

Allometric functional response model: body masses constrain interaction strengths

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Summary

1. Functional responses quantify the *per capita* consumption rates of predators depending on prey density. The parameters of these nonlinear interaction strength models were recently used as successful proxies for predicting population dynamics, food-web topology and stability.
2. This study addressed systematic effects of predator and prey body masses on the functional response parameters handling time, instantaneous search coefficient (attack coefficient) and a scaling exponent converting type II into type III functional responses. To fully explore the possible combinations of predator and prey body masses, we studied the functional responses of 13 predator species (ground beetles and wolf spiders) on one small and one large prey resulting in 26 functional responses.
3. We found (i) a power-law decrease of handling time with predator mass with an exponent of -0.94 ; (ii) an increase of handling time with prey mass (power-law with an exponent of 0.83 , but only three prey sizes were included); (iii) a hump-shaped relationship between instantaneous search coefficients and predator–prey body-mass ratios; and (iv) low scaling exponents for low predator–prey body mass ratios in contrast to high scaling exponents for high predator–prey body-mass ratios.
4. These scaling relationships suggest that nonlinear interaction strengths can be predicted by knowledge of predator and prey body masses. Our results imply that predators of intermediate size impose stronger *per capita* top-down interaction strengths on a prey than smaller or larger predators. Moreover, the stability of population and food-web dynamics should increase with increasing body-mass ratios in consequence of increases in the scaling exponents.
5. Integrating these scaling relationships into population models will allow predicting energy fluxes, food-web structures and the distribution of interaction strengths across food web links based on knowledge of the species' body masses.

Key-words: attack rate, body-mass ratio, food webs and predator–prey interactions, handling time, hill exponent, metabolic theory, optimal foraging, *per capita* consumption rate

Introduction

Understanding constraints on species' interaction strengths is critically important for predicting population dynamics, food-web stability and ecosystem functions such as biological control (Berlow *et al.* 2004; Wootton & Emmerson 2005; Montoya, Pimm & Solé 2006). Empirical and theoretical evidence suggests that predator and prey body masses are among the most important of these constraints (Emmerson & Raffaelli 2004; Woodward *et al.* 2005; Wootton & Emmerson 2005; Berlow, Brose & Martinez 2008; Berlow *et al.* 2009). Conceptually, these nonlinear interaction strengths are described by the magnitude and shape of functional

responses that quantify *per capita* consumption rates of predators depending on prey abundance. One generalized functional response model is based on Holling's disk equation (Holling 1959):

$$F(N) = \frac{bN^{q+1}}{1 + bT_h N^{q+1}}, \quad \text{eqn 1}$$

where F is the *per capita* consumption rate, N is prey abundance, T_h is the handling time needed to kill, ingest and digest a resource individual, b is a search coefficient that describes the increase in the instantaneous search rate, a , with resource abundance, N :

$$a = bN^q, \quad \text{eqn 2}$$

where q is a scaling exponent that converts type II into type III functional responses (Williams & Martinez 2004; Rall,

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Guill & Brose 2008). The hill exponent, h , used in some prior studies (Real 1977) is equivalent to q ($h = q + 1$).

Functional responses can be linear (type I, $T_h = 0$, increase up to a threshold abundance), hyperbolic (type II, $T_h > 0$, $q = 0$) or sigmoid (type III, $T_h > 0$, $q > 0$). While many early studies focused on type I and type II functional responses and ignored the scaling exponent, type III functional responses with scaling exponents larger than zero could occur more frequently than previously anticipated (Sarnelle & Wilson 2008). Under hyperbolic type II functional responses predation risks for prey individuals decrease with prey abundance causing inverse density-dependent prey mortality, which can lead to unstable boom-burst population dynamics (Oaten & Murdoch 1975a, b; Hassell 1978). In contrast, increasing predation risks under sigmoid functional responses can yield an effective *per capita* top-down control that often prevents such unstable dynamics (Gentleman & Neuheimer 2008; Rall *et al.* 2008). Slight differences in functional response parameters can thus have drastic consequences for population and food-web stability in natural ecosystems (Oaten & Murdoch 1975a; Williams & Martinez 2004; Fussmann & Blasius 2005; Brose, Williams & Martinez 2006b; Rall *et al.* 2008).

