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## 4. Articles II.: The effects of environmental temperature

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### 4.1. Temperature, predator-prey interaction strength and population stability

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#### *a) Abstract*

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Warming could strongly stabilise or destabilise 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 due to 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.

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#### *b) Introduction*

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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, Bradley, & Hughes 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

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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; Emmerson & Yearsley 2004; Brose et al. 2006b; Otto et al. 2007; Neutel 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 time (Brose et al. 2006b), inversely related to predator ingestion efficiencies (Vasseur & McCann 2005; Rall et al. 2008; Yodzis & Innes 1992), 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 (de Ruiter et al. 1995; May 1972). Often, interaction strength is measured as the log ratio between prey density in treatments with predators versus prey density in treatments without predators (Berlow et al. 2004, 1999). 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 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

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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; Meehan 2006a; Brown et al. 2004). Despite an intensive debate on the exact exponents, the power-law (body mass) and the exponential (temperature) scaling of metabolism find broad empirical support (Clarke 2004; Kozlowski & Konarzewski 2004; Savage, Gillooly, Woodruff, et al. 2004; Makarieva et al. 2005; Brown et al. 2004).

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; Vucic-Pestic et al. 2010; Brose 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 (Wahlström et al. 2000; Vonesh & Bolker 2005; Brose et al. 2008; Vucic-Pestic et al. 2010). 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). While 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 2002b). Unfortunately, studies that include both, temperature-dependent ingestion and metabolism of predators, are scarce (Vasseur & McCann 2005; Abrahams, Mangel, & Hedges 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 side of the hump-shaped relationship, (Brose et al. 2008)) and small prey (right 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. 2010). All experiments were replicated at three environmental temperatures (8°C, 15°C 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.

## c) *Material and Methods*

### Respiration and ingestion experiments

We investigated how predator metabolism varied with temperature. Specifically, we measured the O<sub>2</sub> consumption of eight carabid beetle species (*Abax paralelepipedus*, *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*). O<sub>2</sub> consumption of the beetles and spiders was measured in an automated electrolytic microrespirometer (Scheu 1992). We converted the individual O<sub>2</sub> consumption [ml/s] into energetic equivalents of metabolism  $I_j$  [J/s] by assuming that 1 ml O<sub>2</sub> equals 20.1 J (Peters 1983).

**Table 4.1.1:** ANCOVA tables of metabolism, ingestion, ingestion efficiency and interaction strength (continuous variables in italic and factors in bold). The metabolism ANCOVA does not include the factor “prey size”.

	metabolism			ingestion		ingestion efficiency		short term interaction strength	
	d.f.	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: <b>Temperature</b> (8°C / 15°C / 22°C)	2	326.35	< 0.001	6.38	< 0.01	63.87	< 0.001	1.43	0.24
3: <b>Prey size</b> (large / small)	1			1385.96	< 0.001	341.83	< 0.001	18.04	< 0.001
4: <b>Predator group</b> (beetles / spiders)	1	56.97	< 0.001	175.4	< 0.001	0.9	0.34	33.15	< 0.001
<i>Predator mass</i> x <b>Temperature</b>	2	0.08	0.92	1.36	0.25	2.27	0.11	2.39	0.09
<i>Predator mass</i> x <b>Prey size</b>	1			189.24	< 0.001	14.54	< 0.001	130.14	< 0.001
<b>Temperature</b> x <b>Prey size</b>	2			4.41	0.01	32.29	< 0.001	2.68	0.07
<i>Predator mass</i> x <b>Predator group</b>	1	26.04	< 0.001	7.35	< 0.01	0.04	0.84	28.14	0.001
<b>Temperature</b> x <b>Predator group</b>	2	0.88	0.41	1.53	0.22	0.68	0.51	3.53	0.03
<b>Prey size</b> x <b>Predator group</b>	1			47.32	< 0.001	1.68	0.2	< 0.01	0.96
<i>I</i> x <b>2</b> x <b>3</b>	2			0.06	0.95	3.21	0.04	0.75	0.47
<i>I</i> x <b>2</b> x <b>4</b>	2	0.13	0.88	0.59	0.56	0.62	0.54	1.5	0.23
<i>I</i> x <b>3</b> x <b>4</b>	1			0.42	0.52	0.02	0.89	20.53	< 0.001
<b>2</b> x <b>3</b> x <b>4</b>	2			0.97	0.38	0.26	0.77	3.39	0.04
<i>I</i> x <b>2</b> x <b>3</b> x <b>4</b>	2			0.83	0.44	0.41	0.66	1.61	0.2

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

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 (*Abax paralelepipedus*, *Carabus auratus*, *Platynus dorsalis*, *Poecilus versicolor* and *Pseudophonus rufipes*) and four spider species (*Alopecosa cuneata*, *Pardosa palustris*, *Pirata*

*latitans* and *Pisaura 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°C, 15°C 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 and right 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 m<sup>2</sup> perspex arenas lined with dental cast to hold moisture during experimental time of 24 hours. Initially, we added 2.35g of re-moistened 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 hours 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],

$$J_{ij} = \frac{N_e M_i \varepsilon}{t_F} \quad (4.1.1a)$$

where  $M_i$  is the individual body mass of a prey individual [g/Ind.] and  $t_F$  is the experimental duration in [s], we assume an energy content  $\varepsilon$  of 7000 J/g wet mass (Peters 1983). Subsequently, we calculated the dimensionless ingestion efficiency (Vasseur & McCann 2005) as

$$y_{ij} = \frac{w_{ij} J_{ij}}{\lambda I_j} \quad (4.1.1b),$$

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, Xu, & Ji 2003; McConnachie & Alexander 2004).  $\lambda$  is a dimensionless constant converting basal metabolic rate into field metabolic rate ( $\lambda=3$  (Savage, Gillooly, Woodruff, et al. 2004)), and  $I_j$  is the metabolic rate of predator  $j$  (calculated according to Eqn. 4.1.2a below). 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.

While 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):

$$\alpha_{ij} = \left| \frac{\ln\left(\frac{N_i - N_e}{N_i}\right)}{t} \right| \quad (4.1.1c),$$

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 that thus natural mortality of the prey species is negligible. This assumption was supported by the lack of mortality in controls without predators.

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### Statistical analysis of experimental data

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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°C, 15°C, 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], and ingestion,  $J_{ij}$  [J/s], of an ectotherm organism depend on its body mass,  $M$  [g], and the environmental temperature,  $T$  [K] as:

$$I_j = i_0 M_j^b e^{\frac{-E_I}{kT}} \quad (4.1.2a)$$

$$J_{ij} = j_0 M_j^b e^{\frac{-E_J}{kT}} \quad (4.1.2b)$$

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

$$y_{ij} = y_0 M_j^b e^{\frac{-E_y}{kT}} \quad (4.1.2c),$$

$$e^{\alpha_{ij}} = \alpha_0 M_j^b e^{\frac{-E_\alpha}{kT}} \quad (4.1.2d).$$

Note that due to the fact that the per capita interaction strength is calculated as the natural logarithm (Eqn. 4.1.1c), we used the exponential functions for investigating the mass and temperature dependence of per capita interaction strength (Eqn. 4.1.2d). 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 equation (4.1.2a-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<sup>2</sup>], and predator density,  $P$  [Ind/m<sup>2</sup>]:

$$\frac{dN}{dt} = r \left(1 - \frac{N}{K}\right) N - c_J J_{ij} N P \quad (4.1.3a),$$

$$\frac{dP}{dt} = \frac{c_J J_{ij} N P}{w_{ij}} - c_I I_j P \quad (4.1.3b),$$

where  $t$  [days] is time,  $r$  [1/day] is the intrinsic growth rate, and  $K$  [Ind/m<sup>2</sup>] is the carrying capacity of the prey species. The feeding interaction follows a linear functional response, where  $J_{ij}$  [J/s] is the ingestion rate of a single predator,  $c_J$  [s N day<sup>-1</sup> J<sup>-1</sup>] is a correction factor that converts the ingestion rate from Joules per second into prey individuals per day.  $I_j$  [J/s] 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 [s P day<sup>-1</sup> J<sup>-1</sup>]. The temperature and mass dependent intrinsic growth rate  $r$  in (4.1.3a) is calculated by

$$r = r_0 M^{b_r} e^{\frac{E_r}{kT}} \quad (4.1.4a),$$

where  $r_0$  ( $r_0 = e^{32.39}$ , Savage, Gillooly, Brown, et al. 2004) is a normalisation constant,  $M$  is the mass [ $\mu\text{g}$ ],  $b_r$  ( $b_r = -0.25$ ) is a constant exponent,  $k$  is Boltzmann's constant ( $8.62 \times 10^{-5}$  eV/K) and  $E_r$  (-0.84 eV) is the activation energy for insects (Savage, Gillooly, Brown, et al. 2004).

