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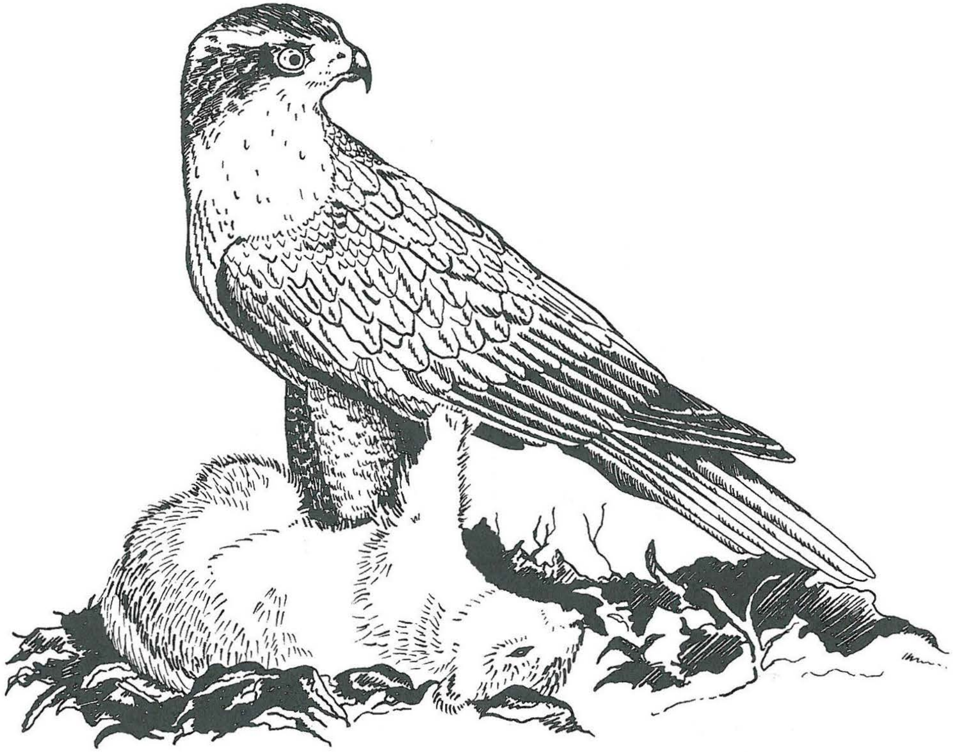
Raptors and Scavengers

FRANK I. DOYLE & JAMES N. M. SMITH



The principal study to date of the responses of raptorial birds to the snowshoe hare cycle was conducted by Lloyd Keith and colleagues in a mixed farmland/aspen parkland landscape at Rochester, Alberta. They found that great horned owls (*Bubo virginianus*) showed strong reproductive and numerical responses to hare abundance (McInvaille and Keith 1974, Adamcik et al. 1978). In contrast, red-tailed hawk (*Buteo jamaicensis*) numbers at Rochester remained stable, even though their reproductive success declined as hares disappeared from the prey base (Adamcik et al. 1979). In Alaska, numbers and breeding success of northern goshawks responded positively to increasing hare abundance (McGowan 1975). Also in Alaska, golden eagles (*Aquila chrysaetos*) reproduced more successfully during a period of high hare and ptarmigan abundance (McIntyre and Adams 1999). The community and population level responses of other raptors to vole cycles have been studied intensively in Europe (e.g., Korpimäki and Norrdahl 1991) and less intensively in temperate North America (e.g., Phelan and Robertson 1978).

Raptorial birds vary greatly in their migratory behavior (see below), but nearly all breed in territorial pairs that rear only a single brood of young per year (Newton 1979). Most raptors exhibit size and behavioral dimorphisms. Females are larger and are solely responsible for building and guarding the nest, incubation, and brooding. They feed small young with food brought to the nest by the male until the chicks are half grown, when the female also starts to hunt to help meet the increased food demands of the growing brood. In corvids, the sexes are more similar in size and share parental duties more evenly.

Raptorial and scavenging birds (hawks, owls, and corvids) composed a substantial fraction (21 of 87 species; table 16.1) of the vertebrates that we studied at Kluane. They varied in size from the 73-g gray jay (*Perisoreus canadensis*), which rarely eats prey larger than a nestling bird, to the 5-kg bald eagle (*Haliaeetus leucocephalus*) that consumes birds, fish, and mammals that often exceed its own mass.

Our aim in this chapter is to describe how these 21 avian predators and scavengers responded to the changes in prey through the hare cycle. Boutin et al. (1995) provided a preliminary account of these responses. For each of 12 breeding species, we describe diets and functional and numerical and reproductive responses to the hare cycle. We also provide some information on mortality factors affecting raptors.

16.1 Methods

16.1.1 General Approach

The methods used in studies of raptors have a long and successful history worldwide (Craighead and Craighead 1956, Newton 1979). Most previous research on avian predators and scavengers has been conducted in developed areas of North America (e.g., McInvaille and Keith 1974, Grant et al. 1991) and in the heavily managed forests of boreal Europe (Hörnfeldt 1978, Newton 1986, Korpimäki 1988, Hörnfeldt et al. 1990). In such areas, roads and tracks allow ready access by vehicle, and breeding pairs and nests can be found readily from the air or ground in open country and deciduous forests (e.g., Craighead and Craighead 1956, Luttich et al. 1971, McInvaille and Keith 1974, Grant et al. 1991). Also, nest boxes have often been used successfully for studying cavity-nesting species (e.g., Hörnfeldt and Eklund 1989, Korpimäki and Norrdahl 1991).

Table 16.1 Status of the 21 species of raptors present at Kluane.

Species	Status	Present Each Year	Breeds in Study Area	Breeds Every Year	Found throughout study area	Habitat
Great horned owl	C	Y	Y	N	Y	C, S, O
Northern hawk owl	C/R	N	Y	N	N	C, S
Short-eared owl	R	N	N	N	U	O
Boreal owl	C/R	U	Y	N	N	C
Saw-whet owl	R	N	N	N	U	U
Great gray owl	R	N	N	N	U	U
Red-tailed hawk	C	Y	Y	Y	Y	C, S, O
Rough-legged hawk	F	Y	N	N	N	C, S, O
Northern harrier	C	Y	Y	Y	Y	O
Gyrfalcon	R	N	N	N	U	O
Peregrine falcon	R	N	N	N	U	O
Merlin	F	Y	N	N	U	O
American kestrel	C	Y	Y	Y	N	O
Northern goshawk	C	Y	Y	Y	Y	C, S, O
Sharp-shinned hawk	R	Y	Y	U	U	S, O
Osprey	R	Y	N	N	U	L
Golden eagle	C	Y	Y	N	N	S, O
Bald eagle	C	Y	Y	N	N	C, S, O, L
Common raven	C	Y	Y	N	Y	C, S, O
Black-billed magpie	C	Y	Y	Y	N	S, O
Gray jay	C	Y	Y	Y	Y	C, S

F = frequently seen or heard (at least once a month); R = rare (<3 records per year) C/R = switched from common to rare; Y = yes; N = no. Habitat key: C = closed forest, O = open forest, S = shrubs/meadows, L = lakes, U = unknown.

Access to most of the Kluane study area was only possible on foot, and most raptor nests were in dense white spruce (*Picea glauca*) foliage and were not visible from the ground or air. We therefore needed to use new methods to assess population densities (e.g., Rohner and Doyle 1992a), and we had to conduct most surveys on foot. We chose not to use nest boxes extensively to avoid confounding our experimental design by increasing the densities of cavity-nesting species. A few nest boxes, however, were erected away from our study plots, and these proved useful for studying diets of boreal owls (*Aeglolus funereus*) and American kestrels (*Falco sparverius*).

For all raptor species and the two larger corvids, common ravens (*Corvus corax*) and black-billed magpies (*Pica pica*), we estimated the population density by mapping territories and nest sites within the "intensive search area" (see below) from March to July 1989–1995. Additional information was available for some species in 1988 and 1996. Three secretive species (northern goshawk, *Accipiter gentilis;* sharp-shinned hawk, *A. striatus;* and boreal owl) could not be enumerated as reliably as other breeding species (see below).

16.1.2 Population Surveys: The Intensive Search Area

We surveyed all species in a 100-km^2 area (see CD-ROM frame 68), that we called the "intensive search area." The intensive search area had habitats and prey species characteristic of the study area as a whole and included most of our experimental treatment plots. The entire intensive area was surveyed on transects 250 m apart each May and June. Transects were mostly walked at a steady pace from dawn to early afternoon (0430–1400 h), but some areas were covered at other times. Night surveys were mainly conducted from roads and tracks. The locations of individuals heard and seen by day and by night were mapped, and we searched for nests at the time or on later visits. In open areas, we looked for perching or flying raptors. In dense forest, we listened for calling raptors or alarm calls from prey and looked for plucking posts and whitewash.

These general methods provided estimates of numbers of breeding pairs in the intensive search area and samples of nests for assessing breeding success. Additional methods for particular species are described in the species accounts below. We also used data from additional nests outside the intensive search area to supplement our studies of diets and reproductive success.

