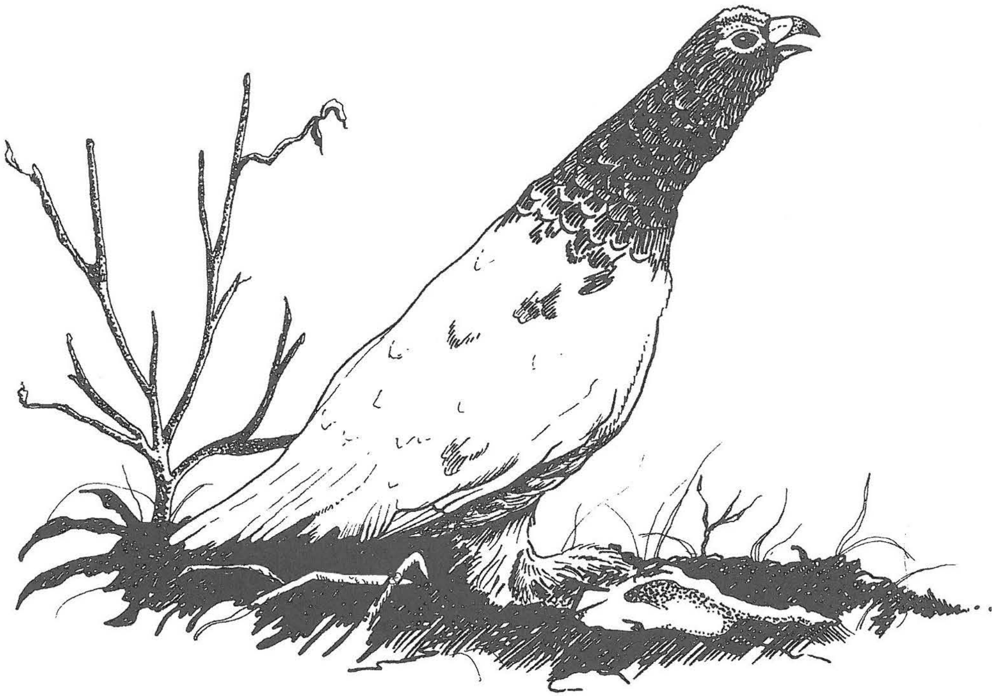
11

Forest Grouse and Ptarmigan

KATHY MARTIN, CATHY DOYLE, SUSAN HANNON, & FRITZ MUELLER



11.1 The Ecological Role of Forest and Alpine Grouse

11.1.1 Trophic Position

The Kluane system harbors five species of grouse. Two species, spruce grouse (*Falcipennis canadensis*) and ruffed grouse (*Bonasa umbellus*), inhabit forest year-round. Three species of tundra grouse, willow ptarmigan (*Lagopus lagopus*), white-tailed ptarmigan (*L. leucurus*), and rock ptarmigan (*L. mutus*), inhabit the alpine and subalpine above treeline in the Shakwak Valley most of the year. Willow ptarmigan descend into the open forest from October to March. All grouse are almost exclusively herbivores; females during egg laying and young chicks also eat a variety of invertebrates. Spruce grouse are conifer specialists, foraging principally on spruce and pine in winter and on forbs and leaves, fruits, and seeds of shrubs in summer and autumn (Boag and Schroeder 1992). Spruce grouse spend significant amounts of time foraging on ground vegetation in summer and thus might compete with hares for food during the breeding season. Ruffed grouse feed principally on buds and leaves of deciduous trees (aspen, bog birch) and shrubs and forbs seasonally (Rusch et al. 2000). Ptarmigan feed on willow buds and leaves throughout the year and on flowers, leaves, seeds and berries of sedges, ericaceous shrubs, and mosses in season (Braun et al. 1993, Hannon et al. 1998). Both forest grouse and ptarmigan form part of the herbivore trophic level year-round in Kluane, as their wide-ranging predators (goshawk, golden eagle, harrier, coyote, lynx, fox, wolverine, wolf) hunt in both forest and adjacent alpine areas.

11.1.2 Life History

Forest grouse have a promiscuous mating system and are assumed to have an equal sex ratio (Johnsgard 1983, Boag and Schroeder 1992). Breeding densities for the *F. canadensis* race of spruce grouse range from <0.1 to 83 birds/km^2 (Boag and Schroeder 1987, 1992). Given their dispersal and migration behavior, a year-round study of spruce grouse will consist of year-round residents, breeding birds, winter residents, and some birds encountered only during spring and autumn migration (Schroeder 1985). Spruce grouse tend to be relatively long lived compared to alpine grouse, with above-average nesting success for ground-nesting birds (Ricklefs 1969). Annual mortality averaged 30.1% (range 22–49%), with the longevity record being 13 years in natural populations (Boag and Schroeder 1992).

Ruffed grouse, a close relative of spruce grouse (Ellsworth et al. 1995), are more sedentary and extend farther south into the northern United States in the Appalachian, Cascades, and Rocky Mountain cordilleras than do spruce grouse. Male ruffed grouse have traditional drumming display stations that make males easy to count. Females of both species are difficult to census because they range over large areas in spring and autumn and have secretive behavior most of the year. Both spruce grouse and ruffed grouse choose nest sites in willow or slash, often at the base of trees in deciduous or mixed forests. Overbrowsing by hares at the peak might reduce nesting cover for forest grouse. Hatching success (proportion of nests hatching at least one chick) for *F. canadensis* populations ranges from 40% to 81% in southern Canada and the northern United States, and 81% in Alaska.

Ptarmigan are monogamous and territorial and breed in open tundra habitats. Ptarmigan are unique in the avian world because they change their plumage from fully white in winter to a cryptic brownish and reddish grey plumage in other remaining seasons. Male willow ptarmigan participate in brood rearing, whereas white-tailed and rock ptarmigan females supply all of the parental care, as is typical for most grouse species. Annual survival of willow ptarmigan ranges from 30% to 64% and varies with sex and age class (Hannon et al. 1998). A long-term population dynamics study of willow ptarmigan conducted in the Chilkat Pass, about 200 km south of Kluane, showed that densities of ptarmigan were strongly correlated with the snowshoe hare cycle (Boutin et al. 1995, Hannon and Martin 1996).

11.1.3 Habitats

Spruce grouse range across the northern boreal coniferous forest from Alaska to Labrador and southward into New England and the northern United States (Boag and Schroeder 1992). Highest spruce grouse densities in North America are in 15- to 25-year-old pine plantations in central Ontario (Boag and Schroeder 1992). Spruce grouse choose microhabitats within forests that vary between the sexes and across seasons. In spring, males choose territorial sites in mature or young forests with sparse canopy cover and openings on the ground for display. Breeding females use areas where food is most available such as open wet and dry meadows with interspersed trees and a well-developed shrub and herb layer. Hens with broods may use forest with much deadfall. The selection of microhabitats for both sexes appears to be a compromise between food acquisition and predator avoidance. Ruffed grouse range throughout northern North America from temperate coniferous rainforest to relatively arid deciduous forest types in both young and mature stands (Johnsgard 1983). The unifying criterion is that all forest stages include deciduous trees, especially *Betula* or *Populus* species.

A winter study (1989–1992) showed that spruce grouse at Kluane feed exclusively on needles of white spruce (*Picea glauca*), and certain individual trees were fed on extensively (Mueller 1993). Captive spruce grouse had a strong preference for young needles from "feeding trees" over control trees of similar age, size, and location. Feeding trees had lower concentrations of two monoterpene antifeedants, camphor and bornyl acetate, and lower resin than control trees. Feeding trees showed increased growth of lateral twigs, longer needles, and decreased cone production.

