

METABOLISM AS A CURRENCY AND CONSTRAINT IN ECOLOGY

Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy

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Summary

1. Environmental temperature has systematic effects on rates of species interactions, primarily through its influence on organismal physiology.
2. We present a mechanistic model for the thermal response of consumer–resource interactions. We focus on how temperature affects species interactions via key traits – body velocity, detection distance, search rate and handling time – that underlie per capita consumption rate. The model is general because it applies to all foraging strategies: active-capture (both consumer and resource body velocity are important), sit-and-wait (resource velocity dominates) and grazing (consumer velocity dominates).
3. The model predicts that temperature influences consumer–resource interactions primarily through its effects on body velocity (either of the consumer, resource or both), which determines how often consumers and resources encounter each other, and that asymmetries in the thermal responses of interacting species can introduce qualitative, not just quantitative, changes in consumer–resource dynamics. We illustrate this by showing how asymmetries in thermal responses determine equilibrium population densities in interacting consumer–resource pairs.
4. We test for the existence of asymmetries in consumer–resource thermal responses by analysing an extensive database on thermal response curves of ecological traits for 309 species spanning 15 orders of magnitude in body size from terrestrial, marine and freshwater habitats. We find that asymmetries in consumer–resource thermal responses are likely to be a common occurrence.
5. Overall, our study reveals the importance of asymmetric thermal responses in consumer–resource dynamics. In particular, we identify three general types of asymmetries: (i) different levels of performance of the response, (ii) different rates of response (e.g. activation energies) and (iii) different peak or optimal temperatures. Such asymmetries should occur more frequently as the climate changes and species' geographical distributions and phenologies are altered, such that previously noninteracting species come into contact.
6. By using characteristics of trophic interactions that are often well known, such as body size, foraging strategy, thermy and environmental temperature, our framework should allow more accurate predictions about the thermal dependence of consumer–resource interactions. Ultimately, integration of our theory into models of food web and ecosystem dynamics should be useful in understanding how natural systems will respond to current and future temperature change.

Key-words: climate change, communities, consumer–resource dynamics, food webs, predator–prey, scaling, species interactions, temperature

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Introduction

Earth's thermal landscape is rapidly changing, and there is growing recognition of associated changes in the geographical distribution, phenology and behaviour of species (Parmesan *et al.* 1999; Hughes 2000; Walther *et al.* 2002; Parmesan & Yohe 2003; Burrows *et al.* 2011). Virtually all organisms have a physiological response to temperature, and these responses have important consequences for higher levels of ecological organization, such as populations, communities and ecosystems (Kingsolver & Woods 1997; Brown *et al.* 2004; Helmuth, Kingsolver & Carrington 2005; Angilletta 2009; Woodward *et al.* 2010; Dell, Pawar & Savage 2011; Buckley & Kingsolver 2012). Thermal response curves describe how biological rates and times (e.g. metabolic rate, growth, reproduction, mortality and activity) vary with temperature (Huey & Stevenson 1979; Huey & Kingsolver 1989). These responses can vary systematically between life stages, populations and species (Angilletta 2009; Dell, Pawar & Savage 2011; Kingsolver *et al.* 2011).

In contrast to individual-level traits, the strength and dynamics of the thermal response of ecological interactions result from the integration of the thermal dependence of the relevant traits of both individuals involved in the interaction. For example, changes in temperature can alter individual body velocities independently for a consumer and a resource, thus increasing (or decreasing) encounter and likely consumption rate between those individuals. Such temperature responses to encounter and consumption may not be predictable by only studying either consumer or resource in isolation (Vasseur & McCann 2005; Dell, Pawar & Savage 2011; O'Connor, Gilbert & Brown 2011; Vucic-Pestic *et al.* 2011).

Consumer–resource interactions are a particularly important class of ecological interactions because they determine most of the flux of nutrients and materials among individuals and through communities and ecosystems. Even small changes in temperature can have major effects on the strength of consumer–resource interactions (Davis *et al.* 1998; Post *et al.* 1999; Sanford 1999). A general framework for predicting how temperature alters the dynamics of ecological interactions, and of consumer–resource dynamics in particular, is therefore necessary for predicting effects on populations, communities and ecosystems (Harrington, Woiwod & Sparks 1999; Walther *et al.* 2002; Helmuth, Kingsolver & Carrington 2005; Vasseur & McCann 2005; Abrahams, Mangel & Hedges 2007; Petchey, Brose & Rall 2010; Rall *et al.* 2010; Woodward *et al.* 2010; O'Connor, Gilbert & Brown 2011; Stegen, Ferriere & Enquist 2012; Stevnbak *et al.* 2012; Cahill *et al.* 2013).

If a consumer and resource possess traits, such as metabolic rate and body velocity, that all respond identically to temperature, then their dynamics should unfold in exactly the same qualitative manner but at an overall accelerated or decelerated pace (depending on whether

temperature was increased or decreased). As long as temperatures are not so extreme that they cause populations to go extinct (due to death or inability to reproduce), static properties like equilibrium densities and coexistence should not change with temperature. This is because static properties are merely outcomes of the dynamics, whether sped up or slowed down. However, when the temperature responses of two interacting species are different (i.e. asymmetric; Fig. 1), changes in interaction dynamics are likely to arise that have important consequences for populations and communities (Frazer & Gilbert 1976; Huey & Kingsolver 1989; Kingsolver 1989; Ives & Gilchrist 1993; Davis *et al.* 1998; Post *et al.* 1999; Sanford 1999; Takasuka, Oozeki & Aoki 2007; Pörtner & Farrell 2008; Barton & Schmitz 2009; Broitman *et al.* 2009; Kingsolver 2009; O'Connor 2009; Rall *et al.* 2010; Kordas, Harley &

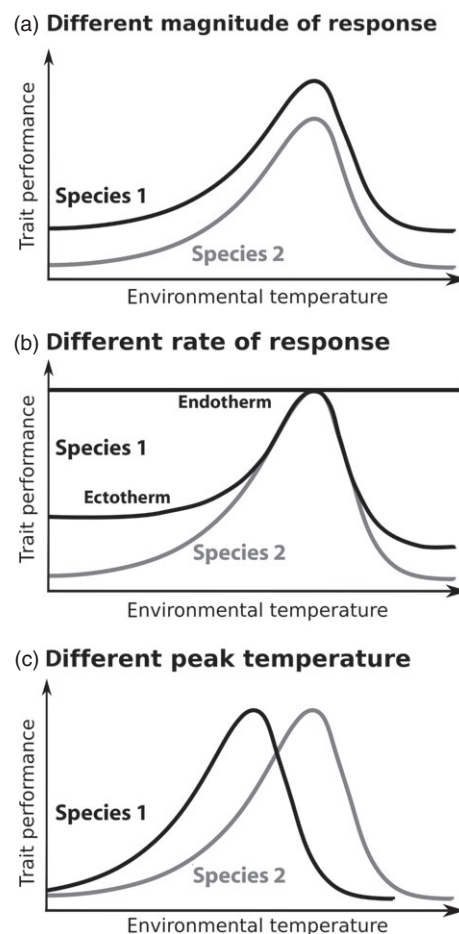


Fig. 1. Three general scenarios for how differences might arise in the thermal responses of individual- or population-level traits (e.g. metabolic rate, body velocity and population growth rate) of interacting consumer–resource pairs (black and grey lines). (a) Differences in the levels of performance, (b) differences in rates of response (either the rise or fall; unimodal black curve), with an extreme case being when one species responds to environmental temperature and the other does not (i.e. endotherm) (horizontal black line) and (c) differences in temperature for peak performance (T_{pk}). These three scenarios can affect consumption rate via effects on encounter rate.

