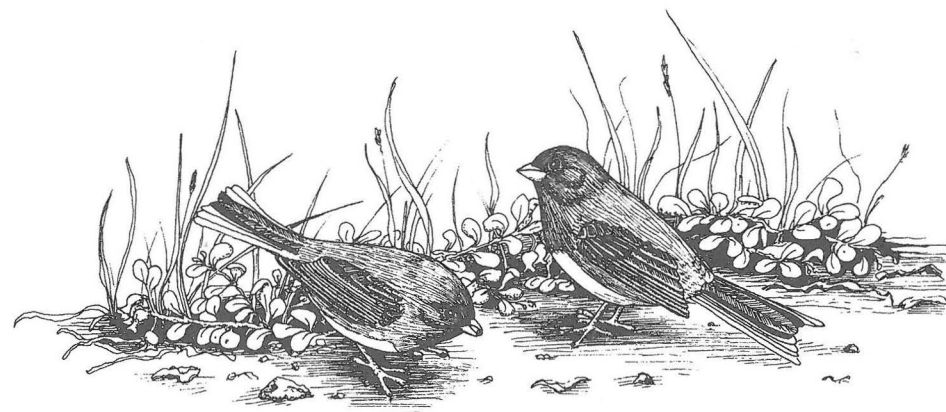# Other Herbivores and Small Predators

Arthropods, Birds, and Mammals

JAMES N. M. SMITH & NICHOLAS F. G. FOLKARD

In this chapter, we discuss the responses of three groups of animals in the center of the Kluane food web (figure 2.8) to the snowshoe hare cycle, to the experimental addition of NPK fertilizer, and to an unexpected natural event, a large outbreak of bark beetles. None of these animals was studied intensively every year, either because we did not expect them to be central players in the drama of the snowshoe hare cycle or because they were rare.

The first group, arthropods, are usually the most diverse and abundant animals in terrestrial food webs (Daly et al. 1998), including the boreal forest (Danks and Footit 1989). Lepidopteran larvae can be dominant consumers of vegetation in temperate forests, removing foliage from almost the entire forest canopy (Myers 1993), and severe defoliation can have large impacts on ecological performance of trees (Kaitaniemi et al. 1999). Defoliating species may generate strong interactions in boreal food webs, including effects on passerine birds (Enemar et al. 1984, Neuvonen 1989). Wood-boring insects, particularly bark beetles (order Coleoptera, family Scolytidae), can kill many species of forest trees (Daly et al. 1998; see below).

Arthropod numbers in boreal systems are strongly constrained by a short warm season. Even in May and August, temperatures are often too low for feeding, mating, and development. Arthropods are the principal foods of a variety of other consumers, including spiders, wasps, passerine birds, woodpeckers, and even small raptors such as American kestrels (*Falco sparverius;* see chapter 16). Adding nutrients to the ground layer, as we did at Kluane by fertilization, may elevate the abundance of herbivorous insects and result in increases in predaceous insectivores (Chen and Wise 1999).

The second group included insectivorous songbirds (order Passeriformes) and woodpeckers (order Piciformes). Songbirds at Kluane are nearly all migratory or nomadic, the only permanent residents being three species of corvids and two species of chickadees. In the boreal forest, distinctly different assemblages of passerines are found in the valley bottoms, compared with the neighboring alpine and subalpine areas (Theberge 1976, Folkard and Smith 1995). The dominant songbird species in the white spruce forests of the valley are the yellow-rumped warbler (*Dendroica coronata*), dark-eyed junco (*Junco hyemalis*), and Swainson's thrush (*Catharus ustulatus*), whereas the subalpine willow shrub zones are dominated by American tree sparrows (*Spizella arborea*) and Wilson's warblers (*Wilsonia pusilla*). Woodpeckers are conspicuous birds at Kluane and serve an important role in avian community dynamics (Martin and Eadie 1999) by excavating cavities that are used by other vertebrates such as boreal owls (*Aegolius acadius*) and northern flying squirrels (*Glaucomys sabrinus*).