Willow and rock ptarmigan have a holarctic distribution that includes arctic, subarctic, and subalpine regions (Hannon et al. 1998), while white-tailed ptarmigan are restricted to alpine regions of western North America from Alaska to New Mexico (Braun et al. 1993). The ptarmigan species in the southwestern Yukon are sympatric in a regional sense, but are stratified altitudinally (Weeden 1963, 1964). In the breeding season, willow ptarmigan occur in the subalpine with clumps of *Salix* and *Betula* (0.2–2.5 m high) interspersed with sedge and grass hummocks or deciduous shrubs. In winter, they descend into open forest with more cover than the subalpine but still with exposed forage (Weeden 1964, Gruys 1993, Mossop 1994). White-tailed ptarmigan remain in the alpine most of the year and descend in winter to willow-dominated basins with considerable snow accumulation (Braun et al. 1993).

11.1.4 Current Understanding of Population Dynamics

For all grouse species occurring in Kluane, there are long-term population studies, ranging from 10 to 30 years, in multiple locations in North America that provide detailed information on life history, population dynamics, and behavior (Mercer 1967, Keppie 1982, Keith and Rusch 1986, Bergerud and Gratson 1988, Martin et al. 1989, Boag and Schroeder 1987, 1992, Braun et al. 1993, Hannon and Martin 1996, Rusch et al. 2000). In general, data for ruffed grouse support top-down regulation of densities by predators that switch from declining hare or vole populations to grouse (Keith and Rusch 1986). Ruffed grouse show 10-year cycles with peaks and declines 1–2 years before hares in the northern part of their range (Keith and Rusch 1986). Population density and recruitment of other forest grouse decreases with increasing age of the forest (Bendell and Elliott 1967, Zwickel and Bendell 1972, 1985). Willow ptarmigan numbers fluctuate on 8- to 11-year cycles in North America (Mossop 1994, Hannon et al. 1998), with populations declining in synchrony with snowshoe hare cycles where these species co-exist (Keith 1963, Boutin et al. 1995). Rock ptarmigan in Iceland function as keystone herbivores, precipitating both functional and numerical responses in gyrfalcon populations (Nielsen 1999).

Despite numerous experiments and long-term correlative studies, there is no overall agreement on mechanisms of population change in grouse. Angelstam et al. (1985), Hannon (1986), and Bergerud (1988) summarized hypotheses proposed to explain population changes in grouse. Regulation may occur through (1) predation or starvation in winter, (2) territorial or spacing behavior in spring or autumn, or (3) variation in chick production during the breeding season. Poor chick production might be caused by poor maternal quality related to food supply or by heavy parasite loads. Declines in ruffed grouse are associated with high predation on juvenile grouse in summer in Alberta (Keith and Rusch 1986), or on all birds in autumn and winter in Wisconsin (Small et al. 1991). In northern Fennoscandia, where forest and tundra grouse show synchronous 4-year cycles with voles and their predators (Angelstam et al. 1985), it is hypothesized that generalist predators such as mustelids switch to grouse nests when vole numbers decline. In summary, forest and tundra grouse are considered an important component of population cycles in southern Alberta, Iceland, United Kingdom, and Fennoscandia. They have functioned as the keystone herbivore in Iceland, but more commonly as the alternative herbivore. The timing of the declines and the life-history stage showing the most dramatic impact (survival of adults or juveniles in spring, summer, or winter, or in nesting success) differed across these studies.

11.1.5 Predicted Responses to Experimental Treatments

Given previous studies, we expected all grouse in the Yukon to decline in synchrony with the hares. We designed the Kluane grouse censusing to describe numerical and reproductive responses of forest and alpine grouse to the hare cycle and to examine potential mechanisms for population change. We tested whether forest and alpine grouse numbers were correlated with changes in hare densities. Given other studies, we expected to see increased predation on grouse by great horned owls, goshawks, lynx, and coyotes as hares declined. Because ptarmigan live above the forest most of the year and thus vary in relative availability seasonally, we expected them to be a seasonal component of the boreal forest trophic structure. Their contribution to prey biomass in winter might improve survival of resident predators and might also improve survival of other forest herbivores through a buffering effect (reduction of predation risk).

We did not expect to see strong responses to our experimental treatments when it became clear that forest grouse were patchily distributed and at much lower density than hares on our plots. Thus, we present a limited number of comparisons among the treatment plots, and given the small number of grouse per plot we make only qualitative inferences for two secondary predictions. First, if predators regulate grouse populations, we expected spruce grouse numbers to remain stable on predator exclosure plots. Second, if hares and grouse have an overlap in summer food supply, then hares might compete with grouse by changing food supplies for grouse due to overbrowsing at the peak. If so, spruce grouse should decline less on the fertilizer addition plots and decline more on food addition treatments after hares severely overbrowse the natural vegetation.

11.2 Methods

11.2.1 *Duration of Grouse Studies*

Data on population trends for forest and alpine grouse at a valley-wide scale are available for the duration of the Kluane study. During the 1990–1997 breeding seasons, we conducted specific studies on spruce grouse on six plots, with less emphasis on ruffed grouse. There are data on spruce grouse abundance for two of these plots in 1987 and 1988. Personnel recorded grouse mortalities encountered during field work. A population study of willow ptarmigan in Chilkat Pass, 200 km southeast of Kluane, from 1979 to 1992 provided concurrent population data (Hannon and Gruys 1987, Boutin et al. 1995, Hannon and Martin 1996).

11.2.2 *Shakwak Valley Population Trends*

The Kluane Seen-Sheet Data Field staff recorded all encounters of 25 avian and mammalian species (including spruce grouse, ruffed grouse, and ptarmigan), the hours afield and mode of transportation used (foot, snowmobile) for the extensive Kluane study area, (Hochachka et al. 2000). A visual detection during daylight hours was required to score a sighting. We recorded trips where individuals saw no animals. Radio-tagged individuals were not included unless encountered accidentally. Observers were trained in species identification. Data were collected year-round from May 1988 through April 1996 by 12–45 observers annually (total of 212 observers and 98,058 field h of observations during the study). The Kluane seen-sheet data is a coarse-grained data set that provides information on relative abundance/activity on multispecies population trends in the valley.

11.2.3 *Numerical and Reproductive Parameters on Treatment Grids*

We measured abundance and reproductive parameters of forest grouse during breeding season on hare grids in response to the experimental manipulations using dawn census data and grouse search and capture data from 1990 to 1997 (CD-ROM frame 30).

Dawn Census In 1990 we began counts of total breeding densities of spruce grouse in relation to experimental treatments over a 10-day period in late April to early May. Counts of breeding displays of both male and female spruce grouse can be used to estimate populations in spring (Herzog and Boag 1977, Schroeder and Boag 1989, Keppie 1992). Females give a cantus call considered to have a spacing or territorial function during prelaying and laying periods (Nugent and Boag 1982). This call broadcasts up to 500 m, and other females answer and may approach the call, occasionally to within meters. Females are most responsive to other females calling around dawn. Males also approach and perform flutter flights (nonvocal displays; Boag and Schroeder 1992) in response to these female calls. We used standardized playback techniques for six grids (control 1, control 4, fertilizer 1, food addition 1, predator exclosure, predator exclosure + food) from 0430 h to 0645 h (about 75 min before sunrise to about 60 min after sunrise). In 1991 and 1993, we tried playback calls at intervals from early April through late May to determine the optimal timing for census.

