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Community consequences of foraging under fear

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Abstract

Non-consumptive effects of predators within ecosystems can alter the behavior of individual prey species, and have cascading effects on other trophic levels. In this context, an understanding of non-consumptive predator effects on the whole prey community is crucial for predicting community structure and composition, hence biodiversity patterns.

We used an individual-based, spatially-explicit modelling approach to investigate the consequences of landscapes of fear on prey community metrics. The model spans multiple hierarchical levels from individual home range formation based on food availability and perceived predation risk to consequences on prey community structure and composition. This mechanistic approach allowed us to explore how important factors such as refuge availability and foraging strategy under fear affect prey community metrics.

Fear of predators affected prey space use, such as home range formation. These adaptations had broader consequences for the community leading to changes in community structure and composition. The strength of community responses to perceived predation risk was driven by refuge availability in the landscape and the foraging strategy of prey animals. Low refuge availability in the landscape strongly decreased diversity and total biomass of prey communities. Additionally, body mass distributions in prey communities facing high predation risk were shifted towards small prey animals. With increasing refuge availability the consequences of non-consumptive predator effects were reduced, diversity and total biomass of the prey community increased. Prey foraging strategies affected community composition. Under medium refuge availability, risk-averse prey communities consisted of many small animals while risk-taking prey communities showed a more even body mass distribution.

Our findings reveal that non-consumptive predator effects can have important implications for prey community diversity and should therefore be considered in the context of conservation and nature management.

Keywords: predator-prey interactions, individual-based model, landscape of fear, home range, biodiversity, foraging

1. Introduction

Predators affect prey populations in two different ways: directly by consuming and indirectly by evoking fear (Brown et al., 1999; Lima, 1998). While it is clear that consumption has negative consequences for prey populations, the impact of fear is not that obvious. Prey individuals sensing the presence of a predator may respond with morphological changes, for example, the development of spines against being eaten in *Daphnia pulex* (Krueger and Dodson, 1981) or behavioral adjustments, such as increased vigilance behavior (Hunter and Skinner, 1998), alterations in group size (Creel and Winnie, 2005) or diurnal vertical migration (Stich and Lampert, 1981) in order to minimize predation risk. Additionally, fear effects can have profound consequences on ecosystem functioning due to cascading impacts on other species (Ripple and Beschta, 2004; Schmitz et al., 2004; Werner and Peacor, 2003). Due to the frequently reported losses of apex predators in many ecosystems (Estes et al., 2011), an understanding of indirect effects of predators on prey is of high importance to better understand and predict consequences for biodiversity and ecosystems.

Common behavioral adjustments of animals perceiving predation risk are modifications in space use during foraging. In order to understand these modifications the “landscape of fear” concept has been developed, consisting of visual maps that quantify the spatial distribution of predation risk (Laundré et al., 2010, 2001). Predation risk perception can be measured by using established methods such as giving-up densities (Brown, 1988) or vigilance patterns (Altendorf et al., 2001). In combination with information about food availability and locomotion costs landscapes of fear can help to decipher and predict animal movement decision (Gallagher et al., 2017). Furthermore, landscapes of fear can be integrated in basic ecological concepts, such as the link between bottom-up and top-down control (Laundré et al., 2014).

Adaptations in prey behavior due to perceived predation risk can have cascading effects on other species. These effects have been summarized under the term ‘behavior-mediated indirect interactions’ (Dill et al. 2003, Werner and Peacor 2003). Behavior-mediated indirect interactions occur in manifold ecological communities with quantitatively significant effects on community dynamics, often exceeding the impact of density-mediated effects (reviewed in Werner and Peacor 2003). Experimental analysis of behavior-mediated effects is often challenging due to difficulties of disentangling direct and indirect effects. Nevertheless, by using playbacks from a predator, the domestic dog, Suraci et al. (2016) could show that increases in fear reduce raccoon foraging on marine biota leading to cascading effects across multiple trophic levels in the intertidal food web. Thereby, fear of predators can act as an important ecosystem service that can structure communities and ecosystems (Ripple and Beschta, 2004).

To date, most studies on behavior-mediated effects of predators on their prey either focused on specific behavioral adaptations on the level of single individuals (e.g. Lima and Dill 1990, Kotler et al. 1991, Jacob and Brown 2000) or on consequences for other trophic levels (e.g. Beckerman et al. 1997, Dill et al. 2003). However, consequences of fear at the prey community level are largely unknown, despite their potential implications for conservation and management. Non-consumptive effects have been shown to have strong negative impacts on reproduction of the prey (Zanette et al., 2011) e.g. via maternal effects (Boonstra et al., 1998; Sheriff et al., 2010). Furthermore, non-consumptive effects can exist in prey communities even if direct predation is low or not present (Creel and Christianson, 2008). An understanding of community responses to predation risk and the underlying mechanisms behind them is therefore important to predict how changing predator abundance affects prey community structures.

In this study, we assessed the consequences of non-consumptive predator effects on prey community structure and composition. Given the challenge to scale up from the behavior of individuals to the whole community structure, we applied an individual-based mechanistic model of home range formation in a mammalian prey community where individual space use is based on the trade-off between food availability and predation risk. It extends a modelling approach by Buchmann et al. (2011) which has been successfully applied to explain community responses to habitat loss and fragmentation (Buchmann et al., 2013), the importance of individual foraging movement for community structure (Buchmann et al., 2012) and to generate realistic landscape patterns of biodiversity in the context of matrix suitability (Prevedello et al., 2016). The incorporation of fear in the model advances our understanding of the impact of predator-prey interactions on home range formation and the consequences for community structure and composition.

A key concept in our model is the premise that behavioral strategies of animals under predation risk can be expected to have consequences on prey community structure. Animals adjust the time they spend in local foraging patches and the amount of food they exploit from them in response to perceived predation risk. Animals can adopt different foraging strategies in order to minimize predation risk. Animals that use a risk-averse strategy reduce foraging in risky patches to decrease the probability of encountering a predator. To compensate for the reduced food intake in risky patches, animals increase foraging activities in safe patches. This adaptation in foraging activities represents a commonly observed pattern in many animals such as fish (Rozas and Odum, 1988; Werner et al., 1983) and small mammals (Jacob and Brown, 2000; Simonetti, 1989). For example, under the presence of owls several gerbil species increase their food intake in bush microhabitats in contrast to open habitats since they offer shelter from avian predators (Kotler et al., 1991). In contrast to the risk-averse foraging strategy, animals with a risk-taking foraging strategy utilize food resources both in risky and safe patches. Risk-taking animals reduce the probability of predation in dangerous patches by using shorter foraging bouts. These animals frequently use refuges or return to their den in order to escape from a predator. An example for this strategy are birds that directly fly to cover when detecting a predator (Schneider, 1984). By implementing contrasting foraging strategies of prey animals (risk-averse and risk-taking) in the model we assessed a possible spectrum of consequences of different strategies on the prey community in concert with landscape of fear effects.

Additionally to the foraging strategy of prey animals under predation risk, refuge availability in the landscape plays an important role. If available, prey animals frequently use refuges in order to reduce predation risk (Lima and Dill, 1990). In aquatic systems, refuges are known to alter the impact of predation risk and can affect prey population dynamics and coexistence (Orrock et al., 2013). By varying the amount of refuges in the landscape we assessed how prey community structures are affected by refuge availability.

Based on these premises, we specifically aim to assess the following hypotheses: (1) Perceived predation risk in the landscape impacting individual space use in prey species can shape prey community structures. (2) The interplay between the availability of high-quality refuges and foraging strategies of prey animals is a driving mechanism of prey community responses to predation risk.

2. Methods

2.1 Model overview

The model simulates home range formation in a mammalian prey community based on food availability and perceived predation risk. It aims to gain a mechanistic understanding about space use behavior under fear and its consequences for community structure and composition. As our model focuses on the indirect effects of predation on space use, it does not include the direct effects of predator-induced mortality on individuals or communities over time. The model predicts how individual changes in behavior can affect the structure and composition of prey communities, in turn allowing us to predict how non-consumptive predator effects can alter prey community metrics. It extends a successfully validated modelling approach developed by Buchmann et al. (2011) by integrating landscapes of fear and different foraging strategies of animals under predation risk. A detailed model description following the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2010, 2006) is provided in the Supplementary material, Appendix A. Here we only give an overview of the general model structure and processes.

The individual-based and spatially-explicit model includes two entities: (1) Landscape cells, which are described by their location, the amount of food resources they contain and the predation risk that animals perceive in this cell, and (2) prey individuals, which are characterized by their body mass and their foraging strategy under predation risk (Tab.1). The body mass is used to calculate physiological traits such as energy requirements per day and movement costs of prey individuals via allometric relationships. In this study we focus on small, herbivorous mammals with a body mass ranging from 10g to 1000g. Predators are not modelled explicitly, but are represented by the predation risk in the landscape cells i. e. the landscape of fear. We assume generalist predators such as eagles, buzzards, foxes or lynxes.

