

LETTER

Temperature dependence of the functional response

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Abstract

The Arrhenius equation has emerged as the favoured model for describing the temperature dependence of consumption in predator–prey models. To examine the relevance of this equation, we undertook a meta-analysis of published relationships between functional response parameters and temperature. We show that, when plotted in lin-log space, temperature dependence of both attack rate and maximal ingestion rate exhibits a hump-shaped relationship and not a linear one as predicted by the Arrhenius equation. The relationship remains significantly downward concave even when data from temperatures above the peak of the hump are discarded. Temperature dependence is stronger for attack rate than for maximal ingestion rate, but the thermal optima are not different. We conclude that the use of the Arrhenius equation to describe consumption in predator–prey models requires the assumption that temperatures above thermal optima are unimportant for population and community dynamics, an assumption that is untenable given the available data.

Keywords

Arrhenius, attack rate, functional response, handling time, optimum, parasitoid, predator, prey, response curve, temperature.

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INTRODUCTION

The relationship between the consumption rate of a predator and the density of its prey, often referred to as the functional response, is a mainstay in predator–prey theory. It was recognised early on that this relationship is crucial for the dynamics of populations and communities (Nicholson 1935; Holling 1959a), and subsequent studies have explored a wide range of behaviours and environmental conditions that influence functional responses (reviewed by Jeschke *et al.* 2002). These studies have produced an impressive diversity of functional response models: Jeschke *et al.* (2002) list as many as 40 different types. One of these, the Holling's type II model (Holling 1959b), also known as the 'disc equation', has been accorded the status of a 'null-model', and it is upon this that much of modern predator–prey theory is built. This model describes the number of prey eaten by a predator per time unit (E) as a hyperbolic function of prey density (N), $E = aN/(1 + abN)$ (Fig. 1a). The parameter a , often called the attack rate or search efficiency, is the per capita prey mortality at low prey densities, and b specifies the maximal intake rate ($1/b$) that is observed at prey densities high enough to cause satiation. Originally, b was defined as the time needed to handle a prey item (Holling 1959b), but for most predators the maximal intake is limited by the rate of gut evacuation rather than the handling time (Jeschke *et al.* 2002). Analogous equations have been proposed for parasitoids, but here, the parameter b reflects the time needed for handling hosts (host inspection, egg laying, etc.).

The effects of temperature on predator–prey dynamics received little attention from theoretical population and community ecologists during the twentieth century, and most published models that included temperature dependence of consumption rates were detailed and system specific (Wollkind & Logan 1978; Berry *et al.* 1991; Petersen & Deangelis 1992; Collings 1995). More recently, predictions of climatic warming have inspired a number of general theoretical studies of temperature effects on predator–prey dynamics (Vasseur &

McCann 2005; van de Wolfshaar *et al.* 2008), interaction strength (Rall *et al.* 2010) and food web connectance (Petchey *et al.* 2010).

Inspired by the Metabolic Theory of Ecology (MTE), these studies have used the well-known Arrhenius equation to describe the temperature dependence of functional response parameters. In its original formulation, the Arrhenius equation describes the temperature dependence of chemical reactions. The reaction rate (y) is given by $y \propto e^{-E_a/TK}$, where T is the absolute temperature, k is Boltzmann's constant, and E_a , which determines the strength of the temperature dependence, is the activation energy of the reaction (Cornish-Bowden 2004). More recently, proponents of the MTE have suggested that the Arrhenius equation also can serve as a mechanistic model for the temperature dependence of basal metabolism and of a range of other biological rates that are coupled to metabolism, including growth, maximal consumption rate and development (Gillooly *et al.* 2001; Brown *et al.* 2004; Savage *et al.* 2004). As all aerobic organisms, from bacteria to mammals, share the same biochemistry of metabolism it has been argued that a universal temperature dependence exists for all ectothermic animals, and that this can be represented by the Arrhenius equation. Gillooly *et al.* (2001) argued that the slope of this relationship (E_a) should vary between 0.2 and 1.2. However, later it was stated that the E_a value should be constrained between 0.6 and 0.7 (Gillooly *et al.* 2006; Allen & Gillooly 2007). Although the mechanistic derivation of this prediction is unclear (see review by Irlich *et al.* 2009), it was explicitly stated as being a prediction from MTE by Gillooly *et al.* (2006) and Allen & Gillooly (2007).

