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POPULATION RESPONSES OF NORTHERN GOSHAWKS TO THE 10-YEAR CYCLE IN NUMBERS OF SNOWSHOE HARES

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Abstract. We studied the abundance, diet, and migratory status of Northern Goshawks (*Accipiter gentilis*) at Kluane, southwest Yukon, Canada, from 1987 to 1993. This period spanned a local increase, peak, and decline in numbers of snowshoe hares (*Lepus americanus*). Goshawk sightings increased from 1988 to 1991, the year after hares reached peak densities, and about 40 pairs of goshawks occupied the 400 km² study area in 1990. As hare numbers fell, goshawk numbers dropped, birds became more nomadic, and their mortality increased within the study area. Goshawks nested mainly in mature but small spruce trees (*Picea glauca*). In the breeding season, male goshawks preyed heavily on hares, arctic ground squirrels (*Spermophilus parryi*), red squirrels (*Tamiasciurus hudsonicus*), and took some Spruce Grouse (*Dendragapus canadensis*) and Willow Ptarmigan (*Lagopus lagopus*). Hares made up 56% of the biomass of prey killed from 1989 to 1991. No successful breeding by goshawks was noted in 1992, after hare numbers declined to low levels. Data from mortality-sensing radio transmitters fitted to hares showed that goshawks accounted for about 10% (summer) to 17% (winter) of mortalities of radio-collared hares from fall 1988 to spring 1993. The number of breeding attempts located and the reproductive success of breeding pairs increased with hare densities. Pairs breeding at the hare peak fledged 2.8 young per nest. We suggest that this population of goshawks is resident year-round during periods of high hare numbers, because snowshoe hares are available as food in winter. In periods of low hare abundance, goshawks become more nomadic in spring, summer, and fall, and virtually disappear from the Kluane area in winter.

Key Words: *Accipiter gentilis*; demography; diet; migration; Northern Goshawk; reproduction; snowshoe hare cycle.

The "10-year cycle" of the northern boreal forest (Keith 1963) is one of the most dramatic ecological events in northern North America. Every 8–11 years, the numbers of snowshoe hares (*Lepus americanus*) rise to a peak, where they dominate the biomass of vertebrates in the boreal forest (Krebs et al. 1986, 1992; S. Boutin et al., unpubl. ms.). Several larger avian predators reproduce well and increase in numbers during the prey bonanza at peak hare densities (Craighead and Craighead 1956, Luttich et al. 1971, McInvaille and Keith 1974, Keith et al. 1977, Adamcik et al. 1978). One of many interesting questions about the 10-year cycle is: how do large raptors respond to the appearance and disappearance of the snowshoe hare from their prey base, at a rate that is rapid relative to their potential lifespan? We studied this question for the Northern Goshawk (*Accipiter gentilis*) at Kluane, Yukon, from 1987 to 1993, during the cyclic rise and fall of snowshoe hare numbers. Our study forms part of a larger experimental project (C. J. Krebs et al. 1992, unpubl. data), on the effects of the rise and fall in hare numbers on the boreal forest food web.

In this paper, we address four specific questions: (1) do numbers of goshawks change as hare numbers rise and fall; (2) does the breeding performance of the goshawk respond to the changing abundance of snowshoe hares; (3) do the diets of goshawks shift from the period of peak hare numbers, to the time when hare numbers are declining; and (4) is this northern population of goshawks migratory?

METHODS

STUDY AREA

We worked at Kluane (60°57′N, 138°12′W) in a 400 km² area of the Shakwak Trench, a broad glacial valley bounded by alpine areas to the northwest and southeast. The part of the valley studied (ca. 30 × 13 km) contains a 30-km stretch of major highway (the Alaska Highway) and about 50 km of secondary roads and tracks. Snowmobile trails in winter generally follow these secondary roads. Most parts of the valley are accessible only on foot. The valley bottom averages about 900 m above sea level and is mostly covered with closed spruce forest, interspersed with shrub thickets, grassy meadows, old burns, eskers, small lakes, marshes, and many ponds.

The dominant tree species is white spruce (*Picea glauca*), with some aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*). The dominant shrubs are gray willow (*Salix glauca*), bog birch (*Betula glandulosa*), and soapberry (*Sherpherdia canadensis*).

