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NORTHERN HAWK-OWLS IN THE NEARCTIC BOREAL FOREST: PREY SELECTION AND POPULATION CONSEQUENCES OF MULTIPLE PREY CYCLES[1]

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Abstract. We studied hawk-owls in the southwestern Yukon, Canada, from 1987–1993. Most information on hawk-owls originates from studies in Europe, and very little is known about the subspecies *Surnia ulula caparoch* in North America. The boreal forest communities in the two continents differ remarkably in the composition of cyclic herbivore populations. Fennoscandia is dominated by 3–4 year microtine cycles, whereas northern Canada and Alaska experience a 10-year cycle in snowshoe hare numbers, with voles fluctuating at lower levels. We studied the diets of nine nesting pairs by pellet analysis, and we observed prey deliveries at five nests. The proportion of voles in the diets was lower than reported from Fennoscandia, and snowshoe hares made up 40–50% during the peak of the hare cycle. Estimates of prey densities by live-trapping revealed that hawk-owls strongly prefer voles over snowshoe hares and squirrels. Among voles, *Microtus* were preferred and *Clethrionomys* were avoided. Hawk-owls showed, however, a functional response not only to voles but also to juvenile hares, and they may be critically dependent on larger prey during certain nesting stages when vole abundance is moderate or low. Breeding densities and winter observations changed concurrently over years of different prey abundance. Prey selection translated into population consequences: hawk-owls did not respond numerically to *Clethrionomys* outbreaks, but to the combined densities of *Microtus* and snowshoe hares. We conclude that the Northern Hawk-Owl is less of a vole specialist and more affected by the prey composition in specific systems than commonly assumed, and we discuss this pattern from an evolutionary perspective.

Key words: Surnia ulula caparoch; *diet; functional response; numerical response; reproduction; snowshoe hare cycle; community dynamics.*

INTRODUCTION

Northern Hawk-Owls (*Surnia ulula*) are among the least studied birds of North America, and there has been increasing concern about their conservation status (Duncan 1993). Although widely distributed across the northern boreal forest from Alaska to Newfoundland, Northern Hawk-Owls have rarely been studied on their breeding grounds. Information on diet and breeding biology is available only from nests that were discovered incidentally. The most intensive study on hawk-owls breeding in North America was based on two nests in Denali National Park, Alaska (Kertell 1986). Estimates of breeding densities are not available. Wintering hawk-owls occur in varying numbers on farmland in southern Canada and the northern United States, and occasionally breed there (Jones 1987, Duncan and Lane 1987). The winter ecology of hawk-owls in the Nearctic boreal forest, and the population dynamics of this species are virtually unknown.

Most research on hawk-owls has been carried out in Fennoscandia on *S. u. ulula.* The ecology of this subspecies is tightly linked to the 3–4 year population cycles of voles. Hawk-owls lead a nomadic life, occurring at places with temporarily high microtine densities, feeding almost entirely on voles, and raising broods as large as 8–13 young (Mikkola 1983). Hawk-owls disappear as vole populations decline, sometimes irrupting

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into more southern latitudes, and probably do not breed until they find high microtine densities again (Hagen 1956, Glutz Von Blotzheim and Bauer 1980, Semenov-Taishanski and Giljasov 1985, Byrkjedal and Langhelle 1986). The Nearctic *S. u. caparoch* has been assumed to behave identically to *S. u. ulula* (e.g., Johnsgard 1988).

We found our first hawk-owl nest in 1988, and we were surprised to observe hawk-owls preying on juvenile snowshoe hares (*Lepus americanus*). Microtines are the predominant cyclic herbivore in Fennoscandia, whereas boreal forests in North America are characterized by the 10-year population cycle of snowshoe hares (e.g., Keith 1963). In this paper we ask: (1) to what degree are Nearctic hawk-owls influenced by the snowshoe hare cycle; and (2) does their ecology in the Nearctic differ from the Palaearctic? We collected data on prey selection, breeding biology, and population trends from 1987–1993, and we present evidence that Nearctic hawk-owls are less dependent on vole cycles than commonly assumed.

METHODS

This study is part of the Kluane Boreal Forest Ecosystem Project (Krebs et al. 1992) and was conducted during 1987–1993. We worked at Kluane Lake (60°57′N, 138°12′W) in the southwestern Yukon, Canada. The study area comprised 350 km^2 of the Shakwak Trench, a broad glacial valley bounded by alpine areas to the northwest and the southeast. The valley bottom averages about 900 m above sea level and is mostly covered with spruce forest (*Picea glauca*), shrub thickets (*Salix* sp.), some aspen forest (*Populus tremuloides*), grassy meadows with low shrub (*Betula glandulosa*), old burns, eskers, marshes, small lakes and ponds.

Owl abundance. We censused breeding hawk-owls in two main ways: (1) All project field personnel were trained to recognize hawk-owls and report observations from a total of 47,276 hours in the study area on foot during both summer and winter. We checked the locations of these observations for breeding pairs. (2) We searched a 100 km^2 "intensive area" systematically for hawk-owls during May–June.

In winter, we used sightings from a total of 2,831 hours driving vehicles on the Alaska Highway, which follows the valley bottom for the whole length of the study area, and we calculated an abundance index of hawk-owls seen per 100 observation hours.

Nest observations. We followed hawk-owls with prey to locate their nests. The breeding pairs were usually not disturbed by careful observations from 30–40 m distance. Only at nest O in 1993 did we need to observe from a blind. We recorded all major activity such as prey deliveries or prey caching in surrounding trees, and searched the ground underneath roost sites for pellets.

Pellet analysis. We removed hair tissue manually and based the analysis on the identification of bone contents in order to establish a minimum count of prey individuals (Marti 1987).

Prey densities. Adult snowshoe hares were live-trapped during sessions of 5–6 days in March and April (4–6 grids of 34 ha in size), and closed population methods were used for calculating numbers (Otis et al. 1978). The numbers of juvenile hares in 1989–1992 were estimated using a population model based on average pregnancy rates, parturition times, stillborn rates, litter sizes, and early survival rates from field results in the study area (details in Rohner and Krebs, unpubl. ms.). We did not have measurements of hare reproduction for 1988 and 1993, but we assume that no major changes occurred in these years, and we used data from 1989 and 1992 respectively. Density estimates of red squirrels (*Tamiasciurus hudsonicus*), ground squirrels (*Spermophilus parryii*), and voles and mice (*Clethrionomys rutilus, Microtus* spp., *Peromyscus maniculatus*) were based on live-trapping (details in Boutin et al., unpubl. ms.; Hubbs 1993). Red squirrels were trapped in spring, ground squirrels in early summer, and voles both in May and August (average used). The number of trapping grids and population densities are given in Appendix 1.

