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18. OUTLINES OF FOOD WEBS IN A LOW ARCTIC TUNDRA LANDSCAPE IN RELATION TO THREE THEORIES ON TROPHIC DYNAMICS

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INTRODUCTION

Generalizations derived from published food webs have been criticized recently by several ecologists (Paine 1988; Hall & Raffaelli 1991, this volume; Martinez 1991; Polis 1994). Food-web charts are abstractions, normally produced to illuminate central properties of different ecosystems. They tend to be neither too complex (since complex charts are difficult to interpret and thus impractical), nor too simple (because simple systems can be described verbally). Computing statistical properties of published food webs is thus likely to be a study of heraldics of graphical communication (Raffaelli & Hall 1995). Paine (1988, 1992) not only questioned the validity of established conclusions but even the utility of constructing connectivity food webs, since such webs need have little to do with the dynamics of the system they represent. Energy flow webs, where quantitative information has been added to recorded trophic connections, can be equally uninformative, because minor energy transfers can have major regulatory impacts and vice versa (Power 1990, 1992; Polis 1994). This problem is especially severe in terrestrial ecosystems, where many organisms obtain most of their energy from plants, but where no consensus exists about their potential impact on standing crops and population processes of plants. Many terrestrial ecologists argue that trophic interactions in general and herbivore–plant interactions in particular are donor controlled and the impact of top-down forces is modest or non-existent (Haukioja & Hakala 1975; White 1978; Price *et al.* 1980; Rhoades 1985; Hunter & Price 1992; Strong 1992; Seldal *et al.* 1994; Polis & Strong 1996).

The hypothesis of donor controlled trophic interactions in terrestrial ecosystems is an interesting and testable proposition. It predicts that interactions between herbivores and plants should not change their characteristics when the density of predators is reduced. This prediction has been tested in a wide array of systems, including: greenhouse tables, where one vole amounts to an extraordinarily high population density (Moen *et al.* 1993a); small, isolated islands, where voles or hares have spread spontaneously (Bergman 1970; Soikkeli & Virtanen 1975; Pokki 1981; Angerbjörn & Hjernquist 1984) or where they have been introduced (Oksanen *et al.* 1987; Lundberg, Ekerholm & Oksanen, unpublished data); islands, where important predators of folivorous insects are absent (Spiller & Schoener 1990); various kinds of fenced herbivore populations (Desy & Batzli 1989; Atlegrim 1989; Marquis and Whelan 1994; Ostfeld 1994); relatively large, predator-free islands where rabbits (Werth 1928) or reindeer (Klein 1987; Leader-Williams 1988) have been introduced; areas invaded by feral reindeer (Höglund & Eriksson 1973); an island where wolves are suffering from inbreeding depression and are thus unable to respond to an increase in moose density (McLaren & Peterson 1994); and an island, where a novel herbivore has evolved in the absence of predators (Hnatiuk *et al.* 1976; Merton *et al.* 1976).

Except for cases where herbivores quickly reach a size that is too large to be included in the predator diet (Schmitz 1993), the story is always the same. Areas with exceptionally low predator numbers are characterized by exceptionally high herbivore density and by exceptionally intense herbivory pressure. Cascading impacts to plants have been weaker in the case of folivorous insects than for grazing vertebrates, but this pattern may have a technical explanation. Experiments on herbivorous invertebrates have normally only considered insectivorous birds and lizards, yet there is persuasive circumstantial evidence for the importance of pupal predators (Hanski 1987) and parasitoids as regulators of folivores (Caughley & Lawton 1981). Gall midges appear to be involved in a strong interaction with parasitoids (Strong & Larsson 1994), and predatory nematodes appear to regulate root herbivores (Strong *et al.* 1995a; Strong *et al.* 1995b). Moreover, most invertebrate work has been done with univoltine species during a single growing season, which precludes the study of folivore population growth between generations. We suspect that stronger impacts could be observed in greenhouse experiments, where folivores could be effectively protected against all natural enemies.

The case of Aldabra, with its strictly resource-limited grazing tortoises and its tightly clipped grazing lawns, is especially instructive. Contrary to the argument of Strong (1992), the tortoises are not aberrantly efficient. They are rather bizarre grazers for this habitat, needing shade and large amounts of fresh water, which makes it impossible for them to eliminate woody plants from the island (Hnatiuk *et al.* 1976; Merton *et al.* 1976). They are currently under threat of being outcompeted by an expanding population of feral goats, which are more efficient herbivores than the tortoises (Hambler 1984; Coblentz *et al.* 1990). Moreover, Aldabra has received 'much of the rich mainland flora', including relatively unpalatable plants, and plants that are morphologically quite different from the prostrate constituents of grazing lawns. Many species of woody plants are present, the atoll being largely covered by woody vegetation at the start of this century, when the tortoise population had been overexploited by man (Stoddart 1971a, b). The ongoing decimation of woody vegetation and the re-expansion of grazing lawns is a direct response to increasing grazing pressure (Hnatiuk *et al.* 1976; Merton *et al.* 1976) and can be reversed by excluding grazers (Gibson *et al.* 1983). This natural experiment even has an evolutionary component. The dominant constituents of grazing lawns belong to genera which are represented by totally different types of plants in adjacent mainland areas (e.g. tall graminoids in the case of *Scirpus* spp., *Panicum aldabarense* and *Sporobolus* spp., exceptionally unpalatable dicots in the cases of *Euphorbia* spp.), indicating that the persistent, intense herbivory has selected for prostrateness and against investments in unpalatable, woody shoots (Braithwaite *et al.* 1973; Merton *et al.* 1976).