We distinguished two main forested habitats: closed spruce forest, with dense stands of spruce and a sparse understory; and open spruce forest, with scattered spruce, occasional clumps of aspen trees, and a dense shrub layer. Trees at Kluane are small (canopy height 8–13 m) because of the proximity to tree line. On the borders of the valley the vegetation changes first to open sub-alpine forest of spruce and dense tall willow (*Salix* spp.) thickets, then to patchy short willows, and finally to open tundra at about 1400 m above sea level. The large Kluane Lake (ca. 300 km²) borders the study area to the northwest. The valley lies in the rain shadow of the St. Elias mountains, and experiences a cold continental climate with only moderate precipitation. Snow depths average about 55 cm by late winter (Krebs et al. 1986).

Survey Methods

We sought information on goshawk numbers in five main ways:

(1) All project field personnel were trained by one of us (FID) to identify local raptors. These observers spent a total 47,276 hours in the study area on foot during both summer and winter and 9777 additional hours driving vehicles on the Alaska Highway and tracks in the study area. At the end of each field day, each worker recorded the numbers of goshawks and other larger animals seen on foot or from a vehicle while in the study area, and the number of foot- or vehicle-hours accumulated each day. We term these observations "seen sheet" data, and expressed them here as goshawk sightings per 100 observer hours.

(2) We designated part of the study area as a 100 km^2 "intensive area." This area was closer to our base camp than the rest of the study area, and thus more easily searched on foot; it also contained most of our sampling plots. The intensive area contained the same sets of habitats and prey species, and had similar vegetation to the remainder of the study area. We searched the intensive area systematically on foot for the presence of breeding goshawks each May and June. From 1990 on, we broadcast tape-recorded goshawk "kakking" calls every 200 m on regularly-spaced transects walked through the intensive area during the nestling period. Kimmel and Yahner (1990) found that such broadcast calls produced responses (calls, flights overhead, or a close approach) from about 50% of breeding pairs tested with single calls broadcast 150 m from known nests. Joy et al. (*this volume*) found somewhat higher levels of response to playbacks of alarm calls by nesting goshawks.

(3) We worked more opportunistically elsewhere in the study area, searching particularly near water (Beebe 1978), near past nest sites, and by broadcasting calls in areas where recent goshawk sightings had been reported. Several parts of the remaining 300 km^2 area contained study plots and a satellite field camp, and these areas were also visited regularly. Ground searches focused primarily on indirect signs of goshawk presence (long streaks of "whitewash" below perches, and prey remains and pellets near plucking sites).

(4) We also searched for nests from a light aircraft in early spring in 1988 and 1989 before leaves appeared on deciduous trees, but while snow was still on the ground (McGowan 1975). This method revealed some nests in deciduous trees. However, we discontinued its use after 1989, when it became clear that most goshawk nests were in white spruce trees and were not visible from the air.

(5) We trapped goshawks using falling-lid traps baited with live rock doves (*Columba livia*) in an inaccessible bottom compartment. Trapped goshawks considered to be likely breeders (adults or yearling females in spring or late winter) were fitted with tail-mounted radio transmitters manufactured by Biotrack Ltd. (Kenward 1978). We monitored the presence of these birds weekly, until they left the study area or molted their transmitters in the fall. In May 1988, we monitored the hunting ranges of a non-breeding adult male and an immature female intensively, using methods outlined by Mech (1983) and Kenward (1987). Bearings were taken from fixed points on the Alaska Highway, and we moved rapidly between points to minimize movements of birds between readings, and spaced the points far enough apart so that successive bearings deviated by 90° or more. We used the program RANGES IV (Kenward 1990) to calculate 95% outer convex polygons for each bird's range.

Reproductive Success and Diet

When nests were located, they were monitored every 2–5 days until the young left the nest. When a nest was first found, we conducted a careful spiral search around the site to locate the plucking sites used by the male bird. The fallen trees and bowed branches used for plucking prey by the male were then flagged and revisited every 2–4 days. Any non-fresh prey remains were removed and discarded on the first visit, and all fresh prey remains were collected and removed on each subsequent visit. At the end of the breeding season, we collected nest remains, sorted them together with prey remains from plucking sites, and matched parts of each prey (tails, heads, wings, etc.) to establish the minimum number of prey individuals captured per species for each nest. Small mammals (mice, voles) are probably under-represented in data from plucking sites, because these require little preparation, and thus generate few remains.