2.2 Landscape design

The landscape is characterized by the distribution of food resources and predation risk. The whole landscape comprises 100x100 cells with each cell representing $4m^2$. 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 and do not refill. Besides food resources, cells either have a high perceived predation risk (*p-safety* = 0.1) or a low perceived predation risk (*p-safety* = 0.9). All non-productive cells have a high perceived predation risk because we assume that a lack of vegetation corresponds with high perceived predation risk. This corresponds to landscapes in which animals have to cope with areas of hostile matrix in their home ranges which is typical for human-dominated landscapes such as clear-cuts in forests.

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. The distribution of perceived predation risk in the landscape represents the landscape of fear for the prey animals. We assume that the landscape of fear is static, i.e. the predation risk in the cells does not change during the simulation.

2.3 Foraging strategies

In the model we implemented two highly contrasting foraging strategies in separate model runs to explore a possible spectrum of consequences of different strategies on the prey community. We assume that individuals of both foraging strategies 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. Foraging strategies were tested separately, i. e. all individuals in a community had the same strategy. Moreover, we compared the two contrasting foraging strategies 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 process home range formation.

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 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. These animals are facing indirect costs of their antipredatory behavior via the costs of missed opportunities. 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. This behavior increases the energy costs of risk-taking animals in risky habitat. To cover the increased movement costs, they need to exploit more food resources to fulfill their daily energy requirements. In refuges, risk-taking individuals have the same activity patterns as animals of the control.

The two foraging strategies represent simplified behavioral strategies of animals foraging under predation risk. The risk-averse foraging strategy allows to explore the consequences of adaptations in food intake under perceived predation risk on prey communities while the risk-taking strategy focuses on consequences of increased movement costs due to perceived predation risk. By using these extreme and contrasting examples, we intend to gain a first overview of the spectrum of consequences that different foraging strategies have on prey community structures.

2.4 Process scheduling

Each simulation starts with the generation of a new landscape with a specific distribution of food and perceived predation risk. After the generation of the landscape, in each step of the model one additional new prey individual characterized by its body mass and foraging strategy searches for a home range in the landscape. The home range has to contain enough food resources to fulfill the animal’s energy requirements. If the individual finds a suitable home range, it exploits the food resources within the home range. Otherwise, the individual is excluded from the community, we assume that the individual disperses to another area outside the simulated landscape or dies. Existing individuals in the landscape are not affected by newly added individuals. The simulation continues until the community is saturated, i.e. 100 individuals (parameter ‘nfail’, see Supplementary material, Appendix A, Table A.2) have consecutively not been able to establish a home range in the landscape because they could not reach their energy requirements. In the following, we briefly describe the processes within the model (see Fig. 1 for an overview of processes in the model).

2.4.1 Trait assignment

In each model step a new prey individual characterized by its body mass and foraging strategy is created. The body mass of the new individual is drawn from a "body mass input distribution", a truncated power-law distribution with an exponent of -1.5 (see Supplementary material, Appendix A, Tab. A.2). This specific exponent was chosen since it yields realistic community structures (Buchmann et al., 2011, 2012). On the basis of the body mass further traits of the animal are calculated by using allometric relationships, namely the feeding rate, locomotion costs, maximum home range size and the share of food resources that is available to an animal per grid cell (see Supplementary material, Appendix A, Tab A.3). In addition to body mass, individuals are attributed a foraging strategy: either risk-averse, risk-taking, or control.

2.4.2 Home range search and food consumption

The key process of the model is the home range search of the newly created prey individual. The home range needs to contain enough food resources to cover the individual’s daily feeding rate and movement costs for foraging within the home range. Individuals are 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 individual 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 eight 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:

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

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:

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

For the control and the risk-taking individuals the amount of exploited food is the arithmetic product of food availability in the cell (*p-food*) and the allometric magnitude of food exploitation (*i-foodshare*).

$$\text{Exploited food} = \textit{p-food} \cdot \textit{i-foodshare} \tag{3}$$

For risk-averse individuals predation risk (*p-safety*) additionally affects food intake.

$$\text{Exploited food} = \textit{p-food} \cdot \textit{i-foodshare} \cdot 2 \cdot \textit{p-safety} \tag{4}$$

The factor 2 was chosen so that the food intake at a medium predation risk (*p-safety=0.5*) equals the food intake of the control. In safe cells (p-safety > 0.5), risk-averse animals have a higher food intake than risk-taking and control animals whereas their food intake is reduced in dangerous cells (p-safety < 0.5). The factor *i-foodshare* leads to different feeding efficiencies in mammals depending on their body size.

For control and risk-averse individuals movement costs are the product of the allometric costs (*i-lococost*) and twice the distance to the core cell ($distance_{core}$) as the individual has to move to the foraging cell and back to the central place.

$$\text{Movement costs} = 2 \cdot i\text{-}lococost \cdot distance_{core} \tag{5}$$

Risk-taking individuals have the same movement costs when predation risk is low (i.e. p-safety ≥ 0.5). However, high predation risk (p-safety < 0.5) causes additional movement costs for risk-taking individuals:

$$\text{Movement costs} = 2 \cdot i\text{-}lococost \cdot distance_{core} + p\text{-}food \cdot i\text{-}foodshare \cdot (1 - 2 \cdot p\text{-}safety) \tag{6}$$

Movement costs in risk-taking individuals thus 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. Furthermore, movement costs in this case can also include costs of other adapted behavior not related to movement such as increased vigilance. Exemplary calculations for the different foraging types during home range search are shown in Supplementary material, Appendix A, Tab. A.4.

If after adding a cell the food gain from the home range meets the daily energy requirements of the animal and the movement costs, the home range search was considered 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 area outside the simulated landscape or dies. 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. Due to fractal characteristics of food resources, animals only exploit a share of the available food resources in a grid cell and do not deplete food resources completely. Therefore, the individuals entering subsequently are able to include cells that already have been exploited, leading to overlapping home ranges. A visual representation of exemplary home ranges for animals with different foraging strategies is shown in Fig. 2.

2.4.3 Community saturation

As the simulation progresses, an increasing number of individuals establish home ranges and deplete food resources within the landscape. This reduction in available food means that new individuals are less likely to establish home ranges. Thus, the community becomes saturated. Simulations were stopped if 100 individuals have consecutively not been able to find a home range. The sequential failure of individuals indicates that most accessible food resources in the landscape have been exploited and a further establishment of home ranges was not possible.

2.5 Design and analyses of simulation experiments

All simulations were conducted in Netlogo 5.3.1 (Wilensky, 1999). To compare the effect of different foraging strategies with a control foraging strategy we performed simulations for risk-averse, risk-taking and control prey communities. All individuals in one simulation had the same foraging strategy. Furthermore, we varied the proportion of refuges in the landscape (from 0 to 1, with an interval of 0.1). 30 repetitions were performed for each combination of foraging strategy and landscape configuration. Model output included body mass, size and location of individuals that successfully established a home range in the landscape and food availability in the landscape cells at the end of the simulation.

To analyze the effect of body mass, initial food availability in the landscape and the proportion of refuges on the home range size we made additional simulations where only one individual established a home range in the landscape. We varied the body mass of the individual (from 10g to 1000g), the initial food availability in the landscape (by reducing the default food availability from 100 to 10% of the initial food availability) and the proportion of refuges in the landscape (from 0 to 100%). While varying one of these parameters, the others were kept constant, the body mass at 50g, the reduction in food resource availability at 0% and the proportion of refuges at 50%. For each combination 30 replicate simulations were conducted.

Statistical analyses were conducted in R version 3.3.2 (R Core Team, 2016). To calculate Shannon diversity, species richness and evenness the package vegan (Oksanen et al., 2017) was used. For the calculation of these community metrics prey individuals were categorized into species depending on their body mass. We used a total number of 100 species. The right border of the body mass interval (in g) representing a species was defined by $10 + S^{1.5}$ with S as the species number from 0 to 100. The left border of the interval was the right border of the previous species. The exponent 1.5 was chosen in order to cover the range of possible body masses in the model. Additionally, we calculated community metrics for evenly spaced body mass intervals and for 10 species. All body mass intervals and species numbers yielded similar results (see Supplementary material, Appendix B, Fig. B.1 for a comparison of community metrics of different body mass intervals and species numbers).

3. Results

3.1 Space use patterns

To gain a better understanding of individual home range formation we compared the addition of cells to the home range between control, risk-averse and risk-taking individuals (Fig. 2). Results show that all individuals avoided including non-productive cells in their home range since they could not gain food resources from these. Individuals of the control consecutively added productive cells closest to the home range core, often resulting in circular home ranges. Risk-averse and risk-taking individuals preferred refuges, although possibly located further away from the home range center. From refuges, individuals could gain more food (risk-averse) or had lower movement costs (risk-taking) than in risky habitat. If the home range contained risky habitat, risk-taking individuals needed to add more cells to their home range than risk-averse individuals to cover the increased movement costs in this habitat.