Allometric scaling theories provide a conceptual framework how body masses could determine foraging interactions (Peters 1983; Brown *et al.* 2004). The maximum consumption rates realized at infinite prey densities are proportional to the inverse of handling time and independent of the success of the attacks (Yodzis & Innes 1992; Koen-Alonso 2007). Consequently, the $3/4$ power-law scaling of maximum consumption with predator body mass (Peters 1983; Carbone *et al.* 1999) suggests that handling time should follow a negative $3/4$ power-law with predator body mass. This trend is qualitatively supported, though studies reported linear (Hassell, Lawton & Beddington 1976; Spitze 1985), power-law or exponential relationships (Thompson 1975; Hassell *et al.* 1976; Aljetlawi, Sparrevik & Leonardsson 2004; Jeschke & Tollrian 2005).

The characteristic components of search rates include the reactive distance between predator and prey (i.e. the distance between predator and prey individuals at which a predator individual responds to the presence of the prey) and the capture success. While the reactive distance increases with the body masses of the predators (i.e. large predators have a larger visual range than small predators), the capture success decreases with predator mass above an optimum body mass ratio (Aljetlawi *et al.* 2004; Brose *et al.* 2008). A further explanation for the low capture success is that the predator's motivation to capture small prey of limited energy content is low (Petchey *et al.* 2008). Together, these patterns in reactive distances and capture success may explain the hump-shaped relationships between search rates and predator-prey body-mass ratios with a maximum search rate at intermediate (optimum) body-mass ratios documented in prior studies (Hassell *et al.* 1976; Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Vonesh & Bolker 2005; Brose *et al.* 2008). However, these studies were either restricted to search rates of single

predator-prey interactions (with variance in individual size) or studied multiple predator-prey search rates at a single, constant prey density. Thus, none of these prior studies has addressed body-size constraints on functional responses across species.

In this study, we quantified systematic effects of predator and prey masses on functional response parameters (handling time, search coefficient and scaling exponent) across different predator-prey interactions. While more complex functional response models accounting for digesting time and interference behaviour exist (Skalski & Gilliam 2001; Jeschke, Kopp & Tollrian 2002; Schenk, Bersier & Bacher 2005; Kratina *et al.* 2009), testing for their body-size dependence was left for subsequent studies. Instead, the allometric functional response model addressed here provide an empirical basis for an understanding of body-size constraints on interaction strengths, food-web topology (Petchey *et al.* 2008) and dynamics (Brose *et al.* 2006b; Otto, Rall & Brose 2007; Brose 2008; Rall *et al.* 2008).

Methods

The predators of our experiment were carabid beetles (*Abax parallelepipedus*, *Carabus nemoralis*, *Pterostichus melanarius*, *Pterostichus oblongopunctatus*, *Harpalus rufipes*, *Calathus fuscipes*, *Calathus melanocephalus*, *Anchomenus dorsalis* and *Poecilus versicolor*; Carabidae; Coleoptera) and wolf spiders (*Trochosa terricola*, *Pardosa lugubris*; Aranea: Lycosidae) sampled in pitfall traps. The juvenile weight classes of 1, 3 and 10 mg of *Trochosa* were considered as trophic species as they vary in consumption rates and preferences for the different prey species (Rickers and Scheu 2005, Brose *et al.* 2008). We used *Alphitobius diaperinus* larvae (Coleoptera; Tenebrionidae; hereafter: *Alphitobius*), flightless adults of *Drosophila hydei* (Diptera; Drosophilidae, hereafter: *Drosophila*) and *Heteromurus nitidus* (Collembola; Entomobryidae, hereafter: *Heteromurus*) as prey.

FUNCTIONAL RESPONSE EXPERIMENTS

To explore fully possible combinations in predator and prey body masses, we studied the functional response of each predator on one small and one large prey. For the beetles, we used flightless *Drosophila* as small prey and *Alphitobius* as large prey. For the spiders, we used *Heteromurus* as small prey and flightless *Drosophila* as large prey. Each experimental unit included one predator individual and prey at different initial densities that were varied between low densities (1, 3, 5, 10, 20, 30 prey individuals per experimental arena) and higher prey densities that were adjusted to each specific predator-prey combination to reach saturation in the predators *per capita* consumption rate (e.g. 120 individuals of *Drosophila* for the small predator *Anchomenus dorsalis* and 4000 individuals of *Drosophila* for the large predator *Carabus nemoralis*). Six replicates per prey density were established. The predator individuals were kept separate in plastic jars dispersed with water and were deprived of food for 1 week prior to the start of the experiments. The experiments were performed in Perspex® (Degussa AG, Darmstadt, Germany) arenas (20 × 20 × 10 cm) covered with lids that had holes to allow gas exchange. The ground was covered with moist plaster (200 g dry weight) to provide constant moisture during the experiments. Habitat structure in the arenas was provided by moss (*Polytrichum formosum*, 2.43 g dry weight) that was first dried for several days at 40 °C

to exclude other animals and then re-moisturized. The experiment was run for 24 h with a day/night rhythm of 12/12 h dark/light and temperature of 15 °C. Initial and final prey densities were used to calculate the number of prey eaten. Control experiments without predators showed that prey mortality or escape did not influence our experiments. The predators were weighed before and after the experiment to calculate the mean body mass of each predator and the body-mass ratio of each predator-prey pair (Table 1).