In 1990, we also watched nests from blinds using a 20–45 power telescope for 68.1 hours, to identify possible biases in the prey remains left at plucking sites. Similar prey items were brought to nests during watches and collected from plucking sites in 1990, but a higher proportion of birds was recorded at plucking sites (54 of 229 items, 23.6%) than in observations at nests (1 of 19 items, 5.3%). Nearly all prey at plucking sites could be identified, but some prey brought to nests were not identifiable. Pellets have yet to be analyzed at the time of writing.

Information on Goshawk Prey and Predators

Snowshoe hares, arctic ground squirrels (*Spermophilus parryi*), red squirrels (*Tamiasciurus hudsonicus*), deer mice (*Peromyscus maniculatus*) and voles (*Clethrionomys rutilus, Microtus* spp.) were live-trapped each summer on 2–3 unmanipulated 34-ha plots in the study area. Squirrels and hares were trapped with live traps (Tomahawk Live Trap Co., Tomahawk, WI). Squirrel traps were baited with peanut butter and placed near middens or burrow complexes on 10-ha plots. Hare traps (Tomahawk Live Trap Co.) were placed each April in runways under cover at 50 sites evenly-spaced on four rows of each 34-ha plot. Hare traps were supplied with apple slices and alfalfa cubes. Mice and voles were trapped in Longworth box-and-tunnel traps (Penlon Ltd., Abingdon, Oxfordshire, U.K.), supplied with cotton batting, baited with whole oats, and covered with 20 × 25-cm wooden boards. Fifty Longworth traps were placed at alternate stations on a 10 × 10 grid with 15-m trap spacing, on a 2.8-ha plot nested within each 34-ha plot. Hares were trapped once each April in a 5–6 day trapping period, and other species were trapped twice over three to five days in June and August. Trapped mammals were given numbered metal ear tags (National Band and Tag Co., Newport, KY). Hare densities on the 34-ha plots were calculated by assuming that the effective trapping area of each plot was 60 ha. Weights of juvenile hares were estimated from the length of their right hind foot using an equation provided by M. O'Donoghue (unpubl. data): weight (g) = $-302.2 + 10.2 \times$ RHF ($N = 1051$, $r^2 = 0.92$). Goshawks did not consume hare feet, and thus these were readily obtained.

Detailed analyses of population changes in other prey species have yet to be completed (S. Boutin et al., unpubl. data), and we report only qualitative trends here. We used numbers of animals trapped to calculate estimates of available adult biomass of each prey species.

A sample of 50–150 trapped hares at any one time was fitted with 40-g mortality-sensing radio collars (made by various manufacturers) on nine 34-ha study plots. When a collared hare was found dead in winter, we could usually (>80% of cases) identify the predator responsible for the kill from tracks, feather-imprints in the snow, and predator hair or feathers (Einarsen 1956). Summer deaths could not be so readily identified because of the absence of tracks, but the way a prey was plucked, and distinctive long streaks of whitewash, identified the goshawk or Red-tailed Hawk (*Buteo jamaicensis*) as the killer. Mortality-sensing radio collars (various manufacturers) were also fitted to 60–100 red squirrels annually from 1989 on, and to 30–100 arctic ground squirrels from 1991 to 1993. Spruce Grouse (*Dendragapus canadensis*) were color-banded and counted on the ground on four sample plots each spring, and ptarmigan (*Lagopus* sp., mostly Willow Ptarmigan [*L. lagopus*]) were counted on transects in the alpine tundra from a light aircraft in spring (late April or early May) from 1990 to 1993. Numbers of passerine birds were estimated in early June using 5-minute point counts at 11 regularly-spaced stations on each of four 34-ha study plots from 1988 to 1992 (Folkard 1990).

The seen sheets yielded estimates of the abundance of several potential predators on goshawks (e.g., Golden [*Aquila chrysaetos*] and Bald [*Haliaeetus leucocephalus*] eagles). The Great Horned Owl (*Bubo virginianus*), the most abundant large predatory bird at Kluane (peak densities of ca. 1 pair per 4 km²), was studied intensively in the valley by C. Rohner (Rohner and Doyle 1992, Rohner, unpubl. data) from 1988 to 1992.

