
Experimental Design and Practical Problems of Implementation

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In this chapter we summarize the experimental design and explore the reasons for particular choices among competing designs. For any given experimental design, the difficulty is in the details of implementing the design, and here we present the practical issues we faced. Part of this discussion may be useful to anyone contemplating a long-term, multidisciplinary ecological field study, but the thrust of this chapter is to discuss the experiments we did at Kluane Lake from 1986 to 1996, why we did them, and how.

4.1 Experimental Design

The experimental design is the Achilles heel of all field ecological research, and it always involves compromise because many ecological factors can impinge on any population or community and one cannot study all of them. Three choices dictate the experimental design. One must first decide on the treatments to be studied. Given the treatments, decisions about the size of the treatment unit and the spatial interspersal of the treatments are next. And finally, one must decide on the level of replication of the treatments. All of these issues have been discussed extensively in the statistical literature (e.g., Fisher 1966, Sokal and Rohlf 1995), and we apply these general statistical principles to the particular question of understanding how the boreal forest community functions.

4.1.1 Choice of Treatments

To understand how a community is structured and how it functions, a food web must be constructed (see figure 2.8). Two choices then must be made. Over a series of years a detailed description of the linkages in the food web could be constructed in the hope that natural variation will be large enough to infer the structure behind the linkages. In the boreal forest, the 10-year cycle of snowshoe hares is a well-known natural perturbation, and consequently this strategy could be used with some effect. Alternatively, you can perturb the system to see how it responds to the manipulations. The history of ecology is littered with decisions of this critical juncture, and it is abundantly clear that the second strategy maximizes our rate of progress toward understanding how communities work (Paine 1984, Krebs 1991, Menge 1995). We note that it is possible to balance these two strategies because it is critical to have a good description of what happens on control areas as well as on the manipulated sites.

In theory any of a wide variety of community variables can be manipulated, and it is not immediately clear what is best for achieving understanding. Most ecologists gravitate toward food supply and predation as two key resources in community organization, and these are the two main variables we chose to manipulate. But we could have manipulated parasites or diseases, temperature or precipitation, soil chemistry, or fire. The crux of this decision is the empirical test: how much understanding can we achieve with the choice of a few variables? At the end of this book we return to this question, but in principle ecology will progress by natural selection favoring those kinds of manipulations that increase our understanding and rejecting those kinds that shed little light on how a community is organized.

If one chooses to manipulate food supplies and predation levels, there is still the decision whether to direct treatments toward the entire trophic level or to concentrate on the

keystone species, which in the boreal forest is the snowshoe hare. In principle for the reasons discussed in chapter 3, it is best to manipulate on a broad scale and direct treatments toward the entire trophic level. It is practical in a vertebrate community to manipulate the plant and the herbivore trophic levels, but there are severe limitations on how much vertebrate predators can be manipulated. In theory trophic levels can be manipulated up or down, but, again, practical constraints intervene to direct manipulations at increasing plants and herbivores and decreasing predators. One could ask how herbivores would respond to cutting their food resources in half, and this may be an interesting experiment but impossible to actually do in the boreal forest. Similarly, one could ask how herbivores would respond to a doubling of their predators, but this would be technically a most difficult experiment to carry out. Because great horned owls occupy territories covering all of the forest every year (see chapter 15), releasing owls into this ecosystem would not add to the predator population. We were constrained by these kinds of considerations to increasing food resources and reducing predator impacts in this ecosystem.

We selected food addition based on our previous experience that this treatment increased snowshoe hare densities two- to three-fold (Sinclair et al. 1988, Smith et al. 1988). Consequently, this manipulation was chosen as the mechanism of increasing the size of the herbivore trophic level. This was the natural complement to the fertilization and predator exclusion experiments, which manipulated the plant and the predator trophic levels. We knew when we began in 1986 that rabbit chow was eaten readily by ground squirrels, gray jays, moose, and grizzly bears but was eaten less by voles, mice, and red squirrels, who respond more to seeds (Gilbert and Krebs 1981, Boutin 1990, Klenner and Krebs 1991, Schweiger and Boutin 1995). Because we were constrained financially from adding both rabbit chow and seeds to areas, we chose to add rabbit chow only, knowing that it may not supplement the food resources of all the herbivores equally. Consequently, the first major manipulation was to add commercial rabbit chow year-round to selected field sites.

We knew less about how to increase the food resources to the plants. Adding fertilizer is the chosen mechanism in all of modern agriculture and intensive forestry, but the consequences of fertilization on all the component species of the boreal forest was not known when we began this study. We searched the literature and found that, although many forest fertilization experiments had been carried out, no one had looked at the entire plant community because trees were the usual target object. We chose a standard agricultural NPK fertilizer with the ratio 35:10:5 and with nitrogen in the form of ammonium nitrate. We chose a level of 17.5 g nitrogen/m² as a target level of addition from Alaskan studies on the response of trees to this level of nutrient addition (Haag 1974, Shaver and Chapin 1980, Van Cleve and Oliver 1982). In chapter 5 we explore on a small scale the impact of fertilization over a broad range of levels. Fortunately, our choice of level was nearly optimal for many species of plants in this part of the boreal forest.

Vertebrate predators such as lynx operate on a large spatial scale, and the only feasible manipulation is to reduce their numbers on target areas. There are two ways to do this. Either predators can be removed continuously from the target area or they can be prevented from entering with some type of barrier. We rejected the predator removal option, partly for aesthetic and conservation reasons (we did these studies at the edge of Kluane National Park) and partly because the logistics are more difficult than one might presume (not all animals enter traps, etc.). By creating a sink by predator removal, we would also face the possibility of continuous immigration of surplus predators from surrounding areas, po-

tentially altering control populations. Predator exclosures are a better design. We discovered a new type of electric fencing made by Gallagher Fencing of New Zealand in 1986, and decided to attempt to fence mammalian predators out of target areas. In principle this was simple, and in the end it worked very well. The details of the problems we ran into are described in the next section.

