
Testing Hypotheses of Community Organization for the Kluane Ecosystem

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In chapter 3 we outlined the general ideas of community organization through top-down and bottom-up processes. In this chapter we review how each experiment has affected the total biomass or nutrient pool of the trophic levels. We compare these results with the predictions for different models of trophic level interactions discussed in chapter 3. We identify the major components that hold the system together and the direction and strength of their interactions. The need is to identify the components most sensitive to change so that they can be used as indicators for long-term monitoring.

Empirical studies have tested models of community organization that involve variations of top-down (pure predator control) hypotheses, bottom-up (nutrient limitation) hypotheses and hypotheses including reciprocal interactions (control by predators that are dependent on the prey; see Menge 1992, Power 1992). These concepts and some related ones (e.g., donor control) have not always been rigorously defined. Consequently, the same terms can apply to several different models, and so it has been difficult to derive testable and generally acceptable predictions.

Bottom-up hypotheses assume that systems are regulated by nutrient flow from below (White 1978, 1984, Lampert 1985, Strong 1992, Polis and Strong 1997). These hypotheses assume there is a shortage of suitable resources (e.g., areas with accessible nutrients, plant parts with sufficiently high quality, prey that are easy to catch), even if resources appear superficially to be abundant. Bottom-up hypotheses can also be regarded as biological null hypotheses because plants are essential to the levels above, whereas the reverse need not be true. One bottom-up hypothesis predicts that an increase in resources, such as soil nutrients, should lead to a biomass increase in all subsequent levels (Abrams 1993). Another hypothesis predicts that the biomass of the top level increases as well as alternating lower levels, while intermediate levels remain constant (Oksanen et al. 1981, Abrams 1993, Schmitz 1998). Yet others predict that higher trophic levels have neither a regulating effect nor any influence on productivity or overall biomass on the levels below them, although the standing crops of subcomponents that make up suitable resources can be depressed (Hawkins 1992, Hunter and Price 1992, Strong 1992). Technically, bottom-up hypotheses require some form of self-regulation because if there were no self-regulation population densities at each trophic level would either decline toward zero or increase ad infinitum.

There are various top-down hypotheses with different implications for population regulation at all levels. According to the hypothesis of Menge and Sutherland (1976), predation pressure increases monotonically from the top of the food chain downward, which implies that top predators can exploit basal organisms. Caughley and Lawton (1981) argued that strong reciprocal interaction exists between herbivores and plants, whereas predators and herbivores are involved in a bottom-up relationship. Their view has been supported by data from arid and arctic ecosystems (Batzli et al. 1980, Caughley and Gunn 1993).

A converse idea was presented by Hairston et al. (1960), who proposed that a tight, reciprocal interaction occurs between predators and herbivores. Consequently, herbivores only have light impact on plants, which are either self-regulated or involved in a reciprocal interaction with mineral nutrients. These ideas imply that removal of the effective top consumer generates cascading impacts down to plants and nutrients.

An alternative hypothesis, combining reciprocal and bottom-up features, suggests that

biomass is regulated from below by nutrient availability but that this effect is strongest at the plant level and becomes weaker at progressively higher levels (Benndorf and Horn 1985, McQueen et al. 1986, 1989, Pace and Funke 1991). Conversely, at the top of the food web, top-down interactions are strong, but these effects weaken with every step down the food chain. Such attenuation could be achieved if the feeding efficiency of predators is reduced by interference, territoriality, or prey refuges (Power 1984, Arditi and Ginzburg 1989, Arditi et al. 1991, Hanski 1991, Leibold 1996).

17.1 Experimental Perturbations of the Boreal Forest

We tested the predictions from the 27 models in chapter 3 by experimentally perturbing the boreal forest food web. In these experiments, each trophic level was perturbed and the subsequent effects on the biomass, productivity, or activity of other levels were measured.

17.1.1 Direct and Indirect Effects

We measured two types of response, biomass change and productivity change. A direct effect occurs in the biomass or productivity at the next trophic level; an indirect effect occurs at one or more levels removed. These indirect effects are a subset of "interaction-chain indirect effects" (Wootton 1993, 1994a,b,c, Billick and Case 1994, Menge 1997) in that they are linear on the food chain. We discuss briefly interactions such as apparent competition (Holt 1977) and indirect mutualism (Dungan 1987) that involve interactions between species within a trophic level and interaction modifications such as effects of predation risk (Hik 1995, Boonstra et al. 1998).

Predictions from the models on the effects of the perturbations are through the direction of change in biomass relative to control areas. For some levels, in particular plants, we also considered changes in productivity as a response to perturbation. The predicted changes in biomass are indicated in table 3.3 as an increase, decrease, or no change. However, where two perturbations are applied simultaneously, both acting in the same direction, an additional prediction can be made on the magnitude of change relative to either single perturbation.

17.1.2 The Experiments

We recapitulate the major experimental perturbations here and highlight the predictions of the trophic level models for each experiment. We refer to the models summarized in table 3.2.

Application of Fertilizer Fertilizer was applied from the air to two 1-km² blocks of forest as described in chapter 4. This manipulation should increase the soil nutrient pool (*N*). Models that suggest that plants (*V*) are responsive to the nutrient pool (i.e., those with right or double arrows between *N* and *V*) predict increases in biomass of higher trophic levels to varying lengths of the food chain (18 of the models).

Models with top-down effects (left arrow) only (nine models) predict that plant biomass is not limited by nutrients and should not respond to fertilizer inputs. However, pro-

ductivity of plants and consumption by herbivores could increase. Similarly, productivity of herbivores and consumption by predators could increase.

Food Addition Commercial rabbit chow was applied ad libitum to two areas (chapter 4). This food is eaten readily by hares and ground squirrels. This treatment had the effect of artificially increasing the food supply for herbivores independently of the natural food and, therefore, increasing the herbivore level independently of the vegetation level. Of the 27 models, 9 assume that herbivores are not limited by food supply and so they predict no response to food addition. The remaining 18 models assume that herbivores are limited by food (bottom-up control indicated by a right arrow). In nine of these models herbivores also have a top-down limiting effect on vegetation (a reciprocal effect indicated by a double arrow).

The Exclusion of Carnivores Carnivores were excluded from a 1-km² area by wire fencing as described in chapter 4. This fence was permeable to hares and squirrels through small holes in the fence. Although some predators occasionally broke into the enclosure, predation by carnivores was considerably reduced within the enclosure. For models predicting top-down effects, herbivores should increase in biomass, plants should decrease, and nutrients should increase.

The Exclusion of Carnivores and the Addition of Food Carnivores were excluded from a 1-km² area by wire fencing, and ad libitum rabbit chow was provided for the herbivores. For top-down models (left arrow) the removal of mammalian predators predicted an increase in herbivores. In addition, for models where herbivores are also responsive to their food supply, we predict an additional increase in herbivore biomass relative to the herbivore increase predicted from the predator enclosure experiment. Hence, in this experiment, there should be increased effects on other trophic levels relative to the single perturbations. The remaining models where herbivores do not respond to food supply predict changes in herbivore biomass similar to that in the predator enclosure experiment.

The Exclusion of Hares Hares were the dominant component of the herbivore biomass in this system, and they were excluded by fencing a 4-ha area. In the 18 top-down models, exclusion of the top two trophic levels predicted that vegetation biomass should increase. In 12 of these models, top-down effects continued to the nutrient level, predicting a decrease in the soil nutrients.

The Exclusion of Hares and the Addition of Fertilizer This experiment was similar to the hare exclusion experiment but with the addition of fertilizer. The two perturbations are predicted to have opposite effects on soil nutrients: fertilizer adds nutrients but removal of hares should result in fewer nutrients. Because the outcome could be any value depending on absolute amounts of inputs and outputs, no qualitative prediction for soil nutrients can be made. However, for vegetation biomass one can predict two alternative responses. In models where plants respond to nutrient levels, there should be a greater increase in plant biomass relative to the hare enclosure experiment. In contrast, the other models predict no difference in plant biomass changes between hare enclosure and hare enclosure + fertilizer.

The Removal of Vegetation Soil nutrient levels were measured in plots where vegetation was removed and compared to an equal number of immediately adjacent control plots with intact vegetation. Soil nutrients should increase in plots where the vegetation has been removed in those models predicting that nutrients respond to plant uptake.

With these seven experiments just described, 21 models out of 27 make unique sets of predictions. There are also three pairs of unique sets (5 and 8, 12 and 19, and 6 and 26; table 3.1; see 3.4.7).

17.2 Methods

Most of the methods for the data discussed here were presented in earlier chapters. We highlight here only a few specific points for methods not described in earlier chapters.

17.2.1 Soil Nitrogen

Fertilizer was applied by air once each year from 1987 to 1994 as described in chapter 4. In 1995, 10 soil samples were collected at sites on experimental treatments and immediately adjacent to them as controls. The treatment grids sampled were fertilizer, food addition, predator enclosure plus food addition, and hare enclosure. In 1996 soils were sampled inside ($n = 100$ samples) and outside the hare enclosure. Also outside this enclosure, vegetation was removed from 156 plots and soil samples were compared with 156 plots with vegetation left intact. Vegetation was killed by using Roundup (Monsanto Corp.) and left in situ. The edges of all plots were cut to a spade-depth to kill roots and so reduce the movement of nutrients into or out from the plot. In 1995, soils were sent to Peace Growers' lab in Fort St. John, British Columbia, and in 1996 to Pacific Soil Analysis in Richmond, British Columbia, for analysis of nitrate nitrogen.

