

Temperature, predator–prey interaction strength and population stability

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Abstract

Warming could strongly stabilize or destabilize populations and food webs by changing the interaction strengths between predators and their prey. Predicting the consequences of warming requires understanding how temperature affects ingestion (energy gain) and metabolism (energy loss). Here, we studied the temperature dependence of metabolism and ingestion in laboratory experiments with terrestrial arthropods (beetles and spiders). From this data, we calculated ingestion efficiencies (ingestion/metabolism) and *per capita* interaction strengths in the short and long term. Additionally, we investigated if and how body mass changes these temperature dependencies. For both predator groups, warming increased metabolic rates substantially, whereas temperature effects on ingestion rates were weak. Accordingly, the ingestion efficiency (the ratio of ingestion to metabolism) decreased in all treatments. This result has two possible consequences: on the one hand, it suggests that warming of natural ecosystems could increase intrinsic population stability, meaning less fluctuations in population density; on the other hand, decreasing ingestion efficiencies may also lead to higher extinction risks because of starvation. Additionally, predicted long-term *per capita* interaction strengths decreased with warming, which suggests an increase in perturbation stability of populations, i.e., a higher probability of returning to the same equilibrium density after a small perturbation. Together, these results suggest that warming has complex and potentially profound effects on predator–prey interactions and food-web stability.

Keywords: food webs, global warming, ingestion efficiency, ingestion rates, metabolic theory, predation theory, predator–prey dynamics

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Introduction

Understanding the impact of global warming on the stability of populations and critical ecosystem processes is one of the most important scientific challenges we currently face (Mann *et al.*, 1998; Hughes, 2000). Warming may affect a species by changing the strength of its interactions (e.g., competition or predator–prey interactions) with coexisting species. By modifying interaction strength warming may not only directly affect population densities, but it may also indirectly affect the population size of coexisting species (Berlow *et al.*, 2009). Indirect effects occur when a species affects the *per capita* population growth rate of a non-adjacent

species within an ecological network such as a food web. These indirect effects among species can be more important than direct effects in driving the outcomes of perturbations (Abrams, 1995; Menge, 1997; Yodzis, 2000; Ives & Cardinale, 2004). Moreover, the pattern and strength of species interactions determine the stability of populations and food webs (May, 1973; de Ruiter *et al.*, 1995; Neutel *et al.*, 2002, 2007; Emmerson & Yearsley, 2004; Brose *et al.*, 2006b; Otto *et al.*, 2007; Brose, 2008). Thus, understanding how temperature affects interaction strengths is of vital importance for predicting consequences of global warming for the stability of populations, communities and ecosystem processes (Hughes, 2000).

Two important aspects of population stability (McCann, 2000) are (1) intrinsic stability expressed as the inverse of variability in population density over

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time (Brose *et al.*, 2006b), inversely related to predator ingestion efficiencies (Yodzis & Innes, 1992; Vasseur & McCann, 2005; Rall *et al.*, 2008), which are defined as the ratio of ingestion to metabolism; and (2) perturbation stability, quantifying the resistance of a population to a small perturbation measured as the probability of returning to the same equilibrium density (Emmerson & Raffaelli, 2004). Perturbation stability decreases with increasing *per capita* interaction strength (hereafter, interaction strength) expressing the effects of a predator individual on the abundance of prey populations (May, 1972; de Ruiter *et al.*, 1995). Often, interaction strength is measured as the log ratio between prey density in treatments with predators vs. prey density in treatments without predators (Berlow *et al.*, 1999, 2004). The time scales used to calculate interaction strength varies between short-term experiments of some days (Emmerson & Raffaelli, 2004) or weeks (Sanford, 1999) and longer experiments over several months (Berlow, 1999). These differences in time scales may result in different outcomes and interpretations of experiments (Walther, 2007). In particular, interaction strengths on a short time scale (days) depend primarily on predator ingestion rates while ignoring numerical responses in predator and prey abundances. However, on a long time scale (month, years), interaction strengths are also influenced by the rates of prey growth and prey abundance (Berlow *et al.*, 2009). Therefore, predicting the consequences of warming requires an understanding of temperature effects on the rates of ingestion and metabolism of the predators (with implications for short-term interaction strengths) and the growth rates and abundances of the prey species (with additional implications for long-term interaction strengths).

The Metabolic Theory of Ecology (MTE) offers a general framework for tackling these questions by suggesting: (i) three-quarter power-law increases in the rates of metabolism, ingestion and growth with organism body mass, (ii) a three-quarter power-law decrease in abundance with body mass within a single trophic level, and (iii) exponential scaling of these rates and abundance with temperature, where the strength of these scaling relationships is determined by an activation energy, E (Gillooly *et al.*, 2001; Brown & Gillooly, 2003; Brown *et al.*, 2004; Meehan, 2006a). Despite an intensive debate on the exact exponents, the power-law (body mass) and the exponential (temperature) scaling of metabolism find broad empirical support (Brown *et al.*, 2004; Clarke, 2004; Kozłowski & Konarzewski, 2004; Savage *et al.*, 2004a, b; Makarieva *et al.*, 2005).

In the case of ingestion, the scaling with body mass and temperature remains hotly debated (see: Peters, 1983; Brown *et al.*, 2004; Vasseur & McCann, 2005;

Carbone *et al.*, 2007; Brose *et al.*, 2008; Brose, in press; Vucic-Pestic *et al.*, in press; and references therein). In contrast to MTE predictions (Peters, 1983), recent foraging studies have documented a hump-shaped relationship between ingestion rates and predator–prey body-mass ratios (Wahlstrom *et al.*, 2000; Vonesh & Bolker, 2005; Brose *et al.*, 2008; Vucic-Pestic *et al.*, in press). This implies that handling and digestion constrain predator ingestion rates at low predator–prey body-mass ratios (i.e., when prey species are relatively large), whereas catching efficiencies limit predator ingestion rates at high ratios (i.e., when prey species are relatively small). Although some prior studies showed that ingestion increases with temperature (Thompson, 1978; Kingsolver & Woods, 1997) others concluded that ingestion is not effected by warming (Woodward & Hildrew, 2002). Unfortunately, studies that include both, temperature-dependent ingestion and metabolism of predators, are scarce (Vasseur & McCann, 2005; Abrahams *et al.*, 2007; but see Kingsolver & Woods, 1997 for an example), and it remains unknown whether the different processes leading to handling and catching limitation of large (left-hand side of the hump-shaped relationship, Brose *et al.*, 2008) and small prey (right-hand side of the hump-shaped relationship), are similarly influenced by temperature.