Using the Arrhenius equation as a mechanistic representation for the temperature dependence of physiological rates has been criticised (Marquet *et al.* 2004; Clarke 2006; van der Meer 2006; Irlich *et al.* 2009), but the equation appears to be a useful empirical generalisation for interspecific data concerning, for example, metabolism, digestion rate and maximum population growth rate (Brown *et al.* 2004; Allen & Gillooly 2007). Here, interspecific data refer to observations of the performance of many different species, each studied at its optimal or normal temperature. However, for population and community

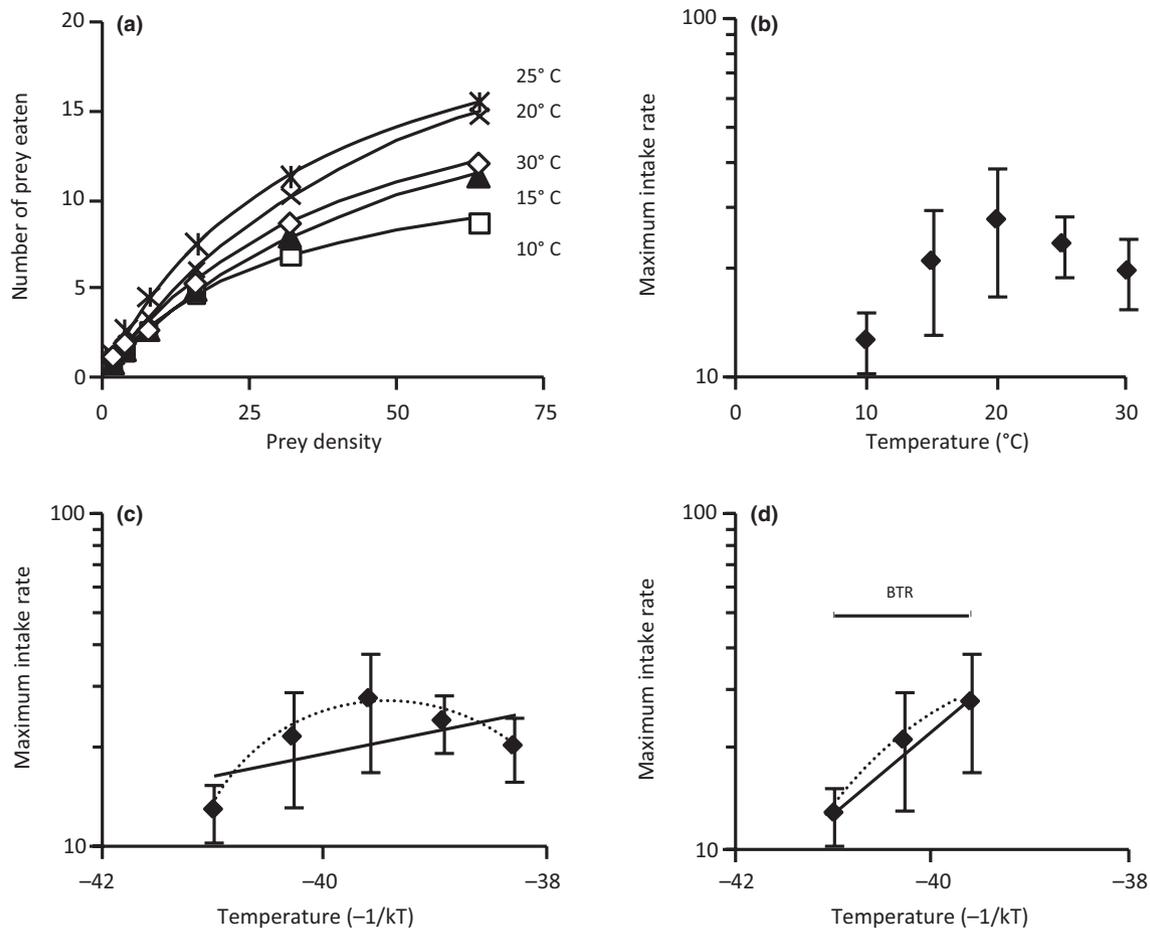


Figure 1 The panels illustrate the different types of data and analyses used in the meta-analysis for one specific example. a) The functional response of the parasitoid *Aphidius matricariae* to densities of the cotton aphid, *Aphis gossypii* at different temperatures (Zamani *et al.* 2006). Plotted lines represent type II functional responses fitted to the data using the disc equation. Each marker (squares, triangles, etc.) denotes the mean of six replicates. Note that the lines for 20 °C and 25 °C are crossing at temperatures higher than those shown in the graph. b) Maximal intake rates estimated as $1/b$ from the functional responses fitted to the data in panel a and plotted against temperature (°C). Error bars denote 1 standard error. c) Maximal intake rates plotted against inverse temperature (Kelvin) and scaled with the Boltzmann constant (k_B). The solid line represents the Arrhenius model (eqn 1) and the dotted line represents the quadratic model (eqn 2), fitted to the data. d) The same data as in panel c with the horizontal bar indicating the 'biologically relevant temperature range' (BTR). The solid line represents the Arrhenius model (eqn 1) and the dotted line represents the quadratic model (eqn 2) fitted to the data that fall within this range.