Avian predators were more difficult to exclude, and a mechanical barrier was the only option available. We were unable to construct an effective barrier against birds of prey, for detailed reasons given below, and this was our largest failure to achieve the original experimental design. Consequently, we were unable to reduce avian predation rates on any of the target areas, and the predator exclusion areas must only be considered as mammalian predator exclusion areas.

We carried out a fourth large-scale experiment designed to examine the potential interaction between food and predation. We combined rabbit chow addition and electric fencing on one area. This experiment does not fit directly into the community trophic-level approach to the Kluane project, but it was pivotal to furthering our understanding of the snowshoe hare cycle. We had many hours of discussion about whether we should replicate the predator exclusion experiment or do this interactive experiment with reduced mammalian predation and increased food resources for herbivores.

Finally, we wanted to know what would happen to the vegetation of the boreal forest if the dominant herbivores, snowshoe hares, were excluded from an area. We constructed two hare exclosures, each 4 ha, to provide a small area with reduced browsing and grazing pressure. By eliminating hares from the area, we also had to eliminate moose browsing, but this was not a problem in general because moose were relatively rare in our system (see 2.6).

In addition to these imposed perturbations, we studied a system with large natural perturbations. For example, spruce seed crops vary over several orders of magnitude among years, and we had no control over when these occurred. Berry crops in the boreal forest vary dramatically from year to year. And, of course, there was the snowshoe hare cycle. These natural perturbations would propagate through our experimental perturbations and give us additional understanding of how the boreal forest community operates.

In summary, we had four available treatments designed to kick each trophic level: add supplemental food, eliminate mammalian predation, add nutrients as fertilizer, and exclude hare browsing. In addition to these experimental treatments, natural variations in cone crops, berry crops, and snowshoe hare abundance could impact populations under study.

4.1.2 Size and Spatial Location of Treatments

We have so far discussed the treatments imposed on target sites but have not discussed the size of the areas used and their spatial interspersal. Our choice was to make the experimental unit a 1-km² block of forest. We did this for two reasons, one ecological and one logistical. Most ecological manipulations have been done on small spatial scales, typically a few square meters (Tilman 1989). We wanted to increase the scale of manipulation closer to a landscape level. We also wanted to manipulate areas that had a large enough population of the main herbivores that we could detect significant changes in their populations. From previous experience we knew that herbivores were affected by experimen-

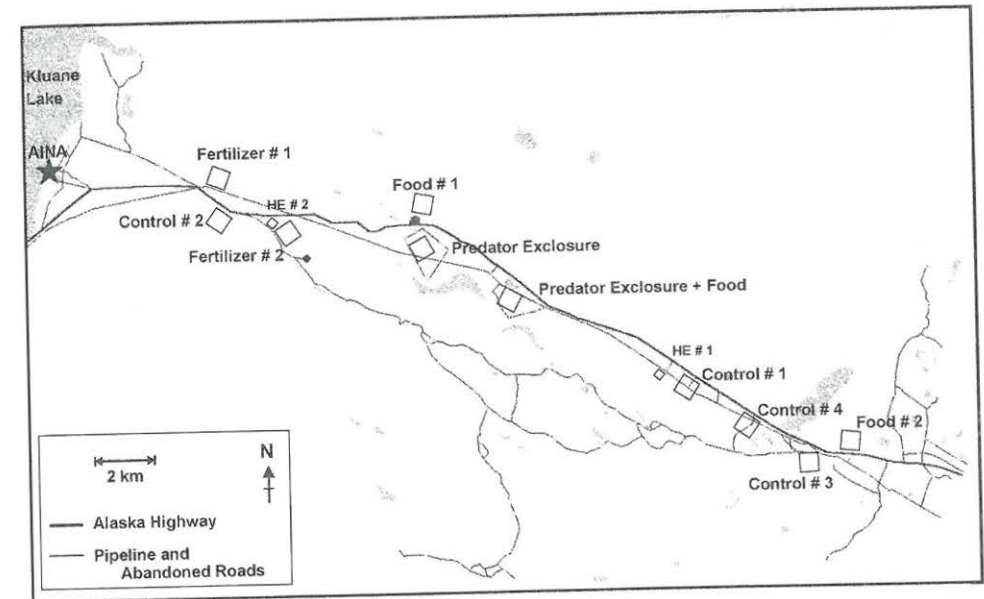


Figure 4.1 Map of the study area for the Kluane Boreal Forest Ecosystem Project. The Arctic Institute of North America Kluane Research Station is at the left edge of the map, on the shores of Kluane Lake.

tal treatments well beyond the boundaries of a trapping grid. We decided for hares that a 35-ha trapping area was a reasonable size for population estimates, and this grid size effectively trapped hares over a 60-ha area. We focused on snowshoe hares, arctic ground squirrels, and red squirrels and calculated that, on 1 km², populations would be sufficiently large that we could detect effects of $\pm 20\%$ change in the herbivore trophic level. This scale is a herbivore scale. Plant experiments can clearly be done at a smaller scale (chapter 5). Direct manipulation of predator numbers would require much larger areas and is currently impossible with a limited budget.

