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NESTING HABITAT OF *ACCIPITER* HAWKS: IS BODY SIZE A CONSISTENT PREDICTOR OF NEST HABITAT CHARACTERISTICS?

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Abstract. In western coniferous forests a general correlation of accipiter size and structural size of nesting stands and nest trees used by sympatric *Accipiter* species has been reported. In this paper we review the literature to evaluate the following predictions: accipiter hawks consistently use nesting habitat in which their body size is (1) positively correlated with nest tree height, and average stand tree diameter, and (2) inversely correlated with average stand tree density and stand % canopy closure. We include in this review summary habitat data collected at 42 Northern Goshawk (*Accipiter gentilis*), 52 Cooper's Hawk (*A. cooperii*), and 16 Sharp-shinned Hawk (*A. striatus*) nest sites in the Jemez Mountains of north-central New Mexico. From our review of the literature, stand % canopy closure, and nest tree height did not consistently follow the expected pattern. Average stand tree density and average stand tree diameter consistently supported the body size predictions. However in several studies, stand densities of goshawk and Cooper's Hawk stands were not significantly different. In addition, there seems to be much variation between studies for mean values for all of the parameters, and the ranges of the mean values overlap among species. This is probably indicative of both habitat variation between study areas and differences in methodology. This review of accipiter habitat studies supports Kennedy's (1988) hypothesis that the correlation between accipiter size and nest stand and nest site structural size is not a widespread phenomenon for all vegetation parameters and may not be adequate for predicting suitable accipiter nesting habitat in all areas.

Key Words: *Accipiter cooperii*; *Accipiter gentilis*; *Accipiter striatus*; Cooper's Hawk; nesting habitat; Northern Goshawk; Sharp-shinned Hawk.

The three North American *Accipiter* species (Northern Goshawk [*A. gentilis*], Cooper's Hawk [*A. cooperii*] and Sharp-shinned Hawk [*A. striatus*]) are sympatric predators in many forested areas in North America (Palmer 1988:304–378, Reynolds 1989). In western coniferous forests Reynolds et al. (1982), Moore and Henny (1983) and Fischer (1986) reported a general correlation of accipiter size and tree size (used as an index of successional stage) of nesting stands and nest trees used by sympatric *Accipiter* species. Kennedy (1988) also observed this correlation for nest tree size and accipiter size in New Mexico. However, in the northeastern U.S., Bosakowski et al. (1992) found Cooper's Hawks nesting in trees with greater diameter than goshawks. In addition, Kennedy (1988) and Bosakowski et al. (1992) found no significant differences for basal area (BA), tree densities, or mean diameter at breast height (dbh) between goshawk and Cooper's Hawk nesting stands in their study areas.

There are two plausible explanations for these equivocal results: (1) a correlation between accipiter size and nest stand and nest tree sizes is not a widespread phenomenon; or (2) a strong correlation does exist but it cannot be detected because of small sample sizes (goshawk N = 11, Cooper's Hawk N = 12 [Kennedy 1988]; goshawk N = 16, Cooper's Hawk N = 19 [Bosakowski et al. 1992]). Our primary study objective is to review the literature to determine if accipiters consistently use nesting habitat in which their body size is positively correlated with nest tree height and average stand tree diameter and inversely correlated with tree density and % canopy closure. We include in this review summary habitat data collected at 42 goshawk, 52 Cooper's Hawk, and 16 Sharp-shinned Hawk nest sites in north-central New Mexico during 1992 and 1993 (Siders and Kennedy, unpubl. data). These data were collected in the same area studied by Kennedy (1988), and thus allow us to determine if her results are maintained when sample sizes of goshawks and Cooper's Hawks are more than doubled and Sharp-shinned Hawk nest sites are included.

APPROACH

In our literature review, we tried to include all published studies, M.S. theses, and Ph.D. dissertations on accipiter nesting habitat characteristics within the United States. We included habitat studies of single *Accipiter* species if the study was conducted in an area where the species was probably nesting sympatrically with congeners. To be included in this review, a study had to have data on one or more of the following parameters: average stand tree density, average stand tree diameter, average stand % canopy closure, and average nest tree height. Of these studies, coniferous forest habitat was the predominant forest cover type, with Bosakowski et al. (1992) and Joy (1990) as the only predominantly deciduous forest cover type for goshawk and Cooper's Hawk.

In reviewing the literature, we encountered various definitions of nest site and/or nest stand, indicating

TABLE 1. COMPARISON OF *Accipiter* NEST STAND TREE DENSITY (TREES/HA) AMONG U.S. STUDIES

Location	Northern Goshawk (N)	Cooper's Hawk (N)	Sharp-shinned Hawk (N)	Source
California, N	749.0 (12)			Saunders (1982)
California, NW	427.0 (10)			Hall (1984)
Missouri		1137.8 (33)	1370.0 (15)	Wiggers and Kritz (1991)
Montana–Idaho	1135.0 (17)			Hayward and Escano (1989)
New Mexico	959.3 (11)	723.9 (12)		Kennedy (1988)
New Mexico	1054.8 (42)	1129.0 (52)	1815.6 (16)	Siders and Kennedy (unpubl. data)
New York–New Jersey	540.1 (16)	633.4 (19)		Bosakowski et al. (1992)
Oregon, E	482.0 (7)	1159.0 (5)	1594.0 (5)	Reynolds et al. (1982)
Oregon, E	1007.4 (34)	1802.5 (31)	2312.0 (15)	Moore and Henny (1983)
Oregon, NW		656.0 (4)	1296.0[1] (3)	Reynolds et al. (1982)
			652.0[2] (2)	Reynolds et al. (1982)[3]
Utah	720.0 (10)	1900.0 (17)	4003.0 (9)	Fischer (1986)
Minimum	427.0	656.0	652.0	
Maximum	1135.0	1802.5	2312.3	

[1] Second growth stands.
[2] Old growth stands.
[3] Goshawk and Cooper's hawk nest stands were not separated into second growth and old growth.

differences in the usage of these terms. We defined a nest stand as the area surrounding a nest tree, including vegetation and topographic features used by a nesting pair during the entire nesting season, exclusive of foraging areas (Reynolds et al. 1982). We defined a nest site as the actual tree in which the nest was placed. In compiling the data from other studies, these definitions were used to avoid confusing nest site and nest stand level comparisons.

In addition to the literature, we included in this comparison unpublished data from our ongoing research on accipiter habitat in the Jemez Mountains and adjacent Pajarito Plateau in north-central New Mexico. In the 1992 and 1993 nesting seasons, we collected habitat data at all known goshawk (N = 42), Cooper's Hawk (N = 52) and Sharp-shinned Hawk (N = 16) nest stands that had not been drastically altered by timber harvest or other disturbance since the sites were identified as active. Each of these nest sites had been occupied (minimally, hawks observed constructing nests during courtship) at least once between 1984–1993.

To estimate the four vegetative parameters of interest, we established 0.08-ha (corrected for slope) circular plots around nest trees. On each plot we measured nest tree height and diameter at breast height (dbh) of all trees (≥2.54 cm dbh) using standard forest measurement techniques (Wenger 1984). To determine % canopy closure, we divided the plot into four quadrants using the four cardinal directions for quadrant boundaries. We measured % canopy closure using a convex spherical densiometer (Lemmon 1956, 1957). Four canopy closure measurements were taken (facing NE, SE, SW, and NW) at each of five locations (center, and at one-half the radius of the plot to the NE, SE, SW, or NW) and averaged for each stand. We determined stand tree density by counting all trees (≥2.54 cm dbh) within the 0.08-ha plot (converting this value to number of trees per ha).

In this comparison, we present mean values of nest tree height, stand tree density, stand tree diameter, and stand % canopy closure for each species in each study. We compared these data qualitatively to determine if accipiters consistently use nesting habitat in which their body size is positively correlated with nest tree height and average stand tree diameter and inversely correlated with average stand tree density and stand % canopy closure. The database cannot be evaluated statistically because sampling techniques and plot sizes varied between studies.

RESULTS AND DISCUSSION

Accipiter nest habitat studies in the U.S. indicate that there is a trend of increasing average stand tree density with increasing accipiter body size (Table 1). However, in three studies (Kennedy 1988, Bosakowski et al. 1992, Siders and Kennedy, unpubl. data) average stand densities for goshawk and Cooper's Hawk stands were not significantly different. It is also interesting to note that Kennedy's average stand densities are lower than the average stand densities we recorded. This is probably due to her small sample sizes and the inclusion of a few riparian cottonwood (*Populus fremontii*) nest stands, which typically have lower stand densities.

This potential effect of sample size on descriptions of accipiter nesting habitat characteristics is also evident in the two studies conducted in the same area in eastern Oregon (Reynolds et al. 1982, Moore and Henny 1983). Both of these studies appear to differentiate between goshawks and Cooper's Hawks by roughly a factor of two in stand density, and between Cooper's Hawks and Sharp-shinned Hawks by 25–30% differences in stand density. Yet, similar to the two New Mexico studies, stand densities for the study with larger sample sizes (Moore and Henny 1983) consistently report larger stand densities than the

TABLE 2. COMPARISON OF *Accipiter* NEST STAND AVERAGE CANOPY CLOSURE (%) AMONG U.S. STUDIES

Location	Northern Goshawk (N)	Cooper's Hawk (N)	Sharp-shinned Hawk (N)	Source
California, N	76.9 (12)			Saunders (1982)
California, NW	94.0 (10)			Hall (1984)
Colorado	95.0 (2)	95.0 (4)	94.0 (14)	Joy (1990)
Missouri		80.9 (31)	82.3 (14)	Wiggers and Kritz (1991)
New Mexico	65.7 (42)	61.6 (52)	77.5 (16)	Siders and Kennedy (unpubl. data)
New York–New Jersey	90.0 (16)	88.7 (19)		Bosakowski et al. (1992)
Oregon, E	59.8 (7)	64.0 (5)	68.3 (5)	Reynolds et al. (1982)
Oregon, NW		75.0 (4)	80.3[1] (3)	Reynolds et al. (1982)
			89.7[2] (2)	Reynolds et al. (1982)[3]
Utah	68.4 (10)	83.1 (17)	81.6 (9)	Fischer (1986)
Minimum	59.8	61.6	68.3	
Maximum	95.0	95.2	97.9	

[1] Second growth stands
[2] Old growth stands
[3] Goshawk and Cooper's hawk nest stands were not separated into second growth and old growth.

study with the smaller sample sizes (Reynolds et al. 1982).

The relationship between stand % canopy closure and accipiter body size is unclear (Table 2). For all three species, average % canopy closure varied from approximately 60% to 95% throughout the range of the studies. In some studies stand % canopy closure was inversely related to body size (Reynolds et al. 1982, Wiggers and Kritz 1991), but in other studies this was not the case. In the eastern U.S., Bosakowski et al. (1992) found goshawks and Cooper's Hawks nesting in stands with similar % canopy closures. In Colorado, Joy (1990) found that all three species were using stands with similar % canopy closures. In Utah, Fischer (1986) found Cooper's Hawks and Sharp-shinned Hawks using stands with similar % canopy closures but with higher % canopy closures than stands used by goshawks. In our study, Cooper's Hawks used stands with more open canopies than did the goshawk which nested in more open stands than did Sharp-shinned Hawks. The values for goshawk and Sharp-shinned Hawk stands in our study are within the range of previously recorded averages for this variable, but the Cooper's Hawk value is the lowest reported stand % canopy closure.

The data on average stand tree diameter supports the prediction that this parameter is positively correlated with accipiter body size (Table 3). The range in stand tree diameters for goshawks was almost a factor of two greater than the reported ranges of its congeners. This is a result of Hall's (1984) study in northwestern California where she reported average stand diameters of 46.0 cm. In contrast, average stand tree diameters for the goshawk and Cooper's Hawk nest stands in our study are the lowest reported

TABLE 3. COMPARISON OF *Accipiter* NEST STAND AVERAGE TREE DIAMETER (DBH-CM) AMONG U.S. STUDIES

Location	Northern Goshawk (N)	Cooper's Hawk (N)	Sharp-shinned Hawk (N)	Source
California, N	27.0 (12)			Saunders (1982)
California, NW	46.0 (10)			Hall (1984)
Missouri		21.8 (33)	20.8 (15)	Wiggers and Kritz (1991)
New Mexico	22.0 (11)	20.0 (12)		Kennedy (1988)
New Mexico	14.8 (42)	13.5 (52)	12.5 (16)	Siders and Kennedy (unpubl. data)
Oregon, E	27.4 (7)	21.3 (5)	18.3 (5)	Reynolds et al. (1982)
Oregon, E	22.1 (34)	15.0 (31)	12.9 (15)	Moore and Henny (1983)
Oregon, NW		24.4 (4)	21.3[1] (3)	Reynolds et al. (1982)
			27.4[2] (2)	Reynolds et al. (1982)[3]
Utah	27.5 (10)	14.7 (17)	10.0 (9)	Fischer (1986)
Minimum	14.8	13.5	10.0	
Maximum	46.0	24.4	27.4	

[1] Second growth stands.
[2] Old growth stands.
[3] Goshawk and Cooper's hawk nest stands were not separated into second growth and old growth.