The individual's home range size was the result of the interplay between its traits and the landscape configuration (**Fehler! Verweisquelle konnte nicht gefunden werden.**). Traits influencing the home range size were the daily energy requirements, the movement costs per distance unit and the foraging strategy under predation risk. The first two traits were determined by the body mass due to allometric relationships. Home range size increased with body mass as the individuals had higher energy requirements and movement costs (**Fehler! Verweisquelle konnte nicht gefunden werden.**a). Risk-taking individuals had larger home ranges than risk-averse individuals and individuals of the control.

Additionally, the landscape configuration affected the home range size. An important factor determining home range size was food resource availability in the landscape. Simulations always started with the same food resource availability but due to the depletion of food resources by animals that already established a home range, individuals that were chosen later in the simulation found a lower food resource availability in the landscape. Since the depletion by animals varied across simulations we reduced the initial overall food resource availability in the landscape to analyze the effect of food availability on individual home range size and compare between different foraging strategies (**Fehler! Verweisquelle konnte nicht gefunden werden.**b). The reduction in food resource availability led to an increase in home range size. Again, home range sizes of risk-taking individuals were generally higher than for risk-averse and control individuals. Concerning individuals of the risk-averse and the risk-taking behavioral type, the proportion of refuges also had an effect on the home range size. With increasing proportions of refuges home range size decreased (**Fehler! Verweisquelle konnte nicht gefunden werden.**c). Risk-averse individuals showed a larger decrease in home range size than risk-taking individuals.

Beside effects on home range formation, the behavioral response of animals to risk had consequences for the landscape usage by prey animals (Fig. 4). The overlap of home ranges per grid cell in low-risk and high-risk areas differed between foraging strategies (Fig. 4a). Risk-averse communities showed a higher overlap of home ranges in risky habitat compared to refuges. The high food intake of risk-averse individuals in refuges caused a strong depletion of these resources. Consequently, these cells were occupied by few individuals (low density) profiting from the good resource conditions. Other individuals had to use risky habitat which could, due to the low food intake in these, be utilized by many individuals, resulting in a high overlap of home ranges in this area.

The reverse pattern was found in risk-taking communities although the difference between risky habitat and refuges was much smaller here. Risk-taking individuals had the same food intake in risky habitat and refuges. Due to the preference for refuges, which bear lower movement costs, the home range overlap was higher in these than in the risky habitat.

Furthermore, modified space use patterns of individuals due to the fear distribution had consequences for the exploitation of food resources in the landscape. The preference for refuges led to an unequal use of food resources in the landscape (Fig. 4b). Due to the increased foraging pressure in refuges, food resources were depleted to a higher degree (i. e. lower giving-up density) than food resources in risky habitat which had a higher giving-up density. This difference in depletion was more distinct for risk-averse individuals.

3.2 Community effects

The median body mass increased for both risk-averse and risk-taking individuals with the proportion of refuges indicating a shift in the community structure towards animals with a larger body mass (Fig. 5a). The increase was steeper in the community with risk-taking individuals than in the risk-averse for low proportions of refuges. For high proportions of refuges, the pattern was inverted, with a higher increase in median body mass of the risk-averse community compared to the risk-taking community. Furthermore, risk-averse communities reached a higher median body mass under high proportions of refuges compared to risk-taking and control communities.

Regarding the number of individuals in the community, risk-averse and risk-taking showed different patterns to increasing proportions of refuges (Fig. 5b). For the risk-averse community the number of individuals decreased with an increasing proportion of refuges, whereas it increased in the community of risk-taking individuals. The total biomass of the community represents the sum of the body mass of all individuals in the community. For the community of risk-taking and risk-averse individuals the total biomass increased with the proportion of refuges and in case of the risk-averse individuals even exceeded the total biomass of the control (Fig. 5c).

Similar to the total biomass and the mean body mass, Shannon diversity and species richness increased with the proportion of refuges (Fig. 5d, 5e). Risk-taking prey communities showed a higher diversity for medium proportions of refuges than risk-averse prey communities. If no refuges were present in the landscape, risk-averse prey communities had a higher diversity than risk-taking communities. For high proportions of refuges the diversity and species richness of risk-averse communities were higher than the control. The evenness of the risk-taking community decreased with the proportion of refuges and was generally higher than the evenness of the control (Fig. 5f). In contrast, the evenness of the risk-averse prey communities showed a U-shaped pattern with the smallest evenness at medium proportions of refuges.

In order to get further insights into the community structure we compared the distribution of body masses within the community for exemplary proportions of refuges (Fig. 6). The risk-averse and the risk-taking communities both showed a clear shift to smaller individuals accompanied by a loss of large individuals for low proportions of refuges (Fig. 6a). In these scenarios, the body mass distribution is similar to the body mass distribution of control communities that are facing a reduced initial food availability of 20% of the default availability.

With increasing proportion of refuges the body mass distributions of the communities approximated each other. For a proportion of 50% of refuges the risk-taking community was nearly equal to the control while the risk-averse community still showed a shift towards animals with smaller body masses (Fig. 6b). If all cells were refuges, the body mass distribution in the control, the risk-averse and the risk-taking community was approximately the same (Fig. 6c).

4. Discussion

In this study we investigated the consequences of non-consumptive predator effects on prey community metrics by using a mechanistic model of individual home range formation. The results support our hypothesis that perceived predation risk shapes prey community structure due to modifications in prey space use. Furthermore, the model gives insights into the role of refuges and foraging strategies of prey animals for prey community structure. The availability of refuges increased general community metrics such as total biomass, mean body mass, species richness and Shannon diversity. Foraging strategies of prey individuals affected the composition of the prey community by shifting the body mass distribution towards smaller individuals occurring in high abundances. This shift was more pronounced in risk-averse than in risk-taking prey communities especially for a medium proportion of refuges.

4.1 Foraging strategies under predation risk

We compared the performance of prey communities using two contrasting foraging strategies under predation risk. Risk-taking animals have increased movement costs in areas with risky habitat since they return more often to refuges in order to escape from predators. To cover the increased movement costs, risk-taking animals need to exploit more food to fulfill their daily energy requirements which results in larger home ranges. Home range overlap of risk-taking animals is slightly higher in refuges since they bear lower movement costs.

Due to the higher food requirements of risk-taking animals, fewer individuals could be supported by the available food resources in the landscape resulting in decreased biomass and species richness at the community level compared to risk-averse communities and the control.

In contrast to risk-taking prey, risk-averse animals face indirect costs of their antipredatory behavior via the costs of missed opportunities. Risk-averse individuals reduce their foraging in risky habitat and thus miss exploiting food resources in these parts of the landscape.

Individuals balance the reduced food intake in risky habitat with intensive foraging in refuges. This behavior caused strong competition for food resources in refuges and a fast depletion of these by only a few animals. Therefore, risk-averse communities show a low overlap of home ranges in refuges. In risky habitat, low food exploitation by risk-averse animals results in a high overlap of home ranges. In comparison to risk-taking prey communities, risk-averse communities showed a higher biomass and species richness since their antipredatory behavior only reduced the access to food resources but did not lead to additional energy costs.

Foraging strategies could be considered to be the result of different personality traits between individuals. The impact of individual differences in traits such as boldness and exploratory behavior on animal space use has been confirmed for many species (reviewed in Spiegel et al., 2017). For example, starlings that spend more time on the ground have larger home ranges compared to starlings that spend more time on perches (Minderman et al., 2010). This is similar to larger home ranges of risk-taking individuals in the model. Nevertheless, empirical studies have shown that animals often adapt their foraging decisions according to specific conditions (Lima, 1998). For example, hungry animals are more likely to use risky areas than well-fed animals (Gotceitas and Godin, 1991; Kohler and McPeek, 1989; Pettersson and Brönmark, 1993), i.e. they switch between a risk-averse and a risk-taking strategy depending on their internal state. Obviously, the implemented foraging strategies in the model do not allow for such an adaptive foraging behavior but they can give an initial overview about the spectrum of consequences that differences in foraging behavior can have. Further studies should refine the implemented foraging strategies by integrating more sophisticated trade-offs such as a direct feedback of perceived predation risk on the fitness of the animal and the possibility of adaptations in the behavior depending on the internal state and external conditions. Additionally, future studies could incorporate communities in which individuals follow different foraging strategies representing for example differences in personalities between individuals. This would allow to investigate which foraging strategies are favored under varying environmental conditions.

Regarding community composition, risk-taking communities consisted of animals with larger body mass and a more even body mass distribution but lower number of individuals compared to risk-averse communities. Risk-averse communities were more shifted towards small individuals occurring at high abundance. The high number of individuals in risk-averse communities caused a high species richness while the uneven distribution of body masses resulted in lower evenness and Shannon diversity compared to risk-taking communities. Differences in community composition of risk-taking and risk-averse communities shed first light on the question which foraging strategy prey animals should use to maximize their fitness. Under low refuge availability a risk-averse strategy is preferable for small animals since their low energy requirements allow them to forage only in the refuges. Large animals with high energy requirements should follow a risk-taking strategy since it allows them to use additional food resources from risky habitat patches.