models, where the focus is usually on interactions between species (e.g. van de Wolfshaar *et al.* 2008; Petchey *et al.* 2010), it is often more relevant to consider intraspecific relationships (i.e. general patterns describing the shape of species-specific response curves). For this type of data, the relationship between temperature and the rate of consumption or growth tends to be hump shaped rather than exponential, as illustrated in Figs 1b–d (De Moed *et al.* 1998; Angilletta 2009; Knies & Kingsolver 2010). Proponents of the Arrhenius equation acknowledge this fact and argue that the equation is valid for a 'biologically relevant temperature range' (BTR) (Fig. 1d), which is defined as spanning temperatures that are lower than the optimal temperature, but high enough to yield positive growth (Savage *et al.* 2004). In opposition to this approach, it can be argued that temperatures outside the BTR are indeed relevant for ecological interactions, especially if climate warming causes species to experience temperatures higher than their optimum (Deutsch *et al.* 2008; Huey *et al.* 2009). Moreover, a recent study of the temperature dependence of intrinsic population growth rate suggests that relationships are not

exponential even at suboptimal temperatures (Knies & Kingsolver 2010).

Given that the Arrhenius equation is in the process of becoming a generally accepted description of the temperature dependence of parameters in models of trophic interactions (Savage *et al.* 2004; Vasseur & McCann 2005; van de Wolfshaar *et al.* 2008; Petchey *et al.* 2010; Rall *et al.* 2010), it is important to evaluate it in relation to available empirical data. Previous reviews of the temperature dependence of consumption rates have focused on maximal intake rates, often measured in the form of gut evacuation rates (He & Wurtsbaugh 1993; Irigoien 1998), whereas attack rates have not been reviewed. Here, we present a meta-analysis of studies that have measured the temperature dependence of attack rates and maximal intake rates of ectothermic animals. As the use of the Arrhenius equation in dynamic population and community models has been inspired by the MTE, we first test predictions from this theory, i.e. we ask whether there is a universal exponential temperature dependence of functional response parameters constrained within the range

predicted by the MTE ($E_a = 0.6\text{--}0.7$). Second, we examine whether attack rate and maximal intake rate exhibit the same temperature responses. This question is of interest because some models have assumed that the two responses are equal (Vasseur & McCann 2005; van de Wolfshaar 2006; van de Wolfshaar *et al.* 2008). Finally, we examine whether the temperature responses of attack rate and maximal intake rate vary between habitats, taxonomic groups, or functional groups of predators and prey. We find that the temperature dependence of attack rate and maximal intake rate is hump-shaped rather than exponential and conclude that the Arrhenius equation should not be used to describe the thermal dependence of functional response parameters, especially in models exploring the influence of temperature on population and community dynamics.

METHODS

Literature search

We searched the Web of Science and reference lists in published papers and found 48 studies that could be used to estimate the effect of temperature on attack rates and maximal intake rates. All studies encountered that were published before 2010 were included. As some studies reported data for several species or life stages (e.g. eggs and adults), the total number of observations was 56. The studied consumers included predators ($N = 38$), parasitoids ($N = 15$) and filter feeders ($N = 3$). The majority of the consumers studied were insects ($N = 36$), followed by fish ($N = 8$), crustaceans ($N = 6$) and mites ($N = 4$). The studies included are listed in the Supporting information, Table S1.

Several authors have noted that meta-analyses of the same body of literature can reach different conclusions because different criteria are used when selecting studies (Englund *et al.* 1999; Whittaker 2010). There is no consensus on how to deal with this problem (e.g. Lajeunesse 2010; Whittaker 2010), and we chose to follow the recommendation of Lajeunesse (2010) to include all relevant studies and use auxiliary information to evaluate variation between studies.

Deriving attack rates and maximal intake rates from data

Some studies reported direct observations of attack rates and maximal intake rates made at different temperatures, but in most cases, these two parameters were estimated by fitting a functional response model to data on consumption rates at different prey densities (see Fig. 1a for an example). If the original study did not provide parameter estimates or used an inappropriate functional response model, we estimated attack rates and maximal intake rates using data extracted from graphs or tables. For experiments without appreciable prey depletion, we used Holling's disc-equation, $E = aN/(1 + abN)$, where E is the number of prey eaten, N is prey density, a is attack rate, and b is handling time. For cases with prey depletion, the integrated form of the disc equation, $E = N(1 - e^{-a(bE-1)})$, was used. For data on parasitoids, we used either the disc equation or Rogers (1972) random parasitoid equation, $E_p = N(1 - e^{-aP/(1-abN)})$, where P is the density of parasitoids and E_p is the number of hosts parasitised. The former was used for cases involving superparasitism, where the recorded response was the number of eggs laid. For data with a pronounced sigmoid shape, we used the maximal attack rate as defined by the slope of the steepest part of the response curve. This

slope was estimated by fitting a type III function to the data, that is, $E = aN^2/(1 + abN^2)$, and calculating the first derivative at the inflection point.