Methodological Problems

Before presenting and discussing our results, we first comment on some methodological problems encountered in this study. First, there is the issue of biases in our data. We are confident that our seen sheet data provided a reliable index of the relative abundance of goshawks among years, despite some variability in the skill of observers. One of us (FID) was present during the collection of most of the seen sheet data, and his observations correlated well with those of other project workers. Most observers spent thousands of hours in the field and became very familiar with the commoner raptors at Kluane, including goshawks. These data stemmed from extensive field work during all seasons, not just from an intensive period of work during spring and summer. It is possible, however, that seasonal differences in sightings were affected to some degree by skill levels of seasonal workers, and by seasonal shifts in the type of field work. Summer workers were slightly less skilled on average, and they spent more time trapping mammals and sampling vegetation, whereas winter workers mainly did snow tracking. As sightings from vehicles showed similar trends to those on foot, we do not think that biases stemming from the type of work were large.

We are also confident that our methods yielded a useful index of the numbers of breeding birds, particularly after 1989, but we are not confident that we tallied all breeding birds present. Northern Goshawks at Kluane did not often fly above the forest canopy, and were thus hard to detect from the ground or air. When active nests were approached closely, females generally attacked us vigorously, but the rugged terrain and the size of the study area made it impossible to search every nook and cranny thoroughly.

As found by Kimmel and Yahner (1990), calls broadcast near known active nest sites at Kluane produced responses from only about half of the pairs tested. Therefore, our methods underestimated the numbers of breeding pairs, perhaps by about 50 per cent, even in the intensive study area (100 km²). We probably detected an even lower proportion of pairs in 1988 and 1989, before we used broadcast calls.

Data on diets reported here are also likely to be subject to biases. Birds were over-represented at plucking sites, and very small prey may have been taken by males but not brought to plucking sites or nests. Adult hares are too heavy (ca. 1.4 kg) for a male goshawk to carry any distance, and large adult hare remains at plucking sites and nests were probably mostly from kills made by the female hunting from the nest. Diets outside the breeding season must have been radically different from those of nesting birds, because of the much simpler prey base available in winter (hares, red squirrels, voles, small mustelids, corvids, chickadees and finches).

RESULTS AND DISCUSSION

Numbers of Hares and Goshawks

Hare densities on unmanipulated plots at Kluane rose over six-fold from about 0.2 hare ha^{-1} in the spring of 1987 to a peak of 1.44 hares ha^{-1} in 1990 (Fig. 1). Hare numbers remained near this level in 1991, but declined fifteen-fold to below 0.1 hare ha^{-1} by the spring of 1993 (Fig. 1). No goshawks were sighted in the winter of 1988–1989, after the first spring with high hare numbers, but goshawk numbers increased sharply during the next three winters. The peak number of goshawk sightings in winter occurred just after the onset of the decline in hare numbers (Fig. 1). Rates of responses to broadcast goshawk calls also declined five-fold from 1990 to 1992 (Table 1).

Winter sightings (November–March) of gos-

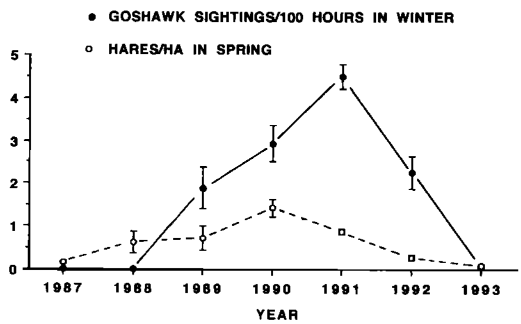

FIGURE 1. Mean number of goshawks sighted per month in winter (November to March), in relation to mean numbers of snowshoe hares live-trapped in spring (mean of two to three plots) at Kluane, Yukon. The bars represent one standard error.

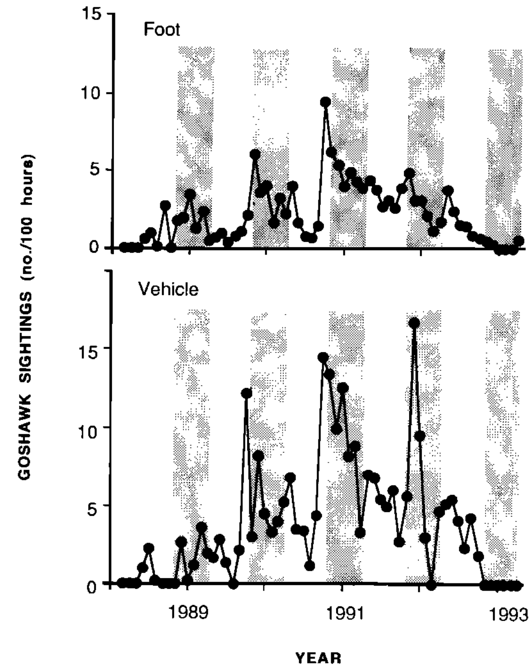

FIGURE 2. Monthly index of sightings (per 100 hours) of Northern Goshawks by observers on foot, and observers in vehicles. Shaded areas display the five winter months (November to March).