The spatial location of the treatments and their control areas was a compromise of interspersal of treatments and controls (as recommended by Hurlbert 1984) and the problem of access. Figure 4.1 shows the study area in the Shakwak Trench just southeast of Kluane Lake. Road access in this area is limited by the Alaska Highway, which transects the valley and sections of the old Alaska Highway as it was upgraded since World War II. Our decisions on the spatial locations of the treatments followed these four rules:

1. All 1-km² blocks must be predominantly open-spruce or closed spruce forest.
2. Every experimental unit must be at least 1 km from the nearest unit.
3. Fertilization plots must be close to the airstrip at the Arctic Institute Base to facilitate aerial fertilization.
4. Vehicle access must be feasible within at least 500 m of the area.

Most of these decisions are self-explanatory. The 1-km spacing rule arose from previous studies which suggested that snowshoe hares almost never moved as far as 1 km. This assumption has turned out to be wrong (see chapter 8), but it is true that few individuals

move as far as 1 km. The greatest restriction on randomization was the necessity to put the fertilizer addition areas close to the only available airstrip (see figure 4.1).

We made other operational decisions that were not random. We separated the three areas that had food addition by at least 4 km so that individual predators would not have more than one of these areas within their home range. We had four control areas scattered throughout the valley. In the final analysis we used nearly all the habitat along the 30-km segment of the Alaska Highway that had suitable forest cover.

4.1.3 To Replicate or Not to Replicate

Given the treatments and the size of the experimental units, our final decision was how much replication to include in the project. We faced the classical statistical dilemma of whether to study many small areas or a few large units. Having decided to use large land units, we were forced by logistics to minimize replication. We began by replicating the control areas four times because we wanted a good description of what was occurring throughout the valley. We replicated the nutrient addition and the food supplementation treatments twice because this was the maximum we could afford to do on our budget. We could not replicate the predator exclusion areas (electric fences) for logistic reasons detailed below. We could not afford to build or keep up more than one electric fence per treatment. This is the Achilles heel of our study: we have only one replicate of the mammalian predator exclusion treatment and one replicate of the predator exclusion + supplemental food treatment (figure 4.1). Table 4.1 summarizes the treatments applied and the number of replicates of each.

Our defense for low replication is simply that we could not do more than this. This is a common problem for all large-scale ecological experiments (Carpenter et al. 1995). The reason for doing large-scale experiments is often to see how large of an effect is produced by a treatment. Interesting effects can then be searched more thoroughly in follow-up experiments. There is a series of statistical procedures that can be used to test for changes in time-series data. Randomized intervention analysis is one of the key methods that can be used (Carpenter et al. 1989). One key to interpreting the results of unreplicated experi-

ments is the amount of variation observed among replicated control populations, but a more important factor is the level of understanding of the natural history of the system under study. Terrestrial vertebrate communities are among the best known in the world for the linkages among the elements in the food web. We think this is more important for the understanding of our experiments than statistical *p*-values (Yoccoz 1990). For statistical purposes it is possible to generate *p*-values by assuming that the variance among controls would also apply to the variance among replicates of the fencing treatments, if we had been able to replicate these.

We were also encouraged by our earlier studies of this boreal forest community (Krebs et al. 1986, Sinclair et al. 1988, Smith et al. 1988), which showed great uniformity among snowshoe hare populations on study areas spaced >100 km apart in the Kluane region. This reflects the general synchrony that occurs in the hare cycle throughout western Canada and Alaska.

4.2 Practical Problems of Implementation

We discuss here some of the practical difficulties we had to overcome to get our treatments to work effectively in the Yukon boreal forest. These details illustrate the problems of trying to do large-scale field manipulations.

4.2.1 The Evolution of a Predator-proof Fence

High-tensile electric fencing was developed in New Zealand for deer farming, and when we began this study we assumed it would be highly effective against mammalian predators. The fence was energized by batteries with 8600 volts pulsed at 4 msec at 1-sec intervals. We began with a 1.8-m tall design with alternating positive and negative wires spaced at 25 cm. The first fence was built in the summer of 1987 at a site called Beaver Pond that had been trapped for hares during the 1976–1985 study. The construction was spearheaded by Tony Sinclair and a large crew of undergraduates and technicians and was completed by late August 1987. Fortunately, this was just after the low of the hare cycle, so predator numbers were minimal. During the winter of 1987–1988, we could snow track predators as they approached the electric fence. We found to our dismay that two lynx, one red fox, and one wolverine walked right through the fence while it was fully operating. Two problems had clearly arisen that we had not anticipated. First, the winter fur of these mammals seemed to insulate them from electric shock. Second, snow is a poor conductor of electricity, so when they did make contact with a live wire there was no ground to pass the current. Fortunately, the predators that moved into the fenced area left almost immediately.

We had a second problem in the winter of 1987–1988 because heavy snowfalls and drifting, along with some icing, shorted out the lower wires of the fence. We found we had to dig out the largest snowdrifts and developed a method of turning off the lower wires of the fence as they became snow covered. We also found we needed to add height to the fence to prevent animals from jumping over it when snow depth was greatest.

In the summer of 1988 we built a second electric fence to use for the predator exclusion + food addition treatment at a site called Hungry Lake. One side of this fence ran along an unused pipeline clearing, which facilitated construction. This fence was built to

Table 4.1 Experimental treatments used in the Kluane Boreal Forest Ecosystem Project, 1986–1996.

Treatment	No. of Replicates	Details
Food supplementation	2	Commercial rabbit chow, year-round ad lib, spread over 35-ha area
Mammalian predator exclusion	1	Electric fence, unable to effectively exclude birds of prey
Predator exclusion + food	1	Electric fence around 1 km ² and rabbit chow ad lib spread over central 35-ha area
Nutrient addition	2	NPK fertilizer added in spring
Hare enclosure	1	4-ha enclosure, moose also excluded
Hare enclosure + nutrient addition	1	4-ha enclosure in fertilizer 2 area

All experimental areas are 1 km² except as noted.

a new standard of 2.3 m height, and we added more wires to reduce the chances of animals squeezing between them.