Another line of empirical evidence is provided by the traditional, extensive grazing systems of temperate Eurasia, where a few, initially native grazers (cattle and horses) and browsers (sheep, goats, and in arid regions, even camels) were protected against predators. While specialized cattle ranching frequently leads to the invasion of woody plants, due to the high degree of grass specialization by bovids, traditional grazing with mixed livestock has invariably led to the replacement of forests by secondary grasslands, heath or cushion plant communities (Walter 1964, 1968; Sjörs 1971; Gimingham 1972; Ellenberg 1978). In areas where grazing has been long lasting and intense, it has led to the evolution of endemic, prostrate plants and to the development of peculiar plant communities, which are now threatened by the relaxation of grazing pressure (Pettersson 1959). The results of this continent-wide experiment clearly show that there is no such thing as an inedible plant. Even the least palatable trees are vulnerable as seedlings (Ostfeld & Canham 1993). Elimination of woody plants by browsing mammals may take some time, but in the end it will always succeed. To witness this, one does not have to travel to Aldabra; corresponding grazing lawns, created by sheep or rabbits, are commonplace all over England, and forest regeneration in many areas has been restricted to the period when rabbits were still vulnerable to myxomatosis (Crawley 1983).

The hypothesis of donor control in terrestrial grazing chains has been tested and, in our opinion, thoroughly falsified. Donor-controlled trophic interactions between animals and plants do indeed occur, involving thousands of species of granivores, frugivores, nectarivores, sapsuckers and other consumers of high-quality plant organs or products. These consumers might live in White's (1978) 'passively harsh world', where the main regulating factor is the production of adequate food. However, there are also true folivores, which have evolved a symbiotic relationship with cellulase-producing microbes, and can thus subsist and reproduce by exploiting vegetative plant organs. Some of these folivores have for millennia been used for the production of meat, milk and wool, while others occasionally defoliate forests and cropfields, causing heavy economic loss. Consequently, top-down forces in terrestrial food webs are not only an interesting academic issue, but vital for resource management as well.

THREE HYPOTHESES AND THEIR PREDICTIONS

From the current debate on trophic dynamics in terrestrial food webs, the *hypothesis of ratio-dependent predation* (Arditi & Ginzburg 1989; Arditi *et al.* 1991; Akçakaya *et al.* 1995) stands out as the one with least-surprising and seemingly most plausible predictions. The core of the hypothesis is that the functional response of predators in the population dynamic time scale depends on the amount of prey per predator. Consequently, the structure and dynamics of food webs is predicted to remain unchanged across productivity gradients, as equilibria at all trophic levels are similarly influenced by primary productivity. If predators are assumed to survive at relatively low prey/predator ratio, the hypothesis of ratio-dependent predation can be regarded as a formalization of the green world hypothesis of Hairston *et al.* (1960) and Hairston and Hairston (1993), according to which plants and carnivores and resource limited and herbivores are predation controlled in all terrestrial ecosystems. With other parameter values, the hypothesis of ratio-dependent predation can be made to approach the donor-controlled ideas of Hunter and Price (1992).

Entirely different predictions are generated by *the hypothesis of exploitation ecosystems* (Oksanen *et al.* 1981; see also Fretwell 1977, 1987), which was deduced by modelling trophic interactions across productivity gradients by means of Rosenzweig's (1971, 1973, 1977) elaborations of Lotka–Volterra type exploitation models. According to this hypothesis, relatively productive ecosystems (e.g. forests and their successional stages) are characterized by three-link trophic dynamics – that is, by resource-limited predators, predation-controlled herbivores and resource-limited plants, as proposed by Hairston *et al.* (1960). Predator and plant communities are structured by resource-based competition, whereas apparent competition (Holt 1977) is the structuring force of herbivore communities. In relatively unproductive ecosystems, such as tundras, steppes and semideserts, depletion of the vegetation arises from a lower density of herbivores than would be required to support a population of predators. Consequently, two-link trophic dynamics prevail. Carnivores can only be present during grazer outbreaks, and are thus relegated to the role of donor-controlled consumers. Herbivores are resource limited and their communities are structured by resource-based competition, which is predicted to create clear niche segregations and to favour those species which can break even at low plant biomass and utilize low-quality forage. Plants are subjected to intense natural grazing pressure, and the vegetation is structured by apparent competition. In the most extreme environments, such as polar deserts, grazers are predicted to be absent. The only trophic interaction in these one-link ecosystems is between plants and physical resources. Consequently, the scanty vegetation is structured by pre-emptive competition for the few sites where growth is possible.

The patterns described above should be found in large-scale productivity gradients. Trophic dynamics within relatively small patches of unproductive habitat can be profoundly influenced by 'spillover predation' (Holt 1984), due to despotic habitat selection in predators (Fretwell 1972; T. Oksanen 1990) and opportunistic behaviour of transient predators (Oksanen *et al.* 1992a). The most simple version of the hypothesis (Oksanen *et al.* 1981) predicts that equilibrium biomass at different trophic levels increases in a step-wise manner along gradients of increasing primary productivity. In two-link ecosystems, the equilibrium herbivore biomass increases whereas standing crop of plants is constant. In three-link ecosystems, equilibrium plant biomass increases, equilibrium herbivore biomass stays constant and equilibrium carnivore biomass may or may not increase (depending on whether herbivores are saturated). Especially in the case of three-link ecosystems, these biomass patterns can become modified by plausible evolutionary and behavioural responses to intense exploitation pressure (Abrams 1984, 1993; Oksanen 1992). This may also happen in nutrient-poor two-link ecosystems, where the evolutionarily stable strategy of plants includes relatively high investment in defence and relatively low palatability (Bryant *et al.* 1983; L. Oksanen 1990a; Herms & Mattson 1992).

