Supplementary Material

Appendix A

ODD-Protocol

Purpose

The purpose of the model is to simulate the effects of perceived predation risk and food availability on home range formation in a prey community of herbivorous mammals. It aims to gain a mechanistic understanding about space use behavior under predation risk and about the consequences of adapted space use for community structures.

Entities, state variables and scales

The model consists of two entities, landscape cells and prey individuals (Tab. A1). Landscape cells are described by the state variables location, food resources (*p-food*) and safety (*p-safety*); the latter feature defines the "landscape of fear". Cells containing food resources (*p-food* >0) are called productive cells. Landscape cells are square cells on a grid with a size of 100x100 cells. Each landscape cell represents 4m². In order to avoid edge effects, periodic boundary conditions were used.

Individuals are characterized by their location, their body mass and their foraging strategy under predation risk. To simplify spatial calculations, the location of individuals can only be on the discrete landscape grid cells. The body mass of the individual is used to calculate further physiological traits by using allometric relationships. The foraging strategy of an individual represents a consistent behavioral strategy that defines the response to perceived predation risk (see *Submodels: Trait assignment* and *Home range search* for details on the different strategies). The model uses discrete time steps. Each step represents the home range search of one individual.

Tab. A.1: Entities and their state variables.

Entity *State variable*	**Unit**	**Description**
Landscape cells *p-food*	Dry biomass, g/(cell · day)	Food resource availability in cell
p-safety	-	Safety of a cell, inverse to predation risk
Individuals *i-bodymass*	g	Body mass of individual
i-fear-type	-	Foraging strategy of individual under predation risk
Allometric traits: *i-feedrate*	Dry biomass, g/day	Amount of food resources that need at least be contained in the home range
i-lococost	Dry biomass, g/cell	Locomotion costs for moving one cell forward
i-maxhr	cells	Maximum home range size
i-foodshare	-	Defines magnitude of food resource exploitation

Process overview and scheduling

In each step of the model a new prey individual is created and performs the processes *trait assignment* and *home range search*. If the home range search is successful, the process *food consumption* is executed, otherwise the individual is excluded from the community. The simulation continues until the community is saturated, i.e. a specific number of individuals (*nfail*, see Tab. A2) have consecutively not been able to establish a home range in the landscape (see Fig. A1 for an overview of the processes). Food resources in the landscape are reduced according to the exploitation by prey animals within the process of food consumption, while the landscape of fear is static. The location and size of the home range are stored after the individual has executed the home range search.

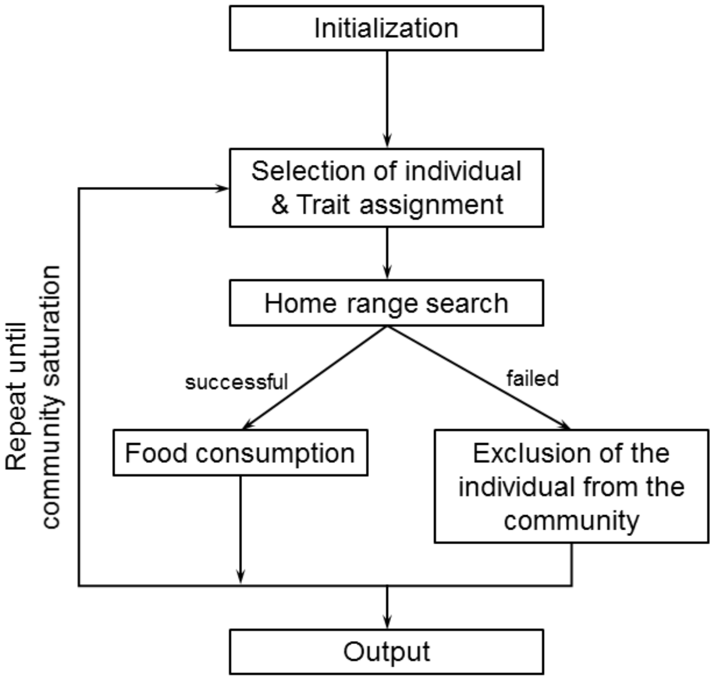

Fig. A.1: Schematic overview of processes in the model. After initialization, a new individual is created and gets assigned certain traits. This individual searches for a home range in the landscape that fulfills its daily energy requirements. The addition of cells to the home range is based on food availability and perceived predation risk in cells. If the home range search is successful, the individual consumes the food resources within, otherwise it is excluded from the community. These steps are repeated until the community is saturated.

