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General Introduction

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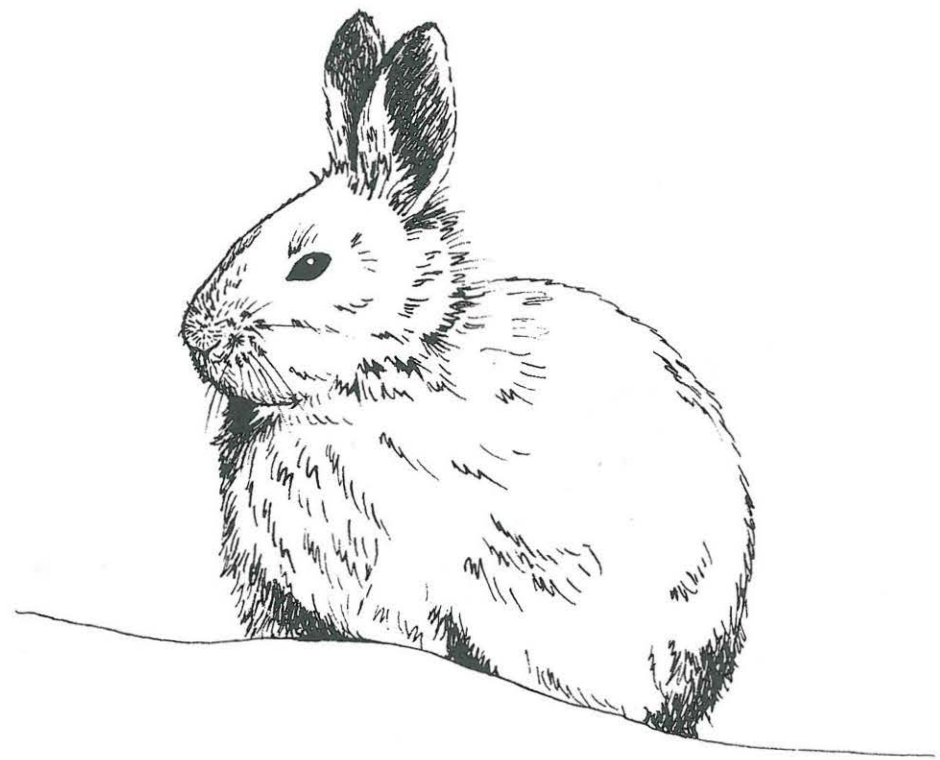

The boreal forest of North America stretches from Alaska to Newfoundland in an unbroken sweep of more than 5 million km^2. The boreal forest is remarkably uniform in overall appearance, dominated by coniferous trees, and an Alaskan feels quite at home in northern Manitoba or in eastern Quebec. But if you turn a botanist loose in the boreal forest, he or she will tell you that it is remarkably diverse in the dominant tree species, the shrubs, and the grasses and herbs of the forest floor. This botanical diversity is reflected in the various classifications of the subdivisions within the boreal forest, and the wide disagreement about what subdivisions to recognize (Rowe 1972, DEMR 1974, Bonnor 1985, Botkin and Simpson 1990). Figure 1.1 gives a general breakdown of the three main sub-

Figure 1.1 Three major subivisions of the North American boreal forest, as defined by the Canadian Forest Service, after Rowe (1972). The middle layer (lightest color) is predominantly boreal forest. The northern edge is a mixture of boreal forest and tundra and the southern edge is a mixture of boreal forest and grasslands. Kluane is part of the Western Mountains stratum of the boreal forest zone. See CD-ROM frame 6 for additional information. Figure modified after Rowe (1972).

divisions within the North American boreal forest and sets the geographical scale for this book.

We focus in this book on one particular part of the boreal forest, the Kluane sector of the Western Mountains region described by Rowe (1972) and Botkin and Simpson (1989). The Kluane region of the boreal forest differs from the surrounding regions in its relatively high elevation and in its location in the climatic rain shadow of the St. Elias Mountains. The white spruce is the only conifer in this area, and typical boreal forest trees such as black spruce, paper birch, lodgepole pine, and larch are absent at Kluane, although they occur within 200 km both northwest and southeast of Kluane. The relatively high elevation of the Kluane area (600–1100 m) is reflected in a colder climate and lower productivity than one finds farther north in central Alaska or in the southeastern Yukon.