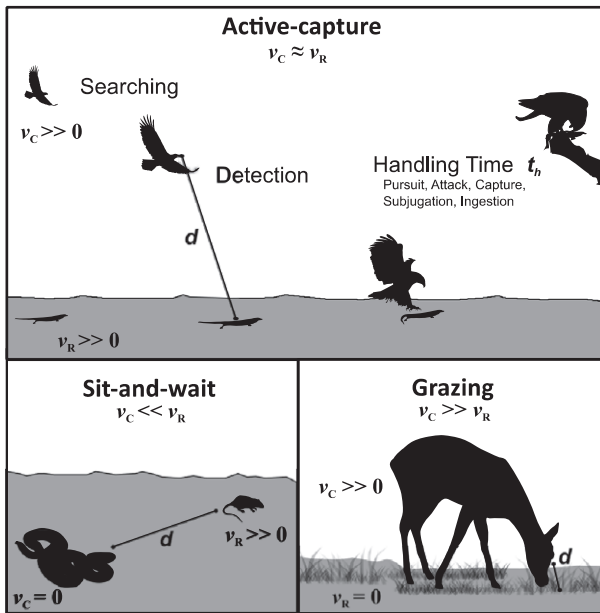


Fig. 2. Three general foraging strategies defined by the relative body velocities of the consumer (v_C) and/or resource (v_R). When both species move throughout the landscape, the interaction is active-capture (top panel). When only the resource moves but the consumer is sessile or stationary, the interaction is sit-and-wait (bottom left panel). When the consumer is active but the resource is sessile or stationary, the interaction is grazing (bottom right panel). The components of a typical trophic interaction are detailed in the top panel and include searching, detection and handling time (see main text). Body velocity varies with temperature whenever $v \gg 0$. In our model, detection distance (d) is independent of temperature.

O'Connor 2011). Note that our use of the term 'asymmetric' in this context does not relate to the nature of the consumer benefitting and the resource suffering from the interaction, but rather differences in how each species responds to temperature. Specifically, differential effects of temperature on the average consumer and resource body velocity would likely alter the rate at which the two species encounter each other, which can drive differences in consumption rate and ultimately their population dynamics. In this paper, we generalize and quantify previous work (references above) by using theory and data to show that consumption rates do vary with temperature and by identifying specific asymmetries in the thermal responses of interacting consumers and resources.

Because most biological rates have a unimodal response to temperature (Dell, Pawar & Savage 2011), there are three general scenarios for how the thermal response of traits may differ between species [Fig. 1; see also Pörtner & Farrell (2008) and Kordas, Harley & O'Connor (2011)]. First, the level of performance of temperature responses could differ between consumer and resource (Fig. 1a). Second, consumer and resource traits may respond to temperature at different rates (Fig. 1b) (Kordas, Harley &

O'Connor 2011). This could be a difference in the rate of increase (rise), the rate of decrease (fall) or both and is likely to be important in nature because differences in reaction and/or denaturation rates are known to exist across taxa and traits (Addo-Bediako, Chown & Gaston 2002; Pörtner *et al.* 2006; Dell, Pawar & Savage 2011). For example, at low temperatures, resources tend to achieve higher escape velocities than consumers, which we previously hypothesized arises because avoiding predation across a wider temperature range is more critical to survival for an individual resource than each attempt by an individual consumer to obtain food (Dell, Pawar & Savage 2011). An extreme version of this scenario occurs when only one species is an endotherm, so that many traits are effectively invariant to temperature (horizontal line in Fig. 1b). Third, both consumer and resource respond to temperature at the same rate, but each has a different temperature for peak performance (T_{pk}), resulting in responses being offset (Fig. 1c) (Pörtner & Farrell 2008; Kordas, Harley & O'Connor 2011). These offsets will be particularly critical when the T_{pk} s are sufficiently asymmetric that one species is responding positively to temperature (i.e. in the rise region for temperatures lower than T_{pk}), while the other is responding negatively (i.e. in the fall region beyond T_{pk}). Other, more complex scenarios that involve a combination of the three cases are of course possible, such as each species varying in response to breadth (Gilchrist 1995). However, to streamline our discussion, we do not explicitly consider such scenarios here. The three scenarios in Fig. 1 (and combinations of them) are likely to become increasingly important as species come into first contact and communities reorganize due to species' shifts in geographical ranges.

Here, we use a trait-based approach (McGill *et al.* 2006; Weitz & Levin 2006; Savage, Webb & Norberg 2007; O'Connor, Gilbert & Brown 2011; Pawar, Dell & Savage 2012) to develop a general framework that applies to a wide diversity of consumer–resource interactions. Our work builds on earlier studies of the thermal responses of consumption rates that have yielded crucial insights (Vasseur & McCann 2005; O'Connor, Gilbert & Brown 2011; Vucic-Pestic *et al.* 2011) and extends our previous theory for the dependence of consumer–resource dynamics on body size and dimensionality of search space (Pawar, Dell & Savage 2012). Our approach differs from previous work because we explicitly consider the thermal dependence of component traits that underlie consumption rate. Despite the extraordinarily diverse ways in which consumers and resources interact, we are able to do this in a general way because we can focus on a few key traits. Virtually all consumer–resource interactions involve some combination of search, detection and handling (Fig. 2). We derive predictions for how these component traits integrate to determine the thermal responses of search and consumption rates, with particular focus on asymmetries. We test our assumptions and

predictions using a comprehensive database of thermal responses that we compiled previously (Dell, Pawar & Savage 2011, 2013). Finally, we examine how thermal responses and their asymmetries could affect equilibrium population densities, a key feature of populations and communities, via effects on consumption rate and its component traits.

Modelling framework

THERMAL DEPENDENCE OF BIOLOGICAL TRAITS

Biological rates are typically unimodal over the full temperature range, with the fall usually occurring faster than the initial rise (Angilletta 2009; Dell, Pawar & Savage 2011). This faster decline may be due to a variety of metabolic mechanisms, including denaturation of proteins (Johnson & Lewin 1946; Hochachka & Somero 1984; Ratkowsky, Olley & Ross 2005; Corkrey *et al.* 2012), or in aquatic environments, due to decreases in oxygen solubility at higher temperatures (Pörtner & Knust 2007). Within the range of temperatures for which the thermal response is rising (except at temperatures near the critical thermal minimum or very close to the peak), the dependence of most rates can be modelled as a Boltzmann–Arrhenius equation (Gillooly *et al.* 2001; Brown *et al.* 2004; Angilletta 2009; Dell, Pawar & Savage 2011; Price *et al.* 2012; but see Clarke 2006; Irlich *et al.* 2009; Knies & Kingsolver 2010; Englund *et al.* 2011) (Fig. 3).

$$P = P_0 e^{\frac{E}{kT}} \quad \text{eqn 1}$$

where P is a trait performance in terms of a rate, E is the average activation energy for the underlying biochemical reactions, k is Boltzmann's constant, T is body temperature in Kelvin, and P_0 is a taxon-, activity- and mass-dependent scaling coefficient (Gillooly *et al.* 2001) that also includes effects of interaction dimensionality (Pawar, Dell & Savage 2012) in the case of search or consumption rate.

The full unimodal response can be described either by extending the Boltzmann–Arrhenius model using thermodynamic principles or by adding a phenomenological decline at higher temperatures (Johnson & Lewin 1946; Ratkowsky, Olley & Ross 2005; Martin Tara & Huey Raymond 2008; Angilletta 2009; Amarasekare & Savage 2012). A unimodal model based on the Boltzmann–Arrhenius model should have the general form

$$P = P_0 e^{\frac{E}{kT}} f(T_{pk}, E_D) \quad \text{eqn 2}$$

where T_{pk} is the temperature at which trait performance reaches its peak value, and E_D is a parameter that partly controls the steepness of decline beyond T_{pk} . In the case of a fully thermodynamic model, E_D can be interpreted as the average energy constant at which proteins denature (Corkrey *et al.* 2012).