On the G and N transect lines (CD-ROM frame 24) on each 36-ha grid, we played calls at a total of seven stations per transect, each station separated by 100 m. At each playback station, we first listened for 30 sec, then played two cantus calls (15 sec) twice, each followed by a 30-sec period to listen for responses (total of 2 min/station). Tape recorder volume was adjusted to broadcast about 200 m. We recorded all responses by females or males and the time and the approximate locations of each, counting only those birds on the plot. Individuals recorded at multiple stations or between lines were only included once in each survey-morning. We also recorded male ruffed grouse heard during the dawn census. Because the prime response period was only about 45–50 min, and responses dropped off quickly after sunrise, each observer was able to conduct a maximum of two transects (one grid) per morning, which took about 75–90 min. Each plot was censused three times (rounds) per season, and the population size was calculated as double the number of the maximum grouse of either sex counted during one of the surveys. There were two main observers (K.M. from 1990 to 1997 and C.D. from 1990 to 1996), and a third individual differed each year. Observers and starting points were rotated for each round. The total of 18 surveys was completed in 6–9 mornings. We did not sample on days with falling snow or moderate to high winds.

Grouse Search and Capture Two to three observers searched for grouse on six grids after the dawn census at intervals from 0630h to 2200 h to monitor population changes across the hare cycle on six treatment plots in spring. Radio-marked birds were included only when encountered accidentally. During each search we used a dog (1987–1994), and occasionally we used female cantus calls. We did not play calls on plots we planned to survey the next morning. Grouse search data are available for fertilizer 1 and control 1 in 1987 and 1988. We recorded all ruffed grouse encountered. During grouse search periods, we captured and banded all spruce grouse located (41 males, 31 of the 46 females banded were also radio tagged), and we measured local survival, body condition, and reproductive parameters such as clutch size, nesting success, and chick survival.

11.2.4 *Data Robustness and Limitations*

The main field observers and dog contributing to our year-round and spring abundance estimates of grouse populations over the hare cycle worked throughout much of the Kluane study. Thus, we have the advantage of continuity, normally difficult to achieve across a long-term study. The seen sheet, grouse search and capture, and dawn census use different spatial scales, observers, and methods to estimate abundance and thus are independent data sets to examine population trends. The concordance across these independent data sets suggests that our general demographic trends are robust. The radio tagging provided data on reproductive parameters over the hare cycle, but the sample is insufficient to assess responses to treatments. Spruce grouse, the most abundant grouse accounting for the highest biomass in Kluane, is the only species for which we can assess responses to the experimental treatments, and here power to detect responses in abundance or reproductive parameters is low, given their low density and patchy distribution.

We have less confidence in our estimates of ptarmigan densities over the hare cycle because we expended limited census effort on them. In winter, ptarmigan occur in flocks, and the seen-sheet data are highly skewed (zero observations for many observer-days) that conform to neither normal nor Poisson distributions (Hochachka et al. 2000). We conducted aerial censusing from 1990 to 1996 to measure ptarmigan breeding densities, but it was difficult to achieve comparable count conditions across years given annual variation in snow melt, weather, and flight conditions (birds are harder to see when snow melt is advanced). An MSc student, Luc Pelletier, conducted replicate sets of aerial spring surveys in 1995 and 1996 and compared these with ground counts for ptarmigan. The aerial census did not provide reliable indices for comparing ptarmigan abundance across years (Pelletier 1996, Pelletier and Krebs 1997) and are thus not presented here.

11.3 Demography of Grouse

11.3.1 Population Trends in the Shakwak Valley

The Kluane seen-sheet data indicate that densities of spruce grouse (both breeding and winter) increased from 1987 to 1988, peaked in the summer of 1989 and the winter of 1989–1990, began to decline during the 1990 breeding season, declined markedly in the 1990–1991 winter, and bottomed out in the 1991 breeding season (figure 11.1). Densities remained low through 1993. In 1994, numbers increased and continued to increase through the end of data collection in April 1996 (figure 11.1). Summer densities of spruce grouse started declining again in 1996 (figure 11.2), but spruce grouse numbers appeared to remain high over the 1997–1998 winter (E. Hofer, personal communication).

The start of the grouse decline was in late winter or early spring of 1990. Data available from the seen-sheet observations show encounters of spruce grouse greatly decreased early in 1990. In November and December 1989, we observed 10.9 grouse/100 h ($n = 830$ hours afield) compared with only 1.9 grouse/100 h ($n = 859$ h) for January and February of 1990. The following year, 1.9 grouse/100 h were seen in November and December 1990 ($n = 859$ h), compared with 1.4 grouse/100 h ($n = 1071$ h) in January and February 1991. The spruce grouse decline appears to be caused by elevated predation on adult grouse. Sixteen grouse mortalities were recorded in the spring of 1990 (when data collection began), and 16 mortalities over the autumn, winter, and spring of 1990–1991. For the same period in 1992, we recorded only two dead grouse. During the spring of 1991, we located four recently killed grouse and only five live birds during 60 h of grouse search (table 11.1).

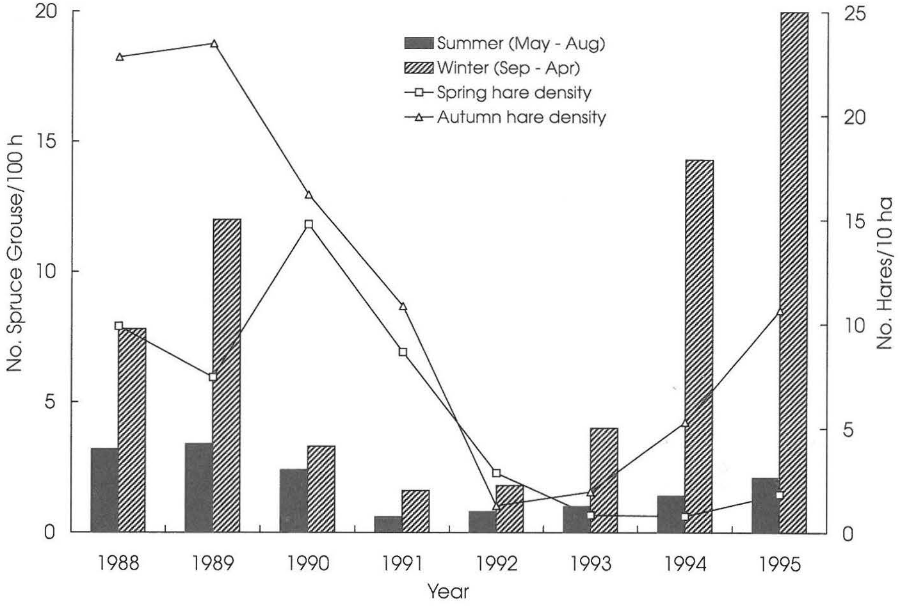


Figure 11.1 Average number of spruce grouse seen by multiple observers on foot in the Shakwak Valley during the breeding season (summer) and the nonbreeding season (winter). Summer 1988 is May–August 1988; winter 1988 is September 1988 through April 1989, and so on. The lines indicate spring and autumn hare densities.

Ruffed grouse at Kluane were confined to patchily distributed aspen (*Populus tremuloides*)-dominated stands and thus occurred at lower overall densities than spruce grouse. Ruffed grouse were found mostly in larger aspen stands, but they occurred also in smaller deciduous stands when population densities were high. Ruffed grouse accounted for 9% of forest grouse detections during grouse search. Ruffed grouse declined and remained low in synchrony with spruce grouse (figure 11.2). Virtually no ruffed grouse were heard in the Shakwak Valley by project personnel from 1991 to 1993 (F. I. Doyle, personal communication).

Ptarmigan were present in the valley only in winter. Seen-sheet data indicate that willow ptarmigan numbers at Kluane peaked in the winter of 1989–1990 and started declining the next winter simultaneous with declines in hare winter densities ($r = .76$, 8 years; figure 11.3). Long-term field studies in the Chilkat Pass showed numbers of willow ptarmigan pairs peaked in 1980–1981 and again in 1990; in both cases, declines began synchronously with changes in hare densities ($r = .84$, $n = 12$ years, $p < .001$; Boutin et al. 1995).