In their recent contributions, Polis *et al.* (1995) and Polis and Strong (1996) have vigorously argued for a third alternative, to be referred to as the *hypothesis of energy shunts*. The basic premises are that omnivory is rampant in all food webs, making the concept of trophic level meaningless (Cousins 1980, 1987) and that most energy fixed in terrestrial ecosystems goes inevitably directly to the detritus chain (Odum 1971). The causal background of this phenomenon was not discussed in detail; possible, uncontroversial causes include the high turnover rate of fine roots, the copious amounts energy directed to mycorrhizas, and the problems of grazers tracking the seasonal pulse of plant growth. Moreover, Polis and Strong argue that detritus-based food chains and food chains based on green plants are tightly intertwined, because consumers ignore the feeding history of their resources (Cousins 1987). The impact of these internal energy shunts can be enhanced by energy transfers from other ecosystems, especially where relatively barren ecosystems are juxtaposed to substantially more productive ones (Polis & Hurd 1995).

Unfortunately, the interesting ideas of Polis and his coworkers have been only vaguely outlined, and aspects of the contributions are logically inconsistent. On one hand, the authors argue for the invulnerability of plants and for the unimportance of herbivory, on the other hand they argue for the hypothesis of Menge and Sutherland (1976), according to which basal organisms are intensely exploited by omnivorous top consumers and exploitation predation pressure increases monotonically from the top of the food web to its base. For us, a reasonable compromise is to assume that there are true folivores, capable of exploiting vegetative plant tissues and of decimating plant biomass (see above) and omnivores, which function as predators of folivores but, in addition, obtain energy from detrital food webs and plants in a donor-controlled way. The variant of the energy shunt hypothesis thus developed is partially our own and does not necessarily conform with the views of Polis and Strong.

The dynamics of such energy shunt systems have been formally studied by L. Oksanen (unpublished data); here we restrict ourselves to intuitively obvious predictions. In the case of productive ecosystems, the dynamics of energy shunt systems by and large converge with the behaviour of exploitation ecosystems and with the green world hypothesis of Hairston *et al.* (1960). Omnivory creates intra-guild predation (Polis *et al.* 1989), which on the guild level dynamically corresponds to direct density dependence and thus tends to reduce the predation pressure experienced by folivores (Wollkind 1976; T. Oksanen 1990). On the other hand, availability of detritus-based prey and direct energy transfers from plants to carnivores increase the equilibrium standing crop of carnivores and the predation pressure on folivores. Thus, the impacts of the additional assumptions incorporated in the energy shunt hypothesis tend to cancel in the case of relatively productive ecosystems. The behaviour of energy shunt systems along gradients of decreasing primary productivity is radically different from the predictions of the two other hypotheses. In unproductive habitats, where foliage lies close to the ground, carnivores can simultaneously search for herbivores and for detritus-based predators of similar size. This creates intense apparent competition between herbivores and detritus-based predators, and in apparent competition, folivores are handicapped by the load of their internal 'fermentation factory' (see Oksanen 1992). Consequently, decreasing primary productivity leads to elimination of folivores from energy shunt systems even in the absence of direct energy transfers from plants to carnivores.

Standing crops of plants, herbivores and carnivores along gradients of primary productivity have been frequently used in the debate on trophic dynamics (Oksanen *et al.* 1981; Oksanen 1983; McNaughton *et al.* 1989; Arditi & Ginzburg 1989; Arditi *et al.* 1991; Moen & Oksanen 1991; Oksanen *et al.* 1992; Persson *et al.* 1992; Diehl *et al.* 1993; T. Oksanen *et al.* 1995; Akçakaya *et al.* 1995; Crête & Manseau 1996). While many interesting points have been raised by such data, we doubt that they will ever settle the issue. Heavy human impacts on top predators are commonplace, and many populations of terrestrial herbivores are hunted and managed, making the relevance of most data points dubious. Standing crops of

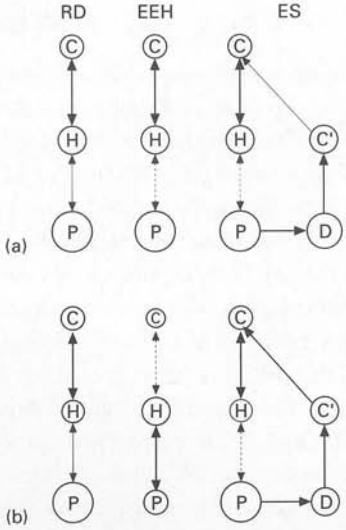

FIG. 18.1. Outlines of food chain dynamics in (a) productive and (b) unproductive terrestrial ecosystems according to the hypotheses of ratio-dependent predation (RD), exploitation ecosystems (EEH) and energy shunts (ES).

plants are normally measured at the end of the growing season, whereas the prediction of constant plant biomass in two-link ecosystems refers to the end of the winter or the dry season. Moreover, the hypothesis of exploitation ecosystems predicts that many two-link ecosystems are characterized by non-equilibrium dynamics (Oksanen *et al.* 1981; L. Oksanen 1990b). In such systems, mean standing crop of plants should correlate positively with primary productivity, even if the theoretical equilibrium standing crop remained constant (Abrams & Roth 1994; Lundberg & Fryxell in press).