Here, we address these deficiencies by quantifying the temperature dependence of metabolism and ingestion (of small and large prey) of terrestrial arthropods (beetles and spiders) across a range of body masses. The predator and prey species of our experiments were chosen to reflect the predator–prey body-mass ratios of natural food webs (Brose *et al.*, 2006a) and both sides of the hump-shaped relationship between ingestion and body-mass ratios documented in a prior study with the same species (Brose *et al.*, 2008; Vucic-Pestic *et al.*, in press). All experiments were replicated at three environmental temperatures (8, 15 and 22 °C) representing the natural gradient of spring and summer temperatures in central Germany (Deutscher Wetterdienst, 2007). Based on these experiments, we quantified how temperature affects ingestion efficiencies, short-term and long-term interaction strengths, which provides the information required to address the effect of temperature on both intrinsic and perturbation stability of populations and food webs.

Materials and methods

Respiration and ingestion experiments

We investigated how predator metabolism varied with temperature. Specifically, we measured the O₂ consumption of eight carabid beetle species (*Abax paralle-*

pipedus, *Carabus auratus*, *Harpalus affinis*, *Notiophilus biguttatus*, *Platynus dorsalis*, *Poecilus versicolor*, *Pseudophonus rufipes* and *Pterostichus oblongopunctatus*) and six species of lycosid and pisaurid spiders (*Alopecosa cuneata*, *Pardosa lugubris*, *Pardosa palustris*, *Pirata latitans*, *Pirata piraticus* and *Pisaura mirabilis*). O₂ consumption of the beetles and spiders was measured in an automated electrolytic microrespirometer (Scheu, 1992). We converted the individual O₂ consumption (mL s⁻¹) into energetic equivalents of metabolism I_j (J s⁻¹) by assuming that 1 mL O₂ equals 20.1 J (Peters, 1983).

For a subset of these predators, we investigated how ingestion varied with predator and prey body mass, and temperature. Logistic constraints restricted our study to five beetle species (*A. parallelepipedus*, *C. auratus*, *P. dorsalis*, *P. versicolor* and *P. rufipes*) and four spider species (*A. cuneata*, *P. palustris*, *P. latitans* and *P. mirabilis*). For each predator species, the experiments were replicated six times: with large prey (beetle prey: fly larvae *Lucilia caesar*, spider prey: cricket *Gryllus sigillatus*) and with small prey (beetle prey: fruit fly *Drosophila hydei*, spider prey: springtail *Heteromurus nitidus*) in climatic chambers at three temperature levels (8, 15 and 22 °C). These two prey size groups represent the whole range of body size ratios found in nature (Brose *et al.*, 2006a), including the left-hand and right-hand side of the hump-shaped relationship between predation rates and predator-prey body-mass ratios documented in a prior study (Brose *et al.*, 2008). For both predator groups, we used two prey species with similar escape behaviour. Crickets and springtails avoid spider predation by jump-escaping in the case of emergency. Flightless fruit flies and the fly larvae escape beetle predation by crawling. Ingestion experiments were performed in 0.04 m² perspex arenas lined with dental cast to hold moisture during experimental time of 24 h. Initially, we added 2.35 g of remoistened dry moss (*Polytrichum formosum*) as habitat structure, 30 prey individuals, N_i , and one predator individual to each arena. The number of the remaining prey individuals was counted after 24 h to calculate the number of prey individuals eaten (N_e). The full-factorial combination of the independent variables (nine predators, two prey sizes, three temperatures) with six replicates per combination resulted in a total of 324 experimental units.

For every combination of predator j and prey i , we calculated the ingestion rate, J_{ij} (J s⁻¹)

$$J_{ij} = \frac{N_e M_i \varepsilon}{t_F}, \quad (1a)$$

where M_i is the individual body mass of a prey individual (g per Ind.) and t_F is the experimental duration in

seconds, we assume an energy content ε of 7000 J g⁻¹ wet mass (Peters, 1983). Subsequently, we calculated the dimensionless ingestion efficiency (Vasseur & McCann, 2005) as

$$y_{ij} = \frac{w_{ij} J_{ij}}{\lambda I_j}, \quad (1b)$$

where w_{ij} is the dimensionless assimilation efficiency ((ingestion-faeces)/ingestion). We assumed a constant assimilation efficiency ($w_{ij} = 0.85$; Lawton, 1970; Peters, 1983; Yodzis & Innes, 1992) that does not vary with environmental temperature as documented in most empirical studies, e.g., of carnivorous insects (Lawton, 1970), caterpillars (Kingsolver & Woods, 1998) and lizards (Chen *et al.*, 2003; McConnachie & Alexander, 2004). λ is a dimensionless constant converting basal metabolic rate into field metabolic rate ($\lambda = 3$ Savage *et al.*, 2004b), and I_j is the metabolic rate of predator j [calculated according to Eqn (2a)]. The ingestion efficiency expresses the ingestion gain of a consumer relative to its metabolic loss, and it is thus closely related to biomass gains or losses.

Although there is a wide range of different metrics that can be used to calculate *per capita* interaction strengths (Berlow *et al.*, 1999, 2004), we focused on the most widely used: the log response ratio, (Berlow *et al.*, 1999; Emmerson & Raffaelli, 2004)

$$\alpha_{ij} = \left| \frac{\ln((N_i - N_e)/N_i)}{t} \right|, \quad (1c)$$

where t (days) is the experimental duration, N_i (Ind.) is the initial prey abundance and N_e (Ind.) is the number of prey eaten. In our case, the short-term interaction strength is the log ratio between the prey abundances at the end and at the start of the experiment. This approach assumes that prey abundance without predators equals the initial prey density, and thus natural mortality of the prey species is negligible. This assumption was supported by the lack of mortality in controls without predators.