Prey biomass. Prey masses were taken from individuals trapped during June (Appendix 1). The mass of juvenile hares was estimated in two steps: (1) We measured hind foot length of juvenile hares cached by hawk-owls, or transformed the width of proximate ends of femurs in pellets into hind foot length (regression from a known sample; $y = 8.49x - 5.15$, $r^2 = 0.96$, $n = 43$). (2) We calculated the average age of juvenile hares in pellets by using the almost linear growth of hind foot length in the field ($y = 1.49x + 34.93$, $r^2 = 0.93$, $n = 844$; M. O'Donoghue, unpubl. data), and obtained the corresponding mass for this age from O'Donoghue and Krebs (1992). For vole and mouse species not listed in Appendix 1 we used a mass of 30 g. Masses for

TABLE 1. Summer diet of hawk-owls at Kluane Lake, Yukon. Results from pellets collected at roost sites near nests in nine territories from 1988–1993, expressed as percentage of the number of prey items (%*n*) and the percentage of biomass (%mass).

	1988 (*n* = 3)		1989 (*n* = 1)		1990 (*n* = 3)		1993 (*n* = 2)		1988–1993 (*n* = 9)	
	%*n*	%mass	%*n*	%mass	%*n*	%mass	%*n*	%mass	%*n*	%mass
Microtus pennsylvanicus	31.6	21.2	15.0	4.5	3.1	1.4	51.8	49.7	27.6	16.0
Microtus olm[1]	25.4	17.1	22.5	6.7	27.6	12.6	18.1	17.3	24.3	14.1
Microtus sp.	20.6	13.9	20.0	6.0	23.5	10.7	0.0	0.0	17.4	10.1
Synaptomys borealis	6.1	4.1	0.0	0.0	7.1	3.3	7.2	6.9	6.0	3.5
Peromyscus maniculatus	0.4	0.2	0.0	0.0	1.0	0.4	0.0	0.0	0.4	0.2
Phenacomys intermedius	7.0	3.5	5.0	1.1	9.2	3.2	7.2	5.2	7.3	3.2
Clethrionomys rutilus	0.9	0.3	10.0	1.5	7.1	1.6	7.2	3.5	4.2	1.2
Voles, total	92.0	60.3	72.5	19.8	78.6	33.2	91.5	82.6	87.2	48.3
Lepus americanus juvenile	3.5	14.1	15.0	27.0	14.3	39.3	0.0	0.0	6.2	21.7
Lepus americanus adult	0.4	10.3	2.5	26.2	0.0	0.0	0.0	0.0	0.4	9.1
Snowshoe hares, total	3.9	24.4	17.5	53.2	14.3	39.3	0.0	0.0	6.6	30.8
Eutamias minimus	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.1
Tamasciurus hudsonicus	2.2	10.3	5.0	10.5	2.0	6.5	0.0	0.0	2.0	8.1
Spermophilus parryii	0.0	0.0	5.0	16.5	4.1	20.6	1.2	12.7	1.6	10.0
Mustela nivalis	0.4	0.3	0.0	0.0	1.0	0.5	1.2	1.2	0.7	0.4
Sorex sp.	0.0	0.0	0.0	0.0	0.0	0.0	4.8	1.2	0.9	0.1
Other mammals, total	3.0	10.9	10.0	27.0	7.1	27.6	7.2	15.1	5.4	18.7
Dendragapus canadensis	0.4	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.2	1.6
Perisoreus canadensis	0.4	0.6	0.0	0.0	0.0	0.0	1.2	2.3	0.4	0.5
Birds, total	0.8	4.3	0.0	0.0	0.0	0.0	1.2	2.3	0.6	2.1
Total %	100	100	100	100	100	100	100	100	100	100
Total prey items, biomass	228	13.57 kg	40	5.34 kg	98	8.56 kg	83	3.46 kg	449	30.93 kg

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[1] *Microtus oeconomus*, *M. longicaudus*, *M. miurus*.

TABLE 2. Prey deliveries at selected hawk-owl nests in Kluane, Yukon.

	1988 nest B	1988 nest F	1989 nest F	1990 nest B	1993 nest J
Voles, mice	21	8	2	0	9
Juvenile snowshoe hares	3	1	6	4	0
Red and ground squirrels	0	2	2	3	0
Unknown items	2	0	2	2	0
Total prey items	26	11	12	9	9
Vole proportion (numbers)	0.81	0.73	0.17	0.00	1.00
Vole proportion (biomass)	0.41	0.19	0.02	0.00	1.00
Hours observed	81.7	29.8	39.3	20.0	17.5
Deliveries/hour	0.32	0.37	0.31	0.45	0.51

other mammals and birds were taken from Banfield (1974) and Dunning (1984).

Breeding biology. Nestling ages were estimated using the equation wing length = 13 + 5.6 × age (Huhtala et al. 1987). Laying dates (dates of clutch initiation) were then back-calculated, assuming incubation of 30 days beginning with the first egg (Glutz Von Blotzheim and Bauer 1980). We estimated hatching asynchrony by calculating a "hatching interval" from the age difference between the oldest and the youngest chick, divided by ($n - 1$) nestlings in the brood to obtain the average time interval between chicks. Information on nestling growth for these calculations was only available for the European subspecies, which is about 6% smaller than the North American *S. u. caparoch* (Earhart and Johnson 1970, Mikkola 1983). Our nestling ages are therefore provisional and probably slightly overestimated.

Statistical calculations. We used SYSTAT for statistical analysis. All correlations were calculated as Spearman rank correlations. If not indicated otherwise, all probabilities are two-tailed.

RESULTS

DIET

We identified a total of 449 prey individuals from nine nests, including at least seven species of voles, five other species of mammals, and two species of birds (Table 1). The diet of breeding hawk-owls consisted almost entirely of mammals; birds were taken only occasionally. Voles were the most numerous prey (87.2%), but their proportion varied considerably from year to year.

In terms of biomass, the overall proportion of voles was surprisingly low (48.3%). In 1989, the biomass of voles in hawk-owl diets reached only 19.8%. Among other mammals, juvenile snowshoe hares, red squirrels, and ground squirrels were highly represented in the prey biomass consumed by hawk-owls.

We found the same result when we observed prey deliveries at five hawk-owl nests during a total of 188.3 hours (Table 2). The proportion of vole deliveries varied considerably between nests and years, but was certainly not constantly high. Some successful nests were supplied with less than 20% voles.

Hawk-owls took juvenile hares of an average age of 22 days, which is equivalent to a weight of about 240 g ($n = 11$, see methods for age estimation). This corresponds approximately with the expected sizes available in the environment during the sampling period in early June (O'Donoghue and Krebs 1992; Rohner and Krebs, unpubl. ms.).