Predictions concerning the structure and dynamics of food webs, summarized in Fig. 18.1, are more robust. Statistical analyses of published food webs (Pimm 1982; Briand & Cohen 1987; Cohen *et al.* 1990) have been supportive to the hypothesis of ratio-dependent predation. However, according to a re-analysis of these food webs by L. Oksanen *et al.* (1995), predaceous connections between herbivorous and carnivorous vertebrates become less frequent along the gradient from boreal to high arctic areas. The same trend appears to exist in a mesoscale gradient in northern Fennoscandia. The shortcomings of the chapter, Oksanen *et al.* (1995), include a clear vertebrate bias and heavy reliance on unpublished data from northernmost Fennoscandia. Below, we broaden the taxonomical perspective and provide the reader with access to those primary data that have not yet been published and which are critical to the food webs outlined by L. Oksanen *et al.* (1995).

STUDY AREA AND METHODS

Since 1977, we have studied interactions between plants, microtine rodents and small predators on the tundra plateau of Finnmarksvidda, northernmost Norway. The area of 16 km^2, where our studies have been conducted since 1986, has been described by Oksanen *et al.* (1992b), L. Oksanen *et al.* (1995) and Oksanen & Schneider (1995). Its southern part consists of lowland tundra, underlain by nutrient-poor Precambrian rocks and dominated by barren lichen heaths and palsa bogs (Oksanen & Virtanen 1995). We have subdivided this lowland area in two parts, the divide (representing typical, barren low arctic tundra landscape), and the valley, lying in the vicinity of the escarpment of the Scandinavian mountain formation and harbouring relatively large patches of more productive habitats (mesic scrublands and mesic birch woodlands). The slope immediately below the escarpment is south facing, moist, nutrient rich and occupied by moderately productive (e.g. mesic heaths) and luxuriant habitats (e.g. herb-rich willow thickets and birch woodlands). Above the escarpment, there is a highland plateau, underlain by nutrient-poor silicaceous nappes and occupied by various types of unproductive alpine vegetation (lichen-rich dwarf birch–crowberry heaths, sedge–cottongrass bogs and moss–dwarf willow snowbeds, see Oksanen & Virtanen 1995).

Plants and microtine rodents have been studied both experimentally and by means of descriptive methods. In the context of these studies, we have also recorded observations of other herbivorous vertebrates (reindeer, mountain hare, willow grouse, rock ptarmigan). The composition of the guild of grazing vertebrates in different subareas has been presented by L. Oksanen *et al.* (1995), the numerical dynamics of microtine rodents during 1977–90 have been summarized by Oksanen and Oksanen (1992). Mammalian predators have been studied by means of snow-tracking and live-trapping (Oksanen & Oksanen 1992; Oksanen *et al.* 1992b; Oksanen & Schneider 1995; Aunapuu, unpublished data). The study area has been annually surveyed for breeding avian predators. In the peak year of 1988, the raptor study area was extended to cover an area of 70 km^2, and the survey was initiated in the spring, when snow allowed rapid moving and made the arriving predators visible. Since 1993, we have used the same method, but extended the raptor study area to 100 km^2, and recorded inhabited fox dens. The impact of mammalian predators on lemmings in the highland was studied in spring 1989, immediately after a lemming crash, by recording indications of winter nest predation (fur-lined winter nests, see MacLean *et al.* 1974) and by looking at signs of physical injury (e.g. broken spinal cords) in dead lemmings. When live-trapping microtine rodents, we have also recorded shrews.

We have studied invertebrates by means of pitfall traps in 12 localities, on a transect from the divide through the valley and slope to the highland. Pitfall samples have been identified to species, counted, converted to biomass equivalents using the third power of the body weight as a scaling factor and pooled into four trophic categories (carnivores, herbivores, detritivores and others). L.O. conducted line transect studies of breeding passerine birds and waders in the same general area in 1976, with the Finnish line transect method (transect length 50 km, main belt width 50 m, transects followed co-ordinate lines to yield an unbiased sample of the landscape; for details, see Järvinen and Väisänen 1976). The areas covered by this survey can be regarded as representative of lowland and highland habitats in Fennoscandia, whereas the slope subarea is essentially more productive than the areas covered by the transect lines. We thus conducted similar line transect survey (transect length 2 km) in the most luxuriant part of the slope subarea in June 1995.

HERBIVOROUS VERTEBRATES AND THEIR PREDATORS

The dominant components of the guild of grazing vertebrates are the man-managed reindeer and the microtine rodents. In the luxuriant slope area and in the most productive lowland habitats, microtines have had regular, cyclic density fluctuations, where declines have been accompanied by relatively high numbers of small mustelids (Oksanen & Oksanen 1992). Tracking in these habitats has indicated high mustelid activity (Oksanen *et al.* 1992b). In the 1990s weasels have remained rare, and the period of the vole cycle has increased from 4 to 5–6 years, the typical peak syndrome with high densities in spring has not been observed, and minimum vole densities have been exceptionally high. Except for the years of lowest vole numbers (1990 and 1995), the density of stoats within the slope subarea has consistently exceeded one individual km^{-2}. The number peaked in late summer 1994, when 10 stoats were captured (corresponding to 3.4 stoats km^{-2}). In the valley part of the lowland subarea, stoat density has ranged from 0.2 to 0.8 km^{-2} during our tracking and trapping periods in the 1990s. Both in the lowland and in the valley, the activity of small mustelids has been concentrated in the most productive habitats, but not restricted to them (Table 18.1; Oksanen *et al.* 1992b). The dynamics of the microtine–mustelid part of the grazing chain in the slope and productive valley habitats thus seems to conform to the model of L. Oksanen (1990b), where productive habitats are predicted to be characterized by a stable mustelid–microtine limit cycle (for a slightly different approach to the same issue, see Hanski *et al.* 1991 and Hanski *et al.* 1993). In any case, predators show a persistent presence and the impact of microtines on the vegetation is modest (Moen 1993).