Statistical analysis of experimental data

All data were analysed by ANCOVAs with the statistical software R 2.9.0 (R Development Core Team, 2009) to distinguish between effects of the factors (1) predator group (beetle or spider) and (2) prey size (large or small, only for ingestion experiments), (3) level of environmental temperature (8, 15 and 22 °C), and the continuous variable (4) predator mass [ln(g)]. Subsequently, we generated multiple regression models following the MTE (Brown *et al.*, 2004) predicting that *per capita* rates of metabolism, I_j (J s⁻¹), and ingestion, J_{ij} (J s⁻¹), of an ectotherm organism depend on its body mass, M (g),

and the environmental temperature, T (K) as

$$I_j = i_0 M_j^{b_j} e^{-\frac{E_j}{kT}}, \quad (2a)$$

$$J_{ij} = j_0 M_j^{b_j} e^{-\frac{E_j}{kT}}, \quad (2b)$$

where i_0 and j_0 are normalization constants, b is an allometric exponent, k is Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV K}^{-1}$) and E (eV) is the activation energy. In the same way, we analysed the temperature and body-mass dependence of ingestion efficiencies and interaction strengths as

$$y_{ij} = y_0 M_j^{b_y} e^{-\frac{E_y}{kT}}, \quad (2c)$$

$$e^{a_{ij}} = \alpha_0 M_j^{b_z} e^{-\frac{E_z}{kT}}, \quad (2d)$$

Note that because of the fact that the *per capita* interaction strength is calculated as the natural logarithm [Eqn (1c)], we used the exponential functions for investigating the mass and temperature dependence of *per capita* interaction strength [Eqn (2d)]. Consistent with prior studies (Brown *et al.*, 2004; Meehan, 2006a, b), we made multiple linear least-squares regressions with the GLM procedure of the statistical software R 2.9.0 (R Development Core Team, 2009) to estimate the parameters of Eqn (2a–d) after ln-transformation.

Long-term interaction strength

Calculations of long-term interaction strengths were based on a population dynamic model (Yodzis & Innes, 1992; Vasseur & McCann, 2005; Rall *et al.*, 2008) of prey density, N (Ind. m^{-2}), and predator density, P (Ind. m^{-2}):

$$\frac{dN}{dt} = r \left(1 - \frac{N}{K} \right) N - c_F J_{ij} NP, \quad (3a)$$

$$\frac{dP}{dt} = \frac{c_j J_{ij} NP}{w_{ij}} - c_I I_j P, \quad (3b)$$

where t (days) is time, r (1 per day) is the intrinsic growth rate and K (Ind. m^{-2}) is the carrying capacity of the prey species. The feeding interaction follows a linear functional response, where J_{ij} (J s^{-1}) is the ingestion rate of a single predator, c_j ($\text{s N day}^{-1} \text{J}^{-1}$) is a correction factor that converts the ingestion rate from Joules per second into prey individuals per day. I_j (J s^{-1}) is the metabolic rate of the predator and c_I is a correction factor that converts metabolism from Joules per second into predator individuals per day ($\text{s P day}^{-1} \text{J}^{-1}$). The temperature- and mass-dependent intrinsic growth rate

r in Eqn (3a) is calculated by

$$r = r_0 M^{b_r} e^{-\frac{E_r}{kT}}, \quad (4a)$$

where r_0 ($r_0 = e^{32.39}$; Savage *et al.*, 2004a) is a normalization constant, M is the mass (μg), b_r ($b_r = -0.25$) is a constant exponent, k is Boltzmann's constant ($8.62 \times 10^{-5} \text{ eV K}^{-1}$) and E_r (-0.84 eV) is the activation energy for insects (Savage *et al.*, 2004a).

The carrying capacity K in Eqn (3a) depends on environmental temperature, body mass, the trophic level of the prey and the net primary production of the habitat (Allen *et al.*, 2002; Meehan, 2006a) following:

$$K = K_0 M^{b_K} e^{-\frac{E_K}{kT}} \sigma^z e^{tl_0(tl-1)}, \quad (4b)$$

where K_0 is a normalization constant, b_K is a constant exponent, E_K is the activation energy, σ is the annual net primary productivity of the habitat [$\text{g(C) m}^{-2} \text{ yr}^{-1}$], z is a constant exponent, tl_0 is a constant and tl the trophic level. We used constants found in other studies with similar soil invertebrates as in our study: $K_0 = e^{-31.15}$, $b_K = -0.72$; $E_K = 0.71$; $tl_0 = -2.68$; $z = 1.03$; $tl = 1.5$ for decomposers, fungivores and herbivores (Meehan, 2006a). The net primary productivity in Eqn (4b) is temperature dependent (Allen *et al.*, 2005)

$$\sigma = \sigma_0 e^{-\frac{E_\sigma(T_0-T)}{kT_0}}, \quad (4c)$$

where σ_0 is the net primary productivity at the temperature T_0 (K) and E_σ is the activation energy [-0.35 eV , of the net primary production that is mechanistically derived from the activation energy of photosynthesis (Allen *et al.*, 2005)]. We assumed an average net primary production, σ_0 , of $600 \text{ g(C) m}^{-2} \text{ yr}^{-2}$ for temperate regions (Cramer *et al.*, 1999) at an average temperature T_0 of 9.5°C (282.65 K) which is approximately equal to the annual average temperature in Germany since 2000 (Deutscher Wetterdienst, 2007).

The long-term population densities of Eqns (3a) and (3b) are calculated assuming that the system is at equilibrium (i.e., $dN/dt = 0$; $dP/dt = 0$), which yields equilibrium densities (P' , N') of

$$P' = \frac{(K - N')r}{c_F J_{ij} K}, \quad (5a)$$

$$N' = \frac{w_{ij} c_I I_j}{c_F J_{ij}}. \quad (5b)$$

Subsequently, the long-term *per capita* interaction strength between i and j , A_{ij} , is calculated according to the log ratio interaction strength used in prior studies

(also known as dynamic index) (Berlow *et al.*, 1999; Emmerson & Raffaelli, 2004):

$$A_{ij} = \left| \frac{\ln(N^+/N^-)}{Y} \right|, \quad (6)$$

where N^+ is the prey abundance when the predator is present and N^- is the prey abundance when the predator is absent and Y is the predator abundance. We can replace N^+ by N' and Y by P' (see Eqn (5a) and (5b)). Moreover, in absence of a predator the prey is growing to its carrying capacity (Eqn (4b)), and we can replace N^- with K , which yields

$$A_{ij} = \left| \frac{\ln(N'/K)}{P'} \right|. \quad (7)$$

Inserting Eqn (5a) and (5b) in Eqn (7) and using the temperature dependencies of I_j [Eqn (2a)], J_{ij} [Eqn (2b)], K [Eqn (4b)] and r [Eqn (4a)] yields the long-term interaction strengths depending on environmental temperature.