TABLE 4. COMPARISON OF *Accipiter* NEST SITE AVERAGE NEST TREE HEIGHT (M) AMONG U.S. STUDIES

Location	Northern Goshawk (N)	Cooper's Hawk (N)	Sharp-shinned Hawk (N)	Source
California, N	34.4 (13)			Saunders (1982)
California, NW	43.0 (12)			Hall (1984)
Colorado	26.0 (2)	23.0 (4)	19.0 (14)	Joy (1990)
Montana–Idaho	26.0 (17)			Hayward and Escano (1989)
New Mexico	25.9 (11)	24.1 (12)		Kennedy (1988)
New Mexico	28.6 (42)	20.8 (52)	15.9 (16)	Siders and Kennedy (unpubl. data)
New York–New Jersey	24.1 (16)	25.2 (19)		Bosakowski et al. (1992)
Oregon, E	33.5 (22)	22.6 (15)	11.0 (10)	Reynolds et al. (1982)
Oregon, NW		22.3 (18)	27.1[1] (6)	Reynolds et al. (1982)
South Dakota	18.3 (21)			Bartelt (1974)
Utah	22.4 (10)	12.2 (17)	8.5 (9)	Fischer (1986)
Minimum	18.3	12.2	8.5	
Maximum	43.0	24.1	27.1	

[1] Second growth stands.

values. In addition, average stand diameter for the three species in our study area are not significantly different (Siders and Kennedy, unpubl. data). We cannot evaluate how much of these differences in nest stand parameters between our study and other studies can be attributed to differences in methodology and/or habitat variation.

Most of the studies that included nest tree height found that the taller nest trees were used by the larger species and the shorter nest trees were used by the smaller species (Reynolds et al. 1982 for eastern Oregon, Fischer 1986, Kennedy 1988, Joy 1990, Siders and Kennedy, unpubl data), but not in all cases (Reynolds et al. 1982 for northwestern Oregon) (Table 4). Similar to stand tree diameters, mean nest tree heights were more variable for goshawks than their congeners.

The goshawk, Cooper's Hawk, and Sharp-shinned Hawk are morphologically similar species at three different sizes. Studies that compare habitat characteristics of all three *Accipiter* species are few, and some of these studies have indicated a relationship between the size of the species and the size of elements of its habitat. However, from our review of the literature, not all habitat characteristics follow this pattern for all studies. Stand % canopy closure did not follow the expected pattern in four studies. Stand density trends did follow the expected pattern in most studies; however, differences between goshawk and Cooper's Hawk stands were non-significant in three studies. Nest tree height did not follow the expected pattern in northwestern Oregon (Reynolds et al. 1982). Average stand tree diameter was the only parameter that consistently supported the prediction of increasing habitat scale with increasing body size. In addition, there seems to be much variation among studies for mean values for all the parameters, and the ranges of the mean values overlap between species. This is probably indicative of both habitat variation among study areas and differences in methodology, particularly sample size. Our review of accipiter habitat studies supports Kennedy's (1988) hypothesis that the correlation between accipiter size and nest stand and nest site structural size is not a widespread phenomenon for all vegetation parameters and may not be adequate for predicting suitable accipiter nesting habitat in all areas.

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NORTHERN GOSHAWK DIETS IN PONDEROSA PINE FORESTS ON THE KAIBAB PLATEAU

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Abstract. We recorded 385 prey deliveries at a mean delivery rate of 0.25/hr at 20 Northern Goshawk (*Accipiter gentilis*) nests in ponderosa pine (*Pinus ponderosa*) forests on the North Kaibab Ranger District (NKRD), Kaibab National Forest, Arizona, 1990–1992. Golden-mantled ground squirrels (*Spermophilus lateralis*) and cottontail rabbits (*Sylvilagus* spp.) were the most common mammalian prey species (41%). Steller's Jays (*Cyanocitta stelleri*) and Northern Flickers (*Colaptes auratus*) were the most common avian prey species (16%). Mammals and birds accounted for 76% and 24% of the observed prey, respectively. Mammals accounted for 94% of the biomass used by Northern Goshawks, and cottontail rabbits made up the greatest proportion of the biomass (26%). Goshawks on the NKRD fed slightly less equitably upon different prey taxa than goshawks in California, New Mexico, and Oregon, but size of prey taken by goshawks varied little among geographic locations.

Key Words: *Accipiter gentilis*; Arizona; diet; Northern Goshawk; ponderosa pine.

Habitat alteration by timber harvesting is one of the most significant factors affecting Northern Goshawk (*Accipiter gentilis*) populations (Reynolds 1989). Timber harvesting alters the structure of vegetation in mature forests and may reduce the suitability of stands as nest sites for goshawks (Reynolds 1983). Timber harvesting may also influence prey populations by changing the structure and composition of vegetation in areas where goshawks forage (Moore and Henny 1983). For example, densities of Kaibab squirrels (*Sciurus aberti kaibabensis*) are lower in harvested stands of ponderosa pine (*Pinus ponderosa*) than in uncut stands (Patton et al. 1985), red squirrels (*Tamiasciurus hudsonicus*) decrease up to 80% following thinning (Sullivan and Moses 1986), and golden-mantled ground squirrels (*Spermophilus lateralis*) increase in numbers following timber harvesting (Tevis 1956).

Populations of Northern Goshawks on the North Kaibab Ranger District and elsewhere in the western United States may be declining (Bloom et al. 1986, Kennedy, unpubl. data, Crocker-Bedford 1990, Zinn and Tibbitts, unpubl. data, Reynolds et al. 1992), although the evidence is equivocal. Prey abundance influences the reproductive success of raptors (Newton 1979). Northern Goshawks generally nest in areas with high prey densities (Hantage 1980, Kenward and Widén 1989, Kennedy 1988), and in years when availability of prey is low they experience nest failures (Hantage 1980). Other studies also suggest that the abundance of prey has an important influence on goshawk populations. Schnell (1958) found that days of increased food consumption by nestlings did not correspond with an increased delivery rate of prey, suggesting that foraging rate was controlled by prey abundance rather than food requirements. Wikman and Linden (1981) observed that goshawk numbers declined and brood sizes decreased in response to a reduction in grouse (Tetraoninae), their principal prey species, despite adequate available nesting habitat. Finally, sizes of goshawk ranges are inversely related to prey availability (Kenward 1982).

Northern Goshawks are opportunistic foragers with diets reflecting the diversity of available prey species (Opdam 1975, Widén et al. 1987, Kenward and Widén 1989, Kennedy 1991). Diet information is a principal component of management plans, but goshawk prey varies regionally. Diet studies of individual goshawk populations are necessary to understand their food habits on a regional scale (Storer 1966, Kenward and Widén 1989). Little diet information exists for goshawks in the southwestern United States, and our objective was to document the diet of Northern Goshawks during the breeding season on the Kaibab Plateau, 1990–1992.

STUDY AREA AND METHODS

The study area was on the North Kaibab Ranger District (NKRD), Kaibab National Forest, Coconino County, Arizona. The NKRD is approximately 259,000 ha located on the Kaibab Plateau, and is situated along the northern border of Grand Canyon National Park. The Kaibab Plateau ranges from 923 to 2830 m in elevation. The topography of the Plateau is typified by gentle slopes interspersed with shallow to deep drainages. The Plateau descends to sage flats on the north, east, and west sides, and is bounded by the Grand Canyon to the south. Ponderosa pine forests are found between 2075 and 2500 m elevation and comprise approximately 99,200 ha of the District.

All goshawk nests observed in this study were in stands of ponderosa pine or stands dominated by ponderosa pine. Other overstory trees include quaking aspen (*Populus tremuloids*) and white fir (*Abies concolor*). Gambel's oak (*Quercus gambelii*), New Mexico locust (*Robinia neomexicana*), and Utah juniper (*Juniperus*

osteosperma) were common understory species found along drainages and slopes in all stands.

We observed eight Northern Goshawk pairs each year in 1990 and 1991, and six pairs in 1992. One pair failed each year, and we obtained insufficient data from the failures in 1990 and 1991 to include them in our analyses. We collected dietary data for the remaining 20 nesting goshawk pairs during 1539 hours of observation ($\bar{X}$ = 76.8 hour/nest ± 19.3 SD); we did not study any nesting pair for more than one successful breeding season.

Reproductive Success

We documented nest site productivity for all nests observed in this study. We estimated hatching and fledging dates when not actually observed and we attempted to date and identify causes of nestling mortalities.

Prey Deliveries

We determined food habits by directly observing prey brought to the nest by adult goshawks. Observations at the nest are considered the least biased and most accurate way to assess diet of diurnal raptors (Errington 1930, 1932; Mader 1975; Snyder and Wiley 1976; Zeisemer 1981; Marti 1987; Mersmann et al. 1992; Bielefeldt et al. 1992). The technique, however, does have weaknesses, including: (1) it requires considerable time; (2) the probability of identifying different prey types is not always equal because the prey often are plucked, decapitated, or skinned prior to delivery to the nest; and (3) no information can be collected about the items consumed by adults away from the nest.

We located active goshawk nests from mid-May to early June by visiting historic nest sites in ponderosa pine forests on the NKRD. The only constraints on our selection of nesting pairs to study were that the pair had not been used in previous years of the study, and the nest was situated in such a way that it could be observed from ground or tree blinds. The order of nest observations was randomly selected during the first rotation, and followed the initial order during following rotations until fledging except when the nest failed or weather prevented access to nest sites. We began observations at each nest in the afternoon and continued until sundown, resuming at dawn until the time of initiation the previous day. We observed the nests from cloth blinds located on the ground or in trees a mean distance of 53 m (±17.6 SD) from the nest trees. Blinds were constructed over a 2–3 day period to decrease disturbance to the nesting pair (Fyfe and Olendorff 1976, Marti 1987). We initiated our observations during late incubation or early nestling stages. Approximately 5–7 days after fledging we discontinued observations because prey deliveries often occurred away from the nest.

We identified prey deliveries to species with binoculars and 15–45× spotting scopes. We tabulated the identified prey and used an Analysis of Variance for Ranked Data test (Winer 1971) to investigate variance among nests. We used chi-square tests (Sokal and Rohlf 1981) to examine changes in diet composition on basis of mammal and avian prey, and individual species for which there were sufficient samples, through the nesting season.

We categorized prey into a priori size classes based on Storer's (1966) cubic function size class system. We calculated the mean weights for adult mammalian species from the collection weight of museum specimens in the University of Arizona mammal collection; museum specimens were from various regions throughout their ranges in Arizona. We only used adult weights when calculating average mammal biomass. Weights for adult avian species were taken from Dunning (1984). Estimates of avian weights for the age classes of nestling-fledgling, subadult, and unknown age were computed following Bielefeldt et al. (1992).

We categorized unidentified mammals as being small or large and assigned them the average weight of identified mammals occurring in size classes 1–12 ($\bar{X}$ = 164.8 g ± 61.4 SD) for small mammals, and size classes 13–20 ($\bar{X}$ = 676.4 g ± 42.2 SD) for large mammals. We categorized unidentified avian prey as small, medium, or large and assigned them the average weight of identified birds occurring in size classes 1–3 ($\bar{X}$ = 19.8 g ± 0 SD), 4–6 ($\bar{X}$ = 45.6 g ± 14.1 SD), and 7–8 ($\bar{X}$ = 96.7 g ± 7.2 SD), respectively. We also noted when prey was cached or retrieved from a cache, and excluded the cache retrievals from diet assessment (Johnson 1981).

Prey Remains

Goshawks often remove plumage and pelage from their prey in the nest area or at the nest structure. We collected prey remains (i.e., feathers, fur, skin, skeletal parts) found in the nest area following each observation period. We also removed prey remains from nests whenever nest trees were climbed to band nestlings.

We cataloged prey remains to nest number and date of recovery on a master list. We packaged samples and assigned each a random identification number to alleviate observer bias when identifying remains. The master list was referred to only after remains were identified.

We reconstructed mammalian and avian remains following Reynolds and Meslow (1984). Remains were identified by comparison to specimens held in the University of Arizona mammal and avian collections. We excluded single feathers from analysis as they may have come from molting birds.