We did not conduct systematic diet studies of hawk-owls wintering in our study area. We compiled, however, occasional observations of hawk-owls with prey (Table 3). We observed three unsuccessful attacks on prey as large as adult snowshoe hares, and 12 cases of hawk-owls feeding

TABLE 3. Evidence for large prey items in the winter diet of hawk-owls at Kluane Lake, Yukon. Observations were collected opportunistically from October–April 1989–1991.

	Unsuccessful attacks	On kill (scavenging possible)	Killed by hawk owls	Total
Snowshoe hare	2	5	3	10
Red squirrel	–	–	3	3
Spruce grouse	1	–	1	2
Voles	–	–	1	1
All species	3	5	8	16

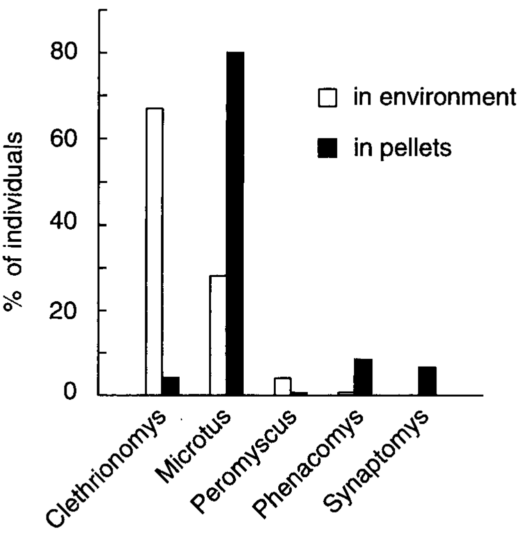


FIGURE 1. Use of different vole species by hawk-owls during the breeding season (May and June, 1988–1990). We compared the percent occurrence in pellets (seven nests, 316 prey individuals) with the availability in the environment (12 grids, 557 trapped individuals).

on prey larger than a vole. For seven of these cases we know from direct observation or from tracks in fresh snow that hawk-owls had killed these prey. Most of this information was collected during checks of snowshoe hares with mortality-sensitive radio-collars. Therefore the proportions of different size classes of prey in Table 3 probably do not represent the actual winter diet of hawk-owls in our area, because they are biased in favor of snowshoe hares.

DIET PREFERENCES

The boreal forest in the southwestern Yukon provided a relatively simple array of prey species for hawk-owls. We distinguished four major prey categories in owl pellets: voles (*Clethrionomys* and *Microtus*), squirrels (*Tamiasciurus* and *Spermophilus*), juvenile and adult snowshoe hares. We compared the proportion of these categories in the owl diet with the proportion available in the environment (Appendix 1), based on biomass and using Manly's alpha as a preference index (Krebs 1989). If there is no preference, this index equals 0.25 with four prey categories. During 1988–1990, when all major prey densities were high enough to be reflected in hawk-owl pellets, the averaged values of Manly's alpha were: 0.887 for voles, 0.059 for juvenile hares, 0.033 for squirrels, and 0.022 for adult hares. Hawk-owls therefore used voles about 15 times more than juvenile hares, about 25 times more than squirrels, and about 40 times more than adult hares. Despite changes in prey densities, the ranking of these preferences was consistent in all of the three years.

We also compared the proportions of the different vole and mouse species in pellets with their proportions in our live traps (Fig. 1). The red-backed vole *Clethrionomys rutilus* was the most abundant of all small mammal species in the environment. Despite its high proportion in traps (0.66), it was hardly taken by hawk-owls. In contrast, *Microtus* species represented only 0.28 in traps, but were by far most preferred (0.80) in hawk-owl pellets. Deer mice (*Peromyscus maniculatus*) and heather voles (*Phenacomys intermedius*) were not frequently trapped, and were also taken at a low proportion by the owls. Almost all bog lemmings (*Synaptomys borealis*) were found in pellets from a single nest close to a large marsh, which was not covered by our trapping.

DIET RESPONSES TO CHANGING PREY DENSITIES

Predator responses to changing prey densities have been characterized by functional responses (review in Fujii et al. 1986). Figure 2 shows prey deliveries from direct observations at five hawk-

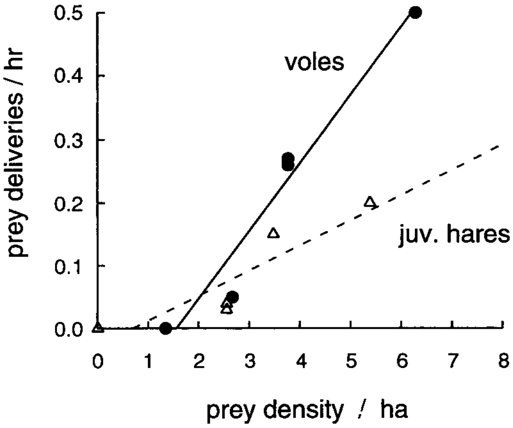
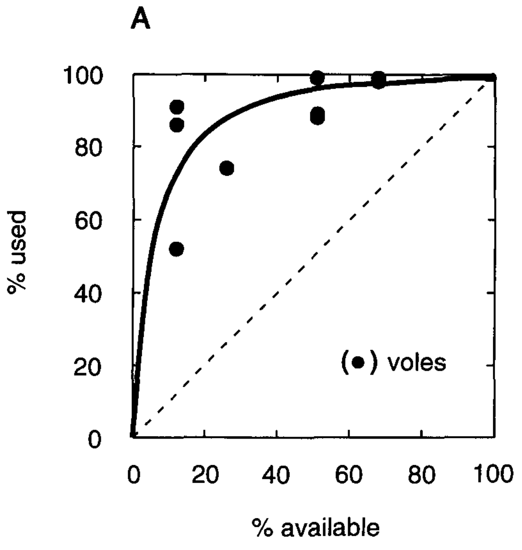


FIGURE 2. Functional responses of hawk-owls to changing densities of voles and juvenile snowshoe hares. Prey deliveries were observed at five nests from 1988–1993 (Table 2). Voles: $y = 0.11x - 0.17$ ($r^2 = 0.96$, $P < 0.01$). Juvenile hares: $y = 0.04x - 0.03$ ($r^2 = 0.81$, $P < 0.05$).