Design Concepts

Basic principles

The model is based on a modelling approach developed by Buchmann et al. (2011). We extended this approach by including perceived predation risk. The model is individual-based (Grimm and Railsback, 2005) and uses the body mass as a main trait of individuals. By applying allometric relationships further traits such as energy requirements and locomotion costs can be calculated. Individuals choose a home range in the landscape depending on food availability, predation risk, physiological parameters and foraging strategies. The home range search is based on principles from optimal foraging theory, the area-minimizing principle (Mitchell and Powell, 2004) and the trade-off between foraging and predation risk (Brown, 1988). The model provides insights how adapted space use on the individual level due to different behavioral strategies, food and predation risk distributions affects community structures.

Emergence

Community structure and composition emerges from the group of individuals that successfully established a home range in the landscape. Home range establishment is driven by individual traits, food availability and predation risk in the landscape.

Adaptation

The decision of individuals which cell they add to their home range is driven by a trade-off between food availability and perceived predation risk in a cell. Individuals add cells with minimum predation risk and maximum food availability to their home range in order to achieve a high food gain with minimum costs. Depending on their foraging strategy, individuals adapt the food intake (risk-averse) or the movement activity (risk-taking) according to the predation risk in a cell.

Objectives

Animals aim to satisfy their energy requirements with the smallest possible home range (area-minimizing-principle, Mitchell and Powell, 2004). Therefore, they add cells with the maximum food gain to their home range which is achieved in cells with a high food availability and a low predation risk.

Sensing

Individuals sense the food availability and the predation risk in the eight neighbouring cells to their current location.

Interaction

Individuals indirectly interact via resource competition during community assembly. By consuming resources after a successful home range search, individuals decrease the food availability in the landscape leaving less food resources for following individuals. We thus do not include territorial behavior, i.e. individuals do not defend territories.

Stochasticity

Landscape generation and the selection of body masses from the input distribution is stochastic. To account for this variability, 30 replicate simulations are executed for each scenario. During home range search animal decisions can be stochastic if several cells have the same suitability. In these cases, the incomplete knowledge of individuals about the landscape is the reason for stochasticity.

Observation

The values of all state variables of the landscape cells are collected at the beginning and the end of a simulation. Individual traits, home range sizes and cells within the home range are collected at the end of a simulation.

Initialization

Before each simulation a new landscape is generated and general model parameters are initialized (

Tab. A.2). The landscape is characterized by the distribution of food resources and perceived predation risk. Landscape cells can be either productive i.e. they contain food that can be consumed by animals or they are non-productive and do not contain food resources. We assume that 30% of the landscape cells contain food. Productive food cells are distributed randomly in the landscape. Each productive cell initially contains food resources reflecting the average daily productivity in grass- and shrublands ($0.685g/(m^2 \cdot day)$, Whittaker, 1975). From these food resources, we assume that 80% of the food resources are lost to other taxonomic groups or not suitable for animal consumption so that only 20% of the average daily productivity can be used by prey animals (see Buchmann et al., 2011 for further discussion on this value). Food resources are exploited by animals during the simulation leading to a decrease in food availability and variation in the amount of food resources in the productive cells. Besides the productivity, cells either have a high predation risk (p-safety = 0.1) or a low predation risk (p-safety = 0.9). All non-productive cells have a high predation risk because we assume that a lack of vegetation corresponds with high predation risk. Productive cells can have a high or a low perceived risk of predation. In the following, we use the term “risky habitat” for productive cells with a high perceived predation risk and “refuge” for productive cells with a low perceived predation risk. The proportion of refuges is a systematically tested model parameter. We assume that the landscape of fear is static, i.e. the predation risk in the cells does not change during the simulation.

The main characteristic of the individuals in the model is their body mass. This is chosen from a "body mass input distribution", a truncated power-law distribution defining the probability density of a specific body mass (Buchmann et al., 2011, 2012). The body mass input distribution represents the regional species pool. It defines possible body masses for the individuals as well as their density. Additionally, the length of a simulation run is initialized. It is defined by the number of individuals that are consecutively not able to establish a home range (nfail).

Tab. A.2: Initialized parameter values of the model.

Parameter	**Value**	**Unit**	**Description**
Food resources in productive cell (*p-food*)	0.548	Dry biomass, g/cell	20% of the average productivity in grass- and shrublands (Whittaker, 1975; Buchmann et al., 2011)
Number of failed individuals (*nfail*)	100	-	Number of individuals that consecutively failed to find a home range in the landscape, used to stop the simulation
Body mass input distribution	M^{expo}	M in kg	Truncated distribution from which body masses of individuals are chosen
Exponent (*expo*)	-1.5	-	Exponent that yields realistic community structures (Buchmann et al., 2011)
Lower boundary (*lowB*)	0.01	kg	Lowest possible body mass of individuals
Upper boundary (*upB*)	1	kg	Highest possible body mass of individuals

Input data

The model does not include any external input.

