Ecology of fear; anomalous or common?

Master essay
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Title page: Picture of a European roe deer (*Capreolus capreolus*) taken in the Netherlands. You can see that the deer is vigilant and that its behavior is influenced through non-lethal effects induced by the photographers presence.

Abstract

In old predator-prey models, prey were not able to respond to the presence of the predator. New models which included this feature showed that non-lethal effects of the predator might play a huge role in a predator-prey interaction. These non-lethal effects on the prey lead to changes in behavior which induce cascading effects that might influence other parts of the ecosystem. Empirical data from Yellowstone National Park showed that these non-lethal effects play a major role in the interaction between wolves and elk and shape the ecosystem. This concept is called the ecology of fear. It is however unknown how common this ecology of fear. By looking at the definition of the ecology of fear and see if other predator-induced changes in behavior match these definitions I can conclude that the ecology of fear is widespread across a wide variety of predator-prey interactions and that this might influence our understanding of ecosystem conservation.

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Introduction

Between 1920 and 1935 population ecology started to emerge and became a well-founded discipline. In this field there was much interest in the dynamics of a single-species population growth. Population ecologist started the foundation of the research on predator-prey interactions to be able to better explain the distribution and abundance of species populations. However, in natural populations, predator-prey interactions cannot be studied easily and therefore several models were made to get a better understanding of the dynamics of these predator-prey interaction (Hassell, 1978). The old models (Taylor, 1984; Lima & Dill, 1990) were organized in a way that individuals were treated as unresponsive- 'particles'. New models included the responsiveness of the prey and predator in the system and results indicated that predator-mediated changes in preys behavior, also referred to as the non-lethal effects of a predator, might be more important than the lethal effects (Brown, Laundre, & Gurung, 1999). Several empirical studies showed that big mammalian predators can have a huge effect on the ecosystem through these non-lethal effects, this is also called 'the ecology of fear' (Ripple & Beschta, 2004). The ecology of fear can be seen as "the melding of the prey and predator's optimal behavior with their population and community-level consequences", as stated by Brown et al. (1999), which nicely include the predator-mediated changes in preys behavior and its effects on the ecosystem.

In ecological research, a lot of predator-mediated behavior changes in prey have been found, but only a very small part of them are referred to as the ecology of fear and it is unclear if the remaining findings can be placed within in this concept as well. In this thesis I focus on the question whether these changes in behavior are also a result of the ecology of fear and discuss if this concept can be generalized over a far wider range of predator-prey interactions. For example in predator-prey interactions between species of fish or insects, that are found on lower trophic levels within an ecosystem. First I will explore how models on predator-prey systems have developed over time to give a short history on the research of predator-prey systems and to show how this research led to the concept of the ecology of fear. Second I will show how predators affect herbivore behavior and how that translates into changes in vegetation and eventually influences other parts of the ecosystem (also called 'cascading effects'), with the help of an example from Yellowstone National Park. To further investigate the commonness of the ecology of fear I will give an overview of studies that show that predators can alter ecosystems through predators changes behavior. Then I will give an overview of studies that show other predator-mediated changes in behavior in prey, but are not referring to the ecology of fear. In the end I discuss whether these behavioral changes can be placed within the concept of the ecology of fear as well.

Predator-prey models

In the last decades several different models have been made to investigate the dynamics behind a predator-prey interaction. Population ecologist haven been looking for answers on how predators influence prey population sizes and dynamics over time. There used to be two different but somewhat complementary approaches to model predator-prey interaction, but both treat the individuals as behaviorally unresponsive 'particles' (Brown et al., 1999). The first focuses on the fact that predators kill prey and that the predator is always lethal (Taylor, 1984). This is of course not the case and prey could respond to the presence of the predator by, for example, moving away. This response is not embedded in this model and therefore the outcome of the model can largely differ from empirical outcomes (Brown et al., 1999). The next model does include the ability of the prey to respond the predators' presence (Lima & Dill, 1990) and is largely based on the optimal foraging theory (Emlen, 1966; McArthur & Pianka, 1966). Models of this theory predict that prey should balance their demands for food and safety (Abrams, 1991; Brown, 1988, 1992, 1999; Gilliam & Fraser, 1987; Houston, McNamara, & Hutchinson, 1993). This is a good improvement of the model, but the model is not suitable for the research on the interactions in large mammalian predator-prey systems, since the foraging theory deals mostly with systems in which the predator consumes large amounts of 'unresponsive, particle-like' prey (Brown et al., 1999).