To assist the small team of raptor specialists, we trained other project workers to identify raptors by sight and vocalizations. These reports provided indices of change in numbers for all raptor species and clues about the locations of pairs and nests for the specialists to follow up.

16.1.3 Reproductive Success

We obtained information on reproductive success by visiting nests after hatching and by counting large young in the nest shortly before fledging or newly fledged young near the nest. Because we generally did not check nests during incubation, we obtained few data on clutch sizes.

16.1.4 Diets

Traditional methods for studying raptor diets can be intrusive (e.g., the use of nest platforms and nest boxes; Newton 1979). Diets of most species at Kluane were only studied at natural nest sites, although we used nestling platforms for horned owls in some years (see chapter 15). We minimized disturbance at nests early in the breeding season (when adults and chicks are most vulnerable to food shortages and poor weather) by only beginning to visit nests when young were about 1 week old. Regurgitated pellets and prey remains left near nests provided most information on diets. In a few species (northern hawk owl, American kestrel, northern goshawk, northern harrier), information from pellets and remains was supported by direct observations from blinds or natural vantage points.

Pellets and Prey Remains Pellets were collected every 2–5 days at nest sites and oven dried at 60°C for 48 h. Pellets were then teased apart (Marti 1987), and prey species were identified using skeletal, nail, beak, dental, hair (color, banding patterns, scale and cell pattern), and feather (color, shape, and size) traits. We maintained a reference collection of local prey specimens and also used the collections of Cowan Vertebrate Museum at the University of British Columbia and published keys (Moore et al. 1974, Kennedy and Carbyn 1981). All prey individuals in pellets were counted, using the minimum number of individuals possible from the diagnostic fragments found (e.g., three left jaws of a species = three individuals; Rohner et al. 1995). Prey remains were collected at the same time as pellets from in and around raptor nests. We also sexed and aged individual prey when the remains allowed us to do so (see Doyle and Smith 1994).

We obtained other information on raptor diets from chance encounters with birds consuming prey. Although such information is probably biased toward larger prey, which take longer to consume, these encounters provided data on diets outside the breeding season and revealed some surprising linkages between predators at Kluane.

Radio Tagged Prey Part of the population of several larger prey species (spruce grouse, red squirrel, ground squirrel, and snowshoe hare) was radio tagged throughout the study. These collared prey were monitored daily, and we could often determine the identity of their killers.

Scavenging Experiment We set up a scavenging experiment to estimate rates of removal of dead radio-collared hares. Twenty road-killed hare carcasses were fitted with radio collars and laid out on the snow surface in March 1991 and checked daily. Tracks or wing marks in the snow or location of the radio collar often revealed the identity of the scavengers of these carcasses.

16.1.5 Data Analysis

We related raptor and corvid population densities and breeding success to fluctuations in prey population density and the timing of breeding in spring using linear and logarithmic regression and Pearson and Spearman correlation coefficients. Because the number of study years was limited and many species were studied, we used correlation coefficients primarily as descriptions of data. Hare densities in spring were mean values from all control grids (chapter 8). Densities of squirrels and voles were taken from chapters 9 and 10, respectively.

We used Levins's (1968) niche width index, $B = 1/p_j^2$ where p_j is the proportion of prey taxon j in the diet, to quantify the diet breadths of raptors. This index ranges from 1 to n, where 1 is the narrowest diet width possible.

16.2 Predicted Responses of Raptors and Corvids

We expected the large resident species that feed on hares in winter (horned owl, goshawk) to show strong numerical and reproductive responses to varying hare densities (Adamcik et al. 1978, chapter 15) and to broaden their diets to include alternative prey as hare populations declined. Based on previous work (Adamcik et al. 1979), we did not expect a strong population response from the migratory red-tailed hawk, but we expected all larger raptors to show functional responses to hares near the peak of the cycle. Because of the large spatial scales at which most of these birds operate, we did not expect to see strong responses to our experimental treatments (but see chapter 15 for an exception). As a result, we did not routinely compare data from different experimental treatments.

We expected the small raptors to depend on small prey species and not to respond directly to changes in hare numbers. We looked, however, for indirect effects in the food web (Bonsall and Hassell 1998)—for example, release from predation (Crooks and Soulé 1999)—that could influence these small species. We expected corvids to respond positively to the hare peak because of increased scavenging opportunities at high hare numbers.

16.3 Responses by Groups and Individual Species

We now treat each group of raptors in detail in light of these predictions. For each group, we first summarize patterns of diet and the functional, numerical, and reproductive responses to the hare cycle. We then present detailed information for each well-studied species, except for the horned owl, which was treated in detail in the previous chapter. We do, however, present some data for horned owls in the figures in this chapter to facilitate comparisons with other raptors. In the species accounts, we describe our methods and present data on diets and on functional responses to hares and other prey. We then consider numerical and reproductive responses. Information on body mass is taken from Dunning (1993) and from accounts in the *Birds of North America* series.

16.3.1 Large Resident Raptors

The large resident raptors group includes two species, the great horned owl and the northern goshawk, both of which varied strongly in abundance through the hare cycle (figure 16.1a,b). Both horned owls and goshawks fed heavily on hares when they were available, but the horned owl relied on hares to a greater extent than did the goshawk (tables 15.5, 16.2), and was unable to breed when hares were scarce (figure 16.2a). As a result, the horned owl showed a stronger numerical response to the hare cycle than the goshawk, and hare densities affected its dynamics with a 2-year lag (figure 16.1a).

Northern Goshawk Northern goshawks are large but inconspicuous forest hawks (mean female mass [MFM] = 1.14 kg, mean male mass [MMM] = 0.91 kg). Goshawks from the boreal forest are generally considered to be migratory (e.g., Mueller et al. 1977), but they were resident at Kluane. During the hare decline in 1990–1991, some goshawks may have migrated south in winter, but others remained resident and several birds died *in situ* that winter (Doyle and Smith 1994).

We trapped goshawks in late winter with falling-lid traps and fitted some individuals with tail-mounted radios (Doyle and Smith 1994; CD frames 23, 31), which allowed us to locate a sample of nests. Most nests were in dense spruce stands, often near water. Once nest sites were known, we checked these each spring and looked for additional nesting pairs by broadcasting female alarm calls (Squires and Reynolds 1997) and listening for responses.

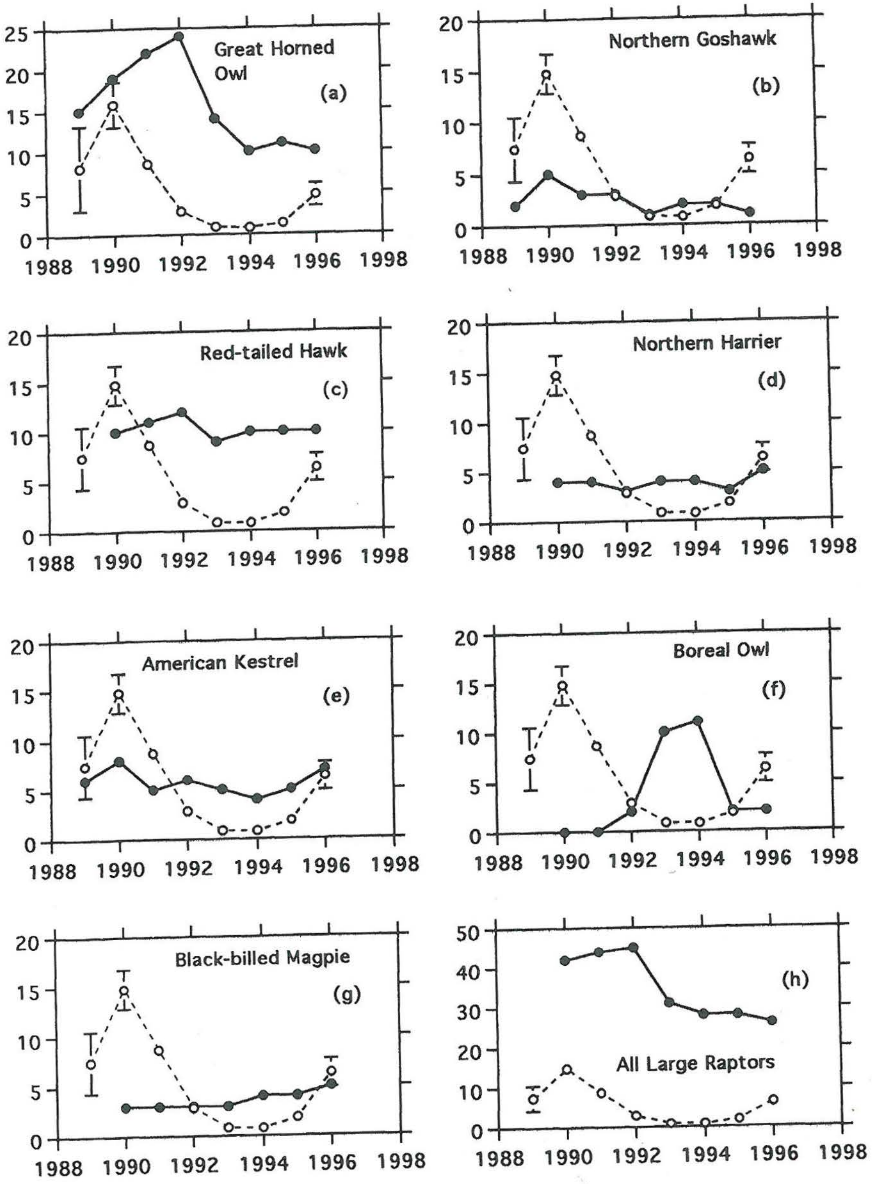


Figure 16.1 Numbers of breeding raptor pairs (filled circles) in standardized survey areas (methods vary with species; for details, see text) in relation to snowshoe hare densities in spring (hares/10 ha, open circles) at Kluane from 1989 to 1996.