Submodels

Trait assignment

In each step of the model a new individual is created. Individuals are characterized by different traits, mainly by their body mass and their foraging strategy. The body mass of the individual is drawn from a truncated body mass input distribution (see 5. Initialization). Similar to the model by Buchmann et al. (2011), allometric relationships are used to calculate further traits (Tab. A3). We assume that individuals are central place foragers frequently returning to a central place, their den. The den is an absolute refuge where individuals do not face predation risk. A further characteristic of individuals is their foraging strategy under predation risk. Foraging animals need to balance energy intake against predation risk, especially if profitable patches have a higher predation risk than less profitable patches (Lima, 1998). Common responses of animals foraging under predation risk are adaptations in space use and/or activity levels (Lima, 1998). To explore the effects of different strategies we here implemented two exemplary foraging strategies under predation risk and compare them to a control foraging strategy in which animals do not respond to predation risk in the landscape i.e. their food intake only depends on food availability and physiological constraints. The rationale of these two strategies is described in the following; their implementation is described below, in the processes home range formation and food consumption.

The foraging strategy of risk-averse individuals focuses on adaptations in food intake between patches with different predation risk. Risk-averse animals show a reduced food intake in risky habitat patches to minimize the time they are exposed to this high risk. To compensate the lower food intake under high risk, they forage more intensively in refuges and show an increased food intake in these patches compared to control individuals. An example for such a foraging strategy are gerbils, which reduce foraging in open areas under the presence of owls and shift their foraging activities to bush areas that offer cover (Kotler et al., 1991). Similar patterns were shown for other small mammals (Simonetti, 1989; Jacob and Brown, 2000) and fish (Werner et al., 1983; Rozas and Odum, 1988).

Risk-taking individuals deal with predation risk by adapting their activity patterns. In risky habitat, risk-taking animals show short foraging bouts with frequent returns to the den and hiding in refuges in order to minimize encounters with a predator. These behaviors increase the energy costs of risk-taking animals under high predation risk. In refuges, risk-taking individuals have the same activity patterns as animals of the control. Exemplary for this strategy are birds that directly fly to cover when detecting a predator (Schneider, 1984) or animals that carry food item to their home to reduce the time they are exposed to the predator (Lima, 1985; Lima et al., 1985).

Tab. A.3: Allometric relationships used to calculate further traits of the individuals. M is the body mass of the individual in g.

Trait	Allometric relationship	Unit	Description and references
Feeding rate (*i-feedrate*)	$0.323 \cdot M^{0.744}$	Dry biomass, g/day	Least amount of food that individual needs to gain from home range cells for successful search Nagy (2001)
Locomotion costs (*i-lococost*)	$\frac{0.0976 \cdot M^{0.68}}{14 \cdot 10^{3}}$	Dry biomass, g/m	Costs of individual for moving from one place to another Garland (1983); Calder (1996); Nagy (2001)
Magnitude of food exploitation (*i-foodshare*)	$\gamma \cdot M^{-0.25}$	-	Fractal characteristics affect the resolution at which individuals can exploit resources, γ was set to 1 Haskell et al. (2002); Buchmann et al. (2011)
Maximum home range size (*i-maxhr*)	$0.0138 \cdot M^{1.18}$	ha	used as a constraint for home range size, if *i-maxhr* is larger than the landscape size, it is set to the landscape size Kelt and Van Vuren (2001)

Home range search

The key process of the model is the home range search of the newly created individual. The home range needs to contain enough food resources to cover the individual's feeding rate and movement costs. We assume individuals to be central place foragers frequently returning to a central place, their den, within their home range. This is implicitly represented in the model by calculating the movement costs for the distance to a cell and the return. The home range search starts with the choice of a core cell, the central place of the home range where the den of the animal is located. This cell is chosen randomly from the pool of productive cells. The addition of a cell to the home range consists of two steps, the choice of which cell is added and the calculation of the food gain from the cell. The cell that is added next to the home range is chosen from the neighboring cells of the cell that was added last to the home range. We assume that the animal has a perceptual range of one cell, i.e. it can sense the food availability and the predation risk in the neighboring cells. For the decision, which of these cells is added to the home range the suitability of a cell is calculated by the product of food availability and predation risk:

$$\text{Suitability} = \textit{p-food} \cdot \textit{p-safety} \tag{A.1}$$

The cell with the highest suitability is added to the home range. For the control, only the food availability is taken into account (Suitability = *p-food*). If several cells have the same suitability, the cell with the minimum distance to the core is chosen.

