Predators in low arctic tundra and their impact on community structure and dynamics

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Abstract

The abundance of predators and their impact on ecosystem dynamics is a vividly discussed topic in current ecology. In my studies, incorporating field observations, field experiments and theoretical modeling, I explored the importance of predators and predation in a low arctic tundra ecosystem in northern Norway. This involved observing the abundance and spatial activity of predators (raptors and small mustelids); manipulating the abundance of predators (spiders and birds) in an arthropod community; and exploring the theoretical consequences of intraguild predation on the coexistence among predators.

The results show that predation is important both in the arthropod assemblage and, depending on the productivity of the community, in the vertebrate assemblage. In arthropod communities predators are at least as abundant as their prey, whereas in the vertebrate part of ecosystem, predators are substantially less abundant than their prey. Still, in both cases predators had strong impact on their prey, influencing the abundance of prey and the species composition of prey assemblages. The impact of predation cascaded to the plant community both in the reticulate and complex arthropod food web and in the linear food chain-like vertebrate community. In the vertebrate-based community we could even observe the long time scale effect on plant community composition.

Within the predator community, exploitation competition and intraguild predation were the structuring forces. As the arthropod communities consist of predators with different sizes, intraguild predation is an energetically important interaction for top predators. As a consequence, they reduce the abundance of intermediate predators and the impact of intermediate predators on other prey groups. Moreover, being supported by intermediate predators, top predators can have stronger impact themselves on other prey groups.

In vertebrate communities, intraguild predation seems to be unimportant as energetic link, instead it manifests as an extreme version of interference competition. Therefore intraguild predation reduces the likelihood of coexistence, as it is due limited prey diversity and intense exploitative competition already precarious in the low arctic tundra.

In conclusion, predators have strong impact on their prey, especially in the more productive parts of the low arctic tundra. This applies even to the food webs with complex and reticulate structure, and these effects carry through the community both in the short time scale of population growth and on the long time scale of population generations.

Key words: arthropods, coexistence, community dynamics, competition, food webs, hypothesis of exploitation ecosystems, intraguild predation, small mustelids, trophic cascades.

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The Road goes ever on and on
Down from the door where it began.
Now far ahead the Road has gone,
And I must follow, if I can,
Pursuing it with eager feet,
Until it joins some larger way
Where many paths and errands meet.
And whither then? I cannot say.

J.R.R.Tolkien

Cover: by Karin Nilsson

LIST OF PAPERS

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals.

I. Oksanen, L., **Aunapuu, M.**, Oksanen, T., Schneider, M., Ekerholm, P., Lundberg, P.A., Armulik, T., Aruoja, V. and Bondestad, L. 1997. Outlines of food webs in a low arctic tundra landscape in relation to three theories on trophic dynamics. In *Multitrophic interactions in terrestrial systems.* (A.C. Gange and V.K. Brown, eds.), pp. 351-373. Blackwell Scientific Publications, Oxford.

II. **Aunapuu, M.**, Oksanen, T., Oksanen, L., Grellmann, D., Schneider, M. and Rammul, Ü. Biomass patterns in European tundra as a test of hypotheses on trophic dynamics. *Manuscript.*

III. **Aunapuu, M.** and Oksanen, T. 2003. Habitat selection of coexisting competitors: a study of small mustelids in northern Norway. *Evolutionary Ecology* 17: 371-392.

IV. **Aunapuu, M.**, Oksanen, L. and Oksanen, T. Intraguild predation and coexistence in vertebrate predators. *Manuscript.*

V. **Aunapuu, M.**, Oksanen, T. and Atlegrim, O. Predation structures the low arctic tundra arthropod community. *Manuscript.*

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Contributions
In paper I my role was performing the vertebrate predator studies in 1994 and 1995 and analyzing the predator data from 1988-1995. In papers II-IV my role has been planning and performing field studies (in paper II since 1994), experiments, modeling, and analyzing the data. In paper V my responsibility was collecting of the plant and predator data and analyzing all the data except the Highland experiment. I have been responsible for writing the papers II-V.

CONTENTS

BACKGROUND

In 1998 when I started as PhD student the great controversy of 1990's concerning the role of bottom-up and top-down forces in community dynamics (see Matson and Hunter 1992) was fading (Persson *et al.* 1996, Leibold *et al.* 1997, Menge *et al.* 1997).

However, on the ground of the previous debate a new topic was blossoming – the occurrence and importance of trophic cascades (Abrams 1996, Persson *et al.* 1996, Pace *et al.* 1999). As with the previous debate, two distinct, opposing sides could be distinguished: on one side proponents of trophic cascades, claiming trophic cascades to be general and dominating phenomena (Hairston and Hairston 1997, Moen and Oksanen 1998, Moran and Hurd 1998, Pace *et al.* 1998). And the other side manned with those arguing for trophic cascades being small extracts from large community assemblages, restricted to few species or special cases (Polis and Strong 1996, Polis 1999).

As a new member of Joatka research group my task was to study the impact of predators in a low arctic tundra, with emphasis on the importance of interactions among predators. Here I explain what and why I did and what I discovered.

Trophic cascades

The term 'trophic cascade' was used first by Paine (1980), though the concept was presented already two decades earlier by Hairston *et al.* (1960), in what has become known as the green world hypothesis (abbreviated as GWH or HSS from authors' names). The basic idea of HSS (Fig. 1) is that predators regulate the abundance of herbivores, in turn releasing plants from consumer (i.e., herbivore) regulation. Under such a scenario there would be so much vegetation that the world would be experienced as green.

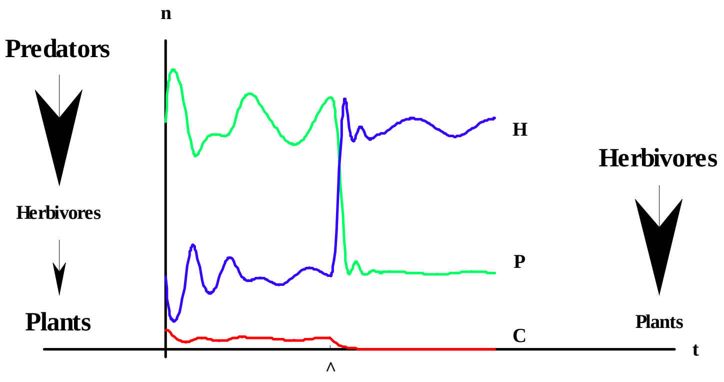

Figure 1. *Community dynamic according to HSS, and the occurrence of trophic cascade after the elimination of predators (C) at '^'. Other labels are: 'H' – herbivores, 'P' – plants, 't' – time, 'n' – abundance. Left side of the graph represents the community before and right side after the elimination of predators. Size of the arrows and font represent the energy and material flow between the trophic levels, and the relative abundance of groups. The abundance scale on the plot is arbitrary and absolute levels of population abundance are not comparable.*

Two important assumptions are made here. First, that species can be agregated, depending on where they get their energy from, into distinct groups – so called trophic levels (Lindeman 1942). In the case of HSS the levels are predators (top trophic level), herbivores (intermediate level) and plants (basal level). The second assumption is that there are strong interactions (sensu Paine 1980) between these groups and therefore they are able to impact each others abundance. When the top trophic level goes extinct (at '^' in the Fig. 1) there will be large changes in the abundance of the remaining trophic levels. As herbivores are released from predation pressure they can now increase and consequently suppress the abundance of plants. The term 'trophic cascade' seems to be used both directly for the event of actual change of community structure (i.e., what happens on the right side of the Fig. 1) and indirectly, assuming that an abundance pattern in a community we observe is due strong interactions among species (the left side of the Fig. 1).

Classic examples of trophic cascades come from aquatic systems. On Aleutian Islands, Alaska, the over harvesting of sea otters *Enhydra lutris* by fur industry in 20th century caused a decline in population numbers (Estes *et al.* 1978). Consequently, populations of the sea urchin *Strongylocentrotus droebachiensis*, the main prey of sea otters, increased dramatically. Grazing by sea urchins in turn reduced the abundance of algae and kelp, lowering even the diversity of other plants and animals in the community. In aquatic ecology, several experimental studies have demonstrated how trophic cascades can occur (Strong 1992, Carpenter & Kitchell 1993, Pace *et al.* 1999). However, trophic cascades are not limited to aquatic systems. There is ample of evidence for trophic cascades in terrestrial communities also (reviews by Schmitz *et al.* 2000, Halaj and Wise 2001, Shurin *et al.* 2002).

It is worth to note that for a trophic cascade to occur, the lumping of species into trophic levels is not necessary. Polis (1999) distinguished between 'species cascades' and 'community-level cascades'. In first case, changes in predator numbers affect few plant species, e.g., birds preying on insects which are foraging on a single plant species (Atlegrim 1989, Marquis and Whelan 1994, Moran and Hurd 1998). In the case of community-wide cascade, as in above cited sea otter example, 'plant biomass changes substantially throughout an entire system' (Polis 1999, p. 10).