As others have found (Squires and Reynolds 1997), goshawks had broad diets. They ate arctic ground squirrels, red squirrels, spruce grouse, ptarmigan, and other birds in summer, and they were the only raptors recorded eating northern flying squirrels (*Glaucomys sabrinus;* table 16.2). They did not, however, exhibit strong functional responses to any of these smaller prey species. During the hare peak, hares made 50% of the biomass of prey brought to nests, but a wide range of prey species continued to be eaten (table 16.2). When adult hares were dropped from the diet entirely in 1993, the biomass of grouse

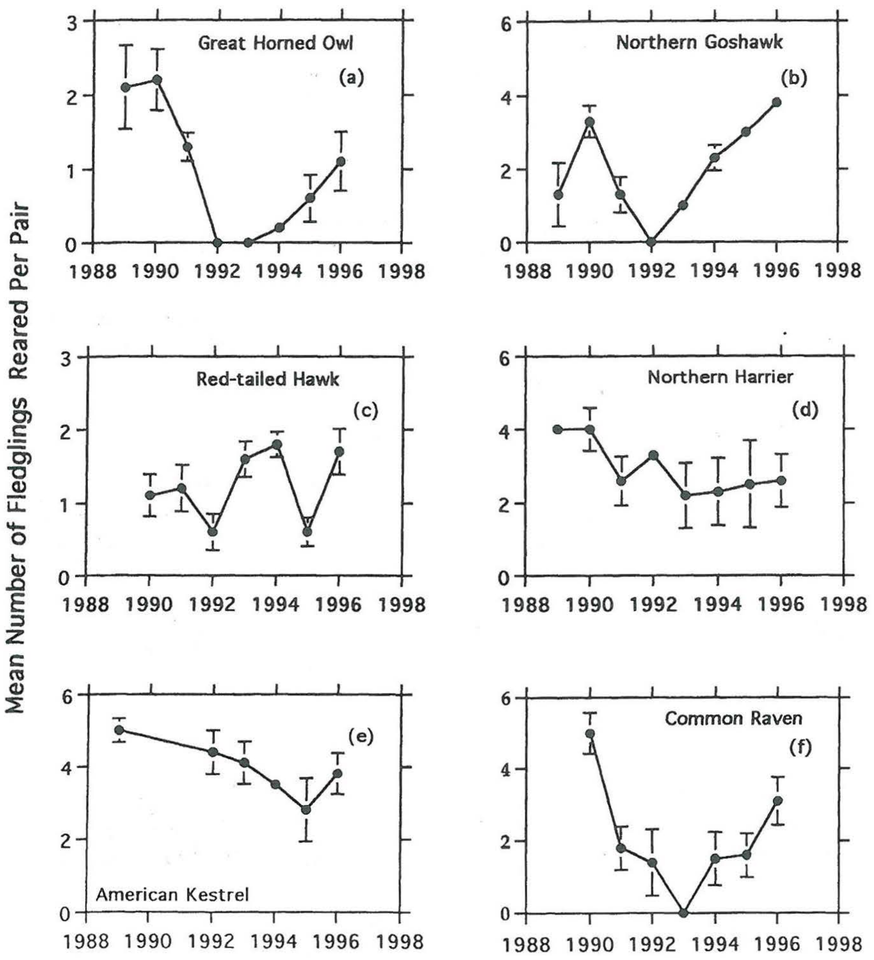


Figure 16.2 Annual variation in fledgling production by six species of predatory birds followed consistently through the hare cycle.

and ptarmigan eaten increased sharply and remained high through 1995 (table 16.2). Goshawks exhibited a type-1 or type-2 functional response to hare densities (figure 16.3a). They usually took live prey, but also fed on 2 of the 20 hares used in the scavenging experiment (C. Doyle personal communication, see also Squires and Reynolds 1997).

The number of territories in the intensive area (figure 16.1b), peaked at five in 1990, the year of peak hare numbers, and then declined to one by the summer of 1993. Goshawks showed a significant numerical response to spring hare densities ($r^2 = .537$, $p = .039$). Goshawks laid their eggs in late March and early April, with chicks fledging in the first and second week of July (figure 16.4). Successful nests were found in every year except 1992, and the number of young reared per pair was unrelated to hare density in spring (figure 16.5b).

Table 16.2 Diets and diet widths of northern goshawks during the breeding season each year.

Prey Species or Group	1989	1990	1991	1992	1993	1994	1995	1996
Lepus americanus (adult)	14	14	20	11	0	3	9	19
Lepus americanus (juvenile)	10	25	17	0	0	5	5	6
Spermophilus parryii	18	33	21	11	17	15	12	13
Tamiasciurus hudsonicus	34	4	21	0	8	19	9	19
Ptarmigan and grouse	13	14	11	22	33	37	38	21
Other birds	9	10	10	56	33	21	28	19
Glaucomys sabrinus	1	0	0	0	0	0	0	2
Mice and voles	1	0	0	0	8	0	0	0
Prey animals	91	229	81	9	14	73	66	47
No. of nests	3	8	4	1	1	3	3	3
Diet width (prey remains)	4.3	3.4	4	2.6	3.9	4.1	3.8	5.1

Values for each prey species are percentages of all individuals identified in pellets.

16.3.2 Large Migratory Raptors

The two species in the large migratory raptors group were the red-tailed hawk and the bald eagle. Red-tails were specialized predators of squirrels at Kluane. They showed a functional response to hare densities, but no numerical response. Bald eagles (MFM = 5.35 kg, MMM = 4.13 kg) were not studied intensively, and we thus do not consider them in detail. We did, however, find that some bald eagles shifted from being migrants to being resident near the peak of the hare cycle and that their reproductive success was low. Only 3 of 16 nesting attempts by the 2 resident pairs that bred near two large lakes in the study area (CD frame 68) were successful, with four chicks fledged in total.

Red-tailed Hawk Red-tailed (Harlan's) hawks of the northwestern boreal forest (*Buteo j. harlani*) are usually dark and often lack the red tail (Mindell 1983). Of the 21 species discussed here, this large migratory hawk (MFM = 1.22 kg, MMM = 1.03 kg) was 1 of only 4 raptors that bred at Kluane every year (table 16.1).

We studied red-tails from 1990 onward by noting the presence of soaring birds and following them to their traditional nest sites, which were then monitored annually. Variable plumage helped us to identify many individuals, which stood out due to the fortunate mix of dark- and light-phase morphs. Each year from 1990, 56–80% of birds had unique markings. Nests were usually near the top of an open spruce tree on the edge of a clearing or along a ridge. Pairs were regularly spaced throughout the study area (table 16.1; CD-ROM frame 68). Diets were estimated by climbing to accessible nests at the end of the breeding season to collect prey remains. Some nest trees, however, were too exposed to climb safely.

Red-tailed hawks elsewhere prey mainly on medium-sized mammals (e.g., Adamcik et al. 1979, Restani 1991). This was also true at Kluane. Arctic ground squirrels and red squirrels dominated the diet in 6 of 7 years, and these two squirrels made up >47% of diets at nests in all years (table 16.3). The proportion of pairs that successfully fledged young

