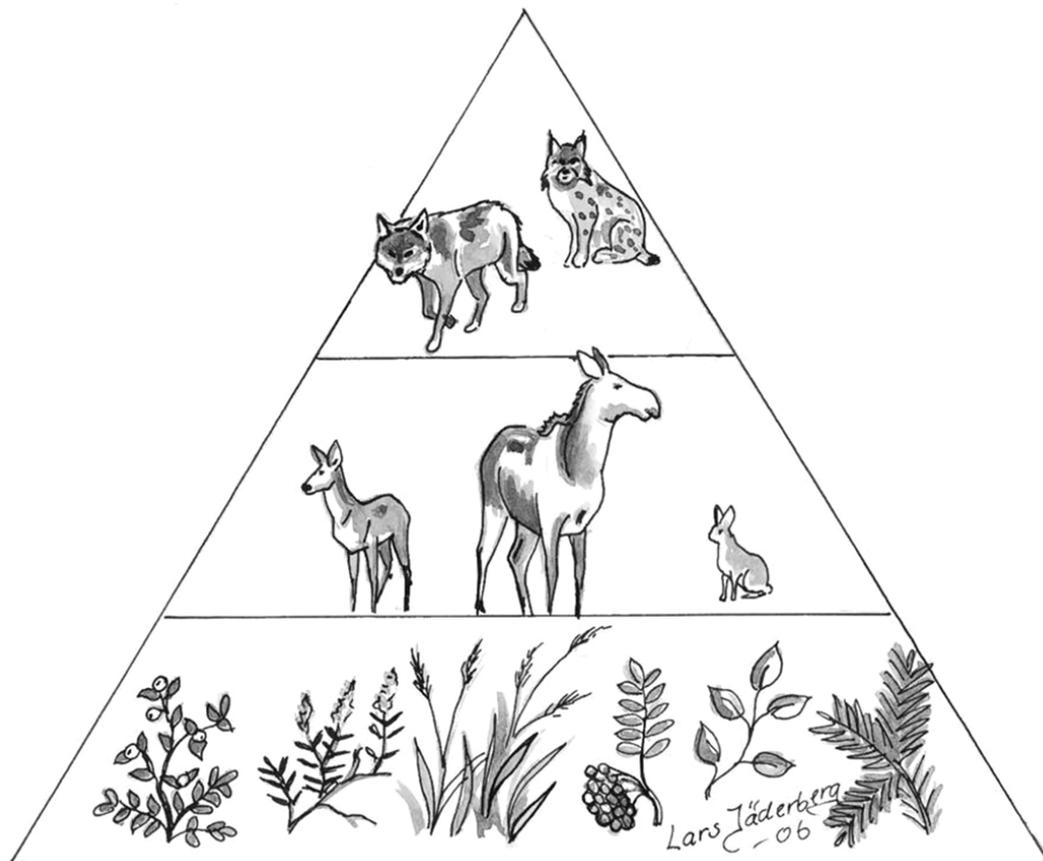




The role of large carnivores in trophic cascades

Camilla Wikenros



The role of large carnivores in trophic cascades

Contents

1. Introduction

2. Number of trophic levels

3. Density- or behavioural-mediated indirect interactions

4. Trophic cascades caused by large carnivores

4.1 Density-mediated indirect interactions

4.2 Behavioural-mediated indirect interactions

5. Comparison between terrestrial and aquatic ecosystems

6. Strength of top-down processes

7. Levels of trophic cascades

7.1 Species cascades

7.2 Community cascades

8. Compensatory mechanisms

8.1 Herbivore behaviour

8.2 Plant responses

8.3 Meso-carnivores

8.4 Top predators

9. Cascading effects in theoretical models

10. Discussion

10.1 Definition of trophic cascade

10.2 Further research

10.3 Importance of long-term studies

10.4 Wildlife management

10.5 Conclusion

11. Acknowledgements

12. Literature cited

Camilla Wikenros
Grimsö Wildlife Research Station
Department of Conservation Biology
Swedish University of Agricultural Sciences
SE-730 91 Riddarhyttan

1. Introduction

It has been widely debated since the 1960's whether ecosystems are regulated by top-down or bottom-up processes. Hairston *et al.* (1960) proposed the three-trophic-level hypothesis (also called the HSS-hypothesis after the author's last names). They were the first to suggest that because 'the world is green'; it is obviously not overgrazed by herbivores. Therefore, if it is not food that limits herbivores, it must be predation. Consequently, they concluded that density dependent processes control predators at upper trophic levels as well as producers and decomposers at lower trophic levels. Also, interspecific competition does occur in those trophic levels. In turn, density independent processes like predation are limiting herbivores in the middle level. Following this, herbivores do not compete for food. Hairston *et al.* (1960) also argued that predators at the top of food webs might control the abundance and distribution of producers at the bottom level. This model was soon criticised. Murdoch (1966) stated that the world is green because all plant material may not be edible as plants use toxic chemicals to defend themselves against herbivores, thereby proposing bottom-up regulated ecosystems.

The importance of competition was supported by Connell (1961) who concluded that the intensity of competition decrease with increased predation pressure. Later, Paine (1966) focused on predation as the driving force structuring the ecosystem. He reported that when predators are absent, the ecosystem is less diverse as large carnivores prevent monopolization by one species. However, an ecosystem can be regulated by both top-down and bottom-up processes (Oksanen *et al.* 1981, Fretwell 1987). If predators regulate herbivores, herbivores can not regulate plants and the vegetation is therefore regulated by nutrients, water and sunlight.

Paine (1980) was the first to use the term 'trophic cascade' but the concept is the same as proposed by Hairston *et al.* (1960). A trophic cascade is defined as a predator and prey interaction that has effects further down through more than one level in a food web. Plant biomass is ultimately affected by changes in predator abundance, via a series of intermediate links (Pace *et al.* 1999, Schmitz *et al.* 2000). Removing a top predator will therefore result in a greater abundance of consumers and less abundance of producers.