STATISTICAL ANALYSES

In the present study, the prey densities changed during the experimental period with each consumption event. To account for this prey depletion during the experiments, we used a generalized model of Rogers's random predator equation (Rogers 1972; Juliano, Scheiner & Gurevitch 2001):

$$N_e = N_0(1 - \exp(bN_0^q(T_h N_e - T))), \quad \text{eqn 3}$$

where N_e is the number of prey eaten, N_0 is the initial prey density, b is the search coefficient (search rate $a = bN_0^q$), T_h is the handling time, T is the experimental duration time and q is the scaling exponent. We fitted eqn (3) to the experimental data using Newton's method in sas 9.1 (Juliano *et al.* 2001) to obtain parameter estimates. We prevented (i) negative scaling exponents (i.e. decreases in search rates with prey density) and (ii) negative handling times.

Subsequently, we tested for effects of predator and prey masses on handling times, search coefficients and hill exponents. We used linear,

least-squares regressions to test for relationships between \log_{10} handling time vs. \log_{10} predator mass and \log_{10} prey mass:

$$\log_{10} T_h = p \log_{10} M_P + n \log_{10} M_N + \log_{10} T_{h(0)} \quad \text{eqn 4}$$

with T_h as handling time, M_P as predator mass, M_N as prey mass, and p , n , $T_{h(0)}$ as constants.

Hump-shaped relationships between \log_{10} -transformed search coefficients, b , and predator-prey body-mass ratios, R , were tested by fitting the following size-search-coefficient curve in R (R-Project 2.8.1, free statistic software; The R Foundation for Statistical Computing, Vienna, Austria):

$$\log_{10}(b(R) + 1) = A \frac{\exp(\varepsilon(\Phi - \log_{10}(R + 1)))}{1 + \exp(\beta\varepsilon(\Phi - \log_{10}(R + 1)))}, \quad \text{eqn 5}$$

where A is a constant, Φ represents the body mass ratio at which 50% of the maximum search coefficient is reached, ε is the rate of change in search with size controlling the steepness of the curve, R is the body-mass ratio and β determines the asymmetry of the curve (Vonesh & Bolker 2005). To find the optimum body mass ratio, R_0 , where the maximum search coefficient is reached, the first derivative of eqn (4) has to be set equal to zero and solved for R_0 , resulting in the following equation (Vonesh & Bolker 2005):

$$\log_{10}(R_0 + 1) = \frac{\Phi + \log_{10}(\beta - 1)}{\varepsilon\beta} \quad \text{eqn 6}$$

The solution of eqn (6) can be inserted in eqn (5) to calculate the maximum search coefficient, $b_{\max}(R_0)$.

Table 1. Mean predator and prey weights, predator-prey body-mass-ratios, and functional response parameters: N = number of replicates, b = search coefficient ($\text{cm}^2 \text{day}^{-1} \text{ind}^{-q}$ Arena^q), T_h = handling time (day ind^{-1}), SE = standard error, q = scaling exponent, weight = mean predator weight (mg) and R = predator-prey body-mass ratio