Nevertheless, we found in autumn 1988, when the snow returned, that lynx were still walking through the electric fences. By this time hare numbers were increasing rapidly, along with predator numbers, so we faced an emergency situation. Stan Boutin developed a new design of fence by adding 5-cm chicken wire to the inside of the electric fence to serve both as a barrier but more importantly as a ground wire. We first put chicken wire up to 1 m height but then added it to 2 m height to cover deep snow years (figure 4.2). To prevent lynx from climbing over and coyotes from digging under the fence, we placed live wires 20 cm from the chicken wire at ground level, at 1 m, and at 2 m. Once the lower wires were covered by snow in winter, they were turned off. The chicken wire posed one further problem. The holes were not large enough to allow anything except voles to move freely through it. We did not want to confound our experiment with the "fence effect" (Krebs et al. 1969, Ostfeld 1994), so we cut holes in the wire large enough for hares to pass through (CD-ROM frames 62–64). The chicken-wire solution worked well and the problem was largely solved because once lynx received an electric shock, they learned immediately to avoid the fence and the predator-exclusion experiments were effective. The electric fences were completely effective by December 1988. Although the electric fences protected hares inside the fence from mammalian predators, hares could move through the fence, and this caused some problems with lynx in particular hunting hares along the fence and catching hares that moved outside of the electric fence.

We had originally intended to eliminate avian predation on a small subset (10 ha) of the predator enclosure. We began in summer 1987 to set out a physical barrier by stringing old gill nets in the trees of the target area (CD-ROM frame 65). Because so much gill netting is damaged each year in the Pacific salmon fishery, there was an unlimited supply of netting that could be had for nearly no cost. The work of stringing it in the spruce forest was formidable, and many students labored mightily to cover a few hectares with netting. To our dismay, it all collapsed under the weight of snow and hoarfrost in the first winter, 1987–1988. Our next attempt in 1988 was to replace the netting with monofilament fishing line strung out in parallel lines about 45 cm apart. We used both steel-reinforced and standard monofilament line and again found that over the winter hoarfrost built up on the lines and caused them to sag or break. We covered about 10 ha with fishing line on one site (predator enclosure treatment), but in spite of all the effort, we judged these mechanical barriers to be relatively ineffective in preventing avian predation on herbivores. Even where the netting or monofilament remained intact, we found that goshawks could walk under the net to kill hares and squirrels. Some reduction in predation occurred under the monofilament for ground squirrels (see chapter 9). We do not know of any simple way to keep avian predators out of large areas of forest and, in spite of much effort, we failed to manipulate this guild of predators in the way we had planned.

Moose were one problem that continually plagued the electric fence. Periodically, about every month or two, a moose would walk through the electric fence. We checked the fences every day to make sure they were operating correctly, so we would immediately find the breakage and repair it. Clearly the moose would receive a shock in doing this, because once inside, they would often not go near the electric fence to attempt to leave. The evolutionary history of moose had not preadapted them to understanding electric fences, and this problem was an intermittent headache of maintenance. The timing of

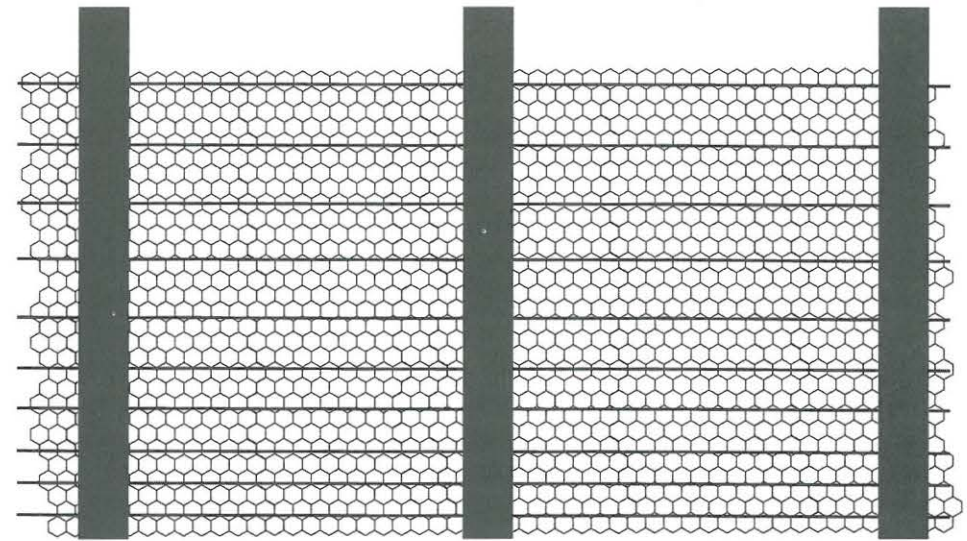


Figure 4.2 Schematic illustration of the electric fence for the mammalian predator enclosure experiments. The 2.2-m fence was lined with chicken wire, which acted as a ground for predators challenging the fence. Holes in the chicken wire would permit hares to come and go from the fenced area but were too small for predators to use. Two such fences were built around 1-km² forest blocks.

the moose entering the fence seemed impeccable. The Kluane Project was funded by the Natural Sciences and Engineering Research Council of Canada, and, as part of the review process, a committee visited our field sites in the summer of 1989. There was considerable skepticism among the committee that we could carry out these large-scale experiments, so of course we were concerned that everything was in working order. Frank Doyle did one last check of the fences on the morning of the review, and all was in order. The review committee was led to the fence, and Stan Boutin suggested that they might wish to test the fence themselves. The normal way to do this was with a voltmeter, but a simple test was to hold a piece of grass and slide it along the wire until one could feel the tingle of the electrical pulse. No one took Stan up on this offer, which was fortunate because the fence was completely dead. Not more than 100 m from where the group stood, a moose had just walked through the fence and shorted the wires. Fortunately, Jamie Smith saved the day by leading the group off to look at an interesting bird he had sighted. After the committee recommended that the project be continued, word of this episode leaked back to Jack Millar, the committee chairman, who claimed that the committee knew about the calamity all along! We owe a lot to the support of the members of the original review committee—Jack Millar, Lloyd Keith, and Dan Keppie—who showed foresight in giving us the chance to do this work.

