Supplemental Information

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1 ODD protocol for feeding simulation model

1.1 Overview

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

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1.2 Purpose

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

1.3 Entities, state variables and scales

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

The environment consists of a two-dimensional square area whose size and habitat complexity can be modified. To manipulate habitat complexity in form of refuges for the prey, each cell in this area is characterized by the boolean state variable 'prey hiding'. This variable is set to 1 if prey individuals staying in this cell cannot be found by a predator, and to 0 otherwise. The predator and prey can move continuously in the area via random walk. Predator and prey are both able to enter all the cells, but the predator is not able to find prey in refuge cells. We implemented non-periodic wall-like boundary conditions (Attard, 2006) to simulate a finite-sized patch.

In terms of scales, one grid cell always represents 1 cm $*$ 1 cm and the spatial extent of the patch can be modified from 20 cm $*$ 20 cm to 1000 cm $*$ 1000 cm to account for different patch sizes. One time step represents one second and simulations were run for 3600 time steps corresponding to one hour.

1.4 Process overview and scheduling

The first process that is applied in this discrete-time model is prey movement (random walk with randomly chosen direction and allometric distance, i.e. the velocity of an individual scales with its body mass). The following processes are the predator's decisions and actions (Fig. 1 from main text). First, the predator digests prey if it has caught prey and is still handling it. Subsequently, if the predator is not handling prey anymore and its gut is full ('gut-fill' $>=$ 60%), it rests, i.e. it does not take any actions. If the predator is not handling prey and is hungry ('gut-fill' $<$ 60%), the predator moves according to the same rules as prey. After reaching the new position, the predator investigates if it encounters a prey in the cell. If there is a prey individual in the same cell and it is not hidden by habitat complexity, the prey will be attacked. If the attack is successful, another prey item is placed randomly into the grid to keep prey density constant. The predator starts to handle the prey in the next time step.

1.5 Design concepts

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

1.6 Initialization

Random values are used to initialize the spatial coordinates of all agents and choose prey hiding cells. All other initial parameters are listed in Table 1.

Table 1: Agents' state variables and parameters

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

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

$$V = v_0 \, M^{a_v} \tag{1a}$$

$$G = g_0 \, M^{a_g} \tag{1b}$$

$$D = d_0 \, M^{a_d} \tag{1c}$$

$$T_h = h_0 \, M_p^{a_{h,p}} \, M_n^{a_{h,n}} \tag{1d}$$

$$S_a = a_0 \, m_0 \, \frac{M_p}{M_n} \, e^{1 - m_0 \, \frac{M_p}{M_n}} \tag{1e}$$

where v_0, g_0 and d_0 are constants, a_v, a_g, and a_d are the allometric exponents, and M is the body mass of the corresponding individual. Subscripts $_p$ and $_n$ of M indicate predator and prey, respectively. As only few relevant studies were found on digestion mechanisms, we developed our own equation for attack success, Eq. (1e), inspired by Wahlström et al. (2000), in which a_0 is maximum attack success and m_0 is optimal prey-predator body mass ratio. Predator and prey also possess some state variables to assist their decision making and activities, i.e. 'position' for all individuals; 'gut fullness' and 'still handling' for the predator; 'prey identity' for prey.

1.7 Submodels

1. Prey move. This process is the first one for each time step. Prey individuals do random walks consecutively according to their identity number. A random direction is generated and position changes in two dimensions are calculated according to prey velocity. Before updating the actual coordinates, wall boundary conditions are considered, checking if values of the coordinates would be beyond the boundaries. If so, the value is set close to

the coordinate value of that edge but with a distance to the edge of 10^{-6} .

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

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

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

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

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

7. Replace caught prey. If attack succeeds, the killed prey item (i.e. its identity

number) would be randomly given a set of spatial coordinates, but body mass never changes.