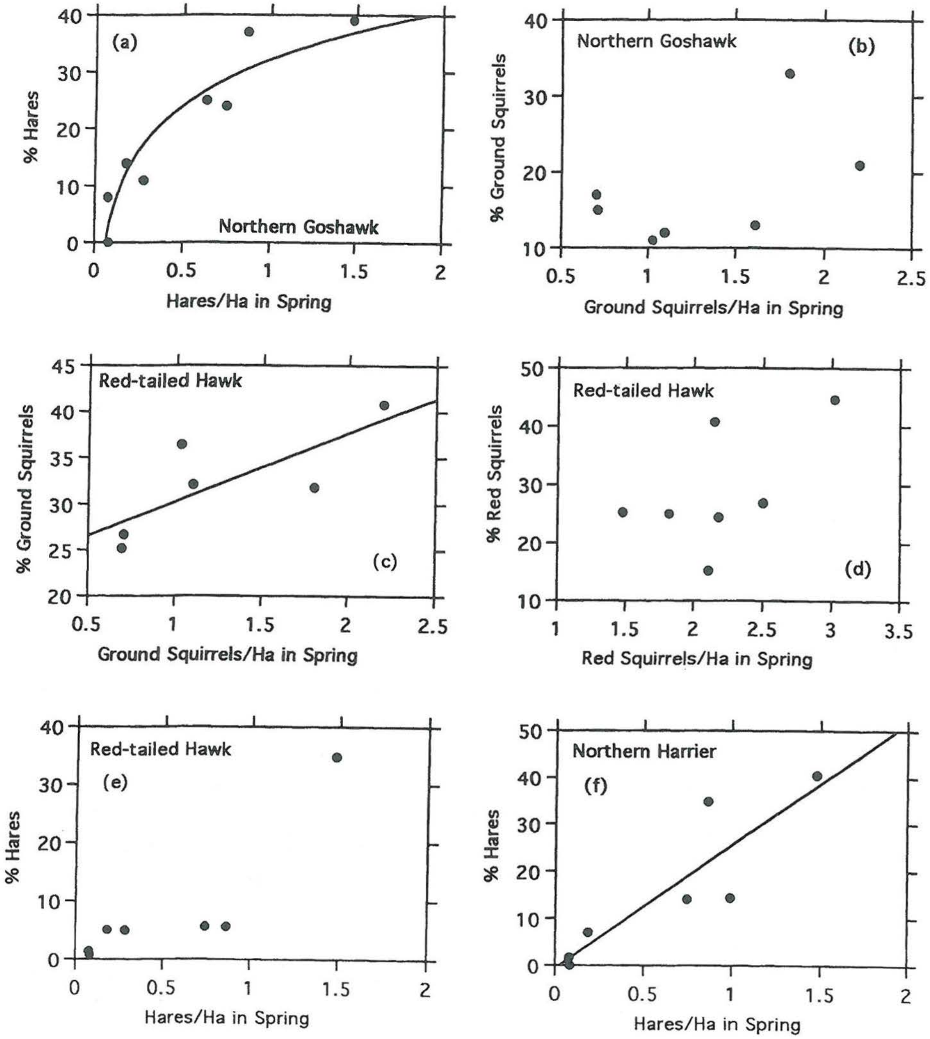


Figure 16.3 Functional responses by three species of predatory birds to changing prey densities. Best-fit lines or curves are shown when regressions were statistically significant ($p < .05$) and not dependent on a single outlying point.

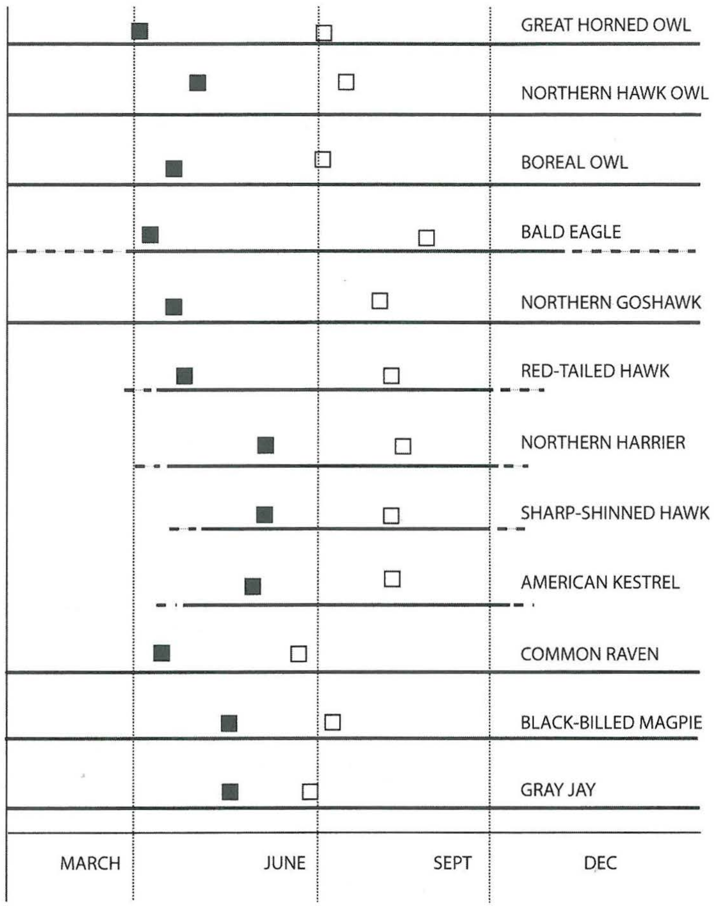


Figure 16.4 Timing of breeding by raptors and corvids at Kluane. Solid line = species present; dashed line = species' presence/absence alters annually; solid squares = timing of egg laying; open squares = timing of fledging.

was higher in years when young red squirrels ($r_s = .81, n = 8$) and arctic ground squirrels ($r_s = 1.0, n = 6$) emerged from the nest early (F. I. Doyle in preparation). The proportions of both squirrels brought to nests increased with their densities, but the relationship was tighter for the arctic ground squirrel (figures 16.3c,d). Hares were taken more frequently than any other prey only at the peak of the hare cycle in 1990, but otherwise were taken at similar frequencies regardless of hare density (figure 16.3e). Voles were taken commonly, particularly during the high vole years of 1992 and 1993 (table 16.3, chapter 10), but they contributed only a small portion of the total biomass of food brought to nests. Birds also contributed regularly to diets, but again the biomass consumed was small relative to that of squirrels (table 16.3). Weasels (*Mustela erminea* spp.) were taken on two occasions.

Unlike the goshawk and horned owl, neither the density nor the breeding success of red-tails was related to snowshoe hare densities (figures 16.1c, 16.2c). The density of occupied territories remained almost constant throughout the study (figure 16.1c), with only a slight increase in the numbers of females because of polygynous trios of a male and two females on three territories in 1991 and 1992 (Doyle 1995b). Breeding success was variable (figure 16.2c), but all known females attempted to breed each year. In 1992, the second year of the hare decline, 9 of 12 nests (75%) failed. Four of these failures were due to predation by horned owls; the cause of the other five failures was unknown. After this poor year, however, breeding success was high for the next 2 years (96% of 23 nests) and

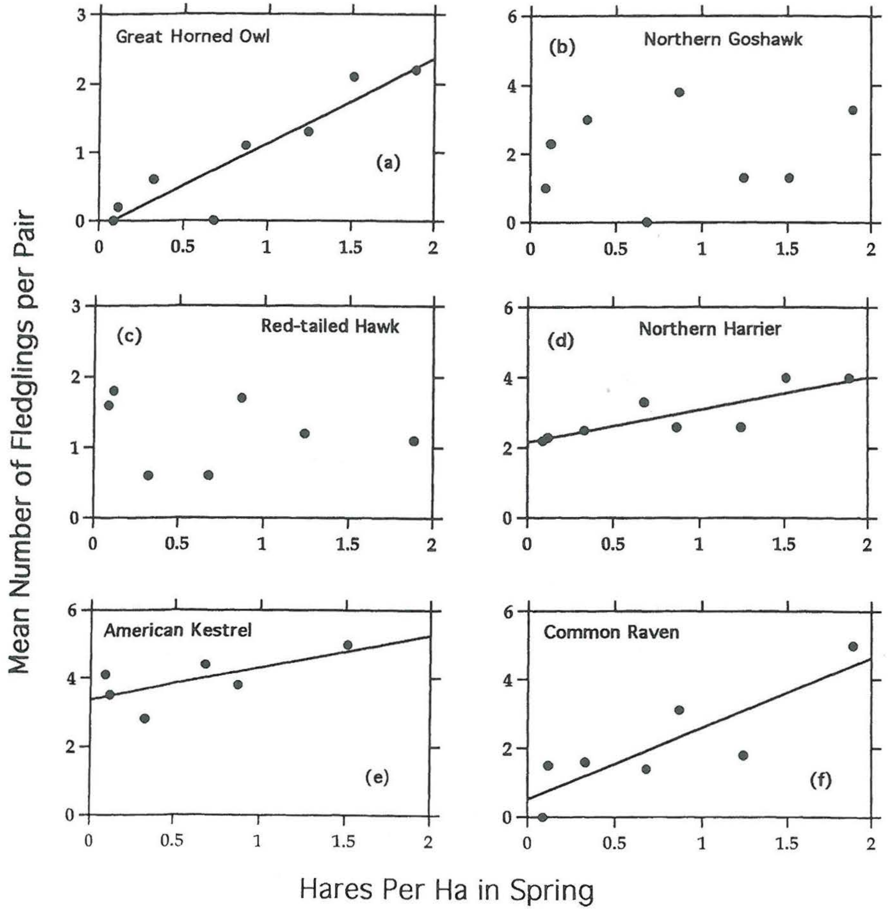


Figure 16.5 Reproductive responses of six predatory birds to variation in snowshoe hare densities in spring. Lines fitted by linear regression, where relationships where statistically significant.

in 1996 (figure 16.2c), but success was poor (44% of 16 nests) in 1995, a time of low hare and declining vole numbers.

