Abstract

The scope of the work was to test and to develop the theory of exploitation ecosystems, according to which herbivores are regulated by predators in relatively productive ecosystems, whereas in barren ones (productivity < 700 g/m^2/yr), herbivores are strictly resource-limited and predators are practically absent. The test system consisted of microtine rodents and small mustelids in North Fennoscandian taiga and tundra.

Data from the taiga and from productive tundra habitats were consistent with the idea of a predator-prey limit cycle and data from a homogenous, barren highland tundra were consistent with the idea of strictly resource-limited herbivores. Difference in mechanisms of population regulation offered a possible explanation for the failure of Norwegian lemmings to establish permanent populations in taiga lowlands. However, data from relatively barren taiga and lowland tundra habitats did not conform to predictions. Small mustelids were present and indications of microtine dynamics fundamentally different from those in adjacent productive habitats could not be observed.

The data thus suggested that the hypothesis of exploitation ecosystems is useful but in its present form insufficient for explaining population dynamics within local habitat complexes. Thus, the theory was further developed by explicitly including the dispersal of consumers between different habitat types, in accordance to the ideal-despotic model of habitat choise. The revised theory contains the original one as a special case, applicable to habitat complexes where patches are infinitely large or where the fraction of land covered by the more productive habitat type is infinitely small. In habitat complexes where a substantial fraction of the land is covered by the productive habitat, its dynamics tend to 'spill over' to the barren habitat, too.

Predator-prey dynamics in small mammals along gradients of primary productivity

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LIST OF PAPERS

The dissertation is based on the six papers listed below.
References to these publications are made by using the Roman
numerals.

I.   Oksanen, T., Oksanen, L. and Fretwell, S. 1985. Surplus
        killing in the hunting strategy of small predators.
        - American Naturalist 126:328-346.

II.   Henttonen, H., Oksanen, T., Jortikka, A. and Haukisalmi,
        V. 1987. How much do weasels shape microtine cycles in
        the northern Fennoscandian taiga? - Oikos 50:353-365.

III.   Oksanen, T. The stoat, Mustela erminea and the
        weasel, M. nivalis as predators of voles in northern
        Fennoscandian taiga: a test of the hypothesis of
        exploitation ecosystems. - Manuscript.

IV.   Oksanen, L. and Oksanen, T. Long-term microtine
        dynamics in North Fennoscandian tundra: is there a case
        for a mustelid-microtine limit cycle? - Manuscript.

V.   Oksanen. T. 1990. Does predation prevent Norwegian
        lemmings from establishing permanent populations in
        lowland forests? - Biological Journal of Linnean
        Society: (in press).

VI.   Oksanen, T. 1990. Exploitation ecosystems in
        heterogeneous habitat complexes. - Evolutionary ecology:
        (in press).

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SUMMARY OF THE THESIS

1. Introduction

    The importance of different regulatory processes for
community structure is continuously debated (Diamond and Case
1986ab, Schoener 1989). MacArthur (1972a) proposed a theory of
community ecology as a direct extension of the theory of
competition-structured guilds. This set the tune of studies in
community ecology in early 70'ies (e.g. Cody 1974), although
potential limitations of this approach had already been pointed
out by MacArthur (1972b) himself. A major shortcoming of this
approach has proved to be lack of attention to predation which
can modify competitive interactions (Paine 1974) and even
render them irrelevant (e.g. Strong 1984). Thus, Menge and
Sutherland (1976) suggested that the competition-centered
approach only applies at the highest trophic level, while the
importance of predation increases towards the base of the food
chain. Another possibility was much earlier proposed by
Hairston et al. (1960). They suggested that competition is
important at the top and the base of terrestrial food chains,
while predation prevails in between. Their reasoning was based
on the fact that carnivores cannot normally forage on plants.
Thus, if carnivores regulate herbivores, plant populations can
increase until resources become limiting.
    The hypothesis of Hairston et al. (1960) tried to explain,
why 'the world is green', plants are big and abundant while

herbivores are much less abundant and less conspicuous. Fretwell (1977) noted that this observation is not globally valid. There are also ecosystems, where plants are small and scanty while herbivores are big and abundant, at least as compared to the scanty vegetation. His explanation was that the hypothesis of Hairston et al. (1960) only applies to relatively productive 'three-link' ecosystems. Less productive habitats harbour 'two-link' (herbivores - plants - physical resources) or even 'one-link' (plants - physical resources) ecosystems, whereas 'four-link' food chains are encountered in extremely productive areas. The proposed general law was that competition prevails at the top of each food chain and at even numbers of trophic links below the top, while predation prevails at trophic levels which are an odd number of trophic links below the top. The dynamic food chain length was proposed to be linked to primary productivity. The model of Oksanen et al. (1981) showed that, except for four-link ecosystems, Fretwell's proposition was logically sound.