Diet Breadth

We examined regional variation in diet breadth between Northern Goshawks in Arizona (this study), California (Bloom et al. 1986), New Mexico (Kennedy 1991), and Oregon (Reynolds and Meslow 1984). We used Levins' (1968) equation

$$B = 1/\sum P_i^2$$

to calculate diet breadths for the niche dimensions of prey taxon and prey size. The value P_i is the proportion of prey in each category, and B ranges from 1 to n, n being the number of categories. If B equals n, prey are used equally from all categories. On the other hand, if B is close to 1, the diet breadth is narrower and categories of prey are not used equally. The number of categories varied among studies. To compare diet

TABLE 1. SPECIES CONTRIBUTING ≥5.0% OF THE IDENTIFIED PREY DELIVERED TO NORTHERN GOSHAWK NESTS, NORTH KAIBAB RANGER DISTRICT, KAIBAB NATIONAL FOREST, ARIZONA, 1990–1992

Species	N	Percent observed	Percent biomass
Golden-mantled ground squirrel	86	28.0	14.9
Cottontail rabbit	41	13.3	26.1
Chipmunk	38	12.4	2.0
Steller's Jay	33	10.7	2.7
Red squirrel	31	10.1	5.8
Tassel-eared squirrel	26	8.5	15.0
Rock squirrel	18	5.9	9.8
Northern Flicker	16	5.2	1.5
Total	289	94.1	77.8

breadths among regions we standardized diet breadth values with the equation

$$B_{\text{standard}} = (B - 1)/(n - 1)$$

(Reynolds and Meslow 1984), which allows diet breadths to be compared on a scale of 0 to 1, the larger the value corresponding to increasing breadth of diet.

RESULTS

REPRODUCTIVE SUCCESS

Goshawks had a nestling rate of 2.4 ± 0.7 SD and 2.6 ± 0.5 SD nestlings per active (reached at least incubation) and successful (fledged young) nest, respectively. Forty-two of 53 nestlings survived to fledge, with a fledging rate of 1.9 ± 1.0 SD and 2.2 ± 0.7 SD fledglings per active and successful nest, respectively. We identified Great Horned Owl (*Bubo virginianus*) predation as the principal cause of nestling mortality (45.4%; N = 5) at our study nests, and a likely factor in some of the unidentified causes of death (36.4%; N = 4). The other identified cause of nestling mortality was falling from the nest (18.2%; N = 2).

PREY DELIVERIES

We observed a mean delivery rate of 0.25 prey items/hour, and identified 370 (97%) of the prey items to class. Only mammals (76%) and birds (24%) were delivered to the nest. We identified 241 (89.2%) of the mammal prey items to at least genus. We identified 59 (65.6%) of the avian prey to species, and six to the Family *Picadae* (6.7%); seven mammalian genera and eight avian genera were represented in goshawk diets.

There was no difference in the mean prey rank between nests (χ^2 = 5.0, df = 19, P = 0.99) for prey species contributing ≥5.0% of the diet. Thus, we pooled the data from all nests to characterize the diet of the goshawk population. Mammalian prey contributing ≥5.0% of the identifiable prey were golden-mantled ground squirrels, cottontail rabbits (*Sylvilagus* spp.), chipmunks (*Tamias* spp.), red squirrels, tassel-eared squirrels (*Sciurus aberti*), and rock squirrels (*Spermophilus variegatus*) (Table 1). Steller's Jays (*Cyanocitta stelleri*) and Northern Flickers (*Colaptes auratus*) were the only avian species contributing ≥5.0% of identifiable prey (Table 1).

We found no significant difference in the proportions of mammal and avian prey taken through the nesting season (χ^2 = 8.9, df = 4, P = 0.06) over 10 day intervals. Neither were there significant differences through the nesting season in the proportions of the three most frequent goshawk prey, golden-mantled ground squirrels (χ^2 = 14.9, df = 9, P = 0.09) over 5 day intervals, or cottontail rabbits (χ^2 = 4.1, df = 4, P = 0.39) and chipmunks (χ^2 = 5.6, df = 4, P = 0.23) over 10 day intervals. Insufficient samples prevented analysis of cottontail rabbit and chipmunk use over five day intervals.

PREY BIOMASS

We used only prey delivered to the nest when computing biomass of goshawk prey. Mammals accounted for 94% and birds accounted for 6% of the biomass in goshawk diets. Only mammals contributed ≥5.0% of the biomass, with cottontail rabbits, golden-mantled ground squirrels, and tassel-eared squirrels accounting for most of the biomass (Table 1).

PREY REMAINS

Mammals accounted for 47.5% and birds accounted for 52.5% of the remains collected (N = 179) at the 20 study nests. Cottontail rabbits (N = 49), Steller's Jays (N = 47), and Northern Flickers (N = 22), the three species represented most frequently in remains, accounted for 65.6% of all remains.

DIET BREADTH

Though goshawks from different regions have similar diet breadth, the goshawks on the NKRD use the available prey slightly less equitably than goshawks in the other regions (Table 2). Size class of prey used by goshawks on the NKRD was also

TABLE 2. STANDARDIZED FOOD NICHE BREADTH OF BREEDING NORTHERN GOSHAWKS IN ARIZONA, CALIFORNIA, NEW MEXICO, AND OREGON BASED ON NUMBER OF PREY GENERA

	Nests	Food niche breadth: Prey genera[1] (total no. genera)	Food niche breadth: Size class (total no. classes)	Source
Direct observation				
Arizona	20	0.32 (15)	0.33 (9)	This study
New Mexico	8	0.62 (9)	0.47 (6)	Kennedy (1991)
Prey remains				
Arizona	20	0.29 (18)	0.25 (11)	This study
California	114	0.41 (21)	0.30 (12)	Bloom et al. (1986)
New Mexico	8	0.36 (22)	0.39 (10)	Kennedy (1991)
Oregon	4	0.42 (30)	0.38 (14)	Reynolds and Meslow (1984)

[1] We pooled *Sphyrapicus* and *Picoides* due to difficulty in distinguishing between them during direct observations.

similar to the goshawks from other regions (Table 2).

DISCUSSION

REPRODUCTION

We studied nests that were active and in late incubation or early nestling stages. Thus, our data on reproduction do not take into account goshawk nests that failed prior to reaching at least late incubation. Nor did we determine the frequency of failed eggs in successful nests. Though it is uncommon for accipiters to experience reproductive losses early in the breeding cycle (Snyder and Wiley 1976), there is a potential bias in our observed rate of 1.9 fledglings per active nest.

Nestling goshawks in successful nests on the NKRD have a high probability (84%) of fledging. Mortality at our study nests appeared to be related to factors other than food availability. For example, Great Horned Owl predation was the single greatest factor contributing to nestling mortality. Only one of the three nesting failures we observed was due to factors other than predation. Eggs in this nest failed to hatch in 1990, but the same nest produced 2–3 young in the following years. One possible cause of the failure was disturbance by a slash cutting crew operating within 100 m of the nest for ≥2 days during incubation. This disturbance may have kept the female away from the nest long enough to allow the eggs to chill.

Our data suggest that food availability was not limiting goshawk productivity at the active nests we studied in ponderosa pine forests on the NKRD during 1990–1992.

PREY FREQUENCY AND BIOMASS

Northern Goshawks purportedly possess an inherent inclination to prey on avian species (Sutton 1925). This suspected proclivity has been supported by numerous studies of diet during the breeding season in which avian prey accounted for ≥55% of the diet (Meng 1959, Opdam 1975, Reynolds and Meslow 1984, Bloom et al. 1986, Widén et al. 1987). These studies used the indirect methods of pellet analysis and/or prey remains identification to determine goshawk diets. Many early anecdotal accounts of goshawk nesting behavior, however, suggest that goshawks take a greater proportion of mammals than these studies indicate (Sutton 1925, Gromme 1935, Dixon and Dixon 1938).

Our data, based on direct observations, indicate a 3:1 mammal to avian ratio in the diets of goshawks in our study on the NKRD. To our knowledge, this is the largest proportion of mammals reported in the diet of a breeding goshawk population. In addition, mammals accounted for 94% of the biomass due to the larger body size of most mammalian prey compared to avian prey. The high use of mammalian prey may be a phenomena associated with the forest structure and available prey found in our study area, or it may be common to the species across its range but only apparent through direct methods of diet analysis (Boal and Mannan, unpubl. data).

Reynolds et al. (1992) recommended that habitat for Northern Goshawks be managed for the 14 prey species that are consistently used by goshawks. Although preliminary information from our study was part of the database used to develop the management recommendations, our final results further support this aspect of the recommendations. All 14 of the listed species occurred in goshawk diets on the NKRD. In addition, six of the seven species accounting for ≥5% of the goshawk diets on the NKRD are among the 14 listed prey species in the management recommendations. The single exception is rock squirrels, which the recommendations list as a potential prey species for which importance is unknown (Reynolds et al. 1992).

Goshawks on the NKRD use the available prey less equitably than is reported elsewhere. This is probably a reflection of predation on golden-mantled ground squirrels at a rate of >2:1 over any other species. Ground squirrels are undoubtedly an important part of goshawk diet during the nesting season. A dependence upon one prey species could conceivably lead to a decline in a predator population if that prey species declined (Dymond 1947, Craighead and Craighead 1956, McGowan 1975, Newton 1979). We think this is unlikely on the NKRD because the prey base of goshawks, though inequitably used, is varied (≥19 species) and is likely to buffer affects of individual prey species fluctuations. The inequitable pattern of predation may be a functional response to the most abundant or available prey species, which appears to have been the golden-mantled ground squirrel during this study. It is possible that during periods when ground squirrels are less abundant, goshawks shift to other species that may be more abundant. Long-term studies of goshawk diet and long-term monitoring of the abundance of prey populations will be necessary to address this issue.

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Population Ecology

BREEDING BIOLOGY OF NORTHERN GOSHAWKS IN NORTHEASTERN OREGON

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Abstract. Ten of 25 historical Northern Goshawk (*Accipiter gentilis*) nest stands in Wallowa County had active nests in 1992. Young fledged at 10 of 12 nests at an average of 1.4 young per successful nesting attempt, or 1.2 young for all nests. Incubation occurred in late April and May, and nestlings were present in June and July. The earliest and latest fledging dates were 22 June and 27 July; the mean fledging date was 8 July. All nests were in old growth or remnant old-growth stands; however, most of the stands searched were old growth. Nest trees averaged 65 cm diameter at breast height and 34 m tall. Diet determined from prey remains consisted of 58.5% birds and 41.5% mammals.

Key Words: *Accipiter gentilis*; breeding biology; Northern Goshawk; northeastern Oregon.

The Northern Goshawk (*Accipiter gentilis*) has generated interest throughout the western United States because there is concern that populations and reproduction of this species are declining (Reynolds et al. 1992). In addition, the Northern Goshawk has been designated as a Management Indicator Species, and the National Forest Management Act regulations require that such species be monitored. Therefore, site specific information on breeding biology is needed to monitor populations of this species. Our objectives were (1) to search historical goshawk nest sites to ascertain how many still had active goshawk nests, and (2) to determine nesting chronology, nest habitat characteristics, and diet during the breeding season.

METHODS

STUDY AREA

The study was concentrated in 42 stands that ranged in size from 10 to 109 ha; these stands were contained within a 350,000-ha area on the Wallowa Valley Ranger District and adjacent portions of the Eagle Cap Ranger District and Hells Canyon Natural Recreation Area, Wallowa County, northeastern Oregon. The study areas were a mixture of stands including ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), grand fir (*Abies grandis*), and Engelmann spruce (*Picea engelmannii*). Elevations within the study areas range from 1200 m to 1800 m, and topography varies from flat to steep canyons.

NEST LOCATION AND HABITAT

To locate active Northern Goshawk nests, we searched 25 historical goshawk nest stands and 17 additional stands containing old growth. A historical nest stand was one where goshawks had nested at least once in the last 20 years based on records kept by the Wallowa Valley Ranger District. Additional sites were selected on the basis of having a stand with >12 trees/ha that were >50 cm dbh, with >60% canopy closure, and >10 ha in size. Stand boundaries were delineated by changes in successional stages. Only the blocks of forest that met the criteria listed above were searched.

Searches for nests were conducted between 16 April and 17 July 1992; however, the majority of the search effort occurred in May and June. We used a silent search and a broadcast of taped calls to search for nests. We searched 75% of the stands with the silent search technique where we walked through the stand looking for nest platforms, white-wash, prey remains, and goshawks. Approximately one person-day was spent searching stands >40 ha in size, and one-half a person-day was spent in smaller stands.

