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Structure and Dynamics of Arctic-Subarctic Grazing Webs in Relation to Primary Productivity

Lauri Oksanen, Tarja Oksanen, Per Ekerholm, Jon Moen, Peter Lundberg, Michael Schneider, and Maano Aunapuu

Introduction

Current discussion on structure and dynamics of food webs includes two seemingly incompatible views on the role of energy supply for food chain length. Authors of food web reviews (Pimm, 1979, 1982, 1991; Briand and Cohen, 1987; Cohen et al., 1990) conclude that the energy constraint is trivial and that chain length is determined by other factors (population dynamics according to Pimm, dimensionality of the habitat according to Cohen and his coworkers). According to the hypothesis of exploitation ecosystems (Fretwell 1977, 1987; Oksanen, 1988; Oksanen et al., 1981), however, the grazing chain shortens along gradients of decreasing primary productivity. In relatively productive ecosystems (e.g., forests and their successional stages), the grazing chain harbors three trophic links (plants-physical resources, herbivores-plants, and carnivores-herbivores). The first and third links are strong, whereas the second represents a weak interaction, as proposed by Hairston et al. (1960). Less productive ecosystems (tundras, steppes, semideserts) are supposedly characterized by two-link dynamics, with strictly resource-limited grazers and grazing-controlled vegetation. In extremely barren areas, the only strong trophic link is between plants and physical resources.

The conflict might be more apparent than real, because the two groups are addressing two different questions. For Pimm, Cohen, and Briand, food webs are the primary object of study, and all kinds of webs are equally

interesting. The hypothesis of exploitation ecosystems focuses on the intensity of natural herbivory and population dynamics and life history strategies of grazers and plants (Fretwell, 1977, 1987; Oksanen et al., 1981, 1992a; Oksanen and Oksanen, 1989; Oksanen, 1988, 1990a, 1990b, 1990c, 1992, 1993). An area is to be called a two-link ecosystem if any grazer guild capable of exploiting the entire vegetation assemblage is not controlled by predators, even if predators were physically present (Oksanen and Ericson, 1987a) and the majority of organisms would belong to considerably longer food chains.

To some extent, the apparent conflict between the two approaches is due to bad data. Pimm (1982) states that three to four trophic levels are present in a subweb consisting of endothermic vertebrates even at Kevo, Finnish Lapland, in spite of extremely low primary productivity. According to Sonesson et al. (1975), the annual primary productivity of the three dominant habitats at Kevo—pine forests, mesic mountain birch forest, and birch brushwoods (referred to as low alpine heaths)—is only 75, 125, and 70 g m⁻² yr⁻¹. However, the reported values are preliminary estimates, which exclude the production of trees and shrubs (i.e., the main components of the vegetation). The mesic mountain birch forest has a close counterpart in the parallel Norwegian project. Its estimated primary productivity is 780 g m⁻² yr⁻¹ (Sonesson et al., 1975).

Unfortunately the differences between the issues addressed and the ambiguities of the

data are not always recognized. Results of food web reviews have been recurrently used as arguments against the idea of tundras as two-link ecosystems (e.g., Hairston and Hairston (1993). Consequently, there is a need to reanalyze published data pertaining to the structure and dynamics of arctic and subarctic grazing webs, with a focus on endothermic vertebrates, because this part of the grazing chain has the lowest ecoenergetical efficiency and is thus likely to be the first to collapse from three links to two links along gradients of decreasing primary productivity. We will also summarize the main results of our own studies on trophic interactions along subarctic productivity gradients in northernmost Norway.

The Case of Truelove Lowland

Truelove Lowland, Devon Island, NWT, Canada is the northernmost thoroughly studied ecosystem in the world. It represents a relatively large (43 km²) oasis of tundra within a polar desert. The primary productivity of sedge-moss meadows is 100–300 g m⁻² yr⁻¹, i.e. comparable to values obtained at Barrow, AK. (Miller et al., 1980). Other lowland habitats (beach ridges and rock outcrops) are considerably less productive (only 20–50 g m⁻² yr⁻¹), and the polar deserts of surrounding areas have a primary productivity of only 7 g m⁻² yr⁻¹ (Bliss, 1977).