Modelling temperature responses

We tested whether the slopes of temperature responses for attack rates and maximal intake rates were within the range predicted by the MTE (0.6–0.7). For each study, we described attack rates (a) and maximal intake rates ($I_{\max} = 1/b$) as functions of $-1/(kT)$, where k is Boltzmann's constant given in eV K⁻¹ ($= 8.617 \times 10^{-5}$ eV K⁻¹), and T is temperature in Kelvin (see Gillooly *et al.* 2001). Although $-1/(kT)$ measures energy (the unit is eV⁻¹), it is often referred to as 'Arrhenius temperature' and we follow this convention here. 'Arrhenius temperature' and untransformed temperature scale almost identically (Figs 1b and c). Use of the former allowed us, however, to fit the Arrhenius equation:

$$Y = ce^{E_a(-1/kT)} \quad (1)$$

to the data (Fig. 1c), where Y is the attack rate or maximal intake rate, c is a fitted constant and E_a is the fitted activation energy (eV) that describes the slope of the response (Gillooly *et al.* 2001).

In c. 40% of the studies, attack rate or maximal intake rate exhibited a maximum (subsequently called a 'thermal optimum') within the investigated temperature range. To restrict the analyses to the BTR, we followed Irlich *et al.* (2009) and excluded all data points above the temperature where the highest rate was observed. Subsequently, eqn 1 was fitted to these restricted data sets (Fig. 1d).

To examine whether the temperature responses of attack rates and maximal intake rates deviated from the Arrhenius model, we fitted a quadratic model:

$$Y = ce^{b(-1/kT)+q(-1/kT)^2} \quad (2)$$

to the data, where c , b and q were fitted parameters. We fitted eqn 2 to three data sets: (1) the full data set (excluding studies that only included two temperatures, $n = 49$); (2) the restricted BTR data set (excluding data above the thermal optimum, $n = 40$); and (3) a data set including only studies that exhibited a thermal optimum (hereafter 'optimum data', $n = 22$ for attack rate and $n = 23$ for maximal intake rate). When b is positive and q is negative, the quadratic model describes a thermal optimum (Fig. 1c) or a downwards concave relationship (Fig. 1d). In such cases, b can no longer be interpreted as the activation energy.

Meta-analyses

We used the parameter estimates from the curve fitting exercises in four types of meta-analyses:

- (1) To test whether the temperature dependence of functional response parameters is quantitatively constrained to the range predicted by the MTE, we performed a meta-analysis using the E_a values obtained from fitting the Arrhenius model (eqn 1) to both the full data set and the BTR data set.
- (2) To test whether temperature relationships deviated qualitatively from the Arrhenius model, we performed a meta-analysis using the values of b and q obtained from fitting the quadratic model (eqn 2) to the full and the BTR data sets.

- (3) To characterise the nonlinear temperature relationship found in step 2 more accurately, we repeated the meta-analysis using b and q , but only included studies where a thermal optimum was observed over the investigated temperature range ('optimum data').
- (4) We tested whether heterogeneity in fitted activation energies could be explained by the type of consumer (predator, parasitoid or filter feeder), the taxonomic classifications of predators and prey (Table S1 in the Supporting information), or the type of habitat (aquatic or terrestrial).

Hypothesis tests were based on weighted means, as is common in meta-analyses. This approach has two important advantages over non-weighted analyses, which are normally used in tests of body size and temperature scaling (Brown *et al.* 2004; Knies & Kingsolver 2010). It allows the down-weighting of studies with low precision, and it allows testing of the hypothesis that all studies reflect the same underlying slope, even in situations where the processes generating heterogeneity are unknown (Hedges & Olkin 1985). We chose not to use an analysis based on phylogenetic relationships because the functional response is the result of the interaction between two species, predators and prey, which are often only distantly related.

The inverse of the sample variance was used to weight each observation (Hedges & Olkin 1985). Observations for which the sample variance could not be extracted were weighted using the mean weight of the studies for which the variance could be extracted. Four observations were excluded because the distance to the mean was > 5.5 SD. If a study provided several estimates for the same predator-prey combination, we formed a weighted mean using the inverse of the sample variance as the weight. This mean value was then used as an observation in the meta-analyses.

MetaWin (Rosenberg *et al.* 1997) was used for statistical analyses. We used a fixed effects model and Cochran's Q-statistic (Hedges & Olkin 1985) to test the hypothesis that all studies estimated a single, common slope. As the assumption of a common slope was rejected in all tests, we used random effects models to test the significance of differences between groups and to calculate confidence intervals (Hunter & Schmidt 2000).