Fretwell (1977) called his proposition 'the food chain theory'. However, this name caused associations to the food web theories of Cohen (1977) and Pimm (1982) which focus on different issues (e.g. connectance of food webs, descriptive as opposed to dynamical food chain length). 'The theory of exploitation ecosystems' was thus regarded as a more appropriate name by Oksanen et al. (1981). The term had been introduced by Rosenzweig (1971), whose ideas were important in the development of the arguments of Fretwell and Oksanen et al. (1981).

The basic difference between the approaches of Menge and

Sutherland (1976) and Hairston et al. (1960) is related to the question, whether trophic structures are diffuse and contain much omnivory or whether they are divided into relatively distinct trophic levels. Opinions on this issue are still divided. Some ecologists totally reject the concept of a trophic level and work exclusively on taxonomical subdivisions of ecological communities (e.g. Cousins 1987). To others, trophic levels are as good as any other abstractions in ecology, and the approach of Hairston et al. (1960) is seen as a good start for understanding population dynamics and community structure (Schoener 1989).

For a terrestrial ecologists, the latter position seems more reasonable. The fiber-rich plants are just too different from mobile animals to be efficiently exploited by the same consumers. This was tacitly accepted even by Cousins (1987), who tried to get around the problem by arguing that plants herbivores and carnivores can be regarded as taxonomically defined groups of organisms. In many cases, however, the taxonomical relatedness of a consumer guild is remote (e.g. the predator guild preying on voles in southern Sweden consists of carnivorous mammals, raptors, owls, shrikes and snakes, Erlinge et al. 1983, Erlinge, pers. comm.). Moreover, the argument that plants, herbivores and carnivores are taxonomically defined groups has no relevance for the viewpoints of Hairston et al. (1960), Fretwell (1977) and Oksanen et al. (1981), as long as the groups are also distinct trophic guilds.

In the paper of Oksanen et al. (1981), the focus was mainly on terrestrial ecosystems where the vertebrate branch of the grazing chain was proposed to shift from three-link to two-link

dynamics along gradients of decreasing primary productivity. However, the works of e.g. Carpenter et al. (1985) and Persson et al. (1988) suggest that also in pelagical aquatic systems, trophic levels seem to be distinct enough to generate the kind of alternation between resource-limited and predator-regulated trophic levels discussed by Hairston et al. (1960) Fretwell (1977, 1987) and Oksanen et al. (1981).

2. The place of my work in testing and developing the
   theory of exploitation ecosystems

The terrestrial productivity gradient best accessible for a Nordic ecologists consists of tundra and taiga ecosystems in northern Fennoscandia and along the Norwegian mountains. The community of vertebrate grazers in these ecosystems basically consists of microtine rodents and reindeer. The quantitative importance of remaining herbivorous vertebrates is marginal (Wielgolaski 1975). As reindeer are under direct human management, only the microtine community and its predators is left for studying natural carnivore-herbivore-plant interactions. Thus, I became immediately connected with the question of sustained population fluctuations in small mammals and their predators.

In early 80'ies, the assumption of carnivorous vertebrates as regulators of their prey populations was in conflict with the established views that, independent of primary productivity, herbivorous vertebrates are limited by their resources (White 1978, Caughley and Lawton 1981) or by social

interactions (Krebs and Myers 1974). For small herbivorous mammals, the idea of predation being unimport was bolstered by the disparity between the population growth rates of predators and their prey. Different growth rates tend to lead to decreasing predator/prey ratios during the increase phase of a prey population. Thus, even those researchers who did pay attention to predation (e.g. Pearson 1966, Hansson 1969, 1979) only regarded it as a factor which extends and deepens population declines of herbivores after numerical changes have been initiated by other factors. However, the supposed relevance of numerical predator/prey ratios is based on the premise that the functional response curve of the predator levels off already at moderate prey densities, when the predators are able to satisfy their immediate food needs (Krebs and Myers 1974, Caughley and Lawton 1981). This assumption did not seem to be well-founded: (1) reports of pronounced surplus killing abound in the litterature on small predators, (2) the assumption of surplus killing is evolutionarily plausible and (3) my island experiment suggested that a single weasel can decimate a fairly large vole population (T. Oksanen 1983).