Results

Respiration and ingestion experiments

The metabolic rates of the predators, beetles and spiders, increased significantly with their body mass and temperature (Fig. 1a and b; ANCOVA, Table 1). The significant interaction term between predator mass and predator group (Table 1) suggests that the exponent for beetles ($b_1 = 0.72$; Table 2; Fig. 1a, circles) is higher than the exponent for spiders ($b_1 = 0.46$; Table 2; Fig. 1a, crosses). In contrast, the interaction term between temperature and predator group was not significant (Table 1) suggesting that the activation energy was similar for beetles ($E_1 = 0.87$; Table 2; Fig. 1b, circles) and spiders ($E_1 = 0.80$; Table 2; Fig. 1b, crosses).

We found significant effects of predator body mass and temperature on ingestion rates (ANCOVA, Table 1). Significant interaction terms with predator mass indicate that the allometric exponents differ for predator groups and prey size (Table 1): exponents were higher for beetles than for spiders and while ingestion increased with predator body mass when prey were large ($b_1 = 0.82$ and $b_1 = 0.6$ for beetles and spiders, respectively; Table 2; Fig. 1c), it decreased with predator body mass when prey were small ($b_1 = -0.25$ and $b_1 = -0.63$ for beetles and spiders, respectively; Table 2; Fig. 1e). Temperature effects on ingestion were similar for both predator groups (no significant interaction term between temperature and predator group) although they differed with respect to prey size (Table 1). Ingestion increased with temperature when prey were large

($E_j = 0.24$ and $E_j = 0.30$ for beetles and spiders, respectively; Table 2; Fig. 1d), whereas it did not vary significantly when prey were small (Table 2; Fig. 1f).

Ingestion efficiency

From the metabolism and ingestion measures, we calculated the ingestion efficiency (ingestion/metabolism) for each predator. We found significant effects of temperature and predator body mass on ingestion efficiencies (ANCOVA, Table 1). Significant interaction terms indicated that these effects depend on prey type, whereas nonsignificant interaction terms suggest similar mass and temperature effects for both predator groups (ANCOVA, Table 1). For both predator groups, ingestion efficiencies did not vary with predator mass in treatments with large prey (Fig. 2a; Table 2), whereas they decreased in treatments with small prey (Fig. 2c; Table 2). Eventually, ingestion efficiencies fell below unity indicating that metabolism exceeded ingestion (Fig. 2c, red symbols). For both predator groups and both prey sizes, increasing temperature generally decreased the ingestion efficiency, which increased the number of predator individuals that could not balance their metabolic demands (Fig. 2b–d, red symbols; 8 °C: 11 individuals, 15 °C: 20 individuals, 22 °C: 34 individuals). Thus, the critical boundary, at which predator ingestion was insufficient to balance metabolic loss [$y_{ij} < 1$, Eqn (1b)] shifted to a range of lower predator body masses when temperature increased.

Short-term interaction strength

Effects of predator mass and temperature on short-term interaction strengths exhibited a significant dependence on predator group and prey size (significant three-way interaction terms in Table 1). Short-term interaction strengths increased significantly with predator body mass in treatments with large prey irrespective of the predator group (Fig. 3a). In treatments with small prey, short-term interaction strengths decreased slightly with predator mass for spiders, but they remained constant for beetles (Fig. 3c; Table 2). Moreover, short-term interaction strengths increased with warming when predators fed on large prey (Fig. 3b; Table 2) and when beetles fed on small prey (Fig. 3d, circles; Table 2). In contrast, short-term interaction strengths decreased slightly with warming when spiders fed on small prey (Fig. 3d, crosses; Table 2).

Prediction of long-term interaction strength

Calculated long-term interaction strength generally decreased with increasing temperature across all

