

1 Supplemental Information for “How patch size and
2 refuge availability change interaction strength and
3 population dynamics: a combined individual- and
4 population-based modeling experiment”

5 Yuanheng Li^{1,2,3}, Ulrich Brose^{1,2}, Katrin Meyer⁴, and Björn C. Rall^{1,2}

6 ¹German Centre for Integrative Biodiversity Research (iDiv)
7 Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

8 ²Institute of Ecology, Friedrich Schiller University Jena, Dornburger-Str.
9 159, 07743 Jena, Germany

10 ³Johann-Friedrich-Blumenbach Institute of Zoology and Anthropology,
11 Georg-August-Universität Göttingen, Berliner Str. 28, 37073 Göttingen,
12 Germany

13 ⁴Department of Ecosystem Modelling, Georg-August-Universität Göttingen,
14 Büsgenweg 4, 37077 Göttingen, Germany

15 **1 ODD protocol for *in silico* feeding experiment**

16 **1.1 Overview**

17 We modeled allometric predator-prey feeding interactions using an individual-based ap-
18 proach. The model description followed the ODD (Overview, Design concepts, Details)
19 protocol (Grimm et al., 2006, 2010). The model was implemented in C++ using Code::Blocks
20 as development environment.

21 **1.2 Purpose**

22 The purpose of the model is to estimate the dependencies of functional-response parameters
23 on patch size and habitat complexity (represented by refuge availability) in a system with one
24 predator and several prey items. As a preparation, we first investigated the maximum feeding
25 rate without any explicit space properties, as we assumed that the maximum feeding rate
26 is driven by physiological (mechanical) parameters such as chewing and digesting and does
27 not scale with patch size or habitat complexity. Secondly, we assessed functional responses
28 of predators to different prey densities in patches of different sizes and refuge availability.

29 **1.3 Entities, state variables and scales**

30 One predator and several prey individuals make up the agents of the model. The common
31 state variables of predator and prey are individual identity, spatial coordinates (in cm), body
32 mass (in mg), and body-mass dependent velocity. The predator is characterized by further
33 state variables related to hunting and digestion. The parameter ‘gut-fill’ captures how many
34 milligrams of food are currently in the gut of the predator, ‘still-handling’ captures how
35 many time steps are still needed for handling prey, and ‘prey-eaten’ counts the number of
36 prey items consumed by the predator.

37 The environment consists of a two-dimensional square area where its size and habitat com-
38 plexity can be modified. To manipulate habitat complexity in the form of refuge availability
39 for the prey, each cell in this area is characterized by the boolean state variable ‘prey hiding’.
40 This variable is set to 1 if prey individuals staying in this cell cannot be found by a predator,
41 and to 0 otherwise. The predator and prey can move continuously in the area via random
42 walk. Predator and prey are both able to enter all the cells, but the predator is not able

43 to find prey in refuge cells. We implemented non-periodic wall-like boundary conditions
44 (Attard, 2006) to simulate a finite-sized patch.
45 In terms of scales, one grid cell is always $1\text{ cm} \times 1\text{ cm}$ and the spatial extent of the patch is
46 modified from $20\text{ cm} \times 20\text{ cm}$ to $1000\text{ cm} \times 1000\text{ cm}$ to account for different patch sizes. One
47 time step represents one second and the simulations are ran for 3600 time steps corresponding
48 to one hour.

49 **1.4 Process overview and scheduling**

50 The first process that is applied in this discrete-time model is prey movement (random walk
51 with randomly chosen direction and allometric distance, i.e. the velocity of an individual
52 scales with its body mass). The following processes are the predator’s decisions and actions
53 (Fig. 1 in the main text). First, the predator digests and afterwards if it has caught prey
54 previously and is still handling it, the predator does the process of handling. Subsequently,
55 if the predator is not handling prey anymore and its gut is full (‘gut-fill’ $\geq 60\%$), it rests,
56 i.e. it does not take any actions in this time step. If the predator is not handling prey and
57 is hungry (‘gut-fill’ $< 60\%$), the predator moves according to the same rules as prey. After
58 reaching the new position, the predator investigates if it encounters a prey in the current
59 cell. If there is a prey individual in the same cell and this cell is not marked as refuge, the
60 prey will be attacked. If the attack is successful, another prey item is placed randomly into
61 the grid to keep prey density constant. The predator starts to handle the prey in the next
62 time step.