Visualising temperature responses

To visualise commonalities in the temperature dependencies of attack rates and maximal intake rates across studies, we plotted the data from all studies that included a thermal optimum (optimum data set) in a single graph. As maximal attack rates, maximal intake rates and the thermal optima varied between studies, we plotted all data on a standardised scale while preserving the shapes of the original response curves. To do so, we rescaled observed attack and intake rates in relative units using $Y_{i,s} = Y_i/Y_{i,max}$. Here, Y_i and $Y_{i,s}$ are vectors containing the observed and standardised rates at different temperatures from study i (Fig. 1c), and $Y_{i,max}$ is the maximum rate estimated from a second order polynomial fitted to the data in study i . Temperatures were rescaled to the mean optimal temperature, that is, the mean temperature at which the thermal optimum was observed across studies. Temperatures were rescaled as $T_{i,s} = T_i - T_{i,opt} + \overline{T_{opt}}$, where T_i and $T_{i,s}$ are vectors containing the observed and rescaled temperatures used in study i , $T_{i,opt}$ is the optimal temperature in study i , and $\overline{T_{opt}}$ is the mean optimal temperature across all studies. Only studies where the investigated temperature range included the optimum could be standardised using this method ($N = 22$ for attack rate and $N = 23$ for maximal intake rate). To illustrate the central tendency of the rescaled data, we fitted a LOWESS model, with the tension parameter set to 0.55 (Wilkinson 2000).

RESULTS

The temperature dependence of attack rates and maximal intake rates did not fit the predictions of the MTE; fitted activation energies covered a much wider range than that predicted, that is, 0.6–0.7, and the relationships were not exponential. Using the BTR data set, the mean estimate of the coefficient E_a for attack rate was higher than predicted, whereas the mean coefficient for maximal intake rate did not deviate significantly from the predicted range of 0.6–0.7 (Fig. 2b). The variance around these means was, however, very large. Highly significant between-study heterogeneity was noted for both attack rate and handling time ($Q = 373.6$, d.f. = 48, $P < 10^{-10}$ and $Q = 1144.3$,

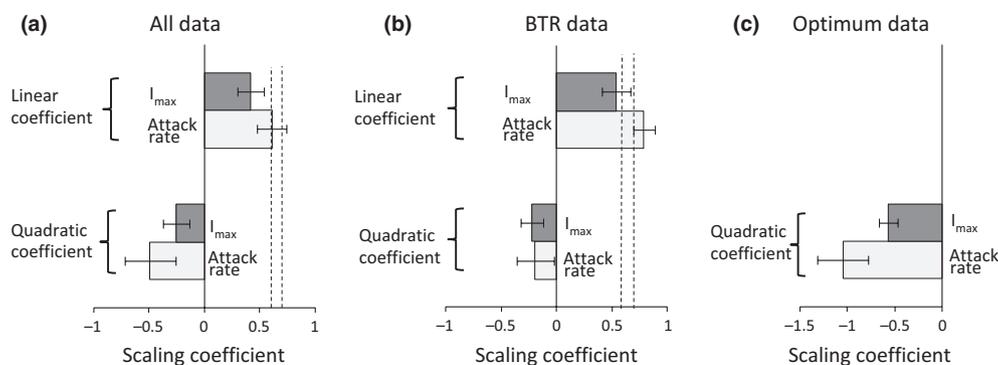


Figure 2 Scaling coefficients (mean \pm 95% CI) for the temperature dependence of attack rates and maximal intake rates (I_{max}) calculated using a) all data, b) data at temperatures below the thermal optimum ('BTR data') and c) all data from studies in which a thermal optimum was observed ('optimum data'). The upper two bars in each panel (labelled 'linear coefficient') represent estimates of the coefficient E_a in eqn 1 ($Y = ce^{E_a(-1/kT)}$). For comparison, the dotted lines indicate the range of E_a predicted by the Metabolic Theory of Ecology (0.6–0.7). The lower two bars in each panel (labelled 'quadratic coefficient') represent estimates of the quadratic coefficient q in eqn 2 ($Y = ce^{b(-1/kT) + q(-1/kT)^2}$). Estimates of the linear coefficient b in eqn 2 (not shown) were significant and positive. The sample sizes were: a) $N = 56$ for linear coefficients, $N = 49$ for quadratic coefficients, b) $N = 53$ for linear coefficients, $N = 40$ for quadratic coefficients, c) $N = 22$ for maximal intake rate, $N = 25$ for attack rate.

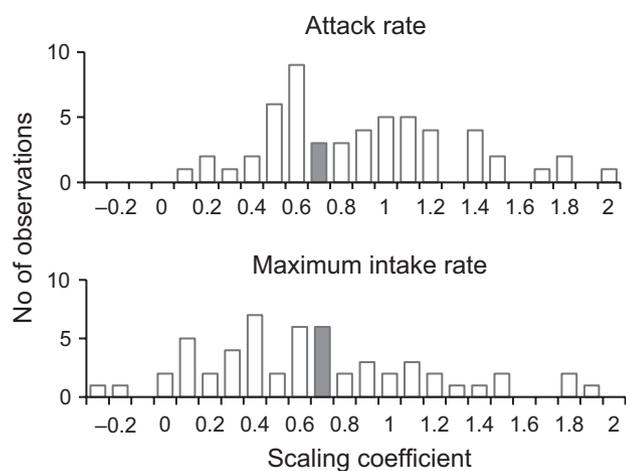


Figure 3 Frequency distributions of the linear scaling coefficients for attack rates and maximal intake rates estimated from the BTR data set using eqn 1. The shaded bars indicate the range 0.6–0.7, which is that predicted by the Metabolic Theory of Ecology.