Cascading trophic interactions has been described mostly in aquatic ecosystems like open ocean (Frank *et al.* 2005), coastal (Estes *et al.* 1998), lakes (Jeppesen *et al.* 1998) and streams (Huryh 1998). It has been suggested that trophic interactions in terrestrial ecosystems are less evident because they may be blocked by complex interactions (Strong 1992, Polis and Strong 1996) or extensive omnivory in food webs (Pace *et al.* 1999). However, there are also trophic cascades described in terrestrial ecosystems (Schmitz *et al.* 2000) although in most cases conducted by invertebrate predators (Spiller and Schoener 1994, Shurin *et al.* 2002).

Regulation of terrestrial ecosystems may be more complicated than just the simple concepts of top-down or bottom-up effects. Polis and Strong (1996) stated that the linear food web theory do not have the diversity and breadth of phenomena found in nature. They also argued that, occasionally, top-down effects and trophic cascades may be triggered by sources outside the focal food web. Also, Pace *et al.* (1999) concluded that communities are complex food webs, not simple chains and they

referred to a wider range of interactions when they described trophic cascades as ‘strong interactions within food webs that influence the properties of the system’. Dawes-Gromadzki (2002) supported the idea that biotic and abiotic heterogeneity, intraguild interactions as well as non-consumptive interactions between trophic levels will result in a more complex food web than the classic top-down or bottom-up regulated ecosystem. However, the debate whether top-down or bottom-up processes, or both, are structuring the ecosystem is still ongoing. Also, the discussion whether small animals (Wilson 1987) or big animals (Terborgh 1988) ‘rule the world’ has not stopped yet. Noteworthy is the argument by Hunter and Price (1992): ‘...the removal of higher trophic levels leaves lower levels intact (if perhaps greatly modified), whereas the removal of primary producers leaves no system at all.’

2. Number of trophic levels

The three-trophic-level hypothesis presented by Hairston *et al.* (1960) was extended by introducing several levels of carnivores by Oksanen *et al.* (1981) and Fretwell (1987). The strength of carnivore-herbivore-plant interactions thus will vary with the number of carnivore levels in an ecosystem (Fretwell 1987). When this number is odd, i.e. one or three levels of carnivores, the plant-herbivore interactions will be weak, whereas an even number of carnivore levels gives strong plant-herbivore interactions. Estes *et al.* (1998) demonstrated declines of marine kelp forests after an increase of herbivorous sea urchins (*Strongylocentrotus* spp.), the main food for the aquatic sea otter (*Enhydra lutris*), after a new top predator, the killer whale (*Orcinus orca*), entered the ecosystem and increased the predation on the sea otter.

3. Density- or behavioural-mediated indirect interactions

Indirect effects of predators on plants may be due to changes in prey density because of predation, known as density-mediated indirect interactions, or evasive behaviour of herbivores known as behavioural-mediated indirect interactions (Abrams 1995). For example, Terborgh *et al.* (2001) presented evidence for density-mediated indirect interactions in a terrestrial ecosystem. They demonstrate that in the absence of top predators of invertebrates on islands outside Venezuela, consumers increased dramatically in numbers and are therefore not limited by food availability or plant defences. In addition, densities of seedlings of canopy trees were strongly reduced on predator-free islands (Terborgh *et al.* 2001).

Schmitz *et al.* (1997) concluded that indirect effects following anti-predator behaviour can cause trophic cascades that are similar to those caused by predation. They demonstrated similar decreases in impact on grass biomass by grasshoppers (*Melanoplus femurrubrum*) both via anti-predator behaviour because of predation risk and directly by spider (*Pisurina mira*) predation. This was a result of grasshopper foraged during the hottest part of the day when spiders were most inactive, as well as shifted diet in response to predation risk by spiders (Schmitz *et al.* 1997). However, this change of anti-predator behaviour may in turn result in increased vulnerability to predation in grasshoppers because the increased heat may induce heat stress.

4. Trophic cascades caused by large carnivores

4.1 Density-mediated indirect interactions

A few studies have been able to demonstrate density-mediated trophic cascades caused by large carnivores in terrestrial ecosystems. In Banff National Park, Canada, Hebblewhite *et al.* (2005) investigated effects of wolf (*Canis lupus*) predation on elk (*Cervus elaphus*) population density, aspen (*Populus tremuloides*) and willow (*Salix spp.*) recruitment and browse intensity, beaver (*Castor canadensis*) density as well as riparian songbird diversity (evenness and abundance). They found evidence that supported a trophic cascade caused by wolves' presence. Wolf exclusion decreased aspen recruitment and willow production, as well as beaver density and riparian songbird diversity and abundance.

A comparable study in Wyoming, USA, showed that the extinction of grizzly bears (*Ursus arctos*) and wolves resulted in high densities of moose (*Alces alces*) that in turn caused changes in the vegetation community (Berger *et al.* 2001). Willows were taller and had a greater volume in areas where moose densities were limited by humans as compared to areas without predation. Also, species richness of breeding birds and nesting density were higher in areas with lower moose densities and Berger *et al.* (2001) concluded a regulation by top-down processes in their study area. Similar relationships between herbivores, riparian habitat and birds have also been shown at sites grazed by domestic livestock (Dobkin *et al.* 1998).

McLaren and Peterson (1994) suggested that the fluctuating population densities of wolves on Isle Royale, Michigan, USA, control the abundance of moose which in turn control the abundance of balsam fir (*Abies balsamea*). However, the latest research conducted on Isle Royale does not support a top-down regulation of wolves on moose and in turn, balsam fir. Vucetich *et al.* (2002) argued that both bottom-up and top-down processes are important processes affecting moose population growth. Vucetich and Peterson's (2004), analysis of wolf-moose dynamics on Isle Royale demonstrated that more variation in moose population growth rate is explained by bottom-up (balsam fir abundance) than top-down processes (wolf predation), but abiotic factors (spring temperature and North Atlantic Oscillation) explained more variation than bottom-up processes. However, most of the variation in moose population growth rate is still unexplained and Vucetich and Peterson (2004) suggested that snow condition, parasites or forage quality might be factors explaining some of this residual variation. They also discussed age selective predation by wolves on moose as a factor affecting the population growth, and if true, this might be a top-down influence. Vucetich and Peterson (2004) explained the contradictory results from the Isle Royale ecosystem in earlier investigations as a result of how previous analyses (McLaren and Peterson 1994) focused on how average moose abundance is affected by mean levels of wolf abundance. Therefore, wolf predation predicts the mean density of moose but predict less of the variation around this mean.