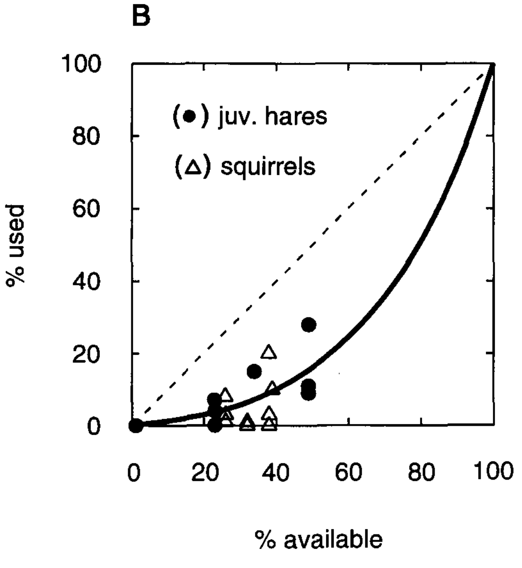


FIGURE 3. Functional responses of hawk-owls to changing prey densities expressed by the relative proportion of each prey species in the environment (*% available*, densities from live-trapping), and in hawk-owl pellets (*% used*, nine nests from Table 1). A: Response to small prey (voles). B: Response to larger prey (juvenile snowshoe hares, red squirrels, and ground squirrels).

TABLE 4. Reproductive performance at nine hawk-owl nests at Kluane, Yukon. Brood size represents fledging success. Laying dates (first egg) and hatching intervals were back-calculated based on estimations of nestling age (see methods for details).

Year	Nest	Brood size	Laying date[1]	Hatching interval[2]
1988	F	2	24 April	1.4 d
	J	4	24 April	1.7 d
	B	2	1 May	1.4 d
1989	C	4	4 May	n.a.
1990	B	4	19 April[3]	n.a.
	R	3	22 April[3]	n.a.
	C	4	24 April	1.5 d
1993	J	5	23 April	2.0 d
	O	5	11 May	1.3 d
Mean		3.7	27 April	1.6 d
Median		4	24 April	1.5 d

[1] Assuming incubation of 30 days (Glutz Von Blotzheim and Bauer 1980).
[2] Maximum age difference within brood)/(brood size − 1).
[3] Estimated from date of fledging.

owl nests. These are absolute estimates of intake rates under fluctuating prey densities (in contrast to the relative estimates of prey proportions in pellets). More voles were brought to nests at higher vole densities. Hawk-owls, however, not only responded to changing vole densities, they also delivered juvenile hares at higher rates when hare densities increased.

The shape of a functional response can be visualized by plotting relative values for availability and use of prey (Murdoch and Oaten, 1975). Figure 3 shows the change of preferences across years with different prey composition in the environment. Use and availability are based on prey items and prey densities, not on biomass, and therefore reflect encounter rates. The dotted line (y = x) indicates the values expected if no preference occurs. Prey switching (type III functional response) occurs only if the values for a species cross the y = x line with increasing prey density. Voles were clearly preferred prey items across all densities, indicating a type II functional response (Fig. 3A). The preferences for snowshoe hares and squirrels are lower (Fig. 3B). Because the proportion of each of those species were never higher than 50% in the environment, there are no data for the upper part of the curve and we cannot exclude prey switching. We plotted the curve in Figure 3 assuming a type II functional response.

BREEDING BIOLOGY

While our sample size of nests is small, we are not aware of studies with an even modest number of hawk-owl nests in a single study area. We therefore present a summary of reproductive pa-

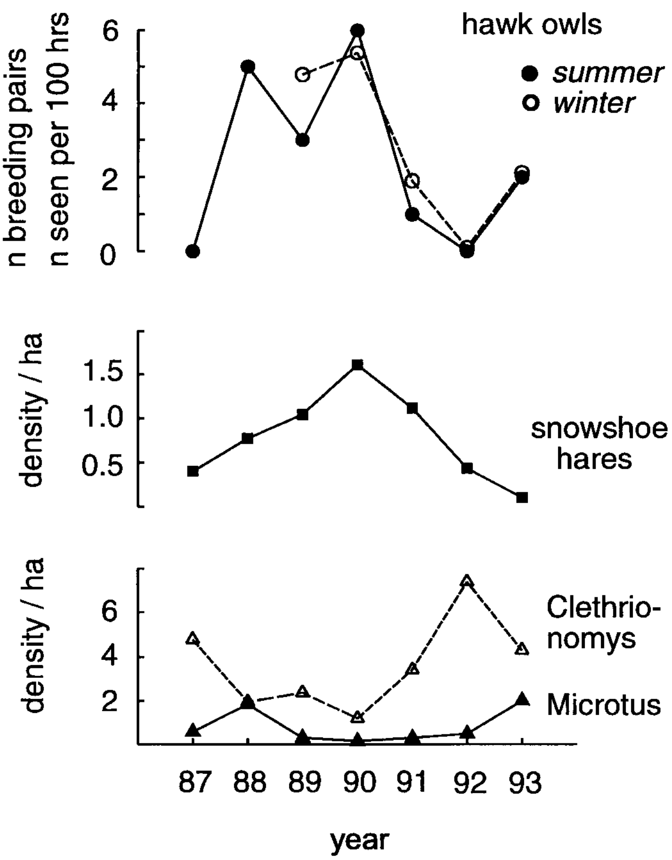


FIGURE 4. Population trends of hawk-owls and their main prey at Kluane, Yukon.

rameters for all nine nests that we found in our study area from 1988–1993.

Seven of nine nest sites were in hollow tops of truncated spruce snags. Two broods were raised in lateral cavities of dead spruce trees, probably where branches had broken off and left an empty space. Nest sites were 3.4–7.1 m above ground, and all cavities were of similar size (measurements of longest diameter, shortest diameter, and depth at two sites were 21 × 18 × 20 cm and 20 × 17 × 10 cm).

We estimated that most clutches were initiated in the last week of April, with a range from 19 April to 11 May (Table 4). Brood sizes varied from 2–5 (mean 3.7). There was no apparent relationship between estimated laying date and brood size. We also estimated the approximate hatching interval from the age differences of nestlings. There were no obvious differences in hatching asynchrony between nests and years.

Fledgling success was complete for eight of nine broods observed (remains of one fledged young at nest J in 1993 was identified as a probable raptor kill). In addition, we found one abandoned nest with two eggs in 1991 (nest site C).

POPULATION RESPONSES

Population densities varied from 0 to 6 pairs in the 100 km^2 area that we searched systematically. Figure 4 shows a conservative count of all hawk-owls that we found nesting or that indicated breeding behavior over the whole study area. The population trends between the breeding seasons were matched by the sighting rates of hawk-owls during the following winters.

A comparison of hawk-owl population trends with changes in density of the major prey populations shows interesting features (Fig. 4). In 1987, hawk-owls were not observed despite high densities of *Clethrionomys*. This situation was repeated in 1991–1992, when hawk-owl numbers reached a minimum as *Clethrionomys* populations peaked.