The carrying capacity  $K$  in (4.1.3a) depends on environmental temperature, body mass, the trophic level of the prey and the net primary production of the habitat (Allen et al. 2002; 2006a) following

$$K = K_0 m^{b_K} e^{\frac{E_K}{kT}} \sigma^z e^{tl_0(tl-1)} \quad (4.1.4b),$$

where  $K_0$  is a normalisation constant,  $b_K$  is a constant exponent,  $E_K$  is the activation energy,  $\sigma$  is the annual net primary productivity of the habitat [g(C) m<sup>-2</sup> y<sup>-1</sup>],  $z$  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 (4.1.4b) is temperature dependent (Allen, Gillooly, & Brown 2005):

$$\sigma = \sigma_0 e^{\frac{E_\sigma(T_0 - T)}{kTT_0}} \quad (4.1.4c),$$

where  $\sigma_0$  is the net primary productivity at the temperature  $T_0$  [K] and  $E_\sigma$  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,  $\sigma_0$ , of 600 g(C) m<sup>-2</sup> y<sup>-2</sup> 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 (4.1.3a, b) are calculated assuming that the system is at equilibrium (i.e.  $dN/dt = 0$ ;  $dP/dt = 0$ ), which yields equilibrium densities ( $P'$ ,  $N'$ ) of

$$P' = \frac{(K - N')r}{c_J J_{ij} K} \quad (4.1.5a),$$

$$N' = \frac{w_{ij} c_I I_j}{c_J J_{ij}} \quad (4.1.5b).$$

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) :

$$A_{ij} = \left| \frac{\ln(N^+/N^-)}{Y} \right| \quad (4.1.6),$$

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. 4.1.5a, b). Moreover, in absence of a predator the prey is growing to its carrying capacity (Eqn. 4.1.4b), and we can replace  $N^-$  with  $K$ , which yields

$$A_{ij} = \left| \frac{\ln(N'/K)}{P'} \right| \quad (4.1.7).$$

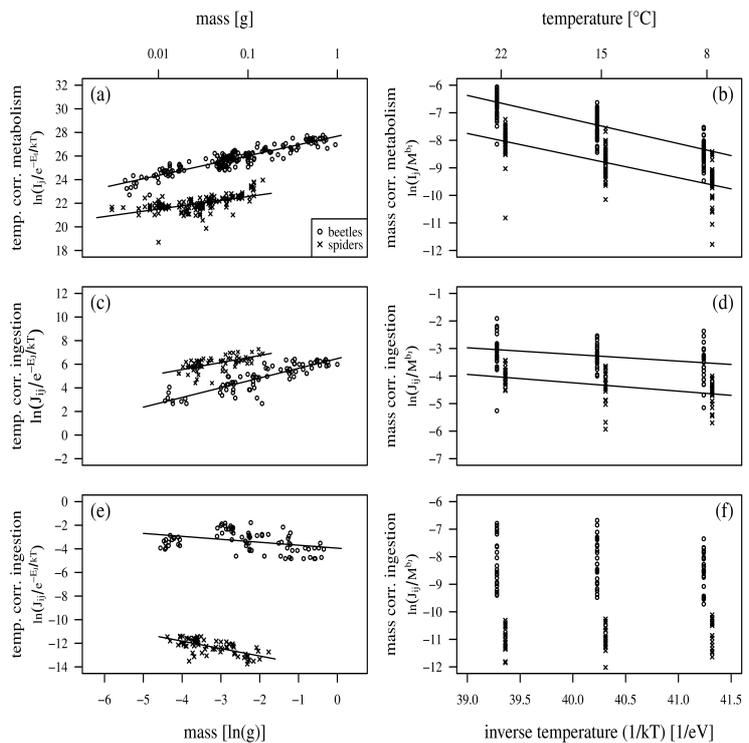
Inserting the equations 4.1.5a and 4.1.5b in equation 4.1.7 and using the temperature dependencies of  $I_j$  (Eqn. 4.1.2a),  $J_{ij}$  (Eqn. 4.1.2b),  $K$  (Eqn. 4.1.4b) and  $r$  (Eqn. 4.1.4a) yields the long-term interaction strengths depending on environmental temperature.

## d) Results

### Respiration and ingestion experiments

The metabolic rates of the predators, beetles and spiders, increased significantly with their body mass and temperature (Fig 4.1.1 a, b; ANCOVA, Table 4.1.1). The significant interaction term between predator mass and predator group (Table 4.1.1) suggests that the exponent for beetles ( $b_I = 0.72$ ; Table 4.1.2; Fig. 4.1.1a, circles) is higher than the exponent for spiders ( $b_I = 0.46$ ; Table 4.1.2; Fig. 4.1.1a, crosses). In contrast, the interaction term between temperature and predator group was not significant (Table 4.1.1) suggesting that the activation energy was similar for beetles ( $E_I = 0.87$ ; Table 4.1.2; Fig. 4.1.1b, circles) and spiders ( $E_I = 0.80$ ; Table 4.1.2; Fig. 4.1.1b, crosses).

We found significant effects of predator body mass and temperature on ingestion rates (ANCOVA, Table 4.1.1). Significant interaction terms with predator mass indicate that the allometric exponents differ for predator groups and prey size (Table 4.1.1): exponents were higher for beetles than for spiders and while ingestion increased with predator body mass when prey were large ( $b_I = 0.82$  and  $b_I = 0.6$  for beetles and spiders, respectively; Table 4.1.2; Fig. 4.1.1c), it decreased with predator body mass when prey were small ( $b_I = -0.25$  and  $b_I = -0.63$  for beetles and spiders, respectively; Table 4.1.2; Fig. 4.1.1e). Temperature effects on ingestion were similar for both predator groups (no significant interaction term between temperature and predator group) while they differed with respect to prey size (Table 4.1.1). Ingestion



**Figure 4.1.1:** 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 normalised by their temperature dependence (a, c, e) or their mass dependence (b, d, f). Upper axes show untransformed body mass [g] and temperature [°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.

increased with temperature when prey were large ( $E_l = 0.24$  and  $E_l = 0.30$  for beetles and spiders, respectively; Table 4.1.2; Fig. 4.1.1d), whereas it did not vary significantly when prey were small (Table 4.1.2; Fig. 4.1.1f).

**Table 4.1.2:** Regression results for the body-mass and temperature dependence of metabolism, ingestion, ingestion efficiency and interaction strength.

