Does fear control population density?

The role of landscape of fear on the strength of bottom-up and top-down control in herbivore populations

Bachelor Thesis
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Abstract

Understanding the factors that influence the population density is an important part of population ecology. The main factors that influence the population density are bottom-up control (food production), top-down control (predation) or parallel control (interspecific competition). However, these factors are not static and shift over species and time. This study tries to analyze the role of landscape of fear in the shifting strengths of bottom-up and top-down control on prey populations. This study focuses on great herbivores as prey model species. By combining multiple studies per species, landscape of fear can be linked to the strength of bottom-up and top-down control. Landscape of fear is defined as the existence of safe and risky patches from predation in the home range of species. Most studies use giving-up density (GUD) as measurement to define the strength of bottom-up control. From the comparison between the herbivore-predator systems that I've considered, I found evidence that in general the strength of bottom-up control reduces if the perceived predation risk increases. The strength of top-down control increases if the perceived predation risk increases. I conclude that landscape of fear does play a role in the shifting of bottom-up and top-down control, but for the precise role and the strength of its effect more research is needed.

Introduction

The mechanisms that control the density of herbivore populations have been extensively studied in ecology. There are in general three main effects that limit the population size: (1) there is bottom-up control, which means that the density of trophic levels in a food web is controlled from the bottom-up. For herbivore populations this means that resources are the limiting factor. The amount of food that is available depicts the density of the herbivore population; (2) there is top-down control, which means that the feeding activities of the top trophic level affect the density of the trophic levels underneath. So, the lethal effect of predation limits the population size; and (3) there is a parallel factor, which is caused by interspecific competition. Different species on the same trophic level compete with each other for the available food and other resources (Laundré et al., 2014). This thesis won't consider parallel factors.
The influence of bottom-up control for herbivores is caused by abiotic factors. In fact, abiotic factors like temperature, rain and nutrients have a direct effect on food supplies, which in their turn affect the

population size of the primary consumers. The population size usually responds with a year lag time. There have been several studies that studied the bottom-up effect on primary consumers (Brown & Heske, 1990; Ernest, Brown, & Parmenter, 2000; Hernández et al., 2005; Hernández et al., 2011; Meserve et al., 2014; Previtali et al., 2009). However, the strength of bottom-up control varied over different studies. Some studies found a very strong effect (Ernest et al., 2000; Hernández et al., 2005) and some studies found no significant effect at all (Brown & Heske, 1990). This difference in the strength of bottom-up control was found between different species but also in studies in which the strength changed over time (Meserve et al., 2014).

Top-down control of a population is caused by the lethal effect of predation and that is density dependent. This means that the strength of this effect is influenced by the densities of the prey and predator populations. The strength increases when the density of the prey or predator population increases. This control mechanism has also been studied in several studies (Estes, 2012; Sih et al., 1985). Again there are studies which found a strong effect of top-down control (Erlinge et al., 1983; Hanski et al., 2001) and studies which only found the effect under specific conditions (Ballard et al., 2001).

Everybody acknowledges the existence of the two mechanisms, bottom-up and top-down control, but the level of impact of these mechanisms has been a point of discussion. The two effects form a dynamic process which can shift over time and over species (Meserve et al., 2003).

In 1999 Brown et al. (1999) formulated the theory of the ecology of fear. There has been several studies that suggest that predators can have a non-consumptive effect on their prey (Laundré, Hernández, & Altendorf, 2001; Riginos, 2014). Prey show different behavior in areas with predation opposed to predation-free areas (Laundré et al., 2001). Prey start to be more vigilant and change their feeding strategies. It seems thus that the presence of the predator can have an effect apart from the lethal effects. The prey avoids the places in which the perceived predation risk becomes higher (Tolon et al., 2009; Willems & Hill, 2009). Perceived predation risk is not the same as predation risk because predation risk only involves the consumptive effects of a predator. Perceived predation risk also involves the non-consumptive effects of a predator which is referred to as fear. The avoidance of certain areas can be mapped, and corresponds with a map of the perceived predation risk for the herbivore. A heterogeneous landscape of risky and safe patches is called “landscape of fear” (Laundré et al., 2014).