In the divide, mustelid activity has been sporadic, mainly occurring during the final phases of microtine crashes in 1989 and 1995 when densities were low in all parts of the study area, and concentrated in the most productive habitats (Table 18.1; Oksanen *et al.* 1992b). The highest density was recorded in summer 1995, when four stoats were trapped (a density of about one individual km^{-2}).

TABLE 18.1. Activity indices for stoats and weasels for the three sample areas during 1991–95 and for the main habitat categories within them. The indices represent percentages of 14 × 14-m grids visited by small mustelids during a 5-day tracking period. Index values smaller than 1 are denoted by + . Unproductive habitats include lichen heaths, heath snowbeds and open bogs. Moderate habitats include scrublands, heathlands, woodlands with a closed field layer, wetlands with herbs and willows and herb-rich snowbeds. Productive habitats are tall herb meadows plus woodlands and scrublands with tall herbs. The percentage contribution of the habitat categories to each subarea are noted in parentheses.

	Stoats	Weasels
Divide		
Over-all	0	1
Unproductive (96%)	0	+
Moderate (4%)	0	16
Slope-valley		
Over-all	8	+
Unproductive (67%)	4	+
Moderate (28%)	14	0
Productive (5%)	39	10
Highland		
Over-all	0	0
Unproductive (99%)	0	0
Moderate (1%)	0	0

In the highland, the occurrence of small mustelids has been even more sporadic. Occasionally, individuals have been tracked along the margins of the highland, but observations from its interior have been confined to December 1988 (one stoat tracked once), and to August 1995 (two juvenile stoats trapped). In spring 1989, after the crash of the lemming population (Oksanen & Oksanen 1992), we located 193 winter nests in the highland; of these only 13 (7%) showed signs of winter predation. Of 51 lemming bodies recovered, only eight (16%) showed any kind of external injury (wounds or broken spinal cord). Except for two preyed-upon winter nests (found in the same area where the stoat had been tracked), these indications of predation were confined to the marginal parts of the highland (Table 18.2). Within our permanent highland plots, the moss cover was totally destroyed and graminoid cover was reduced in 1989 (Moen *et al.* 1993b).

During the 1990s, medium-sized mammalian predators have been relatively common in our study area. American mink (*Mustela vison*) was first trapped in 1990 (three individuals), and again in 1991 (seven individuals). All mink captures were made along creeks in the lowest part of the slope. Mink tracks have been observed outside the vicinity of creeks in the lower parts of the slope in late autumn and early winter. Red foxes (*Vulpes vulpes*), which had been been largely absent during the early and mid-1980s (probably due to the sarcoptic mange) appeared in

TABLE 18.2. Indications of winter nest predation (a) and signs of predation or scavenging recorded in observed dead bodies of lemmings (b) in spring 1989 in the highland proper and in marginal areas (representing transition towards the slope). The border between the two areas was based on limits between drainage systems. Differences between the two subareas were statistically significant in both cases. For winter nest predation, $\chi^2 = 12.62$, $P < 0.001$; for lemming bodies, $\chi^2 = 15.98$, $P < 0.001$.

(a) Winter nests	Predated	Intact
Interior highland	2	117
Transition	11	63

(b) Lemming bodies	Damaged	Intact
Interior highland	0	32
Transition	8	11

1991. The hunting activity of foxes and mink could be assessed by recording areas where microtine live traps had been overturned systematically even in poorly visible sites. In 1993, five red fox dens were located within the raptor study area or close to its borders (Fig. 18.2). One of these was also within the study area proper (in the highland subarea, in an abandoned arctic fox den). The activity of this litter was concentrated around the piece of luxuriant slope immediately south of the den, where we had to pile stones over small mammal traps in order to continue live trapping. The activity of medium-sized mammalian predators thus appeared to be even more confined to the most productive slope habitats than the activity of small mustelids.

Avian predators had been relatively numerous in 1983 (Oksanen & Oksanen 1992), but the only subsequent year with comparable densities was 1988. Highest densities of avian predators were then observed in the slope, where the dominating species was the rough-legged buzzard (*Buteo lagopus*) (Fig. 18.2; notice that the rough-legged buzzards breeding on the escarpment cliff hunted almost exclusively on the slope and in the valley). However, the most numerous avian predator, the long-tailed jaeger (*Stercorarius longicaudus*), preferred wetlands of the divide. Owls, which had been relatively common during previous peaks (Oksanen & Oksanen 1992) were only represented by a single breeding pair. During the 1990s, the highest density of avian predators was recorded in 1993. Except for merlins (*Falco columbarius*), densities were considerably lower than in 1988 (Fig. 18.2). The diet samples analysed so far indicate that rough-legged buzzards are pronounced microtine specialists (96% of samples included microtine remains, birds and shrews were found in 12% and 8% of samples respectively). For long-tailed jaegers and