	N	b	SE	T_h	SE	q	SE	Weight	R
Beetles with large prey <i>Alphitobius diaperinus</i> (23.26 mg)									
<i>Anchomenus dorsalis</i>	3	0	0	0	0	0	0	14.50	0.65
<i>Calathus melanocephalus</i>	3	0	0	0	0	0	0	17.54	0.79
<i>Calathus fuscipes</i>	36	9.33×10^2	1.39×10^{-3}	0.52	0.07	0	0	71.52	3.08
<i>Pterostichus oblongopunctatus</i>	30	3.88×10^3	1.27×10^{-2}	0.62	0.06	0	0	69.65	2.99
<i>Harpalus rufipes</i>	48	1.76×10^3	3.73×10^{-3}	0.41	0.06	0	0	129.10	5.55
<i>Pterostichus melanarius</i>	36	4.07×10^3	7.83×10^{-3}	0.25	0.02	0	0	158.02	6.79
<i>Abax parallelepipedus</i>	24	1.49×10^3	1.01×10^{-3}	0.10	0.01	0	0	302.00	12.98
<i>Carabus nemoralis</i>	42	2.98×10^2	8.62×10^{-4}	0.06	0.02	0.11	0.7	513.14	22.06
Beetles with small prey <i>Drosophila hydei</i> (1.42 mg)									
<i>Anchomenus dorsalis</i>	57	3.63×10^1	1.48×10^{-4}	0.21	0.03	0.86	1.1	14.49	10.21
<i>Calathus melanocephalus</i>	57	8.52×10^1	2.99×10^{-4}	0.20	0.02	0.68	1	17.54	12.35
<i>Calathus fuscipes</i>	46	4.86	2.00×10^{-5}	0.10	0.01	1.42	0.8	81.82	57.62
<i>Pterostichus oblongopunctatus</i>	45	2.53×10^1	7.60×10^{-5}	0.12	0.01	1.08	0.7	65.05	45.81
<i>Harpalus rufipes</i>	54	1.49×10^2	3.03×10^{-4}	0.06	0.01	0.54	0.5	41.85	29.47
<i>Pterostichus melanarius</i>	54	4.78×10^1	1.44×10^{-4}	0.04	0.01	0.53	0.5	148.03	104.3
<i>Abax parallelepipedus</i>	90	5.07×10^1	3.27×10^{-7}	0.02	2×10^{-3}	1.41	0.7	287.58	202.5
<i>Carabus nemoralis</i>	76	3.32×10^1	3.01×10^{-7}	5×10^{-3}	0.01	0.68	0.7	463.84	326.7
Spiders with large prey <i>Drosophila hydei</i> (1.42 mg)									
<i>Pardosa lugubris</i>	54	1.50×10^3	8.25×10^{-3}	0.14	0.02	0.26	1.9	29.37	20.68
<i>Trochosa terricola</i> , 3 mg	42	1.22×10^3	1.64×10^{-3}	0.94	0.09	0	0	3.45	2.42
<i>Trochosa terricola</i> , 10 mg	36	1.90×10^3	4.72×10^{-3}	0.47	0.06	0	0	11.41	8.03
<i>Trochosa terricola</i> , adult	70	2.07×10^2	4.71×10^{-4}	0.03	4×10^{-3}	0.40	0.4	84.81	59.72
Spiders with small prey <i>Heteromorus nitidus</i> (0.15 mg)									
<i>Pardosa lugubris</i>	60	1.27×10^1	3.90×10^{-5}	0.05	0.01	1.10	0.6	25.77	171.8
<i>Trochosa terricola</i> , 3 mg	48	3.43×10^2	6.76×10^{-4}	0.10	0.01	0.5	0.7	3.08	20.51
<i>Trochosa terricola</i> , 10 mg	60	1.27×10^2	3.25×10^{-4}	0.02	0.01	0.40	0.5	10.61	70.75
<i>Trochosa terricola</i> , adult	88	7.66×10^1	1.73×10^{-4}	0.01	1×10^{-3}	0.10	0.3	79.79	532.4

We tested for significant differences in scaling exponents, q , between predator–prey pairs using an ANOVA. Subsequently, we employed two contrast analyses (one for spiders and one for beetles) to test our hypothesis that the scaling exponent is higher for high predator–prey body-mass ratios (small prey) than for low ratios (large prey).

Results

Across the 26 functional responses of the present study (Table 1), we found substantial variance in search coefficients [$4.86 \leq b \leq 4.07 \times 10^3$ ($\text{cm}^2 \text{day}^{-1} \text{ind}^{-q} \text{Arena}^q$)], handling times [$10^{-3} \leq T_h \leq 9.45 \times 10^{-1}$ (day ind.^{-1})], and scaling exponents ($0 \leq q \leq 1.42$). In subsequent analyses, we related this variance in functional response parameters to predator–prey body-mass ratios spanning roughly three orders of magnitude from 0.65 to 532 (Table 1).

The handling time exhibited a power-law decrease with increasing predator mass with an exponent of -0.94 ± 0.09 (mean \pm SE, Fig. 1a) and a power-law increase with prey mass with an exponent of 0.83 ± 0.07 . We caution, however, that these analyses are based on only three prey size classes and the latter exponent illustrates the relationship only qualitatively. Together, predator and prey mass explained 89% of the variation in handling time. The search coefficient followed a hump-shaped relationship with predator–prey body-mass ratios (Fig. 1b, $r^2 = 0.74$). The hump-shaped nature of this relationship depends on two data points with \log_{10} mass ratios smaller than 0.5 (Fig 2b), but other predator species in this body-mass range have not been available. The maximum search coefficient, $b_{\text{max}} = 2161.5$, was reached at intermediate body-mass ratios of $R_0 = 3.15$ (i.e. predators are roughly

three times larger than their prey). As handling time is proportional to the inverse of the predators' maximum consumption rates, the maximum nonlinear interaction strengths increase with the body-mass ratios (Fig 2). These maximum nonlinear interaction strengths are realized at the highest prey densities. At lower prey densities, the nonlinear interaction strengths also depend on successful search rates, which causes hump-shaped relationships with body mass ratios (Fig. 2).