17.2.2 Vegetation

Details of methods are presented in chapters 5–7 as well as in Krebs et al. (1992, 1995) and Turkington et al. (1998). Mammalian herbivores have little influence on biomass of herbaceous vegetation during the summer (John and Turkington 1995). Winter food supply is more likely to be limiting to mammalian herbivores. Winter food plants for snowshoe hares are largely bog birch (*Betula glandulosa*) and gray willow (*Salix glauca*). At certain times when these two shrubs were heavily browsed, hares turned to eating white spruce (*Picea glauca*). We concentrated, however, on measuring the shrubs. Twigs <5 mm diameter were the main food. We measured biomass, growth rates, and browse rates of shrubs as described in chapter 6.

The net effect on plant biomass as defined in this chapter combines the herbivory in one winter and the growth in the subsequent summer. It measures the degree to which an increase in growth rate (g_i) of plant species i in year y compensates for the biomass loss to herbivory (h_i) in the previous winter. The net effect, C_{iy} , is given by:

$$C_{iy} = (1 - h_i)(1 + g_i).$$

If $C_{iy} = 1$, there is complete compensation and no change in biomass, if $C_{iy} < 1$, there is a net loss in biomass, and if $C_{iy} > 1$, there is either an increase in biomass by overcompensation for the herbivory or no herbivory.

17.2.3 Plant Secondary Chemicals

Earlier studies (Sinclair and Smith 1984, Sinclair et al. 1988) have shown that phenolic compounds change over the hare cycle, and of all the secondary compounds, phenols are most sensitive to browsing. These compounds have been identified in other birch species (Reichardt et al. 1984), but they appear to be at low levels in willow species. The product obtained from methanol extraction, as described in chapter 6, can be used as an index of secondary compound content.

17.2.4 Herbivore Biomass

The dominant herbivores in summer are the snowshoe hare and arctic ground squirrel, with red squirrel a minor third species. In winter, although moose are present, they had relatively minor effects, and the snowshoe hare is the dominant herbivore. All smaller mammal species were enumerated by live trapping as described in chapters 8–11.

17.2.5 Predator Activity

For practical reasons we could monitor only the main carnivore species, lynx and coyote, and we could not measure the biomass of these species for each experiment independently. Therefore, we used an index of their total response (numerical \times functional) by counting the number of tracks in winter. After each snowfall, the 4-km perimeters of the control, fertilizer, and food addition plots were surveyed. The number of fresh tracks of each species crossing the 4-km perimeter in the previous day was scored and averaged for that winter.

17.3 Direct Effects of Trophic-level Perturbations

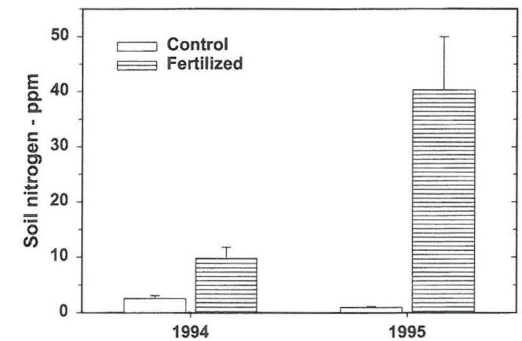
Results for each of the experiments are compared with values from the control sites. We discuss in this section only the direct effects. Indirect effects are seen in the level next to the one perturbed, and double indirect effects are seen two trophic levels removed from the perturbation. To measure direct and indirect effects, data from different years were used. Peak herbivore biomass occurred in 1990. Both maximum browsing by herbivores on winter food and peak predator activity were observed in the winter of 1990–1991. The major decline of herbivore numbers took place in winter 1991–1992. Peak growth of winter food plants (growth index (%), see 6.3.1) occurred in 1992, after browsing declined.

17.3.1 Fertilizer Addition

The mean rate of fertilizer application over the years 1987–1994 was 150 (± 30 SE) kg N per hectare per year in the form of ammonium nitrate (Turkington et al. 1998). Figure 17.1 illustrates the soil nitrate nitrogen in mid-June about 3 weeks after fertilizer application. As expected, there were significant increases in soil nitrate in 1995 after fertilizer was added. Measurement of nitrogen in the soil in mid-June 1995 showed 40.3 ppm (± 9.7 , 95% CL) nitrate nitrogen compared to 0.97 ppm (± 0.19 , CL) in immediately adjacent control samples ($p < .001$; table 17.1).

Figure 17.2 shows the total dry weight biomass of small twigs (<5 mm) of willow and

Figure 17.1 Soil nitrate nitrogen (ppm, with 95% CL) on fertilizer and control sites in 1994 and 1995.



birch obtained from our clip plots. Because each grid had a different absolute biomass, we standardized across grids by setting 1990 as 100%. Both control and fertilizer grids showed an increase in biomass of small birch twigs before the hare peak, followed by a decline in 1991 and 1992. The fertilizer grids, however, showed consistently higher values after 1992 than the controls as a consequence of the added soil nitrogen. Thus, in 1992, addition of fertilizer produced biomass values of 149.6 g/m² compared to 113.6 g/m² on control sites for winter twigs (table 17.2).

Productivity was measured by the growth index (%) in 5-mm twigs (table 17.3; see also figures 6.5 and 6.7). In birch, productivity increased to a peak in 1992, then declined on both fertilizer and control grids. This trend was less evident in willow, but there appeared to be a decline in growth toward the low point of the hare cycle. In both species, however, growth on the fertilizer grids was consistently above that on controls. Productivity of these shrubs in the peak year of 1992 occurred 2 years after peak herbivore biomass. In 1992, birch % growth index was 31.91 (± 1.41 CL) on fertilized grids, compared to 23.88 (± 1.8 CL) on controls. For willow, % growth index was 21.34 (± 1.34 CL) on fertilized grids, compared to 11.98 (± 0.80 CL) in controls.

The percent nitrogen in the growth index of willow twigs on fertilizer grids was consistently higher than that of twigs on control areas (figure 17.3). Thus, the overall availability of high-protein food for hares increased on fertilizer grids. In neither of the treatments was there any trend through the cycle.

In contrast to twig nitrogen, the methanol extract from both willow and birch twigs was similar on fertilizer and control treatments (figure 17.4a,c). Thus, addition of nitrogen did not appear to alter twig defensive chemistry. However, both shrub species appeared to show a response to the hare cycle through an increase of the methanol extract at the hare peak, then a decrease subsequently.

In general, these figures are consistent with models showing direct bottom-up effects (see chapter 3, table 3.1) as a result of increases to the soil nutrient pool.

17.3.2 Addition of Hare Food

On the food-addition sites, hares ate rabbit chow year-round, and arctic ground squirrels ate it in summer. Rabbit chow had the effect of increasing the density of these herbivores. Thus, in spring 1991 at the peak, total herbivore biomass on these sites was 13.34 kg/ha, compared to 2.83 kg/ha on the controls, a fivefold increase. Over the cycle, herbi-

Table 17.1 Nitrate nitrogen (ppm) from soil samples collected at experimental and control sites in 1995 and 1996.

| Site | <i>n</i> | Experimental Site | Control Site | <i>p</i> |
|------------------------------------|----------|-------------------|--------------|----------|
| Fertilizer | 10 | 40.3 | 0.97 | .001 |
| Food addition | 10 | 2.70 | 3.3 | ns |
| Predator enclosure | 10 | 0.37 | 0.18 | ns |
| Predator enclosure + food addition | 10 | 0.85 | 0.33 | ns |
| Hare enclosure | 100 | 8.34 | 5.2 | .0001 |
| Vegetation enclosure | 156 | 6.58 | 5.2 | .0001 |

vore biomass on food-addition sites was consistently above that on controls (figure 17.5). On average, these values were 6.52 kg/ha and 2.48 kg/ha, respectively (table 17.4).

The impact of hare feeding on winter food plants was measured by the percentage of 5-mm twigs browsed. The effect of fertilizer was to increase hare browsing on willows (table 17.5, figure 6.9). However, birch was heavily browsed on controls, and, if anything, there was slightly less browsing on the fertilizer grids in comparison. Thus, higher hare density on this treatment resulted in higher browsing on willow, but not on birch.

Vegetation growth, but not biomass, was measured on food-addition sites (figure 17.6). After the period of high hare numbers, the % growth index of 5-mm twigs was higher on food-addition sites than on controls for both species. Thus, the higher browsing on willow resulted in a significant ($p < .05$) increase in growth on this food-addition treatment 2 years later.

The net effect of peak browsing and one season's subsequent growth (figure 17.7) showed that neither birch nor willow could compensate for browsing during the hare peak. However, because growth responded 2 years after peak browsing, the net effect in 1992 for birch biomass was 1.22, and for willow biomass it was 1.24, indicating a subsequent increase in vegetation biomass once herbivory declined. The methanol extract of these twigs did not differ between food-addition and control sites (figure 17.4b,d).