11.3.2 Reproductive Parameters

To address mechanisms relating to the predation and food competition hypotheses, we measured several survival, body condition, and reproductive variables. Birds banded in

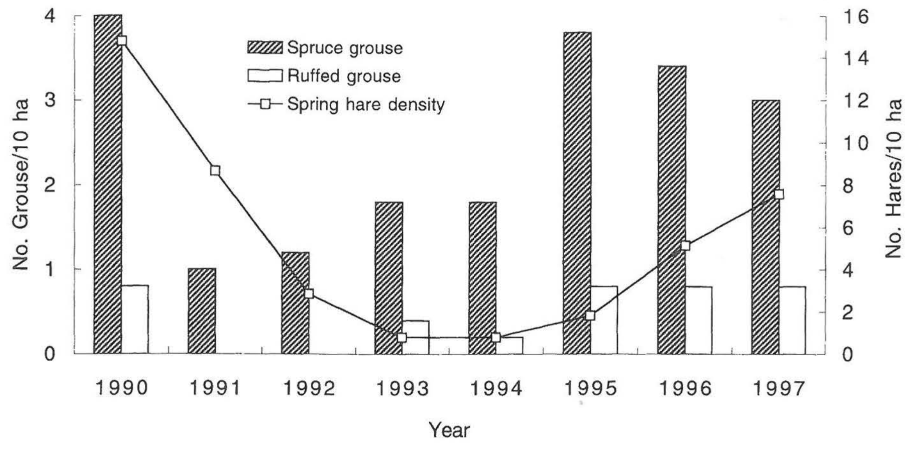


Figure 11.2 Total numbers of spruce and ruffed grouse estimated from the dawn census using playbacks of female cantus calls in late April to early May on six treatment plots (36 ha each, total = 216 ha) in relation to snowshoe hare spring densities (lines).

our study ranged from 1 to 6 years of age. Local survival, as measured by birds returning to the study plots in subsequent years, varied significantly across the cycle from a low of 27% in the hare decline years to a high of 54% at the hare low (table 11.2). As survival of radio-tagged birds during the breeding season remained high throughout the study (80% of 31 females), it appears that spruce grouse declined due to predation over the winter during the hare decline years of 1990 and 1991. At the hare low, local survival of the few remaining birds was high (table 11.2). The proportion of clutches that hatched chicks and the proportion of hatched chicks that survived to late summer remained normal to high for spruce grouse across the study, but data are limited (table 11.2). Although production of independent offspring appeared normal to high during the hare low, we recorded limited recruitment to the breeding population in subsequent years (table 11.1), suggesting that young produced during the hare low did not survive well over winter.

Body condition and reproductive effort indices run counter to the food competition hypotheses as body mass for females was lowest during the hare decline and highest during the hare low ($F = 3.33$, $p = .03$, $n = 35$ females; table 11.2). In addition, clutch size increased through the decline and hare low ($F = 5.82$, $p = .004$; table 11.2). Body mass of male spruce grouse did not vary across the hare cycle ($F = 1.36$, $p = .27$; table 11.2).

11.3.3 Population Trends on Control Plots

On the control plots, forest grouse varied from 0.28 to 3.33 birds/10 ha over the hare cycle. Spruce grouse varied from 0.28 to 2.5 birds/10 ha, and ruffed grouse varied from 0 to 2.2 birds/10ha on control 4 (figure 11.4). The lowest densities were recorded in 1991, two years before the hares reached their lowest spring densities (figure 11.4). Recovery started in 1992 on control 1, but not until 1993 for control 4. The temporal trends on control 4 may be somewhat complicated by the presence of two grouse species. Spruce grouse numbers were greatest in 1993 on control 4, and thereafter remained at or below 1990 levels, but ruffed grouse increased from none in 1991 and 1992 to eight birds in 1997 (figure 11.4). Habitat suitability for each species and sex varied between control plots. Control 1 had a substantial amount of suitable habitat for both male and female spruce grouse, but not for ruffed grouse. Control 4 was basically the reverse, with a large area of aspen in the center comprising the most suitable ruffed grouse habitat of all the census plots, while the periphery had suitable coniferous habitat for female spruce grouse. Ruffed grouse were present only on control 4 grid in 1990 (the first year of dawn census); they were not encountered for 2 years, reappeared in 1993, increased until 1995, and remained high through 1997 (figure 11.4). We recorded one ruffed grouse male on fertilizer 1 in 1995 and 1996 but none in 1997.

Table 11.1 Numbers of spruce grouse (SG) and ruffed grouse (RG) encountered on grouse search in Kluane.

		Grouse Located Alive			*Spruce grouse*		*Spruce Grouse Recruitment*		
Year	Total Search Time (h)	Total Grouse per h	No. RG	No. SG	No. Found Dead	% Dead of Total Located	Total No. Individuals Caught	No. Returns (Banded)	No. New Recruits
1990	52.2	0.38	3	17	3	15	11	3	8
1991	60.6	0.08	0	5	4	44	5	2	3
1992	48.8	0.15	0	7	2	22	5	2	3
1993	57.1	0.19	0	11	0	0	8	4	4
1994	84.0	0.21	3	15	1	6	9	3	6
1995	68.3	0.50	4	30	0	0	18	6	12
1996	64.7	0.42	4	23	0	0	13	9	4
1997	89.5	0.23	6	15	1	6	9	3	6

Total search time is the number of hours searched across 4–6 plots annually and calculated by tallying total person hours in the field. A dog was used from 1990 to 1994. Time required to capture and band spruce grouse was subtracted from the total search time. Grouse/h includes total number of grouse (SG + RG) encountered/total search hours.

11.3.4 Relationship of Changes to the Snowshoe Hare Cycle

Across the valley, spruce grouse breeding densities peaked in 1989 and the winter of 1989–1990 (figure 11.1), about one season ahead of the hare peak in the winter of 1989–1990 and peak hare breeding densities in 1990 (chapter 8). Using breeding season counts for both grouse and hares, serial correlations were strongest for spruce grouse declining 1 year ahead of the hares ($r = .89$, 1988–1995) using seen-sheet data, and also when using dawn census data for spruce grouse ($r = .87$, 1990–1997) or for all forest grouse ($r = .86$, 1990–1997). Using seen-sheet data, correlations of spring grouse populations with autumn hare densities were similar for both the preceding year where $r = .90$ (i.e., lag $= -1$), and for the subsequent winter ($r = .89$, lag $= -2$, 1988–1996). Using dawn census data, the strongest correlations of summer grouse numbers were with autumn hare densities in the preceding winter for spruce grouse ($r = .82$) and for all forest grouse ($r = .82$,

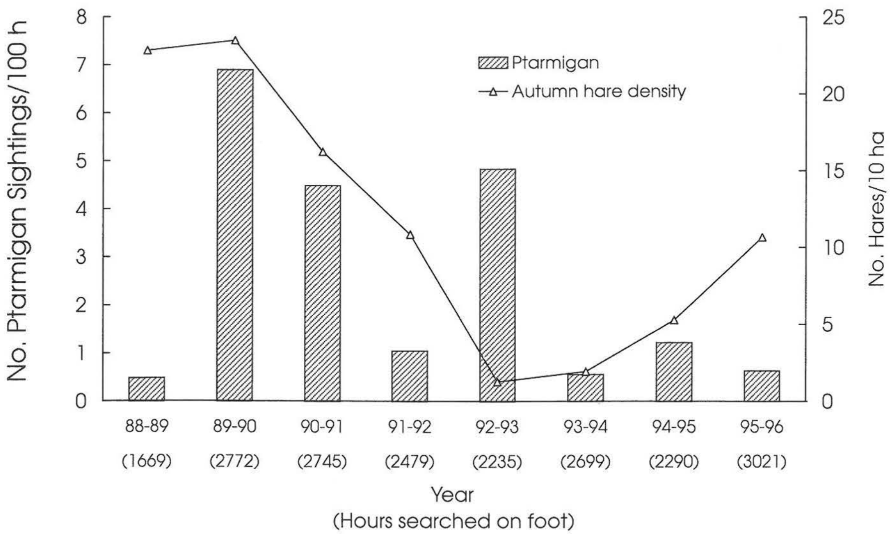


Figure 11.3 Numbers of ptarmigan encountered per 100 h afield from October to March by multiple observers (seen-sheet observation data) in the Shakwak Valley. Total observation hours for each winter are included in parentheses under each year. Autumn hare densities presented as lines.