It is unknown what causes the shifting of the strength of bottom-up and top-down control. One theory is that landscape of fear can play an important role in this. This has already been studied for small herbivores (Laundré et al., 2014). The question that this study aims to answer is: *Can the landscape of fear explain the shifting of bottom-up and top-down control on population density in great herbivores?* Landscape of fear is based on the idea that there are safe and risky patches (Merwe & Brown, 2008; Shrader, Brown, Kerley, & Kotler, 2008). The size, shape and position of these patches form the landscape. Different studies have found that change in perceived predation risk has an effect on the population size and density of the prey (Eggers, Griesser, Nystrand, & Ekman, 2006; Kotler, 2014). Two hypotheses can be formulated:

1. The strength of bottom-up control decreases as the perceived predation risk gets higher.
2. The strength of top-down control increases as the perceived predation risk gets higher.

To test the strength of bottom-up and top-down control there are several methods. Most studies use giving-up density (GUD) as a measure to test for bottom-up control. Giving-up density is defined as the density of food sources that is left after an herbivore ceases foraging (Brown, 1988; Hochman & Kotler, 2006a). A high GUD means that a herbivore population uses less resources then are available. This suggests that the herbivore populations is not limited by resources and that bottom-up control is absent, So the strength of bottom-up control decreases when the GUD increases (Laundré et al., 2014). A theory that combines the factors that influence GUD is the optimal foraging theory (J. S. Brown, 1988). This theory states that an herbivore should stay and forage in a patch as long as the benefits are bigger than the costs. The costs consist of metabolic cost, predation risk and missed opportunity cost, where the metabolic costs are the costs of digesting and extracting the nutrients from the food, the predation risk is the risk an herbivore takes by foraging and not actively searching for predators, and missed opportunity costs are the costs of not engaging in alternative activities. The benefits defined by the optimal foraging theory are food, water and energy (J. S. Brown, 1988).

To test the strength of top-down control several studies (Eisenberg et al. 2015; Grange & Duncan, 2006; Hopcraft et al., 2014) looked at the effect of predators on the prey abundance. They compared different prey species with the same predator. The effect of top-down control on prey “A” is stronger when the abundance of prey “A” is lower compared with prey “B” if they have the same predator. The landscape of fear results in the composition of a mosaic of risky and safe patches for the prey species. There have been used several approaches to determine if a patch is risky or safe in the studies I have considered here. Table 1 shows the methods which were used to measure the risk of a patch in the several ecosystems that are highlighted in this thesis.
This study focuses on large herbivores and considers research done singularly on bottom-up control, top-down control and landscape of fear to try to understand the combination of these three phenomena in an ecosystem. Great herbivores can be considered as good model species because they can also have a big impact on the ecosystem they live in (Manier & Hobbs, 2007; Smit, Bakker, Apol, & Olff, 2010).

Prey	Way perceived predation risk was measured	Predator
Zebra, wildebeest and buffalo, gazelle, hartebeest, elephant, oryx, giraffe, eland and warthog	Presence/absence of predator, tree density, distance to thick woody cover of drainage bed (Grange & Duncan, 2006; Hopcraft et al., 2014; Riginos, 2014)	lion, cheetah, leopard and hyena
Elk	Presence/absence of predator (Eisenberg et al., 2015; Ripple & Beschta, 2012; Ripple, Larsen, Renkin, & Smith, 2001), sight lines and presence of escape barrier (Ripple & Beschta, 2003)	Wolf
European roe deer, wild boar, European bison, moose and red deer	presence of CWD, that is Coarse Wooded Debris (Kuijper et al., 2013)	Wolf
Nubian ibex	Distance from refuge (Hochman & Kotler, 2006a, 2006b; Iribarren & Kotler, 2012a; Kotler, Gross, & Mitchell, 1994), sight lines from food to refuge (Iribarren & Kotler, 2012b)	leopard, wolf, striped hyena, human
White-tailed deer	Snow depth, amount of cover (Nelson & Mech, 1991; Rieucau, Vickery, & Doucet, 2009; Rieucau, Vickery, Doucet, & Laquerre, 2007)	gray wolf, coyote
Mule deer	Amount of kills (Altendorf, Laundré, González, & Brown, 2001)	mountain lion
Roe deer	Amount of kills in an area (Lone et al., 2014)	lynx, human

Table 1. The prey species, predator species and the methods used to measure perceived predation risk of the different ecosystems considered in this thesis.