The final group examined here included larger mammalian herbivores, such as moose (*Alces alces*) and bears (order Carnivora), and some smaller herbivores including the riparian-associated muskrat (*Ondatra zibethica*) and beaver (*Castor canadensis*), and the arboreal porcupine (*Erithezon dorsatum*). During the study, the largest herbivores provided us with both excitement (especially when cantankerous grizzly bears [*Ursus arctos horribilis*] decided they "owned" our food grids), and repeated frustration, when moose and bears repeatedly damaged our fenced exclosures.

12.1 Methods

12.1.1 Arthropods

We sampled arthropods between 1988 and 1989. Samples were collected (by N.F.) on four plots: control 1, control 2, fertilizer 1, and fertilizer 2. In 1988, 40 sticky traps per plot were used to sample flying insects, and 20 pitfall traps (8 cm in diameter, 12 cm deep) per plot were used to sample ground arthropods. Both types of sampling were conducted at 30-m intervals along a 600-m transect. In 1989, we used 30 pitfall traps dispersed nonrandomly across open grassy areas on each plot to sample ground-dwelling species. Foliage-dwelling arthropods were sampled by beating a nonrandom sample of thirty 1×1.5 m willow bushes dispersed widely across each plot. The bush was beaten with a 1 m stick and falling arthropods were collected on a 1-m square tray or sheet below the bush. Similarly, arthropods were sampled from 30 white spruce trees by beating foliage up to 3 m in height against a wire mesh screen (details in Folkard 1990). We sampled trees and bushes three to four times between 1330 h and 1800 h, the time of day when arthropods are most active, from mid-May to early August.

Arthropods were identified to order or family and sorted by size. An index of biomass trapped was calculated by cubing the length of each individual and summing these values per sample.

12.1.2 Songbirds and Woodpeckers

We estimated relative abundances and species richness of songbirds and woodpeckers using point counts with an unlimited radius in 1988 and 1989 and a 100-m radius thereafter. We sampled 11 stations per plot on each of the same four plots where arthropods were sampled (details in Folkard and Smith 1995). Birds flying overhead or through the plot within 100 m of the observer were included in the samples.

Counts were conducted from late May to early July, and the numbers of cycles of counts varied from year to year. In 1988, we censused both fertilizer plots four times and both control plots three times. In 1989, fertilizer 1 was censused five times and the other three plots four times. In 1990, 1991, 1995, and 1996, there were two censuses per plot, and in 1992 only one. Counts were conducted by N.F. from 1988 to 1989, by J.S. from 1990 to 1992, and by M. Evans from 1995 to 1996. The only obvious difference among observers was that N.F. and M.E. did not recognize the thin and insectlike song of the blackpoll warbler, *Dendroica striata*. Consequently, this species was only recorded by J.S. in 1990–1992, when it was moderately common.

In addition to the plot-based surveys, Delehanty (1995) studied the detailed use of space by gray jays (*Perisoreus canadensis*) from 1991 to 1993. Birds from nine groups were trapped and color banded on three control plots and three fed plots.

12.1.3 Other Herbivores

Numbers of other herbivores were estimated from opportunistic sightings on the seen-sheet records (see chapter 4.3.3; Hochachka et al. 2000). Muskrat dens (pushups) were

counted from a low-flying aircraft in 8–11 lakes and ponds in early spring in 1988 and from 1990 to 1996.

12.2   Predicted Responses to Experimental Treatments

We expected herbivorous insects and vertebrates to increase in response to fertilization through increased foliage volume and plant quality (chapters 5–7). We also examined whether such a bottom-up effect might extend to passerine birds, because they are specialized predators on arthropods. We expected numbers of food-hoarding birds such as jays and chickadees to increase on food addition plots.

During the Kluane Project, there was a severe outbreak of spruce bark beetle (*Dendroctonus ruficollis*). The outbreak began in 1994 and, by late 1996, about half of the mature spruce trees in the valley had been killed, with particularly heavy mortality on south-facing slopes (CD-ROM frame 22, more photos button). For example, even on the north-facing control 1 in April 1997, beetles had recently killed 91 of 246 mature white spruce trees (37%), and a further 37%, were defoliated, but still alive. Only 26% of trees were free from noticeable beetle attack. Therefore, in addition to the effects of fertilization and food addition, we expected an increase in numbers of woodpeckers, which feed on wood-boring insects (Winkler et al. 1995), and perhaps a decline in the abundance of foliage-gleaning birds.