As noted by Pimm (1982), Riewe's (1977b) food web for Truelove Lowland nevertheless includes several predators. However, the web is a heuristic illustration of the trophic position of the Inuit in the Jones Sound region and includes trophic connections not mentioned in primary reports (e.g., between owls and lemmings and between wolves and muskoxen). We have therefore constructed a food web for Truelove Lowland (Figure 22.1) on the basis of primary data (Fuller et al., 1977; Hubert, 1977; Pattie, 1977; Smith and Wang, 1977; Riewe, 1977a; Ryan and Hergert, 1977). Numbers in the boxes refers to maximum and minimum numbers recorded on Truelove Lowland. The numerically dominant components of each trophic level are indicated by thick frames. Thick lines in animal-animal interactions de-

note cases where the prey was recorded as a dominant diet component and the predators as a major source of mortality. In herbivore-plant interactions, thick lines stand for interactions between abundant herbivores and their principal resources. Solid thin lines indicate other cases, where mortality was recorded, Hairston (1995). Consequently, there is a need to reanalyze. Dashed lines stand for other interactions between consumers and quantitatively important food items, and dotted lines represent interactions between consumers and minor food items. When lists of food items were not accompanied by quantitative information, the first-mentioned food item was assumed to be the dominant one.

The food web thus obtained (Figure 22.1) includes only one documented predaceous connection between carnivores and herbivorous vertebrates: winter predation by stoats (*Mustela erminea*) on collared lemmings (*Dicrostonyx groenlandicus*), accounting for approximately 10% of winter mortality of lemmings. Trophic connections between arctic foxes (*Alopex lagopus*) and lemmings and between peregrines (*Falco peregrinus*) and rock ptarmigans (*Lagopus mutus*) are probably predaceous. The connection between arctic foxes and musk oxen refers to carrion feeding. The numerically dominating predators, long-tailed and parasitic jaegers (*Stercorarius longicaudus*, *S. parasiticus*), are reported to feed on invertebrates and on eggs and nestlings of passerines and waders. Only one examined stomach of long-tailed jaegers contained lemming remains, and only one case of successful breeding has been recorded during the entire International Biological Program (IBP) period. The data from Truelove Lowland are thus consistent with the idea of a two-link ecosystem, where the strongest interactions in the grazing chain are between grazers and plants, and where the presence of even sparse predator populations is dependent on external energy inputs and detritus-based resources.

The reports cited above indicate that all grazers stay in Truelove Lowland or move along the coast between different lowland areas. No herbivores are reported to forage in the polar desert. Polar deserts thus seem to be genuine one-link ecosystems, devoid of grazing vertebrates.