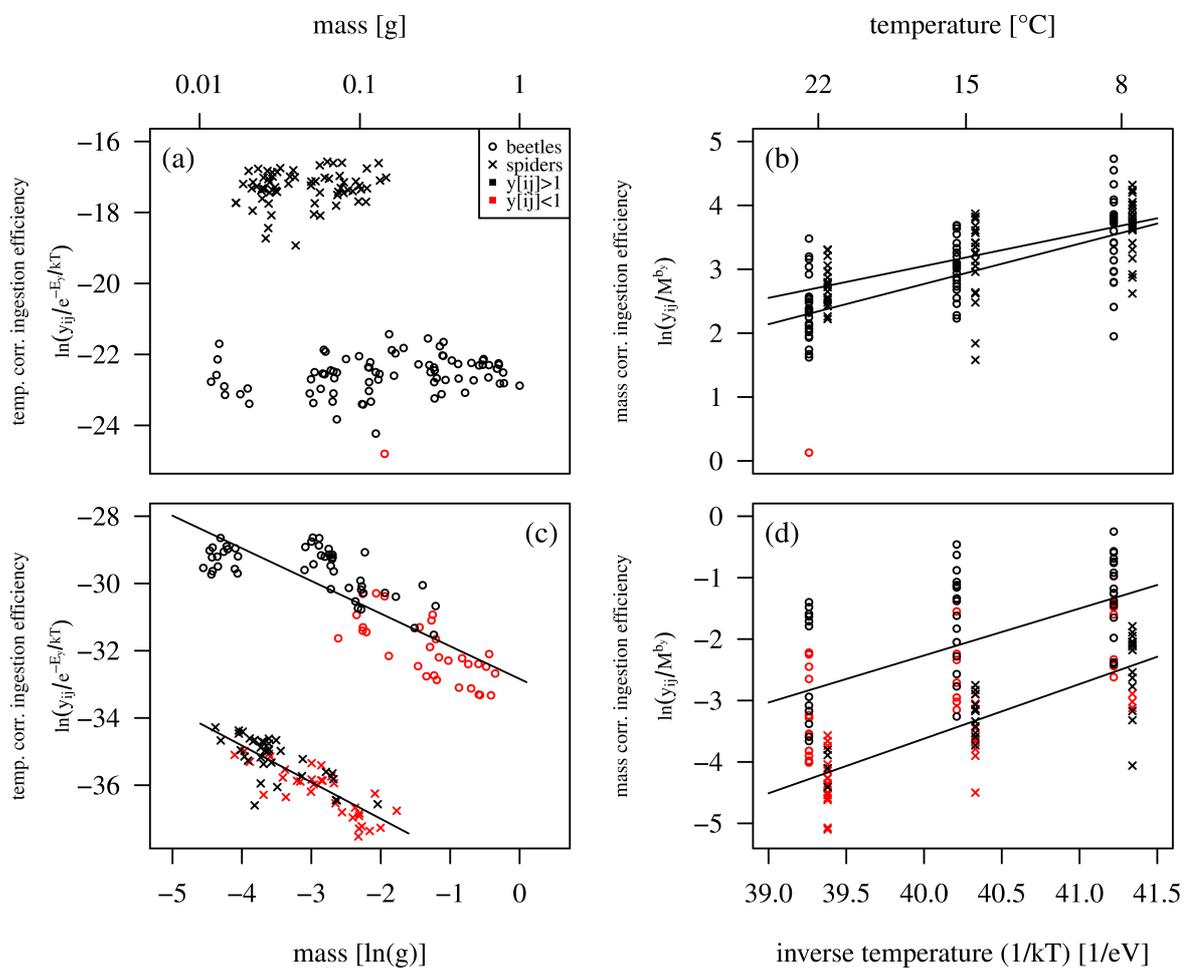
	ln(c)	p	lower CI	upper CI	b	p	lower CI	upper CI	E	p	lower CI	upper CI	r <sup>2</sup>	AIC	n
<b>metabolism</b>															
beetles	27.68	***	24.72	30.64	0.72	***	0.68	0.77	0.87	***	0.80	0.95	0.89	192.19	183
spiders	23.62	***	19.17	28.07	0.46	***	0.36	0.55	0.80	***	0.69	0.91	0.64	265.06	162
<b>ingestion of large prey</b>															
beetles	6.47	*	0.13	12.82	0.82	***	0.71	0.93	0.24	**	0.09	0.40	0.75	142.11	80#
spiders	7.93	*	2.05	13.81	0.60	***	0.40	0.79	0.30	***	0.16	0.45	0.42	96.26	67#
<b>ingestion of small prey</b>															
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	***	-0.80	-0.46	-0.09	-	-0.23	0.06	0.44	97.04	68#
<b>ingestion efficiency – large prey</b>															
beetles	-22.40	***	-28.74	-16.05	0.10	-	-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	-0.50	***	-0.64	-0.36	0.45	96.48	67#
<b>ingestion efficiency – small prey</b>															
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#
<b>absolute interaction strength with large prey</b>															
beetles	3.33	***	1.46	5.20	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	0.20	0.07	***	0.04	0.11	0.44	-92.85	67#
<b>absolute interaction strength with small prey</b>															
beetles	2.80	*	0.22	5.39	-0.04	-	-0.08	0.00	0.07	*	0.00	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. Level of significance: \*\*\* p < 0.001; \*\* p < 0.01; \* p < 0.05.

### 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 4.1.1). Significant interaction terms indicated that these effects depend on prey type, whereas non-significant interaction terms suggest similar mass and temperature effects for both predator groups (ANCOVA, Table 4.1.1). For both predator groups, ingestion efficiencies did not vary with predator mass in

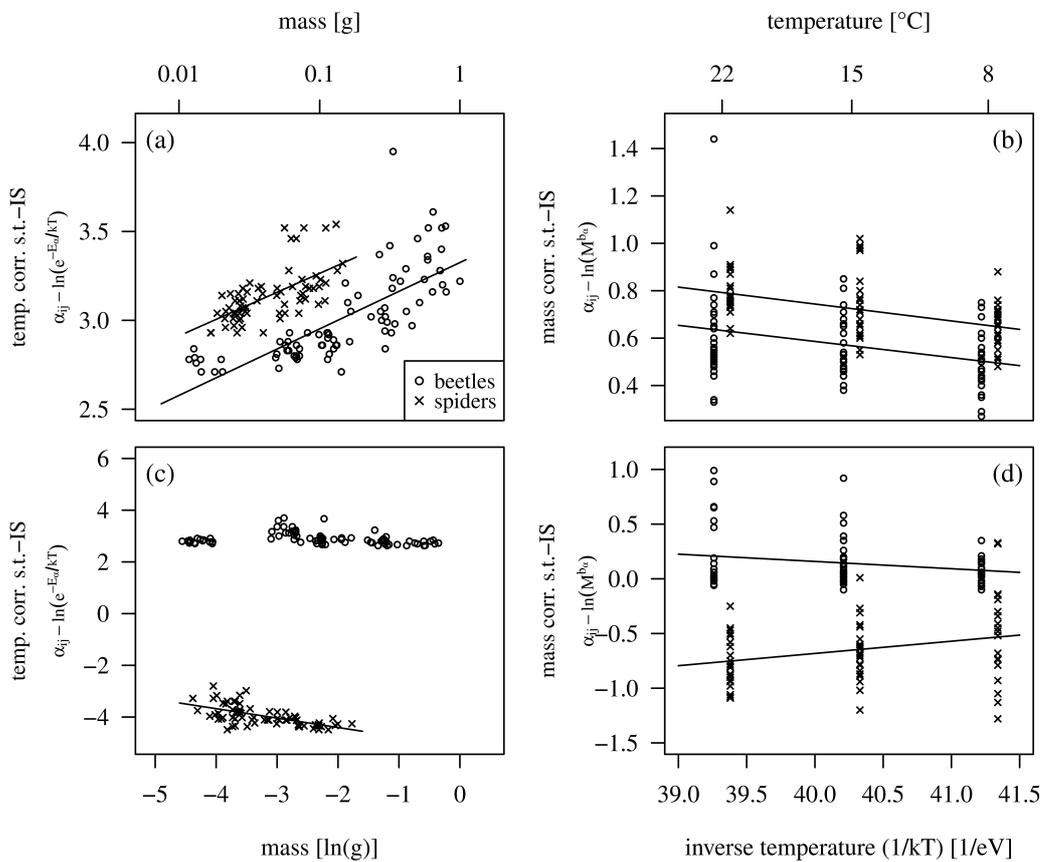
treatments with large prey (Fig. 4.1.2a; Table 4.1.2), whereas they decreased in treatments with small prey (Fig. 4.1.2c; Table 4.1.2). Eventually, ingestion efficiencies fell below unity indicating that metabolism exceeded ingestion (Fig. 4.1.2c, red symbols). For both predator groups and both prey sizes, increasing temperature generally decreased the ingestion efficiency, which increased the number of predator individuals that could not balance their metabolic demands (Fig. 4.1.2b, 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. 4.1.1b) shifted to a range of lower predator body masses when temperature increased.