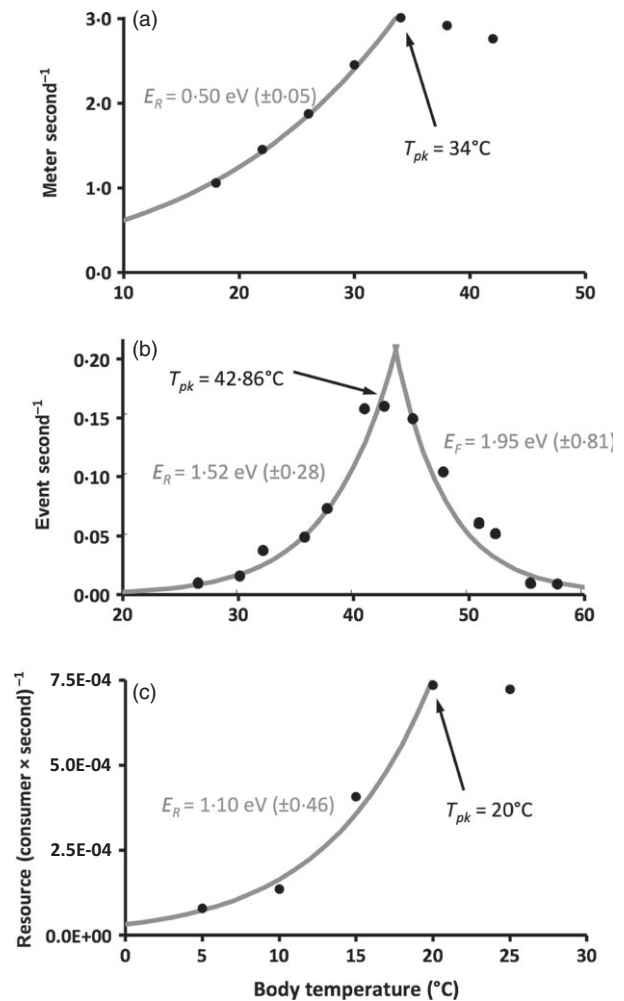


Fig. 3. Three example thermal response curves and the identification and estimation of rise activation energies (E_R), fall activation energies (E_F) and peak temperatures (T_{pk}) when there are sufficient data. These examples are all for traits relevant to consumer–resource interactions: (a) escape body velocity of an agamid lizard (*Agama savignyi*) (Hertz, Huey & Nevo 1982), (b) encounter rate of western harvester ants (*Pogonomyrmex occidentalis*) with an arbitrary line (Crist & MacMahon 1991) and (c) the rate of consumption of backswimmers (*Notonecta glauca*) feeding on mosquito larvae (Cockrell 1984). Gray curves are OLS regressions based on the Boltzmann–Arrhenius model (eqn 1) fitted to the rise (E_R) and fall (E_F) component of each response (eqns 1 and 2). Values shown are estimated activation energies with 95% confidence intervals for the respective rise and fall components. Arrows denote T_{pk} – the temperature at which the trait value is optimal (eqn 2).

In this paper, we focus our theory on the rise component of thermal responses (eqn 1; Fig. 3). This allows us to more easily connect to previous theoretical and empirical work (Savage *et al.* 2004; Deutsch *et al.* 2008; Martin Tara & Huey Raymond 2008; Angilletta 2009; Dell, Pawar & Savage 2011). Also, organisms typically live at temperatures below T_{pk} (Deutsch *et al.* 2008; Martin Tara & Huey Raymond 2008; Angilletta 2009; Huey *et al.* 2009a), so concentrating on rises is necessary for understanding the initial physiological and ecological responses to

temperature change (but see Englund *et al.* 2011). Finally, by focusing on the rise response, we show that even for the simplest version of the model, asymmetric responses can lead to large effects. Including a full unimodal model (see Discussion) should amplify effects based purely on the rise response, because of large asymmetries created by differences in peak temperatures (Fig. 1) and the differential rates of falls compared with rises.

SEARCH RATE

For a consumer–resource interaction to occur, organisms must first encounter each other. The search rate of a consumer throughout the landscape (α) governs the number of potential attacks that a consumer can make (units of area or volume per time), and can be expressed as (McGill & Mittelbach 2006; Pawar, Dell & Savage 2012)

$$\alpha \propto v_r d^{D-1} \quad \text{eqn 3}$$

where d is the distance at which the consumer and/or resource can detect one another, D is the dimensionality of the consumer search space, and v_r is relative velocity of the consumer and resource. When individuals move randomly (Gerritsen & Strickler 1977; Okubo 1980; Barrett & Lowen 1998; see Discussion) prior to detection (i.e. before they come within distance d of each other), relative velocity can be shown to be proportional to the root-mean-square of average velocities of the consumer (v_C) and resource (v_R) (i.e. $v_r = \sqrt{v_C^2 + v_R^2}$). When the consumer moves with a velocity much faster than the resource or if the resource is sessile (grazing; Fig. 2, bottom right panel), relative velocity is well approximated by the velocity of the consumer ($v_r \sim v_C$). In contrast, when the resource moves much faster than the consumer or the consumer is sessile (sit-and-wait foraging; Fig. 2, bottom left panel), relative velocity is well approximated by resource velocity ($v_r \sim v_R$).

The consumer must invest time and effort in pursuing, subduing and ingesting each individual resource. These components can be combined with search rate using a type II functional response to yield a saturating per capita consumption rate (c) (Holling 1959):

$$c = \alpha g(R) \quad \text{eqn 4}$$

Here, R is resource density (individuals \times area⁻¹ or volume⁻¹), and the function $g(R)$ is the risk function that determines the shape of the functional response (Murdoch, Briggs & Nisbet 2003), which in principle can be any form. This choice of notation allows us to treat different functional responses simultaneously and facilitates direct comparison between different functional responses for thermal effects. Here, we restrict our focus to type I and type II functional responses with the associated risk functions, but additional forms could be used instead.

$$g_I(R) = R \quad \text{eqn 5}$$

$$g_{II}(R) = \frac{R}{1 + \alpha t_h R} \quad \text{eqn 6}$$

When handling time is instantaneous, eqn 6 reduces to eqn 5. Equation 4 implicitly includes the probability of a successful attack by the consumer, which we assume is largely temperature invariant. If attack success probability is temperature dependent, it will need to be dealt with more explicitly, most likely through an extra factor that multiplies the search rate or possibly through handling time.

THERMAL DEPENDENCE OF COMPONENT TRAITS

We now derive the thermal dependence of search rate (eqn 3). For consumers that search for prey visually, detection distance (d in eqn 3) is expected to depend on properties of the eye, height of the eye above the foraging surface (Kirschfeld 1976; Kiltie 2000; Pawar, Dell & Savage 2012) and the size of the prey. Because none of these are known to depend on temperature directly, detection distance is also not expected to vary with temperature. Consequently, effects of temperature will also not differ according to interaction dimensionality (D in eqn 3) of the system (Pawar, Dell & Savage 2012). For sensory modalities such as hearing, smell or touch, the temperature dependence is also expected to be weak. For example, hearing and smell may vary as a square root due to how temperature influences diffusion (for smell) and the density of the environmental medium through which sound waves travel (for hearing). Because of the mathematical form of this dependence, these effects are expected to be much weaker than the exponential thermal dependencies of many other traits and rates.