In spite of the vegetation differences that occur across the broad expanse of the boreal forest in North America, the vertebrate community is remarkably constant. Among the large mammals, moose and mountain caribou are spread across the entire boreal region, and snowshoe hares and red squirrels predominate among the mid-sized vertebrates. Canada lynx, coyotes, wolves, red foxes, and wolverine are the main mammal predators. Red-backed voles and deer mice are typical small mammals, along with several less common vole and lemming species. Typical boreal forest birds also occur across this 7000-km stretch. Spruce grouse and ruffed grouse occupy the grouse niche, and the three most common songbirds at Kluane—the dark-eyed junco, the yellow-rumped warbler, and Swainson's thrush—are ubiquitous across the boreal forest. Great horned owls and northern goshawks, two common birds of prey at Kluane, are typical raptors across the entire North American boreal forest zone. Figure 1.2 shows the average biomass pyramids for herbivores and carnivores in the Kluane area. Snowshoe hares and the two squirrels are major herbivores, while lynx, coyotes, wolves, and great horned owls are major predators at Kluane. The relative importance of snowshoe hares in this community is shown even more graphically if we convert these biomass values to energy flow through the community. Figure 1.3 illustrates the average energy flow pyramid for the Kluane community.

If the vertebrate community is so similar across this great expanse of boreal forest, there is a good chance that the ecology of this community is governed by a set of general rules common to the Yukon, Quebec, and Alaska. We start with this large assumption. The major objective of the Kluane Project was to study the organization of the vertebrate community in the Kluane region of the Yukon. To do this, we needed to know the abundance of all the major species, their food habits, and how these change over time. The native people of the boreal region have long known about one of the dominant changes in the boreal forest—the 10-year cycle of snowshoe hares and their predators. By focusing our studies on the entire vertebrate assemblage, we hoped to achieve a better understanding of how the cycles of snowshoe hares are controlled and how other vertebrates are affected by the hare cycle. Are red squirrels affected when snowshoe hare numbers decline, or, conversely, are snowshoe hares affected when red squirrels are abundant? How do predators respond to a collapse of their major food source?

In studying community organization, the critical question we need to answer is *what would be the effect of removing a particular species from the community?* If red squirrels were to disappear in the Kluane region because of some disease, for example, what would happen to the other species in this community? If lynx were removed by excessive fur harvests, what would be the effects on other predators and on prey species in this system?