The scaling exponent, q , was significantly higher for beetles and small prey ($q = 0.89 \pm 0.15$, mean \pm SE) than for beetles with large prey ($q = 0.02 \pm 0.11$, Fig. 1c). This indicates that the nonlinear interaction strengths between beetles and their prey were best described by type III functional responses for high predator–prey body mass ratios when beetles fed on small prey (Fig. 2c), whereas type II functional responses characterized their interactions under low predator–prey body-mass ratios with large prey (Fig. 2a). While a similar pattern of type-III functional responses with small prey (high body-mass ratios; $q = 0.52 \pm 0.16$, mean \pm SE) and type-II functional responses with large prey (low body-mass ratios; $q = 0.17 \pm 0.23$, mean \pm SE) was found for spiders (Fig. 2d, b), this difference in the scaling exponent was not statistically significant (Fig. 1c, contrast analysis for spiders: $P = 0.17$).

Discussion

We studied the influence of predator and prey body masses on 26 functional responses of common terrestrial arthropod predators. We found: (i) power-law scaling in handling times with predator and prey masses, (ii) hump-shaped relation-

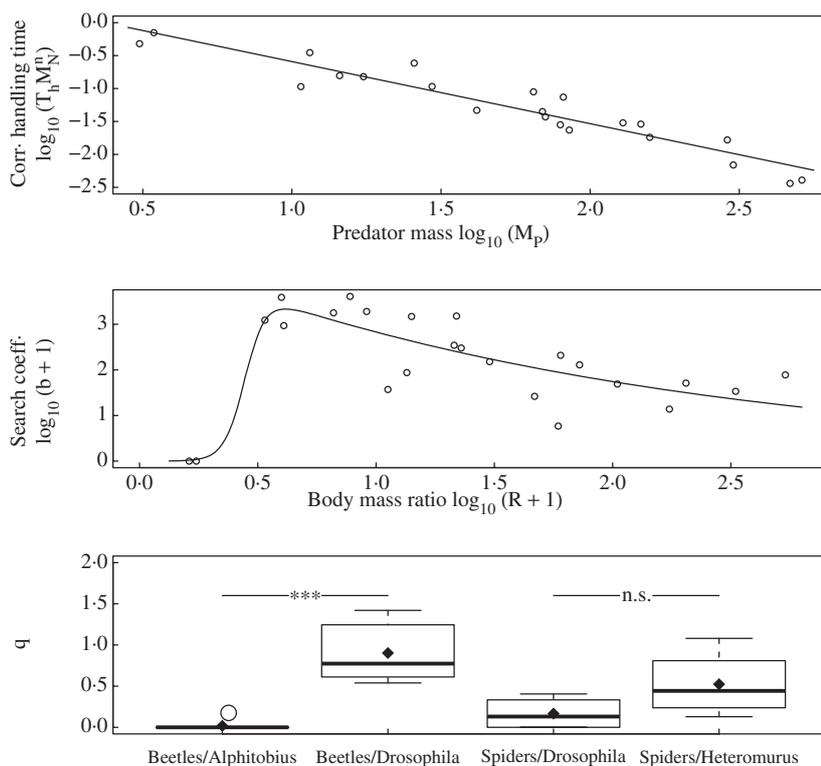


Fig. 1. Allometric scaling of functional response parameters: (a) \log_{10} handling time (min ind.^{-1}) decreases with \log_{10} predator mass (mg); eqn (4): $p = -0.94 \pm 0.09$ (mean \pm SE, $P < 0.001$), $n = 0.83 \pm 0.07$ ($P < 0.001$), $T_{h(0)} = 0.35 \pm 0.14$ ($P < 0.01$), $r^2 = 0.887$; note that handling time was normalized by the prey body-mass term in eqn (4): $\text{corr}T_h = \log_{10}T_h - n\log_{10}M_N$; (b) search coefficients ($\text{cm}^2 \text{day}^{-1} \text{ind}^{-q} \text{Arena}^q$) follow a hump-shaped relationship with predator–prey body-mass ratios; eqn (5): $A = 3.69 \pm 0.52$ ($P < 0.001$), $\varepsilon = 0.48 \pm 0.11$ ($P < 0.001$), $\Phi = 0.45 \pm 0.154$ ($P < 0.01$) and $\beta = 47.13 \pm 88.67$ (n.s.), $r^2 = 0.74$; (c) scaling exponents, q , and predator–prey pairs: Beetles/Alphitobius = low body mass ratio, Beetles/Drosophila = high body mass ratio, Spiders/Drosophila = low body mass ratio and Spiders/Heteromurus = high body mass ratio; significant differences among groups according to contrast analyses.