4.2 Refuge availability

Changes in prey community structure emerged from modified home range formation on the individual level. Individuals integrated areas with the maximum food availability and the lowest predation risk in their home ranges. In the model we used landscapes of fear varying in the proportion of refuges to risky habitat in order to investigate the role of refuge availability for prey communities. On the individual level, prey home range sizes decreased with increasing availability of refuges (Fig. 3c). Within refuges, food gain of prey individuals was higher compared to risky habitat since they could exploit more food (risk-averse strategy) or had lower movement costs (risk-taking strategy). Therefore, the integration of refuges in the home range allowed animals to fulfill their food requirements by foraging in a smaller area.

The use of refuges is a common strategy among animals in order to minimize predation risk (Lima and Dill 1990). Many animals show modifications in their space use due to changes in the landscape of fear, either on the scale of shifting their home ranges to other areas or by adapting the space use within the home range. For example, wild boars respond to variation in predation risk during the hunting season by shifting their home ranges towards protected areas where hunting is not allowed (Tolon et al., 2009). Deer and black bears respond to increased predation risk with adaptations within the home range e. g. by decreasing the usage of ecotones and roads, respectively (Padié et al., 2015; Stillfried et al., 2015), the distance travelled and exploratory behavior (Marantz et al., 2016). Furthermore, refuge use leads to a heterogeneous distribution of food resources in the landscape. Due to the lower giving-up density in refuges food resources are depleted to a lower level compared to food resources in risky habitat (Fig. 4b). These differences in food resource exploitation can induce trophic cascades (Werner and Peacor, 2003).

On the community level, modifications in space use due to increased refuge availability had positive effects on prey community metrics, leading to higher species richness, diversity and total biomass. These results are in good agreement with empirical patterns found in coral reef fish assemblages showing increased species abundance and richness with refuge availability in reefs (Caley and St John, 1996; Hixon and Beets, 1993). Additionally, these results support the habitat heterogeneity hypothesis stating that environmental heterogeneity increases species diversity (Bazzaz, 1975). Increasing availability of refuges causes a heterogeneous distribution of fear in the landscape and therefore allows more species to coexist.

Moreover, refuge availability drives community composition in risk-averse and risk-taking animal communities. While there is a large difference in the number of individuals between risk-averse and risk-taking animals under low refuge availability, both communities show similar numbers of individuals under high refuge availability.

In risk-averse communities low food availability in risky habitat allows only small animals the establishment of a home range while large animals are not able to find enough food to cover their food requirements. With increasing refuge availability, more food becomes available. As a result, large animals can establish home ranges and replace small animals. Due to higher food requirements of large animals the number of individuals in the community decreases while median body mass increases.

By contrast, risk-taking animals face increased movement costs in risky habitat. Under low refuge availability these movement costs strongly increase the food requirements of the animals. Therefore, food resources in the landscape are depleted by fewer animals compared to risk-averse communities. With increasing refuge availability, movement costs decrease and more and larger animals can establish a home range in the landscape. Therefore, the number of individuals and the median body mass increase.

For high levels of refuge availability, biomass, diversity and species richness of risk-averse prey communities even exceeded the values of the control. The high availability of refuges allows risk-averse animals to use nearly the whole landscape so that competition for refuges is reduced. Due to the intensive foraging in refuges, risk-averse animals can exploit even more food than animals of the control. However, the consumption of food resources at such a high rate would in reality only be possible if food resources refill very quickly, otherwise it would soon lead to a breakdown of food resources. Cases of mesopredator release have shown strong increases in the population of mesopredators under the absence of predation risk from top predators accompanied by increased consumption of prey animals which can lead to the breakdown of prey populations (Elmhagen and Rushton, 2007; Ritchie and Johnson, 2009). Low levels of refuge availability led to a reduction of large animals and an increase of smaller animals in risk-averse and risk-taking communities compared to control communities. This shift towards animals with smaller body mass is similar to the shift that can be observed in control communities facing a decreased initial food availability. Similarities arise because the reduced food gain of risk-aware individuals in risky habitat is comparable to the food gain of control individuals in cells with a decreased food availability.

4.3 Scaling up from the individual level to the community level

Linking different hierarchical levels the model bridges the gap between behavioral and community ecology. In our model, patterns emerge from underlying processes, which is crucial to understand complex interactions in ecosystems (Cabral et al., 2017) and to tease apart effects of bottom-up vs. top-down control on biodiversity.

One reason why models often cover only one hierarchical level is the increasing complexity when integrating more levels (Grimm et al., 2017). Nevertheless, several examples show that it is possible to develop individual-based community models (e.g. for forests: Köhler and Huth 1998, for fish communities: Giacomini et al. 2009). The crucial point to reduce the complexity in such models is to find a way to represent all species in a community, and their interactions, with the same basic approach. In forest ecology, gap models (Botkin et al., 1972; Bugmann, 2001) have used this approach for decades. Animal community ecology has made progress in this direction, the key being a trait-based approach where species differ only in their parameterization, but not in their representation (Jeltsch et al., 2013b). In the presented model we further reduced complexity by using allometric relationships to calculate several physiological traits; again, this approach has been used in forest modelling for a long time.

Thus, individuals can be described only by their body mass and their specific foraging strategy under predation risk.

4.4 Possible extension of the model: Temporal variation in predation risk

The model predicts possible consequences of different landscapes of fear and foraging strategies on prey community structure emerging from adaptations in space use. However, the model focuses on spatial variation in predation risk and does not include temporal variation of that risk. The occurrence of temporal variation in risk is common in nature due to seasonal changes, varying light intensity during the lunar cycle or within a day (Dodson, 1990; Kotler et al., 1994; Werner, 1986). The risk allocation hypothesis states that animals should increase antipredator behavior during pulses of high risk and allocate foraging activities to pulses of low-risk (Lima and Bednekoff, 1999). Several studies have shown temporal adaptations in animals to minimize predation risk, e.g. gerbils that show the highest foraging activities during the darkest hours of the night (Kotler et al., 1994) or elk that shift from diurnal to nocturnal activity to avoid hunters (Visscher et al., 2017). It can be expected that such temporal adaptations have effects on the community level since they can affect competition between prey animals arising from changes in activity times. For the integration of temporal variation in predation risk in the model it would be necessary to explicitly include time and allow modifications of home ranges after an individual has settled at a specific location, including the displacement of individuals with an established home range by other individuals. Depending on the time scale, it might also be necessary to include further processes such as reproduction, mortality and dispersal. Nevertheless, it has been shown that the static approach developed by Buchmann et al. (2011) that we used here can capture realistic features of community composition and structure (Buchmann et al., 2011; Prevedello et al., 2016).

4.5 Implications for empirical research and nature management

Our results reveal that perceived predation risk can shape prey community structures. Although adaptations in behavior and cascading effects on ecosystem functioning are widely known, risk effects on prey communities remain poorly studied (Creel and Christianson, 2008). A study on songbirds highlights the strong impact of perceived predation risk on reproduction (Zanette et al., 2011). Furthermore, landscapes of fear are expected to control the extent of bottom-up and top-down processes in prey populations (Laundré et al., 2014). Additionally, the concept of landscapes of fear can also be applied to apex predators. For example, a study by (Mech, 1977) showed that wolves are afraid of hunting close to the territories of neighboring packs. Thereby, they create buffer zones in which prey animals, such as deer can browse safely which can have cascading effects on the vegetation.

Since risk effects are difficult to assess empirically, a combination of empirical and modelling studies might prove useful to investigate the consequences of fear in different prey communities (Jeltsch et al., 2013a). Empirical studies can provide information about the basic principles from which differences in community structure emerge, such as the configuration of the landscape of fear or the foraging behavior of prey animals concerning their decisions on which locations they choose for their home range. By integrating this information, the model can be applied to specific prey communities and allows the prediction of community structures and composition. Vice versa, the model provides mechanisms that are important for shaping community structure that could then be tested in empirical studies.

The prediction of prey community structure under different conditions can prove useful since in many areas landscapes of fear are changing. Firstly, ecosystems face a loss of apex predators resulting in the loss of top-down control (Estes et al., 2011). Secondly, predators are reintroduced in ecosystems where they have been formerly present, leading to changes in the spatial distribution of prey animals which can affect other trophic levels (Kuijper et al., 2013). Thirdly, human activities affect the predation risk that animals perceive. These can be direct risk effects on hunted species (Bonnot et al., 2013; Tolon et al., 2009) or indirect effects on non-target species (Mori, 2017). Furthermore, human activities and disturbances create landscapes of fear for predators and prey, which can decrease the strength of non-consumptive effects on prey animals due to adaptive behavior of predators (Oriol-Cotterill et al., 2015) and in case of the prey often exceed the predation risk perceived from natural predators (Ciuti et al., 2012). Further research on the consequences for prey communities is necessary to estimate the effect of large predators on biodiversity.