Larger herbivores operate on a spatial scale beyond that covered in our experiments, but we expected bears to respond to food addition by concentrating feeding activity on the food grids. Also, when large herbivores die, they provide carrion on which some of the focal species in our study depend.

12.3   Responses by Species Groups

12.3.1   Arthropods

The different sampling methods yielded different types of arthropods. We mainly captured dipterans and adult lepidopterans in sticky traps, predatory ground beetles (family Carabidae) and spiders (order Aranea, family Lycosidae) in pitfall traps, and lepidopteran and sawfly (order Hymenoptera, family Tenthredinidae) larvae from the foliage of bushes and trees.

Strong seasonal changes in arthropod biomass were detected (table 12.1). Flying insects increased sixfold in biomass from late May to late July in 1988. Arthropods on willow foliage increased nearly 90-fold from early May to late June 1989, and on spruce foliage they increased more than 16-fold from mid May to late June. In 1989, arthropod biomass in June–July was over 40 times greater on willow than on spruce foliage.

In contrast to these large seasonal effects, arthropod biomass was not enhanced by fertilization in either 1988 or 1989. The biomass of ground arthropods in pitfall traps on control and fertilized plots was similar in late summer 1988. The biomass of arthropods from willow foliage in June–July 1989 was over twice as high on control plots as on fertilized plots (figure 12.1). In contrast, the biomass dislodged from spruce foliage in June–July 1989 was about two times higher on fertilized plots (figure 12.1). Because arthropod bio-

Table 12.1 Seasonal changes in mean arthropod biomass on four 36-ha plots using three different sampling methods.

Group	Abundance Index in May (SE)	Abundance Index in late June–July (SE)
Flying insects 1988	188.3 (40.3)	1,126.3 (40.15)
Insects on willows 1989	105.3 (72.5)	9,387.5 (3,338.5)
Insects on spruce 1989	13.9 (3.6)	227.3 (57.1)

mass was much higher on willows, overall arthropod biomass sampled was still two times higher on control plots in 1989. Thus, fertilization reduced the abundance of herbivorous arthropods on foliage in 1989 but seasonal changes in arthropod abundance were much larger than effects of fertilization.

12.3.2   Birds

Responses of Passerine Birds to Fertilization   Forty-five species of passerine birds have been found in the Kluane region (Theberge 1976, Folkard and Smith 1995). Twenty-eight of these species were encountered on the four study plots. Most species were present in all years, except for irruptive seed and fruit eaters (particularly white-winged crossbills, *Loxia leucoptera,* and Bohemian waxwings, *Bombycilla garrulus*), whose presence was irregular.
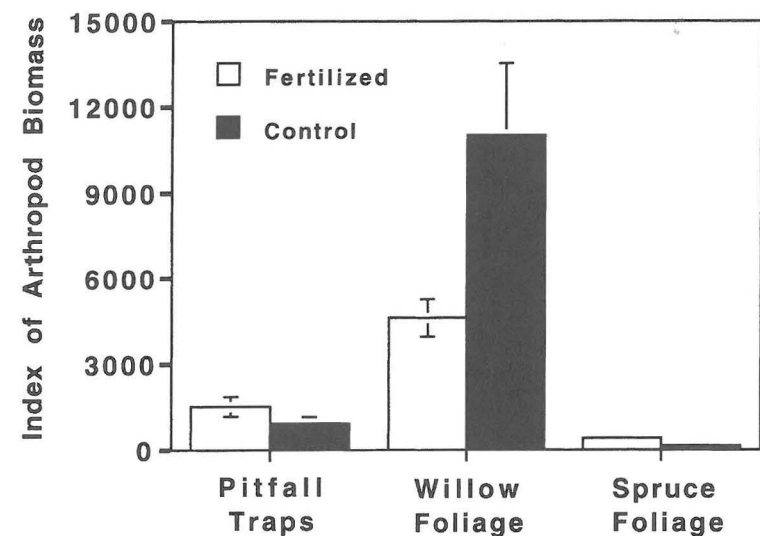