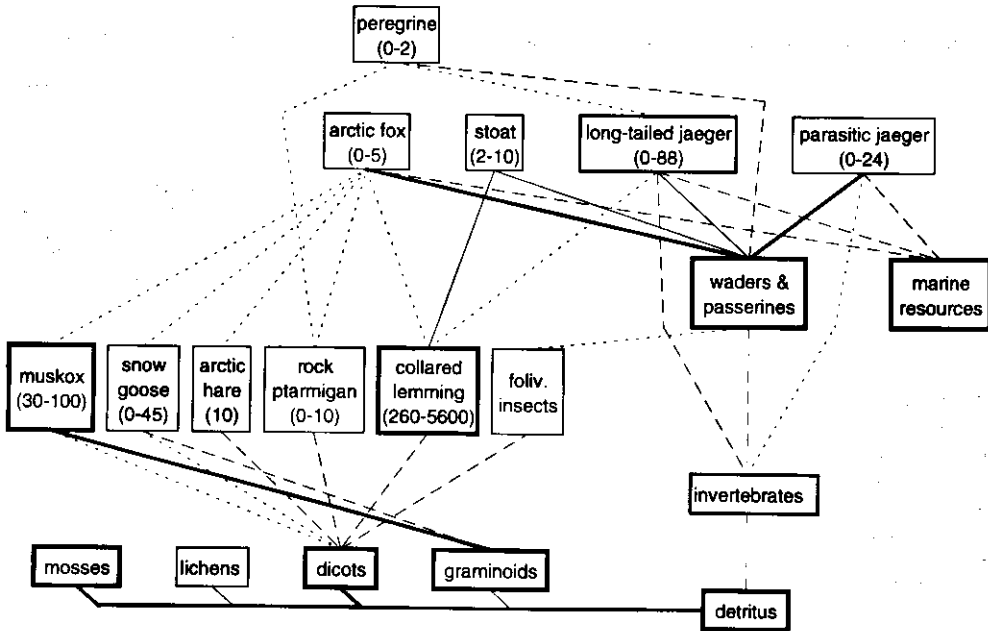


Figure 22.1. The food web for Truelove Lowland, Devon Island, Canada, derived from the primary reports of the IBP team. Thick lines indicate probable cases of strong interaction. Whole thin lines refer to cases of reported prey mortality. Dashed and dotted lines refer to major and minor food items respectively reported in dietary studies.

Grazing Chain Along the Gradient From Boreal to Polar Regions

In order to determine whether or not the case of Truelove Lowland conforms with a consistent pattern, let us examine the presence of predators interacting with grazing vertebrates in different IBP Tundra Project sites (Wielgolaski, 1975; Batzli et al., 1980) and in the terrestrial arctic food webs included in the review by Cohen et al. (1990). Two food webs (Barrow and Prudhoe bays) belong to both categories; therefore priority was given to connections in the final IBP report. The results are presented in Table 22.1, where the areas have been arranged from polar to boreal, in accordance with their positions in the zone system of Aleksandrova (1988) (the chiefly low alpine Hardangervidda is placed between the boreal Kevo and the low arctic Jamal). The data show a clear trend, where predators of grazing vertebrates disappear with increasing latitude (some physically, others by losing recorded trophic connections with the grazing chain). The geographical

isolation of Svalbard probably contributes to the trend (especially in the case of Bear Island). However, potential predators are present in Spitsbergen. The absence of trophic connections between polar bears and Svalbard reindeer has been confirmed by Tyler (1993, and personal communication). He recorded 717 reindeer deaths in the Adventdalen population, where reindeer carry transmitters allowing localization of dead individuals. The overwhelming majority of the deaths are due to starvation. The only recorded case of predation is one calf killed by an arctic fox.

The disappearance of predators from the interaction web and the consequent shift from three-link to two-link dynamics appears to take place between the timberline and the middle arctic tundra. In boreal areas, grazers still seem to be regulated by resident predators (Messier, 1995; Messier and Crête, 1985; Henttonen et al., 1987; Krebs et al., 1992; Bergerud, 1988; Oksanen, 1990b; Hanski et al., 1991, 1993). The middle arctic tundra at Barrow is sometimes invaded by

Table 22.1. Presences (+) and absences (-) of carnivores with recorded interactions with recorded interactions with herbivorous vertebrates in the arctic-subarctic food webs reviewed by Cohen et al. (1990) or studied in the Finnish or Norwegian IBP tundra projects.

Area	Pomarine jaeger	Long-tailed Jaeger	Parasitic jaeger	Merrin	Kestrel	Peregrine falcon	Cyrfalcon	Rough-legged hawk	Goshawk	Golden eagle	Hawk owl	Short-eared owl	Snowy owl	(Least) weasel	Stoat (ermine)	Arctic fox	Red fox	Lynx	Wolverine
Spitsbergen, barren regions	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spitsbergen, reindeer pasture	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Truelove Lowland	-	+	-	-	-	+	-	-	-	-	-	-	-	+	+	-	-	-	-
Bear Island	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Barrow	+	+	+	-	-	-	+	-	-	+	+	+	+	+	+	-	-	-	-
Prudhoe Bay	+	+	+	-	-	-	+	-	-	-	+	+	+	+	+	-	-	-	-
Central Jamal	-	+	+	+	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-
Southern Jamal	-	+	+	+	-	+	-	+	-	-	-	-	+	+	+	+	+	-	-
Hardangervidda	-	+	-	+	+	-	+	+	-	+	+	+	+	+	+	+	+	+	+
Kevo	-	+	-	+	+	-	+	+	+	+	+	-	-	+	+	+	+	-	+