Hawk-owls started nesting in high numbers in

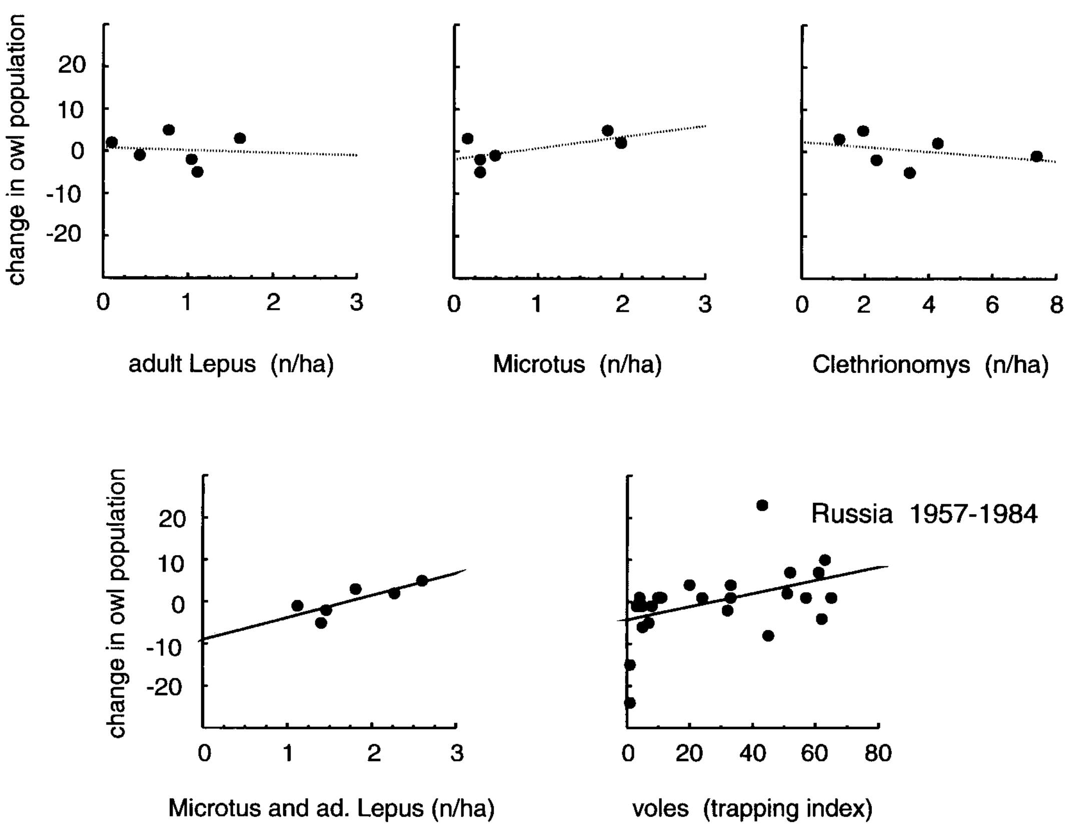


FIGURE 5. Numerical response of hawk-owls (absolute change in breeding pairs from last year to this year) to densities of different prey. Upper panel: Numerical response of hawk-owls *S. u. caparoch* to three prey species at Kluane, Yukon. Lower panel: Numerical response of hawk-owls to the combined prey density of field voles and snowshoe hares at Kluane, Yukon (left; $y = 4.02x - 6.40$, $r^2 = 0.51$, $P = 0.07$, $n = 6$); and numerical response of hawk-owls *S. u. ulula* to combined vole densities in north-western Russia, with data from Semenov-Taishanski and Giljasov (1985) (right; $y = 0.16–4.26$, $r^2 = 0.21$, $P = 0.02$, $n = 27$).

our area in 1988. Both *Microtus* and snowshoe hares increased 1987–1988. Despite the decline of *Microtus* numbers in 1989, hawk-owls remained breeding in the area as hare numbers continued to increase. During this time, hawk-owls fed to a large degree on snowshoe hares. The hare population started to decline in winter 1990/1991, and contrary to previous years hare numbers kept declining throughout the spring and summer (Krebs et al., unpubl. data; Hik 1994). Two hawk-owl pairs may have attempted breeding in 1991, but we found only one nest which had been abandoned at the egg stage.

As hares continued to decline and *Microtus* was at low densities, hawk-owls disappeared almost entirely (three summer sightings during 1,270 observer hours in 1992). They returned in 1993 when *Microtus* reached peak densities and hare numbers were extremely low.

Numerical responses of predators to prey are usually displayed as the rate of increase of a predator population versus prey density. In Figure 5, the change in hawk-owl breeding pairs (from last year to this year) is plotted as a function of densities of different prey. Our sample size is small for this type of analysis (seven years), but it shows the patterns described in Figure 4 more clearly. There is no apparent response to *Clethrionomys*, and the responses to *Microtus* and snowshoe hares are weak and show much variation ($r_s < 0.29$, $r^2 < 0.37$, $P > 0.2$). The best fit is represented by the numerical response of hawk-owls to combined *Microtus* and *Lepus* densities ($r_s = 0.77$, $P = 0.07$, one-tailed). For comparison, we plot the numerical response of the palaearctic subspecies *S. u. ulula* to vole densities in northern Russian Lapland ($r_s = 0.56$, $P < 0.005$, data from Semenov-Taishanski and Giljasov 1985).

DISCUSSION

IMPORTANCE OF SNOWSHOE HARES IN THE DIET

The diet of hawk-owls breeding in Europe consisted of 93–96% voles, mostly field voles *Microtus* and bank voles *Clethrionomys* (review in Mikkola 1983). Meadow voles (*Microtus pennsylvanicus*) accounted for almost all prey in the diet of hawk-owls breeding sporadically at the southern edge of their range in North America (Smith 1970, Duncan and Lane 1987, Duncan and Duncan 1994).

The only study of breeding hawk-owls in the Nearctic boreal forest known to us was based on two nests in Denali, Alaska (Kertell 1986). Voles contributed only 70% to the prey biomass in pellets. More than 20% of prey originated from juvenile snowshoe hares and from red squirrels.

In our study, the proportion of voles in the biomass of successfully breeding hawk-owls was as low at 20–30% (Table 1). Juvenile snowshoe hares contributed 40–50% of the prey biomass during peak years of the hare cycle. Pellet records may even underestimate the hare proportion during the late nestling stage, because they contain pellets produced before the first hare litters are born. Our observations of prey deliveries (Table 2) indicated that successfully breeding hawk-owls may critically depend on hares and squirrels when vole populations are low.