63 1.5 Design concepts

64 *Basic principles* - This model mimics classical functional response experiments in the lab-
65 oratory, but the model allows to explore much larger patch sizes than in a real laboratory
66 arena. Moreover, the model can more easily be used to determine maximum feeding rates
67 than laboratory experiments, because the amount of prey can be held constantly until max-
68 imum feeding rates are reached. *Emergence* - Functional responses are the main emerging
69 pattern from the model, arising from the predator's efficiency at catching prey in patches of
70 different sizes and habitat complexity (refuge availability). *Sensing* - Predator and prey are
71 able to detect each other when they meet in the same cell which is not marked as refuge.
72 Both predator and prey are able to detect patch edges and stop nearby when they reach an
73 patch edge. Next time when this individual needs to move, it just moves according to the
74 same rules as before. *Interaction* - The predator interact with prey by feeding on the prey
75 when they meet on the same cell and the prey is not hidden. When the prey is in a refuge
76 cell, the predator can enter that cell, but does not interact with the prey. *Stochasticity* -
77 Random numbers are used in initialization of most variables, including coordinates of agents,
78 the refuge availability of cells and the state variable 'gut-fill' of the predator. Stochasticity
79 is also involved in the moving direction of agents when random walk applies. Bernoulli-
80 distributed random numbers are drawn to determine the handling time for a prey item as
81 time is a discrete variable in this model. *Observation* - In each *in silico* experiment, the
82 number of prey items eaten by the predator is recorded at each time step. At the end of
83 each simulation run, patch size, refuge availability (percentage of refuge cells), initial prey
84 number, and 'prey-eaten' are recorded.

1.6 Initialization

Random values are used to initialize the spatial coordinates of all agents and choose refuge cells. All other initial parameters are listed in Table S1.

Table S1: Agents' state variables and parameters

sort	variables	unit	note
state variable	gut-fill	rate	randomly initialized
	still-handling	s	initially set to zero
	individual identify	number	
	prey-eaten	number	initially set to zero
calculated parameter	velocity	cm s^{-1}	
	rate of successful attack	rate	
	full gut	mg	allometrically calculated
	digestion rate	rate	
	handling time	s	

Most species traits regulating the processes described above are calculated by allometric rules. These include velocities of predator and prey, V [cm s^{-1}], Eq. (S1a), (Peters, 1983), and the predator-specific traits: gut size, G [mg], Eq. (S1b), (Ibarrola et al., 2012); digestion rate, D [mg s^{-1}], Eq. (S1c), (Ibarrola et al., 2012); handling time, T_h [s], Eq. (S1d), (modified from Rall et al., 2012); and rate of successful attack, S_a unitless, Eq. (S1e), (Wahlström et al., 2000; data from Gergs and Ratte, 2009, and Gergs, 2011):

$$V = v_0 M^{a_v} \tag{S1a}$$

$$G = g_0 M^{a_g} \tag{S1b}$$

$$D = d_0 M^{a_d} \tag{S1c}$$

$$T_h = h_0 M_p^{a_{h,p}} M_n^{a_{h,n}} \tag{S1d}$$

$$S_a = a_0 \left(\frac{R}{R_{opt}} e^{1 - \frac{R}{R_{opt}}} \right)^\lambda \tag{S1e}$$

86 where v_0 , g_0 and d_0 are constants, a_v , a_g , and a_d are the allometric exponents, and M is
 87 the body mass of the corresponding individual. Subscripts p and n of M indicate predator
 88 and prey, respectively. As only few relevant studies were found on digestion mechanisms,
 89 we used generalized Rickers function (Persson et al., 1998; Persson and Brönmark, 2002b,a;
 90 Wahlström et al., 2000; Brose et al., 2008; Rall et al., 2011) to describe the scaling of attack
 91 success (S_a) depending on body size. This function consists of the maximum attack success
 92 a_0 , predator-prey body-mass ratio, R and its optimum R_{opt} and a shaping parameter, λ .
 93 Predator and prey also possess some state variables to assist their decision making and
 94 activities, i.e. ‘position’ for all individuals; ‘gut fullness’ and ‘still handling’ for the predator;
 95 ‘prey identity’ for prey.