16.3.3 Small Migratory Raptors

The small migratory raptors group included the medium-sized northern harrier and the small American kestrel and sharp-shinned hawk. All three species fed on juvenile hares, and the harrier did so extensively at the hare peak. The harrier exhibited both functional and reproductive responses to hare densities, and, to our surprise, the kestrel exhibited a numerical response.

Northern Harrier The northern harrier is a medium-sized (MFM = 513 g, MMM = 358 g), long-winged raptor, adapted to hunt near the ground and specialized to detect prey by sound as well as by sight (MacWhirter and Bildstein 1996). We studied these birds by watching open areas for courtship from a blind or from dense cover. Once nest building and incubation had begun, close observations of the female revealed the ground nest. Aggressive interactions with conspecifics and other species (particularly ravens) also helped us locate breeding sites.

Table 16.3 Diets and diet widths of red-tailed hawks during the breeding season each year.

Prey Species or Group	1989	1990	1991	1992	1993	1994	1995
Lepus americanus	5.6	34.8	5.6	5	0.8	1.4	5.1
Spermophilus parryii	31.5	31.8	40.8	36.4	25.2	26.7	32.1
Tamiasciurus hudsonicus	40.7	15.2	25.3	25	24.4	44.6	26.9
Birds	5.6	6.8	9.9	12.1	13.8	9.1	19.2
Voles	16.7	11.4	16.9	20.7	35	17.2	16.7
Mustelids	0	0	1.4	0	0	0.7	0
Eutamias minimus	0	0.8	0	0.7	0.8	0.4	0
Prey animals	54	132	143	139	244	284	78
No. of nests	2	7	6	4	8	14	7
Diet width	3.34	3.8	3.67	3.92	3.78	3.24	4.12

Values for each prey species are percentages of all individuals identified in pellets.

Harriers bred every year at Kluane in meadows and marshes (table 16.1), and their diets were studied every year except 1992. Harriers arrived in mid- to late April, and most suitable habitat was occupied by early May (table 16.4). Eggs were laid in late May to

Table 16.4 Diets and diet widths of northern harriers during the breeding season each year.

Prey Species or Group	1988	1989	1990	1991	1993	1994	1995
Lepus americanus	14.3	14	40.5	34.8	0	1.6	7
Spermophilus parryii	14.3	5.3	2.4	1.1	3.6	14.1	4.7
Tamiasciurus hudsonicus	10.7	1.8	0	4.3	3	2.1	4.7
Birds	21.4	14	26.2	42.4	26.2	26.7	40.7
Microtus pennsylvanicus	14.3	47.4	19	7.6	38.1	30.9	27.9
M. oeconomus	17.9	12.3	9.5	7.6	17.3	17.3	8.1
M. miurus	0	0	0	0	0.6	0	0
Phenacomys intermedius	0	1.8	0	0	2.4	2.1	2.3
Clethrionomys rutilus	3.4	0	0	1.1	7.1	2.6	0
Peromyscus maniculatus	0	0	0	1.1	0	0	1.2
Eutamias minimus	3.4	1.8	2.4	1.1	0	0.5	0
Shrews	0	1.8	0	1.1	0	0	2.3
Synaptomys borealis	0	0	0	0	1.8	1.6	1.2
Prey animals	28	57	42	92	168	191	86
No. of nests	1	1	2	5	5	6	3
Number of pellets	19	29	32	76	99	124	73
Diet width	6.5	3.5	3.6	3.2	4	4.6	3.8
Diet width (mice and voles summed)	4.4	2.4	3.2	3	2	2.6	2.9

Data from pellets at nests.

early June, and most young fledged by late July. Polygyny is common in southern populations of harriers (MacWhirter and Bildstein 1996), but we only noted monogamous pairs at Kluane.

MacWhirter and Bildstein (1996) reported that harriers in the northern part of their range feed almost entirely on small mammals. Harrier diets at Kluane were dominated numerically by voles and by smaller birds, and juvenile and subadult hares were taken commonly in 1990 and 1991 (table 16.4). Diet width did not change noticeably with changing hare densities, but snowshoe hares were dominant numerically in 1990 and in biomass in 1991. A few arctic ground squirrels, chipmunks, red squirrels, and shrews were also taken. Harriers occasionally fed on road kills along the Alaska Highway. A female harrier was also seen killing a wading bird, which was then stolen by an adult bald eagle (F. Doyle personal observation).

Harrier numbers were fairly stable through the hare cycle (figure 16.1d). The density of pairs fluctuated between 3 and 5 per 100 km ^{2}. Numbers and breeding success were unrelated to densities of either *Microtus* or *Clethrionomys* voles in either the same or in the previous year. During 3 years of high hare numbers (1989–1991) all eight nests fledged chicks, but only 12 of 19 nests (63%) were successful thereafter. Chick production was positively related to hare density in spring ($r^2 = .499, p = .05$; figure 16.5d).

American Kestrel The American kestrel was the smallest (MFM =120 g, MMM = 110 g) migratory raptor at Kluane. Pairs of this conspicuous species were often found perched around open meadows and marshland (table 16.1) near the Alaska Highway. By visiting these habitats, we located all breeding pairs within 500 m of the highway and located their nest cavities by subsequent intensive monitoring. Kestrels arrived in late March and early April, but egg laying did not begin until late May (table 16.4).

Prey brought by American kestrels to eight nests were identified using super 8 cameras in 1995 and 1996. At hatching, cameras were placed 10–20 m from the nest and were gradually moved closer until they were 2 m from the nest hole 2 weeks after hatching. The parent and its prey were photographed as the parent perched on a mechanical trigger at the edge of the nest hole. Voles, small birds, and least chipmunks (*Tamias minimus*) were the main prey (table 16.5). Insects, particularly dragonflies and grasshoppers, were taken more often than any one vertebrate prey, but they contributed little to the biomass delivered to nests. It is likely that hunting males fed mainly on insects while bringing mainly vertebrate prey to nests. The largest prey taken was a small juvenile snowshoe hare. A radio collar was found beneath a kestrel's nest cavity, with juvenile hare fur protruding from the nest hole. The kestrel was the only species at Kluane that ate an amphibian (a wood frog, *Rana sylvatica,* the only amphibian found at such northern latitudes in North America).

Relative densities (figure 16.1e) ranged from four to eight pairs per 12 km of highway over 9 years and were significantly correlated with hare densities in spring ($r^2 = .603, p = .023$), but not with vole densities in spring or in the previous summer. The proportion of successful nests varied from 70% in 1995 to 100% in 1989 and 1990, and the number of chicks fledged per nest (figure 16.2e) was unrelated to vole densities in either spring or summer. Two of six nest failures were due to predation; the other four failed from unknown causes.

Table 16.5 Diets and diet widths of American kestrels in the summers of 1995 and 1996.

Prey Species or Group	1995	1996
Voles	16.7	31
Tamias minimus	13.9	11.9
Small birds	30.6	20.8
Rana sylvatica	1.4	0.6
Shrews	0	0.6
Peromyscus maniculatus	0	0.6
Unidentifiable small mammals	0	10.1
Arthropods	37.5	24.4
Prey animals	72	168
No. of nests	3	5
Diet width	3.6	4.6

Data are from photographs of adults carrying prey at the nest entrance.

Sharp-shinned Hawk The small sharp-shinned hawk (MFM = 174 g, MMM = 103 g) is a specialized predator of small songbirds (Ehrlich et al. 1988). It was a regular, but rarely seen, summer migrant at Kluane (table 16.1). The sharp-shin was the breeding bird that we were least able to study successfully. To locate sharp-shinned hawks, we listened for vocalizations and broadcast their calls by tape recorder (Rohner and Doyle 1992b, Doyle and Smith 1994). The few breeding birds we located behaved inconspicuously, and few data were obtained on numbers or annual changes in diet. The sharp-shin was the last migrant raptor to arrive in the study area (in late April–early May). Egg laying began in late May and early June (figure 16.4), with the first young fledging in late July.

In 1992, prey remains were collected at two nest sites (table 16.6). As expected (Joy et al. 1994, Newton 1979), passerines dominated the diet. The Lapland longspur (*Calcarius lapponicus*), an early season migrant that does not breed at Kluane, was the most commonly taken species. The American robin (*Turdus migratorius*) and Swainson's thrush (*Catharus ustulatus*), two common and large passerines at Kluane (figure 12.2) were also important prey species. A juvenile hare was taken in 1992, when hares were scarce. One to three pairs per 100 km^2 were located annually (CD-ROM frame 68), and three nests found before fledging each fledged five chicks.

No sharp-shinned hawks were brought as prey to the nests by other raptors nor were any taken by mammalian predators in our study area. Thus, it appears that this species really was uncommon and not simply overlooked.

16.3.4 Small Owls

Two species of owls, the hawk owl and the boreal owl, made up the small owl group. They shared a primary diet of voles, and numbers of both species fluctuated, as they are known to do in Europe (Hörnfelt 1978, Sonerud 1997). Both species took juvenile hares, and hawk owls also preyed on adult hares. Boreal owls responded numerically to fluctuating vole numbers, and hawk owls responded numerically to combined hare and vole numbers.