**Figure 4.1.2:** 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 normalised by their temperature dependence (a, c) or their mass dependence (b, d). Upper axes show untransformed body mass [g] and temperature [°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 ( $y_{ij} < 1$ ).

## 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 4.1.1). Short-term interaction strengths increased significantly with predator body mass in treatments with large prey irrespective of the predator group (Fig. 4.1.3a). In treatments with small prey, short-term interaction strengths decreased slightly with predator mass for spiders, but they remained constant for beetles (Fig. 4.1.3c; Table 4.1.2). Moreover, short-term interaction strengths increased with warming when predators fed on large prey (Fig. 4.1.3b; Table 4.1.2) and when beetles fed on small prey (Fig. 4.1.3d, circles; Table 4.1.2). In contrast, short-term interaction strengths decreased slightly with warming when spiders fed on small prey (Fig. 4.1.3d, crosses; Table 4.1.2).



**Figure 4.1.3:** Beetle (circles) and spider (crosses) absolute short term per capita interaction strength  $\alpha_{ij}$  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 normalised by their temperature dependence (a, c) or their mass dependence (b, d). Upper axes show untransformed body mass [g] and temperature [°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.

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## Prediction of long term interaction strength

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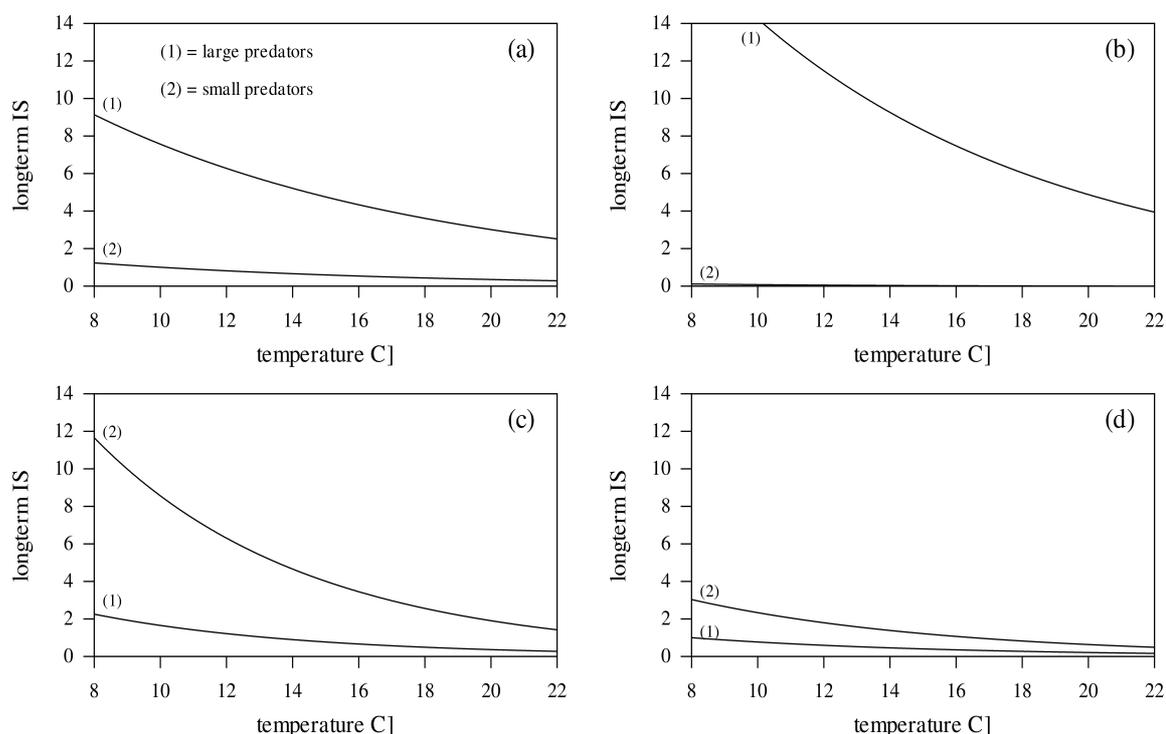
Calculated long-term interaction strength generally decreased with increasing temperature across all combinations of predator groups, predator masses and prey sizes (Fig. 4.1.4). Large predators have a higher impact on the large prey and smaller predators have a higher impact on the small prey (Fig. 4.1.4a & b vs. Fig. 4.1.4c & d). In all cases, the total decrease in long-term interaction strength is stronger when the long-term interaction strength is generally strong (Fig. 4.1.4).

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### e) Discussion

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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 temperature. 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 (Wahlström 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



**Figure 4.1.4:** 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).

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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) 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.

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## Metabolism

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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 ( $b_l = 0.46 \pm 0.09$ ). 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.

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## Body-mass effects on ingestion

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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 body-mass ratios documented by foraging theory (Wahlstrom et al. 2000; Vonesh & Bolker 2005; Brose et al. 2008; Vucic-Pestic et al. 2010; Brose in press). On the left 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

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constraints and ingestion rates increase with body-mass ratios due to 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 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).

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#### **Temperature effects on ingestion, ingestion efficiencies and interaction strengths**

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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 Figure 4.1.2, 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

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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. While 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. 4.1.5b) 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 (Meehan 2006a; Allen et al. 2002). The long-term interaction strengths (Eqn. 4.1.6) 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, due to 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. 4.1.5a).

While short-term interaction strengths were determined by increases in predator ingestion rates under warming (see Eqn. 4.1.1c), 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.

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### **Temperature effects on population stability:**

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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

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& 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 characterised 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 CO<sub>2</sub> levels (Emmerson et al. 2005), which may counteract the direct temperature effects studied here due to increased net primary productivity. Eventually, these two global warming effects need to be reconciled to achieve accurate forecast models.

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### **Caveats**

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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 & Benett 1993; 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.

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## Conclusions

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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) due to lower absolute long-term *per capita* interaction strengths, (3) a higher intrinsic population stability (less fluctuations in population density) due to reduced ingestion efficiencies, and (4) higher extinction risks due to 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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## 4.2. Predicting the effects of temperature on food web connectance

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### a) *Abstract*

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Relatively few models concern how environmental variables such as temperature affect community structure. Here we develop a model of how temperature affects food web connectance, a powerful driver of population dynamics and community structure. We use a Boltzmann factor to add temperature dependence of foraging traits to an existing model of food web structure. The model predicts that temperature change could have large effects on connectance. We predicted temperature sensitive food webs exhibiting slopes of up to 0.01 units of connectance per 1°C change in temperature. This corresponds to changes in diet breadth of 1 resource item per 2°C (assuming a food web containing 50 species). The less sensitive food webs exhibited slopes down to 0.0005, which corresponds to about 1 resource items per 40°C. The sign of the sum of the activation energies of attack rate and handling time determines whether warming increases or decreases connectance. In addition, we found that models of some food webs are much more sensitive to temperature change than models of others. These differences in sensitivity are explained by differences between empirical food webs in the body size distributions of organisms. We conclude that models of temperature effects on community structure and dynamics urgently require more and better empirical data to parameterise and test them.

### b) *Introduction*

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A food web is a network of feeding interactions among the species in a community. If each species eats many other species the food web contains many links and has high connectance. If each species eats few others, the food web has few links and low connectance. Whether food webs have many or few links ( $L$ ), relative to the number of possible links ( $P$ ), turns out to be very important. Connectance ( $L/P$ ) appears to be one of the primary determinants of population stability and community structure.

MacArthur (1955) suggested that a generalist consumer, i.e., one with a large number of links to resources, would fluctuate in abundance less than a specialist. He reasoned that the multiple pathways for gaining energy available to a generalist make any one pathway less influential if lost. Organisms ranging from protists to woodpeckers provide support for this hypothesis (Koenig & Haydock 1999; Petchey 2000). High connectance may, however, contribute to instability of population dynamics (Gardner & Ashby 1970; May 1972). Dynamic models of food webs show that more connections between species lead to a lower

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chance of obtaining a feasible community (all populations with positive population size) and slower recovery from small perturbations (Saunders & Bazin 1975). The consequences of larger perturbations, such as extinction, also depend on the number of connections among species, with more connected species being less likely to remain stable after a deletion. The loss of stability following an extinction can lead to a cascade of secondary extinctions, the extent of which is greatly influenced by connectance (Pimm 1980; Borrvall, Ebenman, & Jonsson 2000; Dunne, Williams, & Martinez 2002).