Relative velocity (v_r in eqn 3), on the other hand, should depend strongly on temperature (Table 1; Table S1, Supporting information). Metabolic rate is the power produced by an organism to be used for maintenance, growth and reproduction. By definition, power equals the product of force and velocity. The force or strength available for movement (e.g. jumping, swimming, flying, running, etc.) (Schmidt-Nielsen 1984) scales with the cross-sectional area of muscle, which should be independent of temperature. Consequently, individual body velocity should depend on temperature only according to how the power (metabolic rate) devoted to locomotion changes with temperature. Using the well-established relationship (eqn 1) between temperature and metabolic rate (Gillooly *et al.* 2001; Savage 2004), we predict that within the rise part of the response, individual body velocity (v) should scale as

$$v \propto \frac{B}{F} \propto e^{\frac{E}{T}} \quad \text{eqn 7}$$

where F is force and B is metabolic rate. Any body mass dependence that may exist is left implicit within eqn 7

Table 1. Theoretical predictions for the temperature dependence of consumer-resource interactions. Differences in the foraging strategies of each consumer-resource pair (Fig. 2) determine whether effects of temperature on relative body velocity (v_r) are driven primarily by the consumer and/or the resource. Asymmetries in the temperature response of the consumer and resource for any of these traits are captured by our asymmetry factor ($\Delta \equiv e^{-1/k(E_R/T_R - E_C/T_C)}$; eqn 8) and are likely to have significant effects on search rate, consumption rate and equilibrium population densities. Differences in interaction thermy (ectotherm or endotherm) also affect temperature dependence and are easily included into our theory (e.g. for endothermic consumers feeding on ectothermic prey $e^{-E_C/kT_C} \sim 1$ and $\Delta \sim e^{-E_R/kT_R}$) (Table S1, Supporting information). The constant a depends on type of locomotion, taxonomy and other factors. Per capita consumption rates (c_I and c_{II}) are for temperature-independent resource population density (i.e. $R \propto T^0$; see main text)

Temperature scaling	Foraging strategy		
	Grazer	Sit-and-wait	Active-capture
Detection distance (d)	T^0	T^0	T^0
Interaction dimensionality (D)			
Relative velocity (v_r)	e^{-E_C/kT_C}	e^{-E_R/kT_R}	$e^{-E_C/kT_C} \sqrt{1+a\Delta^2}$
Search rate (α)			
Consumption rate type I (c_I)			
Handling rate ($1/t_h$)	e^{-E_C/kT_C}	e^{-E_C/kT_C}	e^{-E_C/kT_C}
Consumption rate type II (c_{II})	e^{-E_C/kT_C}	$\frac{e^{-E_R/kT_R}}{1+R\Delta}$	$\frac{e^{-E_C/kT_C} \sqrt{1+a\Delta^2}}{1+R\sqrt{1+a\Delta^2}}$
Risk function [$g(R)$]	T^0	Δ^{-1}	$\frac{1}{\sqrt{1+a\Delta^2}}$
Resource equilibrium density (\hat{R})			
Consumer equilibrium density (\hat{C})	Δ	T^0	$\frac{\Delta}{\sqrt{1+a\Delta^2}}$

because our predictions for consumer–resource interactions are for specific pairs of individuals or species. Therefore, the magnitude of changes in velocity driven by body mass will be negligible in comparison with changes driven by temperature. In addition, any effect of differential allocation of energy to locomotion should be relatively insignificant because the sizes of interacting consumers and resources are typically correlated (Allen *et al.* 2006; Brose *et al.* 2006; Cohen 2008). Substituting the scaling of velocity into search rate (eqn 3) yields a set of predictions that depend upon foraging strategy (Fig. 2; Table 1; Table S1, Supporting information).

Finally, we consider the thermal dependence of handling time (assuming attack success is temperature invariant), which is important for type II functional responses (eqn 6). Once a consumer has attacked and killed a resource, the resource becomes inactive, so its thermy will no longer contribute to handling time. Therefore, for an ectothermic consumer, when the dominant time spent handling a resource involves ingestion (following subjugation) (Fig. 2, top panel), handling rate ($1/t_h$) will scale as e^{-E/kT_C} over the rise part of the response (Table 1). Throughout the remainder of the paper, subscripts C and R on traits, such as body temperature (T), refer to those traits for the consumer and resource, respectively. Handling rate should be temperature invariant for an endothermic consumer (Table 1).

Combining all the components together, we obtain a set of foraging-strategy and thermy-specific predictions for search rate (Table 1; Table S1, Supporting information). For ectotherm consumer–resource pairs, the temperature dependence of search rate for active-capture

strategies is based on both the consumer and resource. For sit-and-wait strategies, it is based on the resource, and for grazers, the thermal dependence of search rate is based only on the consumer. Endothermic consumer–resource pairs should be largely unaffected by shifts in environmental temperature. For interactions between species with a thermy mismatch (i.e. endotherm and ectotherm), thermal dependence will depend on whether the endotherm is sessile (endothermic resource in a grazing strategy or endothermic consumer in a sit-and-wait strategy) or it is moving around the landscape (endothermic consumer in an active or grazing strategy or endothermic resource in an active or sit-and-wait strategy) (Table 1). As we explain below, thermal dependence of consumption rate can be derived from that of search rate, handling time (for type II responses) and resource density (eqn 4; Table 1; Table S1, Supporting information).

THERMAL DEPENDENCE OF CONSUMPTION RATE

We now derive the thermal dependence of per capita consumption rate (eqn 4) for ectothermic consumer–resource pairs (Table 1; also see Table S2, Supporting information). Because most of our data are from the laboratory, resource density (R) does not depend on temperature, but instead is determined by the experimentalist (see Discussion). For type I responses (eqn 5), this implies the thermal dependence of consumption rate is directly proportional to search rate (Table 1). For type II responses, the risk function (eqn 6) has an additional term that depends on the product of search rate and handling time. For grazers, this product is temperature independent

($\alpha t_h \propto e^{-E_c/kT_c} e^{E_c/kT_c} \propto T^0$), so the prediction for grazers for a type II response is exactly the same as for type I (Table 1). For sit-and-wait foraging strategies, the product is equal to a factor that explicitly depends on asymmetries between the consumer and resource (Table 1). That is,

$$\alpha t_h \propto e^{-E_R/kT_R} e^{E_C/kT_C} = e^{-\frac{1}{k} \left(\frac{E_R}{T_R} - \frac{E_C}{T_C} \right)} \equiv \Delta \quad \text{eqn 8}$$

This reveals the critical importance of the asymmetry of temperature responses because it affects the dynamics of consumer–resource interactions. Asymmetries could arise due to differences in either activation energies (e.g. life–dinner principle; Dell, Pawar & Savage 2011), thermy (e.g. ectotherm vs. endotherm) or body temperatures (e.g. thermoregulation) (Fig. 1). Finally, for active-capture foraging strategies, the product is more complicated but can still be expressed in terms of the asymmetry factor Δ and a Boltzmann–Arrhenius dependence for the consumer. Substituting eqn 7 for both the consumer and resource into the equation for relative velocity under random movement (which can be written as $v_r = v_C \sqrt{1 + (v_R/v_C)^2}$), gives the temperature dependence for active-capture (Table 1). Specifically, because $v_R/v_C \propto \Delta$ and $v_C \propto e^{-E_c/kT_c}$, then $v_r = e^{-E_c/kT_c} \sqrt{1 + a\Delta^2}$. Adding the thermal dependence for handling time gives $\alpha t_h \propto e^{-E_c/kT_c} \sqrt{1 + a\Delta^2} e^{E_c/kT_c} = \sqrt{1 + a\Delta^2}$, where a is a constant that depends on the temperature coefficients for the body velocity of the consumer and the resource. This constant depends on body size, type of locomotion, taxonomy and other factors, and could conceivably be estimated from estimates of the difference between consumer and resource velocity and locomotory mode (Schmidt-Nielsen 1984; Dell, Pawar & Savage 2011).

When consumer and resource have the same body temperature and the same activation energies, the asymmetry factor is one (i.e. $\Delta = 1$), and the predictions for type I and type II responses are exactly the same for all foraging strategies. However, when asymmetries exist (i.e. $\Delta \neq 1$), differences between type I and II responses are expected. To illustrate the potential importance of Δ , we now derive the effect of temperature on equilibrium population densities of coexisting consumer–resource pairs.

THERMAL DEPENDENCE OF EQUILIBRIUM POPULATION DENSITIES

We begin with a general model for changes in resource (R) and consumer (C) population densities

$$\frac{dR}{dT} = rR \left(1 - \frac{R}{K} \right) - \alpha g(R)C \quad \text{eqn 9}$$

$$\frac{dC}{dT} = \varepsilon \alpha g(R)C - zC \quad \text{eqn 10}$$

where r is resource intrinsic population growth rate (time⁻¹), K is resource carrying capacity (individuals \times area⁻¹ or volume⁻¹), z is the consumer's mortality rate (time⁻¹), and ε is the consumer's conversion efficiency, or the efficiency of converting ingested resource biomass to biomass of consumers.