96 1.7 Submodels

97 1. Prey move. This process is the first one for each time step. Prey individuals do
 98 random walks consecutively according to their identity number. A random direction is gen-
 99 erated (a double precision floating number from 0 to 2π) and position changes vertically and

100 horizontally are calculated according to prey velocity. Before updating the actual coordi-
101 nates, wall boundary conditions are considered, checking if values of the coordinates would
102 be beyond the boundaries. If so, the value is set close to the coordinate value of that edge
103 but with a distance to the edge of 10^{-6} cm.

104 2. Digest. The state variable ‘gut-fill’ of the predator is subtracted by ‘digestion rate’
105 in this process. It is executed each time step even when the gut is already empty. If the
106 value of gut fill drops below zero, it is set to zero.

107 3. Handle prey. This process is executed under the condition that the state variable
108 ‘still-handling’ has a positive value. The value of ‘still-handling’ is reduced by one in this
109 process.

110 4. Move. The predator does a random walk. If the predator is satisfied, meaning ‘gut-
111 fill’ exceeds 0.6, this process is skipped.

112 5. Encounter and attack? Here, the coordinate of the predator is checked only when it is
113 about to hunt (‘gut-fill’ < 0.6). If the predator is currently in a refuge cell, the hunting pro-
114 cess is forfeited. If it is not forfeited, the following actions are executed. 1) Check potential
115 prey, checking if there exists one prey item that is in the same cell as the predator. Checking
116 order follows the prey’s identity numbers. As soon as one prey fulfills the condition, the
117 checking is finished. 2) If there is a potential prey item, a random number (ranging from 0
118 to 1) is generated and compared to ‘rate of successful attack’ to decide if this prey flees.

119 6. Attack success? If the attacked prey does not flee (attack success), values of ‘gut-fill’
120 and ‘still-handling’ will be increased by the amounts calculated from the prey mass and ‘prey-
121 eaten’ will be increased by one. As time is discrete in our model, a Bernoulli-distributed
122 random number is drawn to make sure that the value of ‘still-handling’ is an integer and on
123 average still satisfying the calculated handling time. If the prey flees (attack unsuccessful),

124 this time step ends.

125 7. Replace caught prey. If attack succeeds, the killed prey item (i.e. its identity number)
126 would be randomly given a new set of spatial coordinates, but body mass never changes.

127 8. Output data. Data are recorded immediately after each of 3600 time steps. The
128 number of prey eaten and relevant input values are recorded, i.e. body masses of agents,
129 patch size, percentage of refuge cells and initial number of prey items.

130 2 Allometric handling time

131 We used data from Rall et al. (2012) to parameterize the equation for handling time (T_h ,
132 Eq. (2d)). We only selected the data for predation (parasitism excluded) and for short
133 experimental duration (≤ 10 minutes) to make the analysis. We fitted 67 data points to
134 a linear mixed-effects model ('lme' in the package 'nlme' in R, Pinheiro et al. (2016); R
135 Core Team (2016)). To correct for differences between studies, study identity was used as a
136 random factor, and all the variables (explanatory variables, body masses of predator and prey
137 species and dependent variable handling time) were ln-transformed. The statistics showed
138 that the handling time increased with increasing prey mass and decreased with increasing
139 prey mass and decreases with increasing predator mass (Fig. S1, Table S2).

Table S2: Statistics for handling time ^a

	Estimate	S.E.	p-value
intercept	3.624	0.839	0.0001
ln.pred ^b	-0.330	0.059	<0.0001
ln.prey ^c	0.173	0.051	0.0013