hawks were about twice as frequent from both vehicles and on foot (Fig. 2) as sightings in the previous summer (June–August) for the four years beginning in June 1988. However, goshawk numbers declined in the winter of 1991 to 1992, and they almost disappeared from Kluane in the winter of 1992 to 1993 (Fig. 2). An index of goshawk numbers at Rochester, Alberta, declined over four successive winters from 1970 to 1974, as hares declined from a peak (Keith and Rusch 1986).

These data all suggest that Northern Goshawk numbers at Kluane responded strongly to declining hare abundance. Declines in goshawk numbers from 1991 to 1993, however, may also have been affected by trends in other prey species, two of which decreased in numbers at about the same time as did hares. Spruce Grouse and Willow Ptarmigan both declined sharply in numbers from 1990 to 1991 and remained scarce up to 1993 (K. Martin and C. Esser, unpubl. data). In contrast to these declines in step with the decline in hare numbers, numbers of red squirrels declined briefly from 1989 to 1990 in response to a poor crop of spruce cones in 1989, but increased again in 1991 and remained stable thereafter (S. Boutin et al., unpubl. data). Arctic ground squirrel numbers remained relatively stable from 1990 to 1993 (A. Byrom, T. Karels, A. Hubbs, and R. Boonstra, unpubl. data). Mice and voles were scarce near the peak in hare numbers in 1990, but numbers of red-backed voles increased about ten-fold from 1990 to 1992, and remained high in 1993 (R. Boonstra et al., unpubl. data). Numbers of passerine birds in summer remained fairly stable from 1988–1992 (Folkard 1990, N. Folkard and J. Smith, unpubl. data).

TABLE 1. Responses of Northern Goshawks to Broadcast Goshawk Alarm Calls during the Breeding Season

Year	Total time of playback (min)	Number of nesting pairs responding	Number of birds without known nests responding	Pairs found per 100 minutes of broadcast
1990	2655	10	3	0.38
1991	3005	6	4	0.20
1992	2460	2	1	0.08

Thus, Northern Goshawks at Kluane, like goshawks and other large avian predators at Rochester (McInvaille and Keith 1974, Adamcik et al. 1978, Adamcik and Keith 1978, Keith and Rusch 1986), showed a strong numerical response in step with a cyclic decline in snowshoe hare numbers. Declines in goshawk abundance at Kluane, however, may have been partly due to declines in other prey species as well as hares.

Nest Site Characteristics

Several other papers in this volume describe and discuss nest site characteristics of Northern Goshawks in detail. Information is also available from neighboring Alaska (McGowan 1975). We therefore present our information on nest sites for comparison with these other reports.

Six nests were located by reading signs left by goshawks on the ground, seven by broadcasting taped alarm calls (1990–1992 only), and two by tracking radios fitted to breeding birds. The remaining five nests were found by checking previously active nests.

We measured the habitat and stand type of 17 of the active nests located during the study. Eleven of the nests were entirely among mature trees and only two were in stands with >50% immature trees. Nine of the 17 nests were in mixed coniferous/deciduous stands, six were in pure spruce, and two in pure aspen. The mean height of ten nests in spruce trees was 7.4 ± 0.7 (SE) m, and spruce nest trees averaged 10.8 ± 0.4 m. Six nests in aspen averaged 5.8 ± 0.4 m in height (mean tree height 8.3 ± 0.3 m). Nests in deciduous trees were much more readily seen from both ground and air, and we thus may have underestimated the proportion of nests in spruce trees. Nests were not particularly close to water ($\bar{X}$ = 258 ± 40 m). Whereas goshawks often nest near water (e.g., Beebe 1978) to provide the incubating female with a nearby place to bathe and drink, water is readily available throughout the Kluane landscape in late spring and early summer from melting snow in small ponds and streams. Nest sites were clustered across years, with pairs often reusing the same stands of trees and nests.