Hypothesis of exploitation ecosystems

The idea of HSS (Hairston *et al.* 1960) was further ellobarated by Fretwell (1977) and Oksanen *et al.* (1981) in what has become known as the hypothesis of exploitation ecosystems (EEH). The basic idea was derived from observations that ecological communities differ in their primary productivity and that there is energy loss in the transfer from one trophic level to the next (Lindeman 1942). Therefore, in unproductive communities only plants are expected to be present – herbivore populations cannot persist as the resource levels are too low for herbivores to sustain themselves. Increasing productivity will cause an increase in plant biomass (Fig. 2) until it reaches a level where herbivore populations can be supported. Further increases in primary productivity allow herbivores to regulate the plant biomass to a constant level, and then only herbivore biomass increases. With an increased primary productivity and no herbivory, plant biomass would continue to increase, as depicted

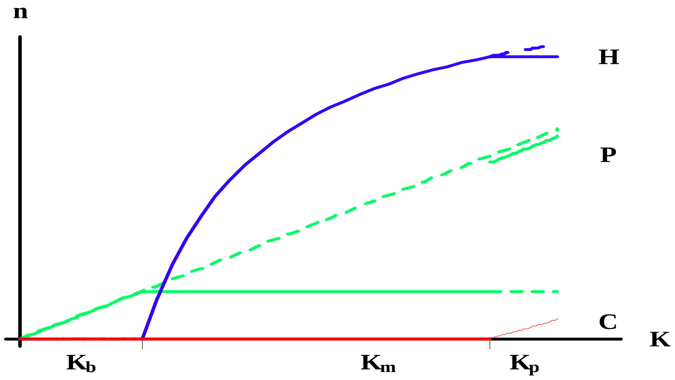

Figure 2. *Equilibrium community biomass (n) along productivity (K) gradient according EEH. In barren communities (K_b) only plants (P) are present. Increase in productivity (K_m – moderate productivity) allows invasion of herbivores (H). In very productive communities (K_p) predators (C) are also present. The abundance scale is arbitrary and absolute levels of population abundance are not comparable. See text for further explanation. Broken lines depict the biomass level that would be reached at given primary productivity without invasion of a higher trophic level.*

by the broken line in the Fig. 2. In even more productive communities, predators can exist. Being the top level, predators regulate herbivores to a constant level and the biomass of predators increases with increasing primary productivity. Without predators, herbivore biomass would continue to increase along the broken line as depicted in Fig. 2. Plants are again released from the herbivore control, and their biomass increases again with increasing primary productivity. Note the abrupt increase in plant biomass with the invasion of predators and that the level of equilibrium plant biomass is lower than it would be in the absence herbivores (Fig. 2).

Summarizing, the essence of EEH is that members of the top trophic level are involved in exploitative competition. The top trophic level regulates the adjacent lower trophic level via consumption. If there exists even a next lower trophic level, then that community is structured by exploitative competition, though the intensity is lower than it would be in a situation with the same productivity and with no higher trophic levels.

Except for the emphasis on the role of primary productivity, EEH has similar assumptions to HSS, but the predictions differ. According to the HSS, predators always regulate consumers and the observed plant biomass is held close to the maximum possible for any given abiotic conditions. According to the EEH, this applies only to productive communities. In moderately productive communities, the trophic level of predators is absent and plant biomass is suppressed by herbivores below the level that could be sustained in the absence of herbivores. Studies, corroborating the predictions of EEH have been performed both in aquatic (Power *et al.* 1985, Persson *et al.* 1988) and terrestrial ecosystems (Fraser and Grime 1997, Olofsson *et al.* 2002, and ref. therein).

Reticulate food webs

The above presented ideas (HSS and EEH) require that communities can be depicted in principle as in Fig. 1, with distinct strongly linked and interacting groups of organisms. However, it has been vigorously argued that natural communities are more complex than this and that species are generally too different to allow meaningful lumping into larger trophic groupings (Cousins 1987, Polis 1994, Persson 1999). Such workers argue that ideally every species should be treated individually. However, in practice even trophic level skeptics pool similar species together into functional groups in order to keep tractability (e.g., Fig. 2 in Polis 1991, with 10 species grouped into the unit 'Termites').

Regardless, when there are many interacting units, either species or functional groups, then each unit will potentially interact with many others, contrary to Fig. 1 where each group interacts only with just one or a maximum of two other groups. There will then be many pathways for energy transfer in a community (Fig. 3 a) and the impact of strong interactions may become diluted (Strong 1992, Polis 1994). In such a scenario, removal of a species would not necessarily lead to large changes in the community assemblage (Fig. 3 b). For example, in the Fig. 3b the consumer 'H4' has been released from regulation by top predator 'C4', but consumer 'H4' is unable to take advantage of this as its resource base is kept low by the competing consumer 'H3'. Or if a basal prey (P2) goes extinct, it may pass more or less unnoticed too, as there are alternative resources for its consumers (i.e., H2 can also forage on P3).

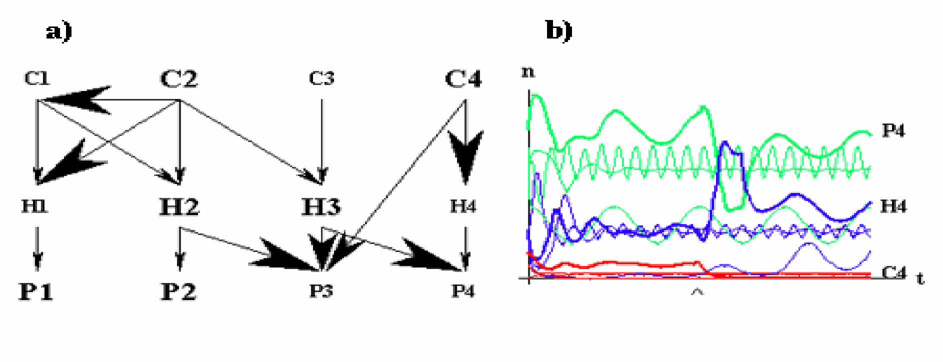

Figure 3. *a) A complex food web with four functional groups in plants (P), intermediate consumers (H) and top consumers (C). There are omnivorous links (from C4 to P3) and intra-guild predation (from C2 to C1). Relative abundance of groups and interaction strength between them are indicated by label and arrow size respectively. b) Removal of a top predator (C4 at '^') may have no (large) observable effect on the community dynamics.*

A second potential complication is that instead of merely regulating the total abundance of the lower trophic level, consumers may change abundance relationships within that lower trophic level (Leibold 1989, Leibold *et al.* 1997, Olofsson *et al.* 2001). Consumption (predation or herbivory) favors resources that are better adapted to apparent competition (Holt 1977), i.e., tolerate higher consumer densities.

Omnivory and intraguild predation (IGP) can further increase the complexity of food webs. Omnivorous consumers can compete with its own resource (Polis 1991, Diehl and Feißel 2000) and intraguild predators both compete with and consume other predators (Polis *et al.* 1989, Finke and Denno 2003, Morin 1999, Fedriani *et al.* 2000). As a result of these additional links, energy can pass between non adjacent trophic levels or within a trophic level (Fig. 3a, Schoener 1989, Hall and Raffaelli 1991). The consequence can be that a top predator can enter the community at lower primary productivity than depicted in the Fig. 2 or that a species' sensitivity to changes in the abundance of its resources can be reduced (Fig. 3 b).

Study area

Our study site Joatka is located conveniently at one-day drive from Umeå, in northern Norway at 69°45' N 23°55' E (Fig. 4). Vegetation and topology are detailed in (Oksanen and Virtanen 1995, Ekerholm *et al.* 2001).

The main study area, where most of the plant, herbivory, and predation studies were carried out, is 16.8 km^2 (Fig. 4 b). Based on the topology and vegetation it can be divided into four sub areas that differ markedly in primary productivity. Highland (maximum altitude 672 m a.s.l.) lies on a higher plateau and is dominated by heath vegetation, open mires and snowbed vegetation. The productive vegetation here consists of dwarf birch (*Betula nana*) bushes mixed with occasional willow (*Salix sp.*) individuals along creeks, reaching a height of approximately half a meter. Snow cover lasts longest on Highland and snow is very densely packed.

For raptor studies, we extended the study area to 105.7 km^2, as raptors have large home ranges and low densities (Fig. 4 a). In this extended part of Highland the altitude decreases slightly (lowest point is 444 m a.s.l.) and it becomes more similar to Divide. Even cloudberry (*Rubus chamaemorus*) bogs and larger stands of willow occur here. To the south, Highland ends abruptly in vertical cliffs, which are occasionally up to dozen meters high. The sub area below the escarpment is called Slope. It runs in east – west direction and has a mean inclination of 20 meters per 100 meters. This southern exposure together with exposure of nutrient rich bedrocks and abundance of water streams has created favorable conditions for vegetation. The tree line reaches up to 500 m a.s.l. and below that there is almost continuous mountain birch (*Betula pubescens*) forest, with heights of up to ten meters. Meadows and willow scrublands occur in some places. Above the tree line there is lush bilberry (*Vaccinium myrtillus*) heath. At the bottom of Slope, where the topography evens out the forest forms a distinct edge and this is used to define the border between Slope and Valley, the next sub area towards south. Valley, with its lowest point at 383 m a.s.l, is characterized by lakes, creeks and open mires. Productive vegetation, i.e., cloudberry bogs, willow mire, and even patches of trees occur along the creeks and on the southern slopes of hills.