This study highlights 7 predator-prey relationships in certain ecosystems:

1. The relationship between zebra (*Equus quagga*), blue wildebeest (*Connochaetes taurinus*), buffalo (*Syncerus caffer*), Grant’s gazelle (*Gazella granti*), hartebeest (*Alcelaphus buselaphus cokei x lelwel*), elephant (*Loxodonta africana*), oryx (*Oryx beisa*), reticulated giraffe (*Giraffa camelopardalis reticulata*), eland (*Taurotragus oryx*), warthog (*Phacochoerus africanus*) as prey, and lion (*Panthera leo*), cheetah, leopard (*Panthera pardus*) and striped hyena (*Hayaena hayena*) *as predators* in the African savannah (Grange & Duncan, 2006; Grange et al., 2004; Hopcraft et al., 2014; Riginos, 2014; Valeix et al., 2009);
2. The relationship between the Nubian ibex (*Capra nubania*), leopard, wolf, striped hyena and human (*Homo sapiens*) in the Negev desert in Israel (Embar, Kotler, & Mukherjee, 2011; Hochman & Kotler, 2006a, 2006b; Iribarren & Kotler, 2012a, 2012b; Kotler et al., 1994);
3. The relationship between elk (*Cervus elaphus*) and wolf *(Canis lupus)* in Yellowstone National Park in America (Barber-Meyer, Mech, & White, 2008; Eisenberg et al., 2015; Halofsky & Ripple, 2008; Laundré et al., 2001; Ripple & Beschta, 2003, 2012; Ripple et al., 2001);

4. The relationship between: European roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), European bison (*Bison bonasus*), moose (*Alces alces*), red deer (*Cervus elaphus*) as preys and wolf and European lynx (*Lynx lynx*) as predators in Białowieża in Poland (Kuijper et al., 2013);
5. The relationship between white-tailed deer (*Oidocoileus virginianus*) and the wolf in Superior National Forest in northeastern Minnesota (Nelson & Mech, 1986, 1991; Rieucau et al., 2009, 2007);
6. The relationship between mule deer (*Odocoileus hemoinus*) as prey and mountain lions (*Puma concolor*) as predator in Cassia and Box Elder counties (Altendorf et al., 2001);
7. The relationship between the European roe deer, Eurasian lynx and human in Hallingdal in South-central Norway (Lone et al., 2014).

Results

African savanna

On the savannas in Africa food sources can be scarce (Hopcraft et al., 2014) . This scarcity resulted in that only herbivores which have very efficient digestive systems could survive. According to theory small grazers are limited by the digestive quality of grass, while large grazers, which can extract sufficient nutrients from low-quality grass, are limited by its abundance instead (Hopcraft, Anderson, Pérez-Vila, Mayemba, & Olff, 2012). The great herbivores considered in the study of Hopcraft (2014) are the zebra, the blue wildebeest and the buffalo. These herbivores are predated by lions, cheetahs, leopards and hyenas. Because the large herbivores need to eat a great amount of food in order to survive, they show migratory behavior. Migration has been studied to look where the herbivores migrate and what influences their movements. The factors that influence the migration of ungulates in Africa are food quality, food abundance and predation risk (Hopcraft et al., 2014). Food quality was quantified by measuring the nitrogen content and the "greenness" of the grass. Predation risk was quantified by measuring the distance to thick, woody cover or drainage beds which increase the predation risk (Hopcraft, Sinclair, & Packer, 2005). On one side the areas with high-quality food attract the ungulates, but on the other side those areas are often the places where the predation risk can be higher. An increased predation risk for the zebra, the blue wildebeest and the buffalo is caused by areas with a lot of cover, such as drainage beds or dense thickets, to conceal predators. Wildebeests and buffalos plan their migration on the presence of high-quality food patches. Zebras plan their migration to minimize risk but get access to enough high-quality food patches (Hopcraft et al., 2014). The migration of zebras display a landscape of fear. However, zebras only tried to minimize risk in the wet season when there was relative enough food. In the dry season when food is most limited, zebras showed the same migration patterns as wildebeests and buffalos and tried to optimize the access to high-quality food.
Another study studied the effect of tree density on the habitat use of herbivores. The study included almost all common large herbivores: plains zebra, Grant's gazelle, hartebeest, elephant, oryx, reticulated giraffe, eland and warthog. An increase in tree density has been associated with an increase in vigilance behavior and predator-avoidance by large ungulates (Underwood, 2015; Valeix et al., 2009). Areas with a high tree density have higher predation rates of lions and thus can be seen as risky patches (Hopcraft et al., 2005). Researchers simulated risky and safe patches by clearing, thinning or doing nothing to certain plots with high or low tree densities. They measured the abundance of fecal pellets on every site to look which tree density plot had the most preference. The abundance of fecal pellets was lower where the tree density was higher. However, in the season with a drought there was a preference for the patches with the high-quality food even if the perceived predation risk was high (Riginos, 2014). This was true for all considered species except the elephants. The elephants have no natural predators on the savanna and preferred the patches with a high tree density. This suggests that elephants don't have a landscape of fear.