Goshawk nests in Alaska (McGowan 1975) were in larger deciduous trees (mean height 9.1 m compared to 5.8 m at Kluane). Most nests studied in Alaska were in birch (*Betula papyrifera*), a species not found at Kluane. McGowan, however, did not search for nests in spruce trees. Elsewhere in North America, goshawks sometimes select stands of very large and old trees for nesting (other papers *this volume*). Large trees are rare at Kluane because of the high elevation and latitude, poor soils, and fire history of the Shakwak Valley. Goshawks, like Sparrowhawks (*Accipiter nisus*), are flexible in their choice of nesting trees and nesting habitat (Newton 1986) and do not require particularly large trees for nesting, provided their principal breeding requirements (an adequate prey base, and fairly open flight lanes) are met.

Reproductive Responses of Goshawks to Hare Density

The numbers of territorial and breeding pairs of goshawks detected changed markedly with hare densities (Table 2). No active nests were located in 1988, despite the presence of two resident birds fitted with radios. At least three pairs bred in 1989, and 11 pairs were located in 1990 at peak hare densities, eight of which bred. Five of the pairs detected in 1990 were in the intensive area, suggesting a minimum density of about 1 pair per 20 km^2. If we assume our index of the number of pairs underestimated the true number by 50% (see methodological problems, above), and if the density of goshawks in the intensive area was the same as in the rest of the study area, there were about 40 pairs of goshawks in the study area in 1990.

TABLE 2. Breeding Performance of Northern Goshawks at Kluane, Yukon, from 1988 to 1992

Year	Number of pairs located	Number of nests located	Mean number of young fledged per pair (SE)	Mean number young fledged per successful nest (SE)
1988	0	0		
1989	3	3	1.3 (0.88)	2.0 (0.35)
1990	11	8	2.8 (0.57)	3.9 (0.37)
1991	7	7	1.3 (0.47)	2.3 (0.25)
1992	3	1	0.0	0.0

Breeding success peaked in 1990, with 2.8 young being produced per pair and 3.9 young per successful pair. There was one nest failure in 1989, and no nest failures in 1990. Four of eight nests were preyed upon during 1991 and 1992. The identity of three of the nest predators was unknown; a fourth was a Great Horned Owl (Rohner and Doyle 1992), and the fifth was a wolverine (*Gulo gulo*). Peaks of sightings of birds each fall (September, October) from 1990 to 1992 suggested the appearance of pulses of newly-independent juveniles in these years.

As hare numbers declined, so did breeding success of goshawks, until in 1992 the single pair detected failed to breed successfully (Table 2, Fig. 3). McGowan (1975) also reported strongly reduced use of traditional nest sites and some reduction in breeding success by goshawks in central Alaska during a decline in hare numbers from 1971 to 1974.

As hare densities changed, the ratio of adult to immature goshawk sightings first declined slightly from 58% adults in 1990 (N = 43) to 49% adults in 1991 (N = 92), and then increased to 70% adults (N = 64) in 1992, and finally to 100% adults (N = 11) in 1993. These data agree with our data from nests in suggesting that reproductive success peaked in 1990, and that there was much less successful reproduction after 1991.

An interesting pattern was a peak in goshawk sightings in the breeding season in 1991, immediately after the onset of the decline in numbers of breeders (Fig. 3). This pattern suggests either (1) a pulse of non-breeding yearlings (see above) raised at peak hare numbers in 1990, (2)

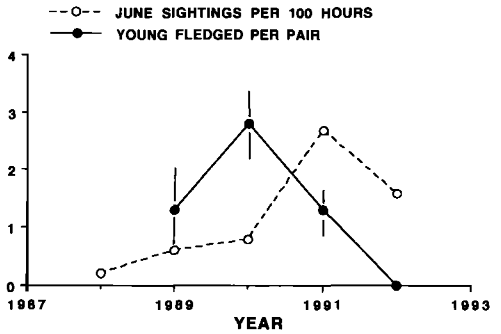

FIGURE 3. Breeding success of Northern Goshawks at Kluane, Yukon (mean number of young fledged per territorial pair), in relation to an index of abundance of goshawks during the breeding season. The bars are one standard error. No data are plotted for 1988, as no breeding pairs of goshawks were detected that year.

an apparent increase caused by non-breeding adult and immature birds ranging more widely in 1991 than in 1990, when they guarded nest areas closely, or (3) increased time spent hunting by goshawks as hare availability declined.