The southernmost part of the study area, Divide is a typical low arctic tundra landscape with slightly rolling hills that are covered dominatingly by barren heaths with moderately productive vegetation at the base. The border between Valley and Divide is defined by the vegetation and the landscape. Divide is characterized by the abundance of smaller and larger lakes and ponds. In favorable places, in topographical

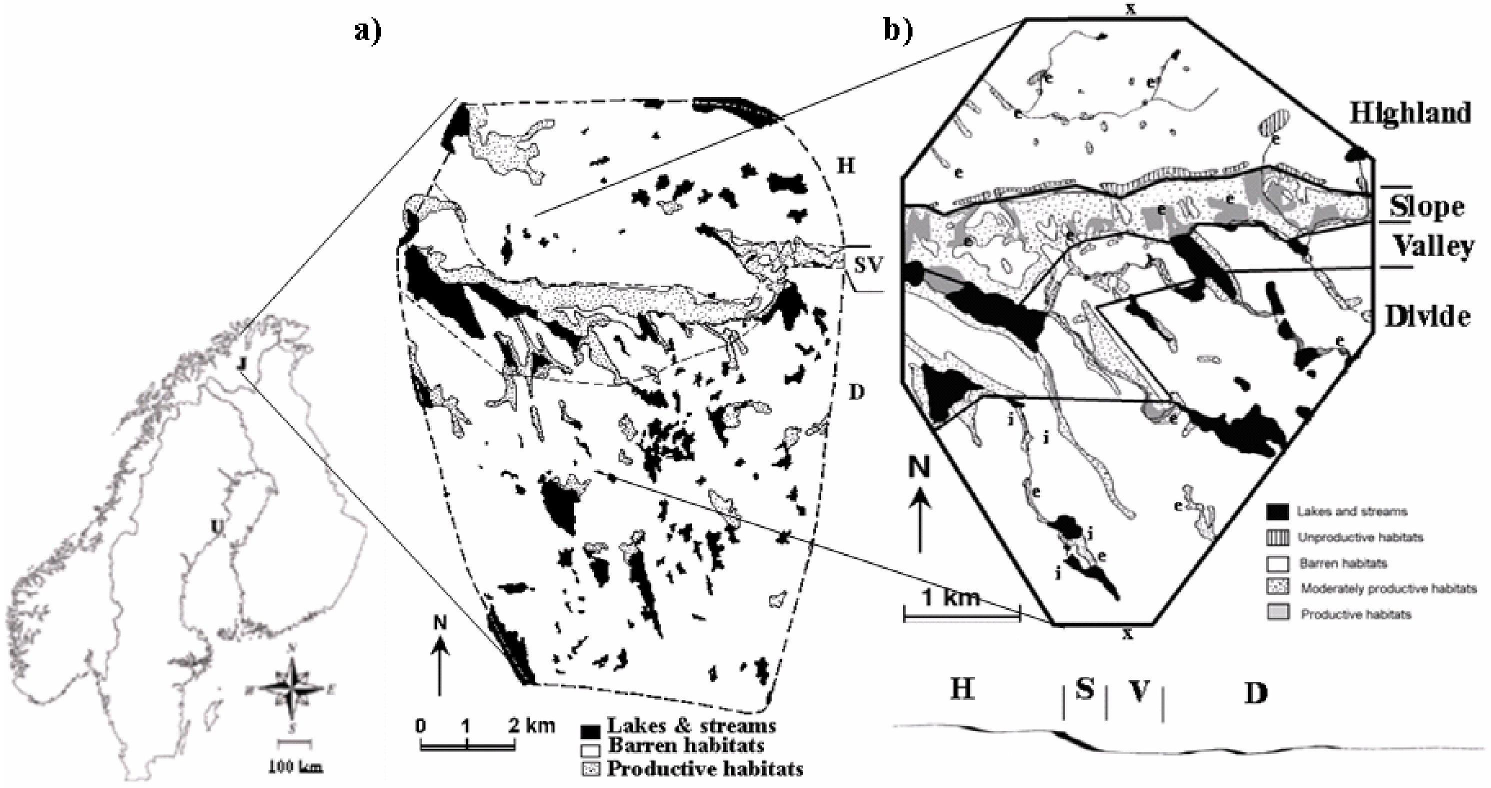

Figure 4. The study area Joatka (J) and its position in Norway (Umeå is marked with U). a) In the extended study area (105.7 km^2) Slope and Valley sub areas are pooled together. b) The main study area (16.8 km^2) is divided, based on altitude and vegetation into four sub areas. The line below the map of the main study area is the height profile, measured between points, marked with *x*. The altitude difference along this line is 214 m. Experimental study of paper **III** was done in places marked with ***i*** and plant and rodent biomass data in paper **V** come from sites marked with ***e***.

depressions and along lake shores, there occur patches of trees, willow and dwarf birch bushes or cloudberry bogs. Highest places are 474 m a.s.l. and 513 m a.s.l. in the main and in the extended part of the study area respectively. When studying raptors, the Slope and Valley sub areas were treated as one, due to the large size of raptor home ranges. In paper **II** we have omitted Valley from the analysis as no vole live trapping has been performed there and we refer to Divide as 'Lowland'.

All these four sub areas can be ranked to form a productivity gradient, starting with Highland, the least productive sub area, to Divide to Valley and to Slope, the most productive sub area. Of course, within each sub area there are habitats that differ in their productivity (**III**). This local productivity gradient allows test the importance of productivity for community functioning in one study area, minimizing the otherwise unavoidable noise when comparing studies, performed in different places.

Finnmarksvidda, as the region is called, has relatively low precipitation (354 mm, (Oksanen and Virtanen 1995) with most precipitation falling usually in July. The length of the growing season depends on topography, with some depressions or otherwise favorable places for snow accumulation having snow until August. In general, snow starts to melt first at the Slope, from the middle of May, and last to be snow free is Highland in the last third of June.

In Joatka there are estimated to be 100 species of macro lichens and 210 species of bryophytes (R.Virtanen, 1997 estimation), 268 species of vascular plants (P.A. Hambäck, 1996), 116 bird species (P. Ekerholm, 1996), one frog species and 17 mammalian species. There are no robust estimates of invertebrate diversity. Although these numbers are relatively large, the low arctic tundra community is still relatively simple making it ideal for studying the community functioning. In a too complex and reticulate community with very many possible pathways for interactions, making of general conclusions would be essentially harder.

Raptor data in paper **I** come from the extended study area, whereas for paper **II** we used raptor data only from the main study area. Small mustelids (**I**, **II**, **III**) were studied in the main study area. Microtine data in paper **I** and **II** come from the live trapping grids (Oksanen *et al.* 1999) marked with the letter '*e*'-s in the Fig. 4b. These live trapping grids were also used as representatives for landscape when collecting plant biomass for paper **II**. Microtine data in paper **III** come from a trapping transect (Ekerholm *et al.* 2001), that could be marked approximately on a line between the '*x*'-is in the Fig. 4b. Locations of experimental study sites for the arthropod community (**V**) in Divide are marked using the letter '*i*' in Fig. 4b.

AIM OF THE THESIS

The objectives of this thesis were to study the distribution patterns of predators in low arctic tundra and their consequences for community dynamics. The main questions I addressed were:

- ✓ How does the abundance of predators and their impact on prey population change along a productivity gradient? (**Paper I**)
- ✓ Do the community dynamics and structure in this ecosystem support the predictions of the hypothesis of exploitation ecosystems? (**Paper II**)
- ✓ What mechanisms regulate the coexistence in the small mustelid guild, the dominant vertebrate predator group in the low arctic tundra? What are the consequences of this on the prey population dynamics? (**Paper III**)
- ✓ What are the theoretical predictions about the importance of intraguild predation for coexistence among endothermic vertebrate predators and for the outcome of competition, along natural productivity gradients? (**Paper IV**)
- ✓ Do predators create a trophic cascade in arthropod communities in the low arctic tundra? What are the consequences of intraguild predation in this community? (**Paper V**)

Setting the stage

Paper **I** is about our study system, summarizing our knowledge about its animal community. This work sails on the last big waves of food web debate (Hall and Raffaelli 1993, Martinez 1995, Polis & Winemiller 1996), a topic that had been so intense for the previous decade (Paine 1980, Peters 1988, Strong 1988, Schoener 1989, Cohen *et al.* 1990, Pimm 1991). Typical of this 'early' period was the topological and statistical description of species richness and their connectance in different communities (e.g., 113 food web matrices in Cohen *et al.* 1990[1]). However, now there appeared a shift from pure topological description to a more dynamic and mechanistic understanding of communities (Paine 1988, Osenberg & Mittelbach 1996, McPeek 1998). The interest was now shifting from 'How it looks' to 'What is the impact of…' The expression 'trophic cascades' turned into new buzzword in community ecology (Fig. 5), althoug the expression 'food web', refilled with new content continued prospering too.

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[1] An intresting and characterizing example of the period is that in their analysis omnivory was not considered as an important phenomena. Omnivory is mentioned only once, in passing by. In a recent re-analyse of their data set Arim and Marquet (2004) found that intraguild predation occurred in 58.4 – 86.7 % of trophic groups.