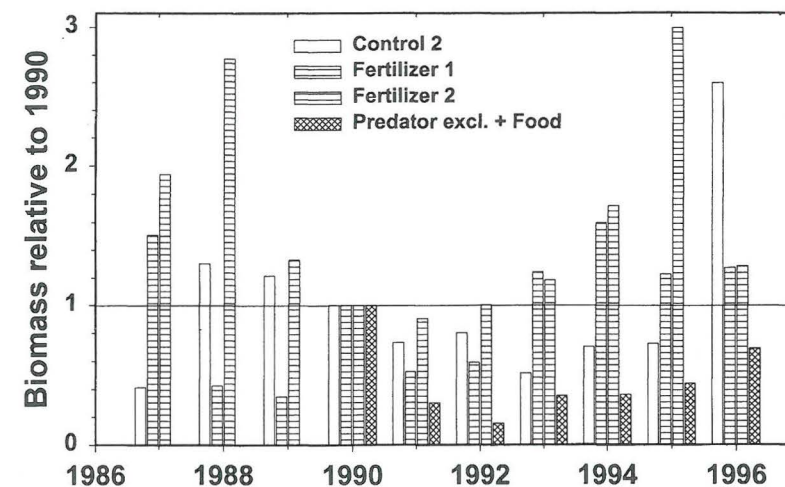
The tracks of lynx and coyote crossing the perimeter of each experimental site were counted after each fresh snowfall and averaged as the number per day in each winter (figure 17.8, table 17.6). In winter 1990–1991, there were 3.5 coyote tracks/day on the food-

Table 17.2 Combined gray willow and bog birch biomass of 5-mm twigs (g/m²) on 2-m² quadrats for 1992, the year following maximum browsing, and as a mean for the 10 years, 1987–1996 (1990–1996 for the predator enclosure plus food addition).

| Site | Year | Peak Biomass | 10-year Mean |
|------------------------------------|------|--------------|--------------|
| Control | 1991 | 133.4 | 94.5 |
| Control | 1992 | 113.6 | 94.5 |
| Fertilizer | 1992 | 149.6 | 133.7 |
| Predator enclosure + food addition | 1991 | 14.3 | 32.9 |
| Predator enclosure + food addition | 1992 | 6.9 | 32.9 |
| Hare enclosure | 1992 | 101.9 | 78.0 |

To make comparisons across grids, values were standardized to 100 in 1990.

(a) Bog Birch



(b) Gray Willow

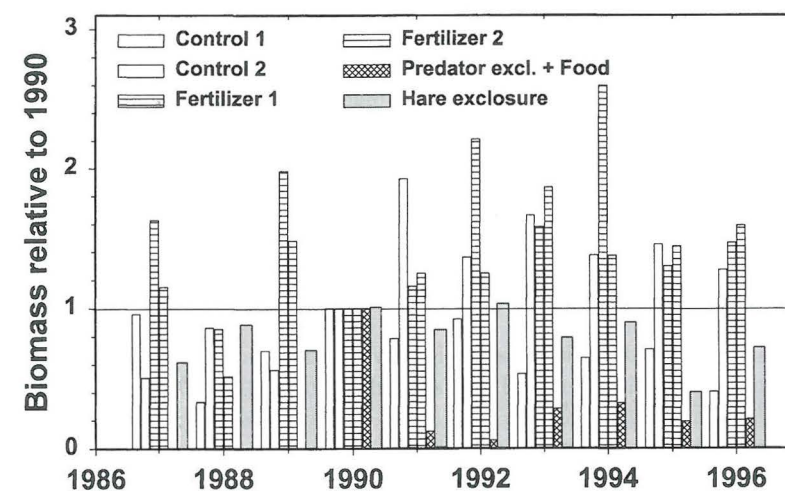


Figure 17.2 Biomass (dry weight) of 5-mm twigs of (a) bog birch and (b) gray willow on all treatments, 1987–1996. Because different areas vary in shrub density, the biomass in 1990 is indexed as 1.0, and all other values for each treatment area are referenced to the 1990 value for that area.

Table 17.3 Percent growth index of 5-mm twigs of gray willow and bog birch in the peak year and as the mean over 1988–1995.

| Site | Year | Peak (95% CR) | Mean (95% CR) |
|------------------------------------|------|---------------------|---------------------|
| Gray Willow | | | |
| Control | 1991 | 12.43 (11.70–13.2) | 15.37 (15.07–15.67) |
| Control | 1992 | 11.98 (11.22–12.78) | 15.37 (15.07–15.67) |
| Fertilizer | 1992 | 21.34 (20.00–22.68) | 19.95 (19.48–20.42) |
| Food addition | 1992 | 31.56 (28.22–35.31) | 22.72 (21.81–23.63) |
| Predator exclosure | 1992 | 16.11 (14.82–17.40) | 16.77 (16.22–17.32) |
| Predator exclosure + food addition | 1992 | 26.68 (24.46–29.09) | 23.22 (22.42–24.02) |
| Hare exclosure | 1991 | 11.27 (9.97–12.73) | 14.82 (14.26–15.38) |
| Hare exclosure | 1992 | 14.84 (13.17–16.71) | 14.82 (14.26–15.38) |
| Hare exclosure + fertilizer | 1992 | 16.91 (15.13–18.69) | 20.22 (19.75–20.69) |
| Bog Birch | | | |
| Control | 1992 | 23.88 (22.13–25.70) | 16.24 (15.85–16.63) |
| Fertilizer | 1992 | 31.91 (30.50–33.32) | 20.56 (20.10–21.02) |
| Food addition | 1992 | 27.16 (25.23–29.16) | 12.08 (11.28–12.88) |
| Predator exclosure | 1992 | 21.11 (19.41–22.89) | 17.54 (17.02–18.06) |
| Predator exclosure + food addition | 1992 | 36.55 (34.02–39.17) | 25.24 (24.44–26.04) |
| Hare exclosure + fertilizer | 1992 | 19.94 (18.54–21.34) | 20.41 (19.69–21.13) |

Growth index = new growth/total twig dry mass. 95% CR = 95% confidence range.

addition areas versus 0.50/day on controls, and 2.89 and 0.96 lynx tracks/day for the two areas, respectively.

In summary, increasing herbivore biomass decreased vegetation biomass, and this decrease could not be compensated for by increased growth the following year. However, once herbivore populations had declined 2 years later, growth more than compensated for herbivory. These results are consistent with top-down effects. At the same time, mammalian predator activity increased by a factor of 3 on the food-addition sites, consistent with bottom-up effects.

17.3.3 Predator Exclosure

Our fence excluded the large carnivores such as lynx and coyote. Avian predators were inhibited in their hunting by overhead lines in a small (10 ha) area, but the inhibitory effect was minor for the whole site. Herbivore biomass during the peak years, 1988–1991, in the predator exclosure was higher than that on the controls, indicating a small but consistent effect from the removal of predators (table 17.4). This indicates a top-down effect of mammalian predators.

17.3.4 Predator Exclosure and Food Addition

The predator exclosure and food addition site received the double treatment of removal of carnivores and addition of rabbit chow. Once the treatment was initiated in summer

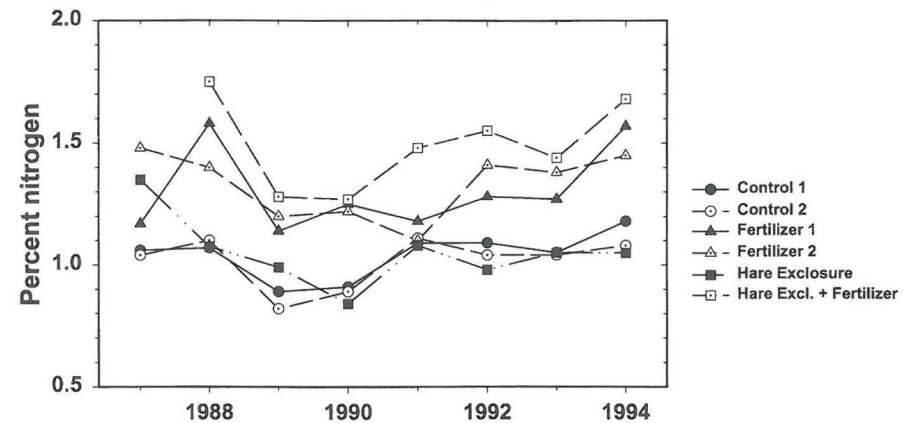


Figure 17.3 Percent nitrogen in gray willow twigs collected at the end of winter each year, 1987–1994.

1988, herbivore biomass increased and remained well above that of the control and predator exclosure sites. However, this treatment maintained similar herbivore densities to those on the food addition up to the peak of the cycle. After the peak, this treatment maintained high densities, while those on the food addition declined (see figure 8.2 and figure 9.10). Thus, food supply was the dominant effect up to the peak, but effects of predator exclosure became detectable after the peak. The mean value for herbivore biomass over the cycle for this joint treatment was 11.30 kg/ha. This density represented a 4.5-fold increase over controls (2.48 kg/ha), a 3.5-fold increase over the predator exclosure alone (3.23 kg/ha), and a 1.7-fold increase over the food addition alone (6.5 kg/ha; table 17.4).

Winter shrub biomass on the predator exclosure + food-addition treatment declined well below that on controls during the period of high hare density. Thus, in 1991 small twig biomass on this treatment was 14.3 kg/ha, one-ninth the biomass on controls (133.4 kg/ha). Mean values over the cycle were 32.9 kg/ha and 94.5 kg/ha respectively, a three-fold difference (table 17.2).