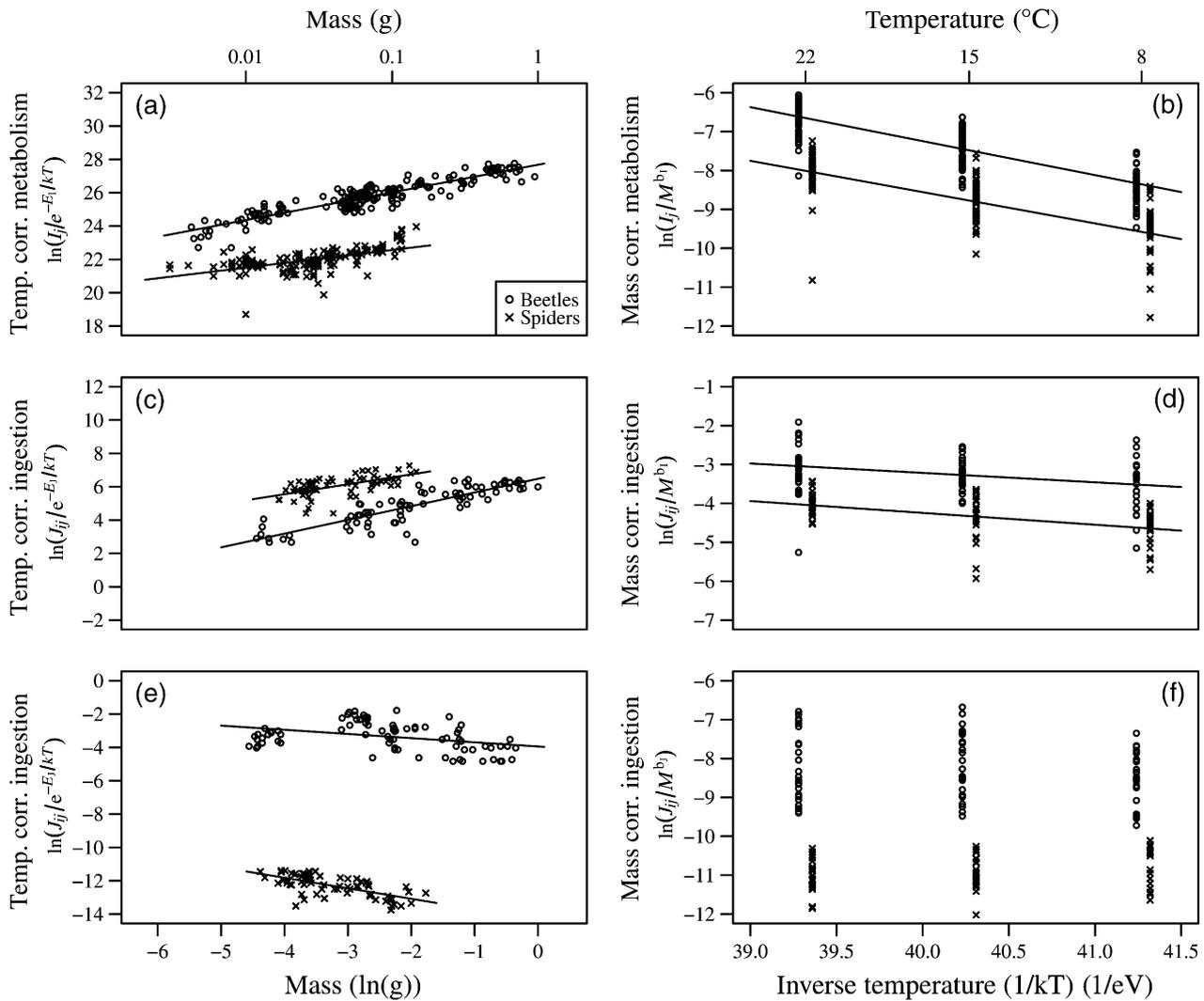


Fig. 1 Beetle (circles) and spider (crosses) metabolism I_j (a, b), ingestion J_{ij} of the larger (c, d) and the smaller prey (e, f) depending on predator body mass (a, c, e) and environmental temperature (b, d, f). Data are \ln -transformed and the dependent variables are normalized by their temperature dependence (a, c, e) or their mass dependence (b, d, f). Upper axes show untransformed body mass (g) and temperature ($^{\circ}\text{C}$) scales. Offsets of -0.04 (beetles) and 0.04 (spiders) were applied to temperature data in panels (b), (d) and (f). Note the inverse scaling of the lower temperature axes.

combinations of predator groups, predator masses and prey sizes (Fig. 4). Large predators have a higher impact on the large prey and smaller predators have a higher impact on the small prey (Fig. 4a and b vs. Fig. 4c and d). In all cases, the total decrease in long-term interaction strength is stronger when the long-term interaction strength is generally strong (Fig. 4).

Discussion

Consistent with the MTE (Brown *et al.*, 2004), our experiments demonstrate that the metabolism of beetles and spiders followed a power law increase with their body mass and an exponential increase with tempera-

ture. However, we did not find similar relationships for predator ingestion rates. As expected based on recent foraging studies documenting hump-shaped relationships between ingestion and predator-prey body-mass ratios (Wahlstrom *et al.*, 2000; Vonesh & Bolker, 2005; Brose *et al.*, 2008), we found differences in warming effects on ingestion rates between treatments with small prey (constant rates) and treatments with large prey (increasing rates). In contrast to our initial expectation based on the MTE, activation energies of ingestion were lower than those of metabolism, and thus ingestion efficiencies (the ratio of ingestion to metabolism) generally decreased with warming. Moreover, short-term interaction strengths (only accounting for ingestion)

Table 1 ANCOVA tables of metabolism, ingestion, ingestion efficiency and interaction strength

	df	Metabolism		Ingestion		Ingestion efficiency		Short-term interaction strength	
		F	P	F	P	F	P	F	P
1: <i>Predator mass</i> [ln(M)]	1	1012.23	<0.001	341.43	<0.001	13.61	<0.001	1.23	0.27
2: Temperature (8 °C/15 °C/22 °C)	2	326.35	<0.001	6.38	<0.01	63.87	<0.001	1.43	0.24
3: Prey size (large/small)	1			1385.96	<0.001	341.83	<0.001	18.04	<0.001
4: Predator group (beetles/spiders)	1	56.97	<0.001	175.4	<0.001	0.9	0.34	33.15	<0.001
<i>Predator mass</i> × Temperature	2	0.08	0.92	1.36	0.25	2.27	0.11	2.39	0.09
<i>Predator mass</i> × Prey size	1			189.24	<0.001	14.54	<0.001	130.14	<0.001
Temperature × Prey size	2			4.41	0.01	32.29	<0.001	2.68	0.07
<i>Predator mass</i> × Predator group	1	26.04	<0.001	7.35	<0.01	0.04	0.84	28.14	0.001
Temperature × Predator group	2	0.88	0.41	1.53	0.22	0.68	0.51	3.53	0.03
Prey size × Predator group	1			47.32	<0.001	1.68	0.2	<0.01	0.96
1 × 2 × 3	2			0.06	0.95	3.21	0.04	0.75	0.47
1 × 2 × 4	2	0.13	0.88	0.59	0.56	0.62	0.54	1.5	0.23
1 × 3 × 4	1			0.42	0.52	0.02	0.89	20.53	<0.001
2 × 3 × 4	2			0.97	0.38	0.26	0.77	3.39	0.04
1 × 2 × 3 × 4	2			0.83	0.44	0.41	0.66	1.61	0.2

Continuous variables in italic and factors in bold.

The metabolism ANCOVA does not include the factor 'prey size'.

Residual standard errors are: metabolism (333), ingestion, ingestion efficiency and short term interaction strength (270).

Table 2 Regression results for the body-mass and temperature dependence of metabolism, ingestion, ingestion efficiency and interaction strength

	ln(c)	P	Lower CI	Upper CI	b	P	Lower CI	Upper CI	E	P	Lower CI	Upper CI	r ²	AIC	n
<i>Metabolism</i>															
Beetles	27.68	***	24.72	30.64	0.72	***	0.68	0.77	0.87	***	0.8	0.95	0.89	192.19	183
Spiders	23.62	***	19.17	28.07	0.46	***	0.36	0.55	0.8	***	0.69	0.91	0.64	265.06	162
<i>Ingestion of large prey</i>															
Beetles	6.47	*	0.13	12.82	0.82	***	0.71	0.93	0.24	**	0.09	0.4	0.75	142.11	80
Spiders	7.93	*	2.05	13.81	0.6	***	0.4	0.79	0.3	***	0.16	0.45	0.42	96.26	67
<i>Ingestion of small prey</i>															
Beetles	-3.94	-	-12.86	4.97	-0.25	**	-0.39	-0.11	0.11	-	-0.11	0.33	0.14	193.17	79
Spiders	-14.34	***	-20.19	-8.48	-0.63	***	-0.8	-0.46	-0.09	-	-0.23	0.06	0.44	97.04	68
<i>Ingestion efficiency – large prey</i>															
Beetles	-22.4	***	-28.74	-16.05	0.1	-	-0.01	0.21	-0.63	***	-0.79	-0.47	0.47	142.23	80
Spiders	-16.88	***	-22.77	-10.99	0.14	-	-0.06	0.33	-0.5	***	-0.64	-0.36	0.45	96.48	67
<i>Ingestion efficiency – small prey</i>															
Beetles	-32.84	***	-41.76	-23.92	-0.97	***	-1.11	-0.83	-0.76	***	-0.99	-0.54	0.74	193.28	79
Spiders	-39.18	***	-45.03	-33.32	-1.09	***	-1.26	-0.91	-0.89	***	-1.03	-0.74	0.81	97.17	68
<i>Absolute interaction strength with large prey</i>															
Beetles	3.33	***	1.46	5.2	0.16	***	0.13	0.19	0.07	**	0.02	0.11	0.58	-53.29	80
Spiders	3.62	***	2.19	5.05	0.15	***	0.11	0.2	0.07	***	0.04	0.11	0.44	-92.85	67
<i>Absolute interaction strength with small prey</i>															
Beetles	2.8	*	0.22	5.39	-0.04	-	-0.08	0	0.07	*	0	0.13	0.09	-2.55	79
Spiders	-5.13	*	-8.95	-1.31	-0.36	***	-0.48	-0.25	-0.11	*	-0.21	-0.02	0.4	38.99	68