^ahandling time is ln-transformed

^bln-transformed predator body mass

^cln-transformed prey body mass

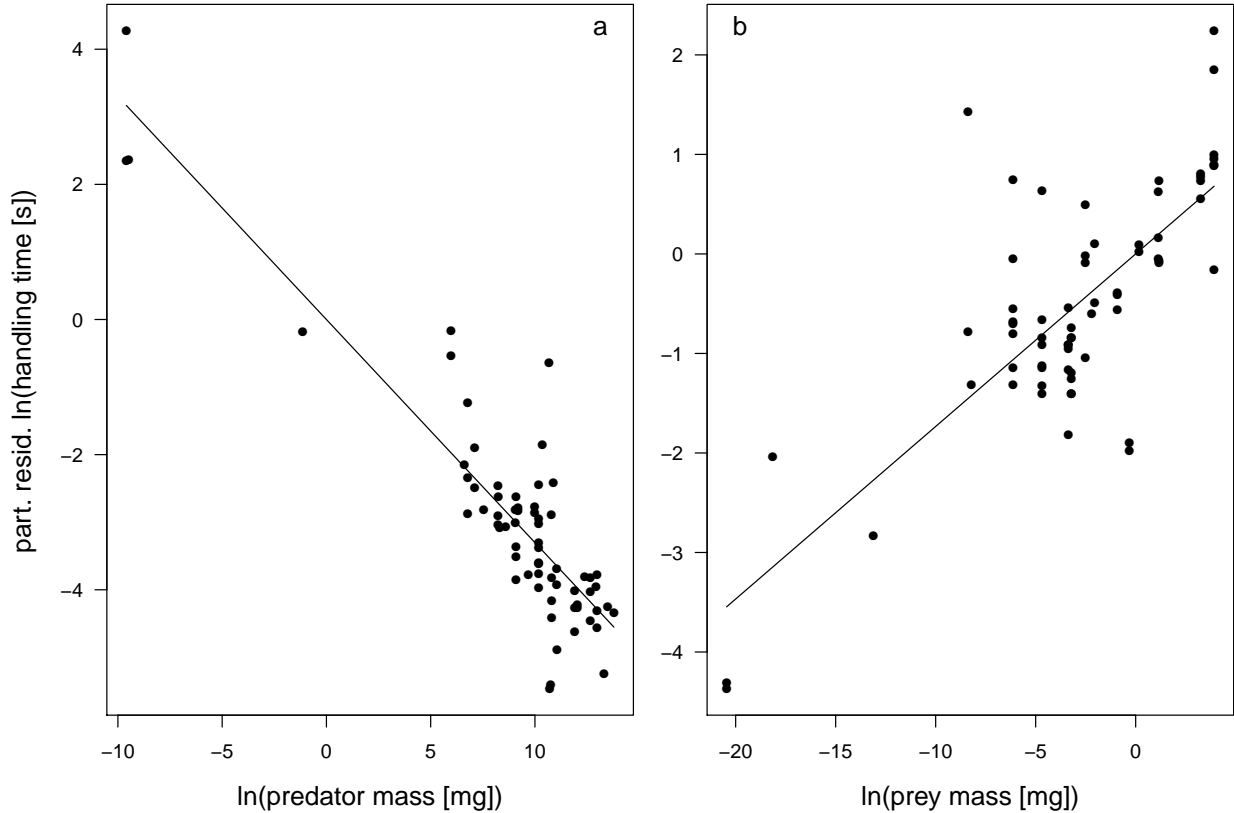


Figure S1: Statistical results for handling time (T_h) show that handling time decreases with increasing predator body mass and increases with increasing prey body mass. Data are ln-transformed before fitting. The partial residual of handling time is used as y-axis.

3 Preliminary model selection

140

141 We listed the statistical results of ‘preliminary tests’ (section “Functional response fitting”
 142 in the main text) on the types of scaling that functional-response parameters had with patch
 143 size or refuge availability, Tab. S3. For the simulations on predator-prey body-mass ratio
 144 of 100 and 200, the selected best model (according to the BIC) includes (1) half saturation
 145 density scaling with power law to patch size and exponentially to refuge availability; (2) Hill
 146 exponent scaling with power law to both patch size and refuge availability. For the simulation
 147 on body-mass ratio of 50, (1) the model is selected for the same scaling relationships of half
 148 saturation density as for body-mass ratio of 100 and 200; thus, (2) Hill exponent scales

149 exponentially with both patch size and refuge availability.