Table 16.6 Diets of sharp-shinned hawks in summer 1992.

Prey Species	Percent
Calcarius lapponicus	21.9
Turdus migratorius	14.6
Catharus ustulatus	12.2
Dendroica coronata	12.2
Wilsonia citrina	7.3
Junco hyemalis	7.3
Bombycilla garrulus	4.9
Zonotrichia leucophrys	4.9
Sialia currucoides	2.4
Dendroica petechia	2.4
Dendroica striata	2.4
Hirundo pyrrhonota	2.4
Perisoreus canadensis	2.4
Lepus americanus (juvenile)	2.4
Prey animals	41
No. of nests	2

Data are from prey remains identified near nests.

Northern Hawk Owl The northern hawk owl (*Surnia ulula;* MFM = 345 g, MMM = 299 g) is noted for its unpredictable population dynamics in Europe (Sonerud 1997), and it sometimes irrupts south from the boreal forests of North America (Duncan and Duncan 1998). Hawk owls at Kluane often perched at the tops of snags close to the nest cavity, so their nests were readily located. They were resident in some years (figure 16.1). In other years, a few birds of unknown status were seen in spring and fall. Egg laying occurred in mid- to late April, and the chicks fledged by mid-June (figure 16.4).

The diets of hawk owls were dominated numerically by voles (table 16.7). However, during the 2 years of peak hare density (1989–1990), juvenile hares up to 240 g in size contributed considerably to biomass in nestling diets (Rohner et al. 1995). Diet width decreased in years with vole peaks and broadened in the 2 years of peak hare densities (table 16.7). Diets were dominated by *Microtus pennsylvannicus* and *M. oeconomus* in 1988 and 1993 when vole numbers were high (chapter 10). We were not surprised to find hawk owls preying on juvenile hares, but we were surprised that a supposed vole specialist ate both adult hares and spruce grouse (Rohner et al. 1995). A hawk owl ate 1 of 20 hares put out in the scavenging experiment in 1991 (C. Doyle personal communication).

Hawk owl numbers were highest (two pairs per 12 km^2 of highway transect) during the hare peak, and numbers were positively related to densities of snowshoe hares in spring ($r^2 = .502$, $p = .049$). Hawk owls were absent in 1992, bred again in 1993, but disappeared during the last 3 years. Only one nest failed, in 1991. Four or five chicks fledged from each of the seven successful nesting attempts. Hawk owl density increased in years of high combined hare and vole numbers ($r_s = .77$, $p = .07$, $n = 6$; details in Rohner et al. 1995).

Table 16.7 Summer diets (from Rohner et al. 1995) and diet widths of northern hawk owls for 4 years.

Prey Species or Group	1988	1989	1990	1993
Microtus pennsylvanicus	31.6	15	3.1	51.8
Microtus oeconomus	25.4	22.5	27.6	18.1
Microtus spp.	20.6	20	23.5	0
Synaptomys borealis	6.1	0	7.1	7.2
Peromyscus maniculatus	0.4	0	1	0
Phenacomys intermedius	7	5	9.2	7.2
Clethrionomys rutilus	0.9	10	7.1	7.2
Lepus americanus (juveniles)	3.5	15	14.3	0
Lepus americanus (adults)	0.4	2.5	0	0
Eutamias minimus	0.4	0	0	0
Tamasciurus hudsonicus	2.2	5	2	0
Spermophilus parryii	0	5	4.1	1.2
Mustela nivalis	0.4	0	1	1.2
Shrews	0	0	0	4.8
Dendragapus canadensis	0.4	0	0	0
Perisoreus canadensis	0.4	0	0	1.2
Prey animals	228	40	98	83
No. of nests	3	1	3	2
Diet width	4.6	6.5	5.8	3.1
Diet width (all mice and voles summed)	1.2	1.8	1.6	1.2

Data are percentages of individuals in pellets collected near nests.

Boreal Owl The small boreal (Tengmalm's) owl (MFM = 167 g, MMM = 101 g) is known as a nomad in Fennoscandia and, like the hawk owl, is known for its ability to track shifting patches of small mammal numbers (Korpimäki 1985). Like goshawks and hawk owls, boreal owls sometimes irrupt southward from North American boreal forests (Campbell et al. 1990, Hayward and Hayward 1993). We surveyed for boreal owls by listening during nocturnal transects and by broadcasting territorial hoots and listening for responses. Eggs were laid from late March to mid-April (figure 16.4).

Insufficient data were collected to examine diets of boreal owls across the hare cycle. Pellets from seven nests in 1994 (table 16.8) contained mostly voles (95%), supplemented by a few small birds and shrews. Heather voles, *Phenacomys intermedius,* and deer mice, *Peromyscus maniculatus,* two forest-dwelling small mammals, were taken much more by boreal owls than by any other raptor, suggesting that boreal owls foraged in closed forest more than other predatory birds (table 16.1). At one nest in 1995, shrews accounted for 15 of the 22 prey items; 2 juvenile hares were also taken. In a separate incident, a perched boreal owl was located eating a freshly killed, radio-tagged juvenile hare.

All nine nests studied produced young, with five chicks fledging from each of six nests in 1994, two from one nest in 1995, and three from one nest in 1996. Fledging success of boreal owls at Kluane was higher than is typical for other populations (Hayward and Hay-

Table 16.8 Summer diets of boreal owls in 1994 and 1995.

Prey Species or Group	1994	1995
Lepus americanus (juveniles)	0.5	9.1
Spermophilus parryii	0.9	0
Birds	5.1	9.1
Microtus pennsylvanicus	15.7	4.5
Microtus oeconomus	31.8	0
Mictotus miurus	9.2	0
Phenacomys intermedius	12.9	0
Clethrionomys rutilus	11.5	4.5
Peromyscus maniculatus	10.1	0
Soricidae	2.3	72.7
Prey animals	217	22
No. of nests	7	1
Diet width	5.6	1.8
Diet width (all voles and mice)	1.2	1.8

Data are percentages of individuals in pellets collected near nests.

ward 1993), perhaps because the principal predator of boreal owl nests, the marten (*Martes americana,* Hayward and Hayward 1993), was absent at Kluane.

Boreal owl numbers fluctuated sharply (figure 16.1f). However, breeding males did not always give territorial hoots in spring (see below), which adds uncertainty to our estimates of numbers. Boreal owls bred in the study area in 5 of 7 years from 1990 (table 16.1). Birds were concentrated in the northwest corner of the study area (CD-ROM frame 68). Numbers of calling males peaked at 11 per 24 km^2 of road transect in 1994 (figure 16.1f), and numbers were positively correlated with combined densities of *Microtus* and *Clethrionomys* voles the previous summer ($r^2 = .735, p = .014$).

16.3.5 Corvids

The three species of corvids at Kluane, common ravens, black-billed magpies, and gray jays, were studied in only moderate detail. Corvids are typically omnivores and scavengers, and this was also the case at Kluane. The large raven showed a strong reproductive response to the hare cycle, and the small gray jay responded to the supplemental feeding experiment by decreasing the sizes of its territories.

Common Raven The common raven is one of the world's largest passerines (MFM = 1.16 kg, MMM = 1.24 kg). Ravens were resident at Kluane, and adults were territorial (see also Ratcliff 1997). Young birds and nonbreeders were not studied at Kluane but are known to live in loose flocks elsewhere and to be subordinate to territorial adults (Heinrich 1994). Territorial ravens were highly visible, and their density was readily monitored from the highway because birds flying along the highway always turned around or flew away from the road at predictable places. Repeated observations of these points allowed us to map territories. Breeding began in mid-March, and eggs were laid in late March to early April (figure 16.4). Chicks fledged in early June.

The limited information available on raven diets corresponded with our expectations (Heinrich 1989, Ratcliff 1997) that they would be habitual scavengers and occasional predators. Ravens were frequently seen taking road-killed squirrels and hares and were regularly found at the remains of adult snowshoe hares killed in the winter. In the scavenging experiment in 1991, 16 of the 20 hares set out were eaten by ravens (C. Doyle personal communication). On another occasion, F. D. saw a pair of ravens attack and kill a juvenile male American kestrel as it left its nest cavity.

The density of breeding ravens was stable at 2/100 km^2, except from 1990 to 1992, at the peak in the snowshoe hare cycle, when a third pair established a territory for 2 years. The number of chicks fledged per pair was greater in springs with higher hare densities ($r^2 = .767, p = .01$; figure 16.2f), and no chicks were reared by four nesting pairs in 1993, at the nadir of the hare cycle (figure 16.2f).

Black-billed Magpie The black-billed magpie is a small (MFM = 166 g, MMM = 189 g) and conspicuous corvid that prefers open habitats and breeds in loose colonies (Birkhead 1991). Magpies at Kluane nested at the base of steep, open hillsides adjacent to a lakeshore. Nests were easily located from a high point or blind above the nest area, as birds called frequently while they carried nest material. Active nests were found every year, with egg laying in early May, and chicks fledging in mid-June (figure 16.4).