c, normalization constant; P, level of significance; CI, confidence interval; b, allometric exponent; E, activation energy; #, zero values omitted for ln transformation. *P < 0.05; **P < 0.01; ***P < 0.001.

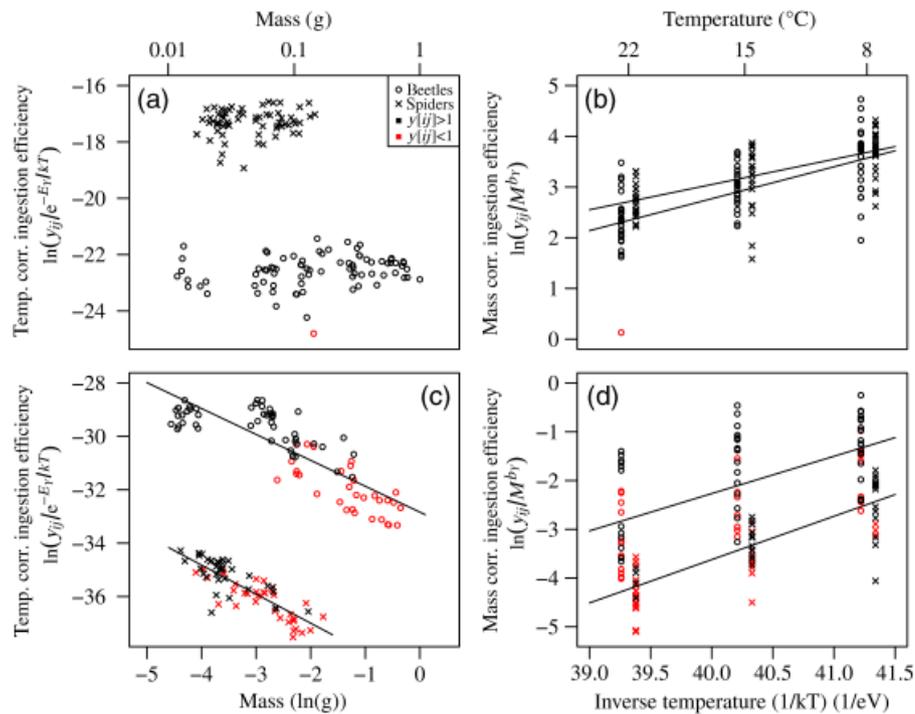


Fig. 2 Beetle (circles) and spider (crosses) ingestion efficiency y_{ij} in treatments with the larger (a, b) and the smaller prey (c, d) depending on predator body mass (a, c) and environmental temperature (b, d). Data are ln-transformed and the dependent variables are normalized by their temperature dependence (a, c) or their mass dependence (b, d). Upper axes show untransformed body mass (g) and temperature ($^{\circ}\text{C}$) scales. Offsets of -0.04 (beetles) and 0.04 (spiders) were applied to temperature data in panels (b) and (d). Note the inverse scaling of the lower temperature axes. Red coloured circles and crosses indicate where the ingestion efficiency was below the critical threshold of unity ($y_{ij} < 1$).

increased with warming in all treatments except for the treatment with spiders and small prey, whereas the long-term interaction strengths (additionally accounting for temperature effects on prey abundance) generally decreased. Together, these results demonstrate that warming may have complex and profound implications for predator–prey interaction strengths, population dynamics and food-web stability.

Metabolism

The MTE predicts a $3/4$ power-law increase in metabolism with body mass and an exponential increase with temperature, where the activation energy should be in the range of biochemical reactions between 0.2 and 1.4 eV (Gillooly *et al.*, 2001; Clarke, 2004). Generally, most of our results corroborate the predictions of the MTE. The exception is spider metabolism, which exhibited a particularly low allometric exponent ($b_1 = 0.46 \pm 0.09$). The low spider exponent may be caused by factors limiting metabolism other than the circulatory transport network (e.g., the relative metabolic tissue is larger in small than in large spiders; but

see (Brose *et al.*, 2008) for more examples), but a mechanistic explanation of allometric exponents is beyond the scope of this study.

Body-mass effects on ingestion

Following assumptions of the MTE, the allometric exponents and the activation energies for ingestion should be similar to those for metabolism (Brown *et al.*, 2004). Consistent with this assumption, the allometric exponents for metabolism were within the 95% confidence intervals of those for ingestion in treatments with large prey. Moreover, the confidence intervals of the allometric exponents of both predator groups in treatments with large prey include the $3/4$ exponent predicted by models based on MTE (Brown *et al.*, 2004). Contrary to the assumptions of the MTE, however, the allometric exponents of ingestion in treatments with small prey were negative, indicating that ingestion rates decreased with increasing predator body mass.