Solving eqns 9 and 10 at equilibrium yields

$$g(\hat{R}) = \frac{z}{\varepsilon \alpha} \quad \text{eqn 11}$$

$$\hat{C} = \frac{r\hat{R}(1 - \hat{R}/K)}{\alpha g(\hat{R})} = \frac{r\varepsilon\hat{R}(1 - \hat{R}/K)}{z} \quad \text{eqn 12}$$

In eqn 11, the term $z/\varepsilon\alpha$ is the ratio of consumer mortality rate to the conversion rate of resources to consumers and can be interpreted as the inverse proficiency of consumer production. Similarly, the term r/α in eqn 12 is the ratio of resource production rate to consumer search rate and can be interpreted as the proficiency of finding prey per area. The term r/z in the last expression in eqn 12 represents the maximum rate of conversion of resources to consumers relative to the consumer mortality rate and can be interpreted as the maximal proficiency of consumer production. Each of these three quantities is the ratio of rates that are temperature dependent. Thus, differences in equilibrium densities will only occur when there are asymmetries in these relative rates. This mathematically captures our earlier comments about asymmetries in thermal responses being necessary for changes in static properties of consumer–resource dynamics with temperature (see Introduction).

For type II functional responses (eqn 6), the equilibrium (eqn 12) may be unstable (Vasseur & McCann 2005; Pawar, Dell & Savage 2012). Our parameter Δ influences local, asymptotic stability of this equilibrium as follows. The Jacobian (de Vries *et al.* 2006) for the system (eqns 9 and 10 with type II response) is

$$\hat{\mathbf{J}} = \begin{bmatrix} -\frac{rz(e + t_h m_C(z - eK(\alpha/m_C)) + Kz\alpha t_h^2 m_C)}{eK(\alpha/m_C)(e - zt_h m_C)} & -\frac{z}{e} \\ r(e - \frac{z}{K(\alpha/m_C)} - zt_h m_C) & 0 \end{bmatrix} \quad \text{eqn 13}$$

The two eigenvalues of $\hat{\mathbf{J}}$ are

$$\lambda(\hat{\mathbf{J}})_{1,2} = \frac{rz(\alpha t_h K(e - t_h z) - t_h z - e) \pm \sqrt{rz(rz(e(1 - \alpha t_h K) + t_h z(1 + \alpha t_h K))^2 - 4eK\alpha(e - t_h z)^2(eK\alpha - z(1 + \alpha t_h K)))}}{2eK(\varepsilon\alpha - \alpha t_h z)} \quad \text{eqn 14}$$

These eigenvalues appear as the arguments of exponential factors that determine the trajectories of the two populations towards or away from fixed points following small perturbations (eqn 12). The system is stable if the eigenvalues have a real, negative part, is unstable if they have a real, positive part, and exhibits oscillations if they have an imaginary part. From eqn 14, we observe that the product αI_h , and thus Δ in eqn 8, will influence whether or not the system is stable.

To quantify these effects we now explicitly introduce and substitute the thermal dependence of each variable in eqns 11 and 12, which have previously been determined (Savage *et al.* 2004).

$$\begin{aligned} z &\propto e^{-E_c/kT_c} \\ r &\propto e^{-E_R/kT_R} \\ K &\propto e^{E_R/kT_R} \\ \varepsilon &\propto T^0 \end{aligned} \quad \text{eqn 15}$$

For conversion efficiency (ε), we assume temperature independence (Peters 1983), similar to the mass independence assumed by Weitz & Levin (2006). Temperature invariance is likely because lower gut passage times at higher temperatures (Dell, Pawar & Savage 2011) probably balance increases in energy uptake within the gut due to increased diffusion at higher temperatures, although it would be straightforward to introduce thermal dependence of conversion efficiency into our model if required (Dell, Pawar & Savage 2011; Lang 2012). The temperature dependence of carrying capacity (K) in eqn 15 assumes that resource equilibrium population density and carrying capacity scale identically with temperature, but the effect of temperature on K may be more complicated, or even invariant, depending on how nutrient supply for the resource population scales with temperature (see Discussion). The temperature dependence of search rate depends on foraging strategy of the interaction and the thermy of both consumer and resource (Table 1; Table S2, Supporting information).

Substituting the temperature dependencies (eqn 15) yields predictions for the thermal dependence of the risk function (eqns 5 and 6) and resource equilibrium density (eqn 11) for ectothermic consumer–resource pairs categorized by foraging strategy (Table 1). It is straightforward to show that the thermal response of resource equilibrium density exactly matches the risk function for both type I and type II functions (Table 1). For grazing foraging strategies, the temperature dependence of consumer mortality rate cancels the increased consumer search and consumption rate. That is, consumers will be able to eat and grow faster, but this effect is exactly balanced by the increased mortality rate at higher temperatures. In contrast, asymmetries arise for both sit-and-wait and active-capture foraging strategies. For sit-and-wait strategy, any asymmetry between the consumer mortality rate and resource velocity will increase encounter rate with the

consumer at higher temperatures and thus result in changes in the risk function and the resource equilibrium density. For active-capture strategies, there is an additional dependence on consumer velocity, and although the resulting prediction is slightly more complicated (Table 1), it is still driven by the same asymmetry factor (Δ). Indeed, when $\Delta \gg 1$, corresponding to resource velocity being much greater than consumer velocity (Fig. 2, lower left panel), the prediction for active-capture reduces to that for sit-and-wait (Δ^{-1}). Similarly, when $\Delta \ll 1$, corresponding to consumer velocity being much greater than resource velocity, the prediction for active-capture reduces to that for grazing (T^0 ; Table 1). If either the resource or the consumer (or both) is an endotherm, then there is the potential for extreme asymmetries to be created or thermal dependencies to be eliminated (Table 1).

In the field, resource density may be temperature dependent, which will alter the temperature dependence of the risk function. Per capita consumption rate depends on this risk function (eqn 4). In the laboratory, resource density is typically independent of temperature, as discussed above. At resource equilibrium density, we substitute eqn 11 into eqn 4 to obtain the per capita consumption rate

$$c = \frac{z}{\varepsilon} \propto e^{-E_c/kT_c} \quad \text{eqn 16}$$

Intriguingly, this result holds across all foraging strategies, is driven completely by consumer mortality, and indicates that per capita consumption rate will increase with temperature for systems at equilibrium.

To obtain the thermal dependence of consumer equilibrium density, we assume that resource equilibrium density and carrying capacity scale identically with temperature, or at least that their difference is weaker than the exponential dependencies in the Boltzmann–Arrhenius model. Given this, we substitute thermal dependencies into eqn 12 to obtain the thermal response of consumer equilibrium density (Table 1). These predictions for ectothermic consumer–resource pairs show that for grazing strategies, consumer equilibrium density is thermally dependent (whereas both the risk function and resource equilibrium density are temperature invariant). In contrast, for sit-and-wait strategies these dependencies are reversed and the consumer equilibrium density is temperature invariant, whereas the risk function and resource equilibrium density do depend on temperature. Together, these represent thermal trade-offs between the consumer and resource populations that are driven by asymmetries in their temperature responses. Predictions for the thermal dependence of equilibrium population densities for species with a thermy mismatch are shown in Table S1 (Supporting information).

Empirical analyses

We test our assumptions about the thermal dependencies of component traits underlying the thermal response of search and consumption rate, and also for the presence of

asymmetries in species thermal responses in real data, by analysing the most comprehensive existing database on thermal response curves of ecological traits (Dell, Pawar & Savage 2011, 2013). Currently, this database contains 2445 intraspecific (i.e. within species) thermal response curves for an ecologically and taxonomically diverse set of species from freshwater, terrestrial and marine habitats. Ideally, one would also like to test the model's predictions about the effects of these asymmetries on population dynamics, but to our knowledge such data are currently not available (see Discussion).