Hawk-owls have been assumed to scavenge on, but not to kill adult snowshoe hares (e.g., Henderson 1919, Kertell 1986, Johnsgard 1988). This is not surprising, because hawk-owls weigh only 300–400 g, about 25% of the mass of an adult snowshoe hare. During winter, we found that hawk-owls repeatedly killed and fed on adult hares (Table 3). It is possible that these hares were in exceptionally poor condition, and that such individuals are more readily available for hawk-owls during peak densities of the snowshoe hare cycle.

PREY SELECTION: ARE HAWK-OWLS VOLE SPECIALISTS?

Hawk-owls clearly preferred voles over other prey during the breeding season (Fig. 3). However, they not only showed a functional response to vole abundance, they also killed more juvenile hares as these increased in density (Fig. 2). Therefore, although juvenile hares were taken at lower proportions than available in the environment on average, they still made up a higher proportion in prey biomass than voles during peak years of the hare cycle, when vole densities were at their lowest (Table 1).

A similar pattern is apparent for prey selection among voles (Fig. 1). *Clethrionomys* are by far the most abundant voles in the study area, but hawk-owls take *Microtus* almost exclusively. *Clethrionomys* live in mature forests and under shrub cover, whereas among *Microtus* particularly *M. pennsylvanicus* prefer open grassland habitat (Krebs and Wingate 1976). Average densities from 1989–1993 in three additional study grids in open habitat were 5.29/ha for *Microtus*, and <0.1/ha for *Clethrionomys*. Hawk-owls primarily hunt from the top of snags and spruce trees overlooking open habitat. We presume that this habitat selection explains the predominance of *Microtus* in hawk-owl diets (see also Sonerud 1986).

Hawk-owls sometimes feed primarily on *Clethrionomys*. Nybo and Sonerud (1990) found a high proportion of *Clethrionomys* in the diet early in spring. This proportion declined rapidly as snow cover melted in the open habitat. *Clethrionomys* is more active above snow, and hawk-owls are forced to hunt in more forested habitat, but as soon as the snow cover begins to disappear, hawk-owls shift their hunting to the more accessible and profitable *Microtus* (Nybo and Sonerud 1990). It is thus possible that high proportions of *Clethrionomys* in some hawk-owl diets (e.g., Kertell 1986) are caused by earlier sampling time, late-melting snow, or denser vegetation.

We conclude that hawk-owls hunt selectively, in particular with respect to habitat, but that the influence of varying environments may have been underestimated. We suggest that the extremely high proportions of voles in the diet of Fennoscandian hawk-owls result not only from high preferences, but also from extremely high availability of voles compared with other prey in these ecosystems. In Nearctic boreal systems, where snowshoe hares reach extremely high densities, the opportunistic potential of hawk-owls becomes more strongly expressed. The situation on the island Ulkokrunni in the Gulf of Bothnia in 1977 can be seen as a replicate: During an outbreak of water voles (*Arvicola terrestris*), two hawk-owl pairs fed up to 99.4% on this species (Pulliainen 1978). This vole weighs 3–4 times more than other voles and comprises only 0.7%

of hawk-owl diets in Fennoscandia and Russia (Mikkola 1972). Opportunism of hawk-owls is also more apparent in winter, when they prey more on birds, particularly at low vole densities (e.g., Fisher 1893, Mikkola 1983, Hogstad 1986).

POPULATION DYNAMICS

Hawk-owls are conspicuous when they are perched on top of snags or spruce trees, but they are very difficult to census systematically in the wide and largely inaccessible boreal forest. The patchiness of muskeg and burn habitat they prefer makes density calculations even more difficult. Hagen (1956) found a density of four breeding pairs in 200 km^2 during high microtine densities in southern Norway. Assumed densities of breeding pairs for suitable habitat in Sweden vary from 0.2–20/100 km^2 (Ulfstrand and Högstedt cit. in Glutz Von Blotzheim and Bauer 1980, Cramp 1985). Our density estimates range from 0–6/100 km^2, depending on specific years and how conservatively we interpreted behaviors indicating breeding when nests were not found (the maximum density of nests found was 3/100 km^2 in 1990). We are not aware of any density estimates for hawk-owls in North America.

Little is known about winter populations of hawk-owls in the boreal forest. Sammalisto (1977, cit. in Glutz Von Blotzheim and Bauer 1980) found unusually high abundances of 0.2–1.6 owls/100 km foot transect in 1976/1977 at about 64°N in Finland. Hawk-owls have been sighted in midwinter in boreal Canada and Alaska (Kiliaan 1989), but we are not aware of systematic winter observations outside our study area.

Are there population consequences of prey selection? Our data on population trends of hawk-owls and prey populations suggest that hawk-owls do not respond directly to fluctuations of vole populations (Figs. 4, 5). *Clethrionomys* is only little represented in the diet, and hawk-owl population changes seem not to be affected by *Clethrionomys* abundance in our study area. *Microtus* species and snowshoe hares were the largest components in the diet, and the changes in combined density of these prey explained most of the variation in owl abundance.

The mechanisms of hawk-owl population dynamics are unknown. Hawk-owls have variable brood sizes, which can account for rapid population increases, and some banded owls in Fennoscandia and Russia are known to have moved over distances of more than 1,000 km (Glutz Von Blotzheim and Bauer 1980). Emigration seems to affect population changes more than local mortality (e.g., Byrkjedal and Langhelle 1986). In addition to food shortage, local mortality may also be caused by other raptors and owls: in our study area at least three hawk-owls were killed by great horned owls (*Bubo virginianus*) during 1989–1992 (C. Rohner, unpubl. data), and we found two more sites with feathers from hawk-owls plucked by goshawks (*Accipiter gentilis*) or great horned owls. Great horned owl populations were highest in 1992, when hares were crashing and these large owls were forced to kill other prey (Rohner 1994, see also Rohner and Doyle 1992). It is thus possible that predation mortality may have substantially contributed to the decline of hawk-owl numbers during 1992–1993.

Brood sizes in Fennoscandia range from 3–13 (average 6.31, $n = 135$, Merikallio cit. in Mikkola 1983). Our brood sizes were small in comparison (average 3.7, $n = 9$). Kertell's (1986) broods from Denali were also relatively small (average 5.5, $n = 6$). Records from other parts of North America show an average clutch size of 6.0 ($n = 17$, review in Duncan and Duncan 1994). Clutches in Finland increase with latitude from 5.13 ($n = 13$) to 7.5 ($n = 17$) towards Lapland (Mikkola 1983). The cause of this latitudinal change is unknown, but it is interesting to notice that the amplitude in fluctuations of microtine populations—and therefore the maximum prey base for hawk-owls—also increases towards northern latitudes in Fennoscandia (Angelstam et al. 1985).