Therefore, Brown et al. (1999) build a model in which prey could respond to the presence of a predator. Due to this change, the dynamical feedback in the model involved changes in the fear levels and catchability of the prey, instead of the dynamical feedback involving prey being killed by predators in the older models. The results of this model showed that a 'fear' driven predator-prey system could be far more stabilizing due to the non-lethal effects than the older models that were often caught in a so called 'Catch-22' (Rosenzweig & MacArthur, 1963). A catch-22 means that in models were the prey cannot respond to the predator by changing their behavior, the outcome resulted in unstable predator-prey systems that will eventually lead to extinction of a prey or a predator species. Thanks to the new model, prey could change their behavior. These behaviorally changes due to the presence of a predator and their impact on the ecosystem are referred to as 'the ecology of fear' (Brown et al., 1999) and might be very important in a lot of predator-prey systems.

Predators can alter ecosystems

Predators can be found on the entire planet and initiate top-down forces and trophic cascades through direct lethal effects, for instance on other animal communities or plant communities in the ecosystem (Ripple & Beschta, 2004; Smit, Peterson, & Houston, 2003). Predators are in a broad way classified as all consumers, and include herbivores and parasites. In a smaller way, we often classify predators as species that hunt/catch and kill their prey (Estes, Crooks, & Holt, 2001). In the past ecologist thought that bottom-up forces regulated populations, meaning that the availability of resources would regulate population sizes. If we look at ecosystems from a bottom-up view, we can argue that top-predators are of minor importance for an ecosystem, since energy flows upwards across trophic levels. This look on ecosystems changed around the 1960's when the focus changed to competition. Species competition for niches was thought to shape population abundances, meaning that predators are of equal importance as any other species in the system.

Recently a new view is getting attention; top down forces are thought to regulate populations (Estes et al., 2001). When we look at ecosystems in this way, predators are getting a lot of credit and are very important, since they are at the top of ecosystem and regulate population of prey in a lower trophic level though direct killing of the prey. Around the year 2000, ecologist know that all these three pathways are important in species interactions and that these often act simultaneously (Estes et al., 2001). Therefore it is important to remember that while studying one of the three pathways, the other two are affecting the ecosystem as well (Estes et al., 2001).

Tropic cascades are “the progression of indirect effects by predators across successively lower trophic levels” (Estes et al., 2001). Predators can have cascading effects on lower trophic levels and influence prey communities thought direct predation, provide food for scavengers and reduce populations of mesocarnivores (Smit et al., 2003). Predators can also alter vegetation can due to the increase of prey numbers when top predators disappear from an ecosystem (Estes et al., 2001) or through direct mortality of the prey, which can lead to less foraging pressure on plant populations (Ripple & Beschta, 2004). This means that the absence of top predators can lead to degraded simplified ecosystems (Soulé, Estes, Berger, & del Rio, 2003). Thus, predation is a major force in the maintenance of biodiversity. But lethal effects are not alone. Last years, empirical evidence have been found for the theory that non-lethal effects might affect prey communities and even ecosystems (Ripple & Beschta, 2004), and theoretical models support this theory (Brown et al., 1999).

Most studies however focus on the lethal effects of the predator on the prey (Terborgh et al., 1999) but since non-lethal effects can also have a huge impact on ecosystem trough trophic cascades it is important to understand how this works. Changes in prey behavior due to the presence of predators are referred to as non-lethal effects or predation risk effects (Lima, 1998). These changes are due to the need of the prey to balance demands for food and safety from predators, described by the optimal foraging theory (MacArthur & Pianka, 1966). Changes include shifts in habitat use of space (habitat preferences and foraging patterns, caused by fear of predation (Lima & Dill, 1990).