After the decision for a cell, the food gain from this cell is calculated. The food gain is the difference between the exploited food and the movement costs:

$$\text{Food gain} = \text{Exploited food} - \text{Movement costs} \tag{A.2}$$

The amount of exploited food is the arithmetic product of food availability in the cell (p-food) and the individual magnitude of food exploitation (*i-foodshare*). For risk-averse individuals predation risk additionally affects food intake. For the different foraging types exploited food is calculated by:

Control:	Exploited food = $\textit{p-food} \cdot \textit{i-foodshare}$	(A.3a)
Risk-averse:	Exploited food = $\textit{p-food} \cdot \textit{i-foodshare} \cdot 2 \cdot \textit{p-safety}$	(A.3b)
Risk-taking:	Exploited food = $\textit{p-food} \cdot \textit{i-foodshare}$	(A.3c)

The factor 2 in eq. A3b was chosen so that the food intake at a medium predation risk (*p-safety=0.5*) equals the food intake of the control.

Movement costs are the product of the allometric costs and twice the distance to the core cell as the individual has to move to the foraging cell and back to the central place. In risk-taking individuals, high predation risk additionally affects movement costs. Movement costs for the the foraging types are calculated by:

Control:	Movement costs = $2 \cdot \textit{i-lococost} \cdot \textit{distance}_{core}$	(A.4a)

Risk-averse:	Movement costs = $2 \cdot \textit{i-lococost} \cdot \textit{distance}_{core}$	(A.4b)
Risk-taking:	Movement costs = p-safety ≥ 0.5: $2 \cdot$ i-lococost $\cdot$ $\text{distance}_{\text{core}}$ p-safety < 0.5: $2 \cdot$ i-lococost $\cdot$ $\text{distance}_{\text{core}}$ +p-food $\cdot$ i-foodshare $\cdot$ (1−2 $\cdot$ p-safety)	(A.4c)

Movement costs in risk-taking individuals increase depending on the amount of food in the cell. We assume that the higher the food intake the more often the individual interrupts foraging to return to the den. In refuges (*p-safety* ≥0.5*)* risk-taking individuals have the same movement costs as risk-averse and control individuals. Exemplary calculations for the different foraging types during home range search are shown in Tab. A4.

If the food gain from the added cells to the home range meets the daily energy requirements and the movement costs of the animal for foraging in the cells of the home range, the home range search is successful and the individual establishes its home range in these cells. If the amount of cells exceeds the maximum home range size before the energy requirements are achieved, the individual fails to find a home range and is excluded from the community, i.e. we assume that it disperses to another landscape part or dies.

Tab. A.4: Example calculations of suitability, exploited food movement costs and food gain for refuges and risky habitat and varying amount of food for the different foraging strategies. Calculations are based on an individual with a body mass of 50g. Exploited food, movement costs and food gain are given in g dry biomass.

	Control	**Risk-averse**	**Risk-taking**
Suitability			
p-food: 0.5 *p-safety*: 0.1	0.5	0.05	0.05
p-food: 0.5 *p-safety*: 0.9	0.5	0.45	0.45
p-food: 0.05 *p-safety*: 0.9	0.5	0.045	0.045
p-food: 0.45 *p-safety*: 0.1	0.5	0.045	0.045
Exploited food			
p-food: 0.5	0.188	0.0376	0.188

p-safety: 0.1			
p-food: 0.5 *p-safety*: 0.9	0.188	0.338	0.188
Movement costs			
p-food: 0.5 *p-safety*: 0.1	$5.98 \cdot 10^{-4}$	$5.98 \cdot 10^{-4}$	0.151
p-food: 0.5 *p-safety*: 0.9	$5.98 \cdot 10^{-4}$	$5.98 \cdot 10^{-4}$	$5.98 \cdot 10^{-4}$
Food gain			
p-food: 0.5 *p-safety*: 0.1	0.187	0.037	0.037
p-food: 0.5 *p-safety*: 0.9	0.187	0.338	0.187

Food consumption

If the home range search was successful, food resources (*p-food*) of cells within the home range are reduced by the amount of exploited food calculated during the home range search. In the last cell it can occur that the calculated animal's resource gain is higher than the amount of resources needed to fulfill the feeding rate of the animal. In these cases only the amount needed to cover the feeding rate is subtracted from the total resource amount in the cell.

Community saturation

During the simulation more and more individuals establish a home range within the landscape and decrease the food resources. Due to the reduction of available food resources new individuals are less likely to establish a home range, i.e. the amount of cells added to the home range exceeds the maximum home range size before the energy requirements of the individual can be fulfilled. During the simulation the number of consecutively failing individuals is counted. The simulation stops if a specific number of individuals (*nfail)* have consecutively not been able to find a home range.