In the remainder of the stands we broadcast adult alarm calls (Kennedy and Stahlecker 1993) at stations about 400 m apart. This distance was used because we determined that the tape could be heard 200 m away. At each station, three calls were broadcast; each call was 10-sec long and 1-min apart. The speaker was oriented at 60°, 180°, and 300° during the calls. We did not use broadcast calls more extensively because the majority of our searching was done when the birds were presumed to be incubating, and birds are not likely to respond to calls during this period (Kennedy and Stahlecker 1993).

Active nest trees (terms defined in Reynolds et al. 1992) were revisited every 1–2 weeks to determine nesting chronology. If there was evidence of occupancy by goshawks (e.g., birds seen, prey remains, white-wash) but no nest was found, the stand was revisited in 2–4 weeks.

At each active nest tree, we recorded tree species, condition (live or dead), diameter at breast height (dbh), and height; exposure of nest (north = 316–45°, east = 46–135°, south = 136–225°, west = 226–315°); and height of nest above ground. In 1 ha around the nest tree, forest type, logging activity, successional stage, canopy closure, landform, slope aspect, and gradient were measured. We climbed seven of the nest trees and recorded: length, width, and depth of the nest structure; depth of the nest cup; and distance of the nest from the bole of the tree.

Forest type was classified using Johnson and Clausnitzer (1992): (1) ponderosa pine, (2) Douglas-fir, or (3) grand fir. Logging activity was classified as high-

graded (logging where only the valuable trees are removed, but the majority of the stand is left), selective (partial overstory removal), and clearcuts and shelterwoods. Clearcuts and shelterwood harvests were combined because neither silvicultural technique leaves habitat structure usable for nesting for many decades. Successional stages were defined as (1) young, trees <30 cm dbh; (2) mature, most trees 30–50 cm dbh; (3) old growth, >12 trees/ha that were >50 cm dbh, >60% canopy closure, and >1 canopy layer; and (4) remnant, some trees >50 cm dbh in the stand but not enough to classify as old growth. Canopy closure was measured with a spherical densiometer. Slope gradient was measured with a clinometer.

Diet and Plucking Posts

We searched for prey remains and pellets within 0.3 km of each nest. All prey remains found in one day of searching at each nest were combined to reduce the chance of counting the same prey item twice (Reynolds and Meslow 1984); however, this method may underestimate common prey types relative to rare prey types (C. Zabel, pers. comm.). Prey remains were identified later with the assistance of skull keys and museum collections.

Places where prey remains were found were called plucking posts. We recorded type of perch (e.g., log, stump, branch), perch height, distance from the nest, tree species, dbh, and condition (live or dead) at each plucking post.

RESULTS

Nesting

Of 25 historical sites searched, 23 had suitable habitat and two had been logged. Ten of the 25 sites had active nests in 1992. Two other active nests were found in the additional 17 stands searched.

The 12 active nests were located between 10 April and 15 July. Five nests were found with defensive adults, three with incubating females, three with nestlings, and one with fledglings. The two nests that failed were found when adults were defensive, and incubating females were seen on the nests before they failed.

Incubation typically started in late April and early May. Nestlings were present in June and early July. The mean fledging date was 8 July among five nests where we knew approximate dates. The earliest fledging date was about 22 June, and the latest was 27 July.

Juveniles fledged from 83% of the nests. Fourteen young fledged from the 10 nests, for an average of 1.4 young produced per successful nest or 1.2 young per nesting attempt. At least two young died before fledging; we could not determine if additional young died because we did not climb to the nests until young were ready to fledge.

Ten of the 12 nest trees were in old-growth stands that either had not been logged or had been high-graded in the past. The remaining two nest trees were in stands that had only remnants of old growth because they had been partially logged. Nine nest trees were in a grand fir forest type, two were in a Douglas-fir type, and one was in a western larch-lodgepole pine-spruce type. The average canopy closure was 81% (SD = 6.9%). Nine nest trees were on the lower third of a slope, and the remainder were at midslope. Slope gradient averaged 31% (SD = 21.2%). Nine nest trees were on a north- or east-facing slope. The average distance from the nest to the nearest water was 70 m (SD = 72.0). None of the nests were >200 m from water. Stands containing an active nest averaged 43 ha (SD = 34.0) in size.

Seven nest trees were Douglas-fir, three were western larch, and two were grand fir. All but two of the trees were alive. Average dbh and height of the nest trees were 65 cm (SD = 23.5) and 34 m (SD = 7.3), respectively. Average nest height was 15 m (SD = 3.3). Aspect of the nest on the tree was south or west at 10 nests and north or east at two nests.

The actual nest platform averaged 94 cm (SD = 18.5) in length, 66 cm (SD = 20.3) in width, and 36 cm (SD = 12.4) in depth. The depression inside the nest averaged 24 cm (SD = 7.0) in length, 21 cm (SD = 4.0) in width, and 8 cm (SD = 7.6) in depth.

Diet and Plucking Posts

We identified 94 prey items collected at nine nests; 58.5% were birds and 41.5% were mammals (Table 1). We collected between one and 32 prey items at each nest. American Robins comprised the majority (29%) of the birds found, and snowshoe hares comprised the majority (33%) of the mammals.

Forty-three plucking posts were found around nest sites; 51% were in trees, 33% on logs, 14% on stumps, and 2% on rocks. Of the standing trees, 63% were live and the remainder dead. Mean dbh and perch height of the standing trees were 32 cm (range = 8–75 cm) and 2.1 m (range = 0.8–4 m), respectively. The type of perch at these trees was a leaning tree trunk (55%), a branch (32%), or the top of the trunk where it had broken off (13%). Logs used as plucking posts averaged 59 cm in diameter (range = 16–110 cm). Perching height on logs averaged 0.5 m (range = 0.2–1.0 m) above the ground because logs were elevated. Three of the plucking posts on stumps were western larch; the remainder could not be identified. Mean diameter and perching height of stumps were 67 cm (range = 40–90 cm) and 0.6 m (range = 0.3–1.0 m), respectively.

Plucking posts typically were clustered around the nest tree, although we did not search >0.3 km from the nest. The distance between nests

TABLE 1. PREY REMAINS AND FREQUENCY (%) COLLECTED AT NINE NORTHERN GOSHAWK NEST SITES IN WALLOWA COUNTY, OREGON, 1992

Prey	N[1]	Birds or mammals (%)	Total (%)
Birds			
American Robin (*Turdus migratorius*)[2]	16	29.0	17.0
Northern Flicker (*Colaptes auratus*)	8	14.6	8.5
Western Meadowlark (*Sturnella neglecta*)	7	12.7	7.5
Western Tanager (*Piranga ludoviciana*)	4	7.3	4.3
Clark's Nutcracker (*Nucifraga columbiana*)	4	7.3	4.3
Steller's Jay (*Cyanocitta stelleri*)	3	5.5	3.2
Gray Jay (*Perisoreus canadensis*)	3	5.5	3.2
Hairy Woodpecker (*Picoides villosus*)[3]	3	5.5	3.2
Ruffed Grouse (*Bonasa umbellus*)	2	3.6	2.0
Dark-eyed Junco (*Junco hyemalis*)	2	3.6	2.0
Long-eared Owl (*Asio otus*)	1	1.8	1.1
Black-headed Grosbeak (*Pheucticus melanocephalus*)	1	1.8	1.1
Northern Goshawk (*Accipiter gentilis*)[4]	1	1.8	1.1
Total	55	100.0	58.5
Mammals			
Snowshoe hare (*Lepus americanus*)	13	33.3	13.8
Ground squirrels[5]	12	30.8	12.8
Red squirrel (*Tamiasciurus hudsonicus*)	11	28.2	11.7
Yellow pine chipmunk (*Tamius amoenus*)	3	7.7	3.2
Total	39	100.0	41.5

[1] Represents number of individuals.
[2] Also may have included Varied Thrush (*Ixoreus naevius*).
[3] Also may have included sapsuckers.
[4] Remains of a nestling were found in pellets at the base of a nest.
[5] Columbian ground squirrels (*Spermophilus columbianus*) comprised 33% of these; the remainder could not be identified to species.

and plucking posts averaged 42 m (range = 7–200 m).

DISCUSSION

We found active nests in ten of the 23 historical nest stands that we considered still suitable. Adult Northern Goshawks were seen in two suitable stands where we did not find nests. Consequently, about half the suitable stands we searched had nests or adults. Because we subjectively selected our stands, our findings do not necessarily indicate a preference for old growth. However, all the goshawk nests we located were in large-diameter trees, which are characteristic of old-growth stands.

The nesting pairs were productive with 83% of the nests successful and an average of 1.2 young fledged per nesting attempt. Similarly, Reynolds and Wight (1978) reported 1.7 young fledged per nesting attempt in Oregon during 1969–1974. The diet we determined from prey remains was similar to that reported by Reynolds and Meslow (1984) in Oregon (55% birds and 45% mammals).

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NEST PRODUCTIVITY, FIDELITY, AND SPACING OF NORTHERN GOSHAWKS IN ARIZONA

RICHARD T. REYNOLDS, SUZANNE M. JOY, AND DOUGLAS G. LESLIE

Abstract. Distribution of nests, nest success and productivity, mate and site fidelity, and diets of Northern Goshawks (*Accipiter gentilis*) were examined on the Kaibab Plateau, Arizona, in 1991–1992. A total of 98 nest attempts was studied, 92 in the Kaibab National Forest and six in Grand Canyon National Park. Of 36 nests in which eggs were laid in 1991, 34 produced young ($\bar{X}$ = 2.15 young/successful nest) and of 59 nests in which eggs were laid in 1992, 49 produced young ($\bar{X}$ = 2.16 young/successful nest). In 1991, 49 adults were banded at nests, including both adults at 21 nests. In 1992 both adults were recaptured at 10 of these 21 nests. At six (60% of 10) of these nests, both adults remained paired and five produced the same or more fledglings in 1992. Three (6% of 49) nesting hawks banded in 1991 moved to new territories in 1992 and each fledged one more young in 1992 than in 1991. The proportion of nesting adults banded in 1991 that were replaced by new hawks at 1992 nests was 23%. In 1992, nine (9.7% of 93) nesting hawks were classed as "young-adult" based on plumage characteristics; young-adults produced significantly fewer fledglings than full adults.

Mean distance between nearest neighboring nests in 1992 was 3.0 km (range = 1.6–6.4 km, N = 59 nests). Alternate nests were used between years in 17 of 34 territories; mean distance between the original and alternate nests was 266.4 m (SD = 157.0 m). Diets in 1991 were composed of 62% mammals and 38% birds by number, and 84% mammals and 16% birds by biomass.

Key Words: *Accipiter gentilis*; Kaibab Plateau; mate and territory fidelity; morphometrics; Northern Goshawk; population; productivity.

The Northern Goshawk (*Accipiter gentilis*) is holarctic in distribution. The North American subspecies (*A. g. atricapillus*) occurs from the northeastern United States across the boreal forests of Canada to Alaska and southward through the montane forests of western United States to northern Mexico (Wattel 1973). The Northern Goshawk nests in most of the coniferous, deciduous, and mixed coniferous-deciduous forests that occur within its range. Northern Goshawks prey on 20 or more species of birds and mammals within nesting home ranges of 15–31 km^2 (Schnell 1958, Meng 1959, Reynolds 1983, Reynolds and Meslow 1984, Bright-Smith and Mannan, this volume).

The Northern Goshawk is listed as a "sensitive species" by the USDA Forest Service Southwestern Region because of potential threats of forest management (e.g., tree harvests, fire suppression, and grazing) to the hawk's nesting and foraging habitats (Reynolds et al. 1982, Herron et al. 1985, Bloom et al. 1986, Reynolds 1989, Crocker-Bedford 1990, Reynolds et al. 1992). In fact, several authors (Herron et al. 1985, Bloom et al. 1986, and Crocker-Bedford 1990) suggest that Northern Goshawk populations have recently declined in Nevada, California, and Arizona due to habitat loss. Crocker-Bedford (1990), for example, estimated that there were 260 pairs of Northern Goshawks on the 120,000 ha North Kaibab Ranger District before timber harvesting began in the 1950s. By 1972, following "light partial" tree harvesting over most of his study area, the number of pairs declined to 130, and to probably half of that in 1988 after the introduction of a more intensive harvesting (Crocker-Bedford 1990).

In 1991 we began a long-term study of individual and population responses of Northern Goshawks to tree harvest and other forest management practices on the Kaibab Plateau. Our objective is to determine the effects of management by measuring Northern Goshawk response variables (e.g., distribution and density of nests, nest success and productivity, diets and prey populations, mate and territory fidelity, time budgets, home range characteristics, and mortality factors) to changes in habitat resulting from forest management. Here we report on nest dispersion, nest success and productivity, mate and territory fidelity, morphometrics, and diets of Northern Goshawks on the Kaibab Plateau in 1991–1992.