5. Conclusions

The consequences of non-consumptive predator effects on prey communities are until now largely unknown since research focuses either on behavioral adaptations on the individual level (e.g. Altendorf et al. 2001, Martin et al. 2003) or on possible effects for other trophic levels and ecosystem functioning (Schmitz et al., 2004; Werner and Peacor, 2003). The presented model integrates behavior on the individual level with effects on the level of the prey community. This approach allows to link patterns at the community level with mechanistic processes on the individual level which is a central goal in ecology (Cabral et al., 2017). Our findings show that modifications in home range formation due to perceived predation risk shape prey community structures with important implications for biodiversity of the whole prey community. An understanding of the consequences of non-consumptive predator effects on prey communities is crucial under the current loss of apex predators in many ecosystems (Estes et al., 2011). Furthermore, anthropogenic land use and hunting modify existing landscapes of fear with potentially extensive consequences for animal communities (Kuijper et al., 2016). The model presented in this study helps to understand and evaluate the magnitude of general mechanisms such as refuge availability and foraging strategy affecting prey community responses under predation risk. Based on these results, further studies combining simulation models and empirical studies can be designed to evaluate the impact of non-consumptive predator effects on prey communities.

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Figures and Tables

Figures in high resolution are uploaded as separate files.

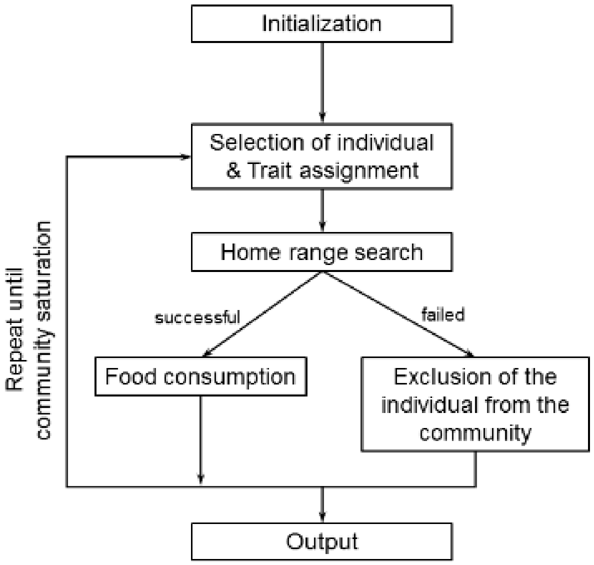


Fig. 1 Schematic overview of processes in the model. After initialization, a new individual is created and gets assigned certain traits. This individual searches for a home range in the landscape that fulfills its daily energy requirements. The addition of cells to the home range is based on food availability 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.

(Single column fitting image)

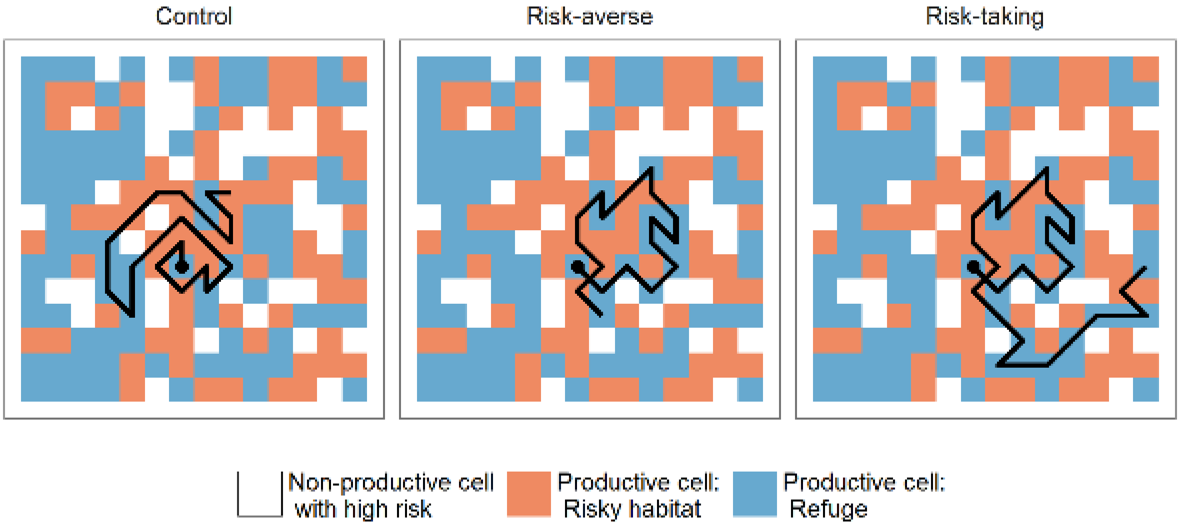


Fig. 2 Example of individuals with a body mass of 50g accumulating cells to their home range. The black dot marks the home range center, the line marks the cells that the individual one after the other adds to its home range. Risk-averse and risk-taking animals both prefer refuges but differ in the food intake and movement costs per cell, resulting in the addition of more cells to the home range for risk-taking animals. For the landscape a proportion of 50% refuges was chosen. All productive cells contained the same amount of food resources, 0.548g dry biomass per cell.

(2-column fitting image)

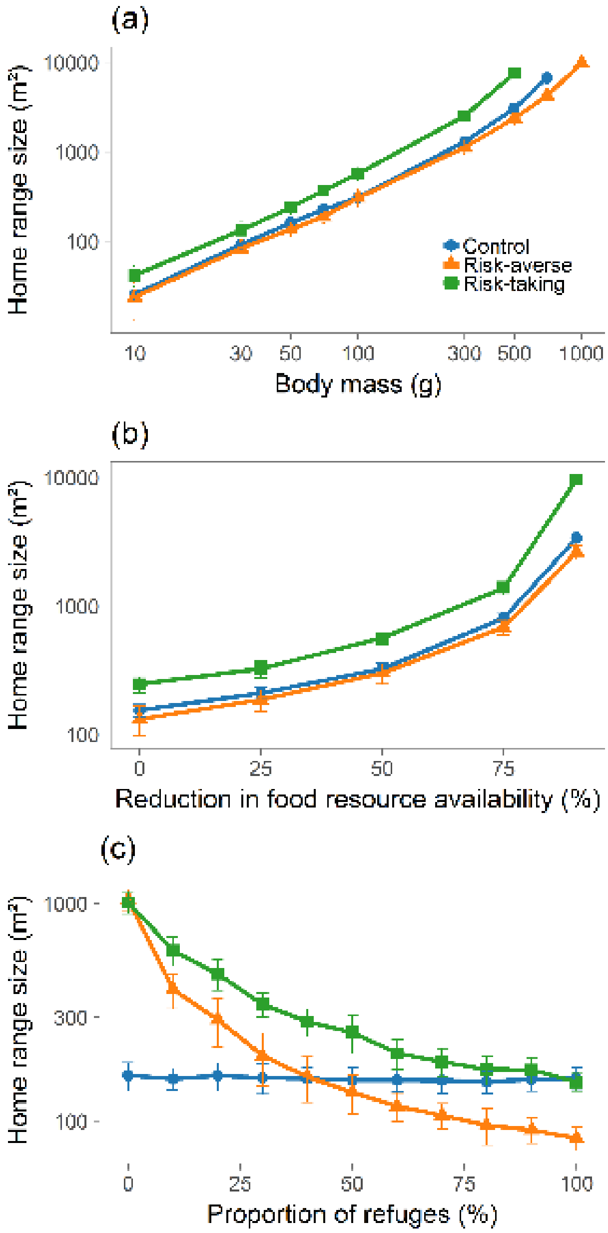


Fig. 3 Effect of body mass (a), resource availability (b), and the proportion of refuges (c) on home range size. The home range size of individuals is affected by the interplay of multiple parameters. To show these effects we analyzed the influence of single parameters on the home range of a single individual while keeping the others constant. The following constant values were chosen: Body mass of the individual: 50g (plot b, c); Food resource reduction: 0% (plot a, c); Proportion of refuges: 50% (plot a, b). Note the logarithmic scale on the y-axes and on the x-axis of plot (a).