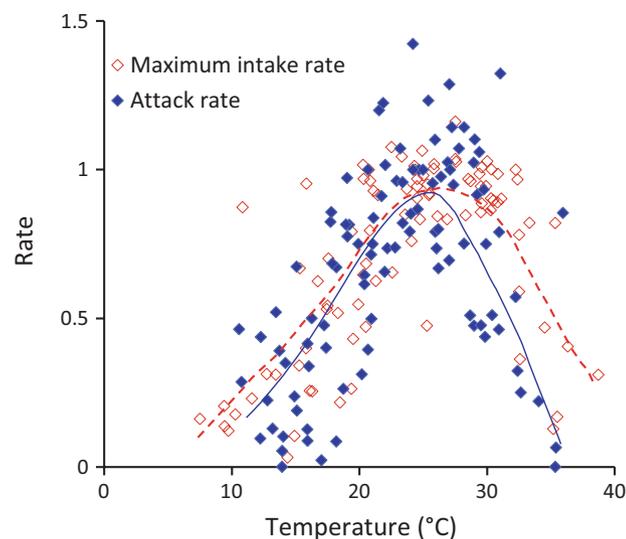


Figure 4 Standardised attack rates (filled diamonds and solid, blue line) and maximal intake rates (open diamonds and broken, red line). Data were standardised as described in the Methods section and centred around the respective optimum temperature (24.9 °C for attack rate and 26.1 °C for maximal intake rate). Only studies from which the value for a thermal optimum could be estimated were included. Lines were fitted using a LOWESS model.

d.f. = 48, $P < 10^{-10}$), and most observations (95% for attack rate and 89% for maximal intake rate) fell outside the range 0.6–0.7 (Fig. 3).

Both temperature relationships were hump shaped as indicated by significant positive linear terms b (data not shown) and negative quadratic terms q (Figs 2a and b). This was true whether we used the full data set (Fig. 2a) or the BTR data set (Fig. 2b). The magnitude of q was smaller, but still significantly negative when we used the BTR data set instead of the full data set (Fig. 2b).

The attack rate and the maximal intake rate depended similarly on temperature. Both attack rate and maximal intake rate increased with temperature (Figs 2a and b linear coefficients) and shared the same thermal optimum (mean \pm CI_{95%} was 24.9 \pm 2.5 °C for attack rate

Table 1 Temperature dependence of attack rate and maximal intake rate for different types of predators and for predators and prey living in different habitats or belonging to different taxonomic groups. Approximate 95% confidence intervals are given within parentheses. Coefficients were estimated by fitting eqn 1 to data for suboptimal temperatures (biologically relevant temperature range data). Q-values refer to Cochran's Q-statistic (Hedges & Olkin 1985), which is used to test for differences between groups

	Attack rate	Q	p	Maximal intake rate	Q	p	N
Predator type							
Predator	0.74 (\pm 0.11)	7.55	0.02	0.45 (\pm 0.15)	6.82	0.03	37
Parasitoid	0.98 (\pm 0.25)			0.84 (\pm 0.33)			13
Filter feeder	1.15 (\pm 0.77)			0.82 (\pm 1.10)			3
Predator taxon							
Insect	0.79 (\pm 0.12)	8.84	0.02	0.49 (\pm 0.15)	3.47	n.s.	35
Fish	0.59 (\pm 0.19)			0.80 (\pm 0.19)			8
Crustacean	1.12 (\pm 0.51)			0.42 (\pm 0.50)			5
Mite	1.17 (\pm 0.67)			0.51 (\pm 0.64)			4
Prey taxa							
Insect	0.75 (\pm 0.13)	5.85	n.s.	0.58 (\pm 0.16)	1.91	n.s.	34
Crustacean	0.69 (\pm 0.33)			0.29 (\pm 0.49)			7
Mite	0.98 (\pm 0.43)			0.53 (\pm 0.48)			6
Algae	1.15 (\pm 0.81)			0.82 (\pm 1.12)			3
Habitat							
Aquatic	0.81 (\pm 0.16)	0.24	n.s.	0.60 (\pm 0.19)	0.74	n.s.	21
Terrestrial	0.76 (\pm 0.14)			0.49 (\pm 0.17)			32

and 26.1 \pm 2.3 °C for maximal intake rate). The attack rate was, however, more strongly affected by temperature than was the maximal intake rate, both above and below the optimum temperature (Fig. 4). The linear slope (E_a) of the attack rate estimated from eqn 1 was significantly steeper than the maximal intake rate using either the full data set ($Q = 4.58$, $P < 0.05$, Fig. 2a) or the BTR data set ($Q = 9.86$, $P < 0.005$, Fig. 2b). Similarly, the weighted mean values of the quadratic term q , which exclusively determines the steepness of the function described by eqn 2 on both sides of its maximum, were significantly higher for the attack rate than for the maximal intake rate (Fig. 2c, $Q = 6.92$, $P < 0.005$).