In addition, Wright *et al.* (1994) studied the effect of exclusion of jaguar (*Felis onca*) and puma (*F. concolor*) on Barro Colorado Island, Panama, and made cross-site comparisons with Cosha Cashu, Peru, where the same predators are present. Even if they failed to prove that these large felids affect prey biomass, top-down processes may still be valid. Among *post hoc* explanations for the absence of a top-down effect of jaguar and puma was that habitat fragmentation and poaching resulted in the

removal of both large felids and herbivores. Alternatively, the explanation for lack of top-down processes may simply be that they do not exist, differences in habitat and methodology among study sites, or that the lack of effect on herbivores by felids is a result of felid dietary differences between the two study areas (Wright *et al.* 1994).

4.2 Behavioural-mediated indirect interactions

Indirect effect of carnivores on plants may depend on resource and habitat use by prey in relation to the presence of predators and predator habitat use and hunting mode (Schmitz *et al.* 2004). However, multiple predators may affect the same prey in different ways and prey may have different anti-predator behaviour against different predators.

Behavioural-mediated indirect effects caused by invertebrates in terrestrial ecosystems have been shown in several studies (for a review see Schmitz *et al.* 2004). However, evidences of behavioural-mediated indirect interactions caused by large carnivores in terrestrial ecosystems are few, but have been demonstrated by Post *et al.* (1999) and Ripple *et al.* (2001). Elk in Yellowstone National Park, Wyoming, USA, used a predation risk foraging strategy where they avoided aspen stands in areas that were highly used by wolves (Ripple and Larsen 2000, Ripple *et al.* 2001). Therefore, wolves had a behavioural-mediated indirect effect on aspen regeneration by changing elk movements.

During the last years the focus on how climate change will affect top predators as well as trophic cascades has increased (Post *et al.* 1999, Wilmers and Getz 2005). On Isle Royale, USA, trophic cascades has been shown to be mediated by wolf behavioural responses to climate. Pack size of wolves is partly regulated by winter snow, which in turn is related to the North Atlantic Oscillation. In turn, hunting pack size of wolves affect wolf kill-rates on moose and ultimately the level of herbivory on balsam fir (Post *et al.* 1999).

Trade-offs in prey can involve reduced foraging activity to increase vigilance (Abrams 1984). It has been shown that elk and bison (*Bison bison*) increased their vigilance level after the reintroduction of wolves in Yellowstone National Park, USA (Laundré *et al.* 2001). Laundré *et al.* (2001) suggested that those behavioural changes may influence on elk and bison ecology more than predation by wolves.

The availability of predator-safe refuges may affect the strength of regulation by predators on prey (Skogland 1991). Therefore, plant biomass can increase in areas without available cover for the prey species but decrease in areas with available cover for the prey species. Predation risk may also cause changes in behaviour of prey i.e. changes in diet, temporal changes in feeding patterns, spatial changes in habitat use or changes in patch selection (Lima and Dill 1990). For example, wolves spend less time along the territory edge due to risk of fatal encounters with other wolf packs (Mech 1977). This might explain why white-tailed deer (*Odocoileus virginianus*) are more numerous in edges of wolf territories as compared to the centre of wolf territories (Rogers *et al.* 1980). Also, White *et al.* (1998) reported new cohorts of aspen saplings, especially near high-use wolf trails, after wolf recolonization in Jasper National Park, Canada.

Ravens (*Corvus corax*) do associate with wolves during winter as a foraging strategy to discover carcasses early (Stahler *et al.* 2002). The extinction of large predators has resulted in a change in behaviour of moose. When predation is relaxed, moose do no longer respond to the sounds of ravens earlier associated with predation risk from wolves (Berger 1999). It has been reported that herbivores are able to quickly learn to adjust their behaviour in order to decrease predation risk after a recolonization of large carnivores. Berger *et al.* (2001) reported that moose quickly changed their behaviour to reduce predation from grizzly bears. However, in Scandinavia, moose did not change their anti-predator behaviour after a recolonization of a large carnivore, the wolf (Sand *et al.* 2006). The lack of response in anti-predator behaviour was explained by the fact that human harvest was the main mortality factor and not predation by large carnivores.

5. Comparison between terrestrial and aquatic ecosystems

It has been suggested that trophic cascades are less common in terrestrial ecosystems than in aquatic ecosystems (Polis and Strong 1996). This may be a result of that terrestrial plants contains anti-herbivore defences (Strong 1992, Polis and Strong 1996), or because of the higher diversity of species in terrestrial compared to aquatic ecosystems (Strong 1992). Schmitz *et al.* (2000) suggested that a decrease of the density of terrestrial herbivores may result in increased food consumption by herbivores due to decreased competition of food. More complex food webs with high species diversity may also reduce trophic cascade effects (Polis and Strong 1996, Schmitz *et al.* 2000). On the other hand, Schmitz *et al.* (2000) concluded in a review of 41 studies that trophic cascades are more common in terrestrial ecosystem than formerly supposed.

Ecosystems that are the most likely to fit the simple assumptions implied by the theoretical trophic cascade models are those that include homogenous habitat, prey population dynamics with rapid turnover in relation to predator dynamics, prey that is uniformly edible, as well as characterized by strong interactions between species (Polis *et al.* 2000). Those characteristics are more often found in aquatic ecosystems than in the more complex terrestrial ecosystem. However, one factor that complicates food web interactions, especially in aquatic ecosystems, is animals that have a juvenile stage that feeds at lower trophic levels than the adults (Persson 1999).

6. Strength of top-down processes

Schmitz *et al.* (2000) reported that the strength of top-down processes is similar in terrestrial ecosystems and aquatic ecosystems. However, these results have been questioned by Shurin *et al.* (2002), who concluded, when considering a wider range of aquatic ecosystems, that top-down control of plant biomass are stronger in marine and still water (lake, pond) ecosystems than on land and in streams. Plant biomass most often increase in the presence of predators but this effect is generally smaller than predicted from the predators' effects on herbivores (Spiller and Schoener 1994, Schmitz *et al.* 2000). The weakness of top-down processes remained in terrestrial ecosystems even when herbivores were reduced to the same extent as in aquatic ecosystems (Shurin *et al.* 2002).