Table S3: Full model selection on scaling rules of functional-response parameters

model scaling rules ^{ab}	BIC		
	100	200	50 ^c
eeee	45061.65	5710.646	3930.403
eepe ^d	45083.81	5709.091	3933.047
peee	45026.84	5709.33	3928.032 ^e
eeep	45057.89	5706.494	3930.711
epee	45219.88	5741.362	3940.024
pepe	45025.2	5707.415	3930.593
eep	45091.41	5705.066	3932.338
eppe	45218.91	5754.17	3944.321
peep	45025.39	5706.341	3928.081
ppee	45228.25	5735.171	3938.638
ep	45231.84	5734.309	3940.953
pepp	<u>45023.57</u>	<u>5703.671</u>	3930.069
pppe	45185.07	5733.498	3941.549
eppp	45223.9	5731.754	3944.204
pp	45236.62	5737.974	3944.041
pppp	45189.86	5729.644	3941.185

^ascaling of N_0 to A , N_0 to R , h to A and h to R , subsequently

^b N_0 half saturation density, h Hill exponent, A patch size, R refuge availability

^cpredator-prey body-mass ratio

^de/p: exponential/power law scaling

^elowest BIC value

150 4 *In silico* feeding experiments on other body-mass 151 ratios

152 We additionally did functional response simulations for predator mass of 200 mg and 50 mg
153 (prey mass of 1 mg). However, we reduced the numbers of patch sizes and refuge availabilities.

154 The simulated patch sizes for both predator masses are 0.04 m², 0.64 m², 2.56 m², 16 m², 49 m²
155 and 64 m²; and the simulated refuge availabilities are 5% to 65%, in steps of 15%. All the
156 following statistics follow the descriptions in the paper.

Table S4: Statistical results of functional-response parameters simulated on other body-mass ratios

		predator mass	parameter ^a	estimate	s.e.	p-value
ht	200		f_{max}	10.56	0.04	$< 2 \times 10^{-16}$
			b_{N_0}	1.504	0.159	$< 2 \times 10^{-16}$
			$\ln(C_{N_0})$	5.338	0.067	$< 2 \times 10^{-16}$
			$\ln(C_h)$	0.25	0.028	$< 2 \times 10^{-16}$
	50		f_{max}	4.12	0.07	$< 2 \times 10^{-16}$
			b_{N_0}	1.423	0.257	3×10^{-8}
			$\ln(C_{N_0})$	4.503	0.110	$< 2 \times 10^{-16}$
			$\ln(C_h)$	0.26	0.047	3×10^{-8}

^arefer to Eq. (5) in the main text

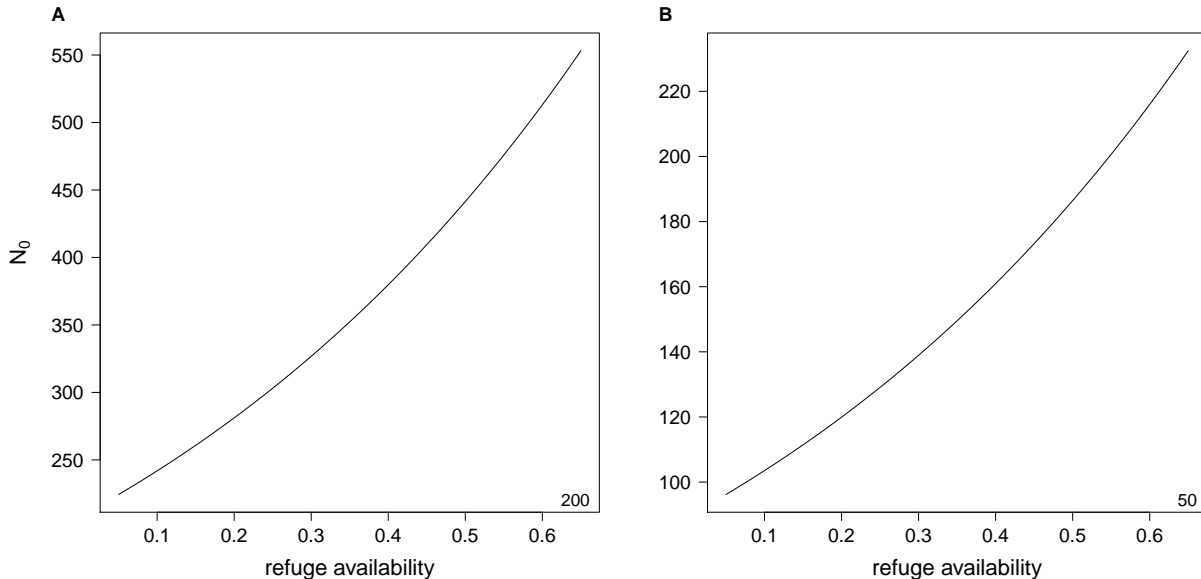


Figure S2: Effect of habitat complexity (expressed as refuge availability) on half saturation density. Panel A and B show the results for body-mass ratio of 200 and 50, respectively (right-bottom corner).

