

# A “death trap” in the landscape of fear

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**Abstract** A crucial element in the “the landscape of fear” concept is that prey animals are aware of varying levels of predation risk at a spatial scale. This often leads to a negative spatial relationship between prey and predator in which prey avoid the most risky sites in the landscape. In this paper, we argue that our understanding of large carnivore-ungulate interactions is biased by studies from highly heterogeneous landscapes (e.g. the Yellowstone National Park). Due to a high availability of refuges and foraging sites in such landscapes, prey are able to reduce predation risk by showing habitat shifts. Besides the spatial heterogeneity at the landscape scale, the ungulate response to predation risk can be affected by the hunting mode (stalking vs. cursorial) of the predator. We propose that prey cannot easily avoid predation risk by moving to less risky habitats in more homogenous landscapes with concentrated food resources, especially where the large carnivores’ assemblage includes both stalking and cursorial species. No distinct refuges for prey may occur in such landscapes due to equally high accessibility to predators in all habitats, while concentrated resources make prey distribution more predictable. We discuss a model of a densely forested landscape based on a case study of the Białowieża Primeval Forest, Poland. Within this landscape, ungulates focus their foraging activity on small food-rich forest gaps, which turn out to be “death traps” as the gaps are primarily targeted by predators (stalking lynx and cursorial wolf) while hunting. No

alternative of moving to low predation risk areas exist for prey due to risk from wolves in surrounding closed-canopy forest. As a result, the prey is exposed to constant high predation pressure in contrast to heterogeneous landscapes with less concentrated resources and more refuge areas. Future research should focus on explaining how ungulates are coping with predation risk in these landscapes that offer little choice of escaping predation by considering behavioural and physiological (e.g. metabolic, hormonal) responses.

**Keywords** Anti-predator response · Behaviourally mediated risk effects · Ecology of fear · Habitat selectivity · Indirect predation effect

## Introduction

Avoidance of predation risk by animals is a widely accepted concept of the dynamic interactions between prey and their predators (e.g. Brown 1999; Verdolin 2006; Hammond et al. 2007; Hochman and Kotler 2007; Valeix et al. 2009b; Thaker et al. 2011; Burkepile et al. 2013; Laundré et al. 2013; Venter et al. 2014). Yet as prey species do not always have the chance to directly confront their predators, perception of predation risk should often rely on indirect cues. The awareness of various potential sources of mortality, including predation, should thus induce behavioural strategies in the prey, which are based on the trade-off between the need for acquiring food and the need for safety (Brown 1999). That prey animals are altering their habitat use or behaviour by trading the decrease in forage quality or quantity over the higher security from predation is well documented (e.g. Sih 1980; Creel et al. 2005; Kauffman et al. 2007; Barnier et al. 2014). However, the mechanism behind this trade-off is not easily understood. Among others, the components of risk can be differently

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perceived by various prey species (Burkpile et al. 2013), can vary with the hunting mode of the predators (Thaker et al. 2011; Bouskila 1995; Verdolin 2006) and be influenced by various environmental factors (Warfe and Barmuta 2004).

Intuitively, habitat structure may play an important moderating role during interactions between predator and prey. It may either facilitate or hamper both survival of the prey and hunting success of the predator. This has been empirically demonstrated for wolf (*Canis lupus*)–moose (*Alces alces*) (Kunkel and Pletscher 2000) and wolf–elk interactions (Kauffman et al. 2007). For the prey, some habitat characteristics, such as openness, can be positive with regard to foraging while negative with regard to predation risk (Brown 1999; Creel et al. 2005; Hernández and Laundré 2005; Hebblewhite and Merrill 2009; Rieucou et al. 2009). For the predator, the same traits may imply the abundance of prey as well as its low accessibility or catchability (Hopcraft et al. 2005). Little is known on how these relationships differ between areas with contrasting landscapes, i.e. heterogeneous landscapes offering a variety of refuges and foraging sites of different quality and homogenous areas consisting of a single habitat type with only highly concentrated food resources. The consequences of the landscape heterogeneity may be particularly important when the presence of predators is highly unpredictable, especially in case of large mammalian carnivores that typically move long distances in short time (e.g. Beier et al. 1995; Valeix et al. 2011). Here, the predator has an advantage over its prey since it may quickly move from one habitat patch to another choosing the best conditions for a successful hunt. As a result, the prey has imperfect knowledge of the predator's current whereabouts and the actual degree of risk at a certain location (Brown et al. 1999). That is likely the reason why the habitat features may constitute one of most important cues for prey species of potential predation risk (Brown et al. 1999; Laundré et al. 2001; Laundré et al. 2010). However, when the prey selects for sites with the highest escape probability, what should then be the most successful strategy for the predator? Should the predator focus on areas where the prey is more easily caught (e.g. Hopcraft et al. 2005) or on the areas with the highest chances of encountering it?