predators from the south (weasels) and from the sea (pomarine jaegers), and their impact on the population dynamics of lemmings can be substantial at times (MacLean et al., 1974; Pitelka, 1973). Nevertheless, each lemming crash is accompanied by massive habitat destruction. The vegetation of lemming exclosures changes radically, the typical trend being expansion of cryptogams (Batzli et al., 1980). The cryptogam biomass in corresponding habitats on Truelove Lowland, where moss-eating brown lemmings do not occur, is orders of magnitude higher than at Barrow (Oksanen, 1983). The data thus suggest that the strongest trophic interactions at Barrow take place between brown lemmings and the dominant components of the vegetation.

Trophic Structure and Trophic Dynamics in the Tundra-Brushwood Landscape of Finnmarksvidda, Northernmost Norway

The results of the above-discussed IBP Projects suggest that the grazing chains of arctic and subarctic ecosystems consist, in essence, of ungulates and microtine rodents. Medium-sized vertebrates are uncommon, probably because they are too small to get access to winter resources by digging through the snow, and yet they are too big to live subni-

vally at the ground surface. The role of folivorous insects can be periodically profound in subarctic areas with relatively mild winters, but not in cold inland areas (Kallio and Lehtonen, 1975; Tenow, 1972; Tenow and Nilssen (1990). On the tundra proper, folivorous insects are but a minor part of the herbivore community probably due to apparent competition with detritus-based invertebrates (Batzli et al., 1980; Ryan and Hergert, 1977; Whitfield, 1977; Wielgolaski, 1975). The dominating ungulate of Fennoscandian tundras, the reindeer, is under direct human control, and also moose numbers are regulated by hunting. Big predators are reduced to remnant populations. Thus, our studies on trophic dynamics along a gradient from herb-rich woodlands and scrublands to high alpine boulder fields on Finnmarksvidda, northernmost Norway, have focused on plants, microtine rodents, and small-to-medium-sized predators.

The study has continued since 1977, with an increase in the level of intensity in the late 1980s. We have monitored the composition of the vegetation and dynamics of plant populations on permanent plots and conducted experiments on plant-plant and herbivore-plant interactions (grazer exclosures, removal of potential competitors). Microtine rodents have been surveyed by twice-a-year snap trapping and, since 1988, by livetrapping. We have introduced voles to virtually preda-

tionfree islands in Lake Iešjávri and constructed a predator enclosure in the mainland. Numbers and habitat use of mammalian and avian predators have been studied sporadically during 1977 to 1985; thereafter systematically by means of livetrapping plus snow-tracking (mammals) and by mapping the distribution of breeding predatory birds. Systematic studies on the habitat use of avian predators have been conducted in 1988 and 1993. The summary of our results, presented below, is based on published papers and unpublished data.

Our data on abundances and habitat use of predators (Oksanen and Oksanen, 1981, 1992; Oksanen et al., 1992b, Oksanen and Schneider, 1995; Oksanen et al., unpublished) suggest that food webs for different parts of the landscape differ substantially from each other. We have thus divided our main study area into three different subareas: the slope valley, the lowland, and the highlands. We present a preliminary food web for these three subareas and for our block field study area, representing an altitudinal counterpart of the polar desert.

The slope valley subarea (elevation 370–500 m) consists of a steep, south-facing slope below the overthrust cliff of the Scandinavian mountain chain and an adjacent piece of Fennoscandian shield with favorable edaphic and microclimatic conditions. The subarea is dominated by relatively productive habitats: mossy dwarf birch scrublands, herb rich gray willow (*Salix glauca*, *S. lapponum*, *S. lanata*) thickets, and patches of herb-rich mountain birch (*Betula pubescens ssp czerepanovi* (Orlova), Hämet-Ahti) woodland. The grazer community is dominated by gray-sided voles (*Clethrionomys rufocanus*), which have a regular 4.5 year cycle (Oksanen and Oksanen, 1992). Root voles (*Microtus oeconomus*), field voles (*M. agrestis*), red voles (*Clethrionomys rutilus*), mountain hares (*Lepus timidus*), and willow grouses (*Lagopus lagopus*) are common. Abundances of these herbivores fluctuate, by and large, in synchrony with the cycle of gray-sided voles. Lemmings (*Lemmus lemmus*) have been relatively abundant in 1978, but practically absent thereafter (Oksanen and Oksanen, 1981, 1992; Oksanen, 1993).