As a consequence of the high herbivore biomass, herbivore browsing was severe in winter 1990–1991. Thus, 88.2% of birch twigs were browsed on the joint treatment, compared to 85.7% on controls, and 62.8% of willow twigs on the treatment, compared to 12.9% on the controls (tables 6.5, 6.6; see also table 17.5). Because browsing on birch was so high on control plots, there was little room for the treatment effects to be higher. However, browsing of willow on the treatment was considerably higher than controls. Consequently, in 1991 the net reduction of biomass in birch twigs was very large but did not differ between treatment and controls (0.15 of the biomass a year earlier on the treatment compared to 0.16 on controls). In contrast, net biomass of willow twigs declined to 0.44 of that a year earlier on the treatment compared to 0.98 on controls. Thus, willow biomass declined to less than half that of controls (figure 17.7, table 17.3). Growth did not compensate for browsing in either species on this treatment.

The joint treatment produced consistently higher growth rates of birch and willow twigs relative to controls. Also, growth of both species on this treatment was higher than

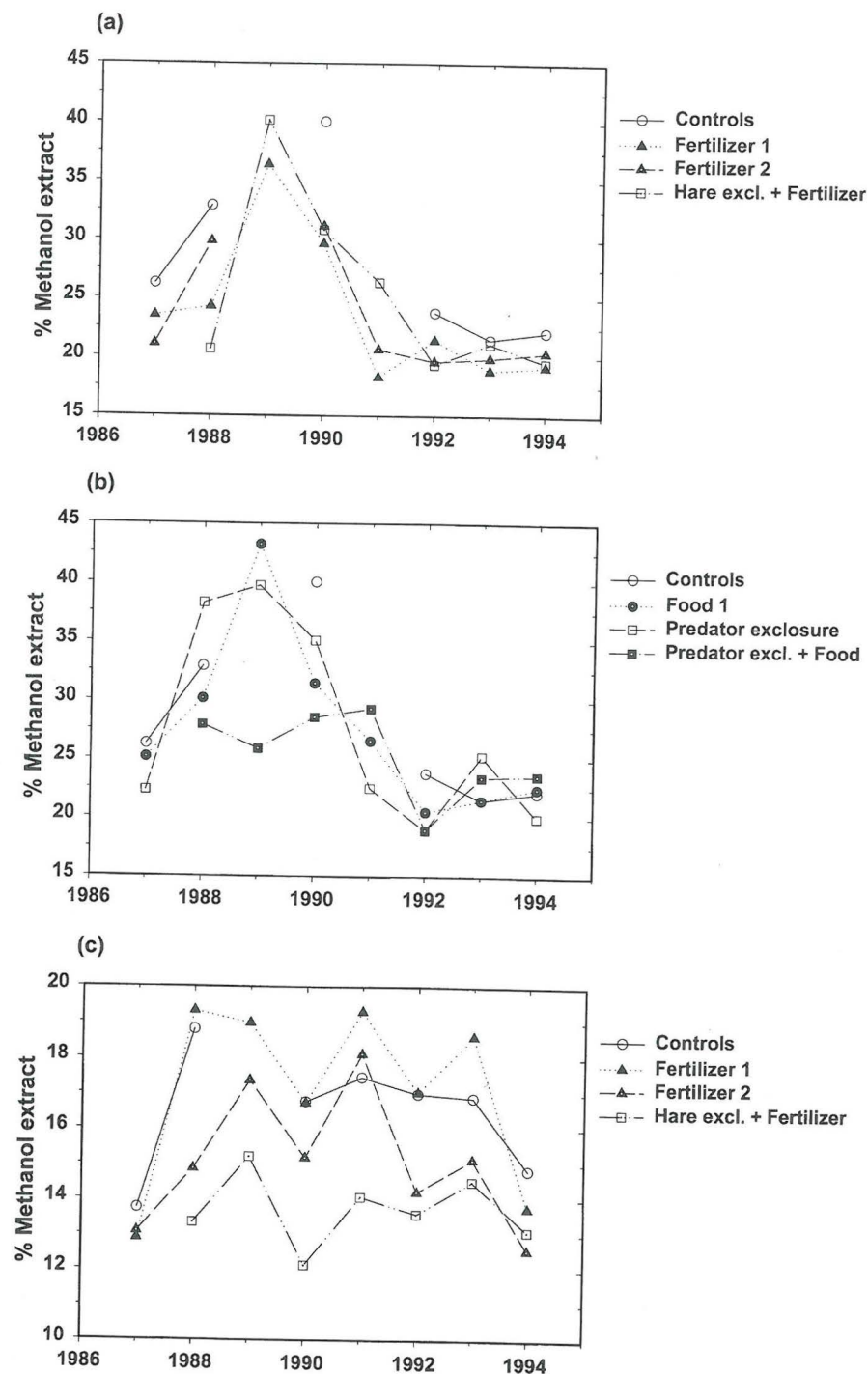


Figure 17.4 Percent methanol extract in twigs collected at the end of each winter. (a, b) Bog birch; (c-e) gray willow. This is a general measure of secondary compounds in the winter twigs.

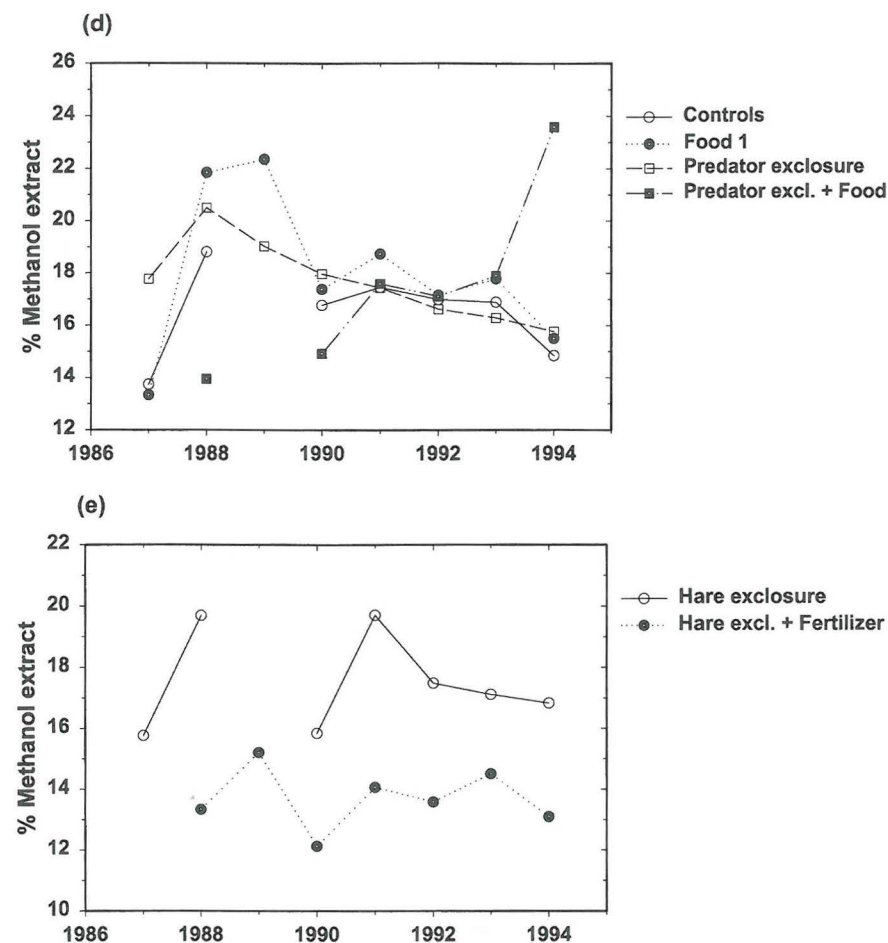


Figure 17.4 continued

that on the predator exclusion, and birch growth (but willow less so) was also higher than that on the food addition (figure 6.4, table 17.3).

In summary, this joint treatment can be compared not only to controls but also to the single treatments. The increase in herbivore density relative to food addition alone indicates the top-down effect from removal of predators after the peak in hare numbers had passed. Similarly, the decrease in plant biomass relative to controls indicates the top-down effect of herbivores. The increase in plant productivity was a response to the herbivory, but it was not sufficient to compensate for the loss of plant biomass.