More recent work has demonstrated that food-webs with random or uniform population traits (e.g., respiration, consumption, growth) are unstable, whereas food webs with a body-size structure and population traits that follow allometric scaling relationships are highly stable (Brose et al. 2006b; Brose 2008). This body-size structure is characterized by consumers that are at least ten times larger than their resources and allometric degree distributions (i.e., the number of consumers and resources of a species decrease and increase, respectively, with its body mass) (Otto et al. 2007). Interestingly, accounting for this body-size structure yields a positive relationship between connectance and food-web stability (Rall et al. 2008) thus matching earlier concepts (MacArthur 1955).

Connectance also plays a large role in determining the types of structures that real food webs display (Vermaat, Dunne, & Gilbert 2009). Other properties of communities, such as food chain length, are strongly influenced by connectance. Indeed, some models of food webs use connectance (and species richness) as an input parameter (Cohen et al. 1990; Williams & Martinez 2000; Cattin et al. 2004; Stouffer et al. 2005). Its pivotal role for population dynamics and community structure has lead researchers to argue for the importance of understanding the determinants of connectance, and how environmental variables affect connectance (Warren 1990, 1996).

Environmental temperature is one such variable. Observed and predicted changes in global and regional temperatures make understanding its effects on ecological communities a priority. Temperature difference may also contribute towards latitudinal and elevational changes in diversity and community structure. Reasonably widely accepted theories and empirical data link temperature and biological variables such as metabolic rate (Clarke 1991; Gillooly et al. 2001; Savage, Gillooly, Brown, et al. 2004; Price & Sowers 2004; Apple, del Giorgio, & Kemp 2006), swimming speed (Olla & Studholme 1971; Winet 1976; Podolsky & Emlet 1993; Wilson, James, & Johnston 2000; Wilson 2005), feeding rate (Bolton & Havenhand 1998; Yee & Murray 2004), growth rate (Savage, Gillooly, Brown, et al. 2004; Rose & Caron 2007), developmental rate (Gillooly et al. 2002), body size (Atkinson, Ciotti, & Montagnes 2003), and phenology (Arft et al. 1999; Wagner & Benndorf 2007). The same is true for abundances (Strecker, Cobb, & Vinebrooke; Rae & Vincent 1998; Baulch et al. 2005), population dynamics (Yodzis & Innes 1992; Beisner, McCauley, & Wrona 1996; Vasseur &

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McCann 2005), ecosystem carbon flux and storage (Allen et al. 2005; Anderson et al. 2006) and ecosystem metabolism (Petchey et al. 1999; Baulch et al. 2005). Indeed, after accounting for size-dependence, temperature explains the largest amount of variation in biological rates (Peters 1983) (though see for example, (Makarieva et al. 2008; Johnson et al. 2009)).

Less well researched are the effects of temperature on aspects of community structure, such as the distribution of biomass across trophic levels, the distribution of diversity across trophic levels, or the extent and distribution of specialism and generalism across species. There are exceptions: evidence and predictions exist of temperature effects on the strength of interspecific interactions (Rall et al.; Sanford 1999; Vasseur & McCann 2005), biomass and production (Petchey et al. 1999; Moss et al. 2003; Brown et al. 2004; Meehan 2006a; Jennings et al. 2008), and food chain length (Arim, Bozinovic, & Marquet 2007). However, very few models exist that are capable of making predictions about the effects of temperature on community structure, and we are unaware of models capable of predicting how connectance changes with temperature. Given the importance of connectance, this seems to be a serious gap in ecological theory.

This article has two aims: 1) to extend an existing model of food web structure to be capable of making predictions about the relationship between environmental temperature and connectance; 2) to understand what in the model and data determine the predicted sensitivity of connectance to temperature change. A test of the predicted relationship against observed relationships between temperature and connectance, is left for when suitable data about food web structure across a temperature gradient is available.

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*c) Material and Methods*

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**Modelling food web connectance**

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Understanding connectance can be accomplished by understanding the determinants of the degree of specialism or generalism (i.e., diet breadth) of a consumer (Warren 1994). Diet breadth can be predicted by models of foraging behaviour, such as the contingency model of optimal foraging (Emlen 1966; MacArthur & Pianka 1966). In this model, diet breadth (specialism / generalism) is determined by the foraging behaviour of consumers (attack rates  $A$  and handling times  $H$ ), the energetic value of resources ( $E$ ), and the density ( $N$ ) of resource items in the environment. The diet is the set of resources that, when consumed, maximises the rate at which the consumer gains energy:

$$\frac{\sum_{i=1}^{d_j} \lambda_{ij} E_i}{1 + \sum_{i=1}^{d_j} \lambda_{ij} H_{ij}} \quad (4.2.1)$$

Here,  $d_j$  is the number of resource items in the consumers diet (i.e., diet breadth),  $\lambda_{ij}$  is the encounter rate of consumer  $j$  on resource  $i$ ,  $E_i$  is the energetic value of resource  $i$ , and  $H_{ij}$  is the handling time of resource  $i$  for consumer  $j$ . Encounter rate is the product of density and attack rate:  $\lambda = AN$ . The value of  $d_j$  that maximises the value of this function is the predicted diet breadth of the species. Connectance is the sum of the diet breadths of all consumers  $\sum_{j=1}^S d_j = P$  divided by the number of possible links  $P = S^2$ , where  $S$  is the number of species in the food web.

Connectance in this model therefore results from diet breadth, which itself results from encounter rates and handling times. More specifically, diet breadth is determined (all else being equal) by the product of the mean handling time and mean encounter rate (hereafter  $\lambda H$ ) (Beckerman et al. 2006, Fig. 4.2.1). This prediction was known previously, for example see Begon et al. (1990, page 307, second edition). As they put it, "searchers should be generalists" and "handlers should be specialists". The term "searchers" refers to consumers that spend little time handling and a long time searching (low  $\lambda H$ ), the term "handlers" refers to consumers that spend much time handling little time searching (high  $\lambda H$ ). When parameterised with data about encounter rates and handling times gathered from 121 empirical studies, the model (termed the Diet Breadth Model, DBM) predicts values of diet breadth and connectance that are not significantly different from those observed in some real food webs (Beckerman et al. 2006).

Foraging traits such as encounter rates, handling times, and energetic value, can be related to body sizes of resources and consumers. For example, larger resources contain more energy, but take longer to consume and digest. Smaller resources are more abundant (higher encounter rate), but may be less visible and so attract lower attack rates (lower encounter rate) than larger resources. These size dependencies create covariances between the foraging traits, and these covariances can result in realistic predictions of the pattern of interactions among species. When coupled with the DBM, these allometries results give what has been termed the Allometric Diet Breadth Model (ADBM), which can correctly predict up to 65% of the links in a real food web (Petchey et al. 2008).