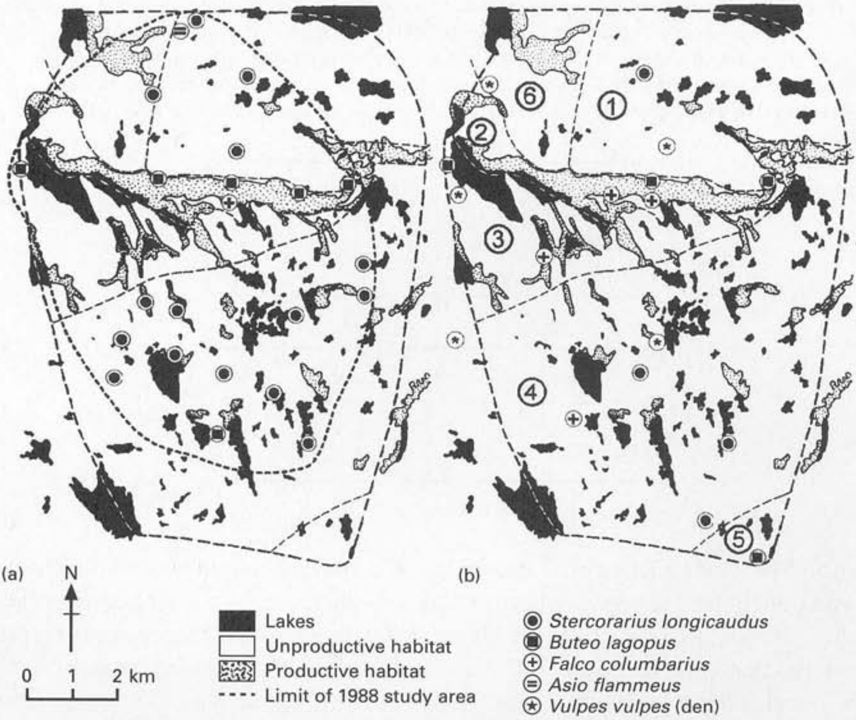

FIG. 18.2. Breeding sites of avian predators in the extended study area in (a) 1988 and (b) 1993, the two summers with highest densities of avian predators between 1986 and 95. Numbers in (b) refer to subdivisions of the extended study area (1, extended highland; 2, extended slope; 3, extended valley; 4, extended divide; 5 and 6 are relatively productive marshy areas, which cannot be directly related to the subdivisions of the main study area.) The merlins attempting to breed on the divide in 1993 failed; other symbols refer to successful breeding.

merlins, microtines and birds are about equally important, occurring in 40–60% of diet samples. Jaegers frequently utilized invertebrates (24%) and plant material (44%) which other predaceous birds did not use at all (see also Andersson 1971, 1976). Dietary data thus amplify the difference in intensity of avian predation of microtines between the slope and other subareas.

INVERTEBRATES, SHREWS AND PASSERINE BIRDS

The dominant trophic groups in all pitfall samples were carnivores and 'others' (Fig. 18.3), the latter group consisting of animals involved in obviously donor-controlled trophic interactions (e.g. feeding on sap or mould). Detritivores were numerous, but their biomass was low due to the predominance of tiny Collembola.

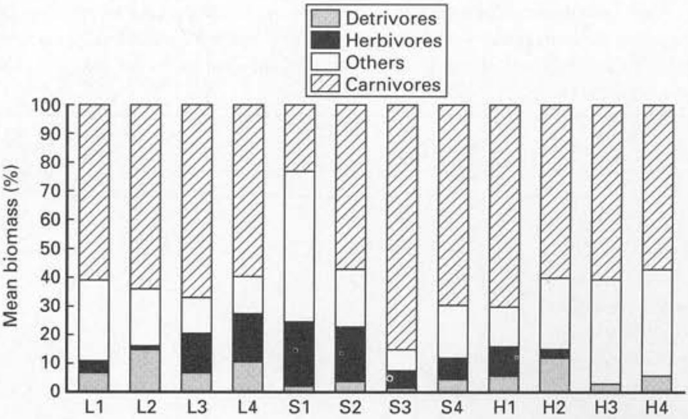

FIG. 18.3. Abundance relationships between main trophic guilds of invertebrates in different parts of the study area according to pitfall trap samples, converted to biomass equivalents. Locations of trapping sites are as follows: L1, southern part of the divide, lichen tundra; L2, valley, lichen tundra; L3, valley, mesic heath; L4, valley, willow scrubland; S1, slope, herb-rich woodland; S2, slope, mesic woodland; S3, slope, timberline; S4, slope, mesic heath; H1, slope-highland transition, mesic health; H2, highland, creekside with low willows; H3, highland, alpine tundra; H4, highland, top plateau.

Herbivores were most abundant in the wooded parts of the slope (sites S1 and S2), moderately abundant in shrubby lowland, slope and highland sites (L3, L4, S3, S4, H1 and H2), rare in typical lowland tundra with scattered dwarf birch shrubs (L1 and L2) and absent from alpine sites with only prostrate vegetation (H3 and H4). Notice that herbivores are more trappable by pitfall traps in tundra habitats, where the dominant taxa (homopterans, hemipterans and chrysomelid beetles; see Solhöy *et al.* 1975) move along the ground, than in the forest, where the dominating taxa (sawfly and moth larvae; Haukioja & Koponen 1975) live in the canopy. The concentration of herbivores in forested slope habitat was thus probably even more pronounced than shown in our data.