To conclude, almost all African herbivores form a trade-off with landscape of fear and limiting food source. There are certain basic conditions to be fulfilled before landscape of fear plays a role in foraging behavior. For instance, zebras are hindgut fermenters and are able to extract more nutrients from low-quality food. They have a more efficient digestive system than the wildebeests and buffalos. This means that they are less dependent on high-quality food patches and thus have a weaker bottom-up control. This could also suggest that if all herbivores have the same top-down control the zebra should be the dominant species (Duncan et al., 1990; Menard et al., 2002). However, the wildebeest and the buffalo are a lot more abundant. The zebra is never the dominant species in all studied areas in the African savanna (Grange & Duncan, 2006). This could be caused by interspecific competition or by different predation pressure (top-down control) (Sinclair, 1985). Indeed Grange et al. (2004) state that the limited density of the zebra population is mainly caused by predation. This suggests that top-down control has a stronger influence on the zebra compared with the ruminants. The study studied if this stronger top-down control could be explained by landscape of fear. The ratio of zebra's compared with the sum of buffalos and wildebeests (Z/BW) was calculated and compared with the abundance of lions. The Z/BW was lower in areas with a high density of lions (Grange & Duncan, 2006). The explanation for this result could be that top-down control for zebras is stronger in perceived risky patches compared with safe patches (where there are less lions). This seems to be in line with the second hypothesis, where the strength of top-down control increases as the perceived predation risk gets higher, and so the landscape of fear can explain the variation in top-down control. The second hypothesis, for which the strength of bottom-up control decreases as the perceived predation risk gets higher, was confirmed by the fact that the GUD is higher, and therefore the bottom-up control is lower, in risky patches compared with the safe patches.

Nubian Ibex

The Nubian Ibex is an endangered species which lives in the Negev Desert in Israel. Ibexes are wild social goats that live on and around steep terrain and cliffs that serve as a refuge for predation (Gross et al., 1995). They live in two different social groups: a group which consists of females and young individuals that can contain more than 100 ibexes, and a group that consists of males of 3 years and older. The ibexes can be predated by: leopards, wolves, striped hyenas and humans (Levy & Bernadsky, 1991). A lot of research that has been conducted focuses on patch use of the Ibexes and what influences it. Before the optimal foraging theory can be applied on an herbivore, the herbivore must be able to determine the quality and benefits of a patch. In a study of Hochman and Kotler (2006a) the giving-up density of Nubian ibexes was compared between patches with different benefits: the ibexes had access to patches with water availability and patches with different quality food. The giving-up density was lower in patches were there was water available or high-quality food (Hochman & Kotler, 2006a). The factor of the cost of foraging that has been most studied is perceived predation risk. Many studies measured perceived predation risk by looking at the distance of the food patch of an herbivore from a cliff. The further away from a cliff means the further away from a refuge and thus a higher perceived predation risk for the ibexes. Hochman and Kotler (2006b) and Iribarren and Kotler (2012b) focused on the apprehension and vigilance of Ibexes compared with the perceived predation risk. Vigilant behavior is a high level of apprehension. Apprehension can be defined as a reduction in attention devoted to performing an activity as a consequence of reallocating attention to detecting or responding to perceived predation risk (Hochman and Kotler 2006). Vigilance is when the herbivore stops foraging, lifts his head and focuses all his attention on looking for predators (Iribarren and Kotler 2012). There is an optimal time spend on vigilant behavior: too little vigilance and there is a high chance the prey gets killed by a predator, too much vigilance and it loses feeding opportunities needlessly (Kotler et al., 2002). Herbivores that can sense the level of perceived predation risk and adjust their time spend vigilant accordingly have a higher survival chance (Lima & Dill, 1990). Iribarren and Kotler (2012) reduced the effectiveness of vigilance by blocking the sightlines between safety (a cliff) and food patches. They not only measured the vigilance and the apprehension of the Nubian ibexes but also the giving-up density in the foraging patches. The ibexes showed more vigilant behavior and had higher GUDs when their sight lines were obstructed or when the patches were further away from the cliff (Iribarren & Kotler, 2012b). Moreover, at an intermediate distance from the cliff, ibexes showed more apprehension but at further distance the vigilance increased (Hochman & Kotler, 2006b). This could mean that ibexes switch from apprehension to the more extreme vigilance as the perceived predation risk increases (Hochman & Kotler, 2006b). Both studies support the optimal foraging theory and confirm that the strength of bottom-up control decreases as the perceived predation risk increases.