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### Temperature scaling of foraging traits

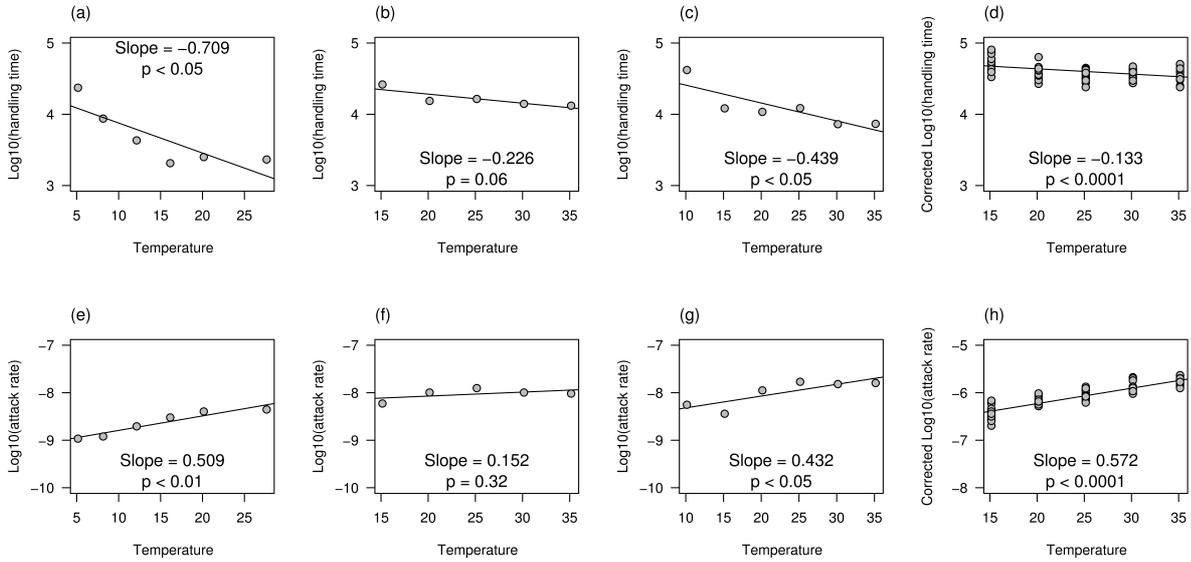
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A starting point for understanding how temperature affects ecological communities is its effect on the rates of metabolism. Rates of biochemical reactions scale with temperature

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according to the Boltzmann factor  $e^{-E/kT}$  where  $E$  is the activation energy,  $k$  is the Boltzmann's constant (in units of electron Volts eV), and  $T$  is temperature in Kelvin. It is the activation energy that determines how metabolism scales with temperature, and values range from 0.27 to 0.79 eV (electron volts) (Gillooly et al. 2001; Vasseur & McCann 2005). Relationships between temperature and metabolic rate holds remarkably well across taxa including microbes, ectotherms, endotherms, and plants (Gillooly et al. 2001). The activation energy of foraging traits are required to predict how community level properties, such as predator-prey dynamics or community structure, respond to temperature change (Brown et al. 2004; Vasseur & McCann 2005). There has, however, been relatively little work on the temperature dependence of these traits. Brown (2004) lists estimates of the activation energy of parasitism rate, attack rate, feeding rate, and grazing rate (0.56-0.81 eV). Activation energies of ingestion rates can also be estimated from temperature dependence of digestion velocity, gastric evacuation, and flow rates in burrows (0.46-0.77 eV) (Vasseur & McCann 2005). Aquatic capture rates are temperature dependent: e.g. a 34-67 % reduction in polychaete ingestion rate has been observed, associated with a 10°C reduction in temperature (Bolton & Havenhand 1998, 2005; Loiterton, Sundbom, & Vrede 2004). This corresponds approximately to an activation energy of 0.50. Similarly, grazing rate of a bacterivore increased twofold from 10-15°C (Delaney 2003); an activation energy of about 0.34 eV.

At least four published datasets contain empirical data suitable for estimating the activation energies of handling time and attack rates. Each is comprised of several functional responses, conducted over a range of temperatures and in one study also with different sizes of predators and prey (Fig. 1). Thompson (1978) recorded functional responses of dragonfly larvae feeding on *Daphnia* at six temperatures from 5-30°C. Zhang et al. (1998) recorded functional responses of large mites eating smaller mites at five temperatures from 15-30°C. Zhang et al. (1999) recorded functional responses of large mites eating small mites at six temperatures from 15-35°C. Xia et al. (2003) recorded functional responses of ladybird larvae feeding on aphids at six temperature (5-30°C), and also prey and predator sizes. We estimated the activation energies by fitting linearised versions of equations 4.2.2 and 4.2.4 (below) to the attack rates and handling times of the functional responses. Activation energy of handling time varied from -0.13 ( $p < 0.0001$ ) to -0.71 ( $p < 0.05$ ), while that of attack rate varied from 0.15 (not significant) to 0.57 ( $p < 0.0001$ ) (Fig. 4.2.1).



**Figure 4.2.1:** Empirical relationships between temperature and handling times (a-d) and attack rate and temperature (e-f) from four published studies. The data are plotted on  $\log_{10}$  y- axis for clarity, while statistics and the slopes are calculated on natural log data with models equivalent to those in equations 4.2.2 and 4.2.4. (a & e) (Thompson 1978), (b & f) (Zhang et al. 1998), (c & g) (Zhang et al. 1999), and (d & h) (Xia et al. 2003). In (d & h) the y-axis variables are corrected to account for variation in prey and predator size among the data. In each plot the activation energy is given as the slope and the significance by the p-value.

### Adding temperature dependence to the ADBM

To extend the ADBM (Petchey et al. 2008) to include temperature dependence of foraging traits we added a Boltzmann factor to the size-scaling of attack rates and handling times. We assume that handling time is a function of prey size, predator size, and temperature via the Boltzmann factor:

$$H_{ij} = h_{T_0} m_i^{h_i} m_j^{h_j} e^{\frac{E_H(T-T_0)}{kTT_0}} \quad (4.2.2)$$

This type of relationship was termed a power handling time function (Petchey et al. 2008). The activation energy of handling times  $E_H$  determines how handling times scale with temperature. Mass scaling is determined by the exponents  $h_i$  and  $h_j$ . The parameters and variables of this and the following equations are described in table 4.2.1.

Another handling time scaling relationship was termed the ratio handling time function, and was found to better predict food web structure via the ADBM (Petchey et al. 2008). Here it is based on a ratio of prey to predator mass with the addition of a Boltzmann factor:

$$H_{ij} = \frac{h_{T_0}}{b - \frac{m_i}{m_j}} e^{\frac{E_H(T-T_0)}{kTT_0}} \quad (4.2.3)$$

Attack rate is a function of prey size, predator size, and temperature via a Boltzmann factor:

$$A_{ij} = a_{T_0} m_i^{a_i} m_j^{a_j} e^{\frac{E_A(T-T_0)}{kTT_0}} \quad (4.2.4)$$

The activation energy of attack rates  $E_A$  determines how attack rates scale with temperature. Mass scaling is determined by the exponents  $a_i$  and  $a_j$ .

Table 4.2.1: Parameters and variables in the handling time and attack rate scaling functions

Parameter or variable	Description
$H_{ij}$	Handling time for prey $i$ and predator $j$ (seconds)
$h_{T_0}$	Normalisation constant for handling time at temperature $T_0$
$m_i$	Mass of a prey individual of type $i$ (grams)
$h_i$	Slope of prey mass dependence of handling time
$m_j$	Mass of a predator individual of type $j$ (grams)
$h_j$	Slope of predator mass dependence of handling time
$E_H$	Activation energy of handling time (eV)
$b$	Critical mass ratio in ratio handling time function (Eqn. 3)
$T$	Environmental temperature (Kelvin)
$T_0$	Temperature offset (293.15 K) for regression
$k$	Boltzmann constant (eV)
$A_{ij}$	Attack rate or predator $j$ on prey $i$ ( $m^2$ per second)
$a_{T_0}$	Normalisation constant for attack rate at temperature $T_0$
$a_i$	Slope of prey mass dependence of attack rate
$a_j$	Slope of predator mass dependence of attack rate
$E_A$	Activation energy of attack rate (eV)