Hawk-owls can successfully breed when sufficient prey other than microtines are available, but they may be most efficient and produce largest clutches when feeding on voles (particularly *Microtus* species). This hypothesis would explain both the latitudinal shift in clutch size in Finland, and the lower clutch sizes in the Nearctic boreal forest, where microtine densities may generally be lower than in Fennoscandian boreal forests (C. J. Krebs, unpubl. data).

Little is known about microtine abundances across boreal North America. It is possible that our area in the southwestern Yukon is exceptionally poor in microtine biomass. It is also possible that there are gradients across the continent along with climatic factors. Temperature, rainfall, and snow depth may affect plant productivity or microtine survival directly (e.g., Pruitt 1978).

More attention should be paid to intra-continental variation in North America, and systematic studies and comparisons with hawk-owls breeding in systems that are not necessarily vole-dominated are needed (e.g., in eastern Siberia, or in Central Asian mountain ranges, Gavrin et al. 1962).

EVOLUTIONARY CONSIDERATIONS

Among owls of the northern hemisphere, hawk-owls are unique in their morphology and behavior, owing their name to their resemblance to *Accipiter* hawks. Taxonomically, they are closest to *Glaucidium* (Ford 1967). They are special in their long tail, relatively pointed wing shape, lack of silent flight, lack of ear asymmetry, high metabolism—these are all signs of a fast and maneuverable visual hunter of the daytime, and are typical for bird-eating diurnal raptors (Johnsgard 1988, 1990; Johnson and Collins 1975). Northern forest owls that feed exclusively on voles, such as boreal owls (*Aegolius funereus*) and great gray owls (*Strix nebulosa*), have developed extreme adaptations for locating and capturing prey (silent flight, ear asymmetry, ability to break through snow cover, e.g., Norberg 1987).

From a morphological perspective, hawk-owls can hardly be considered vole specialists. Two hypotheses could account for this, one non-adaptive, and the other adaptive (sensu Gould and Lewontin 1979). A non-adaptive or "Evolutionary Lag" hypothesis portrays the Northern Hawk-Owl as a species that currently occupies a niche feeding on microtines, but is derived from an ancestor specialized in bird hunting. More advantageous adaptations are lacking because not enough time has passed for those to evolve.

The "Adaptive Generalist" hypothesis posits that voles are the most profitable food item to raise many young during summer, but that hawk-owls critically depend on birds during winter when voles are less accessible under snow. Hawk-owls kill large birds such as ptarmigan in winter, and winter diets can comprise up to 90% of avian prey in Fennoscandia (Mikkola 1972, Cramp 1985, Hogstad 1986, Kiliaan 1989). Finding food may be most difficult in winter, and the most severe selection may take place when hawk-owls in the boreal forest are elusive to observers.

These hypotheses are not exclusive, and they may also relate to the difference between the subspecies *ulula* and *caparoch*. Several owl species are thought to have colonized the Nearctic across Beringia from Eurasia (Voous 1988). Hawk-owls, with their opportunistic potential, may be in the process of adapting to a different array of prey species than in the Palaearctic, particularly to a higher availability of larger prey species such as juvenile (and during winter perhaps even adult) snowshoe hares. There is a general correlation between predator and prey size, suggesting an optimal size ratio for predators to capture prey most efficiently (Rosenzweig 1966, Bozinovic and Medel 1988). In fact, *caparoch* is larger than *ulula* by 6% (Earhart and Johnson 1970, Mikkola 1983). The isolated Central Asian *S. u. tienschanica* is also larger by 5% (Voous 1988). It would be interesting to investigate the feeding ecology and life history of this subspecies comparatively.

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LITERATURE CITED

ANGELSTAM, P., E. LINDSTRÖM, AND P. WIDÉN. 1985. Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia—occurrence and distribution. Holarct. Ecol. 8:285–298.

BANFIELD, A. W. 1974. The mammals of Canada. Univ. of Toronto Press, Toronto.

BOZINOVIC, F., AND R. G. MEDEL. 1988. Body size, energetic and foraging mode of raptors in central Chile. Oecologia 75:456–458.

BYRKJEDAL, I., AND G. LANGHELLE. 1986. Sex and age biased mobility in Hawk Owls *Surnia ulula.* Ornis Scand. 17:306–308.

CRAMP, S. [ED.]. 1985. Handbook of the birds of Europe, the Middle East and North Africa, Vol. 4. Oxford Univ. Press, Oxford.

DUNCAN, P. A. 1993. Status report on the Northern Hawk-Owl *Surnia ulula.* Unpublished Report to the Committee on the Status of Endangered Wildlife in Canada, Environment Canada, Ottawa, Canada.

DUNCAN, P. A., AND J. R. DUNCAN. 1994. Northern Hawk-Owl (*Surnia ulula*). *In* A. Poole and F. Gill [eds.], The Birds of North America, No. XX. The American Ornithologists' Union, Washington D.C.

DUNCAN, J. R., AND P. A. LANE. 1987. Observations of Northern Hawk-Owls nesting in Roseau County. Loon 59:165–174.

DUNNING, J. B. 1984. Body weights of 686 species of North American birds. Western Bird Banding Association, Monogr. 1:1–38.

EARHART, C. M., AND N. K. JOHNSON. 1970. Size dimorphism and food habits of North American owls. Condor 72:251–264.

FISHER, A. K. 1893. The hawks and owls of the United States in their relation to agriculture. U.S. Dept. Agric. Div. Ornithol. and Mammal Bull. 3:1–210.

FORD, N. L. 1967. A systematic study of the owls based on comparative osteology. Ph.D.diss., Univ. of Michigan, Ann Arbor.

FUJII, K., C. S. HOLLING, AND P. M. MACE. 1986. A simple generalized model of attack by predators and parasites. Ecol. Res. 1:141–156.

GAVRIN, V., I. DOLGUSHIN, M. KORELOV, AND M. KUZMINA. 1962. The birds of Kazakhstan, Vol. 2 (in Russian). Alma Ata., Kazakhstan.

GLUTZ VON BLOTZHEIM, U. N., AND K. M. BAUER. 1980. Handbuch der Vögel Mitteleuropas, Vol. 9. Akademische Verlagsgesellschaft, Wiesbaden.

GOULD, S. J., AND R. C. LEWONTIN. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptionist programme. Proc. R. Soc. Lond. B 205:581–598.

HAGEN, Y. 1956. Norwegian studies on the reproduction of birds of prey and owls in relation to micro-rodent population fluctuations. Fauna 22: 73–126.

HENDERSON, A. D. 1919. Nesting of the American Hawk Owl.Oologist 36:59-63.