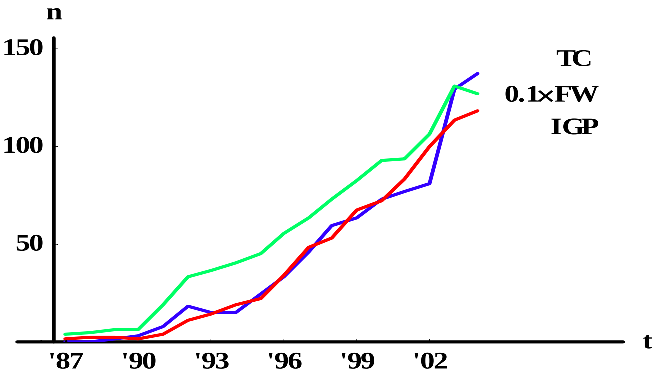

Figure 5. *The number of papers published per year between 1986 – 2003 containing expression 'food web(s)' (FW), 'trophic cascade(s)' (TC) or 'intra(-)guild predation' (IGP) in the title, keywords or abstract according to http://isi3.isiknowledge.com. Publications with 'food web' are scaled down by factor ten.*

For us it was important to describe our community to others, and to describe the structure and the interactions among its members. Criticism directed at our research group around this time (L. Oksanen, pers. comm.) concerned in large part the role of predators. Drawing parallels with study sites from North American tundra (Riewe 1977, Fitzgerald 1981) the predators were expected to be equally common all over Fimmarksvidda low arctic tundra. Thus the importance of predators should be similar over the study area. Somehow the dissimilarity between the continental Joatka study area and North American sites, situated close to the sea with additional non terrestrial resources was missed. This extra input of resources, 'spatial subsidies' from one productive habitat into a juxtaposing barren habitat captured later the attention of the authors of spatial subsidies hypothesis (Polis & Hurd 1996a,b, described further on). Also, discussions on food web complexity (see above) and on plant defenses against consumers (Haukioja *et al.* 1983, Hunter and Price 1992, Seldal 1994) intended to diminish the role of predators, as argued by supporters for the dominance of bottom-up effects.

Predation impact in models

Another theory that we investigated with our data (**I**) was the hypothesis of ratio-dependent predation (Arditi and Ginzburg 1989, Arditi *et al.* 1991, Matson and Berryman 1992, Akcakaya *et al.* 1995). The essence of the hypothesis is that the functional response of predators (i.e., prey consumption rate) depends on the number of prey per predator. Consequently, the structure and dynamics of communities should remain unchanged across productivity gradients, as equilibria at all trophic levels are similarly influenced by changes in primary productivity. This hypothesis was actually by that time falling out of favor (Stow *et al.* 1995, Abrams 1997).

I think this discussion has been important as a debate about how we model predation impact in communities. As a first step in developing ideas, I believe verbal and graphical models are good. Even EEH when published (Oksanen *et al.* 1981) was

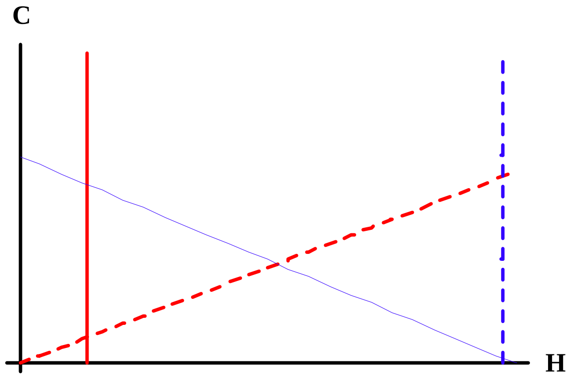

Figure 6. *Isoclines in predation dependent model (e.g., EEH, solid lines) and in ratio-dependent model (broken lines). Prey isoclines are the tilting line, hitting both axes (EEH) and the rightmost vertical broken line (ratio-dependent model). Predator isoclines are the leftmost vertical line (EEH) and the rising broken line (ratio dependent model). The graph is based on models with logistic growth in the prey and type I functional response in the predator.*

not fully mathematical, but partly graphical. Other examples of well known graphical models are the environmental stress model (Menge and Sutherland 1987) and the keystone predation model (Leibold 1996). However, converting the original idea into mathematical terms clarifies the assumptions and predictions and facilitates communication. Many models in community ecology are based on Lotka-Volterra predator-prey model and its derivations (Wangersky 1978, Kuno 1987). Often the analysis of a certain system is done graphically, using the approach developed by Rosenzweig (Rosenzweig and MacArthur 1963). This graphical approach has been also important in the development of EEH.

Returning to the importance of debate over ratio-dependent predation hypothesis, there has been just a slight mathematical modification of the classical Lotka-Volterra predator-prey model (Arditi and Ginzburg 1989), whereby functional response of predator $g(N)$ was replaced with $g(N/P)$. One of the justifications offered by the authors for the modification was to capture the difference between behavioral and population dynamic time scales. The result of this slight change in predators' functional response for predator isocline[1] is visible in the Fig. 6 – predators can survive as long as there is any prey in the community. Therefore, biomass of community members will increase linearly with increasing primary productivity, not in the abrupt way of Fig. 2.

There are other unrealistic aspects in the model resulting from the modification of predator's functional response (Abrams 1994). One surprising features seemingly not

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[1] Isoclines, more specifically null-isoclines, are used to analyse the behaviour of differential models graphically (Rosenzweig and MacArthur 1963). First, abundance of each species' is plotted against that of other community members. Then lines or planes are drawn that mark the abundance combination for given species where its population size does not change. These lines or planes separate the regions of population growth from regions with population decline. If there exists a region were all community members can have positive population growth then those species can (probably) coexist.

taken up in the debate at that time, is the uncertainty of existence of prey isocline in the case of a type I functional response. It does not necessarily lie in the biologically relevant parameter space, and if it exists there, it would be a straight vertical line, and that is difficult to interpret too. Even with type II functional response by predators the existence of a prey isocline in biologically reasonable space depends on the parameter units. The message is that the mathematical formulation has helped, though seemingly not fast enough, the theory to be rejected. Similar logic should be applied by critics of other models (e.g., EEH) and in the current progress of intraguild predation modeling. Instead of verbal attacks one should document the flaws of a model when criticizing. And when supporting a model, it should be shown that the predictions are fulfilled for correct reasons (Englund and Moen 2003).

Observing predators

To understand the functioning of a community, two approaches can be used: observational and experimental (Turchin 2001). Concerning vertebrate predators an observational approach is often the only option. Sometimes the impact of predators on prey populations is studied by creating predator free areas for prey. This is achieved by eliminating predators from fenced enclosures (Krebs *et al.* 1995, Korpimäki *et al.* 2002, Ekerholm *et al.* 2004) or removing predators from larger open areas (Korpimäki and Norrdahl 1998). The opposite manipulation, increasing the abundance of predators or creating artificial prey – predator communities is much harder to achieve (Oksanen and Oksanen 1981).

In 2001 we tried this experimental approach by attempting to establish prey (dominatingly grey-sided voles *Clethrionomys rufocanus*) and predator (stoat *Mustela erminea*) communities on islands occurring in a large nearby lake (Lake Iesjavri). However, the predators disappeared at once from the islands. Unfortunately, also the continuation and modification of the predator exclosure study (Ekerholm *et al.* 2004) suffered from frequent technical troubles. Therefore, my studies on vertebrate predators contain only descriptive data.

As mentioned above, I studied the distribution and abundance of raptors and mammalian predators. Raptors start to arrive at Joatka in the middle of May, when the study area has still the snow cover, and attempt to establish territories. Within the extended study area the raptor survey lasted from the end of May to the beginning of July. At the end of this period, mating pairs had established their territories and commenced breeding. Most non-breeding birds usually had left the area at this point. All observations of raptors were mapped, and breeding pairs were visited regularly during the summer to record breeding success. In August, young were fledged and most of the raptors left the study area by the beginning of September. Raptor droppings found in the field and collected from nests were analyzed to get information about on the raptors' diet. The raptor survey was continued up to and including the 1998 season in the extended study area, following which it was conducted only within the main study area, due time constraints.

Mammalian predators are present all year round. Among the larger ones only red fox (*Vulpes vulpes*) occurs consistently in the study area. Fox dens were mapped and scats found in the field were analyzed. However, the main emphasis was on small mustelids – stoat and least weasel (*M. nivalis*). These two species are considered to be the most important mammalian predators at high latitudes (Henttonen *et al.* 1987, Hanski *et al.* 1991, Korpimäki 1993). During August – September small mustelids were studied via live trapping, using Erlinge type wooden traps (Erlinge 1983). Individuals were measured (species, weight, length, sex, age), marked with Trovan (www.trovan.com) passive senders for later identification on recapture and released. Traps were spread throughout the study area and set up in places where they would be most likely visited by small mustelids, i.e., along creeks and stone blocks and in natural corridors created by depressions on the landscape. During the snowy period, usually in November – December and February – March, I studied the movement of small mustelids by tracking them on the snow, usually over the course of a week. Their tracks were followed throughout the study area and mapped on a topographical map for habitat utilization analysis.