Shurin *et al.* (2002) argued that differences in body size, biomass production, nutritional value of primary producers, and the fraction of the plant that is consumable for herbivores may lead to stronger trophic cascade effects in water than on land. However, they also suggested that variations within ecosystems like species diversity, behavioural responses, primary productivity, habitat or measurement error regulated the strength of trophic cascades more than differences between different ecosystems. It should be noted that evidence of top-down effects, or bottom-up effects, may be biased as researchers may not report studies that do not result in the expected outcome (Schmitz *et al.* 2000).

7. Levels of trophic cascades

7.1 Species cascades

Species cascades occur when changes in predator numbers affect only one or a few plant species. Nearly all demonstrated trophic cascades in terrestrial ecosystems are species cascades (Polis 1999). Also, in cases of demonstrated species-level cascades in terrestrial ecosystems, the result is not a change of a considerable part of plant biomass or productivity and may therefore be more a result of a statistical difference than biologically important (Polis 1999).

7.2 Community cascades

Community-level cascades affect the distribution of plant biomass in an entire ecosystem (Polis 1999). Even if carnivores have a positive indirect effect on some plants, other plant species may be negatively affected because of herbivores adjustment of foraging behaviour or habitat switch, as a result of the presence of top predators (Schmitz 1998). This may cause both negative and positive indirect effects on plants that may cancel each other out, resulting in the wrong conclusion that top predators have no net effect, when in reality a change in species composition is the right conclusion. It is therefore important to investigate more than just one or a few plant species when studying trophic cascades.

8. Compensatory mechanisms

Trophic cascades can be eliminated or reduced by compensatory mechanisms preventing the effects to propagate down the food web. The expression of compensation depends on the potential for individuals to respond to predation and on the diversity and complexity of food webs (Polis and Strong 1996).

8.1 Herbivore behaviour

Herbivores have the ability to reduce plant biomass (Bond and Loffell 2001). However, herbivores affect terrestrial plants less on a global scale but are probably more important at finer scales (Polis 1999). Top-down processes can be prevented by annual changes in the spatial distribution of herbivores, like migrating ungulate species (Skogland 1991, Mduma *et al.* 1999). Messier (1995) reported a three level ecosystem where a non-migrant ungulate, moose, is regulated by predators resulting in low impact of annual forage production. In contrast, Messier (1995) proposed a two level ecosystem for a migrant ungulate, caribou (*Rangifer tarandus*), that through its migratory behaviour avoids regulation by predation and achieves high density and thus might regulate plant production. However, a migratory behaviour by ungulates provide seasons with less predation pressure that may give plants a chance to recover

from high browse intensity. Also, age-differential prey vulnerability could influence the regulation by predators on prey populations and affect top-down processes (Skogland 1991).

8.2 Plant responses

When removing large predators, different categories of plants may be differently affected. Polis (1999) suggested that plant defence, nutritional shortage, abiotic factors, spatial and temporal heterogeneity, intra- and inter-specific interactions (territoriality, intraguild predation etc.), as well as predation, decrease herbivore consumption. The biomass of preferred plants decrease as herbivores feed on them, but a removal of large carnivores may lead to increased biomass of non-edible plants as a result of decreased inter-specific competition with preferred plant species (Schmitz *et al.* 2000). Therefore, examining community-level cascades are more important than species cascades as it otherwise are possible to draw the wrong conclusions (Polis 1999).

8.3 Meso-carnivores

Meso-carnivore (small and mid-sized predators) population densities may increase when a large carnivore is removed, which may have a negative effect on smaller prey due to decreased intraguild predation (Palomares *et al.* 1994). This was demonstrated in Yellowstone National Park, USA, where the coyote (*Canis latrans*) population was reduced with 50-90% after the reintroduction of wolves (Smith *et al.* 2003). However, the presences of wolves may on the other hand benefit scavenger species of meso-carnivores. Winters are getting shorter in Yellowstone National Park, USA, as a result of climate change, and this resulted in less food resources for scavenging species (Wilmers and Getz 2005). However, wolves in Yellowstone provided not only a higher availability of elk carcasses to scavengers as compared to environmental factors e.g. winter starvation (Wilmers and Getz 2005), but also a more even supply of these year round (Wilmers *et al.* 2003). Also, predator behaviour in response to climate variation can cause effects that propagate to lower trophic levels (Post *et al.* 1999).

8.4 Top predators

Pace *et al.* (1999) suggested that omnivory and replacement by other predators may restrict or reduce predatory impact and trophic cascades. In boreal ecosystems where moose are preyed upon by several predator species, moose density typically declined with each additional predator species, including human hunters (Gasaway *et al.* 1992, Peterson and Ciucci 2003). Other factors that influence the occurrence of trophic cascades may be cannibalism in predators (Polis and Strong 1996) or intraguild predation (Polis and Holt 1992). Also, prey choice by top predators may influence the extent of trophic cascades. Fretwell (1987) reported that removal of top predators mainly killing herbivores that have high probability of dying from starvation or other compensatory mortality factors will not increase prey densities. Furthermore, changes in foraging behaviour by one top predator may release the limiting effect of another predator on herbivores resulting in overgrazing of producers (Estes *et al.* 1998).

9. Cascading effects in theoretical models

Theoretical models have shown that the extinction of one species (primary extinction) can trigger a loss of other species (secondary extinctions) and then in turn affect the

whole community (Koh *et al.* 2004, Ebenman and Jonsson 2005). Borrvall *et al.* (2000) concluded, while using model food webs, that the risk of cascading extinctions increases in food webs with few species per functional group as compared to food webs with many species per functional group. In contrast to Pimm (1980), Borrvall *et al.* (2000) reported that the risk of secondary extinctions is higher when a plant species is removed as compared to the removal of a top predator species for a given number of species per functional group. Borrvall *et al.* (2000) explained this by the presence of intraspecific competition within herbivore species in their model food webs that decreased species extinction in lower trophic levels when a top predator is removed. The occurrence of intraspecific competition makes it less possible that herbivore species overgraze and eliminate plant species. Also, the lack of interspecific competition in their model food web makes it unlikely that any herbivore species will be dominant and eliminate other herbivores. Borrvall *et al.* (2000) also found that omnivory stabilized models of food webs. Moreover, Lundberg *et al.* (2000) used theoretical modelling and showed that the loss of a species may lead to permanent changes in the whole community that in turn makes it impossible for the lost species to re-invade the landscape.