METHODS

STUDY AREA

The study area encompassed the coniferous forests on the Kaibab Plateau in northern Arizona. The Kaibab Plateau is an oval-shaped (95 km × 55 km), limestone plateau that rises from a shrubsteppe plain (elevation 1750 m) to a maximum elevation of 2800 m (Rasmussen 1941). It is bounded by escarpments and steep slopes that descend into the Grand Canyon of the Colorado River on its southern half and by more gentle slopes that descend to the shrubsteppe plain on its northern half. Total area covered by forests in the study area, including the Grand Canyon National Park

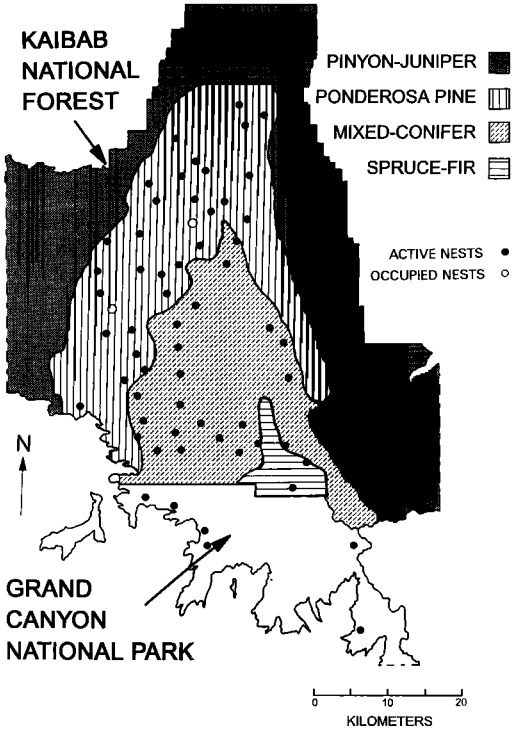

FIGURE 1. Forest types and nest locations of Northern Goshawk on the Kaibab Plateau, including the North Kaibab Ranger District and the Grand Canyon National Park, in 1992 (forest types in the National Park not mapped).

and North Kaibab Ranger District, is about 320,600 ha. Pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodlands occur at lower elevations (1830–2075 m) on the Plateau and occupy about 176,000 ha. Ponderosa pine (*Pinus ponderosa*) forests occur between 2075–2500 m elevation and occupy about 99,200 ha, and mixed-conifer forests (*P. ponderosa, Abies concolor, Pseudotsuga menziesii, Picea engelmannii,* and *Populus tremuloides*) occur above 2500 m, occupying about 45,400 ha (Rasmussen 1941) (Fig. 1). Annual precipitation averages 67.5 cm, with winter snowpacks of 2.5–3.0 m. Mid to late summers are characterized by frequent (2–4 per week) thunderstorms and heavy showers.

The Kaibab Plateau was isolated from established railroad heads in the late 1800s and early 1900s. Thus, forests on the Kaibab Plateau were not subjected to the heavy logging that typically occurred in montane areas on the Colorado Plateau and elsewhere in the southwestern United States during this period (Pearson 1950, Laudenslayer et al. 1989, J. Hanson, pers. comm.). Organized tree harvests did not begin on the Kaibab Ranger District until 1923 and were limited to single-tree cutting to remove dead and dying trees (sanitation cutting) (Burnett 1991). In the late 1960s clear-cutting began in the mixed-conifer forests (total = 922 ha) but was discontinued in the early 1970s; single-tree cutting in ponderosa pine continued through the mid-1980s. Intensive management at the forest stand level began in the mid-1980s with even-aged silvicultural treatments in the pine and mixed-conifer forests; these even-aged treatments continued until 1991. From the 1940s to 1990, the total volume of wood removed from the Ranger District increased by a factor of 5, from 9077 to 48,412 boardfeet per ha (1992 Kaibab National Forest Timber Atlas, J. Ellenwood, pers. comm.). While the early sanitation cutting occurred over much of the North Kaibab Ranger District, the application of stand level management beginning in 1986 resulted in a reduction of the total area harvested (1986–1991) to 12,632 ha, about 14% of the Ranger District (1992 Kaibab National Forest Timber Atlas, J. Ellenwood, pers. comm.).

The suppression of naturally frequent ground fires on the Kaibab Plateau since the 1910s has resulted in an increase in the number of small trees (≤29.4 cm in diameter at breast height) per ha by a factor of almost eight in ponderosa pine forests and by a factor of 11 in mixed-conifer forests (1992 Kaibab National Forest Timber Atlas, J. Ellenwood, pers. comm.). In 1991, due to concerns for the Northern Goshawk population on the Plateau, the focus of management shifted from the level of the stand to small (0.1–1.6 ha) groups of trees combined with an area-wide thinning of the small, understory trees (Reynolds et al. 1992). The objective of this management was to move the ponderosa pine and mixed-conifer forests on the Ranger District toward the species composition and structure that existed prior to fire suppression and intensive tree harvests (Reynolds et al. 1992).

Nests, Morphometrics, Diets, and Movements

To locate active (containing eggs or young) Northern Goshawk nests, we visited all previously documented nests (Goshawk Nest Records, 1990–1992, Arizona Game and Fish Department, Phoenix, Arizona, and North Kaibab Ranger District, Fredonia, Arizona), searched for new nests on foot (Reynolds 1982), and used a vocalization broadcast technique (Joy et al. *this volume*). Each year nest visits and searches were begun in May and continued through August. Broadcast surveys were conducted daily between 08:00 and 16:30 MDT (Joy et al. *this volume*). All nests of Northern Goshawks, and their potential competitors and predators, Cooper's (*A. cooperii*), Sharp-shinned (*A. striatus*), and Red-tailed (*Buteo jamaicensis*) hawks, and Great Horned Owl (*Bubo virginianus*) found were recorded on 7.5-minute USGS topographic maps. We used the Universal Transverse Mercator (UTM) coordinates of all nests to determine the distances between alternate Northern Goshawk nests (nests used in subsequent years by a pair) and to calculate nearest-neighbor distances among nests. Nearest-neighbor distances were the straight-line distances between each active nest and its closest neighbor. Calculation of nearest-neighbor distance included duplicate measures between reciprocal nearest neighbors (Diggle 1983).

The fates of nests (successful = fledged ≥1 young) and nest productivity (number of fledglings produced) were determined by weekly visits to nests. Adults were captured at nests in dho-gaza traps baited with live Great Horned Owls (Bloom 1987). Away from nests,

TABLE 1. NUMBER OF NESTS OF *Accipiter* FOUND ON THE KAIBAB PLATEAU, 1991–1992

Year	Species	Nest search technique			Total
		Visits to historic nests	Broadcast survey	Foot search	
1991	Northern Goshawk	28	5	4	37
	Cooper's Hawk	0	3	4	7
	Sharp-shinned Hawk	0	7	1	8
1992	Northern Goshawk	40	8	13	61
	Cooper's Hawk	5	2	1	8
	Sharp-shinned Hawk	3	3	2	8

adults and juveniles were captured with 5–6 "falling-end" Swedish goshawk traps (Kenward and Marcström 1983) that were baited with domestic pigeons (*Columba livia*) and placed at about 1 km intervals. Swedish goshawk traps were also placed at nests to capture fledglings. All hawks were fitted with U.S. Fish and Wildlife Service aluminum leg bands and anodized aluminum color leg bands with unique alpha-numeric codes. Bands were read from blinds in nest areas or when the hawks were recaptured. Age classes (immature, young-adult, or adult) were determined by plumage characteristics (Bond and Stabler 1941, Stabler 1943) and sex by body mass (see below). Morphometrics of adults included body mass, wing chord, tail, tarsometatarsal length, and condition (good, moderate, or poor based on breast muscle assessment).

Accipiter remove pelage and plumage from their vertebrate prey in the nesting area and on the nest itself. In addition, these hawks regurgitate pellets that contain keratinous body parts of prey. On each visit to a nest, all prey remains and pellets were completely collected. During identification, remains in a day's collection from a nest were lumped and reconstructed by matching the remiges, rectrices, and bills of birds, and the fur, skull parts, and feet of mammals (Reynolds and Meslow 1984). This procedure estimates the minimum number of individuals of each species in a collection (Reynolds and Meslow 1984). Estimates of body mass of birds and mammals in diets were from the literature and museum specimens. We assigned the mass of young prey to be one-half of their adult mass. The mass of prey that could be identified only to genus was determined by averaging mass of all members of that genus in our study area (Reynolds and Meslow 1984). Prey remains collected in 1992 have not been identified and we present only the 1991 diet data.

To determine post-fledging movements and dispersal of Northern Goshawks, 13 adults and 15 fledglings were fitted with tail-mounted (Kenward 1978) and backpack (Kenward 1985) transmitters weighing 6 g ($\leq$0.8% of body mass). We attempted to locate radio-tagged adults and juveniles once a week from the ground in late summer and early fall and from aircraft during winter (2 flights/year).

RESULTS

NEST NUMBERS, NEST PRODUCTIVITY, AND MORPHOMETRICS

A total of 37 occupied Northern Goshawk nests (nests at which adults were observed on two or more occasions during a breeding season) were located on National Forest lands on the Kaibab Plateau in 1991; 28 (76%) of these were located during visits to historic nests, five (13%) during broadcast surveys, and four (11%) during foot searches (Table 1). Active nests of seven Cooper's Hawks and eight Sharp-shinned Hawks were also located during searches and broadcast surveys. In 1992, 61 occupied Northern Goshawk nests were found, 55 nests on National Forest and six on National Park lands. Of these 61 nests, 40 (66%) were found during visits to historic nest areas (including 1991 nests), eight (13%) during broadcast surveys, and 13 (21%) during foot surveys. Three additional Cooper's Hawk nests and five additional Sharp-shinned Hawk nests were found (Table 1).

Of the 2-year total of 98 occupied Northern Goshawk nests, 83 pairs (85%) fledged young, three pairs (3%) either did not lay a clutch or lost their clutch in early incubation, six clutches (6%) were lost during incubation, and six (6%) nests failed during the nestling period. Among active nests there was no significant difference in the rate of nest failure in the two years (one of 34 [5.6%] nests failed in 1991 and 10 of 59 [16.7%] nests failed in 1992) (Fisher's exact test, $N = 93$, $P = 0.13$), nor were there significant differences in the mean number of young fledged in the two years per occupied (Fisher's exact test, $N = 98$, $P = 0.26$), active (Fisher's exact test, $N = 95$, $P = 0.23$), or successful (Fisher's exact test, $N = 83$, $P = 0.44$) nests (Table 2). For both years modal brood size was two, with one fledgling produced at 13 successful nests (16%), two at 44 nests (53%), and three at 26 nests (31%). All but three (8%) of the 37 occupied nests (or alternate nests) in 1991 were reoccupied in 1992. Broadcast and foot searches for active, alternate nests within 2 km of these three nests in 1992 were unsuccessful.

Nestling Northern Goshawks fledged between 7–25 July and eggs hatched between 31 May and 16 June. Assuming a 30–32 day incubation period (Reynolds and Wight 1978), egg-laying occurred in late April and early May. Combining

TABLE 2. FLEDGLINGS PRODUCED PER OCCUPIED, ACTIVE, AND SUCCESSFUL NORTHERN GOSHAWK NESTS ON THE KAIBAB PLATEAU, 1991–1992

	1991			1992		
	$\bar{X}$	SD	N	$\bar{X}$	SD	N
No./occupied nest	2.0	0.83	37	1.7	1.08	61
No./active nest	2.0	0.77	36	1.8	1.05	59
No./successful nest	2.2	0.61	34	2.2	0.72	49

years, the sex ratio of nestlings just prior to fledging for 23 broods was 23 males to 27 females, not significantly different from a 1:1 ratio (Fisher's exact test, N = 50, P = 0.58).

In 1991–1992 we captured and banded 76 fledglings (hatching year), one second-year hawk (after hatching year), and 93 adults (44 males, 49 females). Three (6.8%) males and six (12.2%) females were in the young-adult plumage class (after second year). All of these young adults nested in 1992, and each was paired to an adult hawk. The mean number of fledglings produced by the young-adult females ($\bar{X}$ = 1.0 fledglings, SD = 0.89, N = 6) was not significantly different from the mean produced by the young-adult males ($\bar{X}$ = 1.3 fledglings, SD = 1.33, N = 3) (Fisher's exact test, N = 9, P = 0.71). However, the production of fledglings at active nests of young-adult to adult pairings was significantly less than the production of fledglings at active nests of adult-to-adult pairs ($\bar{X}$ = 1.1 fledglings, SD = 0.9 vs. $\bar{X}$ = 2.3 fledglings, SD = 0.8, N = 21) (Fisher's exact test, N = 30, P = 0.01).