HIK, D. S. 1994. Predation risk and the 10 year snowshoe hare cycle. Ph.D.diss., Univ. of British Columbia, Vancouver.

HOGSTAD, O. 1986. On the winter food of the Hawk Owl, *Surnia ulula*. Fauna Nervegica. Ser. C. Cinclus 9:107–110.

HUBBS, A. H. 1993. Population regulation in the Arctic ground squirrel: the effects of food and predation. M.Sc.thesis, Univ. of Toronto, Toronto, Ontario.

HUHTALA, K., E. KORPIMÄKI, AND E. PULLIAINEN. 1987. Foraging activity and growth of nestlings in the Hawk Owl: adaptive strategies under northern conditions, p. 152–156. *In* R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre [eds.], Biology and conservation of northern forest owls: symposium proceedings. USDA Forest Service, Gen. Techn. Rep. RM-142.

JOHNSGARD, P. A. 1988. North American owls. Smithsonian Institution Press, Washington, DC.

JOHNSGARD, P. A. 1990. Hawks, eagles, and falcons of North America. Smithsonian Institution Press, Washington, DC.

JOHNSON, W. D., AND C. T. COLLINS. 1975. Notes on the metabolism of the Cuckoo Owlet and Hawk Owl. Bull. South. Calif. Acad. Sci. 74:44–45.

JONES, E. T. 1987. Observations of the Northern Hawk Owl in Alberta, p. 149–151. *In* R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre [eds.], Biology and conservation of northern forest owls: symposium proceedings. USDA Forest Service, Gen. Techn. Rep. RM-142.

KEITH, L. B. 1963. Wildlife's ten year cycle. Univ. of Wisconsin Press, Madison.

KERTELL, K. 1986. Reproductive biology of Hawk Owls *Surnia ulula* in Denali National Park, Alaska. Raptor Research 20:91–101.

KILIAAN, H.P.L. 1989. A Hawk-Owl Spruce Grouse encounter in the Northwest Territories. Blue Jay 47:213–214.

KREBS, C. J. 1989. Ecological Methodology. Harper and Row, New York.

KREBS, C. J., AND I. WINGATE. 1976. Small mammal communities of the Kluane Region, Yukon Territory. Can. Field Nat. 90:379–389.

KREBS, C. J., R. BOONSTRA, S. BOUTIN, M. DALE, S. HANNON, K. MARTIN, A.R.E. SINCLAIR, J.N.M. SMITH, AND R. TURKINGTON. 1992. What drives the Snowshoe Hare cycle in Canada's Yukon?, p. 886–896. *In* D. McCullough and R. Barrett [eds.], Wildlife 2001: Populations. Elsevier, London, U.K.

MARTI, C. D. 1987. Raptor food habits studies, p. 67–79. *In* B. A. Giron Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird [eds.], Raptor management techniques manual. Nat. Wildl. Fed., Washington, DC.

MIKKOLA, H. 1972. Hawk-owls and their prey in Northern Europe. Brit. Birds 65:453–460.

MIKKOLA, H. 1983. Owls of Europe. Buteo Books, Vermillion, South Dakota.

MURDOCH, M. W., AND A. OATEN. 1975. Predation and population stability. Adv. Ecol. Res. 9:2–131.

NORBERG, R. A. 1987. Evolution, structure, and ecology of northern forest owls, p. 9–43. *In* R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre [eds.], Biology and conservation of northern forest owls: symposium proceedings. USDA Forest Service, Gen. Techn. Rep. RM-142.

NYBO, J. O., AND G. A. SONERUD. 1990. Seasonal changes in diet of Hawk Owls *Surnia ulula*: importance of snow cover. Orn. Fenn. 67:45–51.

O'DONOGHUE, M., AND C. J. KREBS. 1992. Effects of supplemental food on snowshoe hare reproduction and juvenile growth at a cyclic population peak. J. Anim. Ecol. 61:631–641.

OTIS, D. L., K. P. BURNHAM, G. C. WHITE, AND D. R. ANDERSON. 1978. Statistical inference from capture data on closed animal populations. Wildl. Monogr. 62:1–135.

PRUITT, W. O. 1978. Boreal Ecology. Studies in Biology 91:1–73.

PULLIAINEN, E. 1978. Nesting of the Hawk Owl, *Surnia ulula*, and Short-eared Owl, *Asio flammeus*, and the food consumed by owls on the island of Ulkokrunni in the Bothnian Bay in 1977. Aquila Ser. Zool. 18:17–22.

ROHNER, C. 1994. The numerical response of great horned owls to the snowshoe hare cycle in the boreal forest. Ph.D.diss., Univ. of British Columbia, Vancouver.

ROHNER, C., AND F. I. DOYLE. 1992. Food-stressed Great Horned Owl kills adult Goshawk: exceptional observation or community process? J. Raptor Res. 26:261–263.

ROSENZWEIG, M. L. 1966. Community structure in sympatric Carnivora. J. Mammal. 47:602–612.

SEMENOV-TAISHANSKI, O. N., AND A. S. GILJASOV. 1985. The ecology of the Hawk Owl in the Lapland Nature Reserve (in Russian), p. 130–138. *In* Birds of prey and owls in the nature reserves of the RSFSR. Central Scient. Res. Lab. Agric. and Nature Res., Moscow, Russia.

SMITH, D. A. 1970. Observations on nesting Hawk Owls at the Mer Bleue, near Ottawa, Canada. Can. Field Nat. 84:377–383.

SONERUD, G. A. 1986. Effect of snow cover on seasonal changes in diet, habitat, and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia. Holarct. Ecol. 9:33–47.

VOOUS, K. H. 1988. Owls of the Northern Hemisphere. Collins Sons, London, U.K.

APPENDIX 1. Abundance of prey populations in Kluane, Yukon (S. Boutin et al., unpubl. ms.).

Prey species	Weight in June (kg)	Number of study plots per year	Population density (*n*/ha)					
			1988	1989	1990	1991	1992	1993
Adult snowshoe hares (*Lepus americanus*)	1.40	3–6	0.77	1.04	1.61	1.11	0.43	0.10
Juvenile snowshoe hares (*Lepus americanus*)	0.22	1–4	2.56	3.48	5.38	1.58	0.02	0.01
Ground squirrels (*Spermophilus parryii*)	0.44	2	0.50	0.94	1.24	2.92	1.01	0.47
Red squirrels (*Tamiasciurus hudsonicus*)	0.28	2	2.39	3.08	2.91	2.31	2.76	2.51
Red-backed vole (*Clethrionomys rutilus*)	0.02	12	1.94	2.36	1.19	3.40	7.38	4.29
Field voles (*Microtus* sp.)	0.04	12	1.83	0.31	0.16	0.31	0.49	1.99