If the strategies of predators' detection and avoidance by prey as well as searching for and acquiring prey by predators are to be evolutionarily stable (Maynard Smith and Price 1973; Kriva and Cressman 2009), ideally the prey should seek patches richest in food and lowest in predation risk, and the predator should focus on sites where prey is most abundant and/or most vulnerable to predation (Sih 2005). What emerges from these ostensibly conflicting strategies is that it often leads to a negative relationship between the prey and predators' spatial distribution (Kunkel and Pletscher 2000; Orrock et al. 2004; Creel et al. 2005; Thaker et al. 2011). An experimental study on dragonfly–tadpole spatial

interactions revealed that when predators used a high resource patch more, prey used that patch less (Hammond et al. 2007). The outcome of these interactions in the wild may, however, depend on various factors including a behavioural interplay between predator and prey (Mitchell and Lima 2002). The spatial correlation between predator and prey among the Atlantic fish species was shown to be positive at larger scales and negative at smaller scales, and it was additionally affected by the presence of refuges (Rose and Leggett 1990). Negative spatial correlation of predator and prey may thus be more likely to occur in composite, spatially heterogeneous habitats as suggested by a study of a spider–*Collembola* system (Birkhofer et al. 2010). We expect that in vertebrates, these correlations may be more complex. Mathematical modelling based on “shell-game” theory showed that in systems with predators having good spatial memory, prey should randomize their foraging sites in order to decrease predictability of being encountered (Mitchell and Lima 2002). Accordingly, a recent field study in a wolf–caribou–moose system revealed completely different patterns of encounters for the predators with its prey and for the prey with its predator (Courbin et al. 2013) suggesting there is an asymmetry in relative probabilities of encounters between predators and prey. While there was a high risk of encountering wolves by caribou in a given land-cover type, there could be low probability of crossing caribou's path by wolves in the same area, relative to the time they spend there. It is thus not surprising that asymmetric encounter probabilities may work best in terrestrial heterogeneous ecosystems with clearly distinguished refuges such as the Yellowstone ecosystem where ungulate prey species showed a shift towards low-risk areas on a large scale once wolves returned to this system (Creel et al. 2005; Hernández and Laundré 2005; Fortin et al. 2005; Ripple and Beschta 2006).

Here, by analysing potential factors and conditions which may affect the observed outcome of predator–prey behavioural interactions, we present an alternative concept of responses of ungulates in relation to predation risk. First, we explore how (1) type of predator (cursorial versus stalking) and (2) spatial structure of landscape (patchy versus homogeneous distribution of resources) affect anti-predator behaviour of ungulates. Next, based on recent studies conducted in the densely forested Białowieża Primeval Forest (BPF), Poland, we present a new concept of the interactions between large carnivores and ungulates. As this area is composed primarily of forest habitat, we regard it as a relatively homogenous landscape as compared to well-studied systems in North America (Yellowstone) or African savannahs. In BPF, ungulates live under constantly high risk of predation which are present

virtually everywhere. Under these conditions, we argue that prey cannot easily escape predators in space as shown by many published studies from highly heterogeneous landscapes.