All but four adults were captured with dhogaza nets. The exceptions (three males, one female) were captured in Swedish traps (98 trap-hours/capture). Four juveniles (one male, three females) were also captured in Swedish traps (77 trap-hours/hawk). There were no significant differences between years in the frequency of adults trapped with either method in the three condition classes (Fisher's exact test: males, N = 50, P = 1.00; females, N = 63, P = 0.51). There was a total of three nesting adult males (one in 1991, two in 1992) and five adult females (two in 1991, three in 1992) in the "poor condition" class. All hawks in poor condition were paired with birds in "moderate" or "good" condition. Mean number of fledglings produced per successful nest of pairs with a hawk in poor condition ($\bar{X}$ = 2.3 fledglings, SD = 0.52, N = 6 pairs) and pairs in which both adults were in moderate to good condition ($\bar{X}$ = 2.2 fledglings, SD = 0.73, N = 38) were not significantly different (Fisher's exact test, N = 44, P = 0.62). Also, nest success of pairs with a hawk in poor condition (six of eight pairs, 75%) did not differ from pairs in which both adults were in moderate to good condition (38 of 40 pairs, 95%) (Fisher's exact test, N = 48, P = 0.12).

Overlap between the sexes occurred for all morphometrics (body mass, wing chord, tail length, tarsometatarsal length) except body mass (Table 3). Mean wing chord and tail length were larger and mass smaller for Northern Goshawks on the Kaibab Plateau than for migrating birds in Wisconsin (Mueller et al. 1976). However, variation in all morphological measurements from hawks on the Kaibab Plateau was less than for Northern Goshawks in Wisconsin. Wing chords of Northern Goshawks on the Kaibab Plateau were also longer than for adults of the

TABLE 3. MEASUREMENTS OF BODY MASS, TAIL, WING, AND TARSOMETATARSUS LENGTH OF ADULT NORTHERN GOSHAWKS ON THE KAIBAB PLATEAU, 1991–1992

Variable	$\bar{X}$	SD	Max.	Min.	N
		Males			
Mass (g)	704.4	32.7	774.0	631.0	45
Tail (cm)	23.5	1.1	28.7	21.3	45
Wing (cm)	34.2	0.7	36.2	32.4	45
Tarsometatarsus (mm)	81.4	3.5	87.7	73.8	45
		Females			
Mass (g)	985.5	51.9	1100.0	907.0	49
Tail (cm)	27.7	0.9	29.0	24.7	49
Wing (cm)	37.3	0.9	38.9	35.0	49
Tarsometatarsus (mm)	88.2	4.4	94.9	79.1	49

subspecies *A. g. laingi* reported by Johnson (1989).

Mate Fidelity, Territory Fidelity, and Nest Productivity

Both members of pairs were banded at 21 nests in 1991. In 1992, both sexes were recaptured at 10 of the 21 nests. At six of the 10 nests both sexes remained paired, at two nests one of the original pair was replaced by a new hawk (one new male, one new female), and at two nests both members of the original pair were replaced by new hawks (at one of these nests both replacement hawks had been banded in 1991 at two different nests).

In 1992, all (six) banded pairs that renested on their 1991 territory (in the same or alternate nest, see below) successfully fledged young in 1991 ($\bar{X}$ = 1.8 fledglings, SD = 0.8), and all but one of these pairs produced the same (two pairs) or more (three pairs) fledglings in 1992 ($\bar{X}$ = 2.3 fledglings, SD = 0.5). The exception produced three fledglings in 1991 and two in 1992. In addition there were ten other nests at which only one adult (either the 1991-banded adult or its replacement) was captured in 1992. At these ten nests, one male and none of the females were replaced. Productivity at the nest where replacement occurred decreased from three to zero fledglings in 1992. Of the females, four produced the same number of fledglings in both years, three produced more in 1992, and two produced less in 1992 (one failed). The overall replacement rate of banded hawks at nests from 1991 to 1992 was 23% (seven replacements for 30 previously banded hawks captured or recaptured in 1992).

Of three banded hawks that moved from their 1991 territory to nest elsewhere in 1992, each fledged two young in 1991 and three young in 1992. In two of these cases, the hawks moved to nests in territories adjacent to their original (male RO, 3.5 km; female EB, 2.6 km). In the third case, female (AH) moved 9.2 km over two territories to pair with male RO.

Distances between Nearest-neighbor and Alternate Nests

Nearest-neighbor distances among a collection of nests provides an estimate of the distribution of those nests. Mean distance between 59 nearest neighboring nests in 1992 was 3 km (SD = 834.2 m, range = 6417–1573 m), and 47% of the nests were within 2.0–3.5 km of each other (Fig. 2). Although by the end of the 1992 season only 50% of the forest on the Kaibab Plateau was searched for Northern Goshawk nests, we think the nearest-neighbor distance is representative of the Plateau. Nest searches were systematically

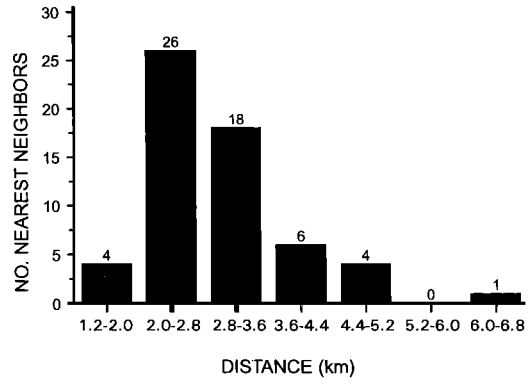

FIGURE 2. Number of occupied Northern Goshawk nests by nearest-neighbor distance in 1992 ($\bar{X}$ = 2.97 ± 0.83 km, N = 59 nests).

conducted in contiguous areas that expanded (and joined) from the northwest toward the southeast of the Plateau, and few nests were likely to have been missed within this area. Two isolated Northern Goshawk nests in the Grand Canyon National Park, discovered in non-systematic nest searches (B. S. Heslin and J. T. Driscoll, unpubl. data), were excluded from the analysis.

Pairs of Northern Goshawks often use alternate nests in different years (Reynolds and Wight 1978, Reynolds 1983). Four pairs of nesting Northern Goshawks banded in 1991 moved a mean distance of 485 m (SD = 130 m, range = 326–635 m) to alternate nests in 1992. In addition, three nesting females banded in 1991 (males not banded) moved a mean distance of 194 m (SD = 50 m, range = 142–241 m) to alternate nests in 1992. Finally, ten unbanded pairs (we presumed one or both sexes to be the same hawks in both years) moved a mean distance of 201 m (SD = 99 m, range = 100–425 m) to alternate nests in 1992. Combining these, the mean distance from 1991 nests to 1992 alternate nests was 266 m (SD = 157 m) (Fig. 3).

Diets

A total of 121 prey items, representing 11 species of birds and eight species of mammals, was identified in prey remains collected at nests in 1991 (Table 4). In descending order of frequency, the most commonly taken species included cottontail rabbit, tassel-eared squirrel, Steller's Jay, red squirrel, black-tailed jackrabbit, and Northern Flicker. By biomass, the most important of the mammals were the cottontail rabbit, tassel-eared squirrel, red squirrel, and jackrabbit and, among birds, Steller's Jay, Northern Flicker, and Williamson's Sapsucker. Overall, mammals con-

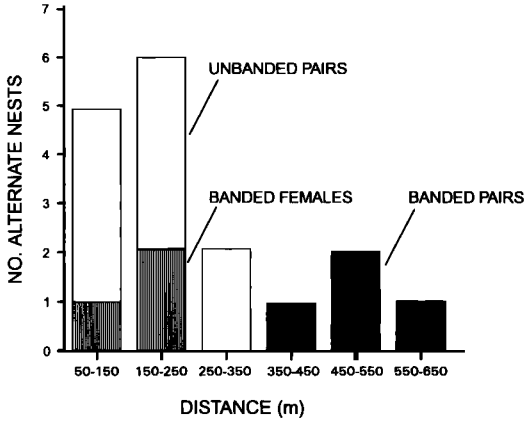

FIGURE 3. Distance between 1991 nests and 1992 alternate nests of Northern Goshawks on the Kaibab Plateau for banded pairs, unbanded pairs, and pairs in which only females were banded.

tributed 62% of number of prey items, while birds contributed 38%.

Post-breeding Movements

Fifteen fledglings were fitted with radio-transmitters in 1991–1992. Dispersal of fledglings from nest areas began in mid August and was completed by late August. Two radio-tagged fledglings in 1991 and four in 1992 could not be relocated after dispersing from nests and two other transmitters, lost by the fledglings, were recovered from the pinyon-juniper woodland on the north end of the Plateau. Five fledglings (two in 1991, three in 1992) were relocated from aircraft one or more times in November and December, and one fledgling was relocated during a March 1993 flight, all on the Plateau. One radio-tagged fledgling was found dead in October 1992, approximately 8 km southeast of Flagstaff, Arizona, a distance of 160 km from its birthplace.

In July and August of 1991 and 1992, five adults (all males) and four adults (two males, two females) were fitted with transmitters, respectively. All adults except one remained on their nesting territories through late October. The exception was a female who left her nesting territory in late August 1992 and spent two weeks in pinyon/juniper woodland on the north end of the Plateau, 13 km north of her nest. The female was relocated in the woodland habitat for two weeks before disappearing. She was again relocated on the Plateau during a March 1993 flight. None of the five males radio-tagged in 1991 were relocated after October 1991, probably because of transmitter failure. Of the other radio-tagged adults, two were relocated from aircraft during a flight in December, both on the Plateau.

TABLE 4. Frequency and % of Total Birds and Mammals in Diets of Northern Goshawks on the Kaibab Plateau in 1991

Species	Frequency	%
Birds		
Cyanocitta stelleri		
Steller's Jay	17	37.0
Colaptes auratus		
Northern Flicker	11	23.9
Sphyrapicus thyroideus		
Williamson's Sapsucker	7	15.2
Accipiter gentilis		
Northern Goshawk	3	6.5
Turdus migratorius		
American Robin	1	2.2
Buteo jamaicensis		
Red-tailed Hawk	1	2.2
Dendragopus obscurus		
Blue Grouse	1	2.2
Corvus brachyrhynchos		
American Crow	1	2.2
Sitta pygmaea		
Pygmy Nuthatch	1	2.2
Siala mexicana		
Western Bluebird	1	2.2
Unknown Emberizidae	1	2.2
Unknown bird	1	2.2
Mammals		
Sylvilagus spp.		
Unknown rabbit	22	29.3
Sciurus aberti		
Abert's Squirrel	13	17.3
Lepus californicus		
Black-tailed Jackrabbit	11	14.7
Tamiasciurus hudsonicus		
Red Squirrel	11	14.7
Unknown Sciuridae	6	8.0
Spermophilus lateralis		
Mantled Ground Squirrel	5	6.7
Spermophilus variegatus		
Rock Squirrel	4	5.3
Eutamius dorsalis		
Cliff Chipmunk	1	1.3
Eutamius umbrinus		
Uinta Chipmunk	1	1.3
Eutamias spp.		
Unknown chipmunk	1	1.3

DISCUSSION

For the North American *Accipiter* species, habitat quality can be regarded as a measure of the abundance and distribution of the structural and floristic elements of forests and woodlands that provide nesting opportunities, hunting perches, and protective cover as well as the accessibility to, and abundance of, suitably-sized prey. Habitat quality can be reflected in a hawk's physical condition (body mass), its nesting suc-

cess and productivity, its degree of fidelity to territory and mate, the size of its home ranges, and population densities of the hawk and its prey (McGowan 1975; Newton 1976, 1986; Moss 1979; Geer 1981; Newton and Marquiss 1981, 1982; Marquiss and Newton 1982). In many raptors, the age of breeding individuals confounds the investigation of habitat quality because age may affect nesting success and productivity. For example, in European Sparrowhawks (*A. nisus*), the number of young produced per nest attempt increases from yearling-to-yearling pairs, through yearling-to-adult pairs, to adult-to-adult pairs (Newton 1986). Furthermore, individuals of some species can improve their annual reproductive performance by pairing with older, more experienced birds and by moving, with or without a previous mate, to territories of higher quality (Newton 1986, Reynolds and Linkhart 1987).

The mean number of young fledged per active nest on the Kaibab Plateau in 1991–1992 was within the range of values (0.69–3.0 young/nest attempt) for the Northern Goshawk in other areas of western North America, including Alaska (see Reynolds 1989 for review). Although the nest failure rate of pairs in which one adult was in poor condition was not statistically higher than for pairs in which both adults were in moderate or good condition, we anticipate that further sampling will demonstrate that physical condition affects nesting success. Additionally, production of fledglings was significantly related to age of nesting adults; younger hawks produced fewer fledglings. Returning to the same territory and pairing with the same mate in most cases resulted in the same or higher production of fledglings. A few adults, however, increased their production of fledglings after changing territories and mates.