Prey can move to areas where rates of encounters with predators are minimized (Taylor, 1984). In a wolf-ungulate system, ungulates might migrate out of wolves core areas or live longer outside these areas (Mech, 1977), creating potential plant refugees (Estes et al., 2001). The ‘terrain fear factor’ represents a model for assessing the relative predation risk effects associated with encounter situations (Ripple & Beschta, 2003), indicating that prey will change their use of space and foraging patterns according the effect the terrain has on the risk of predation. In landscapes with open and close habitats, ungulate might hide from predators in the closed habitat or they might seek open terrain to be able to detect the predator fast (Kie, 1999). Due to these changes, plant refugia could also be created locally thanks to high levels of predation risk at these locations (Ripple & Beschta, 2004).

Environmental factors can also influence the degree of predation risk in different habitats (winter weather, wildfire and the depth and distribution of snow packs). For instance, snow depth variation can affect the ability of ungulates to escape predators (Crête & Manseau, 1996). All these changes in landscape use can lead to trophic cascades and set the foundation for the ecology of fear concept (Brown et al., 1999). The effect of predators on the behavior of prey species may be more important than direct mortality in shaping patterns of herbivory (Schmitz, Beckerman, & O’Brien, 1997) since with the help of trophic cascades non-lethal effects can influence many aspects of ecosystem structure and function, including habitat altering, food web interactions and nutrient cycling (Rooney & Waller, 2003). A nice example of how this can happen has been studied in Yellowstone National Park (Ripple & Beschta, 2004)

Case study; Yellowstone National Park

One of the most prominent examples of the ecology of fear and how predators can shape ecosystems through non-lethal effects can be found in the northern winter range of Yellow Stone National Park (YSNP from now onwards). In this nature reserve the role of elk (*Cervus elaphus*) on shaping woody browse species communities have been a topic of concern for a long time (Ripple & Beschta, 2004). In YSNP there are seven species of ungulates that forage on woody browse species and the wolf (*Canis lupus*) is a major predator of these ungulates.

Unfortunately, wolf numbers have been very low in the history of the park due to uncontrolled market hunting and this might have a huge impact on the elk shaping woody browse species communities. Since 1800 the number of wolves dropped dramatically until in the 1926 the wolves were ultimately extinct in the park (figure 1a). After this extinction the recruitment of deciduous woody species dropped dramatically (Warren, 1926; Ripple & Larsen, 2000). It was concluded that this lack of recruitment was not correlated with indices of climate (Larsen & Ripple, 2003). Due to the removal of the wolves from the park, elk had now a significant effect on the recruitment of deciduous woody species (figure 1c). One would expect that this increased effect of elk on the recruitment of deciduous woody species resulted from increasing number of elk due to the absence of the wolf as a top-predator. However, counts showed that the number of elk remained relatively stable after the extinction of the wolves (figure 1b). The fact that the elk numbers did not rise, but the elk still prevented recruitment of woody browse species indicates that non-lethal effects are important in this predator-prey system. Summarizing this means that the extinction of wolves allowed elk to browse seedlings undisturbed during winter months and that this prevented the recruitment of woody browse species (Beschta, 2003).

This is also confirmed by the efforts of the YSNP to reduce the size of elk herds from the 1926 to 1968. They succeeded in reducing the number of elk from 5,3 to 7,3 elk per square kilometer (1930-1950) to a number of 2,7 to 5,3 elk per square kilometer (figure 1b). However, despite of these reductions in the number of elk, the recruitment of woody browse species did not rise (figure 1c).