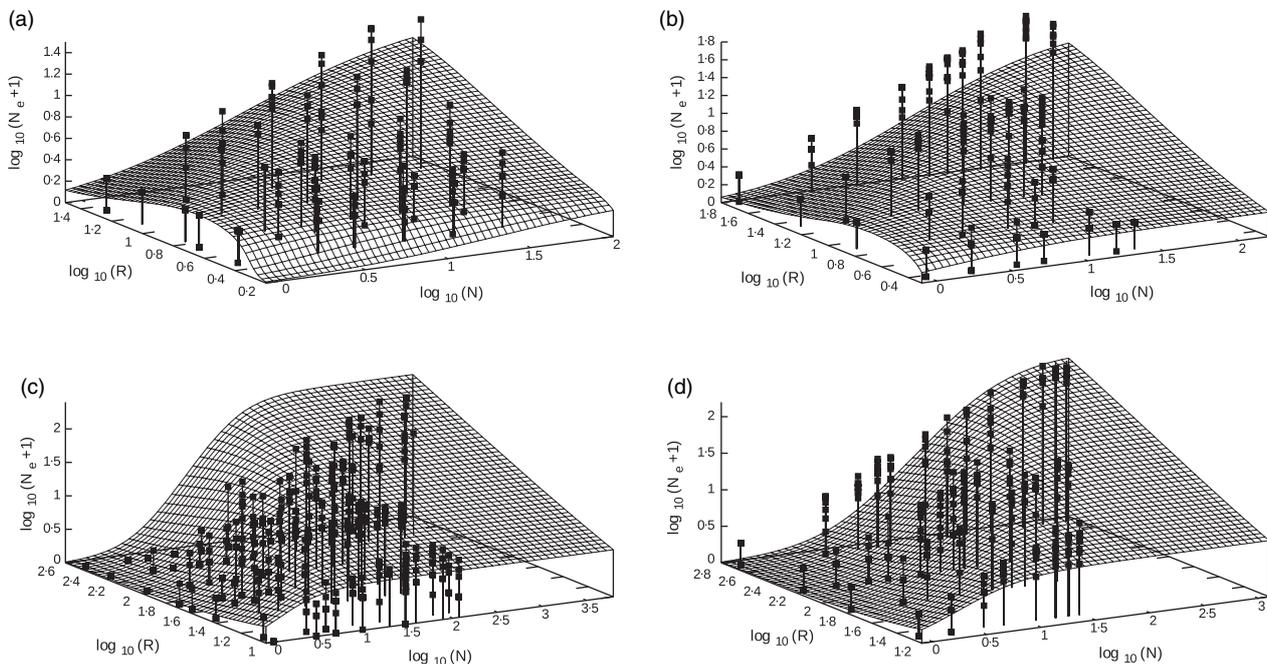


Fig. 2. Experimental *per capita* consumption rates (N_e) depending on predator–prey body-mass ratios (R) and prey density (N) with allometric functional responses according to the allometric scaling functions of Fig. 1 for (a) Beetles/*Alphitobius* (low predator–prey body-mass ratios), (b) Spiders/*Drosophila* (low ratios), (c) Beetles/*Drosophila* (high ratios), (d) Spiders/*Heteromurus* (high ratios).

ships between search coefficients and predator–prey body-mass ratios, and (iii) increases in the scaling exponent with body-mass ratios (only significant for beetles). Our findings provide evidence of how functional response parameters vary across predator–prey interactions of different body-mass ratios. We focused on two groups of generalist predators with different feeding strategies: beetles are mainly nocturnal, tactile and olfactory, whereas spiders are day active and optically oriented. The similarity in our findings for both predator groups suggests the broad generality of our results.