A second problem with the electric fence was trees falling across it during storms. This occurred several times a year during the first 2 years, and again we would recognize the problem because the fence would short out.

Overall, the electric fences worked remarkably well once we overcame the initial problems, with only a few predators gaining temporary access. We had not, however, antici-

pated the amount of work involved in fence maintenance, which was a nearly full-time job in winter. Batteries for the fences had to be changed every 3 days in winter. Solar-powered electrical chargers are not an option in the Yukon winter. These maintenance costs, in addition to the high costs of the fencing itself, prevented us from building replicate fences for these two treatments in 1989.

4.2.2 Food Supplementation

Providing commercial rabbit chow ad libitum to three treatment areas also turned out not to be a simple job (CD-ROM frames 58–60). The problem arose because grizzly bears and moose also love to eat rabbit chow, and, while we did not mind feeding a moose or two, we did not want to conduct a grizzly feeding experiment. We carried out a feeding experiment from 1976–1984 (Smith et al. 1988) using commercial pheasant feeders and fed only in the winter when bears were hibernating. These simple feeders were attacked and destroyed on occasion by moose and bears, so that when we began this study we decided we needed a better method of feeding. One way to keep moose away is to build a corral or fence, and this works well when the fence is strong, but it will not deter bears. We decided to use old 45-gallon oil drums for feeders and to cable these to spruce trees so they could not be moved. Grizzly bears simply destroyed these drums and ripped them off the trees to get at the chow.

Rudy Boonstra suggested the next prototype, the use of road culverts. We used heavy steel road culverts 30 cm diameter and 4–5 m long and placed the rabbit chow in the middle of the culvert. Hares and squirrels could enter and leave easily to get access to the chow, but bears and moose could not. Again, we underestimated grizzly bears. They simply destroyed these culverts or turned them on end to gain access to the chow. We could find no way of rigidly fixing them to the ground so that bears could not rip them up, so we had to abandon culverts in the summer of 1987.

Finally, Stan Boutin, in what is probably the best practical use of optimal foraging theory, recognized that the solution was to broadcast feed. We began in 1988 to spread rabbit chow on four trails transecting the feeding grids (figure 4.3). Chow was spread in summer by a mechanical fertilizer spreader pulled on the back of an all-terrain vehicle (ATV), and in winter by snowmobile. The mechanical spreader sprayed chow over a strip of 4–5 m wide with an average of 2 pellets/10 cm² (or 25 g/m²). Because the chow was spread out and not concentrated, bears and moose were more reluctant to take the time to feed on such small and dispersed items. We still had visits from both bears and moose on the two open feeding grids, but the threat of attack was considerably reduced. About once a summer a bear would tree one of our workers on the food areas, and the most difficult time occurred in 1995, when a particularly aggressive grizzly kept workers off food 1 grid for 4 weeks. On the Predator exclosure + food addition area, there were no problems feeding because bears and moose were typically kept out by the electric fence. From 1990 onward we also spread chow by hand under trees to prevent avian predators from attacking hares feeding along the snowmobile trails in the open in winter.

The frequency of feeding was partly determined by hare numbers and the rate of disappearance of chow, with some constraints from weather. In general we fed every 3–4 days when hare numbers were high and once a week when numbers were low. The amount