10. Discussion

10.1 Definition of trophic cascade

The term ‘trophic cascade’ has been used with different definitions. Mostly a trophic cascade is defined as indirect effects of predators on plants mediated by herbivores (Persson 1999, Schmitz *et al.* 2004). However, trophic cascades have also been used to include horizontal interaction between species (Pace *et al.* 1998). In addition, the conclusion that trophic cascades not only are mediated because of density dependent processes but also mediated by changes in behaviour has caused a broader view on the term. Nowadays, the term trophic cascade has a wider definition not only including the classic three level proposed by Hairston *et al.* (1960) with a top predator controlling the ecosystem. Also factors like climate (Post *et al.* 1999), human activities (Steneck 1998), pollution (Sala *et al.* 1998), rainfall and soil nutrients (Gutiérrez *et al.* 1997), as well as diseases (Lindström *et al.* 1994) can cause trophic cascades. The use of the trophic cascade term can be confusing and the importance of a clear definition has been pointed out by Schmitz *et al.* (2000).

10.2 Further research

How and to what extent large carnivores affect the ecosystem is still poorly known, to a large extent because experimental evidence is missing. This might be a result of both legal and ethical problems as well as practical difficulties to perform experiments on endangered or threatened species (Estes 1996). A top predator removal experiment may also be hard to conduct because of the public opinion. As most of the research on terrestrial ecosystems has been conducted on invertebrates (for a review see Schmitz *et al.* 2000), further research concerning the influence of large carnivores needs to be conducted in order to increase our knowledge of processes in terrestrial ecosystems. Also, more research is needed regarding interactions between species in the same food web and behavioural mechanisms resulting in top-down processes.

Studying trophic cascades, top-down or bottom-up processes is difficult in practice. When removing all large predators from an area one has to deal with problems like different anti-predator behaviour among herbivores and finding areas without

influence from human activity. Humans may affect trophic cascades through fishing or hunting but the intensity of this are likely to vary between ecosystems. Skogland (1991) suggested that, instead of predator removal, the best experiment to study prey regulation might be to reduce the prey population without changing the predator population and then study the prey population's recruitment responses.

Estes (1996) proposed that for large carnivores the best way to investigate trophic cascades is to take the opportunities when large carnivores re-appear in areas where they have been absent. He suggested that changes in ecosystem structure due to variation in number of predators, habitat fragmentation, or changes through time (extinction, recolonization, species recovery or removal) are opportunities that should be taken to investigate trophic cascades. Unfortunately, situations like this, except artificial reintroductions and removals, are hard to predict. In addition they also lack replicates and are uncontrolled. The importance of control areas should be taken in account as the results from experiments without control areas may be unclear (Boutin 1992).

10.3 Importance of long-term studies

Most of the few trophic cascade experiments that have been conducted have been carried out in a short term perspective (Brett and Goldman 1997). Long-term experiments are necessary to determine the total effects on the ecosystem after manipulation. Also, Polis *et al.* (1998) as well as Vucetich and Peterson (2004) point out the importance of studying the effects of annual variation in population dynamics due to annual variations in abiotic processes. However, as demonstrated during the long-term study on Isle Royale, USA, regarding density-mediated indirect interactions of wolves on balsam fir production through predation on moose, both top-down, bottom-up and climate caused effects have been reported to control the ecosystem (McLaren and Peterson 1994, Post *et al.* 1999, Vucetich *et al.* 2002, Vucetich and Peterson 2004). Still, even after this excellent long-term study, most of the variation in moose population growth is unknown (Vucetich and Peterson 2004), despite the fact that the ecosystem on Isle Royale is not as complex and has lower species diversity as compared to many other terrestrial ecosystems. In general, most trophic cascades demonstrated in terrestrial ecosystems are species cascades, not community cascades, and in reality species cascades may be more statistically significant than biologically important for ecosystem processes.

10.4 Wildlife management

The role of top predators and ecological interactions must be known in order to be able to restore biodiversity (Ripple *et al.* 2001). It has been reported that fisheries and fish management change trophic cascades which results in severe consequences for food webs in costal ecosystems (Steneck 1998). Apparently, human-driven environmental change will result in new trophic cascades. Removal, recolonization or reintroduction of large carnivores from an ecosystem can have large effects on other species both through density- and behavioural-mediated indirect interactions. Knowing those consequences are vital for the management of wildlife. An understanding of negative effects caused by humans is required to provide management tools that are necessary for restoration and sustainability goals (Pace *et al.* 1999). However, since top-down processes have been shown to be stronger in aquatic ecosystems than in terrestrial ecosystems, human impact on large carnivores

in terrestrial ecosystems may have less effect on primary producers and ecosystem processes as compared to aquatic ecosystems (Shurin *et al.* 2002).

10.5 Conclusion

If ecosystems are regulated by top-down or bottom-up processes depend on the relative influence of limiting factors (predators) and limiting resources (producers) on community structure and function (Choquenot *et al.* 2001). Also, light and climate determines the greenness of the earth, and human activities play a major role in structuring ecosystems (Polis 1999). Trophic cascades are mostly reported from smaller predators, usually invertebrates, and in simple ecosystems. Even when large carnivores regulate the ecosystem by top-down processes it is not obvious that this result in trophic cascades and affect lower non-adjacent trophic levels. Compensatory mechanisms and interactions within and between adjacent trophic levels may prevent effects to propagate down the food web. The complexity of ecosystems makes it hard to predict when trophic cascades will occur.

11. Acknowledgements

I thank my supervisors Olof Liberg and Håkan Sand, as well as Jonas Nordström and Jens Persson, for valuable comments on earlier versions of this essay, and Lars Jäderberg who illustrated the front page.