DATA COMPILATION AND ANALYSIS

The methods used to obtain, standardize and analyse these data are fully described in Dell, Pawar & Savage (2011, 2013). Briefly, only directly measured thermal response data were used (e.g. estimates of handling time and attack rate derived from fitting functional responses were excluded). All times were converted to rates, and all mass-specific units were converted to per individual (i.e. *per capita*) units. Thermal responses of identical taxa (or combinations of taxa for species interaction traits) and experimental conditions were combined before calculating parameters of the response curve by averaging the trait value at each unique temperature. We calculated the activation energy (E ; eqn 1) together with 95% confidence intervals from the Boltzmann–Arrhenius model for the rise portion of each thermal response in our data set (Fig. 3). We considered the Boltzmann–Arrhenius model to fit a response if $R^2 \geq 0.5$ and the F test P value was < 0.05 . In addition, whenever possible we calculated peak temperature (T_{pk} ; eqn 2) for responses that included a sufficient temperature range. We estimated T_{pk} as the temperature at which the maximum trait value was recorded (Fig. 3). Although we focus on the rise part of the response in our model, analysis of peak temperatures provides additional insights into the effects of asymmetries on consumer–resource trait responses (Fig. 1; see Discussion). No single trait had sufficient data for all rates (E_D ; Fig. 3) to draw robust conclusions about its variation.

Ideally, tests of our predictions for consumption rate and its components would involve data with information about the foraging strategy of each consumer–resource interaction (Table 1; Table S2, Supporting information). However, these data are rarely reported. Therefore, we categorized consumers by trophic group (herbivore, omnivore, carnivore), which to a first approximation likely correlate with foraging strategy (Fig. 2) (Lang 2012). Specifically, herbivores feed on sessile resources (plants) and are thus grazers. Most of the carnivores in our database more closely match an active-capture strategy (Pawar, Dell & Savage 2012) than sit-and-wait or grazing. Consequently, we identified carnivores with the active-capture strategy. Omnivores feed at multiple trophic levels and probably eat both active and sessile resources by employing a mixture of foraging strategies.

The traits we extract from the database are as follows: *body velocity* (v_R or v_C ; units of $\text{m} \times \text{s}^{-1}$) (includes avoidance, escape, foraging, attack, strike and voluntary velocities), *detection distance* (d ; units of m) (includes resource–reaction-to-consumer and strike distances), *search rate* (α ; units of individual or event or area $\times \text{s}^{-1}$) (includes grazing rate, line encounter rate, point encounter rate, resource–habitat encounter rate and voluntary movement rate), *attack rate* (includes attack rate, bite rate), *handling rate* ($1/t_h$; in units of events $\times \text{s}^{-1}$) (includes inverse handling time and inverse subjugation-through-consumption time), *consumption rate* [c ; units of resources \times (consumer $\times \text{s}^{-1}$)] (includes consumption rate and filtration rate) and *conversion efficiency* (ϵ ; a proportion that is introduced in eqn 10) (includes energy assimilation and mass conversion efficiencies).

Results

Our theoretical predictions for the components of consumption rate are largely validated by empirical data. First, available data, though limited, support our assumption of temperature independence of detection distance (d in eqn 3). We found data on the reaction distance of a snake preying on mice and of seven species of terrestrial lizards reacting to an approaching human. Of these, only a single response was thermally dependent and well fit ($R^2 \geq 0.5$ and the F test P value < 0.05 ; Dell, Pawar & Savage 2011) by the Boltzmann–Arrhenius model: a carnivorous lizard with an E of 0.61 eV. Second, mean activation energy (E) for the 70 body velocity responses we analyse is $0.46 \text{ eV} \pm 0.03$ (\pm standard error, used throughout this paper). The median is 0.43 eV, indicating a right skew. These 70 responses cover 62 species, including frogs, fish, snakes, lizards, crustaceans and insects (Dell, Pawar & Savage 2011). Carnivores ($0.45 \text{ eV} \pm 0.04$), herbivores ($0.50 \text{ eV} \pm 0.07$) and omnivores ($0.44 \text{ eV} \pm 0.05$) all have mean activation energies that are statistically indistinguishable from one another (Fig. 4), which supports a central tendency for the thermal dependence of body velocity. Significant variation within trophic groups (Fig. 4) suggests many potentially interacting species do differ in the activation energy of their body velocities, which would lead to the asymmetries illustrated in Fig. 1b. The mean for the 45 body velocity T_{pk} estimates is $30.4 \text{ }^\circ\text{C} \pm 1.30$, and the median was $34 \text{ }^\circ\text{C}$. Categorizing thermal responses of velocities by trophic group reveals that carnivores ($28.8 \text{ }^\circ\text{C} \pm 1.68$) have a slightly lower mean T_{pk} than in omnivores ($30.0 \text{ }^\circ\text{C} \pm 2.28$) and much lower than in herbivores, with a mean T_{pk} of $39.2 \text{ }^\circ\text{C} \pm 2.30$ (Fig. 4). Habitat strongly influences T_{pk} (Dell, Pawar & Savage 2011), so it is not surprising that herbivores have a much higher T_{pk} because all herbivore data were collected in terrestrial habitats, while many carnivore (37%) and omnivore (33%) responses were aquatic (i.e. marine or freshwater). Nonetheless, given the variation in T_{pk} observed, potentially interacting species within habitats are likely to have different peak temperatures that would lead to asymmetries. Third, the few data we could find on conversion efficiency are consistent with our assumption of its

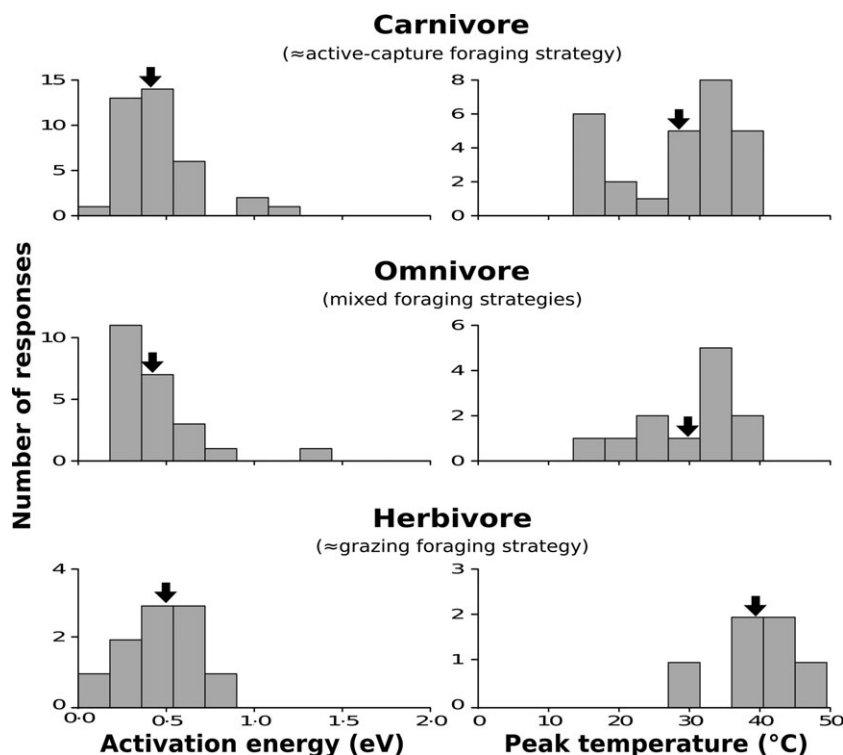


Fig. 4. Distribution of the rise activation energy (E) (left column) and peak temperature (T_{pk}) (right column) estimates from the thermal responses of body velocity ($m \times (\text{individual} \times s)^{-1}$). Responses are categorized by trophic group, which approximate foraging strategy: carnivore (active-capture), omnivore (mixed) and herbivore (grazing). Asymmetries in the thermal response of body velocity of consumer–resource pairs are predicted to lead to differences in equilibrium population densities, likely leading to consequences at the population and community levels (see main text; Fig. 1). Black arrows at top of distributions indicate mean values. See Dell, Pawar & Savage (2011) for further details, including trait definitions and data sources.

temperature independence. Our entire database contains only six estimates of food mass conversion efficiency following consumption (ϵ in eqn 10). Of these, only two had estimates of rise activation energies that were significant: a carnivorous aquatic protist and a carnivorous fish, and their mean activation energy is $0.31 \text{ eV} \pm 0.08$. Three estimates of T_{pk} were obtained for conversion efficiency: a crustacean (omnivore), a fish (carnivore) and a protist (carnivore). The mean T_{pk} for the two carnivores was $18.45 \text{ }^\circ\text{C} \pm 3.45$ and for the omnivore was $20 \text{ }^\circ\text{C}$.