Predator data from late summer, when their populations were maximal, were used to describe the food web of our study area (**I**) and to test the predictions of the EEH concerning the biomass patterns among trophic levels along the primary productivity gradient (**II**). The snow tracking data were used to study coexistence in small mustelids (**III**).

Coexistence among similar predators

EEH treats trophic levels as units, assuming that competition within resource-limited trophic levels causes the members of a trophic level to specialize on utilizing a specific part of the prey community (Oksanen *et al.* 1981). Consequently, 'a rather homogeneous exploitation pressure should be exerted upon the populations on the level below' (Oksanen *et al.* 1981, p.242). It is often neglected fact, that EEH acknowledges the diversity within a trophic level (Oksanen 1992), EEH just assumes that its members are engaged in exploitative competition for resources only.

Working with small mustelids, dominant mammalian predators in our study area and comprising of stoat, least weasel, and an occasionally trapped American mink (*M. vison*) I got interested in the old debate of coexistence in small mustelids (**III**).

For two species of predators to coexist they have to differ along some niche axis (MacArthur 1972, Tilman 1982). Competing species are engaged in exploitative or interference competition (Park 1962). In the first case negative interactions are due to the use of a common resource (MacArthur and Levins 1967, Schoener 1983). Small mustelids prey dominatingly on small rodents and as they show strong dependence on this prey category, the species who can survive on the lowest prey density should exclude the other species'. This assumes of course, that there is a single resource that the species are competing for.

In interference competition, negative effects arise due to territoriality, for example denial of competitor access to prey, by direct aggression, such as fights that can even end with the death of one participant (Paine 1966, Polis *et al.* 1989, Goss-Gustard *et al.* 1995, Tannerfeldt *et al.* 2002). Small mustelids are territorial, and individuals of the same sex or of competing species are expelled from home ranges by direct aggression (King 1989).

Spatial heterogeneity is one of the factors allowing coexistence, as the prey population can have different dynamics in different habitats over the landscape and predators can actually be separated in space and time. Thus predators may not be coexisting at small local scales, but do at the regional scale (Chesson and Rosenzweig 1991, Chesson 2000). Spatial heterogeneity, interspecific dominance and alternative prey resources have been proposed as explanations for coexistence in small mustelids (see **III** for a review).

Intraguild predation

Interference competition can take extreme forms (Polis *et al.* 1989, Holt and Polis 1997) and turn into an energetic link, known as intraguild predation (IGP, e.g., C2 preying on C1 in the Fig. 3a). Thus, apart from foraging at a lower trophic level, predators may prey also on the members of their own trophic level. In size structured populations, e.g., of fish, arthropods and lizards, IGP is very common and has important consequences for community dynamics (Morin 1999, Fedriani *et al.* 2000, Gerber and Echternacht 2000, Finke and Denno 2003).

The term intraguild predation is however not confined to interactions within trophic levels, but is also used to describe the predation by larger (e.g., vertebrate) predators on smaller (e.g., arthropod) predators (**V**, Atlegrim 1989, Marquis and Whelan 1994, van Bael *et al.* 2003, Hooks *et al.* 2003). IGP has several consequences on the dynamics of community, not accounted for in linear food chain models, such as EEH (Oksanen *et al.* 1981, Oksanen and Oksanen 2000). Some consequences of IGP for community dynamics have been assessed by (Diehl and Feißel 2000, Mylius *et al.* 2001). In general these analyses indicate that when IGP occurs, a top predator can invade at a lower primary productivity level than would otherwise be possible, and that a top predator could even exclude its prey from the community. Thus at intermediate levels of primary productivity, two alternative stable states may occur. When IGP occurs, the abundance of intraguild prey is always lower than in communities without IGP.

Modeling predators

Observing organisms on the field gives us knowledge about a particular community. The next step is to investigate how general are the observed phenomena. Do they apply to other systems as well? One way for generalization is gathering and summing knowledge from different studies, known as meta-analysis (Arnqvist and Wooster 1995). Another way is drawing general sketches, mathematical models to describe the processes and produce predictions (Schmitz 2001, Ginzburg and Jensen 2004). A mathematical model can be limited to a description of observations, e.g., logistic growth models, without incorporating the biological mechanisms directly (Olson 1992). Alternatively, a modeling process can start as a theoretical mind game, e.g., the concept of ‘apparent competition’ (Holt 1977) and turn the attention of empirical researchers to important phenomena. And finally, a mathematical model can be formalization of a well known phenomena that suddenly gains attention, e.g., intraguild predation (Holt and Polis 1997).

An advantage of mathematical modeling is that all relevant information about the system can be presented as a set of equations describing all assumptions and predictions. Therefore, in principle all logical weaknesses should be easily detected. However, this is not always the case, as can be seen from the previously discussed ratio-dependent predation debate, when the absence of prey isocline from the models passed unnoticed during the debates. Furthermore, there is always a risk that the modeling will be nothing more than a theoretical mind game. This can be due predictions arising from a model being untestable in reality (Murdoch *et al.* 1992, Englund and Moen 2003) or to an undue focus on the 'wrong aspects' of a system, as occurred in the food web complexity and linkage modeling of 1980's (see critique by Paine 1988, Peters 1988).

Working with two different communities, one being vertebrate dominated and the other being arthropod dominated I became interested in the current intraguild predation debate. There is an ample evidence for the importance of intraguild predation in arthropod communities (see references earlier). It has been argued (Polis 1991, Polis and Strong 1996) that research in vertebrate dominated communities is lagging behind in appreciating the role of intraguild predation. This seems untrue when empirical studies are considered, as the negative impact of larger predators on population dynamics of smaller competitors has been repeatedly demonstrated (Korpimäki and Norrdahl 1989, Maran *et al.* 1998b, Palomares and Caro 1999, Fedriani *et al.* 2000, Tannerfeldt *et al.* 2002, Persson *et al.* 2003).

However, to my knowledge, all theoretical exploration of intraguild predation has been limited to the bacterial, arthropod and fish communities (see previous section for references), whereas mammalian communities have been left out completely, except for an attempt by Rosenzweig (1966).

In my work (**IV**) I tried to see what impact intraguild predation can have on the coexistence of two similar endothermic vertebrate predators, with high maintenance costs, and how intraguild predation affects community dynamics and how the outcome depends on the stability of the community. In communities experiencing large fluctuations in abundance of member species, coexistence possibilities may differ substantially from communities with stable dynamics (Abrams *et al.* 2003).

Manipulating predators

Though it is interesting to observe animals behaving naturally in their natural habitat, to understanding underlying mechanisms in ecological systems it is often necessary to conduct manipulations, whereby animals are forced to exist under our defined conditions while still (hopefully) behaving in a natural manner.

The classical example of weakness of only observational studies is that of lynx-snowshoe hare cycles in the Canadian Arctic. As a result of long term studies an interesting ten year cycle was observed and a multitude of even more interesting hypotheses were put forward starting with sunspots and ending with diseases, encompassing everything else between (Sinclair *et al.* 1993, Krebs *et al.* 1995). Of course, it would be hard to test the importance of the solar cycle hypothesis by applying different levels of sun spot occurrence to a community. However, less grand explanations, e.g., the importance of predation or nutrition are possible to test by manipulating the levels of relevant factors.

The same applies to the role of predators in our study area. Observing a pattern (**I**, **III**) raises usually more questions than it answers. Observing the described (**I**) abundance pattern of prey and predators in community, the next step follows easily – if predators are responsible for the observed pattern then the removal of predators should lead to the changes in their prey. The occurrence of changes and the amplitude of the change can be used to test working hypotheses. This is the reason for perturbation experiments.

The impact of small mustelids on voles, their main prey was studied in a fenced exclosure by Ekerholm *et al.* (2004). Actually, it feels often that ecology is about building fences (Krebs *et al.* 1995, Floyd 1996, Korpimäki *et al.* 2002, Olofsson *et al.* 2002, Hooks *et al.* 2003, van Bael *et al.* 2003).

Spatial subsidies

My interest in arthropod community dynamics arises at least partly from the work by Gary Polis and colleagues (Polis & Hurd 1996a,b, Polis *et al.* 1997, 1998). Their hypothesis of spatial subsidies explores the consequences of adding an additional energy source for community dynamics. Their first argument is that it is misleading to divide systems into simple linear food chains (e.g., Fig. 1). Instead of such simple linear patterns, there are usually complex food webs with plants and detritus at the base and various feeding links between consumer groups, intertwining the 'classical food chains' together (Fig. 7). Because up to 70 – 90 % of primary production from plants passes directly into litter (Polis and Strong 1996), it is the detritus-based part of the community that plays the key role. Also, all organisms after their death contribute to the local nutrient pool.