The spacing of Northern Goshawk nests has only been determined for a few areas. On the Kaibab Plateau, the mean distance to nearest nests (3.0 km) was slightly less than half the nearest-nest distance (5.6 km) among four Northern Goshawk nests in Oregon (Reynolds and Wight 1978) and among European Goshawk nests (*A. g. gentilis*) in Sweden (5.5 km) (Hoglund 1964). The Oregon data, however, consist of a small sample of nests and, when compared to the Kaibab data, the nearest-neighbor distance is biased upward because duplicate measures between reciprocal nearest neighbors in Oregon were not used (Reynolds and Wight 1978). Nevertheless, nests of Northern Goshawks on the Kaibab Plateau appear to occur at a density higher than reported for other populations of the subspecies (see Reynolds 1989 for review).

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APPROACHES TO INVESTIGATING FOOD LIMITATION HYPOTHESES IN RAPTOR POPULATIONS: AN EXAMPLE USING THE NORTHERN GOSHAWK

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Abstract. Food supplementation experiments have been used to demonstrate that food limits reproductive success and recruitment of a given animal population. Of the experiments that have been conducted on terrestrial vertebrates, few have been conducted on raptors. Hence, correlative evidence supporting a relationship between food availability and breeding densities of raptors may not be conclusive. We discuss the strengths and weaknesses of past supplementation experiments and detail an experiment designed to investigate this relationship for a Northern Goshawk (*Accipiter gentilis*) population in northern New Mexico. Our experiment illustrates that food supplementation experiments can be conducted on raptors throughout brood-rearing to rigorously test hypotheses concerning the effect of food availability on raptor demographics.

Key Words: *Accipiter gentilis*; dispersal; experimental design; food supplementation; juvenile survival; nestling size; Northern Goshawk.

It is commonly assumed that food often limits the reproductive success and thus, recruitment of animals into a breeding population (Lack 1954; Newton 1980, 1991). To test this relationship rigorously, a multitude of supplemental feeding experiments have been conducted on terrestrial vertebrates, including nesting birds, and have successfully increased at least one breeding parameter (Boutin 1990). Nearly all of the avian supplemental feeding experiments have been conducted on herbivores (seed eaters) and omnivores (insect and seed eaters) and have examined the influence of food on clutch size and hatching success where supplemental feeding was discontinued after hatching. Advanced laying date and/or increased clutch size as a result of supplemental food have been reported (Yom-Tov 1974, Newton and Marquiss 1981, Dijkstra et al. 1982, Hochachka and Boag 1987, Arcese and Smith 1988) and some experiments demonstrated an increase in nestling and fledgling survival as a result of supplemented diets (Yom-Tov 1974, Hansen 1987, Simons and Martin 1991). However, results of the studies have been variable, and very few studies have been conducted with non-passerines such as raptors. Newton (1980, 1991) noted that only correlative relationships between food abundance and raptor densities have been established. As a result, current evidence supporting a relationship between food availability and breeding densities of raptors is not conclusive.

Another limitation of past avian supplementation experiments is that only three studies have initiated supplemental feeding after hatching (Hochachka and Boag 1987, Simons and Martin 1991, Kenward et al. 1993), so knowledge about the effects of additional food on the post-hatching period and particularly its influence on offspring growth, survival and recruitment is scarce for all birds, and nonexistent for raptors. In three experiments on raptors (Newton and Marquiss 1981, Dijkstra et al. 1982, Hansen 1987), birds were not provided additional food after hatching. Since Boutin's (1990) review, Kenward et al. (1993) conducted a study examining causes of dispersal, providing excess food to goshawk young from three weeks post-fledging until independence (a period of ca. 30 days).

The transition from dependent fledgling to independent juvenile is assumed to be one of the most critical periods for avian survival (Richner 1992). High avian juvenile mortality rates attributed to starvation have been reported during this time (Southern 1970, Hirons et al. 1979, Newton et al. 1982, Korpimäki 1988, Sullivan 1989). Further, both Newton et al. (1982) and Sullivan (1989) speculated that adequate food may be available to the young during the fledgling dependency period, but that juveniles may starve because they are inexperienced and inefficient foragers.

Most of the aforementioned studies were controlled experiments; however, most failed to measure the magnitude of the treatment, supplying unquantified amounts of excess food (but see Yom-Tov 1974, Hogstedt 1981, Dijkstra et al. 1982, Hansen 1987, Hochachka and Boag 1987, Kenward et al. 1993). We believe it is important to quantify the treatment to know how much excess food needs to be provided to yield a true treatment effect. There further exists a need for experimentation on a larger spatial scale over longer periods of time (Boutin 1990).

We are currently examining the potential effects of increased food availability on (1) the size of nestling Northern Goshawks (*Accipiter gentilis*), (2) the time of goshawk fledging, (3) the

TABLE 1. ESTIMATES OF AGE-SPECIFIC ENERGY REQUIREMENTS FOR JUVENILE NORTHERN GOSHAWKS (KELLY AND KENNEDY 1993:TABLE A2.1). AVERAGE AGE OF DISPERSAL FOR TREATMENT JUVENILE GOSHAWKS WAS 12 WEEKS; FOOD SUPPLEMENTATION ENDED AT 22 WEEKS

Age (weeks)	Formula[1]	Energetic requirement (kJ/day)	No. of quail required/ day[2]	Total no. of quail required
0–2	$0.3E^{*n}$	239.1	0.3	4.2
3–5	E^{*n}	797.0	1.0	21.0
6–7	$0.7E^{*n}$	557.9	0.7	9.8
8–22	$0.5E^{*n}$	398.5	0.5	45.5

[1] E^{*n} = peak energy expenditure of an altricial nestling.
[2] Assimilated energy intake of 150 g quail = 792 kJ (based on methods in Kennedy [1991]).

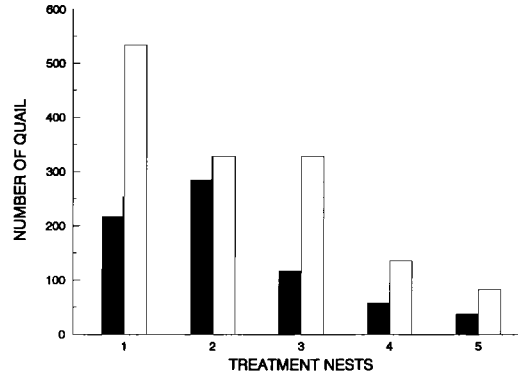

FIGURE 1. Number of quail required (solid bars) to meet 100% of the energetic requirements of the treatment goshawk broods (based on brood size and sex ratio), and the number of quail provided (open bars) at each treatment nest (1–5) during the 1992 experiment.

time of goshawk dispersal, and (4) juvenile goshawk survival. In this paper, we discuss our experimental design as an example of an approach that can be used to evaluate the influence of increased food availability on post-hatching reproductive success and juvenile survival in raptors.

METHODS

STUDY AREA

The experiment was conducted from mid-April to mid-October during the 1992 breeding season and is ongoing for 1993, on a goshawk population in the Jemez Mountains and the adjacent Pajarito Plateau in north-central New Mexico. The majority of the goshawk nests in this area were on land managed by the USDA Forest Service, Santa Fe National Forest. The study area elevation ranges from 1200–3900 m, and the average elevation of the goshawk nests was 2493 m. The mountains are characterized by steep terrain dominated by typical southwestern montane habitat types such as ponderosa pine (*Pinus ponderosa*) and mixed-conifer forests. The Pajarito Plateau, a table-like extension of the eastern flank of the Jemez Mountains, is cut into numerous, narrow, finger-like mesas by southeast-trending, intermittent streams. The mesas are dominated by pinyon-juniper woodland. The drainages contain riparian habitats dominated by ponderosa pine or cottonwood (*Populus* spp.) stands and flow into the Rio Grande. See Kennedy (1988) for a detailed description of the study area.

ENERGETIC CALCULATIONS

To maximize the effect of the treatment, we designed the experiment to supply at least 100% of the broods' (excluding adults) energy requirements at treatment nests. Kennedy (1991) developed an allometric equation describing the relationship between peak energy expenditure of altricial nestlings (E^{*n}, measured in Watts) and adult biomass (M, measured in g), where $E^{*n} = 53.578M^{0.757}$. We used this equation to determine the peak energy expenditure for a nestling goshawk. Peak energy expenditure of nestling males and females was estimated to be 730 kJ/day (where M = 800 g) and 864 kJ/day (where M = 1000 g), respectively. The average of these two estimates, 797 kJ/day, was used as the estimate of E^{*n}. The energetic requirements for young goshawks over the rest of the breeding season can then be calculated as a percentage of E^{*n}. The age-specific energetic requirements are not yet known for the goshawk. However, energetic requirements have been estimated for the Cooper's Hawk (*Accipiter cooperi*), a smaller accipiter that also breeds in the study area (Kelly and Kennedy 1993). We used a modification of the method described by Kelly and Kennedy (1993:Table A2.1) to estimate the age-specific energetic requirements for nestling goshawks (Table 1).

The treatment broods were supplemented with Japanese quail (*Coturnix* sp.) that weighed 120–150 g. The assimilated energy of one 150-g quail is estimated to be about 792 kJ (based on methods used by Kennedy [1991] to estimate assimilated energy of avian prey). According to the age-specific energy requirement calculations, one goshawk offspring required 73.5 quail to meet its daily energy requirements from hatching until mid-October. To maximize the treatment effect, we put out as many quail as the brood would take in addition to the amount provided to meet 100% of the offsprings' estimated energetic requirements. Hence the amount provided at each nest varied with how much excess food the birds would take, and with the number of young at each nest (Fig. 1).

FOOD SUPPLEMENTATION

Twelve of 14 known nest sites were active in 1992; six of the 12 active goshawk nests were randomly assigned as treatments and the remaining six were controls. Sixteen active nests were located in 1993, with eight randomly assigned as treatments and eight as controls. We observed the behavior of the incubating adult bird to determine date of hatching. After hatching, the adult bird on the nest would remain relatively still, except for frequent jerking motions caused by the newly hatched young. It is likely that the hatchlings do

not cause this behavior until they are a few days old. However, since we used the same behavior protocol to determine date of hatching at all nests, any error in age estimation should be equal for all nests.

Food supplementation began the day after hatching was observed (late April) and ended when most birds had dispersed (mid-October). When Newton and Marquiss (1981) provided extra food to sparrowhawks (*Accipiter nisus*), they placed food on or near a regularly used plucking post, and the birds could not remove the food. We modified this technique, placing quail on a podium about 1.5 m tall, located within 10 m of the active nest where the incubating adults could always see the food while on the nest. To entice the birds to take the supplemental food, we initially provided daily 1–2 live quail tethered to the podium. After the live quail were regularly taken, we provided dead quail every other day. In all cases, the quail could be removed by the hawk from the podium. To avoid attracting potential nocturnal predators such as the Great Horned Owl (*Bubo virginianus*), each feeding podium had a motorized cover activated by a solar cell that covered the food by sunset and exposed it by sunrise the following morning. Feeding podiums were also placed at control nests, and were visited every other day to equalize the amount of disturbance at each nest. Each treatment podium was observed 2–3 times during the experiment from sunrise to sunset from a blind approximately 15 m from the feeding podium to verify that the adults, and later, the juvenile goshawks from that territory, were taking the quail. Individual birds were identified by unique alpha-numeric coded color bands.

Data Collection

Size of nestling goshawks

Morphometric measurements were taken for culmen and hallux length, tarsometatarsus width and length, and weight on 29 21-day-old nestling goshawks (16 controls, 13 treatments) in 1992, and 13 nestling goshawks (10 treatments, 3 controls) in 1993. A single observer (JMW) collected all measurements to eliminate observer variability in measurement technique.

Time of fledging and dispersal

When the morphometric measurements were taken, tarsal-mounted transmitters with mortality switches (Advanced Telemetry Systems, Inc., Isanti, MN) were attached to the nestling goshawks. To minimize the impact of transmitter attachment to the offspring, the transmitters were designed to drop off after 3–4 months. After transmitter attachment, the birds were relocated at least once every two days either from the ground or from an airplane. By mid-October the majority of the juvenile birds could not be relocated because they had dispersed, or their transmitter had dropped off or failed prematurely, and the experiment was terminated.