(Single column fitting image)

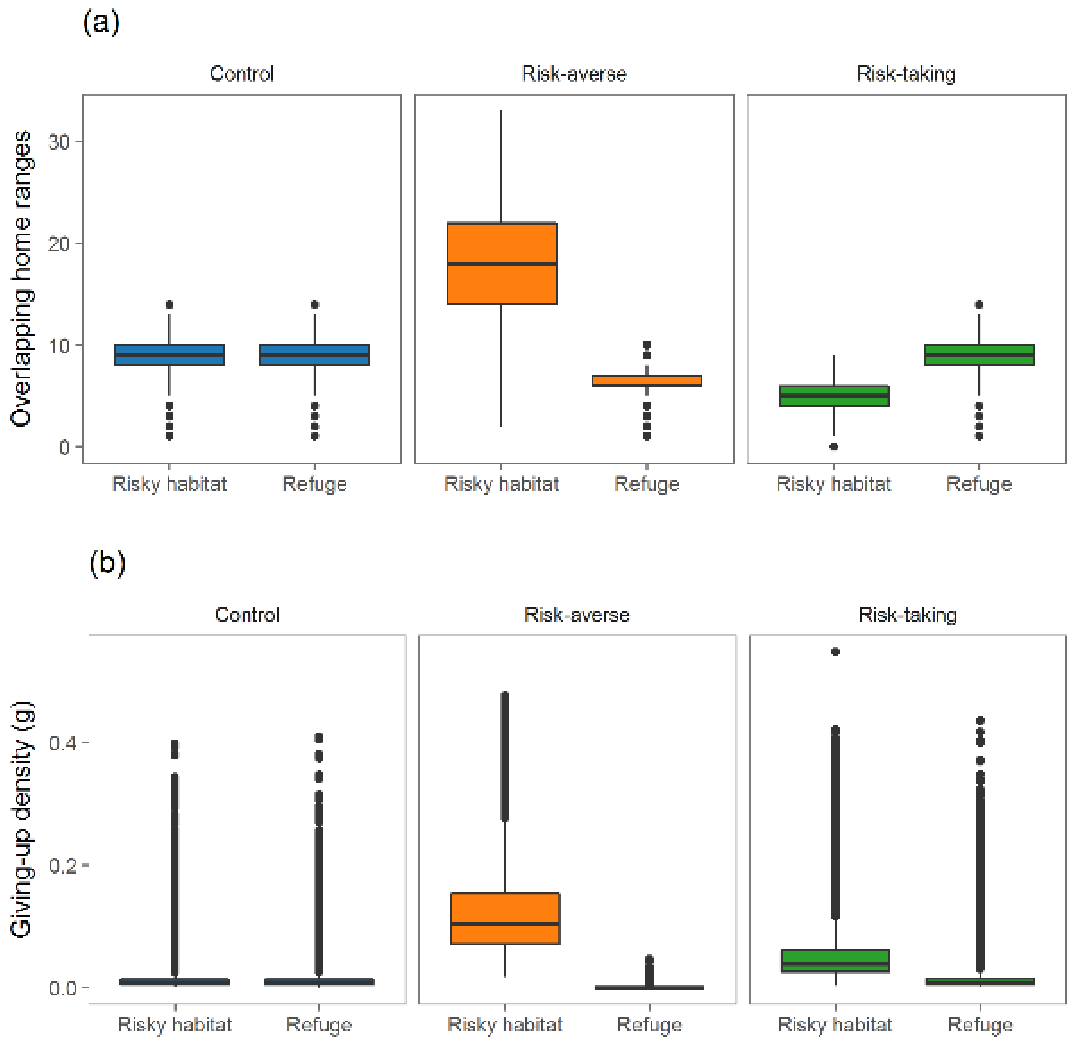


Fig. 4 Comparison between landscape usage in risky habitat and refuges. Figure 4a compares the number of overlapping home ranges per grid cell in risky habitat and refuges for the three different foraging strategies. Figure 4b shows the amount of food resources that are left in risky habitat respectively refuges at the end of the simulation. This represents the food density at which individuals cease including cells in their home range since it is not efficient anymore and is similar to the giving-up density which is often used in field experiments. A proportion of 50% refuges in the landscape was used. Boxplots show the pooled distribution of the number of overlapping home ranges (a) or giving-up density (b) for all 30 repetitions. Black dots represent outliers of the distribution.

(2-column fitting image)

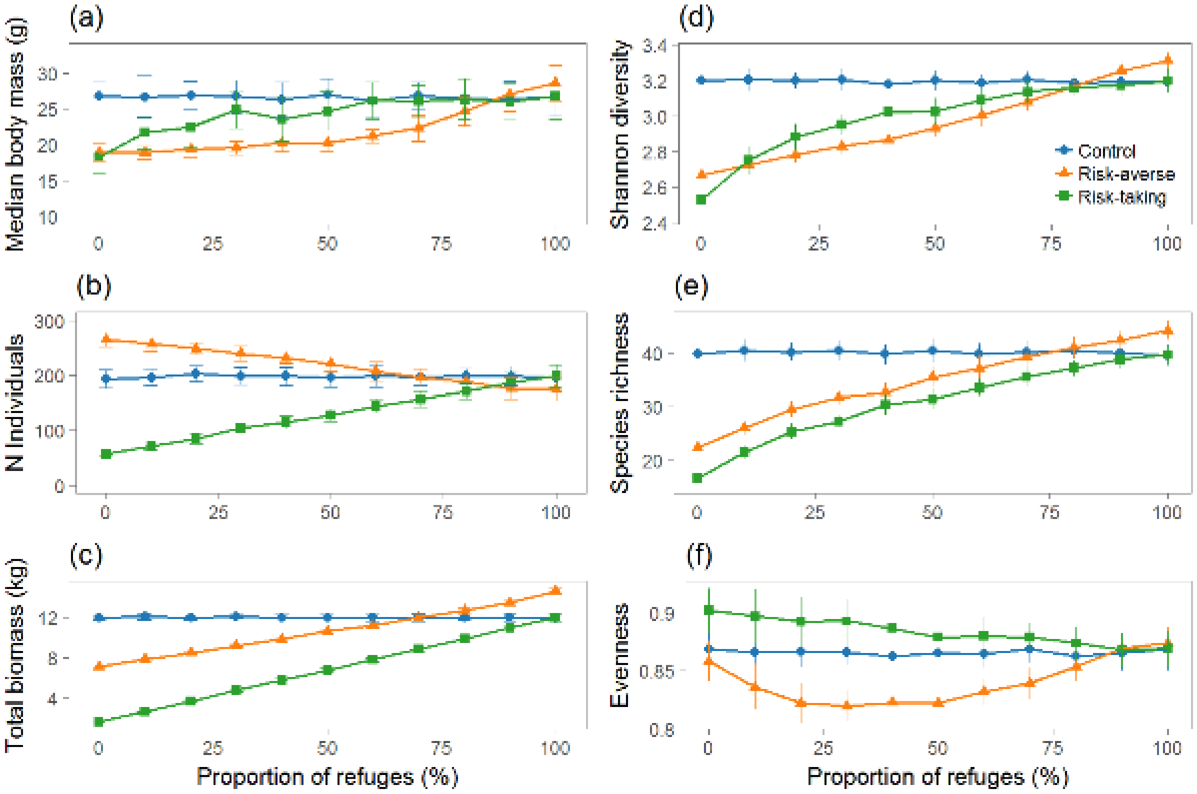
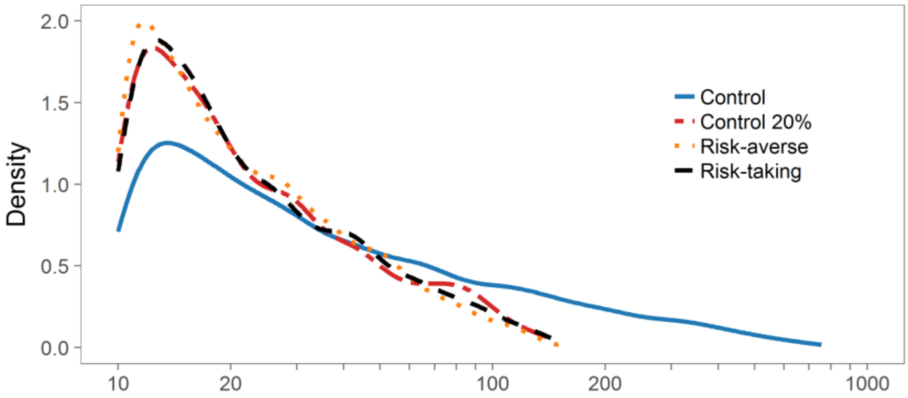


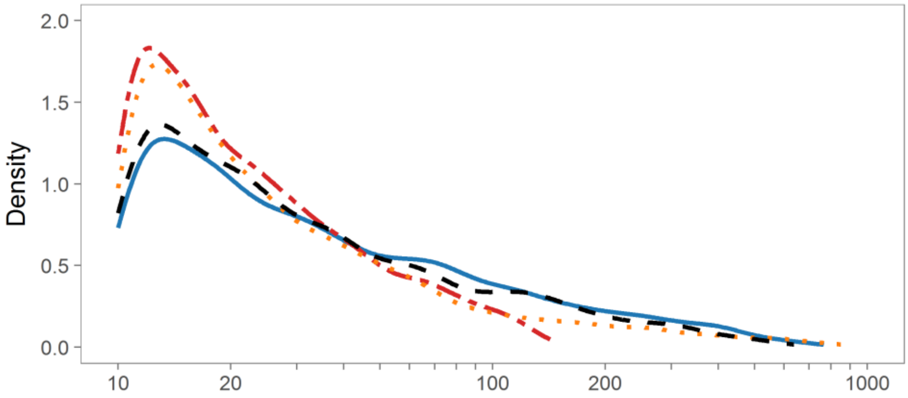
Fig. 5 Changes in general community metrics over the proportion of refuges in the landscape. Results show the effect on the median body mass (a), the abundance (b), the total biomass of the community (c), Shannon diversity (d), species richness (e) and evenness (f) for different proportions of refuges in the landscape.