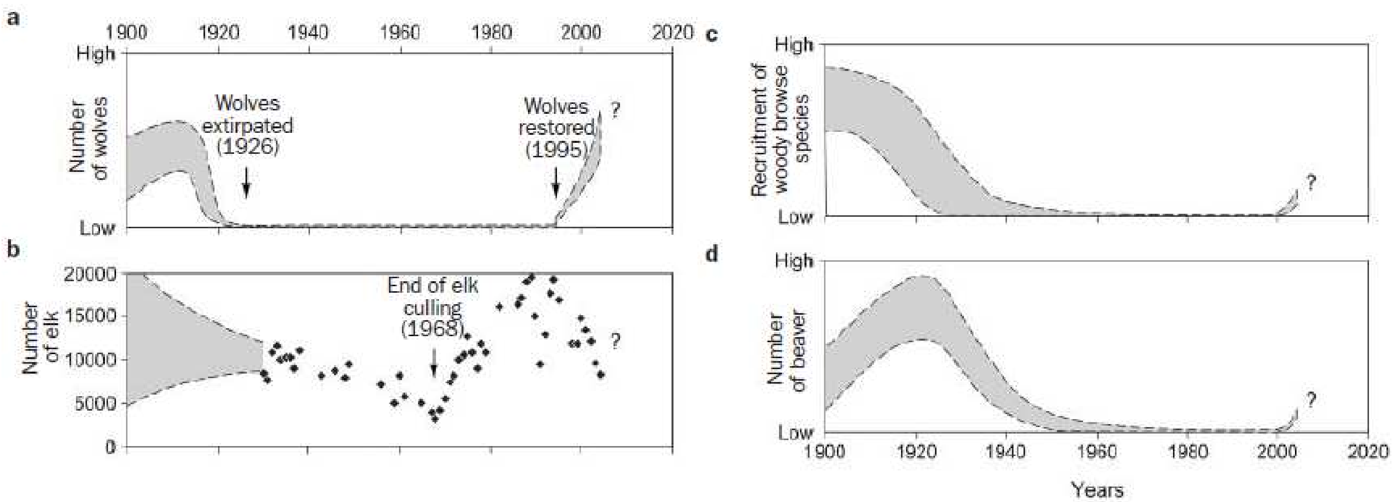

Figure 1. Historical trends for the northern range of Yellowstone National Park since 1900: (a) relative numbers of wolves (Weaver, 1978; Smith et al., 2003); (b) annual elk numbers for the northern range herd (Houston, 1982; YNP, 1997; Barmore, 2003; Smith et al., 2003); (c) relative recruitment of woody browse species (Barmore, 2003; Beschta, 2003; Larsen & Ripple, 2003); and (d) relative numbers of beaver (Warren, 1926; Jonas, 1955; Kay, 1990; Smith et al., 2003). Important events are marked in the graphs (from Ripple & Beschta, 2004)

Cascading effects in the ecosystem ensured that other species were affected by the extinction of wolves as well. With fewer woody browse species available due to the lower recruitment, the amount of provided food by this plant communities declines, affecting other faunal species (Dobkin, Singer, & Platts, 2002)(figure 2). Even beavers are affected by the loss of the top-predator. Before 1900s the beaver population was quite low due to hunting, but the population started to recover in the early 1900s. However, the population suffered from a major decline in the late 1920s. This was probably due to the competition between elk and beaver, beavers need larger trees for the stems to provide food and dam material, while elk would consume all new shoots (NPS, 1961). In the winter of 1995-1996 wolves were reintroduced into YSNP and by 2001 the population of wolves in the northern range has grown to 77 animals (Smith et al, 2003)(figure 1b). In 2001 and 2002 woody browse plants were found that were 2 to 4 meters high, which is in contrast with the 1 meter high plants that were found before reintroduction of the wolves (Ripple & Beschta, 2003). In several high-risk areas (areas were the elk sense a high predation risk due to various terrain conditions and the presence of wolves) the browsing pressure declined on seedlings (figure 1c), this showed that non-lethal effects resulted in selective release from the browsing pressure caused by elk (Ripple & Beschta, 2003). YSNP files