12. Literature cited

- Abrams, P. A.** 1984. Foraging time optimization and interactions in food webs. - *The American Naturalist* 124: 80-96.
- Abrams, P. A.** 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. - *The American Naturalist* 146: 112-134.
- Berger, J.** 1999. Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. - *Proceedings of the Royal Society of London Series B-Biological Sciences* 266: 2261-2267.
- Berger, J., Stacey, P. B., Bellis, L. and Johnson, M. P.** 2001. A mammalian predator-prey imbalance: Grizzly bear and wolf extinction affect avian neotropical migrants. - *Ecological Applications* 11: 947-960.
- Berger, J., Swenson, J. E. and Persson, I. L.** 2001. Recolonizing Carnivores and Naive Prey: Conservation Lessons from Pleistocene Extinctions. - *Science* 291: 1036-1039.
- Bond, W. J. and Loffell, D.** 2001. Introduction of giraffe changes acacia distribution in a South African savanna. - *African Journal of Ecology* 39: 286-294.
- Borrvall, C., Ebenman, B. and Jonsson, T.** 2000. Biodiversity lessens the risk of cascading extinction in model food webs. - *Ecology Letters* 3: 131-136.
- Boutin, S.** 1992. Predation and moose population dynamics: a critique. - *Journal of Wildlife Management* 56: 116-127.
- Brett, M. T. and Goldman, C. R.** 1997. Consumer versus resource control in freshwater pelagic food webs. - *Science* 275: 384-386.
- Choquenot, D., Krebs, C. J., Sinclair, A. R. E., Boonstra, R. and Boutin, S.** 2001. Vertebrate community structure in the boreal forest. - In: Krebs, C. J., Boutin, S. and Boonstra, R. (eds.), *Ecosystem dynamics of the boreal forest: the Kluane project*. Oxford University Press, pp. 437-462.
- Connell, J. H.** 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. - *Ecology* 42: 710-723.
- Dawes-Gromadzki, T. Z.** 2002. Trophic trickles rather than cascades: Conditional top-down and bottom-up dynamics in an Australian chenopod shrubland. - *Austral Ecology* 27: 490-508.
- Dobkin, D. S., Rich, A. C. and Pyle, W. H.** 1998. Habitat and avifaunal recovery from livestock grazing in a riparian meadow system of the northwestern Great Basin. - *Conservation Biology* 12: 209-221.
- Ebenman, B. and Jonsson, T.** 2005. Using community viability analysis to identify fragile systems and keystone species. - *Trends in Ecology & Evolution* 20: 568-575.
- Estes, J. A.** 1996. Predators and ecosystem management. - *Wildlife Society Bulletin* 24: 390-396.
- Estes, J. A., Tinker, M. T., Williams, T. M. and Doak, D. F.** 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. - *Science* 282: 473-476.
- Frank, K. T., Petrie, B., Choi, J. S. and Leggett, W. C.** 2005. Trophic cascades in a formerly cod-dominated ecosystem. - *Science* 308: 1621-1623.
- Fretwell, S. D.** 1987. Food-Chain Dynamics - the Central Theory of Ecology. - *Oikos* 50: 291-301.

- Gasaway, W. C., Boertje, R. D., Grangaard, D. V., Kelleyhouse, D. G., Stephenson, R. O. and Larsen, D. G.** 1992. The Role of Predation in Limiting Moose at Low-Densities in Alaska and Yukon and Implications for Conservation. - *Wildlife Monographs*: 1-59.
- Gutierrez, J. R., Meserve, P. L., Herrera, S., Contreras, L. C. and Jaksic, F. M.** 1997. Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. - *Oecologia* 109: 398-406.
- Hairston, N. G., Smith, F. E. and Slobodkin, L. B.** 1960. Community structure, population control, and competition. - *The American Naturalist* 94: 421-425.
- Hebblewhite, M., White, C. A., Nietvelt, C. G., McKenzie, J. A., Hurd, T. E., Fryxell, J. M., Bayley, S. E. and Paquet, P. C.** 2005. Human activity mediates a trophic cascade caused by wolves. - *Ecology* 86: 2135-2144.
- Hunter, M. D. and Price, P. W.** 1992. Playing Chutes and Ladders - Heterogeneity and the Relative Roles of Bottom-Up and Top-Down Forces in Natural Communities. - *Ecology* 73: 724-732.
- Huryn, A. D.** 1998. Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream system. - *Oecologia* 115: 173-183.
- Jeppesen, E., Sondergaard, M., Jensen, J. P., Mortensen, E., Hansen, A. M. and Jorgensen, T.** 1998. Cascading trophic interactions from fish to bacteria and nutrients after reduced sewage loading: An 18-year study of a shallow hypertrophic lake. - *Ecosystems* 1: 250-267.
- Koh, L. P., Dunn, R. R., Sodhi, N. S., Colwell, R. K., Proctor, H. C. and Smith, V. S.** 2004. Species coextinctions and the biodiversity crisis. - *Science* 305: 1632-1634.
- Laundre, J. W., Hernandez, L. and Altendorf, K. B.** 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. - *Canadian Journal of Zoology* 79: 1401-1409.
- Lima, S. L. and Dill, L. M.** 1990. Behavioral Decisions Made Under the Risk of Predation - A Review and Prospectus. - *Canadian Journal of Zoology* 68: 619-640.
- Lindstrom, E. R., Andren, H., Angelstam, P., Cederlund, G., Hornfeldt, B., Jaderberg, L., Lemnell, P. A., Martinsson, B., Skold, K. and Swenson, J. E.** 1994. Disease Reveals the Predator - Sarcoptic Mange, Red Fox Predation, and Prey Populations. - *Ecology* 75: 1042-1049.
- Lundberg, P., Ranta, E. and Kaitala, V.** 2000. Species loss leads to community closure. - *Ecology Letters* 3: 465-468.
- McLaren, B. E. and Peterson, R. O.** 1994. Wolves, Moose, and Tree-Rings on Isle Royale. - *Science* 266: 1555-1558.
- Mduma, S. A. R., Sinclair, A. R. E. and Hilborn, R.** 1999. Food regulates the Serengeti wildebeest: a 40-year record. - *Journal of Animal Ecology* 68: 1101-1122.
- Mech, L. D.** 1977. Wolf-Pack Buffer Zones as Prey Reservoirs. - *Science* 198: 320-321.
- Messier, F.** 1995. Trophic Interactions in Two Northern Wolf-Ungulate Systems. - *Wildlife Research* 22: 131-146.
- Murdoch, W. W.** 1966. Community structure, population control, and competition: a critique. - *The American Naturalist* 100: 219-226.
- Oksanen, L., Fretwell, S. D., Arruda, J. and Niemelä, P.** 1981. Exploitation ecosystems in gradients of primary productivity. - *The American Naturalist* 118: 240-261.