These ideas were developed and tested in paper I, which elaborated one mechanism by which it is possible to have much higher predation rates than indicated by the numerical predator-prey ratio under high prey densities. The central idea of the paper was that when predators easily satisfy their immediate energy needs due to high prey density, they should use their 'leisure time' in a way which improves their fitness expectations. Males can achieve this by searching and guarding receptive females. However, the fitness of female predators

depends on access to food, and so does the fitness of males outside the reproductive season. The 'leisure time' can be utilized by improving the future food situation in two ways; by territorial defense and by hoarding dead prey. The first-mentioned alternative requires inter- and intraspecific territoriality, and it should thus primarily be found among the largest members of a predator guild. The latter alternative requires good retention of dead prey, and it should be used by small predators in boreal and arctic areas, at least during autumn and winter.

At Pallasjärvi, Finnish Lapland, the small rodent project of Heikki Henttonen has been in process since 1970. In collaboration with his project, I tested predictions of the hypothesis of exploitation ecosystems for the role of specialist predators in regulating prey populations during 1983-1988 (paper II). The combination of long-term snap trapping data, live-trapping and an experiment with supplemental food for the voles of the moist taiga provided a good basis for evaluating the role of predation in microtine dynamics. In addition, a natural experiment was provided by a delayed population peak of weasels.

The long term vole data from Pallasjärvi confirm the existence of sustained microtine cycles, consistent with the idea of a predator-prey limit cycle. Supplemental food caused higher population densities but did not change the pattern of population fluctuations (paper II). As long as weasels (Mustela nivalis) remained absent, the voles were essentially non-cyclic, and density increased in the summer, declined sharply in the autumn and changed little over the winter. With

increasing numbers of stoats (Mustela erminea), the summer rises were weakened. A genuine winter crash only occurred in the presence of weasels, the real vole specialists under snowy conditions. The main problem with predator monitoring was that I could not develop an accurate census method for autumnal densities of small mustelids. My predator censuses, based on snow-tracking in early winter, may indeed be underestimations of true numbers of small mustelids, because it is possible that two individuals did not become distinguished from each other if they were of the same sex. Moreover, a 50% reduction of mustelid numbers between weaning and early winter can be regarded as a minimum estimate (Erlinge 1983). However, underestimations of numbers of mustelids only make my figures of peak numbers conservative.

In addition to numbers of predators and prey, the work at Pallasjärvi also included studies on functional response and habitat choise of small mustelids (paper III). The stoat and the weasel used for studies on hunting behavior showed strong tendencies for surplus killing in a terrarium. Nevertheless, the hypothesis of paper I needs further testing in more natural situations before it can be critically evaluated. Moreover, the data in paper II suggest that continuous surplus killing by predators is responsible for initiating and sustaining population declines at high prey densities. The territory system of Clethrionomys spp. slows down population growth rates at high densities, thus 'helping' predators to catch up.

The snow-tracking study (paper III) showed that stoats and weasels preferred the most productive habitats, as predicted by Fretwell (1977, 1987), Oksanen et al. (1981) and L. Oksanen

(1990). However, this preference was by no means absolute.
Substantial predator activity was also observed on barren pine
heaths and bogs. The impression was that it was a question of
'spillover activity': almost all predators were forced to spend
a fraction of their time in barren habitats while travelling
between patches rich in prey. Moreover, there were indications
that despotic behavior of dominating stoats forced weasels to
less profitable habitats (see also T. Oksanen et al. 1990).
These data, and the lack of conspicuous between-habitat
differences in vole dynamics (paper II), raised the question
whether population dynamics of voles in the barren habitats at
Pallasjärvi really differed from those of the productive ones,
as predicted by Fretwell (1977, 1987) and L. Oksanen (1990).

The project on small mammals, their resources and their
predators in a tundra area of Finnmarksvidda (L. Oksanen and T.
Oksanen 1981) was in 1986 extended to include regular live-
trapping and snow-tracking of small mustelids. In 1988 also
live-trapping of microtine rodents and a predator exclosure
experiment were started (paper IV). Data from the lowland part
of the Finnmarksvidda study area were largely similar to those
from Pallasjärvi. Voles of the lowland tundra were cyclic, and
the decline in 1988-89 was accompanied by high numbers and
intense activity of small mustelids in the most productive
habitats. In Finnmarksvidda, the 'exploitation ecosystems'
hypothesis of Fretwell (1977, 1987), Oksanen et al. (1981) and
L. Oksanen (1990) worked better than at Pallasjärvi. Changes in
lemming numbers in the barren highland were chaotic rather than
cyclic, and predator activity remained very low during all
phases of density fluctuations. However, the mainly barren

parts of the lowlands obtained substantial 'spillover predation' just as the pine heaths at Pallasjärvi. The vole populations appeared to be quite regularly cyclic throughout the lowland (paper IV and T. Oksanen et al. 1990).