## Investigating the temperature-connectance relationship

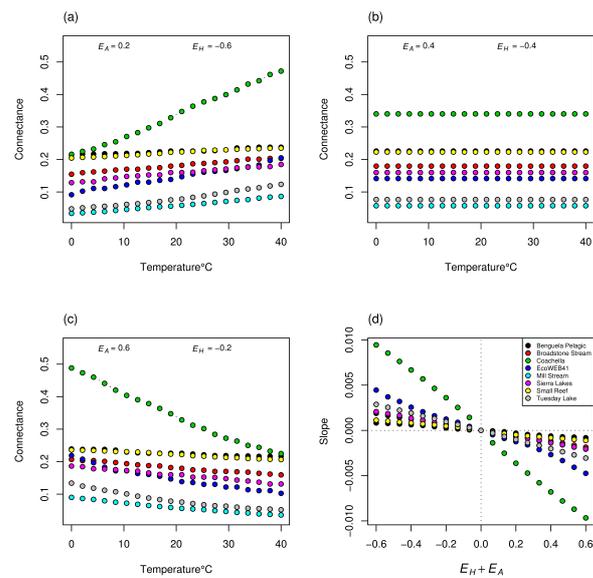
We wish to know how the model parameters control the relationship between temperature and predicted food web connectance. Since analytical solutions of the model are not possible, we used exploration first of the importance of the two activation energies (one for handling time and one for attack rate). The activation energy of handling time was explored from -0.2 to -0.8 eV; values were negative so that handling times decreased as temperature increased. The activation energy of attack rates was explored from 0.2 to 0.8 eV; values were positive to make attack rates increase as temperature increases. Values of all other parameters were taken from Petchey et al. (2008) for the eight best predicted food webs (all > 40% links predicted correctly). This gave eight different combinations of parameters across which to explore the effects of activation energies. It soon became clear that parameters other than the two

activation energies were important for the relationship between temperature and connectance. Consequently, we systematically explored effects of other parameters and variables on the temperature-connectance relationship. The details of this exploration should not be required to understand the generality of the results we found.

#### d) Results

Whether temperature has a positive or negative relationship with connectance depends only on the relative size of the two activation energies (Fig. 4.2.2 and 4.2.3). When the activation energy of attack rate is lower (in magnitude) than the activation of handling time, warming causes increases in connectance (Fig. 4.2.2a and 4.2.3a). If the two activation energies are equal in magnitude, warming has no effect on connectance (Fig. 4.2.2b and 4.2.3b). Connectance decreases with warming if the activation energy of attack rate is larger in magnitude than that of handling time (Fig. 4.2.2c and 4.2.3c). The generality of this result is shown for many relative values of activation energies, for both the power and ratio handling time functions, and for all of the eight modelled food webs (Fig. 4.2.2d and 4.2.3d).

The sensitivity of connectance to temperature change for a particular food web was determined by the relative size of the two activation energies (Fig. 4.2.2d and 4.2.3d). Larger imbalances in activation energies (e.g.,  $E_H = -0.2$  and  $E_A = 0.8$ ) resulted in greater sensitivity to temperature change; smaller imbalances (e.g.,  $E_H = -0.3$  and  $E_A = 0.4$ ) in lower sensitivity (Fig. 4.2.2 and 4.2.3). The relative magnitude of  $E_H$  and  $E_A$  controls sensitivity for the following reason, and recall that diet breadth and connectance are determined in large part by the product  $\lambda H$ . When  $E_H = -0.2$  and  $E_A = 0.8$ , the change in  $\lambda H$  is about  $+1.5 \log_{10}$  units. When  $E_H = -0.8$  and  $E_A = 0.2$ , the change in  $\lambda H$  is about  $-1.5 \log_{10}$  units. Activation energies that are more similar in magnitude cause smaller changes in  $\lambda H$  and therefore smaller changes in connectance. That is, the effect of temperature on  $\lambda H$  is directly



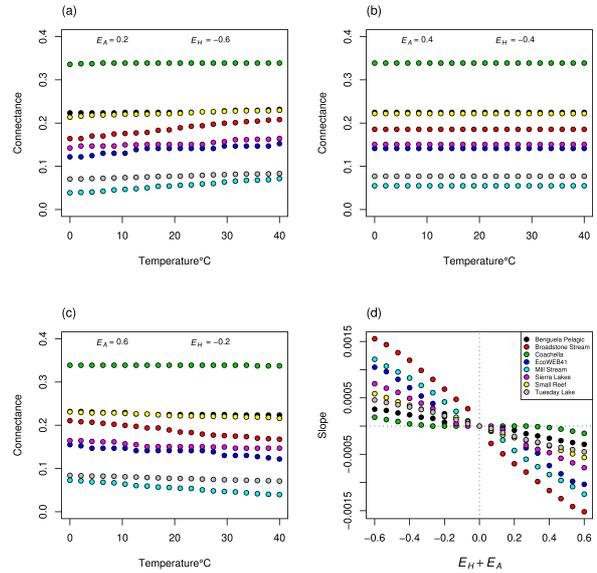
**Figure 4.2.2:** Effects of temperature on food web connectance for different values of activation energies of attack rates ( $E_A$ ) and handling times ( $E_H$ ), using the power handling time function. Colours refer to different sets of parameter values that correspond to models fitted to eight food webs in Petchey et al. (2008). In panel **d**, the x-axis represents the imbalance between effects of temperature on attack rates and handling times; the y-axis represents the slope of the temperature-connectance relationship.

controlled by the relative difference between  $E_H$  and  $E_A$  (Eqn. 4.2.2-4.2.4).

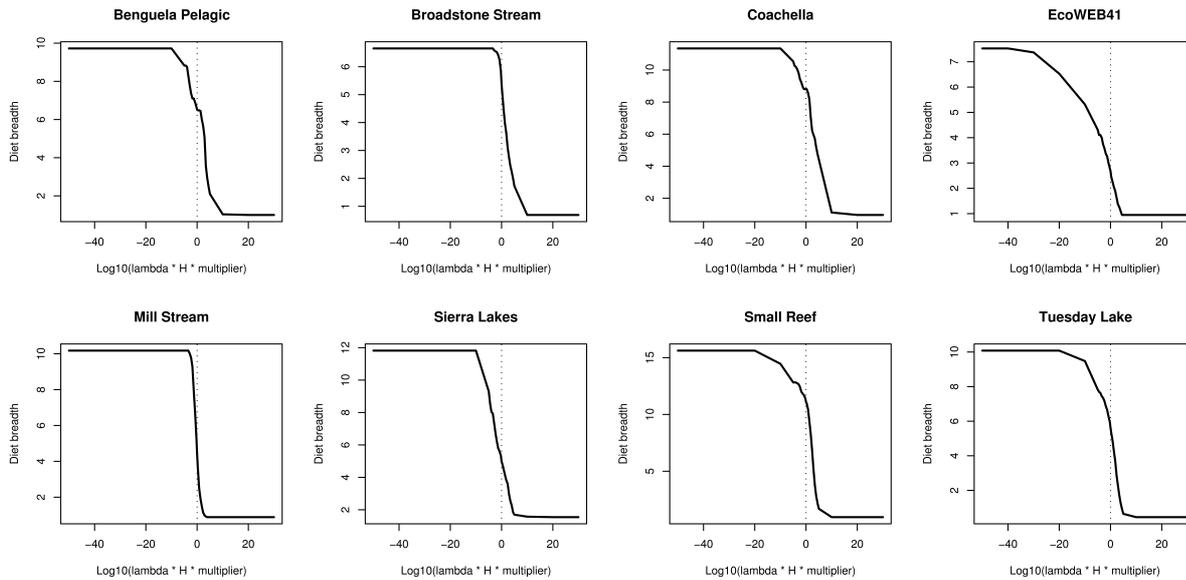
Among the eight food webs the sensitivity of connectance to temperature change, measured as change in connectance per  $1^\circ\text{C}$  change in temperature, varies greatly (even when values of  $E_A$  and  $E_H$  are constant) (Fig. 4.2.2d). For example, the Coachella Valley model is sensitive (up to 0.01 connectance units per  $1^\circ\text{C}$ ), whereas the Benguela pelagic model is insensitive (up to  $\sim 0.001$  connectance units per  $1^\circ\text{C}$ ) (Fig. 4.2.2d). Furthermore, (1) the sensitivities predicted by the ratio ADBM (Fig. 4.2.3d) are generally lower than those predicted by the power ADBM (Fig. 4.2.2d) and (2) the ranking of the eight food webs by sensitivity differs between the power and ratio ADBM (compare the vertical ordering of colours between Fig. 4.2.2d and 4.2.3d). For example, the Broadstone food web is predicted as most sensitive by the ratio ADBM, but is on of the least sensitive according to the power ADBM.