1989–1997). Thus, forest grouse began to decline one season in advance of the hares, their numbers collapsed quickly, and they began their recovery while hares were still declining. Willow ptarmigan started declining in the winter of 1990–1991, 1 year after the forest grouse decline (figure 11.3). The seen-sheet data counts suggest that ptarmigan declined with a 1-year lag with autumn hare densities ($r = .76$, 8 years) or a 2-year lag with spring hare densities ($r = .76$, 8 years). The trends in Kluane ptarmigan counts accord well with patterns in the Chilkat Pass, where ptarmigan densities peaked in 1990, and were still declining in 1992 (Boutin et al. 1995).

11.4 Response of Forest Grouse to Experimental Treatments

Although the size of the manipulated areas for fertilizer addition, food addition 1, predator exclosure, and food addition + predator exclosure was 1 km^2, for consistency, we restricted our grouse census to a 36-ha hare grid area. Here we discuss whether numbers, encounter rates, or timing changed on experimental treatments relative to controls and within plots across the cycle.

11.4.1 Fertilizer Addition

For spruce grouse, the quantity of forage (spruce needles, ericaceous shrubs) was enhanced by the fertilizer treatment (chapters 5 and 6). On fertilizer 1, spruce grouse declined to a low in 1991, numbers increased in 1992, and by 1993 the plot had recovered to peak densities and remained high through 1997 (figure 11.4). This recovery was 2 years earlier than on the other treatment plots and faster than on control 1. The data are consistent with the fertilization treatment resulting in an earlier recovery of spruce grouse from the low than control 4 and more rapidly than control 1.

Table 11.2 Body size, reproductive parameters, and annual survival for spruce grouse across the snowshoe hare cycle stages at Kluane.

	Stage of hare cycle											
	Peak (1987–90)			Decline (1991–92)			Low (1993–94)			Increase (1995–97)		
Parameter	Mean	SD	*N*	Mean	SD	*N*	Mean	SD	*N*	Mean	SD	*N*
Morphometrics and Condition[a]												
Males[b]												
Body mass (g)	570	50	17	620	7	2	601	31	5	586	38	11
Wing chord (mm)	187	4	17	194	1	3	193	3	5	193	2	11
Females[c]												
Body mass (g)	626	39	10	571	58	4	649	26	6	637	43	15
Wing chord (mm)	186	5	10	189	2	4	190	3	6	190	4	15
Survival (%)[d]	—		—	27		15	54		13	45		40
Reproductive Success												
Clutch size[e] *N* = nests	7.6	1.3	5	8.5	0.7	2	9.8	0.8	5	8.7	0.6	14
% nests hatched	80			50			100			79		
Chicks fledged (%) *N* = broods	50		2	44		1	76		2	57		7

[a] Body mass and wing chord measurements were taken from birds captured between 25 April and 15 May 1987–1997.

[b] Male metrics over hare cycle: body mass: $F = 1.36, p = .27$; wing chord: $F = 8.61, p < .001$.

[c] Female metrics over hare cycle: body mass: $F = 3.33, p = .03$; wing chord: $F = 2.74, p < .06$.

[d] Survival is local survival as measured by the return in a subsequent year of birds known to be alive in spring on treatment grids, 1990–1997. Both sexes pooled.

[e] Clutch size across the hare cycle: $F = 5.82, p = .004$. Clutch size did not differ for adult (mean = 8.73, $n = 15$), and yearling hens (mean = 8.78 eggs, $n = 9$) pooled across the study.

11.4.2 Food Addition

It is not clear what, if anything, was manipulated for spruce grouse on this plot. We did not observe spruce grouse eating the rabbit chow. The food-addition plot had average grouse densities in 1990, after which no birds were detected for 3 years and only two were found in 1994 (figure 11.4). The habitat appeared suitable for spruce grouse, but numbers did not recover to 1990 levels by 1997. Spruce grouse may compete with ground squirrels and hares for herbaceous shrubs, forbs, and grasses in spring. Spruce grouse may have experienced increased predation risk because more grouse predators were observed on food 1 during the low and increase phases.

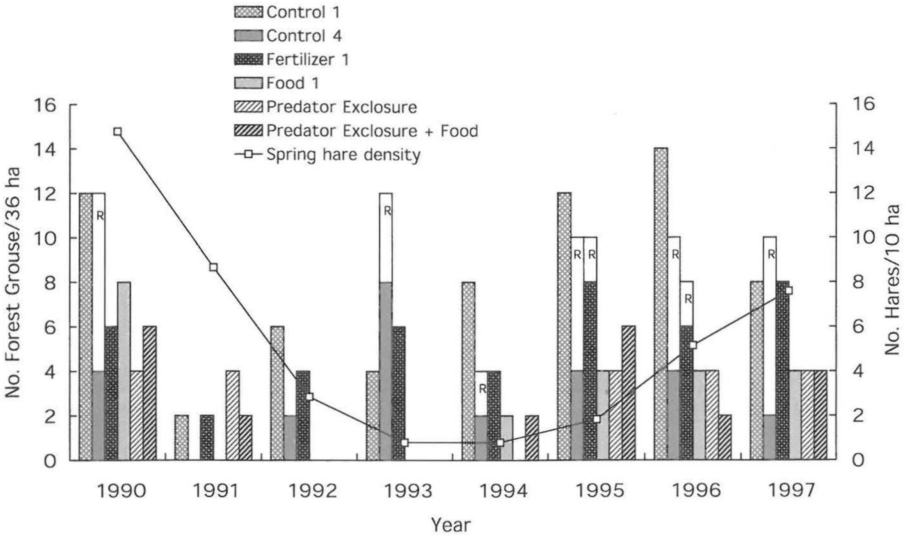


Figure 11.4 Numbers of spruce grouse (filled bars) and ruffed grouse (clear bars labeled R) estimated on control and treatment plots (36 ha each) from the dawn census using playbacks of female cantus calls in late April to early May, 1990–1997, across the hare cycle (spring hare densities as lines). Population size was estimated by doubling the count of the maximum number of birds of one sex (either sex) on the grid in one of three survey mornings.

11.4.3 Predator Exclosure

Risk from mammalian predators was largely removed and the monofilament cover over part of the plot reduced the risk from avian predators, but this would have affected only a few spruce grouse individuals when they were on or close to the ground. Although the predator exclosure had the lowest abundance of grouse in 1990, it was the only plot that remained similar in density in 1991 (figure 11.4). For the next 3 years, we found no spruce grouse on this plot. Grouse reoccupied the plot in 1995, and densities remained at 1990 levels for the next 3 years. The predator exclosure treatment possibly delayed the spruce grouse decline by 1 year. In 1991 we encountered only five spruce grouse in 61 h of search across all plots, and the only female we located was under the monofilament in the predator exclosure plot. Positive effects of the monofilament might have been offset by two pairs of great horned owls nesting near the area (see chapter 15).