### Stalking versus cursorial hunting

Mammalian predators show two basic hunting modes—stalking (e.g. most of felids) and cursorial (e.g. most of canids). Each of these modes is linked to habitat structure in different ways and this may affect a recognizable landscape of fear for prey species. Predators with different hunting modes have been shown to have contrasting effects on prey (Schmitz 2005, 2008). Several recent studies have also suggested that a similar dichotomy in predator effects operate in large carnivore–ungulate ecosystems, with cursorial predators creating the weakest habitat-mediated fear effects (Kauffman et al. 2010; Thaker et al. 2011). Typical cursorial predators, such as wolves, are actively pursuing their prey and they do not require cover to surprise their target as the stalking predators. However, habitat features are linked to hunting success of both cursorial predators (Bergman et al. 2006; Kauffman et al. 2007) and for stalking predators (Hopcraft et al. 2005, Podgórski et al. 2008), but they seem to operate at different scales. The patterns of predation by cursorial predators are shaped by large-scale landscape heterogeneity (Kauffman et al. 2007). Thus, the predation risk cues they are producing are not easily predictable as they are not specifically connected to precise locations. In contrast, hunting activity of stalking predators is closely linked to fine-scale habitat features (Laundré and Hernández 2003; Podgórski et al. 2008) as they need to approach their prey at close distance undetected using habitat features such as a stalking cover. This results in more spatially predictable habitat-linked risk factors at a fine scale. Interestingly, there has been much attention for the effects of cursorial carnivores on the spatial distribution of their prey (for an overview, see Beschta and Ripple 2009), whereas the predicted much stronger indirect effects of stalking predators have been largely neglected (but see Thaker et al. 2011; Laundré et al. 2010).

If predation efficiency is driven by landscape variables, the same traits should affect the perception and response of the ungulates hunted by them when they have the possibility to learn. This concept has been supported by several studies. Elk, the major prey of wolves in the Yellowstone ecosystem, avoid open foraging areas when wolves were in close vicinity and searched for a refuge from predation in woodlands (Creel et al. 2005). Hence, ungulate prey do show large-scale movements resulting from risk effects created by cursorial predators. However, the study by Winnie et al. (2006) showed that the presence of predators may change the threshold of prey sensitivity to environmental conditions. Elk became temporarily

less responsive to habitat variables when wolves were present in comparison to times when they were absent. Other studies demonstrated that elk responded to wolf presence on a short time scale and changed behaviour or movement and grouping patterns (Creel et al. 2005; Creel et al. 2008; Liley and Creel 2008). In other words, prey may decrease its selectivity towards available low-risk habitats when there is an imminent threat of a being killed. This indicates that for a typical cursorial predator, prey is more likely to react to “risky times” resulting from actual presence of the predator, rather than “risky places” related to habitat features (Creel et al. 2008).

Even fewer studies exist on the importance of habitat characteristics in mediating the interactions between prey and stalking carnivores. It can be expected that when faced with predators which require cover for ambushing (e.g. Laundré and Hernández 2003; Hopcraft et al. 2005), prey species can detect predation risk based on indirect habitat cues with higher accuracy and predictability than with a cursorial predator. Therefore, the behavioural response of both predator and prey animals should be tightly linked to fine-scale habitat structure.

Schaller (1972), in his classic study, unequivocally showed that African lions (*Panthera leo*) did not evoke anxiety in prey animals until they remain in sight. In contrast, he noted that “prey is particularly cautious about entering thickets” (p. 235). Therefore, the lions’ presence alone is not enough to induce anti-predatory behaviour in the prey species. This concept was recently studied in detail by Valeix et al. (2009a, b), who clearly showed that many prey species of lions avoided using risky bush-lands and woodlands. Moreover, as lions concentrated their hunting activity around waterholes (Valeix et al. 2010), ungulates responded with behavioural adjustments to reduce predation risk in these risky sites (Valeix et al. 2009a). They reduced the use of waterholes at night when there was highest predation risk and increased their vigilance while drinking. These results show a high wariness in prey animals suggesting that the chance of a successful hunt by lions should decrease at the most attractive and well distinguishable sites. In fact, it was found that lions have higher hunting success in areas with good protective cover rather than in those characterized with a higher abundance of ungulates (Hopcraft et al. 2005; Loarie et al. 2013).