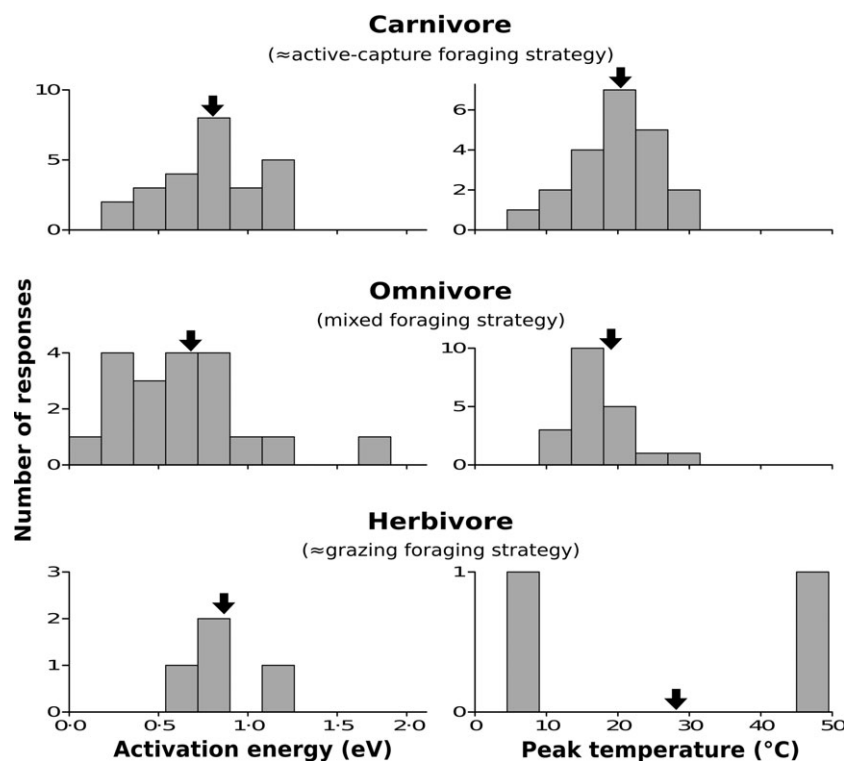
Empirical data on encounter and consumption rate (including attack rate and handling time) show broad consistency in their thermal dependence between trophic groups, although significant variation within groups exists (Fig. 5). Mean rise activation energy from 48 encounter and consumption rate responses is $0.73 \text{ eV} \pm 0.04$. This value is the same for the median, indicating a symmetric distribution. Categorizing responses by trophic group (Fig. 5) reveals that carnivores ($0.78 \text{ eV} \pm 0.05$), herbivores ($0.84 \text{ eV} \pm 0.13$) and omnivores ($0.65 \text{ eV} \pm 0.08$) all have mean activation energies that are statistically indistinguishable. These data include 44 species of worms, arachnids, crustaceans and insects (Dell, Pawar & Savage 2011). The mean for the 43 T_{pk} estimates for encounter and consumption rates is $19.42 \text{ }^\circ\text{C} \pm 1.02$. Categorizing responses by trophic group (Fig. 5b) reveals that carnivores ($20.03 \text{ }^\circ\text{C} \pm 1.22$) have a statistically indistinguishable mean T_{pk} from omnivores ($18.01 \text{ }^\circ\text{C} \pm 1.06$). There were only two T_{pk} estimates for herbivores (Fig. 4d). Again, significant variation in peak temperature is evident within groups, suggesting the likelihood of asymmetries between interacting consumer–resource pairs. Very few

data are available on the thermal responses of attack rates. In fact, we only found a single attack rate estimate from a carnivorous tiger beetle, with an activation energy of 0.66 eV . We did find data on bite rate, which is the number of bites or analogue (e.g. radular scrape) per consumer per time. The four herbivores – two caterpillars and two molluscs – for which estimates of E are available show that bite rate rises have a mean activation energy of $0.46 \text{ eV} \pm 0.03$. Only two T_{pk} estimates for attack rate were found: $34.72 \text{ }^\circ\text{C}$ for a carnivorous tiger beetle and $12.5 \text{ }^\circ\text{C}$ for an omnivorous fish. Four data series for how handling rate ($1/t_h$) varies with temperature were well fit ($R^2 \geq 0.5$ and the F test P value < 0.05) to the Boltzmann–Arrhenius model, confirming our models assumption of the temperature dependence of handling rate (Table 1; Table S2, Supporting information). Handling rate included subjugation-through-consumption rate, which we assume is a constant fraction of handling rate. The mean E for these four responses is $0.68 \text{ eV} \pm 0.14$. Three of these four responses were for carnivores, including a fish, a lizard and an aquatic true bug (Dell, Pawar & Savage 2011), with a mean E of $0.63 \text{ eV} \pm 0.18$.

Discussion

By combining models of the temperature dependence of physiological rates with existing theory for the dependence of search and consumption rate on body size and interaction dimensionality (Pawar, Dell & Savage 2012), we construct a general framework for predicting effects of temperature on consumer–resource interactions. Using this framework, it is possible to make specific predictions about

Fig. 5. Distribution of the activation energy (E) (left column) and peak temperature (T_{pk}) (right column) of combined data for the thermal response of encounter (events/(individual \times s) $^{-1}$) and consumption (resources/(consumer \times s) $^{-1}$) rates. Responses are categorized by trophic group: carnivore (active-capture), omnivore (mixed) and herbivore (grazing). Encounter and consumption rate data can be straightforwardly combined when probability of attack and probability of success are temperature invariant, as assumed in our model (main text). Asymmetries in the thermal response of encounter and consumption rates of consumer–resource pairs are predicted to lead to differences in equilibrium population densities, likely leading to consequences at the population and community levels (see main text; Fig. 1). Black arrows at top of distributions indicate mean values. See Dell, Pawar & Savage (2011) for further details, including trait definitions and data sources.



how temperature change, such as climate change or seasonal variation, might alter the dynamics of interacting species (Table 1; Table S2, Supporting information). We explicitly focus on the rise part of the thermal response (to provide a simpler foundation upon which more complexity can be added and to allow direct connection to previous theory and data), but other models of thermal dependence could easily be substituted. For instance, a full unimodal model (eqn 2) could be used and should amplify effects of temperature because of new asymmetries introduced by differences in peak temperatures and rates of fall among species (Fig. 1) (Deutsch *et al.* 2008; Farrell *et al.* 2008; Pörtner & Farrell 2008; Tewksbury, Huey & Deutsch 2008; Huey *et al.* 2009b; Englund *et al.* 2011).