Levels of breeding success attained by goshawks at Kluane during the peak in hare abundance in 1990 equalled or exceeded those reported for southern populations of the species (see other articles *this volume*). Zachel (1985) also found good breeding success for goshawks in nearby Alaska during a snowshoe hare peak in 1979–1981.

In sum, goshawks at Kluane bred frequently and produced many young during the period of high hare density, but reproduced more poorly as hare numbers began to decline, in part because of increasing predation on goshawk eggs and nestlings. Goshawks virtually ceased reproducing after hares and some other prey species became rare in 1992.

Hunting Ranges

Both birds radio-tracked in May 1988 maintained stable ranges throughout the month, with the male using a 95% range of 40.0 km^2 (50 fixes over 30 days) and the female a 95% range of 28.8 km^2 (49 fixes over 30 days). These ranges are 3–4 times larger than values reported by Zachel (1985) for breeding goshawks in Alaska in 1979 and 1980, at approximately the same phase of the previous hare cycle.

Diets at Plucking Sites and Nests

Our main data on diets came from prey remains near nests (Table 3). Medium-sized mammals, particularly hares and squirrels, made up 77% of prey items and over 85% of biomass from 1989 to 1991. Hares accounted for over 55% of the total prey biomass over these three summers. Because of the over-representation of birds at plucking sites (see above), the use of mammals as prey was probably even greater than these estimates imply. Juvenile hares were taken most frequently in 1990, the year when goshawk reproductive success was highest. Ground squirrels were a dominant item in the diet in 1990, a year when red squirrel numbers were low because of poor over-winter survival, but were about as frequent as red squirrels at other times. Spruce Grouse and ptarmigan were also taken frequently from 1989 to 1991. Other birds taken included American Kestrels (*Falco sparverius*), Gray Jays (*Perisoreus canadensis*), and Northern Flickers (*Colaptes auratus*). Diets of goshawks breeding in boreal forest in nearby Alaska also contained about 90% of mammalian prey by biomass (Zachel 1985). At the southern edge of the boreal forest in Alberta, mammals made up 73% of the biomass in goshawk diets (Keith et al. 1977). Goshawks further south in North America generally killed more birds and fewer mammals (Reynolds and Meslow 1984, Bull and Hohmann *this volume*, DeStephano et al. *this volume*), but Boal and Mannan (*this volume*) also found heavy use of mammalian prey. In Europe, birds made up over 85% of prey items (Opdam 1975, Opdam et al. 1977, Widén 1987) and 91% of biomass (Widén 1987). Widén noted greater use of mammals in winter in Sweden, but Opdam et al. (1977) did not find such a switch in the Netherlands and Germany. These differences in the ratio of birds to mammals in goshawk diets probably occur principally because the goshawk is an opportunist, and the availability and relative sizes of avian and mammalian prey differ among sites.

Few data on goshawk diets were available from the summer of 1992, as the only nest found failed soon after the young hatched. These few data suggested a switch from mammals to birds in 1992, after hares had become scarce, and when grouse numbers were also declining from a peak in 1990. Radio-collared adult red squirrels were rarely taken by goshawks or unknown predators in summer or winter, although young-of-the-year with radios were preyed on by raptors in summer (K. Stuart-Smith and S. Boutin, unpubl. data). Goshawks caused a substantial proportion of winter deaths of radio-collared hares (17%), and we suspect that goshawks depended heavily on snowshoe hares as prey in winter. Widén (1987) also found that female goshawks killed mountain hares (*Lepus timidus*) in winter.

Goshawks accounted for about 10% of radio-collared hare mortalities in summer. The summer value is less reliable, because over half the summer kills could not be assigned to a predator

TABLE 3. MINIMUM NUMBERS OF PREY ITEMS (% OF TOTAL ITEMS PER YEAR) FOUND AT 16 NESTS OF NORTHERN GOSHAWKS AT KLUANE, YUKON