Four species of mammalian predators have been observed as residents of this subarea:

weasels (*Mustela nivalis*), stoats (*M. erminea*), American minks (*M. vison*), and red foxes (*Vulpes vulpes*). Highest densities have been observed for weasels (45 individuals per km²) in fall 1988, but during most years, stoats have been more numerous than weasels (Oksanen and Oksanen, 1992; Oksanen et al., 1992b). Red foxes and American minks have been relatively uncommon until the late 1980s but have dramatically increased since then (Oksanen et al. unpublished). Avian predators have been mainly represented by rough-legged hawks (*Buteo lagopus*) and merlins (*Falco columbarius*), which have bred every year in the area. Hawk owls (*Surnia ulula*) invaded the area in 1983 and 1988, and gyrfalcons (*Falco rusticolus*) have been regular visitors. Occurrence of other predators has been sporadic (Oksanen and Oksanen, 1981, 1992; Oksanen et al., 1992b, unpublished; Oksanen and Schneider, 1995).

At the start of our study, we observed signs of heavy vole impact even in most lush areas (willows and mountain birches killed or injured by bark-gnawing voles in 1974–1975). Moreover, we also observed (Oksanen et al., 1987) and experimentally created (Lundberg and Ekerholm, unpublished data) similar situations on productive islands. In productive mainland habitats, such devastating impacts have been limited to uppermost willow thickets at about 500 m elevation. Abundances of woody plants increased on our permanent plots, and the response of the vegetation to exclusion of grazers was modest (Oksanen and Oksanen, 1981; Oksanen, 1988; Moen, 1993). Conversely, exclusion of predators has led to increases in vole numbers (Ekerholm, unpublished data). The data summarized above suggest that there is a potential for strong grazer-plant interactions in luxuriant habitats (see also Moen et al. (1993a) but this potential is not normally realized due to predation. We thus propose that the grazing web of the slope valley subarea has the structure outlined in Figure 22.2. Consequently, we interpret the sustained fluctuations of voles as a vole-mustelid limit cycle (or chaos with a strong, periodic component), which appears to be characteristic for northern Fennoscandia as a whole (Henttonen, 1987; Henttonen et al., 1987; Oksanen, 1990a; Hanski et al., 1991, 1993).