Interestingly, we found an exponent of -0.94 ($SE = \pm 0.09$) in the relationship between handling time and predator body mass, which is significantly different from the exponent of -0.75 initially predicted based on metabolic theory (Peters 1983; Yodzis & Innes 1992; Carbone *et al.* 1999; Brown *et al.* 2004). Thus, larger predators had lower handling times and smaller predators had higher handling times than expected based on metabolically driven processes. Assuming that metabolism mainly drives the digestive part of handling, it follows that the speed of morphologically constrained handling processes such as killing and ingesting the prey increases more steeply with predator mass than metabolic processes. For instance, if gut and stomach size are proportional to body size the maximum ingestion will also be proportional to body size. Consequently handling time should be inversely proportional to body size, which is consistent with our results. Consistent with most other functional response experiments, the short 24-h time period of our experiments thus emphasizes morphological over digestive constraints on handling times. An improved mechanistic understanding of the scaling exponents thus requires differ-

entiating between ingesting and digesting times in studies with varying experimental duration (Jeschke *et al.* 2002). While metabolic arguments suggest power-law scaling of digesting times with predator masses, ingesting times could be inversely proportional to body mass.

Instead of the expected linear increase in handling time with prey mass (exponent of unity), we found a scaling exponent of 0.83 ± 0.07 (mean \pm SE). One plausible but speculative explanation for this difference could be that the energy content of the prey does not increase proportional to the prey mass. In this case, larger prey would contain more indigestible body parts (e.g. exoskeleton) that impose limitations on ingesting or digesting the prey body. However, a detailed analysis of the morphological and energetic structure of the prey biomass was beyond the scope of the present study. Moreover, we caution that our results were based on only two prey types for each of the predator groups, which may confound the prey-mass scaling relationships presented here. While our study demonstrates that handling time-scales with prey mass, subsequent studies should include a broader variation in prey body masses to more specifically address the exact exponent of this scaling relationship.

Consistent with prior studies investigating search coefficients at constant prey densities (Wahlström *et al.* 2000; Brose *et al.* 2008), our results corroborate the hump-shaped relationship between search coefficients and predator–prey body-mass ratios (Figs 1b and 2). While the present study was lacking data of direct behavioural observations, we follow prior studies in suggesting that the following behavioural constraints could be responsible for this hump-shaped relationship. Small predators (with low predator–prey

body-mass ratios) have a small search area, and they have difficulties in subduing prey larger than themselves leading to inefficient attacks. Large predators (with high predator–prey body-mass ratios) have difficulties in catching small prey individuals, since the much smaller prey have faster reaction times and high escape efficiencies (Brose *et al.* 2008). At intermediate predator–prey body-mass ratios, however, the highest search coefficients were found, because predators are less restricted in subduing or catching the prey individuals. While the hump-shaped scaling of search coefficients with predator–prey body-mass ratios is supported by our data, these behavioural constraints remain hypotheses to be tested.

In our study, the two different predator groups were most efficient at a predator–prey body-mass ratio of $R_0 = 3.15$ (i.e. when predators were roughly three times larger than their prey). In a prior study, however, the group-specific capture mechanism of predators (e.g. sit-and-move vs. chasing predators) was shown to have a large effect on the optimum predator–prey body mass ratio (Troost, Kooi & Dieckmann 2007) suggesting that the optimum body-mass ratio documented here for epigeic spiders and beetles should not necessarily apply to other predator groups. Interestingly, in other ecosystems, a negative relationship between prey density and search rates could occur if the prey employs group defence mechanisms such as swarming (e.g. mammals or fish) (Jeschke & Tollrian 2005). With respect to defence mechanisms of prey, the prey type may thus also influence these scaling relationships.

Moreover, prior studies reported maximum search coefficients of differently sized perch at $R_0 = 49.8$ for planktonic prey of 0.5 mm and at $R_0 = 78.9$ for prey of 1 mm size (Wahlström *et al.* 2000), and $R_0 = 103.1$ for wolf spiders and $R_0 = 83.1$ for ground beetles in terrestrial ecosystems (Brose *et al.* 2008). These studies were based on the simplifying assumption of constant prey densities, whereas the present study overcame this assumption by varying prey densities to estimate search rates of functional responses. While our results support the predicted hump-shaped search rates under varying prey densities, they also demonstrate that optima in the search coefficients were realized at body-mass ratios of $R_0 = 3.15$, which is approximately one order of magnitude lower than the optimum body-mass ratios of a prior study with the same species (R_0 of 83.1 or 103.1; Brose *et al.* 2008). This difference suggests that studies at constant prey densities might yield inaccurate estimates of optimum body-mass ratios. Interestingly, the optimum body-mass ratio of the present study is highly consistent with the geometric average body-mass ratio of 3.98 between invertebrate predators and their prey found in terrestrial food webs (Brose *et al.* 2006a). This implies that many interactions in terrestrial communities might be realized with maximum instantaneous search rates.