Some of the variation we found in E_a (Fig. 3) could be explained by the type of predator and by taxonomic differences between predators. Using E_a values from the Arrhenius model (eqn 1) fitted to the BTR data set, we found that the scaling coefficients for attack rate E_a varied between taxonomic groups of predators (fish < insects < crustaceans \approx mites), and both attack rate and maximal intake varied significantly between different types of consumers (Table 1). However, scaling coefficients did not differ between taxonomic groups of prey or between aquatic and terrestrial habitats. It should be noted that sample sizes were low for several of the groups, indicating that the observed patterns may change if more data can be included.

DISCUSSION

The Arrhenius equation has emerged as the preferred model for incorporating temperature dependence of consumption and growth into general population and community models (Savage *et al.* 2004; Vasseur & McCann 2005; van de Wolfshaar *et al.* 2008; Petchey *et al.* 2010; Rall *et al.* 2010). This practice has been inspired by recent developments of the MTE. When evaluating the usefulness of the Arrhenius model we, therefore, first examine the claims made by MTE. According to this theory, there is a universal temperature

dependence for biological rates that can be derived from the enzyme kinetics of basal metabolism (Brown *et al.* 2004). Specifically, it is hypothesised that temperature scaling coefficients are constrained to the range 0.6–0.7 eV, with a mean value of 0.65 (Gillooly *et al.* 2006; Allen & Gillooly 2007; see also the review by Irlich *et al.* 2009).

The existence of a universal temperature dependence for attack rates and maximal intake rates was not supported by our data. All analyses indicated that there was highly significant heterogeneity, and as many as 89–95% of the observations fell outside the 0.6–0.7 range of activation energies predicted by the MTE (Fig. 3). Similar conclusions have been reached for metabolic rate and development rate (Irlich *et al.* 2009), and for fitness curves (Knies & Kingsolver 2010). More detailed analyses showed that some of this heterogeneity occurred because the temperature dependence varied between taxonomic groups and/or types of consumers (Table 1). Significant heterogeneity remained, however, after accounting for these effects (tests not shown). An additional source of heterogeneity was suggested by our finding that relationships were concave downwards rather than linear in plots of $\log(\text{rate})$ vs. inverse temperature, even when data were restricted to temperatures below the optima. If the true response is concave, then the slope of a fitted straight line will depend on the range of temperatures investigated, relative to the position of the optimum. Thus, heterogeneity may occur because different studies investigated different temperature ranges. The finding that maximal intake rate and attack rate had different temperature responses also argues against the existence of a universal temperature dependence.

Even though a universal temperature dependence was not supported by the data, it can be argued that the Arrhenius equation may be useful as a coarse empirical generalisation. For minimal or strategic predator–prey models, tractability requires a high degree of simplification. Thus, at least for very general research questions, it may be reasonable to ignore the fact that the temperature response is concave in lin-log space, or that it differs between attack rate and maximal intake rate. However, using the Arrhenius equation as an empirical generalisation can only be justified if we can ignore interactions that occur at temperatures above the optimum, because in this range, the Arrhenius model predicts an increasing response when it is, in fact, decreasing.

A crucial question is therefore whether it is reasonable to consider temperatures at and above the optimum as being outside of the BTR (*sensu* Savage *et al.* 2004). The answer to this question depends on the match between performance optima and the temperature experienced in the habitat where the organisms occur. If thermal optima are, in general, higher than environmental temperatures, then it makes sense to use the Arrhenius equation. This question has recently received interest because the effects of future warming on ecological communities critically depend on its answer (Deutsch *et al.* 2008; Huey *et al.* 2009; Asbury & Angilletta 2010). Several empirical data sets do indeed suggest that thermal optima often are higher than environmental temperatures (Deutsch *et al.* 2008; Huey *et al.* 2009). However, there are important problems that complicate the interpretation of these data. It is likely that, to some extent, these patterns reflect experimental artefacts. Thermal optima of the most common performance measures, that is, individual and population growth rates, are usually estimated in laboratory experiments where organisms are fed *ad libitum* and temperatures are kept constant. In contrast, natural conditions are typically associated with scarcity of food and variable temperatures. As reduced food intake rate lowers the thermal optimum, it is likely that optima estimated in the laboratory are too

high (Elliott 1982; Boehlert & Yoklavich 1983). This effect can be substantial; Elliott (1982) found that the thermal growth optimum of brown trout varied from 4 °C to 14 °C, depending on food availability. Also, the use of constant temperatures may lead to overestimated thermal optima if response curves are skewed to the left (Martin & Huey 2008).