(2-column fitting image)

(a) 0% refuges



(b) 50% refuges



(c) 100% refuges

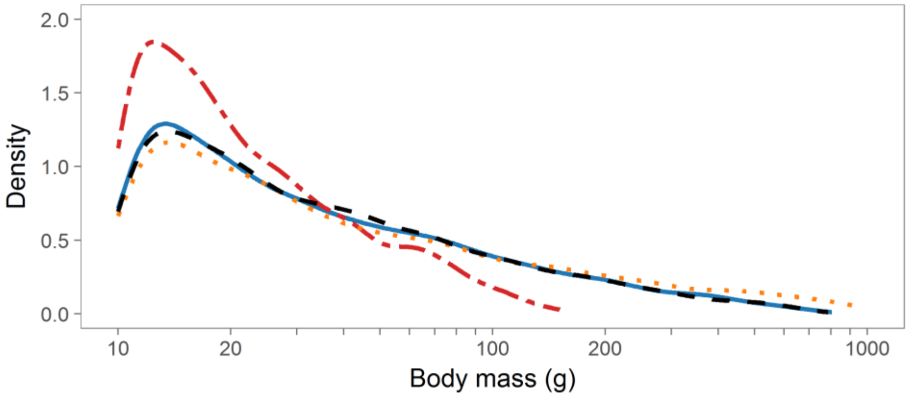


Fig. 6 Body mass distribution in the community for different proportions of refuges. To estimate the effects of overall habitat productivity on body mass distribution an additional control was added with a reduced initial food availability of 20% of the default food availability. Density plots show the relative occurrence of body masses in the community to compare distributions with different absolute body masses. Note the logarithmic scale on the x-axis.

(1.5-column fitting image)

Tab. 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

Declaration of interest: none

Supplementary material:

- Appendix A: ODD-Protocol
- Appendix B: Comparison of community metrics for different body mass intervals and species numbers.

References

Altendorf, K.B., Laundré, J.W., López González, C.A., Brown, J.S., 2001. Assessing effects of predation risk on foraging behavior of mule deer. J. Mammal. 82, 430–439. doi:10.1644/1545-1542(2001)082<0430

Bazzaz, F., 1975. Plant Species Diversity in Old-Field Successional Ecosystems in Southern Illinois. Ecology 56, 485–488.

Beckerman, A.P., Uriarte, M., Schmitz, O.J., 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. Proc. Natl. Acad. Sci. USA 94, 10735–10738. doi:10.1073/pnas.94.20.10735

Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F., Hewison, A.J.M., 2013. Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. Eur. J. Wildl. Res. 59, 185–193. doi:10.1007/s10344-012-0665-8

Boonstra, R., Hik, D., Singleton, G.R., Tinnikov, A., 1998. The impact of predator induced stress on the snowshoe hare cycle. Ecol. Monogr. 68, 371–394. doi:10.1890/0012-9615(1998)068[0371:TIOPIS]2.0.CO;2

Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Some Ecological Consequences of a Computer Model of Forest Growth. J. Ecol. 60, 849–872. doi:10.2307/2258570

Brown, J.S., 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behav. Ecol. Sociobiol. 22, 37–47. doi:10.1007/BF00395696

Brown, J.S., Laundré, J.W., Gurung, M., 1999. The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. J. Mammal. 80, 385–399. doi:10.2307/1383287

Buchmann, C.M., Schurr, F.M., Nathan, R., Jeltsch, F., 2013. Habitat loss and fragmentation affecting mammal and bird communities—The role of interspecific competition and individual space use. Ecol. Inform. 14, 90–98. doi:10.1016/j.ecoinf.2012.11.015

Buchmann, C.M., Schurr, F.M., Nathan, R., Jeltsch, F., 2012. Movement upscaled - the importance of individual foraging movement for community response to habitat loss. Ecography 35, 436–445. doi:10.1111/j.1600-0587.2011.06924.x

Buchmann, C.M., Schurr, F.M., Nathan, R., Jeltsch, F., 2011. An allometric model of home range formation explains the structuring of animal communities exploiting heterogeneous resources. Oikos 120, 106–118. doi:10.1111/j.1600-0706.2010.18556.x

Bugmann, H., 2001. A review of forest gap models. Clim. Change 51, 259–305.

Cabral, J.S., Valente, L., Hartig, F., 2017. Mechanistic simulation models in macroecology and biogeography: state-of-art and prospects. Ecography 40, 267–280. doi:10.1111/ecog.02480

Caley, M.J., St John, J., 1996. Refuge availability structures assemblages of tropical reef fishes. J. Anim. Ecol. 65, 414–428. doi:10.2307/5777

Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A., Boyce, M.S., 2012. Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. PLoS One 7, e50611. doi:10.1371/journal.pone.0050611

Creel, S., Christianson, D., 2008. Relationships between direct predation and risk effects. Trends Ecol. Evol. 23, 194–201. doi:10.1016/j.tree.2007.12.004

Creel, S., Winnie, J.A., 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Anim. Behav. 69, 1181–1189. doi:10.1016/j.anbehav.2004.07.022

Dill, L.M., Heithaus, M.R., Walters, C.J., 2003. Behaviorally Mediated Indirect Interactions in Marine Communities and Their Conservation Implications. Ecology 84, 1151–1157. doi:10.1890/0012-9658(2003)084[1151:BMIIIM]2.0.CO;2

Dodson, S., 1990. Predicting diel vertical migration of zooplankton. Limnol. Oceanogr. 35, 1195–1200. doi:10.4319/lo.1990.35.5.1195

Elmhagen, B., Rushton, S.P., 2007. Trophic control of mesopredators in terrestrial ecosystems: Top-down or bottom-up? Ecol. Lett. 10, 197–206. doi:10.1111/j.1461-0248.2006.01010.x

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S. a, Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D. a, 2011. Trophic downgrading of planet Earth. Science 333, 301–306. doi:10.1126/science.1205106

Gallagher, A.J., Creel, S., Wilson, R.P., Cooke, S.J., 2017. Energy Landscapes and the

Landscape of Fear. Trends Ecol. Evol. 32, 88–96. doi:10.1016/j.tree.2016.10.010

Giacomini, H.C., De Marco, P., Petrere, M., 2009. Exploring community assembly through an individual-based model for trophic interactions. Ecol. Modell. 220, 23–39. doi:10.1016/j.ecolmodel.2008.09.005

Gotceitas, V., Godin, J.-G.J., 1991. Foraging under the risk of predation in juvenile Atlantic salmon (Salmo salar L.): effects of social status and hunger. Behav. Ecol. Sociobiol. 29, 255–261. doi:10.1007/bf00163982

Grimm, V., Ayllón, D., Railsback, S.F., 2017. Next-Generation Individual-Based Models Integrate Biodiversity and Ecosystems: Yes We Can, and Yes We Must. Ecosystems 20, 229–236. doi:10.1007/s10021-016-0071-2

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R. a., Vabø, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. Ecol. Modell. 198, 115–126. doi:10.1016/j.ecolmodel.2006.04.023

Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: A review and first update. Ecol. Modell. 221, 2760–2768. doi:10.1016/j.ecolmodel.2010.08.019

Hixon, M., Beets, J.P., 1993. Predation , Prey Refuges , and the Structure of Coral-Reef Fish Assemblages. Ecol. Monogr. 63, 77–101. doi:10.2307/2937124

Hunter, L.T.B., Skinner, J.D., 1998. Vigilance Behaviour in African Ungulates : The Role of Predation Pressure. Behaviour 135, 195–211. doi:10.1163/156853998793066320

Jacob, J., Brown, J.S., 2000. Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. Oikos 91, 131–138. doi:10.1034/j.1600-0706.2000.910112.x

Jeltsch, F., Blaum, N., Brose, U., Chipperfield, J.D., Clough, Y., Farwig, N., Geissler, K., Graham, C.H., Grimm, V., Hickler, T., Huth, A., May, F., Meyer, K.M., Pagel, J., Reineking, B., Rillig, M.C., Shea, K., Schurr, F.M., Schröder, B., Tielbörger, K., Weiss, L., Wiegand, K., Wiegand, T., Wirth, C., Zurell, D., 2013a. How can we bring together empiricists and modellers in functional biodiversity research ? Basic Appl. Ecol. 14, 93–101. doi:10.1016/j.baae.2013.01.001