Prey species	1989	1990	1991	1992	Biomass (%)[1]
Adult snowshoe hare	13 (14)	32 (14)	16 (20)	1	35.4
Juvenile hare	9 (10)	57 (25)	14 (17)	0	22.7
Red squirrel	31 (34)	10 (4)	17 (21)	0	5.6
Arctic ground squirrel	16 (18)	76 (33)	17 (21)	1	22.0
Northern flying squirrel	1 (1)	0	0	0	0.1
Grouse-ptarmigan	12 (13)	31 (14)	9 (11)	2	12.4
Other birds	8 (9)	23 (10)	8 (10)	5	0.9
Voles-mice	1 (1)	0	0	0	0.01
Total prey items	91	229	81	9	

[1] Biomass (kg) values used: adult hare 1.41, red squirrel 0.24, ground squirrel 0.51, grouse/ptarmigan 0.57, other birds/voles 0.05 kg; for juvenile hares, see text. Samples of nests: 1989 = 3; 1990 = 8; 1991 = 4; 1992 = 1.

species and because some kills in summer may have been made by Red-tailed Hawks. The Northern Goshawk is one of the four most important hare predators at Kluane near peak hare numbers; the others are the lynx (*Lynx canadensis*), the coyote (*Canis latrans*), and the Great Horned Owl. These other three predators typically captured hares in open spruce forest, but 33% of 100 kills attributed to goshawks were in dense forest cover, although this comprised only 18% of habitats in the valley. Goshawks thus can capture hares in dense cover, where they are relatively safe from their other major predators in winter. Goshawks may therefore affect the habitat choices of hares, which generally avoid open areas where risk of predation is high (Hik 1994).

MIGRATORY STATUS OF GOSHAWKS AT KLUANE

Goshawk abundance in winter followed hare densities closely (Figs. 1, 2). Birds were present year-round during the period of high hare numbers from 1989 to 1991, and several birds remained in the summer of 1992. Sightings, however, dropped sharply in the winter of 1992–1993, after hare densities had declined to low levels. The sharp drop in numbers could have been because (1) goshawks migrated from the study area during winter in periods of low hare density, or (2) numbers of resident goshawks declined through mortality. Our data (Fig. 2) did not suggest any obvious fall exodus and spring return of goshawks as hare numbers declined, but we did note a change from resident to transient status of birds trapped before and during the hare decline. Thirteen of 14 birds fitted with radios in 1988 to 1990 remained in the study area for at least one month after capture during the periods of increasing and high hare numbers, but only one of five captured birds did so from 1991 to 1993 during the hare decline ($P = 0.002$, Fisher exact test). Mueller et al. (1977), and T. C. Erdman and D. F. Brinker (unpubl. data) have reported large southward flights of goshawks, including many adult birds, south of Lake Superior in years following declines in snowshoe hare numbers.

Concerning the local mortality hypothesis, no natural deaths of adult or immature goshawks were noted during the period of increasing and high hare densities from summer 1988 to spring 1991, but eight birds (five adults and three immatures) were found dead in either summer 1991 or the following winter, during the hare decline. Five of these were found as carcasses revealed after snow melt in spring, and these birds may have starved. Two birds were killed by Great Horned Owls, and another bird by an unknown raptor. Predation and food shortage thus combined to reduce breeding numbers and reproductive success of goshawks in the hare decline. This supports Rohner and Doyle's (1992) suggestion that strong predator-predator interactions occur in the boreal forest as hares become increasingly scarce. The abundant Great Horned Owl may be a key killer of other smaller predators in these interactions.

In summary, our data suggest that many Northern Goshawks at Kluane are resident during periods of high hare abundance. Declines in goshawk numbers from 1991 to 1993 were due to both increased local morality and increased movements induced by declines in the availability of snowshoe hares as prey, particularly in winter.

CONCLUSIONS

Data from boreal areas (McGowan 1975, Zachel 1985, this study), suggest that four factors characterize goshawk populations in the boreal forest: (1) year-round resident status during periods of high hare numbers; (2) increased nomadism and/or migration during hare declines; (3) increased mortality of adults, immatures, and eggs and nestlings, during declines in hare numbers; and (4) a partial or complete withdrawal of surviving birds from large parts of the boreal forest in winter during periods of low hare numbers.

As reported elsewhere (e.g., Beebe 1978, McGowan 1975, Zachel 1985, Widén 1987), goshawks breeding at high latitudes have broad diets, preying mainly on medium-sized mammals, supplemented by some medium-sized to large birds. Goshawks at Kluane preyed heavily on snowshoe hares in summer and winter from 1989 to 1991, but the few remaining breeders switched to smaller prey in 1992 after hare numbers declined markedly.

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