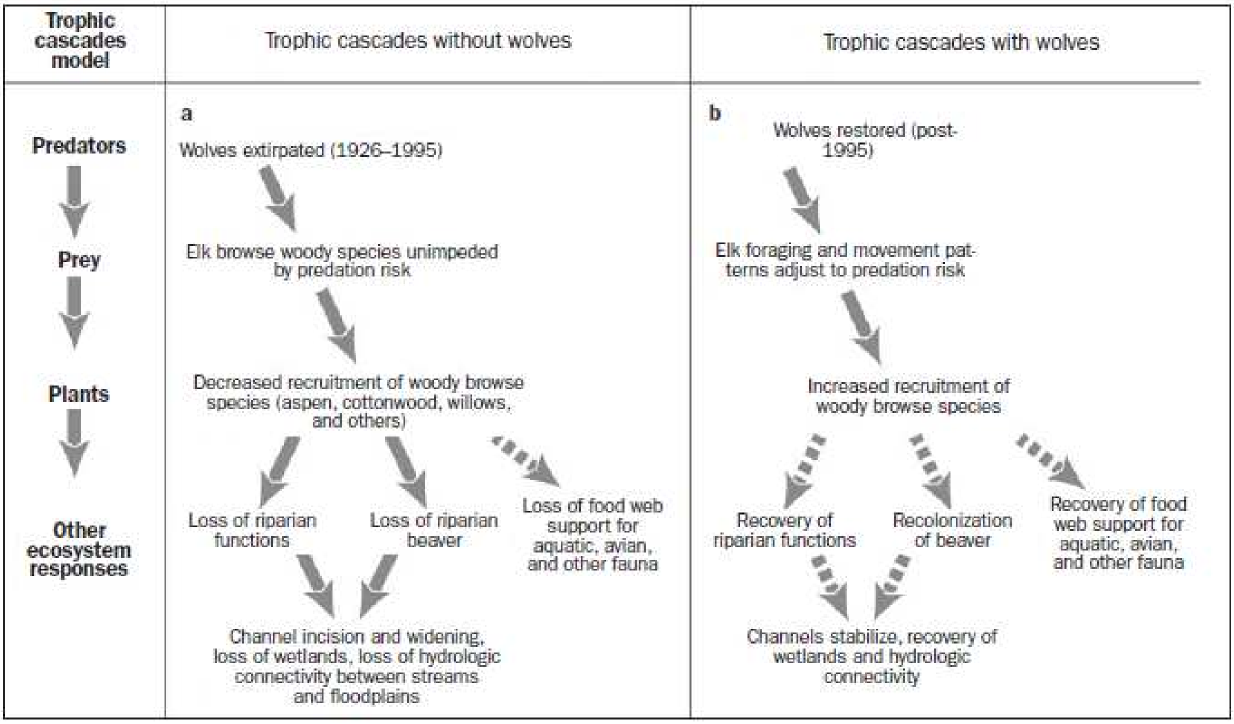

Figure 2: Tropic interaction and cascades with and without the presence of wolves in Yellowstone National Park. Solid arrows show interactions that have been documented. Dashed arrows show interactions that are predicted. (from Ripple &Beschta, 2004)

showed that even the beavers started to respond to the presence of the wolves and by 2003 there were already 7 colonies in the northern range (figure 1d). The changed foraging behavior of the elk due to the presence of predators, together with all cascading effects on other part of the ecosystem (figure 2) is called the ecology of fear (Brown et al., 1999) and plays an important role in shaping the ecosystem in Yellowstone National Park (Ripple & Beschta, 2004).

Ecology of fear in other systems

In a few other systems it has been shown that predators influence prey through non-lethal effects and that due to cascading effects the predator can have a high influence on the ecosystem and the authors refer to the concept of the ecology of fear. For instance, in a puma/mule deer system, it was shown that the mule deer respond to the predators presence by foraging less on high risk areas (Laundre, 2010). But also in completely different systems predators can influence prey's behavior. A good example of this can be found in the Trinidadian guppies. With the help of experiments in the lab it was shown that these guppies reduced food intake when receiving predator cues (water in which a predator was housed), but not being directly in contact with the predator. What is even more important is that the guppies that received predator cues also assimilated nutrient more efficiently resulting in a reduced extraction of nitrogen by 39% compared to the guppies that did not receive predator cues. The reduction of the extraction of this limiting nutrient might influence the ecosystems through cascading effects (Dalton & Flecker, 2014).