11.4.4 Predator Exclosure + Food

Numbers of spruce grouse declined from 1990 to none or two birds for the next 4 years (figure 11.4). Numbers recovered by 1995, but decreased subsequently. Hares remained at or above control peak levels until 1993, and ground squirrels remained high through 1996 (Krebs et al. 1995; see figure 9.10). Although risk from mammalian predators was removed, extensive overbrowsing by hares reduced ground cover in some sections such that risk from avian predators might have increased. In addition, grouse may have continued to experience high predation risk here if avian predators concentrated activities on this plot. Natural vegetation was strongly affected, despite food addition, as both hares and ground squirrels were maintained at high densities for 4 years on this plot (Krebs et al. 1995; see chapters 8 and 9). Thus, spruce grouse possibly competed with ground squirrels and hares for the remaining herbaceous shrubs and forbs in spring.

11.5. Discussion

11.5.1 Hypotheses Related to Grouse Population Trends

Our results suggest that densities of all grouse in the valley were strongly influenced by the hare cycle. We found the strongest support for the predator regulation hypothesis because grouse body condition and fecundity measures did not decrease across the hare decline. Grouse appeared to decline due to harvest bycatch by predators when hares were still abundant. The goshawk was the only predator observed switching to grouse during the hare decline (see chapter 16). At the low of the hare cycle, avian predators might switch during the winter to young-of-the-year grouse. This switch could explain the slow recovery of grouse, despite good summer production. Thus, grouse may require mainly a reduction in predation to permit density increase. We have little evidence for bottom-up regulation, but because little direct work was done on grouse foraging and competition with other herbivores, we incur the usual risk of biological error associated with nonequivalent testing of alternative hypotheses.

11.5.2 Did the Experiments Change the Dynamics for Grouse?

The major treatments failed to change grouse population dynamics. However, our census grids were small given the spatial scale and patchy distribution of forest grouse. We observed a possible delay of 1 year in decline of spruce grouse on the predator exclosure (with monofilament) plot. Fertilizer 1 had the least severe decline, the most rapid recovery of grouse, and postfertilization numbers exceeded 1990 levels (figure 11.4). Given these qualitative patterns, the simplest model to predict density changes for grouse is a top-down predator control model that primarily influences survival of adult grouse just before the peak of hare populations.

11.5.3 Linkages on the Same Trophic Level

Except for females with broods, spruce grouse feed primarily on spruce needles and ruffed grouse on aspen, and competition with other major herbivores is not expected to be strong, especially since grouse can access the upper parts of trees that are unavailable to hares. Hares may compete with ptarmigan in winter as both species rely on willow, but we expect the magnitude of competitive interactions to be small because ptarmigan select more open areas than hares and willow is abundant.

The relative contribution of forest grouse to the overall herbivore biomass in the Kluane vertebrate community varied from <1% at the peak to 5–6% at the low (see figure

1.2). Hare demography just before the hare peak had a large impact, via predators, on the density of forest grouse in summer and likely all grouse in winter.

11.5.4 Linkages to Other Trophic Levels

Trophic Level Above In the Kluane ecosystem, most predator species can integrate over a spatial scale from valley bottom to the alpine and thus can prey on grouse year-round. Most avian and mammalian predators present in Kluane were recorded feeding on adult or juvenile grouse (see figure 2.8). However, the magnitude of trophic interactions between grouse and their predators was asymmetrical. Predators usually have a large impact on population dynamics of most grouse (Braun et al. 1993, Hannon et al. 1998), and this appeared to be the case in Kluane. Predation on adult grouse in winter and early spring appeared to be responsible for the crash in grouse populations. Many grouse mortalities were found in 1990 and 1991, but no one predator species appeared to be responsible for the grouse declines.

We have no compelling evidence that grouse had a large impact on the population dynamics of any predator species, except during the low. Grouse were a minor diet item for most predators examined; they comprised 1% of 208 kills by coyotes and 2.5% of 572 kills by lynx, and furthermore 56% of 16 recorded grouse kills occurred when hares were still abundant (see chapter 14). Over the study, data on prey remains and pellets at raptor nests indicated that grouse composed 20% of diet items for goshawks and less for northern harriers, red-tailed hawks, and great horned owls (see chapters 15, 16). During the low, red squirrels were the most important alternative prey, but great horned owls, harriers, red-tailed hawks, and goshawks all preyed on grouse during this period. Thus, grouse may be most important to avian predators when both they and hares are at low densities, as they contributed to maintaining the few remaining individuals of several predator species. At the hare low, grouse comprised about 80% of the diet for the only breeding pair of goshawks left on the study (chapter 16).

Trophic Level Below All grouse are primarily herbivorous. Spruce grouse foraging on new needles can have a significant impact on individual spruce trees and occasionally on patches of trees (Mueller 1993). The impact of spruce grouse herbivory on spruce trees was quite localized at wintering sites and may have been mitigated by feces deposition in this nutrient-limited system. During winter, ptarmigan flocks move irregularly over distances of up to 50 km (Hannon et al. 1998) and thus local impact on willow by ptarmigan is likely minimal.

Importance of Interactions for the Community The association of ruffed grouse with aspen and spruce grouse with conifer may result in a rather even availability of grouse biomass to boreal forest predators. Because coniferous forest is predominant in Kluane, spruce grouse contributed about 85% of forest grouse biomass in summer (figure 11.2; 91% of grouse located/search hour). In winter, both species occur in flocks, and given their similarities in body mass and apparent vulnerability to predation at Kluane, spruce and ruffed grouse may be interchangeable prey for most mid-sized and larger predators. Ptarmigan augment the prey base year-round for predators because they winter in open willow areas at lower elevations and because goshawks and harriers hunt for them at high elevation in summer. The overlap of the forest and tundra grouse may increase the reliability of the winter food supply to predators. Winter concentrations of grouse may be vital to maintaining low densities of several avian predator species during the hare low.

11.6 Conclusions

11.6.1 Comparison with Other Studies

The timing of the forest grouse and hare peaks and declines at Kluane agree with previously documented fluctuations of ruffed grouse in southern populations where grouse decline in abundance 1 year ahead of hare declines (Keith and Rusch 1986). Spruce grouse and snowshoe hares are sympatric over much of their ranges, but despite several long-term grouse population studies, the Kluane study is the first to record a strong cycle in numbers of breeding and wintering spruce grouse in synchrony with hare densities. Annual harvest data in the Yukon support the hypothesis of spruce grouse cycling with hare densities. Peak numbers of spruce grouse were harvested in the autumn of 1989 (in agreement with peak abundance data for Kluane) and 11 years earlier in 1978, and lows were recorded in 1982 and 1992 (last year reported; Mossop 1994). Cyclicity has also been observed in Alaskan spruce grouse (D. Mossop, personal communication). In northern Ontario, where snowshoe hares cycle, and elsewhere, there is little evidence of spruce grouse and hare densities changing in synchrony (J. F. Bendell and D. M. Keppie personal communications). Other spruce grouse populations studied do not coexist with cyclic populations of snowshoe hares (Fritz 1979, Keppie 1987, Boag and Schroeder 1992).

Reproductive potential of Kluane spruce grouse females was exceptional. The mean clutch size of 8.7 + 0.2 S.E. eggs ($n = 26$ clutches, range 7–11 eggs) for Kluane spruce grouse was 3.1 eggs more than previously reported for the species (Keppie 1982). Furthermore, clutch size varied over the study with the largest clutches being laid during the low. Other researchers have not recorded density-dependent effects of clutch size for grouse or ptarmigan (D. M. Keppie unpublished data for three other spruce grouse populations in Canada; Hannon and Martin 1996).