Kotler, Gross and Mitchel (1994) and Iribarren and Kotler (2012a) focused more on giving-up density and food preference of ibexes. Kotler et al. (1994) found that ibexes tend to forage in patches until the food occurs in similar densities across all the patches (Kotler et al., 1994). Iribarren and Kotler (2012a) mapped the giving-up density by creating a five by five array of feeding trays in a varied landscape. They combined the map of GUD with the map of terrain characteristics and created a map of the landscape of fear. They concluded that the two most important factors that influence landscape of fear were vegetation cover and distance from a refuge (Iribarren & Kotler, 2012a). Both studies support the hypothesis that the strength of bottom-up control decreases when the perceived predation risk increases.

Wolf

In 1995 the wolf was reintroduced in Yellowstone National Park (YNP) after it was absent for over 70 years. This gave researchers the unique opportunity to study the effect of the introduction of a predator in a stable ecosystem. The main herbivore living in YNP is the elk. Before the reintroduction, predictions were made of the impact of the wolves on the elk population. Most of the studies predicted a decline of the herbivore population to be between 5-30%. However, the elk population decreased 50% from 19.045 individuals in 1994 to 9.545 individuals in 2005 (White & Garrott, 2005). Not only the population of elk started to decrease, they also started to behave differently. Elk started to show more vigilant behavior. The female elk showed more vigilant behavior than male elk and the female elk with calves showed the most vigilant behavior. This increase of vigilance only happened in the part of YNP where the wolfs were introduced (Laundré et al., 2001). The elks also started to avoid certain areas with a high predation risk. This spatial distribution of vigilance levels and avoidance of the areas where predators where around can be seen as a landscape of fear. Before the introduction of the wolves, browsing intensity of the elks was very high. Because the elks started to avoid certain areas and the browsing intensity of those areas declined, certain trees got the chance to grow. This phenomenon is called trophic cascade and has been studied for two plant species: cottonwood (*Populus* spp.) (Ripple & Beschta, 2003) and quacking aspen (*Populus tremuloides*) (Ripple et al., 2001). Both studies showed that the growth of plants was higher in patches with higher perceived predation risk (Ripple & Beschta, 2003; Ripple et al., 2001). The perceived predation risk was differently measured between Ripple and Beschta (2003) and Ripple et al. (2001). In the study that considered the trophic cascade on the cottonwood, patches with low visibility and presence of escape barriers were compared to nearby patches in open areas. In the study that considered the trophic cascade on quacking aspen, patches in high wolf-use areas were compared to patches in low wolf-use areas. The increase of growth of both plant species can be linked to a lower browsing intensity of the herbivores in those risky areas. A lower browsing intensity can be linked to a higher GUD which on his turn can be linked to a lower bottom-up control.

Eisenberg, Hibbs and Ripple (2015) compared three valleys: Saint Mary, Waterton and North fork which had respectively low, moderate and high presence of wolves and thus high predation riskfor the elks. The study analyzed the density of elk and wolf pellets in the valleys and on a site-specific level. Elk pellet density was lowest in North fork in which the predation risk was the highest. On site-specific level the elk pellet density became lower as obstacles to detecting and escaping wolves increased, this even happened in the valley with a low wolf-use (Eisenberg et al., 2015). This suggests that even with a very low wolf presence elk tend to avoid risky patches which means that obstacles that increase the perceived predation risk can have a big impact, even when the predation risk is low.