Shrews (mainly *Sorex araneus*) were largely confined to the slope; in 1992, the abundance of shrews was at its highest, and we trapped four in the highland and three in the valley, while slope captures were in double figures. Densities of passerine birds declined from luxuriant birch forests to barren tundra habitats, but not dramatically, and this was balanced by an opposite trend in the abundance of waders (Table 18.3), especially in palsa bogs of the lowland. The exceptionally high density and species diversity of waders in the tundra in general, and palsa bogs in particular, is a regional phenomenon (Järvinen & Väisänen 1976, 1978) and obviously detritus based. In terms of primary productivity, palsa bogs are more barren than lichen heaths (Sonesson *et al.* 1975).

TABLE 18.3. Estimated densities of breeding birds (pairs km^{-2}) in the main habitat categories of Finnmarksvidda on the basis of line transect censuses (main belt observations only, main belt width 50 m). In the slope forests, birds observed outside the main belt but no further than 200 m from the transect line are denoted by +.

	SLOPE		LOWLAND		HIGHLAND	
	Forest	Scrub	Bog	Heath	Bog	Heath
Passerines						
Anthus pratensis	–	8	19	4	17	6
Calcarius lapponicus	–	42	38	43	22	25
Carduelis flammea	+	8	–	–	–	–
Emberiza schoeniculus	+					
Fringilla montifringilla	50	17	–	–	–	–
Luscinia svecica	40	17	19	2	22	–
Oenanthe oenanthe	–	–	–	–	–	3
Phylloscopus trochilus	130	33	8	1	9	–
Plectrophenax nivalis	–	–	–	–	–	2
Turdus iliacus	–	–	3	3	–	–
Total	**220**	**125**	**87**	**53**	**70**	**36**
Waders						
Calidris alpina	–	–	8	–	4	2
C. temmincki	–	–	5	–	–	–
Eudromias morinellus	–	–	–	–	–	2
Philomachus pugnax	–	–	8	1	9	–
Phalaropus lobatus	–	–	5	–	–	–
Pluvialis apricaria	–	–	3	13	4	13
Tringa glareola	–	–	8	–	–	–
T. erythropus	–	–	3	–	–	–
Total	**–**	**0**	**40**	**14**	**17**	**17**
Larids						
Stercorarius longicaudus	–	–	–	1	–	–
Sterna paradisaea	–	–	5	–	–	–
Gallinaceous birds						
Lagopus lagopus	–	17	–	1	–	–
Corvids						
Corvus corone	+	–	–	–	–	–
Raptors						
Falco columbarius	+	–	–	–	–	–
km of transect line	2	2	7	21	5	12

OUTLINES OF FOOD WEBS

The data presented above can be summarized in the form of two food webs (Fig. 18.4). The one for slope, productive valley and divide habitats (Fig. 18.4a) is characterized by three-link trophic dynamics in all parts of the grazing web. The vegetation is little influenced by herbivory and dominated by obviously competition-adapted, broad-leaved plants. Herbivores are exploited by numerous predators, especially in the most luxuriant slope habitats. The dynamics of microtines appear to be changing from weasel–vole limit cycle, which used to be typical for boreal Fennoscandia (L. Oksanen 1990b; Hanski *et al.* 1991, 1993), to seasonal density fluctuations where generalist (fox, mink) and intermediate predators (stoats) play a central role. The absence of typical peak years with high spring densities has

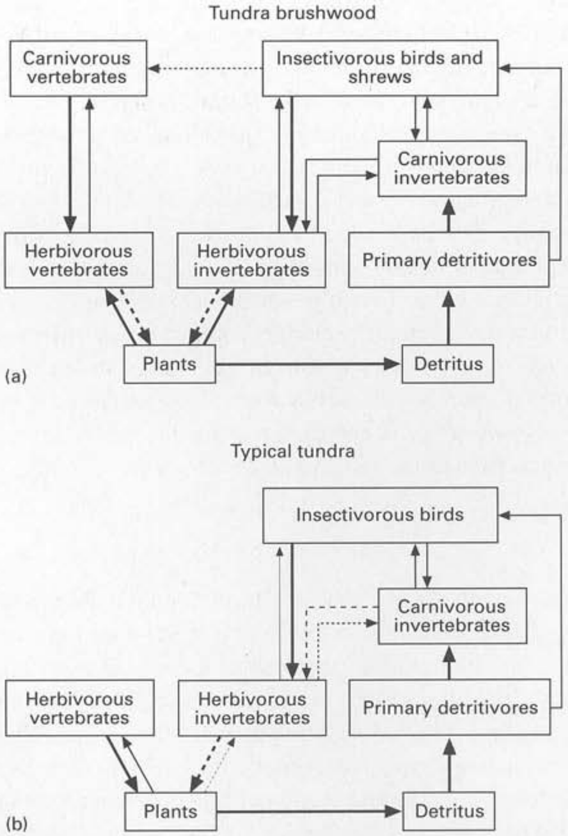

FIG. 18.4. Food-web outlines for the most productive parts of (a) tundra–brushwood landscape at Joatkanjávri and (b) typical low arctic and alpine tundra within the study area. Arrows pointing from resources to consumers represent energy transfers; their thickness indicates the relative magnitude of the flow. Arrows pointing from consumers to resources indicate top-down impacts, their thickness indicates the strength of the top-down control. Dashed lines from consumers to resources indicate potential top-down impacts which are not realized due to top-down controls higher up in the food web.

been reflected by low numbers of avian predators. In the invertebrate branch, detritus-based predators abound, and shrews are likely to feed on both folivores and detritus-based predators. For passerines, the existence of a substantial detritus shunt is less certain, because of three common species, two are foliage gleaners and only one (the brambling *Fringilla montifringilla*) is a partial ground feeder. In somewhat less productive habitats, the detrital shunt is stronger, owing to the higher abundance of ground-feeding birds. The detrital shunt continues to carnivorous vertebrates but can hardly play a major part in their resource supply, as vole numbers normally exceed the numbers of passerines and shrews by an order of magnitude, and voles are easier to catch than birds.