17.3.5 Hare Exclusion

The hare exclusion treatment excluded hares and moose (*Alces alces*), which were the only herbivores in winter. Moose were rare, and the treatment reflected the effects of ex-

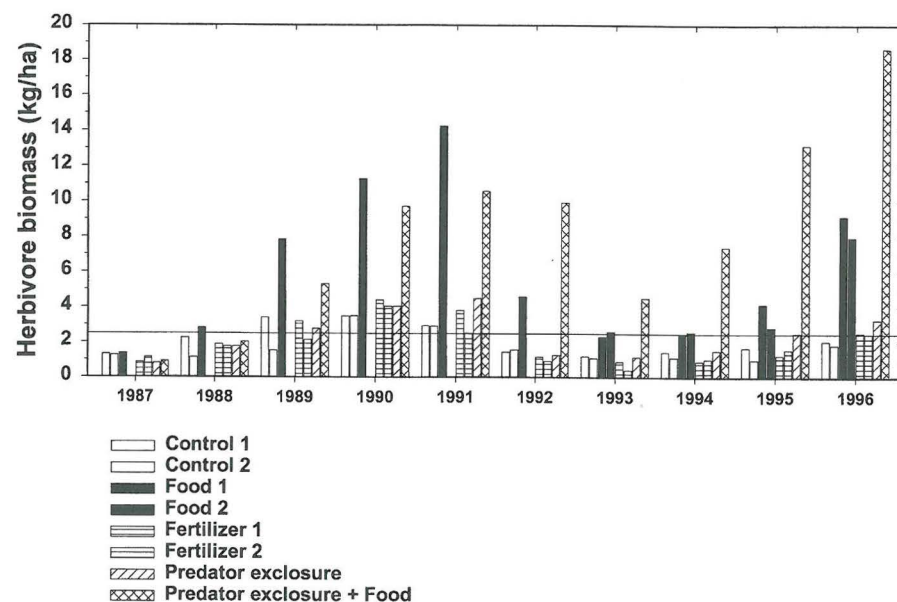


Figure 17.5 Annual changes in herbivore biomass (kg/ha) in the spring of each year from 1987 to 1996 on all control and treatment areas. All herbivore species are included in these totals. The average herbivore biomass for control areas is indicated by the horizontal line.

cluding hares as the dominant herbivore. Willow was the only winter shrub species in the hare enclosure. In 1992, biomass of 5-mm twigs was 101.9 kg/ha in the enclosure, compared to 113.6 kg/ha on the controls. When standardized to 100 in 1990 there was no difference in twig biomass between the enclosure and control in the period 1990–1996 (figure 6.3).

Growth of willow twigs in the hare enclosure did not follow the cycle as it did outside, but rather appeared to decline slightly over the 8 years (figure 17.6b). In 1992 growth in the enclosure (14.84%) did not differ markedly from willow on controls (11.98%), and

Table 17.5 The percentage of 5-mm twigs of willow and birch that were completely browsed in the peak winter 1990–1991.

| Site | Willow | | Birch | |
|------------------------------------|----------|------------|----------|------------|
| | % Browse | Net Effect | % Browse | Net Effect |
| Control | 12.9 | 0.98 | 85.7 | 0.16 |
| Fertilizer | 34.9 | 0.78 | 61.7 | 0.49 |
| Food addition | 47.1 | 0.63 | 57.3 | 0.51 |
| Predator enclosure | 10.8 | 1.01 | 51.5 | 0.56 |
| Predator enclosure + food addition | 62.8 | 0.44 | 88.2 | 0.15 |
| Hare enclosure | 0 | 1.13 | — | — |
| Hare enclosure + fertilizer | 0 | 1.18 | 0 | 1.23 |

The net effect is the net biomass in September 1991 relative to that in September 1990 as a result of browsing followed by growth in summer 1991. Net effect <1 indicates undercompensation, >1 overcompensation of growth.

over the cycle mean growth was similar (14.82% enclosure, 15.37% controls). Nitrogen values of these twigs also did not differ from those of controls (figure 17.3).

In 1991, the year of highest browsing impact, net biomass of willow for the enclosure increased by a factor of 1.13, compared to 0.98 on controls. Thus, the removal of herbivores allowed a small net increase in willow twig biomass. Over the whole cycle, willow biomass showed a net increase in the enclosure by 1.15, compared to 1.09 on controls (figure 17.7d). In general, exclusion of hares showed small but significant impacts of herbivory on productivity but not on biomass of willows. Because birch were absent from this site, we could not measure the equivalent impacts. However, we anticipate that herbivory would be greater on birch.

17.3.6 Hare Enclosure Plus Fertilizer

The growth of willow twigs on the hare enclosure + fertilizer plot was consistently above controls (figure 17.6). Over the cycle, growth remained approximately constant and averaged 20.2% compared to 15.4% on controls. Similarly, for birch, % growth index was usually above that on controls. Over the cycle, birch growth also showed no trend in the enclosure and averaged 20.4% compared to 16.2% on controls.

Both willow and birch had similar high growth rates on the fertilizer grids and on the fertilized hare enclosure (figure 17.6). However, growth on the fertilizer grids increased to a peak, then declined, reflecting the changes in browsing during the hare cycle. Growth in the hare enclosure did not show this pattern, and it merely declined over time. In 1992, after peak browsing, the growth rate (% growth index) on fertilizer plots (21.3% for willow, 31.9% for birch) was significantly higher than that in the fertilized hare enclosure (16.9% for willow, 19.9% for birch). Therefore, browsing by herbivores at peak densities on the fertilizer areas stimulated productivity of the vegetation. Nitrogen values in the twigs of willow in the fertilized hare enclosure were similar to those on the fertilizer plots and consistently higher than those of controls (figure 17.3).

Because there was substantial browsing of twigs on the fertilizer plots, the higher

Table 17.4 Total herbivore biomass (kg/ha) on the experimental sites in the year of peak biomass and as a mean over 1987–1996.

| Site | Year | Peak | 10-year Mean |
|------------------------------------|------|-------|--------------|
| Control | 1990 | 3.34 | 2.48 |
| | 1991 | 2.83 | |
| Fertilizer | 1990 | 4.22 | 2.73 |
| Food addition | 1991 | 13.34 | 6.52 |
| Predator enclosure | 1991 | 4.49 | 3.23 |
| Predator enclosure + food addition | 1991 | 10.59 | 11.30 |

Herbivores include hares, squirrels, small mammals, and grouse.

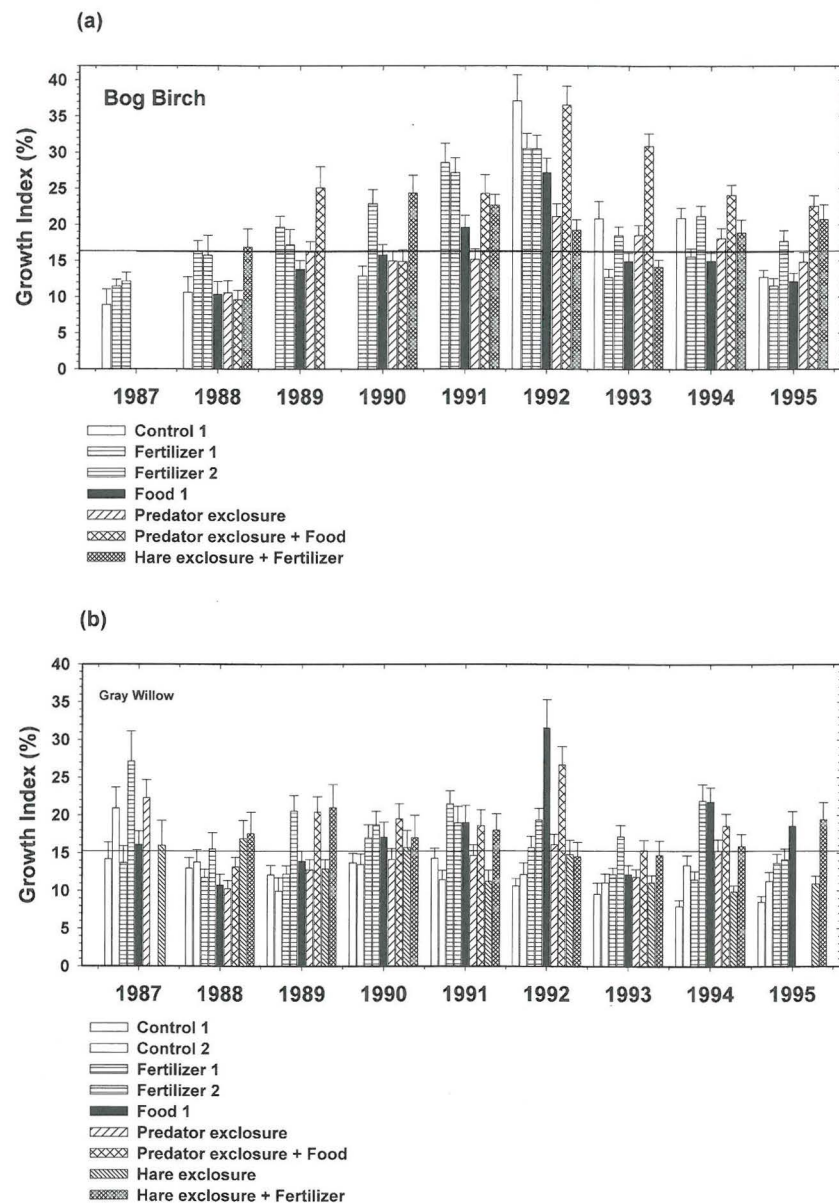


Figure 17.6 Annual changes in the growth rates (± 1 SE) of (a) bog birch and (b) gray willow. Growth is indexed as the percentage dry weight of current annual growth to total 5-mm twig biomass. The horizontal line marks the average growth rate for control areas over 1987–1996.