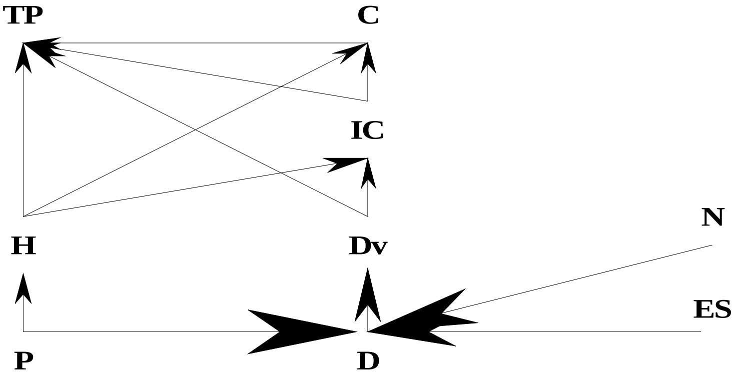

Figure 8. *Schematic representation of hypothesis of spatial subsidies. Plant-based part of community (**P**lants, **H**erbivores, **T**op**P**redators) and detritus-based part of community (**D**etritus, **D**etritivores, **I**ntermediate **C**arnivores, **C**arnivores) are tightly intertwined into one reticulate food web. Arrow size and direction represent the movement direction and relative amount of nutrients and energy.* ***ES*** *stands for external energy and nutrient sources and* ***N*** *represents the nutrients from dead community members. See text for more explanations.*

Their second argument is that very often habitats with large differences in primary productivity are close to each other. This results in a transfer of energy and nutrients from the more productive to the less productive, thereby supporting higher consumer populations. Polis and Hurd (1996a,b) called this phenomena an 'apparent trophic cascade' in the spirit of 'apparent competition' (Holt 1977). They justified this by arguing that a trophic cascade may not be triggered by the removal or addition of predators, but rather by the fact that predators can be supported by extra resources and so are able to suppress the local resources.

In our study area we probably do not have the exceptionally large differences in primary productivity of neighboring habitats as observed in coastal deserts (Polis & Hurd 1996a,b). However, the amount of litter is large (personal observation) and detritivores are abundant (**I**). We have suggested (**I**) that the scarcity of herbivores in relation to other feeding groups in tundra is due the detrital energy shunt. That is, detritus functions as subsidies for predators in plant-based part of the community. As the litter increases in abundance, so too does the abundance of detritivores, which in turn become prey for various predators. As the predators can thrive on detritivores, they are able to more strongly impact herbivores, which can be even eliminated from the community.

To study the possible effects of such a subsidy on community structure and see if this can cause an apparent trophic cascade, I returned to the fencing approach (**V**). I excluded birds and spiders and observed the changes in arthropod community. On two plants species, dwarf birch (*Betula nana*) and bilberry (*Vaccinium myrtillus*) leaf damage was recorded to study the eventual effects on the plant community.

RESULTS & DISCUSSION

Distribution and abundance of predators

Those who argue that predators can be found everywhere are correct. Predators that move around in the landscape will in the long run visit almost all places. Another pattern emerges, however, when the impact of predators is studied.

First – not all areas are equally inhabited by predators. Areas that are more productive and therefore can sustain more prey and/or higher prey turn-over rates have more predators. This pattern applies both to number of predator individuals and their activity (**I**, **III**) and to collective biomass of predators (**II**). The general pattern of more vertebrate predators in prey-rich habitats is observed also in other ecosystems (Erlinge 1983, Jędrzejewski and Jędrzejewska 1992, Korpimäki and Norrdahl 1991a, Klemola *et al.* 1999). In our study area, Slope, the most productive sub area supported the greatest abundance of predators and Highland, the most barren sub area supported the least (Fig. 18.2 in **I**, Fig. 1 in **II**, Fig. 3 in **III**). As is seen from Fig. 1 in paper **II** there is an abrupt change in predator abundance – a slight change from Highland to Lowland (= Divide) and large increase from Lowland to Slope. A reminder – raptors leave the area in September, whereas small mustelids are present year round. However, predators were found also in both Highland and Lowland, which seems inconsistent with EEH. The reason may be in the fluctuating nature of abundance in community members, i.e., the microtines in our study area are exhibit 4 – 5 year population cycles (Oksanen *et al.* 1999, Ekerholm *et al.* 2001, Fig. 1 in **III**). There is thus a large variation in prey profitability in a given habitat. During the peak phase of prey even the otherwise barren areas contain prey. The phenomena is called 'spill-over' predation (Holt 1984, Oksanen 1990) – predators produced in productive habitats hunt in barren habitats where they can not survive in the long run. This is similar to the ideas of G. Polis and coworkers (Polis and Hurd 1996a,b, Polis *et al.* 1997) relating to the consequences of having productive habitat next to a barren habitat. Although, they were concerned about the transfer of energy and material from productive habitats into the barren one, and not with the consumer movements. Beside fluctuations in prey numbers, this discrepancy also reflects the heterogeneity of the landscape. Specialist predators in barren areas are confined to the productive corridors (**II**), which link to the more productive areas.

Another aspect that is notable from Fig. 18.2 in paper **I** is the spatial change in relative taxonomic composition of predator trophic level. In Divide and Highland the dominating predator is the long tailed jaeger (*Stercorarius longicaudus*), a generalist raptor that forages also on insects, berries and carrion. These alternative resources allow this species to persist in the area even when microtine rodent densities are low. However, breeding appears to occur/succeed only when the density of microtine rodents is above a certain threshold (Aunapuu, unpublished data). On Slope, the always present merlin (*Falco columbarius*) preys on birds, except during the microtine rodent peak phases when voles comprise a large proportion of its diet (Aunapuu 1998). A third species, rough-legged buzzard (*Buteo lagopus*) is a rodent specialist preying dominatingly on rodents (Aunapuu 1998). In contrast to these observations for the raptor predators, composition in the small mustelid guild changes in time rather than in space (Fig. 1 in **III**). During the 1980's the least weasel was as common as stoat. We have speculated elsewhere (Oksanen *et al.* 2001) that invasion by mink at the beginning of 1990's may have switched the balance so that stoats came to dominate. The reason is that the least weasel depends on access to *Microtine* vole species, that can have high densities over a small area and have fast reproduction (Henttonen 1987). In our study area those *Microtine*-habitats are small and found dominatingly along the creeks, which are easily accessed by minks (T. Oksanen and M. Schneider, unpub. data) or on the Slope, harboring also hares and willow ptarmigans, alternative prey for stoats. Those habitat patches along the creeks are usually too small and isolated from larger productive habitats to be included in home ranges of stoats. Therefore, as the home ranges of weasels are smaller (King 1989), the least weasel could utilize those habitats. Having an exclusive access to this prey allowed the least weasel to persist in the system and even invade other habitats. Due to appearance of the American mink, suddenly the least weasel was confronted with stronger competitors is all habitats.

Among arthropods the opposite pattern to vertebrate predators was observed (Fig. 18.3 in **I**, Fig. 1 in **V**). Here predators were the major group in terms of abundance. The less productive habitat, bilberry heath, actually had slightly more arthropod predators than the more productive dwarf birch scrubland. Similar patterns have been observed in other tundra communities (Danilov 1972, MacLean 1980). Besides arthropod predators, insectivorous birds also have strong impacts on the arthropod assemblage.

Predators, prey and trophic cascades

We argue in paper **II** that regulation by predators is the reason why biomass of herbivores does not differ between Lowland (= Divide) and Slope, though there is an increase in primary productivity. As a consequence, plant biomass increases significantly, as predicted by EEH (Oksanen *et al.* 1981). In addition, predators have also an indirect impact on plant community composition. The abundance of most palatable plant species (**II**) increases once predators start to regulate herbivores. Vegetation studies from islands where predators have been absent confirm the role of herbivore regulation by predators in structuring the plant community (Terborgh *et al.* 2001, Hambäck *et al.* 2004).

It has been suggested that these strong effects, cascading from top predators down to the plant community are typical to simple, linear food chains. In reticulate food webs strong effects may get attenuated as they pass from one interacting unit to another (Strong 1992, Polis 1994). However, we demonstrated (**V**) that even in an arthropod community, which is far more complex then our vertebrate dominated assemblage strong impacts can cascade through all trophic levels. Removal of predators led to increased plant damage. Increased damage does not necessarily lead to changes in plant biomass (Schmitz *et al.* 2000). However, these strong interactions indicate that changes in plant biomass might occure in the long run.

As effects of predation cascaded down to the plant assemblage, intermediate trophic levels in the food web were affected too. This applies both to vertebrate and invertebrate dominated components of ecosystem. In the arthropod community, we could demonstrate that predation reduces abundance of some prey groups (**V**). However, the results did not confirm the suggestion that predation is the proximate cause of low herbivore abundance (Oksanen *et al.* 1997). Nevertheless, the plant damage data indicate that predation influences herbivorous insects. Increased activity by herbivores at the reduced predation pressure might cause these results (see also Schmitz *et al.* 1997). If so, then the observed trophic cascade was not density mediated (via an increase in consumer abundance), but rather was trait-mediated, whereby changes in consumer behavior was the cause (Schmitz *et al.* 2004). Unfortunately I did not have the possibility of concentrating on behavioral aspects in my research. This would be an informative avenue for future research, as some interactions among predators led firstly to behavioral responses which in turn had consequences for population dynamics (see next section).