A corollary of the Fretwell-Oksanen theory on trophic dynamics is that herbivores adapted to resource-limited dynamics in barren habitats should be poorly equipped to cope with the intense predation pressure characteristic for productive habitats (Fretwell 1977, 1987) and for complexes where productive habitats abound (paper VI). This perspective offered an explanation why Norwegian lemmings failed to establish permanent populations in lowland forests and on small, isolated patches of hilltop tundra (paper V). The explanation was tested in Finnmarksvidda during the lemming outbreak 1987-88. The data conformed to the prediction as lemmings mainly occurred in barren plains (chiefly in the highland but also in the most barren parts of the lowland). Conversely, the luxuriant thrust slope with high predator activity remained almost devoid of lemmings, in spite of habitats which ought to be ideal for lemmings (snowbeds followed by meadows and wetlands, compare to Kalela 1971).

The theory of Fretwell (1977, 1987) and Oksanen et al. (1981) appeared to be most successful on a regional scale, i.e. when comparing the highland tundra of Finnmarksvidda with the lowland taiga at Pallasjärvi. It seemed to work fairly well also in a local scale when the sizes of the subareas were measured in tens of square kilometers. However, the theory appeared totally inapplicable to small-scale habitat patchiness in areas where productive habitats abound. The reason for this

discrepancy seemed to be 'spillover predation'. Due to social interactions, a predator population supported by productive habitats inevitably also generates predator activity in adjacent barren habitats. In paper VI, the Oksanen-Fretwell theory is modified to incorporate this phenomenon. After the modification of the theory, the model of L. Oksanen et al. (1981) becomes a special case where patches are infinitely large making between-patch dispersal rates zero. However, in habitat complexes where productive habitats are relatively abundant, the predictions of the new model differ substantially from those of Oksanen et al. (1981). This also concerns qualitative predictions as decreasing productivity may imply increasing predation pressure.

3. Concluding remarks

The empirical and theoretical results summarized above should constitute a step towards better verification of the basic premises of the theory of exploitation ecosystems and towards higher a degree of realism with minimal loss of generality. In any case they suggest that the ideas of top-down population control in terrestrial ecosystems and the keystone role of carnivores in productive areas are realistic possibilities which have to be paid attention to. Decimation of carnivores may alter the dynamics of herbivore and plant communities. The data from Finnmarksvidda also suggest that some relatively rare habitats with exceptionally high productivity can set the tune for the dynamics in an entire habitat complex. Thus, besides keystone species (Paine 1974),

there may also be relatively rare keystone habitats whose removal would have profound impacts on population dynamics of the entire area.

As the implications of the food chain theory are so profound, it would be highly desirable to develop the theory further, and to test it more rigorously than has been possible so far. The model presented in paper VI is, strictly spoken, restricted to dispersal in an equilibrium community. An analysis of the impacts of opportunistic predation by transient predators is on its way (T. Oksanen and L. Oksanen, unpubl.), and it has so far yielded similar predictions as paper VI. Moreover, there are obvious reasons to relax the assumptions of equilibrium conditions. The systems discussed in papers II-V are clearly cyclic or chaotic. A non-equilibrium version of the model of Oksanen et al. (1981) has been published (L. Oksanen 1990), but the model does not include dispersal of carnivores or herbivores. Simultaneous relaxation of the assumptions of a stable equilibrium and lack of dispersal will probably require replacement of analytical work by computer simulations (T. Oksanen and K. Rainio, unpubl.).

In the future, testing the predictions of the theory of patchy exploitation systems (paper VI) with experiments is critical. Working with herbivores and plants at the transition from moderately barren to extremely barren habitats (e.g. on highland tundra) would probably give faster results as compared with carnivore studies. However, as carnivores are predicted to be keystone organisms in all productive habitats, their study is motivated.