No quantitative information was collected on the diet of the magpie. We saw them foraging on open hillsides (probably for grasshoppers and other arthropods), on road-killed insects in the summer, and on road-killed mammals throughout the year. F. D. saw a magpie kill a red-backed vole that had just been released from a trap. Elsewhere, magpies primarily eat insects in summer (Linsdale 1937), but also carrion, birds' eggs, and small mammals. In winter, fruit and seeds form a large part of the diet (Birkhead 1991).

The density of pairs was stable at 3/100 km^2 from 1990 to 1993, and it increased to 5/100 km^2 by the end of the study in 1996 (figure 16.1g). The number of chicks fledging per nest ranged from 3 to 5 from 12 nests, with means ranging from 1.29 per pair in 1994 to 3.14 in 1995. The proportion of pairs fledging young ranged from 3 of 7 in 1994 to 4 of 5 in 1992, but information was not collected every year.

Gray Jay The gray jay, our smallest corvid (mean mass = 73 g), was resident throughout the study area in forested habitats (Delehanty 1995). Some gray jays were trapped in hare live traps and color banded in 1993 and 1994. They lived on territories of 15–25 ha (Delehanty 1995) and were the only predators or scavengers to respond numerically to the food addition treatment (see Chapter 12). Breeding pairs were located every year (table 16.1) when independent young jays joined their parents in mid-May, suggesting that most eggs were laid in late March or early April. In the two nests that we found, eggs were laid in early May and the chicks fledged in early June, unusually late dates for the species (Strickland and Ouellet 1993).

We lacked quantitative information on jay diets, reproduction, and densities through the cycle. Gray jays are omnivores, relying heavily on stored food in winter (Strickland and Ouellet 1993), and are probably major predators on the eggs and nestlings of shrub-nesting passerines at Kluane (Pelech 1999). A gray jay was seen killing a newborn snowshoe hare on one occasion (Sovell 1993).

16.3.6 Other Raptors

Nine other raptor species were seen in the study area (table 16.1). Some, like the small merlin (*Falco columbarius;* MFM = 218 g, MMM = 163 g) and large golden eagle (*Aquila chrysaetos;* MFM = 4.91 kg, MMM = 3.48 kg), were seen throughout summer every year and bred on the mountain slopes around the study area. Golden eagles are migrants at Kluane and in interior Alaska and arrive in late March or early April (McIntyre and Adams 1999). We have no information on their diets or breeding success, but they undoubtedly took snowshoe hares and arctic ground squirrels from our study area, and possibly also nestling red-tailed hawks and great horned owls. We kept an injured adult horned owl briefly, and it was extremely attentive to golden eagles soaring 1000 m above its perch. Merlins probably ate smaller birds in open habitats. Peregrine falcons (*Falco peregrinus*) were seen less frequently, but we believe that they also bred near Kluane.

The remaining species were all uncommon to rare. Two were annual migrants through the area: rough-legged hawks, *Buteo lagopus,* and ospreys, *Pandion haliaetus,* in spring and fall. Two of the four remaining species, gyrfalcons (*Falco rusticolus;* MFM = 1.76 kg, MMM = 1.17 kg) and short-eared owls (*Asio flammeus;* MFM = 378 g, MMM = 315 g), were only seen occasionally. A third species, the great gray owl (*Strix nebulosa;* MFM = 0.90 kg, MMM = 0.80 kg) is a boreal forest resident (Bull and Duncan 1993), but prefers moist forest habitat, which was scarce at Kluane. It was only seen once. Finally, the northern saw-whet owl (*Aegolius acadicus;* MFM = 91 g, MMM = 81 g) is at the very northern limit of its range at Kluane. A hooting male was heard in 1992.

16.3.7 Intraguild Predation

During our studies at Kluane, raptors sometimes killed each other, or mammalian predators took them (O'Donoghue et al. 1995). For example, a horned owl killed an adult female goshawk and her nestlings in 1991 (Rohner and Doyle 1992b), and a wolverine (*Gulo gulo*) killed and ate a second brood of goshawk nestlings in the same year (Doyle 1995a).

Most of our evidence for intraguild predation (O'Donoghue et al. 1995) came from raptor parts identified in the pellets or prey remains of other raptors. Raptor–raptor predation was surprisingly common. Fifty-two cases of intraguild predation by five avian and one mammalian predator species were accumulated over the hare cycle (table 16.9). Intraguild predation affected both large and small species. The abundant great horned owl was the most frequent predator on other raptors, including other horned owls (table 16.9). There were many more cases of predation on raptors by birds (42) than by mammals (6). Even young of the large bald eagle were taken (by a wolverine).

Intraguild predation rose sharply, particularly on broods of nestlings, in 1991, the first year of the snowshoe hare decline (figure 16.6). It remained common for the next 3 years, but declined sharply in 1995 (figure 16.6).

We suspected that predation risk had strong behavioral effects on the predatory birds at Kluane. Young "floater" horned owls behaved inconspicuously and did not hoot (chapter 15). Breeding boreal owls, which are often eaten by larger predators (Hayward and Hayward 1993; table 16.9), seldom gave territorial hoots in 1992 and 1993, during the peak period of intraguild predation (figure 16.6). On one occasion when we broadcast boreal owl hoots, an adult horned owl flew in silently to the speaker.

Table 16.9 Cases of intraguild predation involving raptors over the study.

Predator Species	Prey Species									
	HO	NG	RTH	NH	RV	NHO	BO	AK	BE	UNK	Total
Horned owl	2	5	4	1	1	4	2	0	0	0	19
Northern goshawk	0	0	0	0	0	1	0	2	0	2	5
Red-tailed hawk	0	0	0	0	0	0	4	1	0	0	5
Northern harrier	0	0	0	0	0	1	0	1	0	2	4
Raven	0	0	0	0	0	0	0	1	0	0	1
Unknown bird	2	0	3	0	0	2	0	1	0	1	9
Wolverine	1	1	0	0	0	0	0	0	1	0	3
Unknown mammal	0	0	0	4	0	0	0	0	0	0	4
Unknown	0	1	1	0	0	0	0	0	0	0	2
Total	5	7	8	5	1	8	6	6	1	5	52

Cases include depredation of young at nests and killed fledglings and adult birds in summer and winter. HO = horned owl, NG = northern goshawk, RTH = red-tailed hawk, RV = common raven, NHO = northern hawk owl, BO = boreal owl, AK = American kestrel, BE = bald eagle. UNK = individual raptors of unknown species identified from parts (e.g., beaks, legs) found in pellets at nests of known predators.

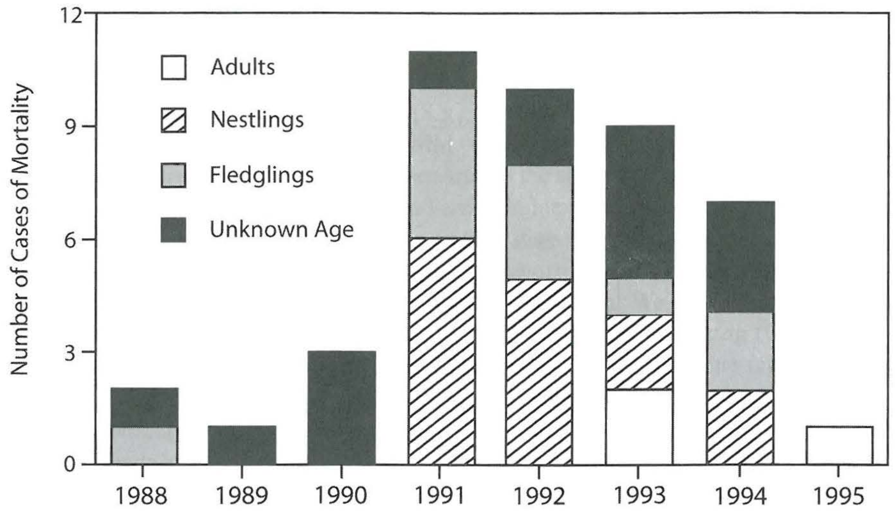


Figure 16.6 Temporal distribution of cases of predation on avian predators detected mainly during analysis of pellets and prey remains. The different shading patterns represent different age categories of the prey species.

16.4 Discussion

16.4.1 Functional, Numerical, and Reproductive Responses to Hare Densities

Functional Responses We were able to calculate functional responses for four species: the great horned owl (see chapter 15), the northern goshawk, the red-tailed hawk, and the northern harrier. All four species responded by increasing the proportion of hares in their diets at high hare densities (figures 15.7, 16.3). The horned owl and the northern harrier showed particularly strong responses by rarely bringing hares to their nestlings when hares were rare, but by bringing little else when hares were common (figure 15.5, table 16.4). In contrast, the northern goshawk commonly brought hares to nests even when hares were scarce (table 16.2), whereas the red-tailed hawk only fed hares to its young often in one year at the peak of the hare cycle (table 16.3).