In the vertebrate assemblage, we see that predators have similar direct effects on their prey as they had indirectly on plants. In addition impacting the abundance of their prey, predators cause also changes in prey community composition (**II**, Rammul and Oksanen unpub. data). Among small rodents, dominance in exploitative competition is positively correlated with body size (Henttonen *et al.* 1977). Smaller species usually require higher quality forage, but are in turn better able to respond to higher predation pressure by being more agile. As a consequence, predators exclude some of larger species (e.g., lemmings *Lemmus lemmus*) from productive areas, and indirectly contribute to the persistence of smaller species (e.g., red vole *C. rutilus*) by preying more efficiently on competitively dominant species (Oksanen 1993).

Over shorter population time scales predators are mostly tracking changes in abundance of prey. Raptors that are nomadic and can easily travel between areas with higher prey densities probably do dampen prey fluctuations (Korpimäki and Norrdahl 1991b, Norrdahl and Korpimäki 1996, Oksanen *et al.* 2001). In contrast, small mustelids roam over a more restricted area, and cause first an intense localized decline in the prey population, from which a low population phase follows (Korpimäki *et al.* 1991, Korpimäki 1993, see also Ekerholm *et al.* 2004). As we suggested (**III**, Oksanen *et al.* 1999), specialist predators, such as the least weasel may contribute to fluctuations of microtine rodents by tracking patches with higher prey abundance whereas more generalist predators such as stoat, suppresses prey in the habitats where alternative prey, mountain hare (*Lepus timidus*) and willow ptarmigan (*Lagopus lagopus*) also occur.

Interactions among predators

Even though tundra ecosystems are relatively simple there are still a variety of predators, differing in their natural history. Besides impacting lower trophic levels, predators interact also among themselves. Our results indicate that when describing large scale patterns (**II**), individual characteristics of predators can be ignored. However, when trying to understand the underlying mechanisms and causes for these patterns, the details of interactions among predators can be important.

Our results suggest that classical exploitative competition structures the small mustelid community (**II**). The main prey for small mustelids, and actually even for raptors is microtine rodents. As the prey diversity is low, there is intense competition. The least weasel has slightly lower absolute food requirements due small body size, and because of smaller body size it can also enter vole runways, inaccessible to larger competitor stoat (King 1989). This would result in the exclusion of the stoat, as the least weasel could suppress vole abundance below the level needed to sustain stoat population. However, as there is some alternative prey (hare, willow ptarmigan), the outcome is opposite. Species larger then voles are too large to be included in the least weasel diet, at least as regular items. This has been the reason for exclusion of least weasel also in other areas with for the least weasel unfavorable prey size distribution (King 1989). In our study area, the stoat can exclude the weasel due alternative resources, by suppressing the abundance of main prey, voles below the level needed to sustain least weasel population.

In addition, some of the researchers have proposed, that direct aggression by the larger stoat on the smaller least weasel can be as important as competition for resources (King and Moors 1979, Erlinge and Sandell 1988). Interference competition has been argued to be important in structuring also other mammal communities (Sunde *et al.* 1999, Tannerfeldt *et al.* 2002). We found no evidence from our winter habitat utilization data for a significant role of interference competition in the dynamics of small mustelid community inhabiting our study area (**III**). There was an indication that the smaller least weasel avoided places (e.g., frozen surfaces of streams) where it could be more easily detected by the stronger competitor, the stoat. Similar patterns were observed for both species during summer periods, when both of them were trapped only in areas with good cover (M. Aunapuu, unpublished data). This may reflect avoidance of predation by foxes and raptors (Korpimäki and Norrdahl 1989, Jędrzejewska and Jędrzejewski 1998). Thus even among the vertebrate assemblage behavioral responses can impact community dynamics. If small mustelids avoid some areas in order to minimize predation risk by larger predators, then prey populations should be slightly greater there than in the presence of small mustelids. Prey populations would be expected to be greater in the absence of mustelids even when larger predators are present, because larger predators are less efficient than small mustelids. However, the difference cannot become too great as then small mustelid predation would be reimposed as the potential foraging rewards would balance the mortality risk imposed by larger predators (Brown *et al.* 1999). In vertebrate communities, this mortality, imposed by larger predators on smaller guild members, seems to act overwhelmingly as an extreme version of interference competition (**IV**). Intraguild predation, as it is called, gives only a small energetic profit to the IG predator, though the impact on the IG prey may be strong (Erlinge and Sandell 1988, Tannerfeldt *et al.* 2002). The consequence of IGP among vertebrate predators is a reduced likelihood of coexistence (**V**).

The more reticulate nature of the arthropod food web, characterized by more interacting groups with large size differences among them, probably explains the greater importance of IGP, in comparison with the vertebrate assemblage (**IV**). However, size difference is not the only explanation for this contrast, since the weight difference between the least weasel and fox is pronounced (around 100 times). The abundance of the intermediate predator is also important, since it has to be energetically profitable to forage on IG prey. For avian and mammalian top predators, the intermediate predators will be never abundant enough to specialize on IG prey instead of basal prey.

For top predators in arthropod communities, intermediate predators are an important food resource and the effect of IGP on dynamics and composition of community is usually strong (Floyd 1996, van Bael *et al.* 2003, but see Low and Connor 2003 for opposite observation). We demonstrated that the release of spiders (intermediate predators) from mortality imposed by birds (top predators) resulted in an increase in spider abundance, with cascading (increased) impacts on their own prey populations (**V**). In arthropod communities there are even large size differences among intermediate predators. As such, they do prey also on each other, and this was actually the original idea of intraguild predation (Polis and McCormick 1987), extended later to encompass all interacting predators. We do not have any data about interactions among spiders, though studies carried out in other ecosystems have shown IGP among spiders to be common (Polis and McCormick 1987, Wise and Chen 1999). Despite the probably strong IGP among spiders even in our study system, this did not eradicate the impact of spiders on other prey groups.

CONCLUSIONS

In communities where predators are present, they usually have an important role. By preying on the lower trophic groups, predators influence the number and composition of their prey. These effects cascade down to the plant community, and can influence biomass and species composition of vegetation, at least when the vertebrate assemblage is involved.

In some parts of the low arctic tundra, vertebrate predators are not present due to natural causes. When the primary productivity is too low, prey populations do not reach levels that can sustain predators. As a consequence, it is consumption by herbivores that regulates plant communities, which have adapted to high herbivory pressure. The removal of predators by human activities on the other hand causes changes in the ecosystem that is not easily able to adapt to. As a result, large decreases in vegetation biomass with possible nutrient losses may follow.

In arthropod assemblages, the predators seem to be abundant along the whole productivity gradient, due to the availability of an extra resource – detrital prey. Bacause of this, these predators in arthropod assemblages are capable of imposing strong impact on prey groups. As we speculated, these extra energy inputs via the detritus link may explain the low abundance of herbivores in the low arctic tundra. As a consequence, plants are released from consumption by herbivores.

Predators do not live in isolation, but they compete intensely with other predators, and often even prey on their own competitors. Whereas in some assemblages (e.g., among arthropods) predation on competitors (intraguild predation) is common, in others (e.g., mammals) it seems to be rare and has a generally destabilizing impact on coexistence. This knowledge could be used in conservation biology. My results are directly connected to the problem of introduced and invading predators (e.g., American mink, or invasion of red fox into the mountains), that often results in decline of native species (e.g., European mink, arctic fox). The situation could be switched, by active management into the favor of the native species. After the population of native species has recovered, it may be able to keep the competitors out by itself. For example, the introduced American mink (*M. vison*), seen as a pest in Europe (Maran *et al.* 1998a). Being a semi-aquatic species and smaller than another semi aquatic species, the otter (*Lutra lutra*) American mink is out competed from the best watercourses (Bonesi and Macdonald 2004). However, on the land it can be out competed by similarly sized, but more efficient polecat (*M. putorius*). A speculative suggestion is that, by favoring the native species, otter and polecat, it would be possible to reduce the abundance of the introduced one, the American mink.

The effects of predation can cascade through an entire food web, even though it consists of many interacting units with many possible pathways for effects to travel along. To understand the impact of predation on community functioning, the usage of relatively simple models is justified. These models can predict the impact of predation when applied at correct scale of resolution.

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SAMMANFATTNING

En central fråga inom ekologin är betydelsen av rovdjur och hur de påverkar samhällets struktur och dynamik. Mina studier är koncentrerade på rovdjurens roll i ett låg arktisk tundra område, i norra Norge. Jag har observerat rovdjur i fält (rovfåglar och små mustelider), manipulerat rovdjurens (insektätande fåglar och spindlar) mängd i ett insektsamhället, och undersökt hur predation mellan rovdjur påverkar deras möjlighet att samexistera i ett samhälle.

Resultaten visar att rovdjur är viktiga både i vertebrate- och evertebrate baserade delar av ekosystemet. I vertebrate-baserade delen är rovdjur mycket mindre förekommande än deras byte. Däremot är rovdjur minst lika vanliga som bytesdjur bland evertebrater. Ändå hade rovdjur stark påverkan i båda fallen och rovdjur påverkade både tätheten och artsammansättningen hos bytes populationen. Rovdjurens påverkan nådde fram ända till växtsamhället. Som följd av minskad predation i insektsamhället kunde vi observera ökade skador på växter. I däggdjur-baserad samhället kunde vi även observera långtids-effekter på växt biomassan och art-sammansättningen.