Although lions are typically stalking predators while hunting, they are often exceptionally conspicuous on other occasions, particularly during their social activities. Thus, the interplay of periods when lions disappear and come back into sight may give a good cue as to which prey can predict predation risk. We would then expect that yet stronger reliance on habitat structures as a cue of predation risk occurs in ecosystems with solitary stalking carnivores, which are hardly visible to prey. In line with this, Holmes and Laundré (2006) showed that pumas (*Puma concolor*) focused their foraging activity within forest edges, which resulted in the most successful hunting occurring there (Laundré

and Hernández 2003). This transitory habitat allowed pumas to ambush ungulates as they moved between forest and open patches. As a result, ungulates perceived higher predation risk in the edge habitat and responded by higher foraging activity in open habitat and higher vigilance at the forest edges (Altendorf et al. 2001). Similarly, it was found that leopards (*Panthera pardus*) were selecting habitats with sufficient vegetation cover for stalking prey, though not too dense to impede their chase, whereas their prey was most abundant in habitats characterized either by high visibility or by cover dense enough to prevent successful pursuit by leopard (Balme et al. 2007).

To conclude, one can expect that stalking, solitary predators rather than cursorial predators are more likely to generate consistent cues for predation risk which are strongly linked to fine-scale habitat characteristics and therefore clearly identifiable by prey animals. This can induce a situation in which prey show a shift in fine-scale habitat selection and increase their use of low-risk habitats. In other words, if the prey chooses sites with the lowest predation risk, the predator would be forced to hunt in areas with the lowest abundance of prey (Laundré 2010). However, the question is if such a strategy can guarantee the persistence of the predator's population. We agree with Laundré's (2010) hypothesis that the final outcome of these opposing strategies of the predator and prey can be notably influenced by the share of habitat types with different predation risk. Landscapes dominated by protective cover for ungulates (safe habitats) should promote a high prey–predator ratio (and high prey densities), whereas in landscapes dominated with risky habitats the opposite should be expected. Therefore, especially in ecosystems with stalking predators present, and habitat conditions favouring hunting success by predators, the prey may have little chance to avoid predation.

## Effects of the landscape structure

If the trade-off between the quality of a foraging patch and predator avoidance is one of the main mechanisms driving the habitat selection and spatial distribution of prey animals, one can expect that a similar strategy should be valid regardless of the type of ecosystem. However, the majority of empirical data originate from relatively heterogeneous and large North-American (e.g. Yellowstone, Zion, Banff National Parks) or African (Serengeti, Hwange NP) ecosystems. In such landscapes, the risky habitats and refuge areas for prey species are often clearly identifiable, even for researchers (Fig. 1). The low-risk patches for ungulates may consist of either places with good visibility and a long escape distance in case of stalking predators (e.g. Holmes and Laundré 2006) or with protective cover decreasing the probability of being detected by cursorial predators (Creel et al. 2005). In contrast, risky patches may be characterized by having structures which limit the possibility of the prey's escape or the visual assessment of the predator's presence and therefore facilitate ambush by a predator (Halofsky and Ripple 2008).

Heterogeneity of the environment has been proposed as the factor allowing the elk to reduce the risk of predation from wolves in the Yellowstone National Park (YNP; Kauffman et al. 2007). Surprisingly, elk are not necessarily avoiding even the riskiest locations in YNP (Fortin et al. 2005; Kauffman et al. 2007; Mao et al. 2005). Nevertheless, owing to the heterogeneity of habitats offering a range of food quality in combination with varying levels of predation risk within the park, elk are able to balance the predation risk and feeding requirements with various behavioural responses. These included either aggregation in open places, which facilitated the detection of predators and the lowering of predation risk by dilution effects (Mao et al. 2005), or switching habitat preferences at finer scale to safer habitats (Fortin et al. 2005; Thaker et al. 2011).



**Fig. 1** Two contrasting ecosystems with potentially different effects on creating the landscape of fear: *left*—Yellowstone National Park (photo courtesy of Dan Zachariah)—a heterogeneous landscape with clearly distinguishable foraging and refuge patches, USA; *right*—Białowieża

Primeval Forest, Poland (photo courtesy of Jan Walencik)—a relatively homogeneous landscape constituting a relatively uniform body of the forest with very concentrated foraging sites in small forest gaps. Both ecosystems are inhabited by large carnivores and ungulates



Although identifying qualitatively the levels of predation risk in strongly differentiated habitats does not seem to raise many difficulties, interpreting its effect on predator–prey relationships is not so obvious. Even more complex interactions may occur within more homogenous landscapes which are, as

yet, virtually unexplored. In such environments, risk may be more evenly dispersed over the landscape (Fig. 1). Moreover, the indirect cues of predation risk based on habitat features might primarily act at fine spatial scale (Kuijper et al. 2013, 2014; Wikenros et al. 2015).