Consistent with prior studies, our results suggest that predators efficiently exploit prey within a specific size range. While our present results suggest that terrestrial predators are less specialized than previously anticipated (Brose *et al.* 2008), striking differences in optimum body-mass ratios, R_0 ,

between these studies are evident. Disentangling whether these differences depend on the organisms investigated (e.g. beetles and spiders vs. fishes) or on ecosystem characteristics (terrestrial vs. pelagic) would require additional studies of varying predator groups in different ecosystem types. Eventually, these studies will allow addressing evolutionary and ecologically relevant questions of different optimum body-mass ratios and degrees of specialization across organism groups and ecosystem types.

In this study, we present evidence from systematic laboratory experiments that the scaling exponent, q , may increase with the predator–prey body-mass ratio, though this difference was only significant for ground beetles. This corroborates prior findings that type III functional responses could occur more frequently than previously anticipated (Sarnelle & Wilson 2008). Interestingly, a similar increase in the scaling exponent with prey size was reported based on gut content analysis of marine minke whales (Smout and Lindstroem 2007). Together, these results could indicate a potentially broad universality of increases in scaling exponents with predator–prey body-mass ratios across different ecosystems.

It has been stressed that functional response experiments should apply a realistic habitat structure in the experimental arenas to create more natural experimental settings, since prey density often also relates to habitat structure (Real 1977; Crawley 1992). Moreover, it was hypothesized that adding such habitat structure could lead to a change of the functional response type as a consequence of potential hiding refuges for the prey (Hassell, Lawton & Beddington 1977; Real 1977; Crawley 1992). Accounting for this fact, our experimental design included a constant density of moss as a natural habitat structure. Certainly, it would be important to replicate the functional responses of the present study across different moss densities to address how the body-mass effects documented here interact with effects of habitat complexity. Thus, the scaling exponents and attack coefficients of the present study should be interpreted only qualitatively, because different levels of habitat complexity should affect the absolute values of these parameters.

As a general, qualitative pattern, we found that this moss provided refuges for small prey from predation by large predators (high body-mass ratios) resulting in sigmoid, type III functional responses with scaling exponents higher than zero. In contrast, predators of similar body mass as their prey (i.e. low body-mass ratios) were able to follow the prey into the hiding places within the habitat structure resulting in functional responses of type II with scaling exponents of zero. These observations during the experiments provide an explanation for the observed shift from functional responses of type II at low predator–prey body-mass ratios to functional responses of type III at high predator–prey body-mass ratios.

Interestingly, this suggests that population dynamics are stabilized by increasing body-mass ratios as a result of increasing scaling exponents (Oaten & Murdoch 1975a, b; Williams & Martinez 2004; Brose *et al.* 2006b; Rall *et al.*

2008). While previous studies documented that high body-mass ratios stabilize population and food-web dynamics via reductions in the per unit biomass rates of metabolism and consumption (Emmerson & Raffaelli 2004; Brose *et al.* 2006a; Brose 2008), the increases in the scaling exponent documented here suggest an additional mechanism of how high body-mass ratios stabilize natural ecosystems.

We have presented the scaling of functional response parameters with predator and prey body masses with quantitative parameter estimates. This might be interpreted as an opportunity to estimate quantitatively functional responses based on body masses. However, we caution that this would be a misuse of our model: even in the case of the functional responses of the present study (Table 1) backward estimation of the *per capita* consumption rates based on the allometric functional response model yields substantial over- or under-estimations (Fig. 2). As other scaling models such as species–area relationships or metabolic scaling theory, the results presented here should be interpreted as a documentation of patterns across a body-mass scale. For instance, nobody would seriously estimate the species richness of Borneo based on a global species–area relationship, whereas this scaling model certainly has a tremendous value as conceptual cornerstone of biogeography. In the same vein, we suggest using the allometric functional response model presented here as an indication of scaling behavior in foraging ecology. Integrating these scaling relationships into population models will allow predicting general trends in energy fluxes (Brose *et al.* 2008), food-web structures (Petchey *et al.* 2008), and the distribution of interaction strengths across food-web links (Bersier, Banasek-Richter & Cattin 2002). Eventually, combining allometric functional response models with those of food-web structure (Williams & Martinez 2000; Cattin *et al.* 2004; Petchey *et al.* 2008) may allow a more detailed understanding how the distribution of body masses across species in natural ecosystems determines population and food-web stability (Brose *et al.* 2006b; Otto *et al.* 2007; Rall *et al.* 2008).

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