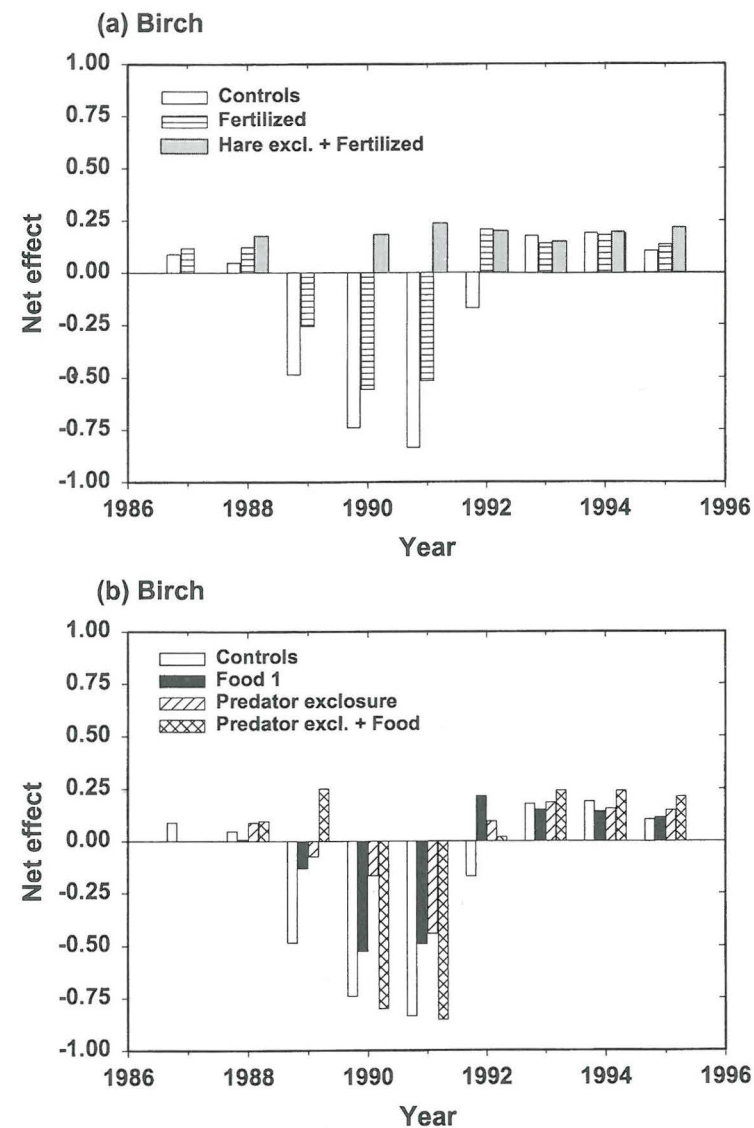


Figure 17.7 The net effect of winter browsing and summer growth on the standing crop of (a, b) bog birch, and (c, d) gray willow. Negative values indicate years in which browsing exceeds growth.

growth rates could not compensate sufficiently for the loss of biomass. Net biomass of willow twigs on fertilized grids decreased by a factor of 0.78, and that of birch decreased by a factor of 0.49 in 1991 (table 17.5). In contrast, on the fertilized hare exclosure, net biomass of 5-mm willow twigs increased by a factor of 1.18 and that of birch increased by 1.23, showing that protection from browsing allowed an increase of vegetation biomass, while exposure to browsing caused a decrease by as much as half.

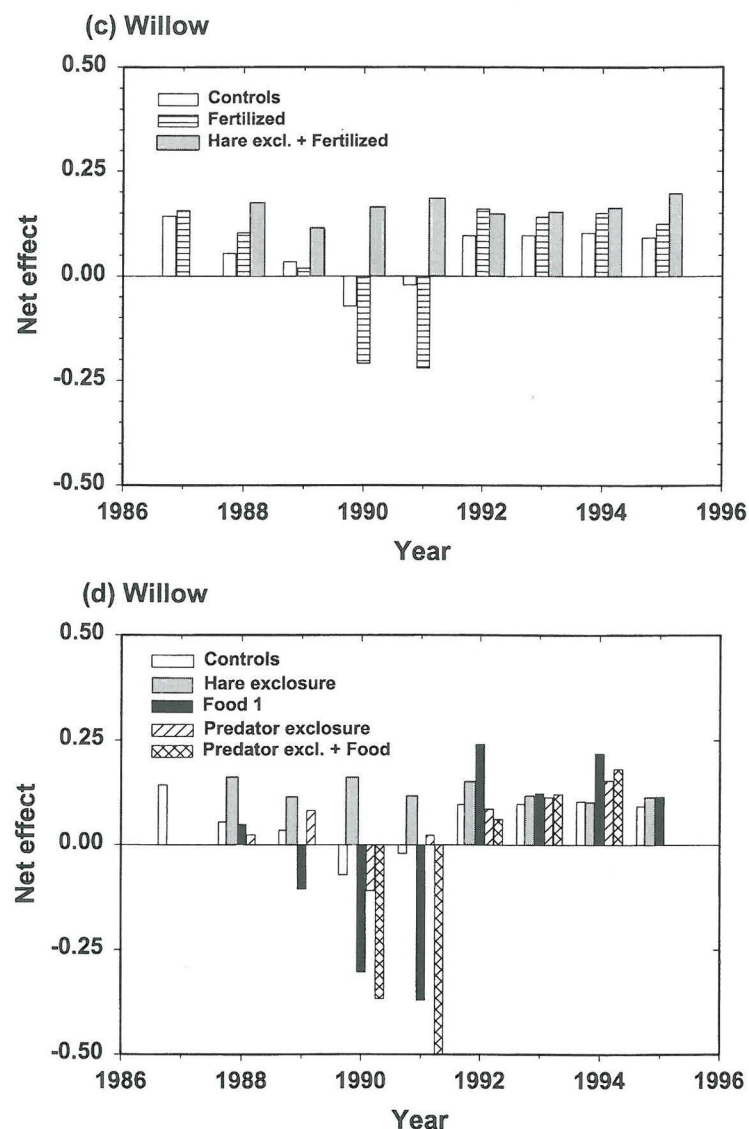


Figure 17.7 continued

Comparing the fertilized hare enclosure with the unfertilized hare enclosure, the increase in net biomass of willows did not differ between the two, despite the higher growth rate of the former. Therefore, fertilizer had little bottom-up effect, and hare removal rather than fertilizer was the major effect observed with this experiment. In summary, top-down effects were observed both through the decrease in vegetation biomass and through an increase in subsequent vegetation productivity.

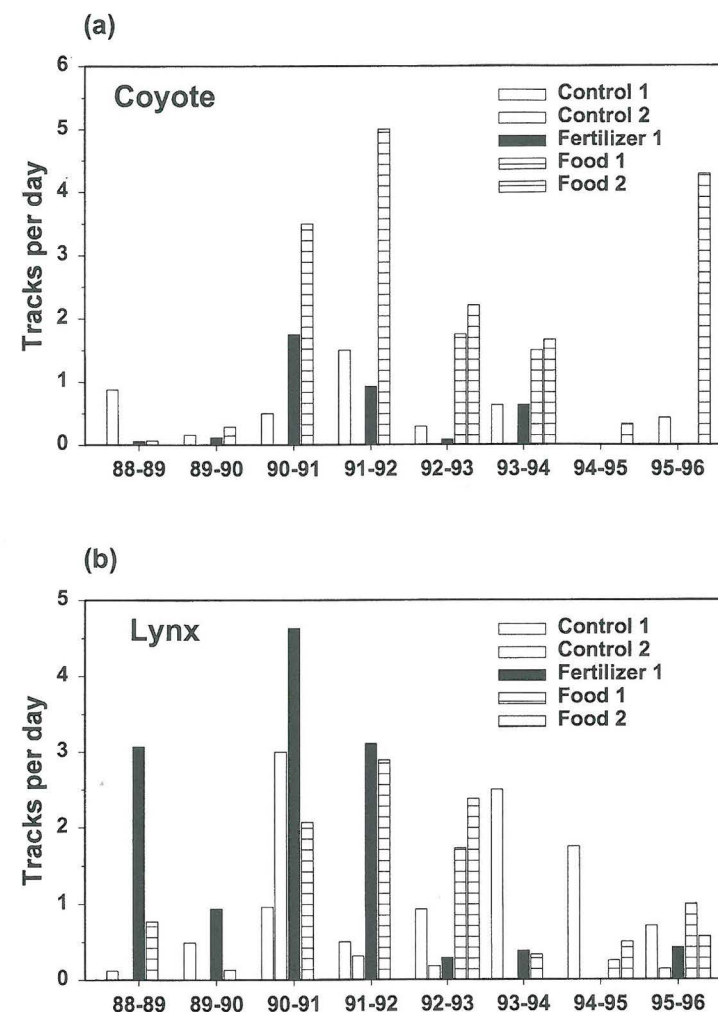


Figure 17.8 Average number of (a) coyote and (b) lynx tracks around experimental and control areas. Transects were 4 km in length and were done only within 24 h after fresh snowfall.

17.3.7 Vegetation Removal

In 1996 soils were sampled from 156 vegetation removal plots and 156 control sites with vegetation present immediately adjacent to them (table 17.1). The nitrate nitrogen value on the 156 removal plots was $6.58 (\pm 0.41, 95\% \text{ CL})$, compared to $5.2 (\pm 0.34)$ on the control plots. The removal plots were significantly ($p < .0001$) higher in soil nitrogen compared to those with vegetation, indicating that herbaceous vegetation reduced the nitrogen content of soils.