#### Box 1. The use of forest habitat by two large carnivores in the Białowieża Forest

The Białowieża Primeval Forest (BPF) is a relatively large and compact forest complex (approximately 1,500 km<sup>2</sup>). The BPF constitutes a patch of forest habitat relatively clearly distinguished from the surrounding agricultural matrix. Despite of high diversity of tree communities (Faliński 1986), it consists mainly of forest habitat (80–90 %) with small gaps resulting from natural gap formation or small clear cuts. It is inhabited by two large predators, wolf and Eurasian lynx (*Lynx lynx*), and their main ungulate prey species red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*). Both predators almost exclusively reside within the main forest complex (Fig. 1) and avoid venturing into the surrounding open areas which are largely utilized as agricultural and rural lands. Therefore, most of the direct and indirect predator–prey interactions occur within a relatively homogenous environment consisting of closed forest.

Due to its size and continuous forest cover, the chance to encounter a wolf or lynx is relatively evenly spread in the area (both in space and time) and no predator-free areas can be found (Fig. 1). There are four packs of wolves and circa 20 lynx residing within the forest (Jędrzejewski et al. 2007; Schmidt 2008). Despite showing preferences for certain forest types, the ungulates are also distributed throughout the whole area of the forest. Distribution of both carnivores and deer largely overlapped within the BPF (Schmidt 2008; Theuerkauf and Rouys 2008). As these carnivores utilize very large home ranges (Schmidt et al. 1997; Herfindal et al. 2005) and move long daily distances, the access to prey is not limited spatially and temporally within the individual territory.

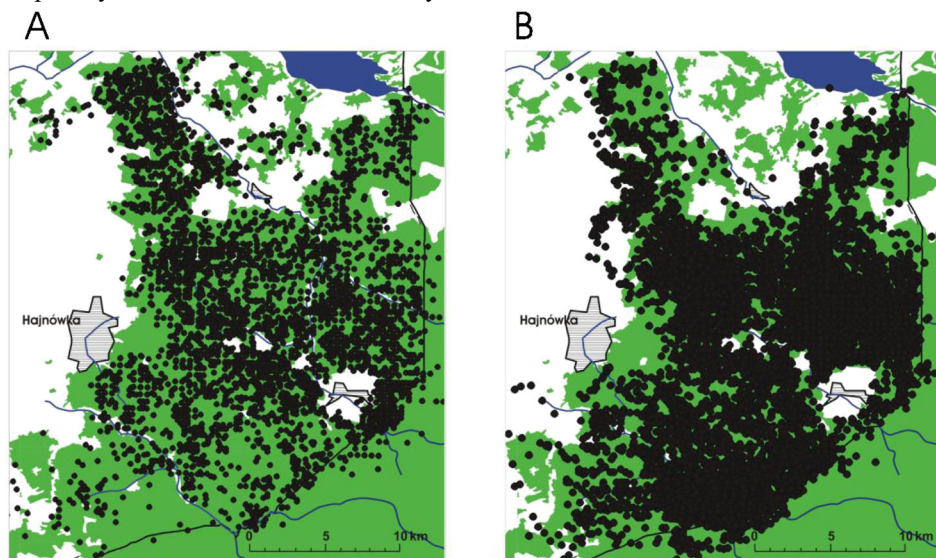


Fig. 1. Map of the Białowieża Primeval Forest, Poland, with radio-locations of lynx (A:  $n = 9,449$  locations of 25 individuals radio-tracked from 1992 to 2007) and wolves (B:  $n = 28,857$  locations of 8 individuals belonging to 4 packs radio-tracked from 1994 to 1999) showing the extensive use of available habitat by large carnivores (based on Schmidt et al. 2009). The area close to the village Hajnówka without locations for both lynx and wolf is a military area which is inaccessible to researchers. The least used south-western part of the forest by lynx has resulted from lower trapping efforts in that area. Meaning of the colours: *green*–forest; *white*–agricultural area; *grey*–villages; *blue*–lake.