In our theory, the effects of temperature on consumer–resource interactions arise primarily through effects on body velocity. Therefore, when one species is sessile, such as the consumer in a sit-and-wait interaction or the resource in a grazing interaction, effects of temperature on encounter rate can arise only through the mobile species (Table 1; Fig. 1) (Vucic-Pestic *et al.* 2011). When both species are mobile, such as in active-capture interactions, temperature dependence can arise by influencing the body velocity of both species. This mechanism has been proposed previously (Vucic-Pestic *et al.* 2011), but not in a generalized way that applies to all foraging strategies. Temperature effects also depend on the thermy of the interacting species. Endothermic body temperature remains relatively constant despite changes in environmental temperature, so their average body velocity is largely invariant to temperature change. In contrast, the body temperature of ectotherms varies with environmental

temperature and so does their body velocity. Our thermal predictions for consumer–resource interactions are therefore contingent on both the foraging strategy and the thermy of the interacting species (Table 1; Table S2, Supporting information). Therefore, our model has the potential to yield additional insights and explain more variation in population dynamics than previous models (e.g. Vasseur & McCann 2005). In this paper, we assume random movement of animals throughout the landscape, but nonrandom patterns of movement (Cantrell, Cosner & Lou 2006; Chen, Hambrook & Lou 2008; Humphries *et al.* 2010; Smouse *et al.* 2010) could be easily substituted. Indeed, provided that the directional movement of the consumer relative to the resource is independent of body temperature, many of our results will still hold.

A key insight of our paper is how asymmetries in the thermal response of interacting species (Fig. 1) qualitatively and quantitatively affect their population dynamics. These asymmetries are captured by our newly defined asymmetry factor, Δ (eqn 8). When consumer and resource have equivalent body temperatures and activation energies, the asymmetry factor equals one, and changes to temperature should not quantitatively affect consumer–resource population dynamics. However, asymmetries will exist when $\Delta \neq 1$, and thus, changes in consumer–resource dynamics and their outcomes, such as equilibrium population densities, are expected (Fig. 1; Table 1; Table S2, Supporting information). Asymmetries could arise due to differences in activation energies (e.g. life–dinner principle; Dell, Pawar & Savage 2011), thermy (e.g. ectotherm vs. endotherm) or thermoregulation (e.g. two ectotherms with different body temperatures) (Fig. 1b). For example, we

predict that across most temperatures ectotherms will likely be relatively slower at low temperatures, and endothermic consumers feeding on these ectothermic resources will therefore have higher success rates for capture and attack at these lower temperatures (Table S2; Christian & Tracy 1981). When both consumer and resource are ectothermic, escapes and failed attacks may be more common at low temperatures because escape body velocity typically remains close to peak levels and is thus higher than attack body velocity (Fig. 1b) (Dell, Pawar & Savage 2011). For ectothermic pairs, consumers should also be much better at attacking resources when temperatures exceed T_{pk} for the resource but not for the consumer (Fig. 1c). For interactions involving two endotherms, there should be little or no temperature dependence.

Conditions promoting asymmetries in the response of traits relevant to trophic interactions will exist in virtually all ecosystems. Moreover, each of the scenarios in Fig. 1 should become more likely as species change their geographical and temporal niches in response to climate change. It is now well-established that warm-adapted species are moving into regions that were previously too cold and that climate change is altering the phenology of many plants and animals (Walther *et al.* 2002; Parmesan & Yohe 2003; Logan, Wolesensky & Joern 2006; Logan 2008; Pörtner & Farrell 2008; Burrows *et al.* 2011; Chen *et al.* 2011; Urban, Tewksbury & Sheldon 2012). Climate change could elicit such shifts when warming cues occur earlier in the year, while other cues, such as seasonal light conditions, remain constant. These differences in environmental drivers could potentially cause matched species interactions to become uncoordinated (Pörtner & Farrell 2008) and new combinations of interacting species to arise.

A prediction of our theory is how differently consumer and resource densities can respond to temperature (Table 1; Table S2, Supporting information). If this holds in real systems, it suggests susceptibility to extinction due to overexploitation could become widespread as climate changes. An important caveat is that this conclusion depends on the scaling of carrying capacity, and it is still being debated whether that is most likely to be temperature independent (Allen, Brown & Gillooly 2002; O'Connor, Gilbert & Brown 2011) or has an inverse Boltzmann–Arrhenius dependence (Savage *et al.* 2004). It has also recently become clear that population density can affect metabolic rate (DeLong, Hanley & Vasseur 2013), which means effects of temperature may become more complicated as consumer densities vary. However, these effects are likely to be secondary in comparison with effects of body size and temperature.

We validate the predictions and assumptions of our theory with data from a diverse range of taxa and habitats (Dell, Pawar & Savage 2011, 2013). We use trophic group as a proxy for foraging strategy, but future analysis should use data for which the foraging strategy of the consumer–resource pair is explicitly known. Similarly, a

new generation of thermal response data from directly interacting species should be a high priority for empiricists. In experiments currently underway, we are using video and automated tracking software to better characterize temperature effects on the mechanics (e.g. foraging strategy, attack and escape body velocity, encounter rates, attack success probabilities, consumption rates) of specific consumer–resource pairs. New data at the mesocosm and microcosm level (e.g. Yoshida *et al.* 2003) should be useful for determining how temperature influences the population dynamics of consumer–resource pairs.

Importantly, our theory can be easily modified to account for additional factors that may be important in natural systems. First, we assume that consumer search space dimensionality (D in eqn 3) is independent of temperature, but a correlative dependence might exist because aquatic environments are likely to be dominated by 3D interactions (Pawar, Dell & Savage 2012) and also have a lower variance in temperature. Second, influence of temperature on decision-making behaviour, such as anti-predator tactics (Hertz, Huey & Nevo 1982; Mori & Burghardt 2001, 2004), likely alters trophic dynamics. Although predicting the thermal dependence of behaviour will be more difficult than for body velocity, it is probably also connected partly to physiology (Mori & Burghardt 2001; Herrel, James & Van Damme 2007), suggesting the possibility for integration into these types of scaling models. Third, we implicitly assume that the probability of a successful attack by the consumer is temperature invariant. However, future work should test this assumption, and if systematic temperature dependence is found, it could easily be introduced into our theory, for example with an extra factor that multiplies the search rate by handling time. Fourth, we did not undertake a comprehensive analysis of the stability of equilibrium densities for our model, and indeed, some equilibrium densities may be unstable in certain instances (Vasseur & McCann 2005; Pawar, Dell & Savage 2012). Future work within our framework should lead to predictions about the effect of thermal asymmetries on coexistence and cycling, and data on this would be important to collect. Lastly, it should be useful to integrate our theory with models characterizing the daily routine and behaviour of animals, such as what time of day is optimal to forage, for how long, and the dependence of the physical environment on these patterns (Houston & McNamara 2013). Similarly, integration with models of temperature effects on other types of ecological interactions, such as competition (Reuman, Holt & Yvon-Durocher 2013), should ultimately prove enlightening for understanding and predicting effects of temperature on natural communities.

The framework presented here should prove useful for studying temperature effects on consumer–resource interactions, extinctions and invasions. Indeed, it should be straightforward to make predictions about how consumer–resource interactions will be affected by climate change when assuming that ectoderm body temperature is equivalent or

proportional to ambient temperature. Of course the relationship between body and ambient temperature is likely to be more complex (Huey *et al.* 1989; Broitman *et al.* 2009), and ultimately it would be useful to include this in our model once more patterns emerge. Nonetheless, our theory has the potential to apply to diverse taxa and habitats and ultimately it should be possible to extend it to other types of ecological interactions that rely on the movement of individuals, such as pollination, parasitism and even competitive interactions (DeLong, Hanley & Vasseur 2013; Reuman, Holt & Yvon-Durocher 2013). Predicting trophic interactions strength is key to understanding effects in complex food webs, such as indirect interactions and polyphagy (Laska & Wootton 1998; Rip & McCann 2011). Our framework can be used to make predictions about how food web organization differs between tropical and temperate regions, potentially explaining distributions of foraging strategies between habitats and across latitudes. Integration of our theory for thermal dependence with theory for other environmental drivers (e.g. light, moisture, habitat dimensionality) should account for even more variation in the dynamics of consumer–resource interactions. Understanding how temperature controls each component trait of a consumer–resource interaction would be a major step forward in predicting how seasonal variation and climate change affect the strength of species interactions and specifically consumption rate and associated effects on population dynamics.

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Supporting Information

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

Table S1. Theoretical predictions for the temperature dependence of consumer-resource interactions, and effects of foraging strategy and interaction therapy.