Figure 12.1 Mean indices of arthropod abundance (± SE) for three different sampling methods on two fertilized and two control plots in 1989.
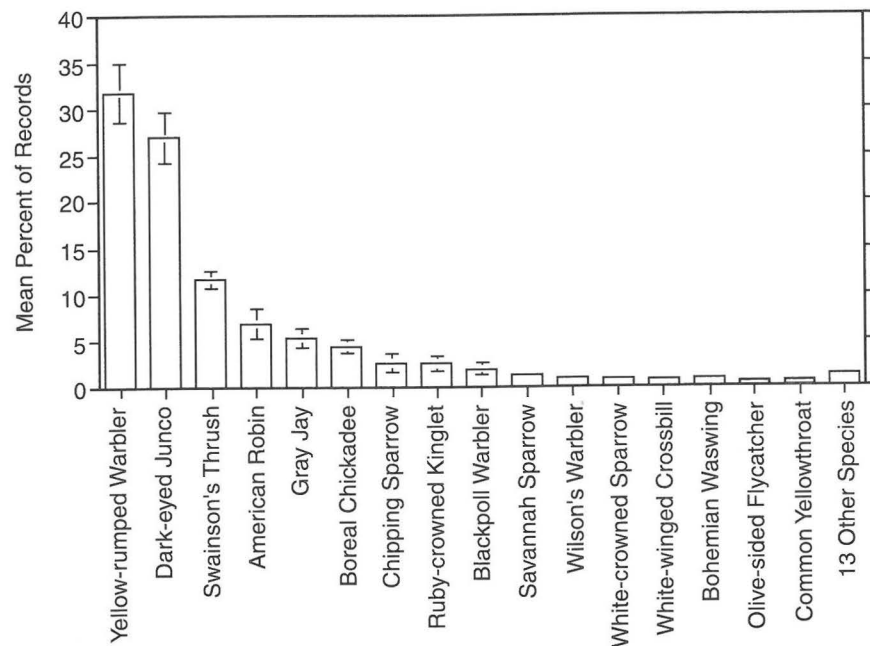
Figure 12.2 Relative abundances of songbirds at Kluane. Data from 1988 and 1989 are for all records, regardless of distance from the observer. Data for 1990–1995 are for records within 100 m of the observer. Plotted values are mean percentages of detections per species per year (±1 SE). Values for the blackpoll warbler are for 1990–1992 only, as observers did not count this species in other years.
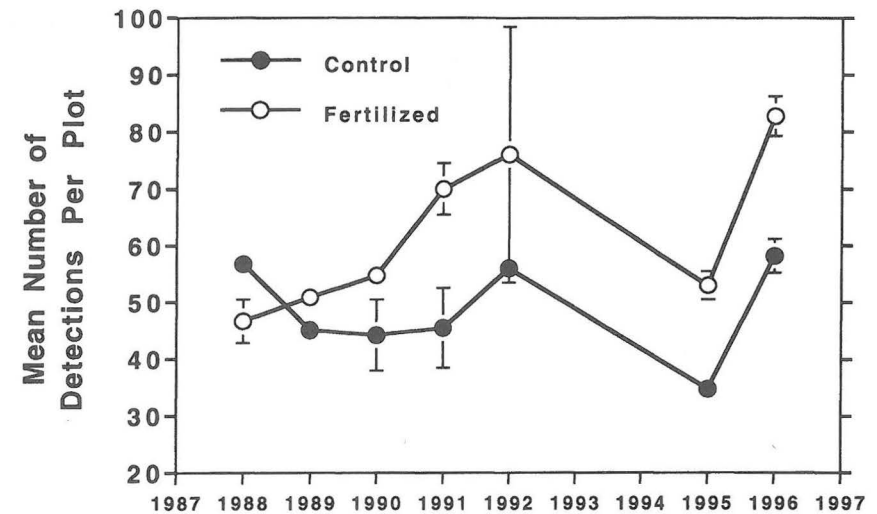

Figure 12.3 Responses of passerine birds to fertilization on two 36-ha control plots compared with two 36-ha fertilized plots. Bars denote standard errors.