- Pace, M. L., Cole, J. J. and Carpenter, S. R.** 1998. Trophic cascades and compensation: Differential responses of microzooplankton in whole-lake experiments. - *Ecology* 79: 138-152.
- Pace, M. L., Cole, J. J., Carpenter, S. R. and Kitchell, J. F.** 1999. Trophic cascades revealed in diverse ecosystems. - *Trends in Ecology & Evolution* 14: 483-488.
- Paine, R. T.** 1966. Food web complexity and species diversity. - *The American Naturalist* 100: 65-75.
- Paine, R. T.** 1980. Food webs: linkage, interaction strength and community infrastructure. - *Journal of Animal Ecology* 49: 667-685.
- Palomares, F., Gaona, P., Ferreras, P. and Delibes, M.** 1995. Positive Effects on Game Species of Top Predators by Controlling Smaller Predator Populations - An Example with Lynx, Mongooses, and Rabbits. - *Conservation Biology* 9: 295-305.
- Persson, L.** 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. - *Oikos* 85: 385-397.
- Peterson, R. O. and Ciucci, P.** 2003. The Wolf as a Carnivore. - In: Mech, L. D. and Boitani, L. (eds.), *Wolves: Behavior, Ecology and Conservation*. University of Chicago Press, pp. 104-130.
- Pimm, S. L.** 1980. Food web design and the effect of species deletion. - *Oikos* 35: 139-149.
- Polis, G. A. and Holt, R. D.** 1992. Intraguild Predation - the Dynamics of Complex Trophic Interactions. - *Trends in Ecology & Evolution* 7: 151-154.
- Polis, G. A. and Strong, D. R.** 1996. Food web complexity and community dynamics. - *American Naturalist* 147: 813-846.
- Polis, G. A., Hurd, S. D., Jackson, C. T. and Sanchez-Pinero, F.** 1998. Multifactor population limitation: Variable spatial and temporal control of spiders on Gulf of California islands. - *Ecology* 79: 490-502.
- Polis, G. A.** 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. - *Oikos* 86: 3-15.
- Polis, G. A., Sears, A. L. W., Huxel, G. R., Strong, D. R. and Maron, J.** 2000. When is a trophic cascade a trophic cascade? - *Trends in Ecology & Evolution* 15: 473-475.
- Post, E., Peterson, R. O., Stenseth, N. C. and McLaren, B. E.** 1999. Ecosystem consequences of wolf behavioural response to climate. - *Nature* 401: 905-907.
- Ripple, W. J. and Larsen, E. J.** 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. - *Biological Conservation* 95: 361-370.
- Ripple, W. J., Larsen, E. J., Renkin, R. A. and Smith, D. W.** 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. - *Biological Conservation* 102: 227-234.
- Rogers, L. L., Mech, L. D., Dawson, D. K., Peek, J. M. and Korb, M.** 1980. Deer distribution in relation to wolf pack territory edges. - *Journal of Wildlife Management* 44: 253-258.
- Sala, E., Boudouresque, C. F. and Harmelin-Vivien, M.** 1998. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. - *Oikos* 82: 425-439.
- Sand, H., Wikenros, C., Wabakken, P. and Liberg, O.** 2006. Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? - *Proceedings of the Royal Society B-Biological Sciences* 273: 421-427.

- Schmitz, O. J., Beckerman, A. P. and Obrien, K. M.** 1997. Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. - *Ecology* 78: 1388-1399.
- Schmitz, O. J.** 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. - *American Naturalist* 151: 327-342.
- Schmitz, O. J., Hamback, P. A. and Beckerman, A. P.** 2000. Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. - *American Naturalist* 155: 141-153.
- Schmitz, O. J., Krivan, V. and Ovadia, O.** 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. - *Ecology Letters* 7: 153-163.
- Shurin, J. B., Borer, E. T., Seabloom, E. W., Anderson, K., Blanchette, C. A., Broitman, B., Cooper, S. D. and Halpern, B. S.** 2002. A cross-ecosystem comparison of the strength of trophic cascades. - *Ecology Letters* 5: 785-791.
- Skogland, T.** 1991. What Are the Effects of Predators on Large Ungulate Populations. - *Oikos* 61: 401-411.
- Smith, D. W., Peterson, R. O. and Houston, D. B.** 2003. Yellowstone after wolves. - *Bioscience* 53: 330-340.
- Spiller, D. A. and Schoener, T. W.** 1994. Effects of Top and Intermediate Predators in A Terrestrial Food-Web. - *Ecology* 75: 182-196.
- Stahler, D., Heinrich, B. and Smith, D.** 2002. Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. - *Animal Behaviour* 64: 283-290.
- Steneck, R. S.** 1998. Human influences on costal ecosystems: does overfishing create trophic cascades? - *Trends in Ecology & Evolution* 13: 429-430.
- Strong, D. R.** 1992. Are Trophic Cascades All Wet - Differentiation and Donor-Control in Speciose Ecosystems. - *Ecology* 73: 747-754.
- Terborgh, J.** 1988. The big things that run the world – a sequel to E. O. Wilson. - *Conservation Biology* 2: 402-403.
- Terborgh, J., Lopez, L., Nunez, P., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G. H., Lambert, T. D. and Balbas, L.** 2001. Ecological meltdown in predator-free forest fragments. - *Science* 294: 1923-1926.
- Vucetich, J. A., Peterson, R. O. and Schaefer, C. L.** 2002. The effect of prey and predator densities on wolf predation. - *Ecology* 83: 3003-3013.
- Vucetich, J. A. and Peterson, R. O.** 2004. The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. - *Proceedings of the Royal Society of London Series B-Biological Sciences* 271: 183-189.
- Vucetich, J. A., Smith, D. W. and Stahler, D. R.** 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. - *Oikos* 111: 259-270.
- White, C., Olmsted, C. and Kay, C.** 1998. Aspen, elk, and fire in the Rocky Mountain National Parks of North America. - *Wildlife Society Bulletin* 26: 449-462.
- Wilmers, C. C., Crabtree, R. L., Smith, D. W., Murphy, K. M. and Getz, W. M.** 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. - *Journal of Animal Ecology* 72: 909-916.