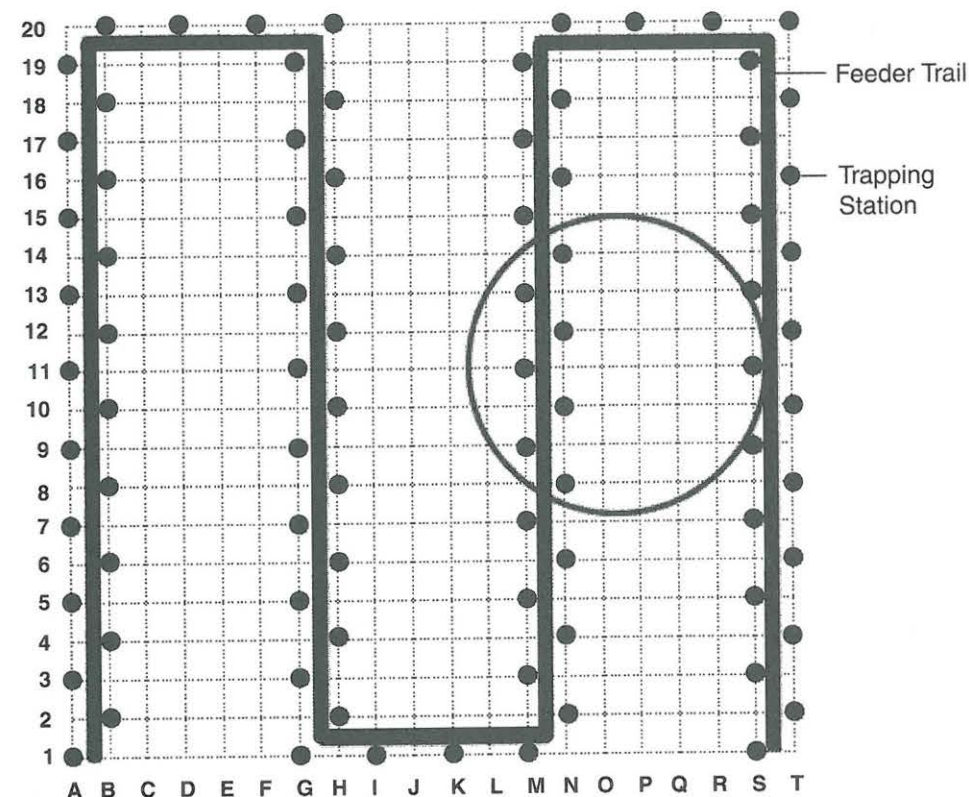


Figure 4.3 Schematic illustration of the method of adding supplemental food to treatment areas. A snowshoe hare trapping grid (20 × 20 stakes) was provided with supplemental rabbit chow in four strips as illustrated. A fertilizer spreader in summer spread the chow over a 4-m strip up and down these rows, and a snowmobile was used during winter. Food was added as the supplies on the ground became exhausted, and consequently frequency of feeding was affected both by hare density levels and by the weather. Three such areas were provided with rabbit chow from 1987 to 1995. The large circle shows a typical snowshoe hare home range of 5 ha to illustrate that all hares would have access to a feeder row.

of feed was adjusted largely by the frequency of feeding rather than by the amount spread per unit area. Table 4.2 gives the amount of rabbit chow put out during this study.

The feeding treatments were highly successful with only minor problems once we determined how to spread the feed. None of the animals using the feed relied entirely on chow for their food supplies, so this food addition must be thought of as a supplementation. The food experiments, as we discuss in later chapters, were specifically designed to supplement the herbivore trophic level by increasing it independently of the plant trophic level. Snowshoe hares in particular feed extensively on woody plants in winter and herbs in summer in addition to the rabbit chow we added, so that natural food plants are impacted by the treatment of supplementing with chow.

Table 4.2 Amount of rabbit chow supplied to the food addition grids throughout the study.

Time Period	Food 1 Grid	Food 2 Grid	Fence + Food Grid
Winter 1988–89	3160	2320	2240
Summer 1989	2240	1960	4600
Winter 1989–90	3800	4400	4080
Summer 1990	3380	3620	5120
Winter 1990–91	3220	4260	4920
Summer 1991	4500	5280	5620
Winter 1991–92	2640	4100	5760
Summer 1992	1680	2080	4880
Winter 1992–93	1160	780	3120
Summer 1993	1140	1160	3620
Winter 1993–94	1360	1240	1900
Summer 1994	2400	2380	5840
Winter 1994–95	1280	1520	2240
Summer 1995	3600	3720	8040
Winter 1995–96	3080	3580	1440

Units are kilograms delivered for each 6-month period.

4.2.3 Fertilizer

In 1985 we conducted a pilot fertilizer experiment. With the help of Scott Gilbert, we fertilized a 5-ha area at the center of fertilizer 2 grid by hauling fertilizer by hand and spreading it by hand from buckets. This experience taught us that we needed to mechanize fertilization and that we needed to cover a large area. Susan Hannon planned the fertilizer treatments by canvassing the leading boreal forestry specialists and reviewing the literature. She quickly found that the boreal forest was believed to be nitrogen limited, but recognized that we did not know if phosphorous and potassium might also be limiting. We elected to put out commercial NPK fertilizer to cover the possibility of phosphorous and potassium being in short supply.

In 1987 we began to add nutrients to the soil and thus to the vegetation of two 1-km² blocks of boreal forest by means of aerial fertilization. Given that we wished to put out NPK fertilizer (35:10:5) at 17.5g N/m² on 100 ha, we needed to distribute 55 metric tons of fertilizer to each of the two areas at the start of the growing season. Fertilizer was brought by truck to the airstrip at the Kluane Research Station, and at the end of May each year a commercial agricultural aircraft from Alberta came north to spread the fertilizer (CD-ROM frames 53 and 54). In 1988 we put out a series of test plots to measure the uniformity of fertilizer fall on the ground and were convinced that the pilots were doing a very good delivery job. The growth stimulus to the plants, particularly the grasses (see chapter 5) was so strong that one could visually inspect the areas fertilized to see the uniformity of the vegetation response.

Aside from the amount of work involved, the aerial fertilization was carried out without any significant problems. Because of budget restrictions, we had to reduce the fertilizer amount by half in 1989. In 1987, we used only nitrogen fertilizer at 25 g/m² ammo-

nium nitrate, but in all the other years from 1988 through 1994 we used the full amount of NPK fertilizer. We stopped aerial fertilization after the 1994 treatment.

The only significant problem we had with the fertilizer treatments was with horses on fertilizer 1. A local Kluane outfitter let his horses free-range for 10 months of the year from 1987 to 1990, and they concentrated their grazing on the enhanced plant growth of the fertilizer 1 area. About 15 horses were involved and the result is that net productivity of grasses and herbs was reduced on this area in those years. In 1990 new restrictions were placed on free-range horses, and they were moved to another location. Fertilizer 2 area was never affected by this problem.