157 The maximum feeding rate, f_{max} , were 4.12 and 10.56 individuals for predator mass of 50
158 mg and 200 mg (Tab. S4). The final models for predator mass of 50 mg and 200 mg based
159 on the BIC selection showed the same dependencies, including an exponential scaling of half
160 saturation density with refuge availability but no scaling with patch size (refer to Eq. (5a)).

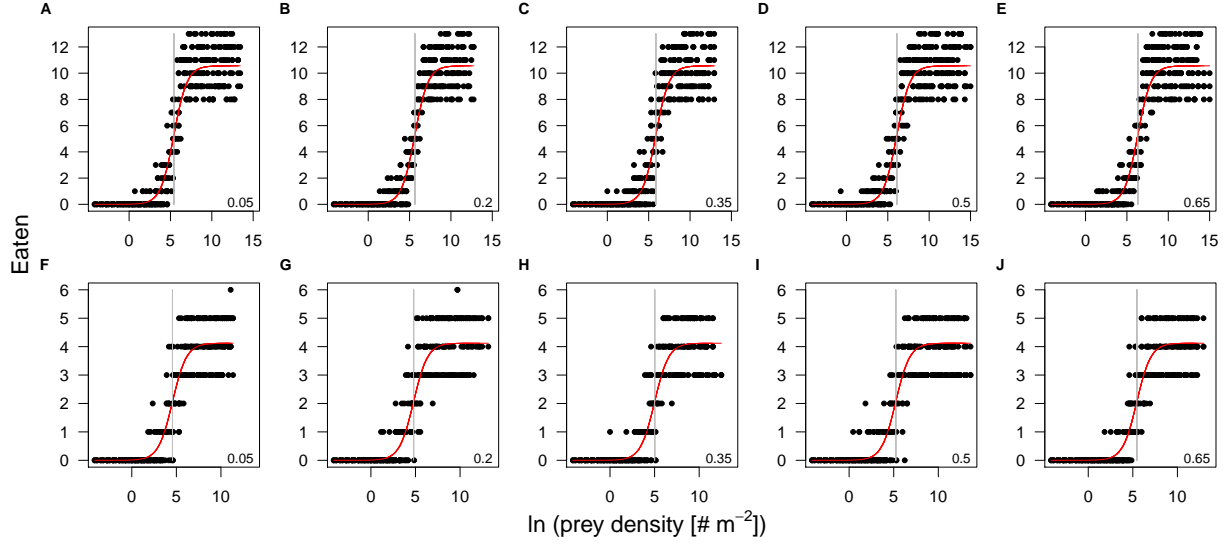


Figure S3: Results of *in silico* functional response experiments (black dots) and their corresponding fits (red lines). The panels are arranged by increasing refuge availability and increasing body-mass ratios of predator-prey. The upper row (panels A to E) are for body-mass ratio of 200 and lower (panels F to J) for 50. Each row starts with data of 5% refuge availability (A, uppermost left) to 65% (O, lowermost right). All prey densities are ln-transformed. The grey vertical lines denote the half saturation densities.

161 Consistent with the result for predator mass of 100 mg in the main text, they did not include
 162 any scaling of Hill exponent for both predator masses (refer to Eq. (5b)). The half saturation
 163 densities increased with increasing refuge availability, $b_{N_0} = 1.504$ for predator mass of 200
 164 mg and $b_{N_0} = 1.423$ for predator mass of 50 mg, see Fig. S2 and Tab. S4. The ln-transformed
 165 intercepts of the half saturation density were 5.338 and 4.503 for predator mass of 200 mg
 166 and 50 mg, respectively (Tab. S4). The estimated Hill exponents across all patch sizes and
 167 refuge availabilities were 1.284 for predator mass of 200 mg and 1.300 for predator mass of
 168 50 mg (Tab. S4). The fitted functional response curves are of the same shape but feedings
 169 are realized at higher densities with increasing refuge availabilities (Fig. S3).