The dominant species in all years and plots was the yellow-rumped warbler, followed by the dark-eyed junco and the Swainson's thrush. These three species made up an average of 70% of all records (figure 12.2). Six other species were moderately common: boreal chickadees (*Parus hudsonicus*), American robins (*Turdus migratorius*), gray jays, chipping sparrows (*Spizella passerina*), ruby-crowned kinglets (*Regulus calendula*), and blackpoll warblers (figure 12.2). The remaining species were uncommon or rare and tended to be restricted to habitats (e.g., riparian areas) that were uncommon on the plots.

Densities of passerines were low, averaging 122–155 males/km^2 for the 8 most common species on all plots in 1988–1989 (Folkard and Smith 1995). Given that these eight species made up 90% of all records, and assuming that (1) only singing males were detected in counts and (2) there was an even sex ratio, total adult densities in 1988–1989 were about 272–344 birds/km^2.

We assessed how passerine birds responded to fertilization by summing the abundances of the eight dominant species (see above) and calculating an average for the control and fertilized plots. These eight species clearly responded to fertilization, but only after a 3-year time lag (figure 12.3). Fertilizer was first applied in 1987; from 1990 onward, we averaged 41.6% more detections on the fertilized plots than on the control plots (figure 12.3). The effect of fertilization after 1990 was statistically significant (one-way AN-

COVA, $p < .001$). Although fertilization ceased in 1994, numbers on the two fertilized plots remained elevated in 1995 and 1996 (figure 12.3). Because some birds undoubtedly bred on the same plot from year to year, we also analyzed the data using a two-factor repeated-measures ANOVA; the result remained marginally significant ($p = .049$).

All eight dominant species showed positive responses to fertilization. The magnitudes of the responses of the three most dominant species were +36.9% for the yellow-rumped warbler, +70.8 % for the dark-eyed junco, and +96.0% for the Swainson's thrush averaged over all years after 1990.

Responses of Gray Jays to Supplemental Food Delehanty (1995) mapped the territories of nine groups of gray jays. Five groups on the control grids had a mean territory area of 23.2 ha (SE = 1.4), whereas four fed groups defended a mean area of 15.8 ha (SE = 1.9), a significant reduction ($p = .02$, t test). Jays on fed plots also maintained better body condition throughout the year and cached food at faster rates than jays on control plots (Delehanty 1995).

Effects of the Spruce Beetle Outbreak Two species of woodpeckers, the migratory northern flicker (*Colaptes auratus*) and the resident three-toed woodpecker (*Picoides tridactylus*) occurred commonly at Kluane. A third fire-dependent species, the black-backed woodpecker (*P. arcticus*), was also present, but we never encountered it in our censuses.

From 1990 to 1992, before the spruce beetle outbreak, we detected an average of 2.0 three-toed woodpeckers and 1.0 northern flickers per survey per plot. In 1995 and 1996, these averages rose to 7.5 three-toed woodpeckers and 7.0 flickers. This increase for flickers was significant (one-way ANOVA on log [$x + 1$] transformed numbers of detections per survey per plot per year, $p < .001$), but the response by the three-toed woodpecker

was not ($p = .30$). However, 29 of 30 records of three-toed woodpeckers during the beetle outbreak were from the 2 plots with the oldest spruce trees (fertilizer 1 and control 1). Three-toed woodpeckers at Kluane forage mainly by scaling pieces of bark from large spruce trees. When only the two old-growth plots were considered, the increase in three-toed woodpeckers became significant ($p = .03$, one-way ANOVA). Because there were no bird surveys in 1994 when the beetle outbreak began, we cannot tell if the increase in abundance of woodpeckers was immediate or if it had a 1-year time lag.

Foliage-gleaning passerines were apparently not greatly affected by the beetle outbreak. Relative numbers of individuals of the eight dominant species were lower in 1995 than in earlier years (figure 12.3), but they rebounded to an all-time high at the peak of the beetle-induced foliage damage in 1996. The yellow-rumped warbler, a species that nests and forages mainly in spruce trees, remained the dominant species in 1995 and 1996.