Within a model type (power or ratio) these differences in sensitivity are reflected in differences in the relationship between diet breadth and  $\lambda H$  (Fig. 4.2.4). At  $20^\circ\text{C}$  (0 on the x-axis in Fig. 4.2.4) some webs have a very steep relationship between diet breadth and  $\lambda H$ , whereas others show shallower slopes. The steepness of the slopes in figure 4.2.4 correspond with the sensitivities shown in figure 4.2.2d. That is, the models of different real webs exhibit different sensitivities to changes in handling times and encounter rates. The same is true of the ratio ADBM (compare Fig. 4.2.5 and 4.2.3d).

What causes these differences in sensitivity? First recall that whether a consumer includes the  $i^{\text{th}}$  most profitable resource in its diet depends on if the profitability of this resource ( $P_i = E_i / H_i$ ) is larger or smaller than the overall profitability ( $P_{1 \text{ to } i-1}$ ) of including all of the  $i-1$  most profitable resources (Emlen 1966; MacArthur & Pianka 1966; Begon et al. 1990). If  $P_i$  and  $P_{1 \text{ to } i-1}$  are very similar to each other, it will take only small changes in attack rates or handling times to switch their relative values, with the result the  $i^{\text{th}}$  resources is in or out of the diet. Larger differences between  $P_i$  and  $P_{1 \text{ to } i-1}$  mean that larger changes in attack rates of handling



**Figure 4.2.3:** Effects of temperature on food web connectance for different values of activation energies of attack rates ( $E_A$ ) and handling times ( $E_H$ ), using the ratio handling time function. Colours refer to different sets of parameter values that correspond to models fitted to eight food webs in Petchey et al. (2008). In panel **d**, the x-axis represents the imbalance between effects of temperature on attack rates and handling times; the y-axis represents the slope of the temperature-connectance relationship.



**Figure 4.2.5:** Sensitivity of diet breadth in eight food webs to changes in the product of attack rates and handling times (ratio handling time function). The x-axis is an arbitrary multiplier applied to  $a_{70}$  to create variation in  $\lambda H$ . The value of  $\lambda H$  equivalent to  $20^{\circ}\text{C}$  is shown at x value of zero (vertical dotted line). The gradient of the solid line where it crosses the dotted line is the sensitivity of diet breadth to temperature change at  $20^{\circ}\text{C}$ . These gradients match the relative sensitivities shown in figure 4.2.3d.

times are required to switch their relative size. In the ADBM, larger differences in resource mass translate directly into larger differences between  $P_i$  and  $P_{1 \text{ to } i-1}$ .

For a simpler but less accurate explanation, consider a species that consumes (for some reason) resources that are larger than  $x$  grams and smaller than  $y$  grams. If the diet range changes (for some reason) to have an upper limit of  $z$  grams, the change in number of resource items in the diet is altered by the number of items that are between  $y$  and  $z$  grams. Clearly it is the distribution of resource sizes that determines this number.

To confirm this reasoning we manipulated the similarity between species masses by drawing masses from log normal distributions with different standard deviation. Model food webs that were constructed from mass distributions that resulted in small differences between  $P_i$  and  $P_{1 \text{ to } i-1}$  (mass distributions with a low standard deviation) were on average sensitive to changes in  $\lambda H$  (Fig. 4.2.6). In contrast, mass distributions that resulted in larger differences between  $P_i$  and  $P_{1 \text{ to } i-1}$  were relatively insensitive to changes in  $\lambda H$ .

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e) *Discussion*

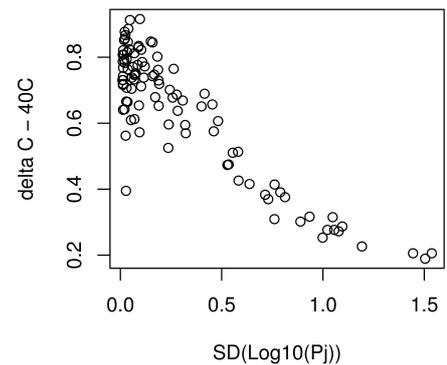
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Temperature change could have large effects on connectance. We predicted temperature sensitive food webs exhibiting slopes of up to 0.01 units of connectance per  $1^{\circ}\text{C}$  change in temperature. This corresponds to changes in diet breadth of 1 resource items per  $2^{\circ}\text{C}$

(assuming a food web containing 50 species). The less sensitive food webs exhibited slopes down to 0.0005, which corresponds to about 1 resource items per 40°C. Dynamical food-web analyses suggest that these changes in connectance can cause substantial variation in population stability and species persistence depending on the body-size structure of the communities (Rall et al. 2008). The importance of connectance for ecological structure and dynamics makes improving and testing these predictions essential for developing a better understanding of how temperature change will affect populations, communities, and ecosystems.

Whether warming increases or decreases connectance in our model depends only on the relative sizes of the activation energies of attack rate and handling times (Fig. 4.2.2 and 4.2.3). There is an enormous amount of available data regarding the scaling of metabolic and other vital rates with body size and temperature. However, there is a dearth of information about the temperature scaling of foraging traits, such as handling times, attack rates, and maximum ingestion rates. This appears to represent a sizeable gap in ecological knowledge, one that limits progress about how temperature change will affect interspecific interactions. The limited empirical data makes it difficult to make an empirically based predictions about even whether connectance will decrease or increase as a result of warming. Recent theoretical developments, including the one described above, urgently need more and better empirical data to parameterise them, and require critical testing.

The sensitivity of connectance to temperature change differs greatly between our models of eight real food webs. This is a result of the differences between models in their sensitivity to changes in encounter rates and handling times (Fig. 4.2.4 and 4.2.5). These differences are largely determined by the mass distribution of the resource items (Fig. 4.2.6). More similar masses result in a more sensitive model food web, whereas greater differences between masses results in food webs less sensitive to changes in attack rates and handling times. This might imply that the structure of terrestrial food webs, in which species are more equally sized than in aquatic food webs (Brose et al. 2006a), could be more sensitive to environmental warming. This finding represents a link between the body size distributions of organisms and the sensitivity of food web structure to temperature change. Many types of environmental drivers (e.g., enrichment, habitat simplification, exploitation) can affect encounter rates and or handling times, therefore this link may be used to make predictions about the sensitivity of



**Figure 4.2.6:** Sensitivity of diet breadth depends on the magnitude of differences in profitability. Sensitivity is measured as change in connectance ( $\Delta C$ ) per 40°C. Differences in profitability are measured as the standard deviation of  $\log_{10}$  profitabilities.

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food web structure to other aspects of environmental change.

We know of no empirical data appropriate to test these predictions. Datasets of changes in diet breadth or connectance with changes in temperature would provide a first test. Such datasets could result from observation of “natural experiments”, for example ecosystems that are in close proximity but that differ in temperature. If observations included individual diets collected by gut content analysis, as well as body sizes of consumers and their resources, one could look for differences in diet breadth and connectance across the temperature gradient. Attributing any observed relationships between temperature and diet breadth to a particular mechanisms would require additional measurement and probably experimentation. Required would be measurements of activation energies of handling times and foraging traits, abundances of organisms in the environment, and changes in body size along the temperature gradient. Manipulative experiments would be required to unambiguously attribute changes in diet breadth and connectance to changes in temperature, otherwise factors confounding the natural temperature gradient could not be ruled out.

Predictions here are made by modelling one general pathway of temperature effect on community structure: effects of temperature on connectance via changes in foraging rates. It seems likely that other pathways, such as effects of temperature on energy requirements, growth rates, death rates, dispersal, body sizes, etc., will likely also be important. In addition, changes in vital and foraging rates could affect species' abundances and dynamics (Vasseur & McCann 2005) and the trophic structure of communities (Arim et al. 2007). Despite the importance of predicting the ecological consequences of temperature change, and with some notable exceptions (Rall et al.; Brown et al. 2004; Vasseur & McCann 2005; Meehan 2006a; Arim et al. 2007), a great remaining challenge for community ecology is to produce general models of mechanistic effects of temperature change on interspecific interactions. Only with these can we plan for how biological communities and ecosystems will respond to temperature change. The model presented above represents a new piece in the theoretical jigsaw of how temperature change can influence ecological communities.