YNP isn’t the only park in which the predator-prey relationship with wolf was studied. In Białowieża primeval forest (BPF) in Poland there was also a study on the effect of the presence of the wolf on the behavior of local prey. The herbivores in BPF were the European roe deer, wild boar, European bison, moose and red deer. This study focused on the microhabitat level in the patches that make up the mosaic of the landscape of fear. They studied the effect of coarse wooded debris (CWD) on browsing intensity. Coarse wooded debris forms an obstacle which both blocks the sight to see a predator and an escape route in case a predator is present. They compared the browsing intensity of the herbivores in patches near CWD (within a 5m radius) to patches outside this range. The browsing intensity was lower near a CWD compared with a patch outside this range (Kuijper et al., 2013). This means that landscape of fear not only works on an area but is even present at microhabitat level which means that a heterogeneous area can form a very complex landscape of fear due to effects on microhabitat level. However, the effect of lower browsing intensity near CWD only occurred in the core area of wolf activity. Outside the core area there was no correlation found (Kuijper et al., 2013). This is in contrast with the study of Eisenberg (2015) which found that even with a low presence of a predator landscape of fear is present.

Deer

To be able to forage in the winter a large part of the white-tailed deer population in north-America and Canada migrate to areas called yards (Morrison, Forbes, & Young, 2002). The yards offer the deer shelter and food and the migration to these areas is induced by snow depth and lower temperatures (Sabine et al., 2013). By migrating to these yards the white-tailed deer lower the predation risk and thus their top-down control. However, moving to these yards is dangerous because during the migration there is a higher predation risk. Not all deer in the population migrate and the deer that stay behind have a higher change to die from predation. The main predators of the deer are the wolf and the coyote (Nelson & Mech, 1991). In Minnesota the yards are altered by humans because there are power lines which go straight through the habitat. These power lines are being kept clear from trees and therefore offer less cover for the deer. The power lines form a unique trade-off, in fact the cleared area forms a higher perceived predation risk for the deer caused by the absence of cover, but it also has a higher production of food caused by the sunshine which can reach the earth. The high perceived predation risk makes the cleared area a risky place, so a weaker effect of bottom-up control could be expected. This was confirmed by Rieucau et al. (2007) who showed that the GUD in the power line patches was higher. Surprisingly, the GUD was the lowest at the edge of the cleared patch (Rieucau et al., 2007). This suggests that deer try to balance the avoidance of perceived predation risk and the quality of the food they eat. Rieucau et al. (2009) studied the effect and the strengths of the costs involved in the optimal foraging theory on giving-up density using foraging behavior of white-tailed deer in the cleared patches. They concluded that the strength of missed opportunities cost was very low while predation risk and metabolic cost had a great impact on GUD. High predation risk or metabolic cost correlated with high GUD (Rieucau et al., 2009). The yards consists mostly of coniferous species which reduce the snow depth and facilitate escapes for deer from predators. However, in the cleared patches snow depth increases, which forms an obstacle for escaping from potential predators. Because of high snow depth cleared patches have a higher predation risk and a higher predation risk (Nelson & Mech, 1986). GUD was highest on the places where the snow depth was the highest (Rieucau et al., 2009). In the cleared patches the strength of bottom-up control was found to be lower, confirming the first hypothesis stating that the strength of bottom-up control decreases as the perceived predation risk gets higher.

Mule deer in Idaho are being predated by mountain lions. A study sets up several feeding trays which are in the forest, at the edge or in the open field. They measured the predation risk by analyzing where mountain lions had killed mule deer previously. The highest amount of kills was at the edge of the forest, at second in the forest and the least kills were in the open field. Then they analyzed the GUD and the vigilance behavior. The mule deer had the highest GUD in the forest and decreased to edge and even more to open field. The mule deer were the most vigilant at the edge and showed lower vigilance levels in the forest and the open field (Altendorf et al., 2001). The GUD didn’t correlate with the predation risk in this case. On the other hand, vigilant behavior, that gives a measure to a part of the perceived predation risk, does correlate with the real predation risk. The effectiveness of vigilance is lower within the forest compared with the open field which could explain why vigilance behavior in the forest is lower but the GUD is higher. This makes the forest riskier than the open field. So the GUD was higher in a riskier patch. Higher GUD is linked to weaker bottom-up control so this confirms the first hypothesis.