Studies on the habitat selection of both large carnivores and ungulates in a densely forested ecosystem were conducted in the BPF, Poland (Box 1). Despite its rich composition at the scale of forest stands (forest types, vertical and horizontal forest stand structure), the entire area can be regarded as very homogenous at the landscape scale as it is all covered with forest habitat (lacking large river valleys, open grass planes, etc.) in contrast to well-studied systems in North America and Africa. This entire area is mainly composed of lowland mixed forest, with only 0.8–3 % of it covered with open habitats (Michalczyk 2001; Kowalczyk 2010). These open areas include marsh lands and small gaps in forest stand resulting from natural gap formation (inside the protected part of BPF—the Białowieża National Park, up to 1 ha of size) or removing a few trees ( $\leq 0.5$  ha) in the managed part of the forest. However, these gaps do not disrupt the general habitat homogeneity due to its small size as compared to the total available habitat (Fig. 1).

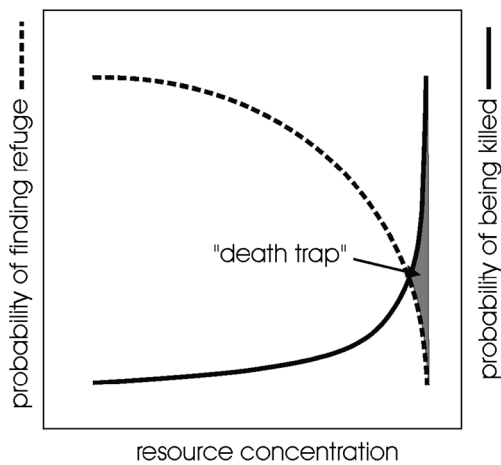
In this system, the stalking predator, Eurasian lynx (*Lynx lynx*), was found to hunt most successfully in the forest gaps; the lynx kills were located in these gaps 37 % more often than the random locations (Podgórski et al. 2008). Likewise, red deer killed by wolves were also found more often in open places than in closed forest (Theuerkauf and Rouys 2008). The choice of the forest gaps may be advantageous for the predator due to good view of the prey provided by the gaps while it approaches from the closed forest being concealed from the prey. At the same time, forest gaps in BPF are highly attractive foraging sites for ungulates which concentrate their foraging activity there (Kuijper et al. 2009). Gaps provide an abundance of forage due to the higher intensity of regeneration of woody browse and higher cover of herbaceous vegetation (Bobic 2007). As a result, patches with higher ungulate visitation and expected higher hunting success are very predictable for the predators in this system. Moreover, good foraging but high risk areas for ungulate prey is likewise very predictable. Ungulates likely have to concentrate foraging in these rich forest gaps, simply because food availability is very low under the surrounding closed canopy with sparse regeneration and low or lacking herbaceous vegetation cover.

Although intuitively correct, and in accord with the optimal foraging theory (MacArthur and Pianka 1966), the equal preference for gaps by predators and prey requires more attention. Stalking predators like lynx select for forest gaps because of higher prey encounter rate and higher chance for a successful ambush of their prey. Ungulate prey may be forced to select for these sites to forage as there is little tree regeneration under a closed canopy (Bobic 2007). Having no alternative low-risk high quality forage patches, ungulates are