12.3.3 Other Herbivores

Numbers of muskrat dens peaked in 1988, 2 years before the peak in the hare cycle, but dropped in concert with the hare decline from 1990 onward (figure 12.4). Overall, there was about a fivefold change in numbers of muskrat dens. Patterns of change in muskrat sightings in the seen-sheet records were less clear. Only one year (1989) revealed high numbers of muskrats (table 12.2).

Among the larger herbivores, moose were detected most commonly, followed by grizzly bear and American black bear (*Ursus americanus;* table 12.2). Grizzly bears were recorded about five times as often as black bears. Sightings for these species did not vary

Table 12.2 Numbers of records of larger herbivores per 100 h from seen sheets (vehicle and foot records are combined).

Year	Moose	Grizzly Bear	Black Bear	Muskrat	Porcupine
1988	0.12	0.02	0.02	0.00	0.03
1989	0.25	0.09	0.00	0.08	0.00
1990	0.18	0.08	0.01	0.01	0.01
1991	0.32	0.08	0.02	0.02	0.06
1992	0.24	0.11	0.01	0.00	0.02
1993	0.24	0.18	0.01	0.01	0.01
1994	0.19	0.20	0.03	0.01	0.00
1995	0.28	0.08	0.09	0.03	0.00

predictably across years. Grizzly bears were attracted to the food addition grids, and this fact undoubtedly increased numbers of sightings. Grizzly bears were encountered particularly often in the summer of 1996, after the end of the seen-sheet records. We doubt if the seen-sheet data provide reliable indices of abundance for these large species. The pattern of sightings probably indicates the habits and degree of habituation of individual animals to humans.

Other species of larger herbivores detected included beaver, which were rarely recorded in the seen sheet data because of the distribution of wetlands relative to our study plots, and white-tailed deer (*Odocoileus virginianus,* one record).

12.4 Discussion

12.4.1 Links to the 10-Year Cycle

Only one of the species that we considered in this section exhibited a 10-year cycle, the muskrat. Muskrats exhibit 10-year cycles in boreal Canada, with more southern populations showing weaker cyclic dynamics (Elton and Nicholson 1942). The magnitude of the cycle suggested by the increases, about fivefold, is similar to that found in fur returns by Elton and Nicholson (1942). Presumably, cycles in muskrats are linked to cycles in snowshoe hares by their shared predators. Young muskrats are vulnerable to terrestrial predators such as lynx and coyote when they disperse in spring (Errington 1963).

Songbirds were commonly taken as prey by predatory birds (chapter 16), but the strength of this interaction was insufficient to affect songbird numbers markedly. The most specialized predator of small songbirds at Kluane, the sharp-shinned hawk (*Accipiter striatus*), was both secretive and uncommon (chapter 16), but the more abundant kestrels and northern harriers also commonly took songbirds. Goshawks took some larger songbirds as prey, but concentrated on mammals, grouse, and ptarmigan (table 16.2).

12.4.2 Effects of Fertilization

Arthropod abundance in 1988 and 1989 was not consistently higher on fertilized plots. In fact, the largest difference between control and fertilized plots (for insects from willow
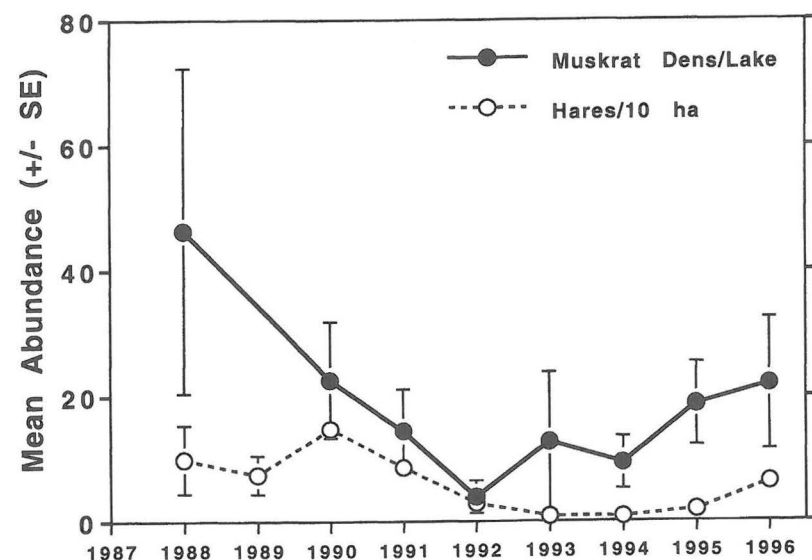