The pattern of increasing and decreasing ingestion rates documented here is consistent with hump-shaped relationships between ingestion and predator–prey

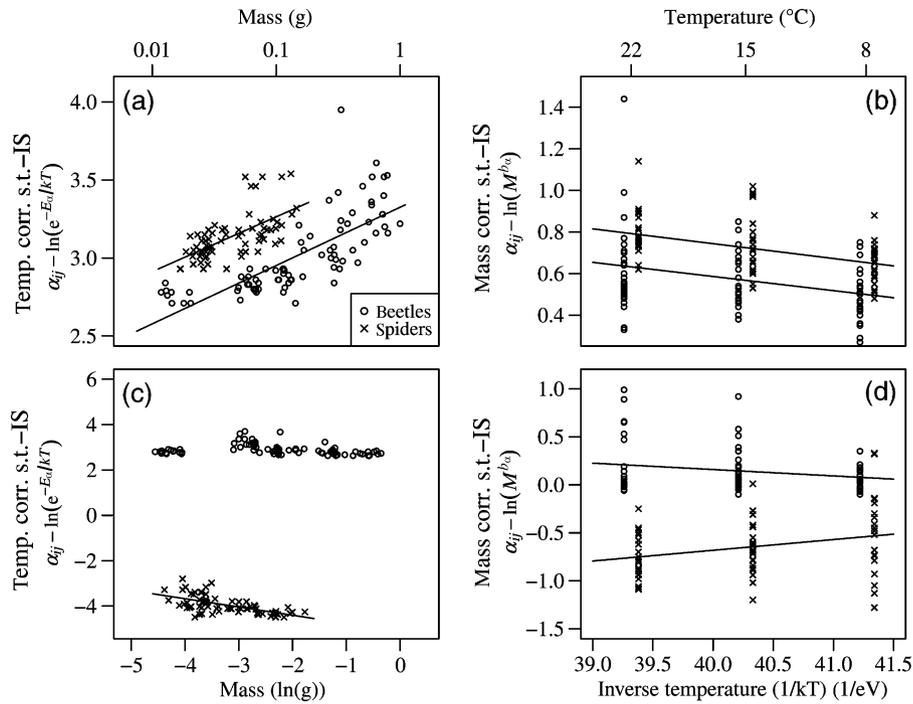


Fig. 3 Beetle (circles) and spider (crosses) absolute short-term per capita interaction strength α_{ij} in treatments with the larger (a, b) and the smaller prey (c, d) depending on predator body mass (a, c) and environmental temperature (b, d). Data are ln-transformed and the dependent variables are normalized by their temperature dependence (a, c) or their mass dependence (b, d). Upper axes show untransformed body mass (g) and temperature ($^{\circ}\text{C}$) scales. Offsets of -0.04 (beetles) and 0.04 (spiders) were applied to temperature data in panels (b) and (d). Note the inverse scaling of the lower temperature axes.

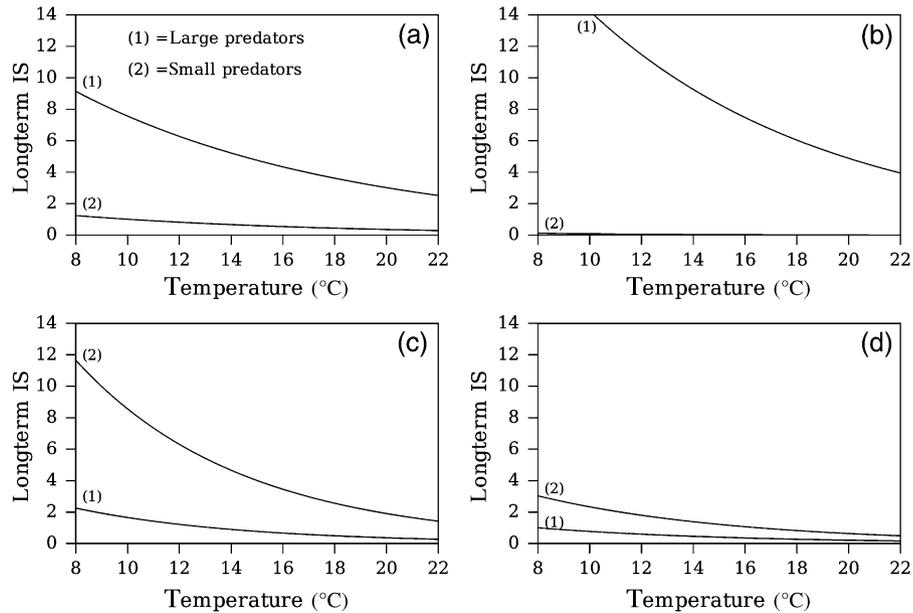


Fig. 4 Beetle (b, d) and spider (a, c) long-term per capita interaction strength A_{ij} in treatments with the larger (a, b) and the smaller prey (c, d) in dependence on environmental temperature. Lines marked with (1) denote largest predators in our experiments (beetles: 1000 mg, spiders: 170 mg) and lines marked with (2) denote smallest predators in our experiments (beetles: 11 mg, spiders: 13 mg).

body-mass ratios documented by foraging theory (Wahlstrom *et al.*, 2000; Vonesh & Bolker, 2005; Brose *et al.*, 2008; Vucic-Pestic *et al.*, in press; Brose, in press). On the left-hand side of the hump at low body-mass ratios (e.g., large prey in our experiments), predator effects on prey are limited by handling-time constraints and ingestion rates increase with body-mass ratios because of decreasing handling time (i.e., the disparity in predator and prey body mass increases and large predators are able to handle small prey with ease). On the right-hand side of the hump, when body-mass ratios are large (e.g., small prey in our experiments), predator ingestion is constrained by the rate at which they can catch small prey and ingestion rates decrease with body-mass ratios, because the predators' attacks become increasingly inefficient (Aljetlawi *et al.*, 2004; Brose *et al.*, 2008). Predators may either not perceive prey, or there is a trade off between the time taken to capture a very small prey item and the energetic benefit derived from the interaction. Thus, the effects of increasing predator body mass on ingestion should deviate from a simple power law when a wider range of predator and prey body masses is considered. As in prior studies over a more limited range of body-mass ratios (Peters, 1983; Emmerson & Raffaelli, 2004), we found that the increasing slope of this hump-shaped relationship at low body-mass ratios (i.e., large prey) is well described by an increasing power function. However, documentation of a hump-shaped relationship required extension of the range of body-mass ratios studied to include decreasing ingestion rates at high body-mass ratios (i.e., small prey in our study).