4.2.4 Hare Exclosures

In 1988 Rudy Boonstra recognized the need for areas without hare browsing, and consequently we built two hare exclosures, one within fertilizer 2 area and one in open spruce forest just to the north of control 1 (figure 4.1; CD-ROM frame 56). We constructed these exclosures of 5-cm plastic-mesh construction-type fencing (L-77 Vexar, Dupont Canada), 1.5 m high, which was convenient for building because it was light and long lasting. We used two heights of this mesh, so that the total fence reached 3 m height. The high-visibility orange mesh would, we hoped, prevent moose from knocking down the fence and walking through it. This turned out to be only partly correct, and we had a moose inside the fertilizer 2 hare exclosure twice, in 1988 with only minor impact and in 1994 (after a tree fell on the fence) with significant feeding impact. We also found that snowshoe hares would chew through the plastic mesh. The resulting immigrant hares were immediately removed, since we kept hare traps in these exclosures at all times, so the experimental design was only slightly affected. To solve this problem in the winter of 1989–1990, we were forced to put 4-cm mesh chicken wire 1.5 m high around these exclosures to reinforce the bottom strand of plastic mesh. Hares did not attempt to chew through the metal chicken wire. Ground squirrels and red squirrels could move freely over or under the fence, so these species were not excluded, and voles and mice could move through the mesh freely. The only other problem with these hare exclosures was trees that occasionally fell across the fence during windstorms, but fortunately this happened only a few times.

4.3 Organization, Personnel, and Equipment

Our original plan was to have three full-time technicians in charge of the Kluane Project year-round because faculty members could not be away from their teaching duties during the academic year. It quickly became clear that we required more people to achieve our goals. Meeting these needs was relatively simple in the summer because we could hire summer students. In most years we used three summer interns hired by the University of Calgary for the Arctic Institute of North America and hired an additional two to five summer students from the University of British Columbia and one or two students from the University of Alberta and the University of Toronto. In any given year there were also two to five graduate students working on thesis projects related to the Kluane Project as well. In winter we quickly found that the snow tracking of mammalian predators could produce

a gold mine of information (see chapter 13), and we needed more winter workers. We were able to use the Yukon government's winter unemployment programs from 1988 through 1996 to employ, on average, three or four additional workers through each winter season. Winter snow tracking is a specialized craft, and it required people with a range of talents for working in difficult winter conditions. We were extremely fortunate to find excellent winter snow trackers in the Yukon throughout this study, and this permitted us to achieve the goals we had set out for winter predator studies.

Over the 10 years of this study we have tallied a total of 157 person-years of effort to complete the work we summarize here. It is to these many individuals who contributed over the years that this project owes its success.

4.3.1 Organizational Structure

As the project began in 1986 we grappled with the problem of designing an organizational structure that would work effectively to accomplish our research goals with a minimum of bureaucracy. We decided on a four-tier structure. The project leader, Charles Krebs, was the top tier. His job was to coordinate the entire project to achieve a balanced experiment. His authority, we all agreed, had to be absolute in making decisions about conflicts within the project and about allocating resources. The second tier included all the faculty cooperating in the project, and these were assigned to particular sectors. Charles Krebs was in charge of snowshoe hares. Stan Boutin was in charge of predator research and red squirrels. Rudy Boonstra was in charge of mice, voles, and ground squirrels. Jamie Smith was in charge of predatory birds and passerines. Tony Sinclair took charge of building the electric fences and organized much of the shrub studies each spring. Susan Hannon and Kathy Martin covered the grouse and ptarmigan portion of the project, and Susan Hannon did all the original work organizing the fertilizer treatments. Mark Dale was in charge of mapping the vegetation, the fertilizer experiments after Susan Hannon got them started, and the tree work. Roy Turkington was in charge of the herbaceous studies and that component of the fertilizer trials. We designed redundancies among the faculty to cover for sabbatical leaves and other absences due to university demands on our time.

Field technicians were organized around a head technician living at the Kluane Research Station, who was in charge of the fieldwork. Vilis Nams was head technician from 1987 to 1990, Sabine Schweiger from 1990 to 1992, Mark O'Donoghue from 1992 to 1995, and Jocelyn McDowell from 1995 to 1996. The head technician reported directly to the project leader Charles Krebs and coordinated the other field workers. Field technicians were assigned particular aspects of the project. Frank Doyle was the key person for avian predator studies, and he maintained the electric fences and the feeding experiments. Cathy Doyle was the key technician for the snowshoe hare studies and the radio telemetry work. Elizabeth Hofer was in charge of winter snow tracking and winter work on mammalian predators. Irene Wingate, based in Vancouver, served as logistics technician, and she kept the field crew supplied with everything from pencils to electric fencing wire. All of these technicians interfaced with the graduate students who worked on particular aspects of the overall project. Any conflicts that arose were referred to the head technician and if necessary to the project leader for a final decision.

Each autumn we had a 2- to 3-day annual meeting in Vancouver or Edmonton of all the faculty participating, the head technician, and as many of the other technicians as we could afford to bring south. These meetings were critical in setting priorities because we reviewed progress each year, pinpointed problems, and agreed on solutions to be implemented. At this meeting we allocated the budget to the different subsections of the project as a group. We were fortunate in having a congenial group that always kept the overall goals in view, and in which conflicts over funding or technical help were infrequent. Most important, when there was a conflict within the group, we all agreed that the decision of the project leader was final.

4.3.2 The Problem of Training and Protocols

One problem that arose immediately in this study was the repeatability of methods. With changes of summer students from year to year and slow turnover of technicians and graduate students, we were concerned that our standard methods did not drift. One way to achieve consistency of field methods is to have one generation of students train the next, and in general this worked quite well for procedures such as hare live trapping or vegetation transects. But we wanted to make these procedures more concrete, and we began in 1989 to publish each year *The Kluane Handbook*. The handbook contained a detailed description of the field procedures for every type of data we were collecting from shrub biomass sampling to winter snow tracking, and it evolved from a 47-page handbook in 1989 to a 117-page handbook in 1995. We included in the handbook a general description of the Kluane Project and a detailed statement of the procedures as well as the means of data entry into computers after the field work was completed. We gave each worker a personal copy of the handbook each year and asked each of the faculty and technicians to revise their sections at the end of each summer field season to make the procedures clearer to newcomers. This was a useful means of standardizing our procedures.