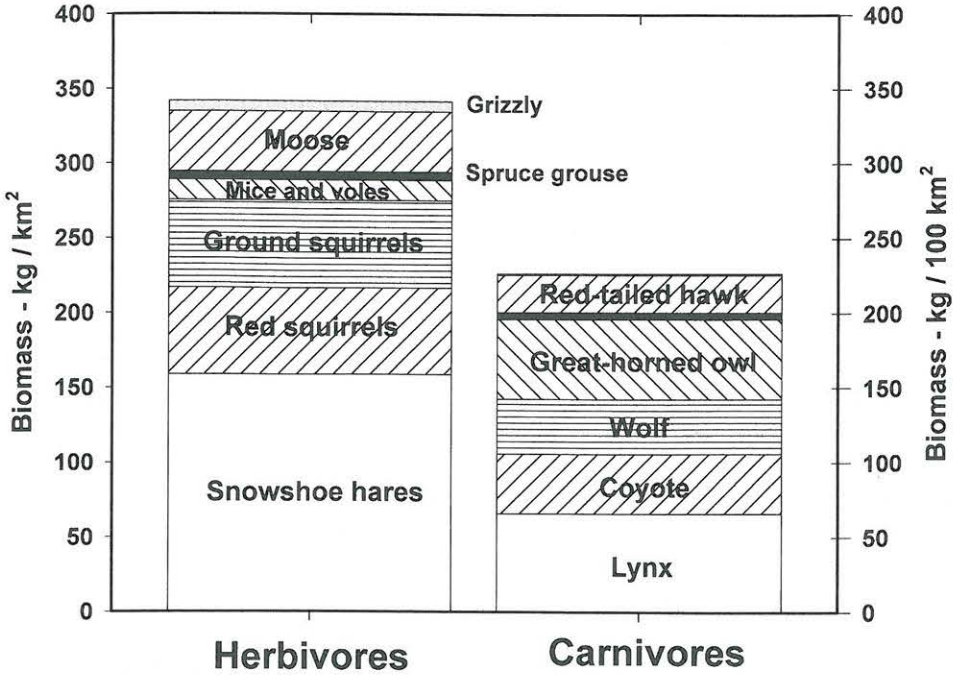

Figure 1.2 Biomass pyramids for herbivore and carnivore species in the Kluane ecosystem. Average values are given for 1987–1995. The herbivore scale is to the left and the carnivore scale to the right. The black bar above the great horned owl is the northern goshawk. The ratio of prey to predators in this ecosystem averages about 150:1. The grizzly bear, an omnivore, is in the herbivore pyramid because the bulk of its diet is herbaceous.

These are complex questions, and ecologists are only now beginning to get some tentative answers for particular ecosystems. If humans were having no impacts on natural communities, such questions about community organization would be of academic interest only. But as human disturbances widen through forestry, agriculture, and tourism, these questions become relevant for conservation, fisheries, and wildlife management.

How can we ecologists study community organization? As the first step, we can describe the food web of the community: who eats whom? This is more difficult than most people imagine because the diets of most vertebrates include many different species and change from winter to summer. There are always problems with diet analysis, but we can approximate the major items in the diet, and some minor items are missed. The second step is to estimate the consumption of each species in the food web by combining the diet information with abundance data. How many snowshoe hares does a lynx eat per day, and how many lynx occupy the study area? How much grass does an arctic ground squirrel eat per day, and how much grass is produced each summer? Once we know all these consumption rates, we should be able to put together an arithmetic balance sheet for the whole community. This simple task has rarely been achieved for any terrestrial vertebrate community. As the third and last step, we can experimentally disturb the system and observe its response. The kinds of experiments we could do on a finite budget in this system are limited to four types of manipulations:

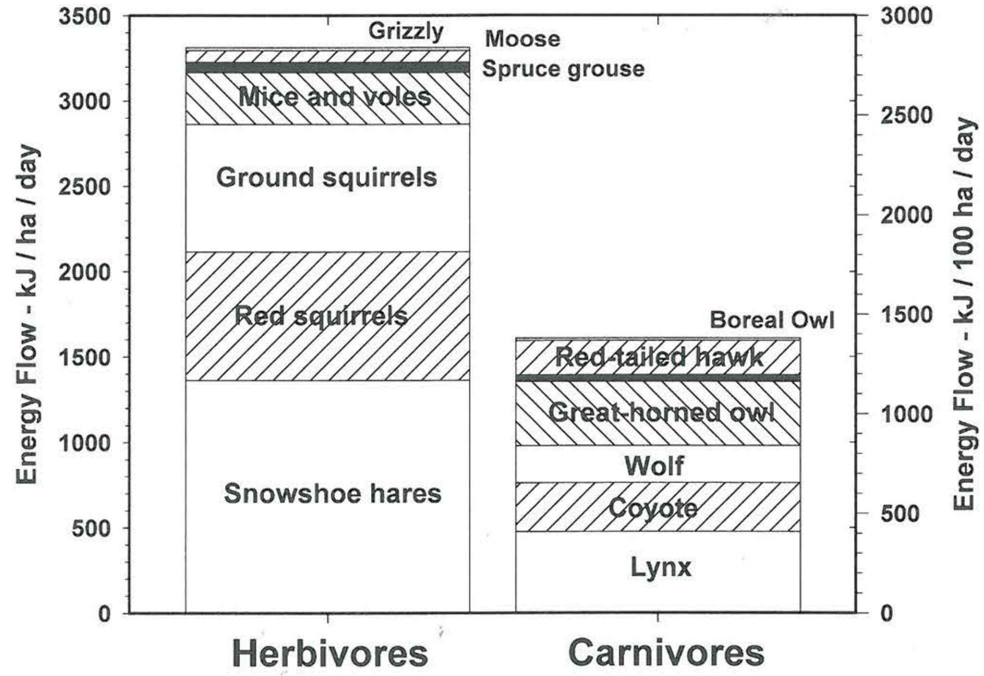

Figure 1.3 Energy pyramids for herbivore and carnivore species in the Kluane ecosystem. Average biomass values were converted to field metabolic energy equivalents with the equations given in Nagy (1987). Average values are given for 1987–1995. The herbivore scale is to the left and the carnivore scale to the right. The black bar above the great horned owl is the northern goshawk.

1. We can add nutrients as fertilizer to change plant production.
2. We can eliminate mammal predators from specific areas by fences and measure the impact of predator elimination on prey populations.
3. We can add supplemental food to the herbivores and measure their responses to enhanced food supplies.
4. We can exclude herbivores from areas and see what happens to vegetation when there is no browsing.

The principle is simple: if you think a community is structured by predation, for example, then you should manipulate predation levels and see what happens to the prey populations. There are two caveats, however, to this simple advice. First, you must do these manipulations on a large enough spatial scale. For most communities we can only guess what scale is large enough. Most ecologists agree that we have not, in general, manipulated large enough areas. In this study we manipulated 1-km^2 blocks of boreal forest, among the largest areas ever manipulated in a terrestrial ecological experiment. Second, the effects of any experiment need time to develop, and ecologists, like all people, are impatient. We have carried out our experiments for 10 years and can address ecological changes on this time scale. For some manipulations, such as logging in the boreal forest, 10 years may not be long enough to see the important impacts. Since most ecological experiments are carried out at the time scale of months to 3 years, our 10-year experiments have extended the range of manipulations in time for this boreal forest community.

In this book we describe the Kluane Boreal Forest Ecosystem Project, which operated from 1986 to 1996 in the southwestern Yukon. We begin by describing the area and its physical setting and then describe the background of the project and the wisdom that had accumulated to 1986 on how this system might operate. The details of the experiments we set up are presented, partly to help the reader appreciate the difficulty of working at −40° and partly to help those contemplating doing similar experiments in the future. Then we examine the three trophic levels of the plants, the herbivores, and the predators in detail to provide some surprises about how the individual species operate within the overall system. Finally, we synthesize these findings in a model of the boreal forest vertebrate community and provide an overview of what we have discovered and what remains to be done. Over the 10 years of this project, nine faculty members from three Canadian universities and 26 graduate students joined with 75 summer assistants and 18 technicians to expend 157 person-years of effort to produce the picture developed here. No one ever thought that ecology was a simple subject like chemistry, but when we began this project we hoped to join forces to make a major advance in our understanding of the boreal forest ecosystem. This book presents our discoveries.

Literature Cited

Bonnor, G. M. 1985. Inventory of forest biomass in Canada. Canadian Forest Service, Petawawa National Forestry Institute, Petawawa, Ontario.

Botkin, D. B., and L. G. Simpson. 1989. The distribution of biomass in the North American boreal forest. *in* Proceedings of the International Conference and Workshop. Global Natural Resource Monitoring and Assessments, Preparing for the 21st century, pages 1036–1045. American Society of Photogrammetry and Remote Sensing, Bethesda, Maryland.

Botkin, D. B., and L. G. Simpson. 1990. Biomass of the North American boreal forest. Biogeochemistry **9:**161–174.

DEMR. 1974. National Atlas of Canada. Department of Energy, Mines and Resources. Ottawa, Ontario.

Nagy, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. Ecological Monographs **57:**111–128.

Rowe, J. S. 1972. Forest regions of Canada. Canadian Forest Service Publication no. 1300, Ottawa, Ontario.