Temperature effects on ingestion, ingestion efficiencies and interaction strengths

The activation energies of ingestion were more than two times smaller than those of metabolism. Thus, the response of ingestion to warming is much weaker than the increase in metabolism. Contrary to expectations based on the MTE, ingestion efficiencies (i.e., ingestion relative to metabolism) thus decreased with warming independent of the prey size and predator group. Eventually, warming leads to ingestion efficiencies below unity (ingestion lower than metabolic demands, see Fig. 2, red symbols), which causes predator starvation. This suggests that many predator-prey interactions could become infeasible under warming. The activation energies of ingestion were slightly positive in treatments with large prey where predators were limited by handling time, which includes biochemical digestion processes (van Rijn *et al.*, 2005). Warming can accelerate these biochemical processes (Gillooly *et al.*, 2001), which leads to faster handling time thus explaining higher

ingestion rates in our experiments with large prey. Interestingly, the activation energies of ingestion were not significantly different from zero in treatments with small prey, where predators were constrained by their ability to catch prey, and ingestion was independent of digestion and satiation (van Rijn *et al.*, 2005). Warming does not affect the catching efficiency, which is primarily driven by constraints such as detectability and mobility. If warming had an equal effect on predator and prey mobility, the net effect of warming on the catching efficiency of predators would be neutral, which could explain the lack of warming effects in our treatments with small prey.

Generally, absolute short-term *per capita* interaction strengths increased with temperature except for the treatment of spiders with small prey. This corroborates a prior field study documenting positive effects of temperature on interaction strengths in a marine intertidal food web (Sanford, 1999). Our study demonstrates that these positive temperature effects are driven by increasing ingestion rates. Although comprehensive field studies investigating temperature and body-mass effects on interaction strengths are scarce, based on metabolic arguments our study suggests the broad generality of positive correlations between temperature and short-term interaction strengths.

Interestingly, the absolute values of the long-term interaction strengths (not taking its sign into account) decrease with warming. This is caused by differences between the activation energies of predator metabolism and ingestion [see Eqn (5b)] yielding higher prey population densities at higher temperatures in simple predator-prey systems. Moreover, the carrying capacity of the prey decreases because abundances of natural populations embedded in a complex network generally decrease with warming (Allen *et al.*, 2002; Meehan, 2006a). The long-term interaction strengths [Eqn (6)] are proportional to the ratio of the equilibrium prey density (increasing with warming) to the prey carrying capacity (decreasing with warming). Consequently, this ratio increases with warming, yielding less negative values, and decreases in absolute strength. Additionally, because of the differences in prey growth rates and predator ingestion rates, the predator density increases with warming causing an additional decrease in absolute *per capita* interaction strength with warming [Eqn (5a)].

Although short-term interaction strengths were determined by increases in predator ingestion rates under warming [see Eqn (1c)], temperature effects on predator and prey densities outweigh these increasing ingestion rates and yield decreasing long-term interaction strengths under warming. This disparity between different measurements of interaction strength on different

time scales is a general problem in ecological sciences, especially in experiments exploring aspects of climate change (Walther, 2007). The approach adopted in this study to calculate long-term interaction strengths might offer a solution to this problem.

Temperature effects on population stability

In our experiments, ingestion rates and short-term interaction strengths with large prey (low body-mass ratios) increased with warming. This may result in a stronger short-term top-down control of prey populations under warming when prey growth rates and densities are negligible. However, long-term interaction strengths generally decrease with warming. As decreasing interaction strengths are inversely correlated with perturbation stability (May, 1972), our results suggest that the perturbation stability of natural communities should increase with warming. Additionally, our results demonstrate decreases in ingestion efficiencies with warming, which should lead to higher intrinsic population stability for all predator-prey interactions irrespective of the body-mass ratio (Yodzis & Innes, 1992; Vasseur & McCann, 2005; Rall *et al.*, 2008). However, decreased ingestion efficiencies combined with higher predator density may lead to starvation of the predator population, even if the prey population also has increased in density. Consistent with this conclusion, warming of microcosm food webs caused an increase in biomass of bacteria and bacterivorous consumers whereas larger predators and herbivores became extinct and the biomass of producers increased (Petchey *et al.*, 1999). Our results indicate that predator-prey interactions characterized by high body-mass ratios (small prey in our experiments) are particularly prone to this predator-starvation effect of warming. Analyses of the body-mass structure of natural food webs (Brose *et al.*, 2006a) may thus facilitate predictions of their sensitivity to global warming. Global warming may also increase the productivity of ecosystems because of increasing CO₂ levels (Emmerson *et al.*, 2005), which may counteract the direct temperature effects studied here because of increased net primary productivity. Eventually, these two global warming effects need to be reconciled to achieve accurate forecast models.

Caveats

As any laboratory study, our approach was based on some simplifying assumptions: (1) simple predator-prey pairs ignore potentially more complex feeding behaviour of predators when multiple prey or predator species or multiple predator individuals coexist (e.g., prey switching or interference competition, compensatory effects of

alternative predators); (2) constant prey densities across all ingestion experiments do not account for non-linearly saturating responses of ingestion to high prey densities. Future more complex extensions of our laboratory approach will need to address effects of these simplifying assumptions. However, our assumption of constant assimilation efficiencies across the temperature gradient is supported by empirical studies of carnivorous insects (Lawton, 1970), caterpillars (Kingsolver & Woods, 1998) and lizards (Chen *et al.*, 2003; McConnachie & Alexander, 2004). As most prior warming experiments, our approach did not account for thermal adaptation of the species, which can reduce their physiological responses to warming (Lenski & Bennett, 1993; Clarke & Johnston, 1999). However, a 76% lower activation energy of metabolism as documented for fish species after thermal adaptation (Clarke & Johnston, 1999) would not affect the qualitative conclusions of the present study. Nevertheless, our approach presents a simplistic, mechanistic null model of temperature effects on predator-prey interactions in which thermal adaptation effects remain to be included. In contrast, prior long-term field studies on the effects of warming avoid some of these simplifying assumptions at the cost of lacking mechanistic explanations. Future studies will need to bridge the gap between simplified but mechanistic laboratory studies and more complex field studies.

Conclusions

Four conclusions arise from our results: warming of natural ecosystems may cause (1) higher feeding rates and short-term interaction strengths yielding higher impacts on a prey population over a short period of time, (2) higher perturbation stability of the populations (higher probability of returning to the same equilibrium density after a small perturbation) because of lower absolute long-term *per capita* interaction strengths, (3) a higher intrinsic population stability (less fluctuations in population density) because of reduced ingestion efficiencies, and (4) higher extinction risks because of predator starvation. As species interactions provide the mechanistic link between global warming and ecosystem functions (Hughes, 2000), our results suggest that predicting the consequences of climate change may be far from trivial. Nevertheless, future extensions of our approach may provide a mechanistic understanding of how warming affects population dynamics, species' extinction risks and ecosystem functions.

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