ACKNOWLEDGMENTS

REFERENCES

Carpenter, S. R., Kitchell, J. F. & Hogson, J. R. 1985.
Cascading trophic intertactions and lake productivity. -
BioScience 35:634-639.
Caughley, G. & Lawton, J. H. 1981. Plant-herbivore systems. -
In: May, R. (ed.), Theoretical ecology: principles and
applications, Blackwell, Oxford, pp. 132-166.
Cody, M. L. 1974. Competition and the structure of bird
communities. Princeton Univ. Press, Princeton NJ.
Cohen, J. E. 1977. Ratio of prey to predators in community food
webs. - Nature 270:165-167.
Cousins, S. 1987. The decline of the trophic level concept. -
Trends Ecol. Evol. 2:312-316.
Diamond, J. & Case, T.J. 1986a. Preface. - In: J.Diamond & T.
Case (eds) Community ecology. Harper & Row, Cambridge, pp
ix-xi.
 - 1986b. Outline of contents. - In: J.Diamond & T.
Case (eds) Community ecology. Harper & Row, Cambridge, pp
xiii-xix.
Erlinge, S. 1983. Demography and dynamics of stoat Mustela
erminea in a diverse community of vertebrates. - J. Anim.
Ecol. 52: 705-726.
 - Göransson, G., Hansson, L., Högstedt, G., Liberg,
O., Nilsson, I. N., Schantz, T. von, Sylvén, M. 1983.
Predation as a regulating factor on small rodent
populations in southern Sweden. - Oikos 40: 36-52.
Fretwell, S.D. 1977. The regulation of plant communities by
food chains exploiting them. - Perspect. Biol. Medicine 20:
 - 1987. Food chain dynamics - the central theory of ecology?
- Oikos 50:
Hairston, N. G., Smith, F. E. & Slobodkin L. B. 1960. Community
structure, population control and competition. - Am. Nat.
94: 421-425.
Hansson, L. 1969. Spring populations of small mammals in
central Swedish Lapland in 1964-68. - Oikos 20: 431-450.
 - 1979. Food as a limiting factor for small rodent numbers:
Tests of two hypotheses. - Oecologia 37: 297-314.
Kalela, O. 1971. Seasonal differences in habitats of the
Norwegian lemming, Lemmus lemmus (L.), in 1959 and 1960 at
Kilpisjärvi, Finnish Lapland. - Ann. Acad. Sci. Fenn.
(A IV) 178: 1-22.
Krebs, C. & Myers, J. 1974. Population cycles in small mammals.
- Adv. Ecol. Res. 8: 267-399.
MacArthur, R. 1972a. Geographical ecology. Harper & Row, New
York.
 - 1972b. Coexistence of species. In: Behnke, J. (ed.)
Challenging biological problems. Oxford Univ. Press, Oxford,
pp. 253-259.
Menge, B. A. & Sutherland, J. P. 1976. Species diversity
gradients: synthesis of the roles of predation, competition
and temporal heterogeneity. - Amer. Natur. 130: 730-757.
Oksanen, L. 1990. Exploitation ecosystems in seasonal
environments. - Oikos, in press.
 - , & Oksanen, T. 1981. Lemmings (Lemmus lemmus) and
grey-sided voles (Clethrionomys rufocanus) in interaction

with their resources and predators on Finnmarksvidda, northern Norway. - Rep. Kevo Subarctic Res. Stat. 17: 7-31.
- , Fretwell, S.D., Arruda, J. & Niemelä, P. 1981. Exploitation ecosystems in gradients of primary productivity. - Am. Nat. 118: 240-261.
Oksanen, T. 1983. Prey caching in the hunting strategy of small mustelids. - Acta Zool. Fenn. 174: 197-199.
- , Oksanen, L. & Norberg, M. 1990. Habitat use of small mustelids in North Fennoscandian tundra: a test of the hypothesis of patchy exploitation systems. MS.
Paine, R. T. 1974. Intertidal community structure: experimental studies on the relation between a dominant competitor and its principal predator. - Oecologia 15: 93-120.
Pearson, O. P. 1966. The prey of carnivores during one cycle of mouse abundance. - J. Anim. Ecol. 35: 217-233.
Persson, L., Andersson, G., Hamrin, S. F. & Johansson, L. 1988. Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. - In: Carpenter, S. R. (ed.), Complex interactions in lake communities. Springer-Verlag, Berlin, pp. 45-65.
Pimm, S. L. 1982. Food webs. Chapman & Hall, London.
Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. - Science 171:385-387.
Strong, D. R. 1984. Exorcising the ghost of competition past: phytophagous insects. In: Strong, D. R., Simberfloff, D., Abele, L. G. and Thistle, A. B. (eds.) Ecological Communities: conceptual issues and evidence. Princeton Univ. Press, Princeton NJ, pp. 28-41.
Wielgolaski, F. E. 1975. Functioning of Fennoscandian tundra ecosystems. - In: Wielgolaski, F. E. (ed.) Fennoscandian tundra ecosystems, part 2. Springer-Verlag, Berlin, pp. 300-326.
White, T. R. C. 1978. The importance of relative shortage of food in animal ecology. - Oecologia 33: 71-86.