The observed discrepancy between environmental temperatures and thermal optima observed in laboratory experiments may also reflect the fact that the mean annual temperature is not a relevant descriptor of the temperature regime in habitats with seasonal temperature variations. In high latitude habitats, the mean annual temperature mainly reflects conditions during the long winter when many ectotherms do not feed or experience much predation (Irlich *et al.* 2009). Activity is usually concentrated during a short period in the summer, and it is the temperature regime during this period that is most crucial for long-term population dynamics. A proper measure of temperature, that accurately reflects the influence of temperature on population dynamics in seasonal habitats, would be a weighted mean temperature, where the weights describe the influence of different temperatures on predator–prey dynamics. Performing such calculations requires information about the temperature dependence of birth and mortality rates, which is lacking for most species. Thus, given that we lack the data required to evaluate the match between thermal optima and local temperature regimes in seasonal environments, we suggest evaluation of this relationship in habitats with little seasonal temperature variation. In both tropical insects (Deutsch *et al.* 2008) and tropical lowland lizards (Huey *et al.* 2009), there is a good match between habitat or body temperatures and thermal optima estimated in laboratory experiments. Other studies show that even rather small increases above the habitat mean temperature lead to decreased performance, for example, in coral reef organisms (Baker *et al.* 2008; Munday *et al.* 2008; Donelson *et al.* 2010) and in marine fish and subtidal invertebrates in Antarctica (Peck *et al.* 2004a,b; Pörtner *et al.* 2007). These data suggest that we need to consider temperatures higher than the optima when modelling predator–prey dynamics. Thus, we cannot recommend the Arrhenius equation as a general model for describing the thermal dependence of consumption.

We emphasise that our conclusion concerns intraspecific data. It is not applicable to models of ecosystem processes, such as primary production or decomposition, where it may be reasonable to use scaling relations based on between-species data, because temperature changes may lead to a succession of species. Note also that the Arrhenius equation may serve well in models of species living at the lower thermal limit of their range.

Irrespective of whether thermal optima have to be taken into account, our results suggest that, as a generalisation across all studies, attack rate has a steeper temperature response than maximal intake rate (Fig. 4). For predators, but not parasitoids, the two parameters often reflect fundamentally different processes (Jeschke *et al.* 2002). Maximal intake rate is intimately coupled to the physiology of the digestive apparatus for most predators. In contrast, attack rate involves both predators and prey and largely reflects behavioural processes such as search, attack, hiding and flight. Attack success will often be influenced by the difference in behavioural performance between the predator and its prey, and activities such as searching for prey and attacking can cease if the expected pay-off is too low. Such cost–benefit considerations may often involve three trophic levels. For example, activity at temperatures where movement capacity is reduced may expose ectothermic consumers to a high risk of

predation from birds and mammals. The ectothermic consumers' expected attack success may then be too low given this predation risk. Thus, we hypothesise that behavioural decisions, rather than differences in enzyme activity, cause the response curve to be steeper for attack rate than for maximal intake rate.

The different thermal sensitivities of attack rate and maximal intake rate imply that consumption is more temperature-sensitive at low prey densities, where attack rate limits consumption, and less sensitive at high prey densities, where digestion or handling limits consumption. A second consequence of the steeper scaling of attack rate is that warming will lead to increased specialisation and decreased connectance, as long as temperatures are below the thermal optima (Petchev *et al.* 2010).

As a final remark, we note that using hump-shaped temperature response curves instead of the Arrhenius equation in predator–prey models has important implications. Model results with respect to the effects of temperature, which are based on Arrhenius scaling, will often be reversed at temperatures higher than the thermal optima of the organisms. For example, Vasseur & McCann (2005) investigated temperature effects in a simple predator–prey model and found that warming may push a system from a stable equilibrium to limit cycles. The critical assumption underlying this result is that the temperature relationship is steeper for consumption than for consumer metabolism. Replacing the Arrhenius equation with a hump-shaped response curve for consumption means that the original prediction may hold for low temperatures, but that warming will stabilise dynamics at temperatures near the optimum, where the temperature dependence of consumption will inevitably be much shallower – or even exhibit the opposite response – than that of metabolism. At even higher temperatures, where ingestion is too low to meet metabolic demands, consumer extinction can be expected. More generally, we expect that the responses of communities to climate warming will, to a large extent, reflect between-species differences in thermal optima. The outcome of pair-wise competitive or predatory interactions will often be reversed if warming pushes one of the interacting species above its thermal optimum. Thus, we argue that our understanding of the effects of warming on communities could be greatly enhanced by incorporating hump-shaped temperature–response curves into general models of species interactions (e.g. Mitchell & Angilletta 2009).

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AUTHORSHIP

GE and GÖ conceived the study. GE, GÖ and CLH extracted data. GE performed meta-analyses and wrote the first draft of the parts other than introduction. GÖ wrote the first draft of the introduction. SB rewrote part of the first draft and suggested additional analyses. All authors contributed substantially to the revision of the manuscript.

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