In spite of this, we still encountered some data that were impossible to accept. Because there were periods of intensive field work, some data would not be analyzed until several months or even a year after collection, and anomalies would then turn up that were impossible to sort out. Although these problems were relatively minimal in this project, we believe that this is the primary problem in large field projects and that data management and data archiving are worth as much effort as possible to make sure that methods do not drift from year to year.

4.3.3 Seen Sheets

Vilis Nams and Frank Doyle developed one of the innovations we used in this project as a way of getting information on uncommon species in the vertebrate community. "Seen sheets" provided a way of monitoring populations by tallying random encounters with animals seen while doing other jobs in the forest. We used 160 field workers from 1986 to 1996 to record 25 species of the less intensively studied vertebrates in the Kluane Region. Each worker would record, for every day in the field, the number of hours in the field, their mode of transport (foot, truck, or snowmobile) and the numbers of each species seen. We trained summer students in the identification of raptors and other species of birds with

which they were unfamiliar. We obtained, on average, 7700 h of observations each year through the study, and we could index species abundances annually by the average number seen per hour. Confidence limits were placed on these indices by bootstrapping techniques. We recognized that observers varied greatly in their sighting abilities, but because we had some observers that spanned much of the study, we had a control group of high-quality observers to use as a baseline for calibration (Hochachka et al. 2000). These data form a valuable addition to our understanding of community dynamics in this system and are used extensively in chapters 11, 12, 14, and 16.

4.3.4 Winter Work at Kluane

Wind and cold were problems during periods of extreme weather in midwinter, and at times long stretches would go by when certain work could not be done. These severe periods were fortunately not common enough to prevent us from doing research in winter. The winter is a special time in the north, and our technicians and students adapted well to the lack of southern amenities such as running water and regular electricity.

One special problem we encountered with this study was winter isolation. This is a common, well-described problem in the north in winter, called "cabin-fever," becoming "bushed," and a variety of colorful euphemisms. In a camp with 8–10 workers who see each other day after day with little outside visitation, personal conflicts could escalate beyond reason. This was a problem in about half of the winters of this study, and we found it difficult to do much about it. One way of alleviating winter problems was for the faculty to visit as much as possible during the winter, but this was constrained by teaching commitments. Because we had e-mail working throughout the project, we could communicate rapidly with the field crews from our southern university posts, and this was a valuable asset. But we never could overcome the overall problem of winter isolation. There were times when we wished that instead of an ecologist we had a resident psychiatrist on the project staff. We think the key to isolated winter work is the personalities of the people involved, but we are not sure that we can determine from knowledge of how people operate in an open summer environment how they will respond to winter isolation.

4.3.5 Equipment

The final practical problem is that of equipment. Field ecological projects are more typically personnel limited than equipment limited, but some pieces of equipment were essential. The major items were all transportation equipment—trucks, snowmobiles, and ATVs. Trucks were always in short supply, and their use on gravel roads and during the winter caused great wear and tear. Research grants for trucks are rare, and we typically made do with older vehicles that were kept running by Donjek Upton, our resident mechanic. Snowmobiles were continually wearing out, partly because most of them were not designed for continuous use in the winter, and we often put up to 4000 km on one snowmobile during the winter season. ATVs were used in summer to carry feed and spread it on the food grids and were useful for electric fence maintenance in summer as well.

Electrical power in winter was essential for running computers and providing some lights for laboratory work, and this was yet one more problem we had to overcome. We found that conventional gasoline generators would not run 8 h a day without excessive

wear and rapid failure. We obtained a small diesel generator that provided 4 kilowatts of power, but had trouble keeping it operational. Electrical generating equipment is oriented toward large units generating more than 30 kilowatts, and these diesel units operate well in the summer at Kluane. But too much fuel is needed to run this large a generator during the winter for small power demands, and the net result was that we were forced to rely on smaller generators that were less reliable.

4.4 Summary

To unravel the structure underpinning vertebrate community dynamics in the boreal forests of Kluane, we carried out four kinds of manipulations to analyze both top-down (predator) and bottom-up (soil nutrient) forces. The two major manipulations were to provide additional food as rabbit chow, to fence out mammalian predators, and to combine both these two treatments on one area. The third type of manipulation was to add nutrients in the form of NPK fertilizer to two areas of forest, and the final manipulation was to fence snowshoe hares out of blocks of habitat to provide areas free of hare browsing. All of the major manipulations were done on experimental units of 1 km² because we wished to work at a large spatial scale. We were unable to replicate the predator fence experiment and the predator fence + food addition experiment because of costs and logistics.

There were a whole series of practical problems that arose while we were attempting these manipulations, and we outline them briefly. The predator-proof electric fence proved illusory until we lined it with chicken wire as a ground to the 8600-volt live wires, and then it worked excellently. Food supplementation had to overcome the attractions of grizzly bears and moose, and by spreading the feed we increased the cost of foraging for these large herbivores and minimized their impact. Fertilizer was spread aerially with no serious problems and good, uniform coverage.

Problems of personnel largely centered on maintaining protocols with changing student assistants, and we wrote a methods handbook to facilitate the transfer of methods from one year to the next. The work carried on winter and summer, and winter work was particularly stressing on personnel because of isolation and difficult weather conditions. Nevertheless, we overcame these many problems to carry out the experimental manipulations with the success outlined in the remainder of this book.

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