Reference

- 170
171 Attard, P. (2006). Non-periodic boundary conditions for molecular simulations of condensed
172 matter. *Molecular Physics*, 104(12):1951–1960.
- 173 Brose, U., Ehnes, R. B., Rall, B. C., Vucic-Pestic, O., Berlow, E. L., and Scheu, S.
174 (2008). Foraging theory predicts predatorprey energy fluxes. *Journal of Animal Ecol-*
175 *ogy*, 77(5):1072–1078.
- 176 Gergs, A. (2011). *Modelling foraging behaviour in the insect predator Notonecta maculata*
177 *using the individuals approach / vorgelegt von: Andr Gergs*. PhD thesis, RWTH Aachen
178 University.
- 179 Gergs, A. and Ratte, H. T. (2009). Predicting functional response and size selectivity of juve-
180 nile Notonecta maculata foraging on Daphnia magna. *Ecological Modelling*, 220(23):3331–
181 3341.
- 182 Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard,
183 J., Grand, T., Heinz, S. K., Huse, G., Huth, A., Jepsen, J. U., Jrgensen, C., Mooij,
184 W. M., Mller, B., Peer, G., Piou, C., Railsback, S. F., Robbins, A. M., Robbins, M. M.,
185 Rossmannith, E., Rger, N., Strand, E., Souissi, S., Stillman, R. A., Vab, R., Visser, U.,
186 and DeAngelis, D. L. (2006). A standard protocol for describing individual-based and
187 agent-based models. *Ecological Modelling*, 198(1-2):115–126.
- 188 Grimm, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Giske, J., and Railsback, S. F. (2010).
189 The ODD protocol: A review and first update. *Ecological Modelling*, 221(23):2760–2768.
- 190 Ibarrola, I., Arambalza, U., Navarro, J. M., Urrutia, M. B., and Navarro, E. (2012). Allomet-

191 ric relationships in feeding and digestion in the Chilean mytilids *Mytilus chilensis* (Hupé),
192 *Choromytilus chorus* (Molina) and *Aulacomya ater* (Molina): A comparative study. *Jour-*
193 *nal of Experimental Marine Biology and Ecology*, 426-427:18–27.

194 Persson, A. and Brönmark, C. (2002a). Foraging capacities and effects of competitive release
195 on ontogenetic diet shift in bream, *Abramis brama*. *Oikos*, 97(2):271–281.

196 Persson, A. and Brönmark, C. (2002b). Foraging capacity and resource synchronization in an
197 ontogenetic diet switcher, Pikeperch (*Stizostedion lucioperca*). *Ecology*, 83(11):3014–3022.

198 Persson, L., Leonardsson, K., de Roos, A. M., Gyllenberg, M., and Christensen, B. (1998).
199 Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-
200 resource model. *Theoretical Population Biology*, 54(3):270–293.

201 Peters, R. H. (1983). *The ecological implications of body size*. Number 2 in Cambridge studies
202 in ecology. Cambridge University Press, New York, repr edition.

203 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team (2016). *nlme: Linear and*
204 *Nonlinear Mixed Effects Models*. R package version 3.1-123.

205 R Core Team (2016). *R: A Language and Environment for Statistical Computing*. R Foun-
206 dation for Statistical Computing, Vienna, Austria.

207 Rall, B. C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmuller, F., Vucic-Pestic, O., and
208 Petchey, O. L. (2012). Universal temperature and body-mass scaling of feeding rates.
209 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1605):2923–
210 2934.

- 211 Rall, B. C., Kalinkat, G., Ott, D., Vucic-Pestic, O., and Brose, U. (2011). Taxonomic versus
212 allometric constraints on non-linear interaction strengths. *Oikos*, 120(4):483–492.
- 213 Wahlström, E., Persson, L., Diehl, S., and Byström, P. (2000). Size-dependent foraging
214 efficiency, cannibalism and zooplankton community structure. *Oecologia*, 123(1):138–148.