facing “death traps” in the forest gaps as the probability of being killed is much higher while foraging there compared to in the closed canopy forest. Although evidences exist that prey animals are often trading the risk of being killed with better food quality (e.g. Cooper 2000; Kittle et al. 2008; Wilson et al. 2012), our example turns attention to specific circumstances where foraging under high predation risk is the best choice for prey animals. Whereas in heterogeneous landscapes prey may find habitats with varying levels of forage quality and quantity and refuges even within the areas highly used by wolves (Fortin et al. 2005), such behavioural responses may not be possible in more homogenous environments, such as a closed forest ecosystem with limited and small food-abundant patches and no refuge areas. While forest gaps are most successful hunting places for both lynx and wolf, the surrounding matrix is not devoid of the risk of being killed by wolves. Despite of the preferential use of forest gaps by deer in BPF (Kuijper et al. 2009), they cannot support long-term occupation by ungulates due to their small size. This contrast to heterogeneous landscapes with both forest and large open spaces, where prey aggregates for considerable amount of time in open habitat (Courant and Fortin 2012; Harvey and Fortin 2013). In our study area, deer use the forest gaps only for short periods of time, with each patch visited less than 2 min, meaning that most of the time they are present in closed forest habitat (Kuijper et al. 2009). Thus, ungulates in homogeneous habitats may experience two sources of predation risk—while foraging in the gaps (“death traps” targeted by both lynx and wolf) as well as while staying out for extended periods of time in the surrounding closed-canopy forest (where they are vulnerable to cursorial wolves). In homogeneous habitats which lack areas free from lynx and wolves (see Box 1) and with concentrated spots of food, prey animals are exposed to chronic high predation risk with little chance to avoid it. As the model of risk allocation hypothesis assumes that maintaining high vigilance under chronically high predation risk is impossible (Lima and Bednekoff 1999), the question becomes what mechanisms allow the prey animals to reduce the predation risk under such conditions is open, particularly because the majority of empirical data on that come from heterogeneous landscapes.

### Synthesis: living under chronic high predation risk in a homogenous environment

It is evident that animals have to trade-off between habitat forage quality and predation risk (Sih 1980; Hebblewhite

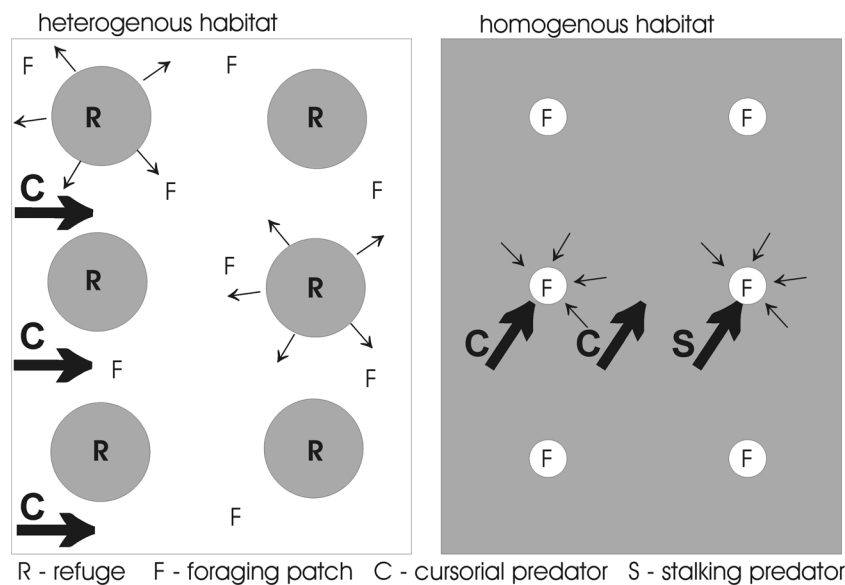


**Fig. 2** Conceptual model showing the hypothetical relationships leading to the occurrence of a death trap. With the increase of resource (food) concentration, the availability of refuges (being related to heterogeneity of habitats) decreases while the probability of being killed by the predator will increase. At highest resource concentration, prey species become highly predictable causing the death trap to occur. The model assumes the probability of finding refuge decreases at low rate within relatively wide range of resource concentrations with the highest rate occurring when resources become highly concentrated and ungulates have no alternative foraging sites. The shape of the kill probability curve is more steep than that of the refuge, indicating that the chance of successful hunt is very high only at the highest resource concentration when ungulates are highly predictable

and Merrill 2009). In various circumstances, this trade-off will result in different outcomes, from an extreme avoidance of risky situations at the cost of limited foraging opportunities

to a seemingly “relaxed” intensive use of food-rich, but very risky habitats. While the occurrence of the latter strategy seems to be rare, we argue that it may characterize multi-species predator–prey communities inhabiting relatively homogenous landscapes with concentrated high quality feeding patches. We believe that the ungulate–predator system in the Białowieża Forest described above may represent a good example for this.