- Wilmers, C. C. and Getz, W. M.** 2005. Gray wolves as climate change buffers in Yellowstone. - *Plos Biology* 3: 571-576.
- Wilson, E. O.** 1987. The little things that run the world (The importance and conservation of invertebrates). - *Conservation Biology* 1: 344-346.
- Wright, S. J., Gompper, M. E. and Deleon, B.** 1994. Are Large Predators Keystone Species in Neotropical Forests - the Evidence from Barro-Colorado Island. - *Oikos* 71: 279-294.

Department of Conservation Biology, SLU, Introductory Research Essays:

1. Glimskär, Anders, 1998. Establishment from seeds in grasslands.
2. Ryberg, Ulrika, 1998. Alternative male mating behaviour: Emphasising alternative male mating tactics in ungulates.
3. Roos, Staffan, 1998. Effects of nest predation on bird communities.
4. Wiklund, Karin, 1998. Population ecology of bryophytes with focus on the epixylic moss species *Buxbaumia viridis*, including a review of metapopulation dynamics in plant populations
5. Mace, Richard, 1999. Large carnivore management in the boreal forest.
6. Azeria, Ermias, 1999. Shortcuts and the ecological foundation in the design of Nature Reserves: possibilities, prospective and drawbacks.
7. Jarnemo, Anders, 1999. Factors affecting neonatal predation in ungulates.
8. Lazdinis, Marius, 2000. Sustainable forest development.
9. Seiler, Andreas, 2001. Ecological Effects of Roads – a review.
10. Johansson, Per, 2001. Abundance, distribution and rarity - general patterns, relationships to species extinction risk and applications in biodiversity monitoring.
11. Danell, Anna, 2002. Modelling Predator-Prey Relationships.
12. Roberge, Jean-Michel, 2002. The umbrella species concept in conservation biology: a critical review.
13. Wretenberg, Johan, 2003. Farmland birds – Agricultural intensification and population trends in Britain and Sweden.
14. Arlt, Debora, 2003. Constraints of habitat selection in birds - On the difficulty to make a decision.
15. Sjögren, Jörgen, 2004. Dead wood in Swedish forests - including aspects on bryophyte ecology.
16. Månsson, Johan, 2004. Factors affecting foraging decisions of deer at different spatial scales.
17. Perhans, Karin, 2005. Reserve selection methods.
18. Hedblom, Marcus, 2005. Urban sprawl and biodiversity.
19. Vanpé, Cécile, 2005. Male mating systems and sexual selection in ungulates.
20. Caruso, Alexandro, 2005. Epiphytic and epixylic lichens: important ecological factors.
21. Wissman, Jörgen, 2005. Effects of management on phenological traits in grassland plants.
22. Gustafson, Tomas, 2005. Nest predation in birds – important concepts and methodological problems.
23. Pihlgren, Aina, 2005. Vascular plants and small-scale spatial heterogeneity in semi-natural grasslands.
24. Nordström, Jonas, 2005. The role of predation as a limiting factor in ungulate populations.
25. Gustavsson, Eva, 2005. The use of historical maps in biodiversity research.
26. Mattisson, Jenny, 2006. Approaches to study intraguild interactions among carnivores.
27. Wikenros, Camilla, 2006. The role of large carnivores in trophic cascades.

Earlier publications in this series were listed as follows: Introductory Research Essays, Department of Wildlife Ecology, SLU. Publications in the earlier series may, if available, be ordered from the Department of Conservation Biology

1. Säterberg, L. 1986. Reproductive modes and intersexual differences in variations of breeding success in urodele amphibians.
2. Edenius, L. 1989. Interactions between large generalist herbivores and plants. Relation to ecological models and hypothesis.
3. Hjältén, J. 1989. Optimal foraging by herbivores and their impact on plant populations.
4. Berg, Å. 1990. Jordbruket och fågelfaunan – en översikt av förändringarna inom jordbruket, jordbruksfåglarnas status och populationsförändringar.
5. Atlegrim, O. 1990. Towards a general theory of community structure?
6. Johnsson, K. 1991. Factors affecting birds using natural tree-holes.
7. Kindvall, O. 1991. Acoustic communication in bushcrickets.
8. Sand, H. 1991. Life history in female cervids – factors affecting reproduction.
9. Nelin, P. 1991. Seasonal changes in food utilization by large generalist herbivores.
10. Mikusinski, G. 1992. Maintaining biodiversity in communities: The keystone species hypothesis.
11. Faber, W.E. 1993. The importance of sodium and potassium in the physiology of wild mammalian herbivores.
12. Edenhamn, P. 1993. Metapopulation dynamics: facts, artifacts and theory.
13. de Jong, J. 1994. The energetics of bats in the temperate region.
14. Welander, J. 1994. Biodiversity by different disturbance regimes and its maintenance.
15. Helldin, J-O. 1994. Responses of boreal carnivores to cyclically fluctuating prey.
16. Jasinski, K.M. 1995. Understanding wildlife needs through the understanding of landscape dynamics.
17. Åberg, J. 1995. Effects of forest fragmentation in boreal forest on birds and mammals.
18. Delin, A. 1995. Population ecology of tree squirrels.
19. Jansson, G. 1995. Indicator systems in conservation biology – objectives and obstacles.
20. Söderström, B. 1995. Agricultural birds and habitat change.
21. Berggren, Å. 1996. Wing polymorphism in insects: its occurrence and impact on population dynamics.
22. Kjellander, P. 1996. Density-dependence and density-independence in ungulate population demography.
23. Uliczka, H. 1996. The importance of habitat continuity in time and space and how to measure it.