Ptarmigan normally cycle with periods between peaks of 8–11 years in North America (Hannon et al. 1998), 4–5 years in England, 4–8 years in Scotland for red grouse (Jenkins et al. 1963), 3–4 years for willow grouse in Norway (Myrberget 1984), and 10 years for rock ptarmigan in Iceland (Nielsen 1999). Angelstam et al. (1985), Hannon (1986), and Bergerud (1988) summarized hypotheses to explain population changes in grouse. Regulation may occur through predation or starvation in winter, by territorial or spacing behavior in spring or autumn, by variation in chick production, or by internal parasite loads during the breeding season (Hudson 1992, Hudson et al. 1998, but see Moss et al. 1996). In most studies, alternative hypotheses were not tested simultaneously. Although there is no overall agreement on mechanisms of population change despite numerous experiments and long-term correlative studies, data for unmanaged grouse with natural population densities tend to support top-down regulation by predators often mediated by densities of keystone herbivores. The keystone herbivores are microtine mammals in Fennoscandia (Angelstam et al. 1985) and hares in the Yukon (this study), Alberta, and Wisconsin (Keith 1963, 1990). In Iceland, rock ptarmigan is the keystone herbivore for gyrfalcons (Nielsen 1999). The critical period for rock ptarmigan in Iceland is during autumn and winter, and during decline years, mortality in this period increases greatly, especially for juveniles (O. Nielsen personal communication). Our study provides indirect evidence that grouse in the Yukon are also vulnerable during the same period. Studies of managed populations of grouse in England and Scotland, with greatly elevated densities and predator control, have found more support for bottom-up limitations of populations through food quality, maternal condition, or intrinsic factors such as weather (Moss and Watson 1984, Watson et al. 1998), as well as through kin-selection social behaviors (Watson et al. 1994).

11.6.2 Unexpected Results

Despite five species of grouse in the Kluane system at reasonable densities, grouse did not appear to be important alternative prey for predators during the hare decline as reported for other studies which had the same predator species (Keith 1963, Nellis et al. 1972, Brand et al. 1976). However, grouse and red squirrels (chapter 9) were important alternative prey in the hare low during winter for maintaining the few predators remaining in the Kluane system.

The Kluane study is the first to record a cycle in spruce grouse in synchrony with the snowshoe hare cycle. There was at least a 75% decline in spring spruce grouse numbers as they had already begun their decline before the start of the dawn census counts in 1990. Also, there was a 10-fold reduction in encounter rates of spruce grouse in winter over a 2-year period from the peak in 1989–1990 (from the seen-sheet data). Density changes of this magnitude over 2–3 years have not been observed in other long-term population studies where the habitat remained unaltered (Boag and Schroeder 1992). After the population decline in 1991, we observed a dramatic behavioral shift, with the remaining spruce grouse being perceptibly wilder and more wary. This is a reasonable response by species undergoing intense predation pressure, but such behavioral shifts have not been recorded for forest or alpine grouse. However, Alden (1947) noted that surviving ruffed grouse during cyclic lows are wilder when being hunted than birds at peak population densities in Pennsylvania.

Despite high predator densities during the hare peak and decline, spruce grouse nesting and fledging success, which was comparable to other populations (Boag and Schroeder 1992), did not change. These results are in marked contrast to hares, where production of 15–19 leverets/summer/female in the increase/peak phase collapsed to about 6.9 in the decline phase (see chapter 8, figure 8.5). Reproduction of hares did not increase again until just after the low. Hares also appeared to show predation risk-induced stress (Boonstra et al. 1998), presumably because they can never reduce their exposure and vulnerability (Krebs et al. 1998). Grouse that survived into the low must have been significantly less vulnerable to predation than those during the decline, as we found high annual survival at the low. Grouse survivors in the low phase may have adopted risk-averse behaviors as suggested for red squirrels, and both possibly used spruce trees as shields against predators (chapter 9).

Despite the dependence of goshawks on grouse at the low phase, grouse maintained their breeding densities at this time. These enigmatic results for grouse may be explained by their migration patterns. There is a partial independence of populations in summer, winter, and during spring and autumn migration in the Kluane system (Boag and Schroeder 1992) that may allow sharing of the local predation risk load with individuals from a considerably larger geographic area. Since ptarmigan can disperse up to 90 km from breeding areas to winter sites, summer and winter populations do not have all the same individuals (Gruys 1993, Hannon et al. 1998). Extensive external dispersal and population rescue are documented for most ptarmigan and forest grouse populations (Small et al. 1991, Beaudette and Keppie 1992, Gruys 1993) and contribute increased stability to grouse breeding densities (Martin et al. 2000).

11.6.3 Unanswered Questions

Forest grouse in the southwestern Yukon have received little study and appear to differ in several life-history parameters from southern and eastern populations. Spruce grouse in Kluane are larger and heavier, have higher potential fecundity, and differ in male and possibly female displays from other populations (unpublished data). The behavioral responses to elevated predation risk in the low phase are fascinating and merit further study. Much remains unknown about migration patterns, scale of dispersal, and life-history differences for all Kluane grouse species—vital information for understanding population dynamics processes and for effective management (Martin 1998).

The Kluane grouse study has precipitated fascinating questions regarding the ecological factors that start and entrain cycles. Why do ruffed grouse and ptarmigan cycle regularly, whereas blue grouse and spruce grouse generally do not? Ruffed grouse do not exhibit cycles in all areas; regular cycles are less prevalent in southern and eastern North America (Keith 1963). We need to address questions about inducing species to exhibit cyclic behavior in locations where forest grouse are regionally sympatric with cyclic alpine grouse such as in Alaska and northwestern Canada to determine which ecological conditions must apply before spruce grouse exhibit cyclic population dynamics with coexisting hares. When forest and alpine grouse assemblages overlap in winter, it may allow interspecific population phenomena at a regional scale, which could result in the cyclicity of one species that might be noncyclic in most of its range.

Literature Cited

Alden, J. A. 1947. Ruffed grouse. A. A. Knight Knopf, New York.

Angelstam, P., E. Lindstrom, and P. Widen. 1985. Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia—occurrence and distribution. Holarctic Ecology **8**:285–298.

Beaudette, P. D., and D. M. Keppie. 1992. Survival of dispersing spruce grouse. Canadian Journal of Zoology **70**:693–697.

Bendell, J. F., and P. W. Elliott. 1967. Behaviour and the regulation of numbers in blue grouse. Canadian Wildlife Service Report Series, no. 4. Department of Indian Affairs and Northern Development, Ottawa. Pages 1–76.

Bergerud, A. T. 1988. Mating systems in grouse. *in* A. T. Bergerud and M. W. Gratson (eds). Adaptive strategies and population ecology of northern grouse, pages 439–472. University of Minnesota Press, Minneapolis.

Bergerud, A. T., and M. W. Gratson (eds). 1988. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis.

Boag, D. A., and M. A. Schroeder. 1987. Population fluctuations in spruce grouse: what determines their number in spring? Canadian Journal of Zoology **65**:2430–2435.

Boag, D. A., and M. A. Schroeder. 1992. Spruce grouse (*Dendragapus canadensis*). *in* A. Poole, P. Stettenheim, and F. Gill (eds). The birds of North America, no. 5. American Ornithologists' Union, Washington, DC.

Boonstra, R., D. Hik, G. R. Singleton, and A. Tinnikov. 1998. The impact of predator-induced stress on the snowshoe hare cycle. Ecological Monographs **68**:371–394.

Boutin, S., C. J. Krebs, R. Boonstra, M. R. T. Dale, S. J. Hannon, K. Martin, A. R. E. Sinclair, J. N. M. Smith, R. Turkington, M. Blower, A. Byrom, F. I. Doyle, C. Doyle, D. S. Hik, L. Hofer, A. Hubbs, T. Karels, D. L. Murray, V. O. Nams, M. O'Donoghue, C. Rohner, and S. Schweiger. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. Oikos **74**:69–80.

Brand, C. J., L. B. Keith, and C. A. Fischer. 1976. Lynx responses to changing hare densities in central Alberta. Journal of Wildlife Management **40**:416–428.

Braun, C. E., K. Martin, and L. A. Robb. 1993. White-tailed ptarmigan (*Lagopus leucurus*). *in* A. Poole and F. Gill (eds). The birds of North America, no. 62. American Ornithologists' Union, Washington, DC.