Numerical Responses The horned owl showed a strong numerical response to hare densities, but it lagged 2 years behind the hare cycle, as it did at Rochester, Alberta (Adamcik et al. 1978). The mechanisms underlying this relationship are clear. Young owls from a pool of nonterritorial floaters continued to recruit to the territorial population after the hare peak in 1990 (figure 15.5), but recruitment eventually stopped in 1993 (figure 16.1a). At the same time, the annual survival of adults fell from 95% in 1989–1991 to 82% in 1991–1992 (chapter 15) and to approximately 60% in 1992–1993 (figure 16.1a). The total numerical response of all large raptors to the hare cycle (figure 16.1h) was dominated by the response of the great horned owl, as the other large species were either uncommon and/or did not respond strongly to changing hare densities.

The American kestrel, the northern hawk owl, and the northern goshawk showed more immediate numerical responses to spring hare density. Numbers of a fourth species, the common raven, increased from two to three breeding pairs at the peak of the cycle in the intensive search area. We speculate that breeding goshawks were in better condition in springs with high hare numbers, and we know that they survived poorly in 1991–92 during the hare decline, when five adults were found dead (Doyle and Smith 1994). We are, however, uncertain of the magnitude of the numerical response because our estimates of goshawk numbers were probably low. The hawk owl and kestrel rarely or never ate adult hares in summer. We speculate that their numerical responses stemmed from good breeding success the previous year (perhaps as a result of feeding juvenile hares to their nestlings) and from poor survival or emigration in winter after hares declined (hawk owl only).

The absence of a numerical response to hare densities by the migratory red-tailed hawk was expected from previous work in Alberta (Adamcik et al. 1979), where red-tailed hawks also showed extremely stable breeding populations through a hare cycle. Red-tails at Kluane only ate hares frequently in the peak year, 1990 (table 16.3).

Because horned owl and goshawk numbers increased at high hare densities, and because hares were a key winter food for them, these resident species added to the high predator pressure exerted on hares by lynx and coyotes (chapter 13) in the early winters of the decline.

Despite approximately synchronous population cycles by *Clethrionomys* and *Microtus* voles (chapter 10), only one species showed a delayed numerical response to fluctuating vole densities, the boreal owl. Boreal owl numbers were high one year after high vole numbers, presumably because young male owls recruited and began to hoot in spring after good chick production the previous year. The boreal owl also responds rapidly to vole cycles in Fennoscandia (Sonerud 1997).

Reproductive Responses Three species showed clear reproductive responses, producing more fledglings in years of high hare density: the great horned owl, the northern harrier, and the common raven (figures 16.2a,d,f). The strongest response was by horned owls, which did not attempt to breed when hares were scarce. Northern harriers had broad diets throughout the hare cycle, but hares dominated numerically in 1990 and 1991 and contributed most of the prey biomass brought to nestlings from 1988 to 1991 (table 16.4). Finally, ravens bred much more successfully in years with high hare numbers, and all nests in 1993 failed when hares were extremely scarce (figure 16.2f). Ravens undoubtedly benefited from increased scavenging opportunities provided by road kills on the Alaska Highway at the peak of the cycle and also may have taken more juvenile hares in peak summers.

We expected the bonanza of hares at the peak of the cycle to generate high reproductive success in species that prey regularly on hares. Indeed, during the hare peak, reproductive success of several raptors and corvids approached the maximum level reported in any study of the species (horned owls, Houston et al. 1999; magpies, Birkhead 1991;

goshawks, Squires and Reynolds 1997, Ethier 1999; ravens, Ratcliff 1997; harriers, MacWhirter and Bildstein 1996; hawk owls, Sonerud 1997). Only the red-tailed hawk, a less enthusiastic hare-eater than the other species, was an exception to this pattern.

16.4.2 Resource Partitioning and Diet Width

Most raptors at Kluane had generalized diets and showed opportunistic shifts in diet as hare and vole numbers fluctuated. Three of the five species for which we had diet data over much of the hare cycle (goshawks, red-tailed hawks, and harriers) took a wide range of prey at all times, but nevertheless showed preferences (tables 15.6, 16.2, 16.3, 16.4, 16.7). Goshawks depended more on hares and adult arctic ground squirrels, whereas red-tailed hawks depended more on red squirrels and juvenile arctic ground squirrels. Goshawks in Europe mainly eat birds (Widén 1987), and this was also true at Kluane in 1993–1995, after hare abundance had declined. Harriers took mainly small mammals and birds, but included many other items in their diets (table 16.4). Data for a small species, the kestrel, also revealed that a variety of prey (voles, small birds, and insects) were taken.

Two species were more specialized in their diet. One, the northern hawk owl, was always a narrow specialist on small mammals, although it ate a variety of vole species (table 16.7) and some hares at the peak of the cycle. The great horned owl switched sharply from specializing strongly on hares at the peak of the cycle (table 15.5) to eating a range of alternative prey in 1992–1995 when hares were relatively rare (figure 15.7). Limited information on the boreal owl also suggested a specialized diet (forest-dwelling voles and shrews) that was similar to the diet of the hawk owl (see also Kertell 1986, Korpimäki 1992).

All of the species that we studied ate juvenile hares at the peak of the cycle. Horned owls may even have timed their breeding to exploit the sharp peak in prey biomass that accompanies the birth of the first litter of hares (F. Doyle unpublished data).

Few studies of northern raptor assemblages have been conducted elsewhere. In the boreal forests of northern Sweden (Hörnfeldt and Eklund 1989) and western Finland (Korpimäki and Norrdahl 1991, Korpimäki 1992) a different suite of avian predators uses a different prey base, mainly composed of regularly cycling voles. Raptors specializing on voles at Kluane took a wider range of prey than the same or similar species did in Sweden and Finland.

16.4.3 Intraguild Predation

Studies of predators in food webs often focus on vertical linkages, but differences in size and strength among predators allow them to prey on each other (e.g., Crooks and Soulé 1999), particularly when herbivorous prey are in short supply. The first substantial evidence that avian predators kill each other regularly came when large numbers of predators were fitted with mortality-sensing radios. In studies reviewed by Newton (1998), other predators killed 38.2% of 178 radio-collared birds of prey. In contrast, in 3,808 cases of mortality of non–radio-collared avian predators, only 4 deaths (of barn owls, *Tyto alba*) were attributed to predation (Newton 1998).

In our study, even though few raptors were radio marked, we found many cases of intraguild predation. It involved a variety of species (table 16.9) and was more frequent during the hare decline and early low phases (figure 16.6), especially when predation involved great horned owls. The data in figure 16.6, however, probably underestimate the frequency of intraguild predation after 1991, as diets of the great horned owl were studied more intensively from 1989 to 1991 (see chapter 15) than from 1992 to 1995. We conclude that, although we were unable to describe the exact pattern of intraguild predation during the cycle, it was frequent enough to have played a significant role in the declines in raptor numbers during the hare decline (figure 16.1). Predation by raptors was mostly of young individuals and may have lowered the recruitment of young to raptor populations after the hare decline, perhaps facilitating the recovery of hare numbers in 1995 and 1996. Also, predation in winters with few hares may have severely limited numbers of resident hawk owls, boreal owls, and goshawks (Doyle and Smith 1994, Rohner et al. 1995). Reduced territorial calling by great horned owls and boreal owls during the snowshoe hare decline suggests that these birds are sensitive to intraguild predation risk.

16.4.4 Methodology and Limitations

Our studies of raptors at Kluane were stretched rather thinly over many species, and much more could have been achieved if we had studied each common species intensively. Such an undertaking would, however, have required many more personnel and more resources. Indeed, we were advised by some expert raptor biologists at the beginning of our studies that the task was too difficult to attempt for even the larger and more common species such as horned owls, goshawks, and red-tailed hawks.

A second limitation to our work is that we mostly studied the diets of nestlings, not those of adult birds (but see table 15.6). It is likely that diets of adults differed from those fed to nestlings. A third limitation that we were only able to overcome in the horned owl is that we only studied the territorial segment of the population. It is possible that numbers of nonterritorial birds varied considerably through the cycle in other species.

16.5 Summary

We studied an assemblage of 21 species of raptorial and scavenging birds, 12 of which were residents or frequent summer visitors to the study area. Most larger raptors at Kluane maintained broad diets through the hare cycle, but the horned owl specialized strongly on hares at the hare peak and took a broader range of prey when hares were scarce. Two species, the boreal owl and northern hawk owl, specialized on voles at all times. Northern harriers ate mainly voles and smaller birds, but also took many juvenile hares at the peak. All four larger species for which we had diet data through the cycle (horned owl, goshawk, red-tailed hawk, harrier) showed functional responses to hare densities. One large species, the northern goshawk, and two smaller species, the American kestrel and the northern hawk owl, showed direct numerical responses to snowshoe hare density, and the horned owl showed a delayed response. Three species, great horned owls, northern harriers, and common ravens, produced more young in years of high hare abundance. The reproductive success of several raptors at Kluane at the peak of the hare cycle reached the maximum level reported for the species in any study. In the decline after the hare peak, raptors at Kluane frequently preyed on each other, and this intraguild predation may have contributed to the rapid decline in total raptor numbers within 3 years of the peak of the hare cycle.

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