The lowland (elevation 400–500 m) con-

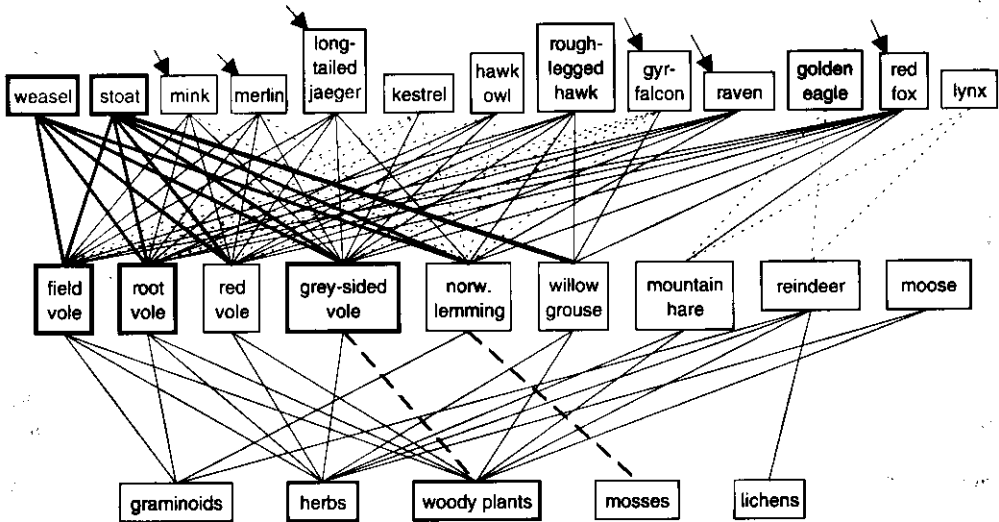


Figure 22.2. Grazing web for the complex of productive subarctic and low arctic habitats on Finnmarksvidda, northeastern Norway. Whole thick lines indicate probable cases of strong interaction, dashed thick lines indicate potentially strong interactions, which are seldom realized due to the predation on the consumers. Entire liners refer to other trophic interactions for which there is positive evidence within our study area (prey remains in nests, within-trap predation on small mammals, field observations of predation) or clear indications (observations of attempted predation, tracks indicating predation or attempted predation). Dotted lines indicate probable trophic interactions (based on published dietary data). Arrows refer to substandard energy inputs from aquatic or detritus-based food webs.

sists of a rolling tundra plateau, largely occupied by lichen heaths and palsa bogs. More productive habitats (scrublands dominated by *Betula nana*, *Salix glauca*, or *S. lapponum*) occupy about 10% of the lowland (Oksanen and Oksanen, 1981). The food web of the lowland appears qualitatively to correspond to Figure 22.2, except that merlins, hawk owls, field voles, and red voles are practically absent, whereas long-tailed jaegers (*Stercorarius longicaudus*) and short-eared owls (*Asio flammeus*) breed regularly during vole peaks. Observations of mammalian predators in the lowland are most frequent during the final stages of small mammal decline. Densities are low even then (maximally 0.5 individuals per km²), and predator activity is concentrated to relatively productive habitat patches (Oksanen and Oksanen, 1981, 1992; Oksanen et al., 1992b, Oksanen et al. unpublished). Avian predator (mainly long-tailed jaegers) density reached 1 breeding pair per km² in 1983. During other microtine peaks, densities of avian predators have been considerably lower (0.3 breeding pairs per km² in 1988, 0.06 breeding pairs per km² in 1993;

Oksanen and Oksanen, 1992; Oksanen et al., 1992b; unpublished). Microtine rodents have a strong impact on plant populations and on the structure of the vegetation of heaths and dry meadows (Oksanen 1988, 1990c; Oksanen and Oksanen, 1981; Oksanen and Ericson, 1987b; Oksanen and Moen, 1994). Moreover, the shoot mortality imposed by voles on dominant dwarf shrubs appears to be density-dependent (higher mortalities in microhabitats with higher shoot densities, Lundberg, unpublished data). Another strong interaction is between reindeer and lichens, whose standing crops are clearly regulated by grazing (Oksanen, 1978; Oksanen and Virtanen, 1995). Impact of reindeer on woody plants is modest, due to the timing of their presence (mainly in late autumn and early winter). In corresponding areas used for summer grazing, reindeer also have strong influence on the uppermost birch brushwoods (Oksanen et al., 1995).

The food web dynamics of the lowland thus seem to vary depending on edaphic conditions. The grazing web for the most luxuriant lowland habitats (willow thickets along

creeks) appears to correspond to Figure 2.22, whereas the grazing web for heaths and bogs is different both qualitatively and quantitatively. The dominating predator is the long-tailed jaeger, and predator densities are too low to have but sporadic impact on grazer dynamics. (The summer decline of 1983 was probably due to predation by jaegers and owls; predation by small mustelids might be significant during the final stages of vole declines, when starving predators sample all habitats.) The strongest regulatory links seem to be between the grazers and the vegetation.

The highland (elevation 500–700 m) is chiefly occupied by lichen heaths, mossy dwarf shrub heaths, and sedge-dominated bogs (Oksanen and Oksanen, 1981). The grazer community is heavily dominated by reindeer (which use the highland primary in late summer and autumn) and lemmings, which had outbreaks in 1978 and 1988. Gray-sided voles occurred in moderate numbers in 1983, 1987, and 1993. Field voles have been occasionally trapped in bogs and meadows. Rock ptarmigans (*Lagopus mutus*) occur on ridges, but only in low numbers (Oksanen and Oksanen, 1981, 1992; Ekerholm, unpublished). Fifteen species of predaceous vertebrates have been observed in the highland (Figure 22.3), the majority of them located near the periphery and only a few times seen in the interior part of the highland (more than 500 m from the edge). The dominant predators are long-tailed jaegers, which are only