Ellsworth, D. L., R. L. Honeycutt, and N. J. Silvy. 1995. Phylogenetic relationships among North American grouse inferred from restriction endonuclease of mitochondrial DNA. Condor **97**:492–502.

Fritz, R. S. 1979. Consequences of insular population structure: distribution and extinction of spruce grouse populations. Oecologica **42**:57–65.

Gruys, R. C. 1993. Autumn and winter movements and sexual segregation of willow ptarmigan. Arctic **46**:228–239.

Hannon, S. J. 1986. Intrinsic mechanisms and population regulation in grouse—a critique. Acta Congressus Internationalis Ornithologici **19**:2478–2489.

Hannon, S. J., P. K. Eason, and K. Martin. 1998. Willow ptarmigan (*Lagopus lagopus*). *in* A. Poole and F. Gill (eds). The birds of North America, no. 369. American Ornithologists' Union, Washington, DC.

Hannon, S. J., and R. C. Gruys. 1987. Patterns of predation in a willow ptarmigan population in northern Canada. International Grouse Symposium **4**:44–50.

Hannon, S. J., and K. Martin. 1996. Mate fidelity and divorce in ptarmigan: polygyny avoidance on the tundra. *in* J. M. Black (ed). Partnerships in birds: the study of monogamy, pages 192–210. Oxford University Press, Oxford.

Herzog, P. W., and D. A. Boag. 1977. Seasonal changes in aggressive behavior of female spruce grouse. Canadian Journal of Zoology **55**:1734–1739.

Hochachka, W. M., K. Martin, F. Doyle, and C. J. Krebs. 2000. Monitoring vertebrate populations using observational data. Canadian Journal of Zoology **78**:521–529.

Hudson, P. J. 1992. Grouse in space and time. The population biology of a managed gamebird. Game Conservancy Ltd, Fordingbridge, UK.

Hudson, P. J., A. P. Dobson, and D. Newborn. 1998. Preventing population cycles by parasite removal. Science **282**:2256–2258.

Jenkins, D., A. Watson, and G. R. Miller. 1963. Population studies on Red Grouse, *Lagopus lagopus scoticus* (Lath.) in north-east Scotland. Journal of Animal Ecology **32**:317–376.

Johnsgard, P. A. 1983. The grouse of the world. University of Nebraska Press, Lincoln.

Keith, L. B. 1963. Wildlife's ten year cycle. University of Wisconsin Press, Madison.

Keith, L. B. 1990. Dynamics of snowshoe hare populations. *in* H. H. Genoways (ed). Current mammalogy, pages 119–195. Plenum, New York.

Keith, L. B., and D. H. Rusch. 1986. Predation's role in the cyclic fluctuations of ruffed grouse. Acta Congressus Internationalis Ornithologici **19**:699–732.

Keppie, D. M. 1982. A difference in production and associated events in two races of spruce grouse. Canadian Journal of Zoology **60**:2116–2123.

Keppie, D. M. 1987. Impact of demographic parameters upon a population of spruce grouse in New Brunswick. Journal of Wildlife Management **51**:771–777.

Keppie, D. M. 1992. An audio index for male spruce grouse. Canadian Journal of Zoology **70**:307–313.

Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. Science **269**:1112–1115.

Krebs, C. J., A. R. E. Sinclair, R. Boonstra, S. Boutin, K. Martin, and J. N. M. Smith. 1998. Community dynamics of vertebrate herbivores—how can we untangle the web? *in* H. Olff, V. K. Brown, and R. H. Drent (eds). Herbivores: between plants and predators, pages 447–473. Blackwell Scientific Publications, Oxford.

Martin, K. 1998. The role of animal behavior studies in wildlife science and management. Wildlife Society Bulletin **26**:911–920.

Martin, K., S. J. Hannon, and R. F. Rockwell. 1989. Clutch size variation and patterns of attrition in fecundity of willow ptarmigan. Ecology **70**:1788–1799.

Martin, K., P. B. Stacey, and C. E. Braun. 2000. Recruitment, dispersal and demographic rescue in spatially-structured white-tailed ptarmigan populations with local and regional stochasticity. Condor **102**:503–516.

Mercer, W. E. 1967. Ecology of an island population of Newfoundland willow ptarmigan. Technical Bulletin No. 2. Newfoundland and Labrador Wildlife Service, St. John's, Canada.

Moss, R., and A. Watson. 1984. Maternal nutrition and breeding success of Scottish ptarmigan *Lagopus mutus*. Ibis **126**:212–220.

Moss, R., A. Watson, and R. Parr. 1996. Experimental prevention of a population cycle in red grouse. Ecology **77**:1512–1530.

Mossop, D. H. 1994. Trends in Yukon upland gamebird populations from long-term harvest analysis. Transactions of the 59th North American Wildlife and Natural Resources Conference, pp. 449–456.

Mueller, F. P. 1993. Herbivore-plant-soil interactions in the boreal forest: selective winter feeding by spruce grouse. MSc thesis. University of British Columbia, Vancouver.

Myrberget, S. 1984. Population cycles of willow grouse *Lagopus lagopus* on an island in northern Norway. Fauna Norv. Ser. C, Cinclus **7**:46–56.

Nellis, C. H., S. P. Wetmore, and L. B. Keith. 1972. Lynx-prey interactions in central Alberta. Journal of Wildlife Management **36**:320–329.

Nielsen, O. K. 1999. Gyrfalcon predation on ptarmigan: numerical and functional responses. Journal of Animal Ecology **68**:1034–1050.

Nugent, D. P., and D. A. Boag. 1982. Communication among territorial female spruce grouse. Canadian Journal of Zoology **60**:2624–2632.

Pelletier, L. 1996. Evaluation of aerial surveys of ptarmigan (*Lagopus spp.*). MSc thesis. University of British Columbia, Vancouver.

Pelletier, L., and C. J. Krebs. 1997. Line-transect sampling for estimating ptarmigan (*Lagopus spp.*) density. Canadian Journal of Zoology **75**:1185–1192.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology **9**:1–48.

Rusch, D. H., S. DeStefano, and D. Lauten. 2000. Ruffed grouse (*Bonasa umbellus*). *in* A. Poole and F. Gill (eds). The birds of North America, no. 515. American Ornithologists' Society, Washington, DC.

Schroeder, M. A. 1985. Behavioural differences of female spruce grouse undertaking short and long migrations. Condor **85**:281–286.

Schroeder, M. A., and D. A. Boag. 1989. Evaluation of a density index for territorial male spruce grouse. Journal of Wildlife Management **53**:475–478.

Small, R. J., J. C. Holzwart, and D. H. Rusch. 1991. Predation and hunting mortality of ruffed grouse in central Wisconsin. Journal of Wildlife Management **55**:513–521.

Watson, A., R. Moss, R. Parr, M. D. Mountford, and P. Rothery. 1994. Kin landownership, differential aggression between kin and non-kin, and population fluctuations in red grouse. Journal of Animal Ecology **53**:639–662.

Watson, A., R. Moss, and S. Rae. 1998. Population dynamic of Scottish Rock ptarmigan cycles. Ecology **79**:1174–1192.

Weeden, R. B. 1963. Management of ptarmigan in North America. Journal of Wildlife Management **27**:673–683.

Weeden, R. B. 1964. Spatial separation of sexes of rock and willow ptarmigan in winter. Auk **81**:534–541.

Zwickel, F. C., and J. F. Bendell. 1972. Blue grouse, habitat, and populations. International Ornithological Congress, Proceedings **15**:150–169.

Zwickel, F. C., and J. F. Bendell. 1985. Blue grouse—effects on, and influences of a changing forest. Forestry Chronicle **6**:185–188.