Jeltsch, F., Bonte, D., Pe'er, G., Reineking, B., Leimgruber, P., Balkenhol, N., Schröder, B., Buchmann, C.M., Mueller, T., Blaum, N., Zurell, D., Böhning-Gaese, K., Wiegand, T., Eccard, J.A., Hofer, H., Reeg, J., Eggers, U., Bauer, S., 2013b. Integrating movement ecology with biodiversity research - exploring new avenues to address spatiotemporal biodiversity dynamics. Mov. Ecol. 1, 6. doi:10.1186/2051-3933-1-6

Köhler, P., Huth, A., 1998. The effects of tree species grouping in tropical rain forest modelling Simulations with the individual based model Formind. Ecol. Modell. 109, 301–321. doi:10.1016/S0304-3800(98)00066-0

Kohler, S.L., McPeek, M.A., 1989. Predation Risk and The Foraging Behavior of Competing Stream Insects. Ecology 70, 1811–1825. doi:10.2307/1938114

Kotler, B.P., Ayal, Y., Subach, A., 1994. Effects of predatory risk and resource renewal on the timing of foraging activity in a gerbil community. Oecologia 100, 391–396. doi:10.1007/BF00317860

Kotler, B.P., Brown, J.S., Hasson, O., 1991. Factors Affecting Gerbil Foraging Behavior and Rates of Owl Predation. Ecology 72, 2249–2260. doi:10.2307/1941575

Krueger, D.A., Dodson, S.I., 1981. Embryological induction and predation ecology in Daphnia pulex. Limnol. Oceanogr. 26, 219–223. doi:10.4319/lo.1981.26.2.0219

Kuijper, D.P.J., de Kleine, C., Churski, M., van Hooft, P., Bubnicki, J., Jedrzejewska, B., 2013. Landscape of fear in Europe: Wolves affect spatial patterns of ungulate browsing in Bialowieża Primeval Forest, Poland. Ecography 36, 1263–1275. doi:10.1111/j.1600-

0587.2013.00266.x

Kuijper, D.P.J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K., Cromsigt, J.P.G.M., 2016. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. Proc. R. Soc. B. 283, 20161625. doi:10.1098/rspb.2016.1625

Laundré, J.W., Hernández, L., Altendorf, K.B., 2001. Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. Can. J. Zool. 79, 1401–1409. doi:10.1139/z01-094

Laundré, J.W., Hernández, L., Medina, P.L., Campanella, A., López-Portillo, J., González-Romero, A., Grajales-Tam, K.M., Burke, A.M., Gronemeyer, P., Browning, D.M., 2014. The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? Ecology 95, 1141–1152. doi:10.1890/13-1083.1

Laundré, J.W., Hernandez, L., Ripple, W.J., 2010. The Landscape of Fear: Ecological Implications of Being Afraid. Open Ecol. J. 3, 1–7. doi:10.2174/1874213001003030001

Lima, S.L., 1998. Nonlethal Effects in the Ecology of Predator-Prey Interactions. Bioscience 48, 25–34. doi:10.2307/1313225

Lima, S.L., Bednekoff, P. a., 1999. Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis. Am. Nat. 153, 649–659. doi:10.1086/303202

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640. doi:10.1139/z90-092

Marantz, S.A., Long, J.A., Webb, S.L., Gee, K.L., Little, A.R., Demarais, S., 2016. Impacts of human hunting on spatial behavior of white-tailed deer (Odocoileus virginianus). Can. J. Zool. 94, 853–861. doi:10.1139/cjz-2016-0125

Martin, J., Lopez, P., Cooper, W.E., 2003. When to Come Out from a Refuge : Balancing Predation Risk and Foraging Opportunities in an Alpine Lizard. Ethology 109, 77–87. doi:10.1046/j.1439-0310.2003.00855.x

Mech, L.D., 1977. Wolf-pack buffer zones as prey reservoirs. Science 198, 320–321. doi:10.1126/science.198.4314.320

Minderman, J., Reid, J.M., Hughes, M., Denny, M.J.H., Hogg, S., Evans, P.G.H., Whittingham, M.J., 2010. Novel environment exploration and home range size in starlings Sturnus vulgaris. Behav. Ecol. 21, 1321–1329. doi:10.1093/beheco/arq151

Mori, E., 2017. Porcupines in the landscape of fear: effect of hunting with dogs on the behaviour of a non-target species. Mammal Res. 251–258. doi:10.1007/s13364-017-0313-5

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. vegan: Community Ecology Package.

Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C., Macdonald, D.W., 2015. Landscapes of Coexistence for terrestrial carnivores: The ecological consequences of being downgraded from ultimate to penultimate predator by humans. Oikos 124, 1263–1273. doi:10.1111/oik.02224

Orrock, J.L., Preisser, E.L., Grabowski, J.H., Trussell, G.C., 2013. The cost of safety : refuges increase the impact of predation risk in aquatic systems. Ecology 94, 573–579. doi:10.1890/12-0502.1

Padié, S., Morellet, N., Hewison, A.J.M., Martin, J.L., Bonnot, N., Cargnelutti, B., Chamaillé-Jammes, S., 2015. Roe deer at risk: Teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. Oikos 124, 1536–1546. doi:10.1111/oik.02115

Pettersson, L.B., Brönmark, C., 1993. Trading off Safety against Food : State Dependent Habitat Choice and Foraging in Crucian Carp. Oecologia 95, 353–357. doi:10.1007/BF00320988

Prevedello, J.A., Gotelli, N.J., Metzger, J.P., 2016. A stochastic model for landscape patterns of biodiversity. Ecol. Monogr. 86, 462–479. doi:10.1002/ecm.1223

R Core Team, 2016. R: A Language and Environment for Statistical Computing.

Ripple, W.J., Beschta, R.L., 2004. Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? Bioscience 54, 755. doi:10.1641/0006-3568(2004)054[0755:WATEOF]2.0.CO;2

Ritchie, E.G., Johnson, C.N., 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecol. Lett. 12, 982–998. doi:10.1111/j.1461-0248.2009.01347.x

Rozas, L.P., Odum, W.E., 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. Oecologia 77, 101–106. doi:10.1007/BF00380932

Schmitz, O.J., Krivan, V., Ovadia, O., 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecol. Lett. 7, 153–163. doi:10.1111/j.1461-0248.2003.00560.x

Schneider, K.J., 1984. Dominance , Predation , and Optimal Foraging in White-Throated Sparrow Flocks. Ecology 65, 1820–1827.

Sheriff, M.J., Krebs, C.J., Boonstra, R., Sheriff, M.J., Krebs, C.J., Boonstra, R., 2010. The ghosts of predators past : population cycles and the role of maternal programming under fluctuating predation risk. Ecology 91, 2983–2994. doi:10.1890/09-1108.1

Simonetti, J. a, 1989. Microhabitat Use by Small Mammals in Central Chile. Oikos 56, 309–318. doi:10.2307/3565615

Spiegel, O., Leu, S.T., Bull, C.M., Sih, A., 2017. What’s your move? Movement as a link between personality and spatial dynamics in animal populations. Ecol. Lett. 20, 3–18. doi:10.1111/ele.12708

Stich, H.-B., Lampert, W., 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. Nature. doi:10.1038/293396a0

Stillfried, M., Belant, J.L., Svoboda, N.J., Beyer, D.E., Kramer-Schadt, S., 2015. When top predators become prey: Black bears alter movement behaviour in response to hunting pressure. Behav. Processes 120, 30–39. doi:10.1016/j.beproc.2015.08.003

Suraci, J.P., Clinchy, M., Dill, L.M., Roberts, D., Zanette, L.Y., 2016. Fear of large carnivores causes a trophic cascade. Nat. Commun. 7, 10698. doi:10.1038/ncomms10698

Tolon, V., Dray, S., Loison, A., Zeileis, A., Fischer, C., Baubet, E., 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. Can. J. Zool. 87, 1129–1137. doi:10.1139/Z09-101

Visscher, D.R., Macleod, I., Vujnovic, K., Vujnovic, D., Dewitt, P.D., 2017. Human risk induced behavioral shifts in refuge use by elk in an agricultural matrix. Wildl. Soc. Bull. 41, 162–169. doi:10.1002/wsb.741

Werner, E.E., 1986. Amphibian Metamorphosis : Growth Rate , Predation Risk , and the Optimal Size at Transformation. Am. Nat. 128, 319–341. doi:10.1086/284565

Werner, E.E., Gilliam, J.F., Hall, D.J., Mittelbach, G.G., 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64, 1540–1548. doi:10.2307/1937508

Werner, E.E., Peacor, S.D., 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84, 1083–1100. doi:10.1890/0012-9658(2003)084[1083:AROTII]2.0.CO;2

Whittaker, R.H., 1975. Communities and ecosystems. Macmillan.

Wilensky, U., 1999. NetLogo. http://ccl.northwestern.edu/netlogo/. Center for Connected Learning and Computer-Based Modeling, Northwestern University; Evanston; IL.

Zanette, L.Y., White, A.F., Allen, M.C., Clinchy, M., 2011. Perceived Predation Risk Reduces the Number of Offspring Songbirds Produce per Year. Science 334, 1398–1401. doi:10.1126/science.1210908