Food webs in unproductive tundra habitats are characterized by a strong energy shunt from detritus-based invertebrates to passerines and waders (Fig. 18.4b). Herbivorous invertebrates are practically absent, probably because of apparent competition with carnivorous invertebrates. Herbivorous vertebrates form a separate branch, presented in detail by L. Oksanen *et al.* (1995a). In this branch, predators are present so infrequently and at such low numbers that their inclusion in the web is questionable. Results obtained at Barrow, where relatively high densities of owls and jaegers are frequently observed (Pitelka 1973) are not transferrable to Fennoscandian inland tundra. The only even moderately common predaceous bird, the long-tailed jaeger, represents a marine shunt in terms of its over-all biology and obtains much of its summer resources via energy shunts from the detritus chain (in the form of insects and insectivorous birds) and directly from the plants. In our study area, however, these energy sources do not suffice to support breeding, unless microtine rodents are already numerous in spring.

DISCUSSION

The energy shunt hypothesis of Polis and Strong (1996) appears to be relevant for the invertebrate-based food web. Its central premise – that most energy fixed by plants goes directly to detritus – applies to arctic and subarctic ecosystems (Wielgolaski 1975; Whitfield 1977; MacLean 1980). This energy flow suffices to maintain relatively high numbers of breeding birds foraging on all kinds of invertebrates, and the ensuing apparent competition between folivorous and predatory invertebrates appears to lead to elimination of folivores from open tundra habitats. The phenomenon seems to be circumpolar. At Barrow and Prudhoe Bay, Alaska, herbivorous invertebrates are so uncommon that they are not even included in the herbivore community of Batzli *et al.* (1980). On Truelove Lowland, Devon Island, Canada, the dominant folivorous insects consumed 0.0001–0.01% of the annual vascular plant production (Ryan & Hergert 1977). At least in our study area, the virtual absence of folivorous invertebrates did not seem to depend on low temperatures *per se*, as the phenomenon was associated with the absence of shrubby vegetation, and was observed both in the relatively warm lowland and on the cooler highland.

On Devon Island, energy shunts support jaegers (though their breeding success was low, see Pattie 1977) and even a few stoats (Riewe 1977), in a system where the densities of lemmings are often so low that predators could not possibly support themselves on herbivores only (Fuller *et al.* 1977). The same seems to apply to the Barrow area, where predation on lemmings can occasionally be intense (Pitelka 1973; MacLean *et al.* 1974; Batzli *et al.* 1980), in spite of the fact that lemming numbers can be very low for long periods, such that predators could not persist without alternative resources. In the inland areas of northern Fennoscandia, detrital energy shunts are insufficient to sustain predators of grazing vertebrates. The same seems to apply to Precambrian Shield areas in the inland of arctic Canada (Krebs 1964). We suspect that the difference reflects distance from the shoreline and the consequent difference in the impact of marine energy shunts (see Polis & Hurd 1995), and that the insufficiency of detrital shunts to support predaceous vertebrates is a generic feature of the tundra. The basic problem is that all arctic insectivores are homeothermic and thus characterized by low ecoenergetic efficiency. Moreover, they are absent in the winter when food would be most needed. In warm deserts, where detritus-based insects are consumed by snakes and lizards, the detrital shunt might be more important.

We agree with Polis and Strong (1996) that the hypothesis of exploitation ecosystems only applies to a small fraction of animal species. However, plants are included in all branches of the grazing chain. As herbivorous vertebrates are resource limited, the plant cover of the tundra is subjected to intense, natural grazing. There is thus no way to understand the ecology of arctic plants without due consideration of grazer–plant interactions, as emphasized already by Tihomirov (1959). Moreover, in spite of their relatively low species diversity, herbivorous mammals are fascinating research objects. The shift from resource limitation to predation control at the transition from arctic to boreal habitats seems to apply to ungulates too (Crête & Manseau 1996), and thus even has implications for game management. Moreover, the feeding ecology and guild structure of arctic mammals can be understood on the basis of classical resource competition, whereas apparent competition seems to be the organizing principle of boreal and temperate communities of grazing mammals (Oksanen 1992). The change in organizing principle is even reflected in the central role of predation at the southern distributional limits of primarily arctic mammals, such as the tundra hare (Holt 1977), the caribou (Bergerud 1988) and the Norwegian lemming (Oksanen 1993).

In research on trophic dynamics, it is useful to see different ideas as abstractions, which are neither perfectly right nor entirely wrong (unless derived in a logically flawed way), but have varying ranges of applicability with shifts in geography, taxonomy, etc. The green world hypothesis of Hairston *et al.* (1960) was one of the great generalizations in ecology, with a wide range of applicability in all respects. It is unlikely that equally big ideas remain to be discovered, and it is counterproductive not to give credit where credit is due. However, even the green world hypothesis has its limitations, which should be vigorously pursued in order to improve our understanding of nature and our ability to prudently manage and protect it. These limitations appear to be especially pronounced in relatively barren areas, where several processes, not included in the green world hypothesis, become critical for trophic dynamics.

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