Figure 12.4 Mean numbers ($\pm$ SE) of muskrat dens counted from a light aircraft on 8–11 lakes and ponds each spring, in relation to hare densities (hares/10 ha) on control grids in spring.

foliage) was a substantially lower biomass on the fertilized plots in 1989 (figure 12.1). Surveys of arthropod abundance after 1989 were clearly needed, and we could not, therefore, measure delayed effects of fertilization on the biomass of arthropods.

Despite the absence of a bottom-up effect on arthropod abundance in 1988 and 1989, we found a clear and consistent effect of fertilization on the numbers of birds after 1989. Fertilizing began in 1987 and, from 1990 onward, fertilized plots consistently supported about 40% more passerines than control plots.

Several mechanisms might explain these changes in numbers. First, arthropod standing crops may have been higher after 1989. Second, fertilization might have increased arthropod production, but songbirds and other small predators such as shrews could have consumed the increase, leaving the standing crop unchanged or even reduced, as seen in 1989. Third, birds might have responded directly to changes in vegetation promoted by fertilization, and not to the arthropods. For instance, fertilized plots were noticeably greener in spring, because of the increased growth by the dominant grass *Festuca altaica* (Turkington et al. 1998; chapter 5). Therefore, cover for nesting on fertilized plots might have been greater, thus encouraging birds to settle there.

12.4.3   Other Patterns in the Food Web

Gray jays responded to supplemental feeding by reducing the sizes of their territories, which presumably resulted in greater jay densities on food grids (Delehanty 1995). Gray jays are efficient predators on the eggs and nestlings of shrub-nesting birds (Pelech 1999), yet gray jays and other common passerine birds increased in response to fertilization. It is commonly believed that food supply and predation (Newton 1998) jointly regulate bird numbers. The above patterns suggest that the positive effects of food on numbers of songbirds are stronger than any negative effects of depredation on nests at Kluane.

The increase in the numbers of woodpeckers in 1995 and 1996 suggests that they increased in response to the spruce beetle outbreak that began in 1994 and continued to the end of the study. Point counts are not the ideal census method for woodpeckers (Martin and Eadie 1999), so there is some uncertainty over the strength of this response. It is not surprising that the resident three-toed woodpecker responded strongly, as it is specialized to feed on bark beetles in mature spruce trees (Winkler et al. 1995). The strong response by the migrant northern flicker was surprising, as flickers prefer open forest and are specialized to feed on ants and fruit (Winkler et al. 1995). Presumably, flickers had sufficient dietary flexibility to exploit the bonanza of bark beetles directly, or they benefited via increased ant numbers associated with the bark beetle outbreak. No marked response to the beetle outbreak was seen in the passerine birds, perhaps because the dominant songbirds at Kluane did not eat bark beetles, nor did they depend greatly on green spruce foliage for food or cover.

12.5   Summary

We examined the patterns of change in numbers of three groups of species that we expected to be largely uncoupled from the snowshoe hare cycle. Numbers of arthropods showed strong seasonal fluctuations, and insects decreased on willows on fertilized plots

soon after fertilization began. Our studies of this important group were too short (1988 and 1989 only) to assess whether fertilization affected numbers of arthropods after 1989. Passerine birds showed a clear response to fertilization. Numbers of the eight dominant species were elevated by more than 40% on two fertilized plots, and all eight species showed a positive response to fertilization. Two species of woodpeckers increased in response to a severe attack by spruce bark beetles that began in 1994 and had killed nearly 40% of mature spruce trees on one plot by 1997. Muskrats exhibited a 10-year cycle with about a fivefold amplitude, but other larger mammalian herbivores showed no consistent patterns of change through the snowshoe hare cycle.

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