Till now we only discussed the existence of one landscape of fear in a predator-prey relationship. However, if one herbivore has two predators that have a different hunting strategy it is possible to have more landscapes of fear. The roe deer in southeastern Norway is one herbivore which has two landscapes of fear. These are caused by lynx and humans both predating on roe deer (Lone et al., 2014). The predation risk of both predators was measured as amount of kills of roe deer from 2006 till 2011. The lynx is a stalk-and-ambush predator which is most dangerous in areas with dense vegetation cover. Humans hunt in the open field in which they have the best visual sight lines. These hunting techniques cause contradictory landscapes of fear for the roe deer. More cover causes a lower predation risk from humans but a higher predation risk from lynxes. A rough terrain increases both predation risks (Lone et al., 2014). This study highlights that predator-prey relationships can be very complex in a multi-predator setting. Landscapes of fear aren't as straight forward as they seem sometimes.

Discussion

The purpose of this study was to research if landscape of fear can play a role and explain a shift from bottom-up to top-down control. The landscape of fear can be defined as the presence of safe and risky patches within an ecosystem and the strength of bottom-up and top-down control could differ between these patches.

Comparing different ecosystems shows that a lot of herbivores display landscape of fear. Landscape of fear is inseparably linked to perceived predation risk. This isn't the same as predation risk because predation risk only involves the consumptive effects of a predator. Perceived predation risk also involves the non-consumptive effects of a predator which is referred to as fear. With this review I found that the factors that influence the perceived predation risk can be categorized in three groups: the presence of a predator, the ability to notice a predator (sight lines) and the ability to escape from a predator (escape barrier, distance from refuge, snow depth). The first hypothesis states that bottom-up control decreases as the perceived predation risk increases. Bottom-up control was measured in GUD or browsing intensity. Almost every study showed that the GUD or browsing intensity was higher in places which had a higher perceived predation risk (Altendorf et al., 2001; Iribarren & Kotler, 2012a; Kotler et al., 1994; Kuijper et al., 2013; Rieucau et al., 2009, 2007; Ripple & Beschta, 2003; Ripple et al., 2001). The increase of the GUD alongside the increase of perceived predation risk shows that bottom-up control is negatively influenced by the perceived predation risk. However GUD isn't only influenced by perceived predation risk. It could be that the changes that were found in GUD were caused by metabolic costs or missed opportunity costs. It's questionable how much bottom-up control can be linked to GUD. A better way to measure bottom-up control is to look at the food production in a certain area. If in a good year the food production increases, caused for example by more rain, it's expected that the abundance of prey also increases with a year lag response (Ernest et al., 2000). To measure this way a long-term study, which measures the total amount of nutrients produced and the abundance of prey, is required. The study on the savanna showed that landscape of fear only exists under certain circumstances (Riginos, 2014). This suggests that there is a threshold that the strength of bottom-up control needs to be beneath for landscape of fear to influence it.

The second hypothesis was that top-down control increases as the patches get riskier. This was found in a study about zebras. The zebras were compared with wildebeests and buffalos which didn't show any behavior according to the landscape of fear. Top-down control was stronger in the riskier patches which the zebra's tried to avoid (Hopcraft et al., 2014). There are no factors known that indirectly influence the strength of top-down control and that can be easily measured. One way to measure the strength of top-down control is analyzing the abundance of prey and predators. If the population of predators increases it should have a certain effect on the abundance of the prey and vice versa. The level of effect can be linked to the strength of top-down control. To study this it takes long-term studies in which both the abundance of prey and predator must be known. Another way is to add or subtract predators from an ecosystem and analyze the effect on the abundance of prey. I found no articles in which this kind of study is performed.

This study confirms that landscape of fear does play a role in the shifting in the strength of bottom-up and top-down control however the precise part of landscape of fear is dependent on the ecosystem. The negative effect of perceived predation risk on the strength of bottom-up control has been confirmed for several species. However the exact role of landscape of fear in the shifting of top-down control is yet unknown and further research is needed.
Besides the scientific value, this landscape of fear can be a help in conservation and management of ecosystems. If the abundance of a prey and even a predator depends on certain landscape characters it can be easily managed by changing the environment. The study in Białowieża showed that even microhabitat changes can have an effect. Currently most conservation management tends to decrease the lethal effects of the predator by killing a part of the predator population. Future conservation could be about creating the right balance between safe and risky patches. Creating more or less risky patches should change the population density of the prey. By using landscape of fear it could be even possible to control the browsing intensity on certain places.

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