Bland rovdjur var resurskonkuransen och intraguild predation de viktigaste faktorerna. Resurskonkuransen förekommer när rovdjur furagerar på samma bytesdjur. Intraguild predation beskriver interaktion där ena rovdjuret prederar på den andra. I en insektsamhället finns stora storleksskillnader mellan olika arter och såväl som inom samma art. Fåglar är topp-rovdjur och spindlar är intermediära rovdjur. En intressant aspekt i insektsamhället är att det i tillägg till växter också finns förna som fungerar som en basresurs. Förnan utgör föda för en stor mängd detritivorer som i sin tur är föda åt spindlar. Spindlar kan därför finnas i större antal och ha större påverkan på andra bytesgrupper, t. ex. små herbivorer som bladlöss. Mina studier visar att om man minskar mängden spindlar, då leder det till ökade skador på växter. Fåglar i sin tur, äter både spindlar och andra större insekter, t. ex. växtätande fjärils larver. Eftersom spindlarna finns i så stor mängd, kan fåglar livnära sig endast på dem och därför kraftigt minska tätheten av eller till och med utrota växtätande fjärils larver. När jag uteständge fåglar, ökande mängd av spindlar, som i sin tur ledde till färre bytesdjur och minskade växtskador. Detta fenomen, där förändring i rovdjurs mängden leder till förändringar hos bytesdjuren och detta i sin tur leder till förändring i växtsamhället kallas för ’trofiska kaskader’.

Jag visar att begränsad tillgång av huvudbytet, sorkar, var den viktigaste faktorn för dynamiken av och samexistensen mellan små mustelider. Vesslor kan trycka bytes populationen till så låga tätheten att större konkurrenten, hermelinen inte kan klara sig. Men om hermelinen även i viss mån kan livnära sig på alternativa byten som hare och ripor, då blir utgången den motsatta. Tack vare det alternativa byten kan hermelinen utkonkurera vesslan. Eftersom hermelinen är större, har det föreslagits att predation från hermeliner på vesslor är en viktigt komponent i interaktionerna mellan dem. Det är en exempel på intraguild predation, precis som fåglarnas predation på spindlar. Mina studier visar att intraguild predation inte är särskild viktigt för små-mustelidernas samexistens. Mina teorestiska analyser visar att intaguild predation mella predatorer skulle minska möjligheterna för samexistens.

Sammanfattningsvis kan man säga att rovdjur var viktiga båda i enkla, linjära födovävar bestående mestadels av vertbrater och i komplexa retikulära födovävar, baserade på insekter. Effekter av predatorer var starkare i produktiva miljöer, precis som förutsagt av en i grunden enkel hypotes om trofiska kaskader, nämligen hypotesen om exploaterande ekosystem.

KOKKUVÕTE

Eluslooduses sobib hästi moto 'Söö või sind süüakse', kuigi tihtipeale pannakse sind sellele vaatamata nahka. Ökosüsteeme võib kirjeldada toiduahelate võrgustikuna, kus kiskjad asuvad kõrgemal tasemel, nende saakloomad allpool ja taimed või muud ressursid asuvad kõige madalamal.

Üks ökosüsteemide dünaamikat kirjeldav teooria, mis lähtub just toiduahelate võrgustikust, on 'ekspluateeritavate koosluste hüpotees' (lühendatult EEH). Sellekohaselt esinevad madala produktiivsusega ökosüsteemides vaid taimed. Produktiivsuse suurenedes taimede biomass kasvab, kuni ta saavutab taseme, mil rohusööjad suudavad sellest hulgast elatuda. Vastavalt EEH'le kaasneb edasise produktiivsuse suurenemisega rohusööjate biomassi suurenemine. Kuna aga rohusööjad tarbivad taimi ja kontrollivad nende hulka, siis taimede biomass ei suurene. Tasemel, mil koosluse produktiivsus on nii suur, et rohusööjate biomass on saavutanud hulga, mis suudab ära elatada kiskjaid, seavad viimased end sisse. Nüüd asuvad kiskjad kontrollima saakloomade arvukust, vabastades sellega taime rohusööjate kontrollist. Seetõttu suureneb edasise produktiivsuse tõusuga nii kiskjate kui taimede biomass, samas kui rohusööjate oma jääb muutumatuks. Kui sellises produktiivsest kooslusest eemaldada kiskjad, kaasneks sellega rohusööjate arvukuse tõus, kuna nad on nüüd vabanenud kiskjate kontrollist. Seetõttu suudavad rohusööjad kontrollida taimede hulka, millega seoses väheneb koosluses taimse biomassi kogus oluliselt.

Seda nähtust, kus ühe liikidegrupi eemaldamisega kaasneb muutus terve ökosüsteemi olemuses, kutsutakse 'troofiliseks kaskaadiks'. See tähendab, et ühe grupi eemaldamine ei avalda mõju ainult tema enda saakloomade arvukusele, vaid läbi muutuste saaklooma arvukuses ka teistele liikidele.

Oma töös uurisin ma kuidas kiskjad ja kisklus mõjutavad looduslike ökosüsteemide koosseisu ja dünaamikat. Ma uurisin kas kiskjatel on oluline osa saakloomade arvukuse dünaamikale ja saakloomade koosluse liigilisele koosseisule ning kas see kiskjate mõju kandub ka edasi teistele ökosüsteemi koosseisu kuuluvatele liikidele. Tööd, millel mu teesid põhinevad, teostasin ma Põhja-Norras, lähis-arktilises tundras. Selle ökosüsteemi saab tingimisi jagada kaheks. Selgroogsete osa, kus ma uurisin röövlindude ja pisikärplaste mõju pisinäriliste arvukusele ja läbi selle taimekooslusele ning selgrootute osa, kus ma uurisin putuktoiduliste lindude ja ämblike mõju taime- ja kõdutoiduliste putukate arvukusele ja seoses sellega ka taimedele. Lisaks huvitusin ma kiskjate endi vahel esinevatest suhetest, mis viis ka teoreetilis-matemaatilise modellerimiseni, uurimaks kiskjate endi vahel esineva kiskluse mõju kiskjate kooseksisteerimisele koosluses.

Tulemused näitavad, et kiskjatel on oluline osa saakloomade koosluse arvukuse ja liigilise koosseisu määramisel, seda nii suhteliselt lihtsas (liigiliselt vaeses) selgroogsete koosluses kui ka keerulises (suhteliselt liigirohkes) selgrootute koosluses. Selgroogsete kiskjate puhul oli selge erinevus kõrge ja vähese produktiivsusega kooslustes. Esimeste puhul olid kiskjad arvukad ja reguleerisid saakloomade kooslust, teiste puhul kiskjad kas puudusid või oli nende arvukus väga väike. Selgrootute kiskjate puhul polnud ökosüsteemi produktiivsus määrav ja nad olid isegi arvukamad kui nende endi saakloomad. Selle üheks põhjuseks on see, et selgrootute seas kasutavad suuremad kiskjad edukalt väiksemaid kiskjaid toiduks (gildisisene kisklus). Selgroogsete kiskjate seas ei ole gildisisene kisklus ei ole otseselt oluline, kuigi pisikärplased üritavad siiski vältida suuremate kiskjate 'jalgu' jäämist. Samas väidan ma, et gildisisene kisklus ei mõjuta imetajate koosluses kiskjate koosesinemist rohkem, kui seda teeb 'konfliktne' konkurents. See-eest on aga selgrootute koosluses gildisisesel kisklusel väga suur osa, mõjutades terve koosluse iseloomu. Lisaks võib käesoleva töö põhjal tõdeda, et isegi küllaltki keeruliste bioloogiliste koosluste olemust saab edukalt kajastada suhteliselt lihtsate matemaatiliste mudelitega.

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ERRATA

The mistakes in published papers should be corrected as follows.

I

Oksanen, L., Aunapuu, M., Oksanen, T., Schneider, M., Ekerholm, P., Lundberg, P.A., Armulik, T., Aruoja, V. and Bondestad, L. 1997 Outlines of food webs in a low arctic tundra landscape in relation to three theories on trophic dynamics. In *Multitrophic interactions in terrestrial systems.* (A.C. Gange and V.K. Brown, eds.), pp. 351-373. Blackwell Scientific Publications, Oxford.

p. 359
Last sentence on the page should be replaced by:
The highest density was recorded in late summer 1994, just before the crash in 1995, when five stoats were trapped. This abundance equals to 0.8 individuals km^2.

p. 360
4th row in the paragraph below the table:
'August 1995' should be replaced by 'August 1994'.

p. 364 Table 18.3
On the row for
Total (for Waders) under sub area Slope '– ' should be replaced by '0'.

III

Aunapuu, M. and Oksanen, T. (2003) Habitat selection of coexisting competitors: a study of small mustelids in northern Norway. *Evol. Ecol.* **17**, 371-392.

Throughout the text ANOVA should be replaced by ANCOVA.

p. 383 Figure 3a
On the graph symbol ' ⊲ ' (left pointing triangle) should be replaced by ' ⊳ ' (right pointing triangle) corresponding to the legend for Divide.

p. 385 legend to Figure 4
In the parenthesis '± SE' should be removed.