We suggest the negative relationship between the spatial distribution of prey and predators, which is emerging from many studies, may be limited to ecosystems with clearly heterogeneous habitat. This notion is in accordance with the conclusion of Birkhofer et al. (2010) that predators and prey may segregate spatially providing habitat heterogeneity is present. We propose that positive spatial relationships between predator and prey are most likely to evolve in relatively homogenous environments with concentrated foraging patches for prey. The system similar to the one reported here (BPF) may occur in the semi-arid savannah with waterholes serving as indispensable spots for ungulates to return to (Valeix et al. 2010; Davidson et al. 2013). The mechanism that may lead to such spatial aggregation (positive relationship) of predator and prey may involve the presence of highly concentrated resources for the prey species in combination with the lack of distinct habitats offering refuges. This relationship can be illustrated by a conceptual model (Fig. 2) predicting that along with the concentration of resources, the availability of refuges (being related with heterogeneity of habitats) should decrease,



**Fig. 3** Conceptual spatial models of interactions between large cursorial (C) and stalking (S) predators (thick arrows) and prey (thin arrows) within heterogeneous and homogeneous landscapes (grey colour represents homogeneous habitat). In a heterogeneous habitat with only cursorial predators, the prey uses distinct refuge patches (R, with low accessibility to predators) from which they disperse to forage in surrounding open landscapes which constitute their foraging areas (F). It allows for a negative relationship between the prey and predators’

spatial distribution. Here, the predictability of both the predator and prey location is low. In homogeneous closed-forest habitats, positive spatial relationships between predator and prey should be expected to occur. Foraging is clearly focused on small food-rich forest gaps, which are highly attractive for ungulates and targeted by both types (C and S) of predators and there are no distinct refuges for prey outside the gaps, as whole available habitat is accessible to (particularly cursorial) predators. The gaps become the death traps as they are easily predicted by predators

and the probability that prey is killed by the predator should increase. This concept may particularly be true in multi-predator systems, especially if there are both stalking and cursorial predators. The risk effect of one predator, which would eventually shift the prey into “safer” habitat, should increase the predation risk from another predator, as it was recently evidenced by Atwood et al. (2009) for a wolf–cougar–elk–mule deer (*Odocoileus hemionus*) system.

The described case of BPF system may also clearly support such interactions due to the wolf and lynx partial overlap in dietary preferences, focusing on both red and roe deer (Jędrzejewska and Jędrzejewski 1998), as well as nearly full overlap in space use (Schmidt et al. 2009). This all contributes to a more evenly distributed predation risk both in time and space through intensive use of all available area by both predators. Under such conditions, the prey is compelled to forage in spots with the highest foraging gains irrespective of the associated lethal consequences (Fig. 3).

Focusing on foraging benefits seems the best option for ungulates in these circumstances, though it leads to death traps because they become very predictable for predators. Following the opinion of Kittle et al. (2008), the potential fitness gain (i.e. higher forage availability) should be still high enough to offset the inevitable risk. However, we speculate a major indirect cost of predation for ungulates lies in feeding under constant awareness of threat rather than in losing foraging opportunities through avoidance of risk. The coexistence and familiarity of prey species with an incessant risk of predation should favor reinforcing their sensitivity to very fine-scale cues of risk, allowing them to efficiently detect and tackle the immediate threat of predators. The prey may thus respond to predation risk at a fine scale within habitats and not between habitats, as shown by recent studies in BPF (Kuijper et al. 2013). The predation risk perceived by ungulates may be yet more precisely fine-tuned based on olfactory cues as they showed unambiguous reaction to a single freshly deposited wolf scat (Kuijper et al. 2014; Wikenros et al. 2015). This ability may help them to perceive the actual vicinity or a recent visitation of a predator indicating near-imminent risk of death.

The question, however, remains what effect the constant predation risk exerts on the prey at the population level. For example, a still unsolved issue is the possibility of affecting the population reproduction rates through predation-induced stress (McArthur et al. 2014). Although its role is not yet well established in shaping ungulate populations (Creel et al. 2009), there is evidence that glucocorticoid stress hormones might play an important role in anti-predator response in prey animals (Thaker et al. 2010). The ungulate prey should utilize a wide array of responses including behavioural and hormonal reactions, of which the effect on their populations

should be farther studied empirically in different types of landscapes including both heterogeneous and homogeneous environments.

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