partially predaceous and have strong connections to the detritus chain (in addition to microtines, they exploit invertebrates and eggs and nestlings of passerines and waders; see Andersson (1971, 1976). The highest numbers (0.3 pairs of long-tailed jaegers per 10 km² plus one stoat home range in our tracking area of 4 km² were observed during the lemming outbreak 1988 (Oksanen and Oksanen, 1992; Oksanen et al., 1992b). During subsequent years, observations of mammalian predators in the interior part of the highland have been restricted to occasional sightings of fox tracks plus to two cases clearly connected to our experiments (Oksanen et al. unpublished).

Lemming peaks in the highland have been accompanied by severe depletion of mosses and graminoids. Stands of woody plants also are frequently injured in moss and graminoid-rich habitats. After a winter crash, the highland is littered with intact lemming bodies. Winter nest predation has been uncommon and practically restricted to the edges of the highland (Oksanen and Oksanen, 1981; Moen et al., 1993b; Oksanen et al. unpublished). Extensive bark-gnawing by voles has been observed in the uppermost scrublands, but in the highland proper, grazing by gray-sided voles is sporadic (Lundberg, unpublished). Summer grazing by reindeer is relatively intense (Oksanen et al., 1995) and probably influences abundances of erect shrubs, broad-leaved herbs, and fructose li-

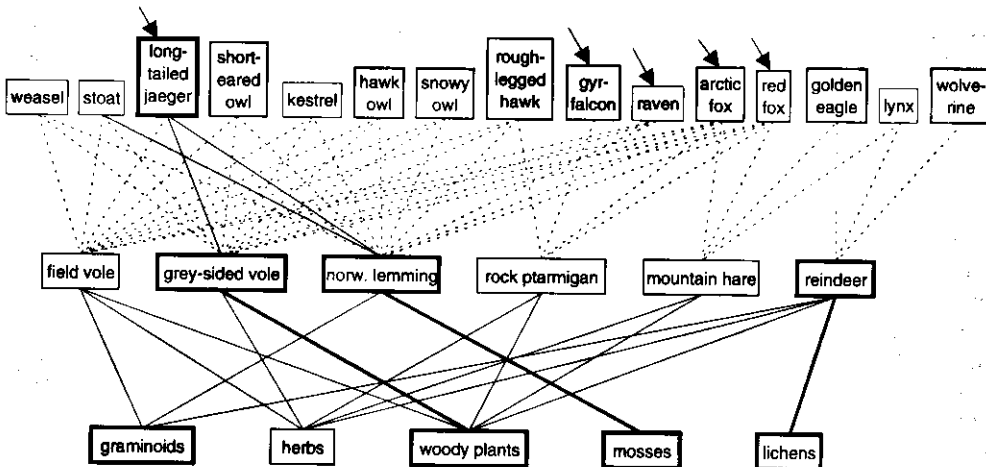


Figure 22.3. Grazing web for the highland tundra of Finnmarksvidda, excluding marginal areas less than 200 m from the 500-m contour. Symbols as in Figure 22.2.

chens (Höglund and Eriksson, 1973; Oksanen, 1978; Oksanen and Virtanen, 1995). Exclusion of grazing vertebrates has led to increases in the abundances of woody plants and herbs in moderate snowbeds (Oksanen, 1988, 1990c; Oksanen and Moen, 1994; Oksanen and Oksanen 1981; Moen 1993) and to expansion of mosses in more extreme ones (Virtanen, unpublished data), where moss biomass also increases as a function of time elapsed since the last lemming outbreak (Kylönén and Laine, 1980; Oksanen, 1983).