Table 17.6 Mean snow track counts per day for lynx and coyote over the winter of peak hare numbers (1990–1991) and the mean over the eight winters 1988–1989 to 1995–1996 (95% CL).

| Site | <i>Lynx</i> | | <i>Coyote</i> | |
|---------------|-------------|-------------|---------------|-------------|
| | Peak | 8-year Mean | Peak | 8-year Mean |
| Control | 0.96 | 0.76 (0.54) | 0.50 | 0.50 (0.36) |
| Fertilizer | 4.63 | 1.61 (1.24) | 1.75 | 0.45 (0.44) |
| Food addition | 2.89 | 1.15 (0.82) | 3.50 | 1.51 (1.08) |

17.4 Indirect Effects of Trophic-level Perturbations

17.4.1 Fertilizer Addition

Indirect effects of fertilizer addition would be experienced at the herbivore level. In 1990, the year of peak biomass, herbivore biomass on fertilizer grids was 4.22 kg/ha and that on controls 3.34 kg/ha, a small but significant difference. However, over all 8 years, there was no difference in herbivore biomass (fertilizer 2.73 kg/ha, control 2.48 kg/ha; figure 17.5, table 17.4), indicating that the effect of fertilizer was only apparent at high herbivore levels.

Double indirect effects would occur at the predator level. Predator tracks on fertilizer grids in the peak winter of 1990–1991 were 4.63/day for lynx and 1.75/day for coyote, compared to 0.96/day and 0.50/day, respectively, for controls (table 17.6). Thus, both predator species used fertilizer grids more than control areas in the peak year. Over the 8 years, there was again no significant difference in mean track counts for either species between fertilizer and control grids (figure 17.8). Thus, bottom-up indirect effects were observed at both higher levels of the food chain, but only when herbivore biomass was high.

17.4.2 Food Addition

The indirect effect of increasing herbivore numbers on the food addition grids would be seen at the soil nutrient level. In 1995 soil nitrate nitrogen on the food addition sites (2.7 ppm) was similar to that on controls (3.3 ppm; table 17.1). Therefore, there were no detectable indirect effects of herbivores on soil nutrients.

17.4.3 Predator Exclosure

The indirect effects from excluding predators would be observed at the vegetation level. In winter 1990–1991, browsing impact in the predator exclosure on birch was 51.5% versus 85.7% on controls, and on willow the values were 10.8% in exclosure and 12.9% on controls. Herbivory in the peak year, therefore, did not increase in the predator exclosure (table 17.5), and may even have declined.

Furthermore, willow growth in the subsequent summer of 1991 completely compensated for this browsing in both the predator exclosure and control (net change in biomass

was 1.01 and 0.98, respectively). Birch growth, however, did not compensate for the higher browsing rate, and biomass declined in 1991 on both the predator exclosure (net change 0.56) and control (net change 0.16; figure 17.7, table 17.5).

In 1992, after herbivore declines, willows had significantly higher growth rates in the predator exclosure than on controls (16.1% vs. 12.0%, $p < .05$), but birch did not (21.1% vs. 23.9%; table 17.3). Thus, in general we did not detect indirect top-down changes in either willow or birch biomass resulting from the higher herbivore numbers on this predator exclosure treatment.

The double indirect effect would be detected at the soil nutrient level. In 1995 soil nitrate nitrogen was 0.37 ppm on the predator exclosure, which was not significantly different from the 0.18 ppm on controls (table 17.1). Hence, indirect effects resulting from higher herbivore biomass were not detected in soil nutrients.

17.4.4 Food Addition and Predator Exclosure

Indirect effects resulting from the high herbivore biomass would be seen at the soil nutrient level. In the exclosure in 1995, soil nitrate nitrogen was 0.85 ppm, while that on controls was 0.33 ppm. No significant differences were detected (table 17.1).

17.4.5 Hare Exclosure

In 1996 soil nitrate nitrogen averaged 8.34 (± 0.45 , 95% CL) ppm, while outside the exclosure nitrogen averaged 5.2 (± 0.36) ppm, a difference significant at $p < .0001$ (table 17.1). A similar difference was detected in 1995 ($p < .02$). Therefore, the indirect effect of herbivores is to increase the uptake of nutrients into the vegetation to compensate for herbivory and so reduce the pool of nutrients in the soil. This result is due to a productivity response at the plant level.

17.5 Discussion

17.5.1 Direct Effects

Table 17.7 summarizes the significant direct effects on biomass derived from each of the experiments. Each of the removal experiments produced an increase in biomass at the level below. The two addition experiments (nutrients on fertilizer grids, food for herbivores on food addition grids) produced an increase in the level above, and for food addition a decrease in the level below. Because we were unable for practical reasons to increase the herbivores directly, we could not test the herbivore (H) \rightarrow predator (P) direct interaction. However, we can see from the indirect effect of food addition, resulting in a higher herbivore biomass and a consequent higher use by predators on those sites (table 17.8), that there is a positive link from H to P . Therefore, putting these interactions together we see the pattern.

$$N \leftrightarrow V \leftrightarrow H \leftrightarrow P,$$

where N is nutrients, and V is vegetation. This is the pure reciprocal model 27 discussed

Table 17.7 Summary of qualitative direct effects on biomass produced by experimental perturbation at the peak values.

| Site | Trophic Level | | | | Predicted by Model 27 | | | |
|---|----------------|-------------------|----------------|----------------|-----------------------|-------------------|----------------|----------------|
| | N | V | H | P | N | V | H | P |
| Fertilizer | M ⁺ | + | | | M ⁺ | + | + | + |
| Food addition | | M ⁺ − | + | + | + | M ⁺ − | + | + |
| Predator removal | | | + | M [−] | + | − | + | M [−] |
| Predator removal + food addition | | M ⁺ −− | ++ | M [−] | ++ | M ⁺ −− | ++ | M [−] |
| Herbivore removal | | + | M [−] | | − | + | M [−] | |
| Herbivore removal + fertilizer addition | M ⁺ | ++ | M [−] | | ? | ++ | M [−] | |
| Vegetation removal | + | M [−] | | | + | M [−] | | |

M⁺ indicates the experimental addition, M[−] the experimental removal. + = increase, − = decrease. N = nutrients, V = vegetation, H = herbivores, P = predators.

in chapter 3, involving two-way interactions at each level. The predictions of this model are provided in table 17.7 for comparison with our results.

17.5.2 Indirect Effects

The above conclusion stems largely from direct effects derived from separate experiments at each trophic level. When we include indirect effects as well, we see other models are equally valid, but no models are entirely consistent with our results. Table 17.8 summarizes the indirect effects on biomass from each experiment. The nutrient addition produced small but positive effects at the peak of the cycle, but over the whole cycle these effects were not evident. In contrast, top-down indirect effects were not detectable despite the strong direct effects. One top-down effect (herbivore removal on soil nutrients [experiment 5]) even went in the direction opposite to that predicted—namely, an increase in the nutrient pool instead of a decrease. This result is most likely due to the fact that although there was less plant biomass, shrubs responded to herbivory by growing more (see below). More growth, therefore, reduced the nutrient pool relative to areas with no herbivory. In contrast, where herbivores were removed, there was less growth and the nutrient pool increased. This result from the nutrient pool illustrates that predictions from simple change of biomass are different from those due to change in productivity.

Table 17.8 presents the models for which the results of each experiment are consistent. Our findings do not match any model completely if we take them strictly at face value because of the anomalous result of herbivore removal on soil nutrients. If we recognize that this nutrient result was due to a productivity response of the vegetation and that there was a top-down effect as seen from the vegetation removal experiment 7 (table 17.7), then models 23, 21, and 27 are all supported.

In general, both top-down and bottom-up indirect effects tend to attenuate rapidly so that there is little effect of perturbations at the far end of the food chain.

Table 17.8 Summary of qualitative indirect effects on biomass.

| Site | Observed | | | | Predicted by Model 23 | | | | Total models |
|---|----------------|-------------------|----------------|----------------|-----------------------|-------------------|----------------|----------------|--------------|
| | N | V | H | P | N | V | H | P | |
| Fertilizer | M ⁺ | + | + | + | M ⁺ | + | + | + | 8 |
| Food addition | 0 | M ⁺ − | + | + | 0 | M ⁺ − | + | + | 2 |
| Predator removal | 0 | 0 | + | M [−] | 0 | − | + | M [−] | 6 |
| Predator removal + food addition | 0 | M ⁺ −− | ++ | M [−] | 0 | M ⁺ −− | ++ | M [−] | 2 |
| Herbivore removal | + | + | M [−] | | 0 | + | M [−] | None | 0 |
| Direct Effects (table 17.7) | | | | | | | | | |
| Herbivore removal + fertilizer addition | M ⁺ | ++ | M [−] | | M ⁺ | ++ | M [−] | | 12 |
| Vegetation removal | + | M [−] | | | 0 | M [−] | | | 18 |

M⁺ indicates the experimental addition, M[−] the experimental removal. + = increase, − = decrease, 0 = no change. N = nutrients, V = vegetation, H = herbivores, P = predators.

17.5.3 Top-down versus Bottom-up

The joint perturbation experiments provide some clues on the relative strengths of top-down and bottom-up effects. In 1991, birch on the fertilized grids (with hares) had a higher growth rate than that on the fertilized hare enclosure by a factor of 1.23, but willow showed no difference in growth rate. This result suggests that the greater hare browsing on birch stimulated growth, but the lesser browsing on willow did not. In contrast, willow on the unfertilized hare enclosure had a much lower growth rate than that on the fertilized enclosure (by a factor of 0.62). This result suggests that in willow, fertilizer produced a stronger stimulation for growth than did hare browsing. Thus, both top-down and bottom-up effects could be detected.