There is also another term that is used for linking the behavior of prey to the ecology of fear. The 'landscape of fear' is the one that is mostly used by the authors that found that prey feed less or are less abundant in high risk areas, which is also a part of the concept of the ecology of fear. Since the ecology of fear is explained as "the melding of the prey and predator's optimal behavior with their population and community-level consequences" (Brown et al., 1999), we can argue that the 'landscape of fear' is a synonym of the 'ecology of fear'. This is because the landscape of fear is a result of the response of the prey to the predators presence and changing its behavior to be optimal in the presence of this predator. The effects of this change on the ecosystem might not be known, but one could imagine that it will at least influence the vegetation in the system, because browsing pressure differ between different areas that have a different predation risk. Therefore we can conclude that the 'landscape of fear' is the same as the 'ecology of fear', only the effects on the ecosystem are not or partly investigated. This results in a few other systems that have shown non-lethal effects of predators on the prey.

For example, the striped mouse (*Rhabdomys pumilio*) from South-Africa avoided high risk wooden patches to lower predation (Abu Baker & Brown, 2010). In a wolf-ungulate system in the dense forests of Poland it was shown that the density of ungulates was lower in wolf core areas due to risk effects that are enhanced by habitat characteristics and that the saplings were less browsed in these areas (Kuijper et al., 2013). In a marine system with help of satellite images it was found that grazing halos (rings devoid of seaweed) are created by prey that seek shelter from predators in reefs and take radiating foraging excursions from this central refugia (Madin, Madin, & Booth, 2011). Even monkeys (*Cercopithecus mitis erythrarchus*) do choose areas with higher canopies and higher understory visibility so they minimize predation risks (Coleman & Hill, 2013). At last, also in a coyotes-rabbit system it was shown that the rabbits (*Lepus californicus* and *Sylvilagus audubonii*) balance food sources and predation risk from coyotes (*Canis latrans*) when choosing to visit or not visit a patch (Arias-Del Razo et al., 2012). This shows that not only mammalian top predators can alter the behavior of prey and influence ecosystems though cascading effects, but that we can find the concept of the ecology of fear or the landscape of fear also in other systems.

Predator-mediated changes in prey species behavior or ecology of fear?

Now we know how and that predators can alter ecosystems in different ways due to the ‘ecology of fear’ or the ‘landscape of fear’. But does this also apply to a wider range of predator-prey systems and is it maybe more common than we currently think? There are a lot of articles that show that predators do induce changes or shape prey’s behavior, but never mention the ‘ecology of fear’ (table 1). The table gives a rough overview of publications made from 2010 until now, but is not complete. The articles were found with the help of the online database ‘Web of Science’, by searching for the terms ‘predator mediated change in behavior’ and ‘non-consumptive effects of predators’ within the topic of publications from 2010 until recent. All included studies show a predator mediated change in the behavior of a wide range of types of prey (insects, birds, fish, etc.). For instance in birds it has been shown that clutch sizes are reduced when predation risk is higher (Travers et al., 2010). In insects it has been shown that larvae of the Colorado potato beetle (*Leptinotarsa decemlineata*) feed less in the presence of the predator the spined soldier bug (*Podisus maculiventris*)(Hermann & Thaler, 2014). Also, in amphibians it was found that tadpoles (*Lithobates sylvaticus*) move less and reduce their time outside refugees in the presence of predators (Carlson & Langkilde, 2014). However most of them lack any consequences of this behavioral change on the ecosystem.

To answer the question whether we can add these finding to the concept of the ecology of fear, we should have a proper understanding of its definition. As proposed by Brown et al. (1999), the ecology of fear is ‘the melding of the prey and predator’s optimal behavior with their population and community-level consequences’. This means that the definition consists of two parts; 1); ‘the prey’s and predators’ optimal behavior’ and 2) ‘with their population and community-level consequences’. The first part says that the prey will adopt the behavior that is most favorable for them under predation risk. This will for example be a balance between their conflicting demands between food and safety, but will at least always maximize their fitness or reproductive success over their lifetime. This can result in changes like a lower metabolic rate, higher assimilation of nutrients, less time spend foraging or a lower clutch size. This means that a lot of publications on the changed behavior of the prey due to the presence of a predator do fall within the first part of the concept of the ‘ecology of fear’.