Our grazing web for the highland (Figure 22.3) thus contains only two cases of strong, coupled interactions, where victims are clearly subjected to density-dependent regulation by their consumers; between lemmings and mosses plus graminoids, and between reindeer and lichens. Herbs interact with several grazers that collectively seem to influence their abundances, but the existence of a reciprocal impact has not been demonstrated. Woody plants are somewhat of an enigma. Their main consumer, the gray-sided vole, appears never to become abundant enough to deplete the supply of dwarf shrubs. We suspect this is because gray-sided voles lack structural adaptations for winter foraging in the open tundra landscape. (Their truly arctic counterpart, the collared lemming, has not managed to cross the dispersal barrier provided by the White Sea.) We cannot, however, rule out the alternative explanation that gray-sided voles are regulated by long-tailed jaegers, which concentrate on the small patches of highland area, where conditions are favorable for voles.

The block field study area on Håldi, 40 km west of the main study area (elevation 800–1100 m) was established in 1988. The most productive habitat of the area, occurring patchwise at elevations below 900 m, is a species-rich meadow dominated by low herbs and graminoids. The meadow habitat is intensely exploited by reindeer. On the basis of captures and signs of foraging, we established the presence of lemmings in this habitat in 1988 and 1994. At higher altitudes, the vegetation consists of crustose lichens and small, scattered patches of vascular plants (mainly: *Ranunculus glacialis* and *Luzula confusa*). Until 1994, when the area was visited by a reindeer herd, the only recorded

vertebrates in this habitat were wheatears (*Oenanthe oenanthe*), which have been captured in stick traps along with spiders (Moen, unpublished). Plants grazed by reindeer, rock ptarmigans, and lemmings have been observed in similar habitats in other parts of the block field (Moen and Lundberg, unpublished data) and in other corresponding areas (Oksanen and Virtanen, 1995). Our data indicate that the zone where the food web approximates Figure 22.3 extends to the lower part of the block field. In the upper part of the block field, the scanty plant cover cannot be profitably exploited, and consequently, interactions between grazers and plants are weak (Figure 22.4).

A problem with interpreting trophic interaction in open tundra areas is that the most important grazer, the reindeer, is privately owned and its predators are practically absent. According to Canadian data, undisturbed trophic interactions involving ungulates depend on primary productivity and follow the same pattern as observed in our study area. In productive areas, moose and caribou populations are controlled by predation and their impact on vegetation is normally modest (Bergerud, 1988; Messier and Crête, 1985 (McLaren and Peterson 1994, Messier 1995, Crête and Manseau 1995). Conversely, caribou populations utilizing subarctic lichen heaths and low arctic or low alpine tundra habitats are food-limited and strongly influence the vegetation of both summer and winter ranges (Crête and Huot, 1993; Messier, 1995; Crête and Manseau 1995). Moreover, reindeer and caribou have a natural tendency to avoid dense woodlands and scrublands, due to the mosquito problem and perceived risk of predation (Henshaw, 1970;

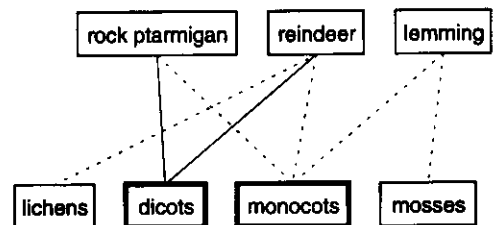


Figure 22.4. Grazing web for high alpine block fields of northernmost Norway. Symbols as in Figure 23.2.

Helle et al., 1990). Thus, the mesoscale pattern observed in our study area is likely to resemble the natural situation.

Conclusion

Along the gradient ranging from subarctic brushwoods and low arctic willow thickets to typical tundras and arctic-alpine deserts, the chain length in the vertebrate branch of the grazing web decreases both in topological and interaction webs. Most predators present in typical tundra habitats are partially dependent on other ecosystems and obtain substantial amounts of energy from the detritus web, which can support relatively high densities of birds in low arctic wetlands (Järvinen and Väisänen, 1976, 1978). The strongest interaction of the typical tundra is between grazers and the vegetation, as pointed out already by Tihomirov (1959). In the most extreme arctic-alpine areas, herbivorous vertebrates are only encountered as infrequent visitors. However, the detritus-based food web seems to harbor several trophic links even in these areas. The answer to the question of whether chain length depends on primary productivity in arctic-alpine habitats thus depends on the kind of food webs studied and the part of the productivity gradient represented in the database.

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