The net effect of browsing and growth on fertilizer grids produced a decline of willow twig biomass by a factor of 0.78, whereas on control areas willow biomass barely declined at all (factor of 0.98). Browsing on birch was much more severe, so that in both fertilizer and control areas net biomass declined to 0.49 and 0.16 of that a year earlier. Thus, fertilizer may have increased growth rate, but it also increased herbivory to an even greater extent so that biomass declined. Therefore, top-down effects outweighed bottom-up effects at the vegetation level in winter. This result is opposite to the summer food situation, where herbivory had a negligible effect on vegetation relative to that of fertilizer addition (John and Turkington 1995).

In the winter of 1991–1992 predators had their most marked effect. Herbivore biomass on the food-addition site declined from spring 1991 to spring 1992 at an instantaneous rate of -1.137 , compared to a decline of herbivore biomass of -0.062 on the food addition plus predator exclosure. The greater rate of decline of herbivores on the food addition is, therefore, due to the presence of predators. Furthermore, the rate of decline on control grids in the presence of predators but without the extra hare food (-0.667) was actually less than that on the food addition in the presence of food. Therefore, predation was the dominant process, and food had no detectable effect in mitigating the decline in herbivores. Thus, top-down effects dominated bottom-up effects at the herbivore level.

17.5.4 Productivity and Biomass Responses

Our main index of trophic-level response was through changes in biomass. However, productivity also responded to top-down effects. Did increased growth rate compensate for biomass loss? The hare exclosure, control areas, predator exclosure, food addition, and the food addition and predator exclosure produced a sequence of increasing herbivory in the peak winter of 1990–1991. Subsequent growth of both willow and birch was positively related to browsing intensity in the previous winter (regression for both species combined, $\% \text{ growth} = 13.03 + 0.216 (\% \text{ browsed})$, $n = 9$, $p < .005$; figure 17.9). At least at the vegetation level, winter food plants responded to top-down effects by an increased growth rate.

In no case, however, did this productivity response compensate entirely for herbivory, and in general the compensatory effect was relatively minor. However, at the next level down, soil nutrient content declined under conditions of herbivory (experiment 5) contrary to the predicted increase, a result consistent with the higher productivity of plants that experience herbivory drawing down the nutrient pool.

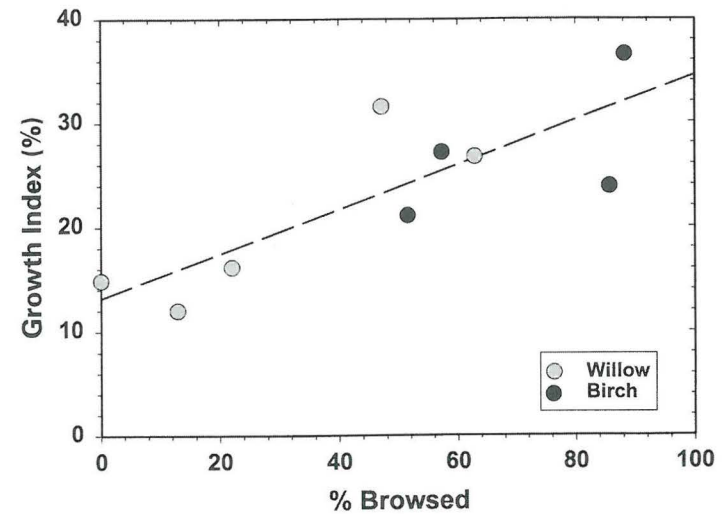


Figure 17.9 Relationship between shrub twig growth rate and the percent browsing in the previous winter for nine different sites in 1991, the year after the snowshoe hare peak.

17.5.5 Other Indirect Effects

Our indices of interaction effects are through changes in biomass over the whole trophic level. Gross biomass values necessarily obscure interactions between species in the same trophic level. In particular, our measures hide the effects of predators through apparent competition or alternative prey, these two processes having opposite results. In apparent competition (Holt 1977), a decrease in primary prey results in fewer predators and an increase in secondary prey. In the alternative prey scenario, a decrease in the main prey causes predators to switch to alternative prey and so cause a decrease in these species as well, though after a time lag.

In our study we have detected some of these indirect interactions. During the hare peak ground squirrel numbers increased (chapter 9), and during the hare decline ground squirrel numbers also declined. Thus, ground squirrels acted as alternative prey to hares. A similar sequence of events occurred with spruce grouse (chapter 11). These birds even reached peak numbers one year ahead of the hare cycle, suggesting that predators were focusing on the increasing hare population and so allowed grouse to reach high numbers.

Another type of indirect effect could arise from the increase in soil nutrients produced by the urine and feces of herbivores at high densities, a result sometimes detected in aquatic studies (Neill 1988). Our soil analyses on the food-addition experiments suggest a minor and nonsignificant increase in soil nutrients. The nitrogen values were low in both treatment and control areas, suggesting that the urine effect is minor relative to other impacts such as plant extraction on soil nutrients.

Exploitation competition is also an indirect effect. At the peak of the hare cycle, hares had little impact on their summer food plants (John and Turkington 1995), and so had little competitive effect on ground squirrels that often ate similar herbaceous species. Hares

had a much larger impact on their winter food supplies (chapter 6; Smith et al. 1988). Ground squirrels were absent in winter, moose were very scarce, and red squirrels ate different foods. The only possible competitor, therefore, was willow ptarmigan, a species that eats gray willow buds. The decline in willow ptarmigan during the hare peak could be interpreted as exploitation competition during winter, but it was more likely the result of increased predation (i.e., apparent competition).

17.5.6 *The Role of Secondary Chemicals*

Secondary compounds in plants that act as antifeedants appear to respond directly to the influence of browsing by hares. The heavier the browsing, the higher the values of crude methanol extract, our index of secondary plant compounds. Thus, regrowth in the following summer acts as a compensatory response to browsing, and elevated secondary compound levels provide an additional deterrent to further browsing. There is experimental evidence that such extracts inhibit both diet selection and digestive abilities (Sinclair et al. 1982, 1988, Rodgers and Sinclair 1997). This effect is most apparent in bog birch and less so in gray willow. Because birch is the preferred species of winter food for hares, chemical defense is perhaps of higher value to this plant. However, where browsing was extremely high, as in the predator enclosure + food-addition treatment, not only was regrowth depressed but also secondary compounds were inhibited. Thus, heavily stressed plants become more prone to browsing.

Fertilizer had the effect of reducing the secondary compounds in both species, although the effect was not great. Our results are consistent with hypotheses proposing that secondary compounds may function to protect nutrients that are hard for plants to obtain (Coley et al. 1985). Where nutrients are provided, there is less stimulus for the plants to produce secondary compounds to defend the nutrients.

17.5.7 *The Dominant Pathways in the Vertebrate Community*

The Kluane boreal forest community is composed of several species of raptors, carnivores, and mammalian herbivores. In addition, there are herbivorous birds such as grouse and many species of granivorous or insectivorous birds. The herbivores feed on a variety of herbaceous plants in summer and several woody shrubs and trees in winter. There are trophic connections among several components between trophic levels. Despite this set of complex interactions, we find that there are only a few strong interactions that dominate the system. In general, a suite of raptor and carnivore species feed on a single dominant herbivore, snowshoe hare. This species, in turn, inhibits the growth of their main winter food plants—namely, gray willow and bog birch—and they stunt the growth of young white spruce trees. Other herbivores (ground squirrels and grouse species) remain relatively scarce, apparently limited by predators whose numbers are determined by snowshoe hares. These predators treat the less abundant herbivore species as alternative prey. Hares appear to be a keystone species in this ecosystem, maintaining the diversity of predators and herbivores. Removal of hares or a major disruption of the hare cycle may cause a profound change in the whole community.

17.6 Conclusion

We conducted either removal or addition experiments on each trophic level of the boreal forest ecosystem at Kluane, Yukon. We measured the response of other levels in terms of biomass, productivity, and activity. The direct effects of the perturbations on the next trophic level are consistent with the pure reciprocal model. The two experiments that produced simultaneous bottom-up and top-down effects indicated that top-down effects were stronger. In contrast to direct effects, indirect effects, although detectable, were relatively weak at all levels. The experiments suggest, therefore, strong reciprocal direct effects and weak, highly attenuated interaction chain indirect effects at all trophic levels in the Kluane boreal forest ecosystem.

Other types of indirect effects between species at the same trophic level are suggested from results in other chapters. Herbivores such as ground squirrels and willow ptarmigan may be secondary prey for predators living primarily on hares. However, there is little evidence for exploitation competition.

17.7 Summary

We used an experiment in the boreal forest of Canada to test predictions of instantaneous changes to trophic levels and distinguish between competing models of trophic level interactions. Seven different perturbations systematically removed or supplemented trophic levels. The predictions resulting from the perturbations were concerned with the direction of change in biomass at the other levels. The direct effects of each perturbation produced strong top-down and bottom-up changes in biomass. At both the vegetation and herbivore levels, top-down effects were stronger than bottom-up, despite some compensatory growth stimulated by herbivory. The combination of experiments produced results consistent with two-way (reciprocal) interactions at each level (model 27; chapter 3). Indirect effects on one or two levels removed from the perturbation were either very weak or undetectable. Top-down effects were strong when direct but attenuated quickly. Bottom-up effects were less strong but persisted as indirect effects to higher levels. Other types of indirect effects between species at the same trophic level were suggested from results in other chapters. Herbivores such as ground squirrels and willow ptarmigan may be alternative prey for predators living primarily on hares. However, there is little evidence for exploitation competition.

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