If we look at the second part of the definition we can explain this as the effects of the changed prey’s behavior on the populations of the prey and cascading effects on other trophic levels of the ecosystem. In a few of the publications that are found these effects are shown to exist, but in most of them they are not. Firstly, this is because in most of the studies included the authors did not intend to study the effects of the changed behavior of the prey but only wanted to prove that predators can have non-lethal effects on the prey of interest. However, in all of the studies one can hypothesize with good arguments what kind of effects the change in the behavior of the prey will have on the ecosystem, even if this effect is just small it might lead to cascading effects affecting the ecosystem. Secondly, one should keep in mind that the ecology of fear concept has been best studied in a wolf-deer system in which the wolf was fully exterminated from the ecosystem and later reintroduced (Ripple & Beschta, 2004). This creates a very special possibility to have a good look at the non-lethal effects of the predator after reintroduction. Of course in most predator-prey systems the predators have always been present and it is therefore harder to show that predators can induce cascading effects on lower trophic levels. Taking all of this together we could say that all of the findings on changed prey's behavior in a very diverse group of species can be seen as part of the concept of the ecology of fear. Hence, the ecology of fear can be found in a very diverse group of predator-prey interactions.

When looking even further into species interactions, one could argue that parasites could also be part of an ecology of fear. Some studies have shown that hosts of parasites avoid places where the parasite densities are high (Rohr et al., 2009; Allan, Varns, & Chase, 2010). Since this alters the behavior of the hosts and this change might influence other aspects of the ecosystems we can call this ecology of fear too, but in this case the fear is induced by parasites instead of predators.

Prey species group	**Number of publications**
Large mammals	7[a]
Birds	4[b]
Small mammals	3[c]
Insects	8[d]
Amphibians and reptiles	3[e]
Other	12[f]

Table 1: Publications from 2010 until now that show a predator mediated change in prey behavior. The publications are sorted on prey species group and found using the online database 'Web of Science' by searching on the topics 'predator mediated change in behavior' and 'non-consumptive effects of predators' ([a]: Gosselin et al., 2015; Le Saout et al., 2014; Marchand et al., 2014; Creel et al., 2013; Creel et al., 2011; Bonnot et al., 2013; White et al., 2014 / [b]: Hua et al., 2014; Travers et al., 2010; Cervencl et al., 2011; Bonnington, 2013 / [c]: Nersesian et al., 2012; Jochym & Halle, 2013; Breviglieri, 2013 / [d]: Hermann & Thaler, 2014; Wu et al., 2014; Schneider et al., 2014; Hernandez & Peckarsky., 2014; Lee et al., 2014; Belovskyc et al., 2011; Li et al., 2013; Fernandez-Ferrari & Schausberger, 2013 / [e]: Carlson et al., 2014; Barry & Syal, 2013; McKeon & Summers, 2013 / [f]: Kintzing & Butler, 2014; Freeman et al., 2014; Robinson et al., 2014; Lasley-Rasher &Yen, 2012; Maire et al., 2010; Molis et al., 2011, Manzur & Navarrete., 2011; Ory, 2012; Premo & Tyler, 2013; Reynolds & Bruno, 2013; Ruehl & Trexler, 2013; Calizza et al., 2013)

Discussion

The reintroduction of the wolves in Yellowstone park have shown us how important non-lethal effects of predators can be on shaping prey's behavior and even through cascading effects influence complete ecosystems. Also in other systems this ecology of fear has been found to exist. Often this ecology of fear is also called the landscape of fear. By looking at the definition of the ecology of fear and recent publications on predator-mediated change in prey's behavior I can conclude that the concept of the ecology of fear is widespread over different predator-prey systems and might also in these systems be very important. Therefore I would recommend authors that study predator-prey interactions to try to focus more on the effects of the changed behavior of the prey on the ecosystem and at least try to argue what kind of effects this might be. In this way we will learn more about the questions how important predators are and how important their non-lethal effects are in ecosystems. Eventually this will help us to better preserve ecosystems and biodiversity on our planet.

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