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

2 allometric handling time

We used data from Rall et al. (2012) to parameterize the equation for handling time (T_h, Eq. (2d)). We only selected the data for predation (parasitism excluded) and for short experimental duration ($\leq$ 10 minutes) to make the analysis. We fitted the 67 data points to a linear mixed-effects model ('lme' in the package 'nlme' in R, Pinheiro et al. (2016); R Core Team (2016)). To correct for differences between studies, study identity was used as a random factor, and all the variables (explanatory variables, body masses of predator and prey species and dependent variable handling time) were ln-transformed. The statistics showed that the handling time increased with increasing prey mass and decreased with increasing prey mass and decreases with increasing predator mass (Fig. 1, Table 2).

Table 2: 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

[a]handling time is ln-transformed
[b]ln-transformed predator body mass
[c]ln-transformed prey body mass

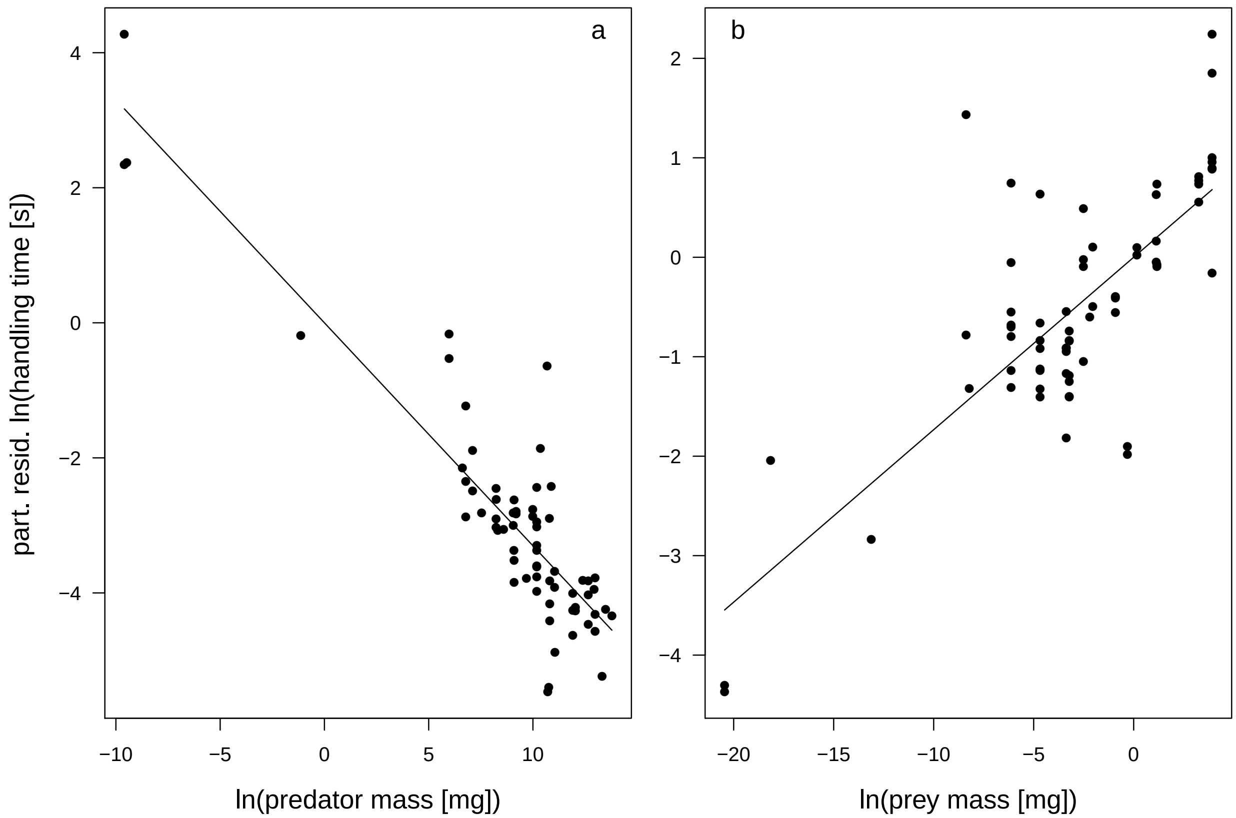

Figure 1: Fitting for handling time (T_h) shows that handling time decreases with increasing predator body mass and increases with increasing prey body mass. Data are ln-transformed before fitting. The partial residual of handling time is used as y-axis.

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