Fledging was defined a priori as the first observation of young perching on a branch (we assume the same fledging date for all young in a nest), and dispersal was defined a priori as the first time a juvenile spent more than a week at least two km away from the nest. Kenward et al. (1993) used a similar definition of dispersal for goshawks in Sweden, defining dispersal as the first day that a hawk was not within 1.5 km of the nest and did not return for at least two days.

RESULTS AND DISCUSSION

The food supplementation experiment was successful, with all treatment birds eating quail. None of the adult birds ate immediately, but all ate within 3–5 days after the experiment was initiated. Adult females and fledgling goshawks were observed taking quail at every treatment nest. However, adult males were never observed taking quail from the podium. In 1992, when the experiment was terminated in mid-October, both adult females and juvenile birds were still taking the supplemental food. On several occasions while delivering quail, we observed goshawks perching on the podium. We also regularly observed molted adult feathers at the base of the podium, and quail feathers were frequently observed at goshawk plucking posts and at the base of frequently used perches. Although we recorded the number of quail taken from the podium, we do not know how many of these quail were eaten by the young and by the adults. Since both parents continued to hunt and were rarely seen in the nest stand during the fledgling-dependency period, we surmise that the young ate most of the quail during this period. The amount of quail eaten varied by nest, which we expected because parental care, habitat quality, and the number of offspring differed at each nest. In 1992, the family that ate the most quail had three offspring and removed 86% of the supplemented quail, whereas the family that consumed the fewest number of quail had one offspring and ate only 22% of the quail.

On several occasions, the podiums were knocked over by black bears (*Ursus americanus*) but the bears did not regularly take quail. There was no evidence of other mammalian predators taking quail. At two of the treatments, Gray Jays (*Perisoreus canadensis*) and Steller's Jays (*Cyanocitta stelleri*) regularly picked at the quail. Also, yellowjackets (Hymenoptera: Vespidae) were an unexpected consumer, sometimes eating the entire quail and leaving only the skeleton. We never observed other avian predators taking food from the podium, which was not surprising since goshawks are such vigorous defenders of their territories. If this technique is used for a less aggressive species or in areas where other consumers are more of a problem, the podium may have to be modified (e.g., metal sheeting placed around the base) to prevent consumption of the supplemental food by other animals.

Although our experiment is an improvement on past supplemental feeding studies (for reasons stated in the introduction), our design also had

some flaws that should be corrected in future experiments. Our sample size is probably not large enough to provide meaningful comparisons of survival of treatment versus control offspring, a common problem in raptor studies. Also, when calculating the energetic requirements of the offspring, the requirements of the adults should be accounted for if the excess food is available to the adults. Another weakness of our experiment is measuring offspring's morphometrics at only one age, the expected time of maximum growth (Kennedy 1991). It is possible that significant differences may be found in the mass of treatment versus control offspring after they reach independence, when the controls have to capture their food and the treatments are still being supplemented. Finally, the fates of goshawk offspring need to be monitored for a longer period of time. We chose tarsal-mounted transmitters because we thought backpack transmitters would adversely affect survival, a parameter we were measuring. The drawback of tarsal-mounts is their short battery life (about 4 months). We suggest using Kenward et al.'s (1993) approach of recapturing fledglings prior to independence and replacing the tarsal-mounted transmitters with backpacks.

This experiment demonstrates the feasibility of conducting food supplementation experiments on birds of prey. We hope our work will encourage other raptor researchers to employ rigorous experiments to demonstrate causality when investigating questions about birds of prey, rather than observational studies that only describe correlative relationships. Possible future research regarding the question of raptor population regulation and food availability may be to conduct an experiment for one part of the breeding season (e.g., courtship) at some nests and another part of the breeding season (e.g., fledgling-dependency period) at other nests during the same year. This would determine if food is limiting during all of the breeding season or only for a portion of it. Other useful experiments would be to provide excess food during the winter when food availability may have a greater influence on raptor survival than during the breeding season. Experimental manipulations of food availability are logistically challenging, but we believe they are necessary to answer conclusively questions regarding food limitation and population regulation in birds of prey.

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BREEDING ECOLOGY OF THE NORTHERN GOSHAWK IN HIGH-ELEVATION ASPEN FORESTS OF NORTHERN NEVADA

JAMES V. YOUNK AND MARC J. BECHARD

Abstract. We examined the habitat requirements of Northern Goshawks (*Accipiter gentilis*) nesting in small, isolated aspen (*Populus tremuloides*) stands in high-elevation, shrubsteppe habitat in northern Nevada. We found 14 and 22 occupied goshawk nests in 1991 and 1992, respectively. Nests were in aspen stands consisting of mature trees with a closed canopy and little understory cover. All were located near water and most were in north- or east-facing stands situated on variable slopes (4–39%). Fourteen breeding pairs fledged 18 young in 1991 and 22 breeding pairs fledged 61 young in 1992 for an average productivity of 2.2 young/occupied nest. Nest observations from blinds indicated that Belding's ground squirrels (*Spermophilus beldingi*) were the primary prey item, followed by various species of birds that were taken in the latter half of the breeding season after ground squirrels had estivated.

Key Words: *Accipiter gentilis*; *Artemisia*; aspen; Belding's ground squirrel; Northern Goshawk; *Populus tremuloides*; *Spermophilus beldingi.*

In the western U.S., the Northern Goshawk (*Accipiter gentilis*) typically nests in mature coniferous forests dominated by ponderosa pines (*Pinus ponderosa*), Douglas-firs (*Pseudotsuga menziesii*), and white firs (*Abies concolor*) (Palmer 1988, Johnsgard 1990). In drier areas of the west such as the Great Basin, goshawks also nest in high-elevation shrubsteppe habitats supporting small, highly fragmented stands of aspen trees (*Populus tremuloides*). Very little information is available on the habitat requirements of goshawks in these shrubsteppe habitats.

METHODS

The study was conducted in the Independence and Bull Run Mountain ranges between the Idaho–Nevada border and a point approximately 50 km north of Elko, Nevada. The ranges are ca. 150 km long and vary from 10 to 30 km in width. Elevations range from 1700 m on the adjacent plain to over 3000 m on the highest peaks. Vegetation is predominately open sagebrush (*Artemisia* spp.) with conifers (*Pinus albicaulis, P. flexilis* and *Abies lasiocarpa*) above 2500 m and aspen (*Populus tremuloides*) growing in riparian areas (Loope 1969). Most of the range is publicly owned and administered by the USDA Forest Service.

We conducted helicopter surveys for all raptor nests in the study area in April of 1991 and 1992 prior to emergence of aspen catkins. In addition, we searched stands of aspens or mixed aspen/conifer that either had a history of occupancy by breeding goshawks or appeared to be suitable nesting habitat. Searches were concentrated in the southern portion of the study area in 1991 but were extended in 1992 to include the northern portion where higher elevations created a shift from aspen to conifer habitat. A nest was classified as occupied if a raptor was seen in the vicinity of a nest structure or if there was evidence of fresh nesting material in nests. Locations of all occupied nests seen from the helicopter were recorded using a Loran C unit and later transcribed onto U.S.G.S. 7.5 min. topographical maps of the region. A nest or nest structure was the platform of sticks on which eggs were laid, and a nesting stand was the stand of trees that contained the nest.

During May and June we checked all goshawk nests on foot to verify occupancy and to determine if eggs had been laid. An occupied nest was defined as a nest where territorial defense, courtship, or a goshawk was seen. Evidence of egg laying included the presence of eggs or young in the nest, or any field sign indicating that eggs were laid (e.g., adults in incubating posture, egg shell fragments in fresh nesting material). Characteristics of aspen stands used by breeding pairs of goshawks were also recorded. Measurements of slope, elevation, aspect, and distances to nearest water were obtained from Geographic Information System (GIS) maps that were developed from data previously collected by USDA Forest Service personnel. We used diameter at breast height (dbh) tapes and increment borers to obtain measurements on sizes and ages of nest trees.

In 1992, we observed eight pairs of goshawks throughout the nesting period from blinds to obtain information on diet and nesting behavior. Blinds were built with lumber and white canvas and placed 30–50 m from a nest tree. Observation periods lasted 3–5 hours and were scheduled to incorporate all times of the day. By continuously recording activities at the nest, observers monitored the types of food that were delivered to nests, the number of food deliveries per hour, and the time spent away from the nesting area by both sexes.

In 1992, adult goshawks were also captured in nest areas in June using a live Great Horned Owl (*Bubo virginianus*) and dho-gaza net. Adults were aged in the hand using plumage characteristics (B. Woodbridge, pers. comm.), and banded with green (male) and blue (female) alpha-numeric, anodized aluminum bands on the left leg and U.S. Fish and Wildlife Service aluminum bands on the right.

RESULTS

In 1991, 123 nest structures were found during helicopter surveys and goshawks were seen at or near ten of these nests. In 1992, only 66 nest

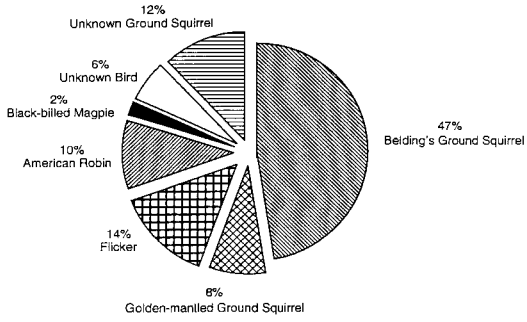

FIGURE 1. Frequency of occurrence of prey species in the diet of Northern Goshawks nesting in shrubsteppe habitats of northern Nevada.

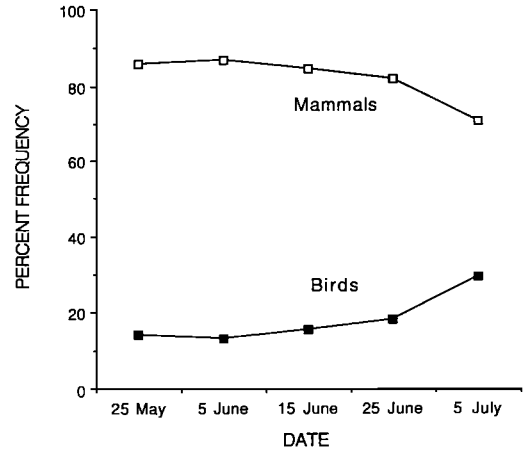

FIGURE 2. Seasonal variation in the frequency of occurrence of prey species in the diets of Northern Goshawks nesting in shrubsteppe habitats of northern Nevada.

structures were found and goshawks were seen at only six of these nests. Subsequent ground searches showed 14 and 22 of the nests to be occupied by goshawks in 1991 and 1992, respectively. The 1992 survey resulted in 11 new goshawk nest sites not located in 1991. Although the 1992 helicopter survey covered conifer forests, and these areas were searched on foot, no goshawks were found nesting there.

All goshawk nest stands had similar characteristics. Mean stand elevation was 2119 m (range 1975–2386 m). Aspens used as nest trees usually had the largest dbh in the stand ($\bar{X}$ = 29 ± 3.8 [SE] cm) and averaged ca. 60 years of age based on core samples. Nest stands were relatively open with a park-like appearance and little understory cover. Although nest stands were small ($\bar{X}$ = 24.9 ± 21.9 ha), the terrain was not steep ($\bar{X}$ slope = 19.4 ± 8.3%) and slopes generally faced north or east. Water, such as a stream or spring, was also usually present within 100 m ($\bar{X}$ = 91 ± 129 m).

Breeding began in April. By backdating from known-aged nestlings and using an incubation period of 33 days, we estimated that egg laying was completed on average by 1 May. We did not observe eggs so could not calculate egg hatchability, but the modal brood size was 3 young. Productivity increased significantly (t-test, $P < 0.05$) from a mean of 1.2 young/breeding pair in 1991 to a mean of 2.8 young/breeding pair in 1992. Young also fledged significantly earlier in 1992 ($\bar{X}$ = 1 July ± 5 days) than in 1991 ($\bar{X}$ = 11 July ± 8 days), possibly because of a very cold and wet spring in 1991.

All 22 adult females and 15 of 22 males were trapped and color marked in 1992. Aging in the hand showed that 11 of the 22 females were in second-year plumage, and none showed 1-year-old plumage characteristics (B. Woodbridge, pers. comm.). We expected the younger females to be less productive, but this was not the case (2.54 vs. 3.0 young per nest). Two-year-old females did fledge young at a significantly later date than older birds (means of 28 June vs. 5 July, t-test, $P < 0.01$). Based on the plumage of birds observed with binoculars in 1991, 5 of 14 breeding females were 1 year of age. We did not trap adults in 1991, so no yearly comparison of 2- and 3+-year-old birds could be made. In both years, only one breeding male was estimated to be less than 3 years of age.

Based on the frequency of occurrence of prey delivered to nests, observations from blinds showed that goshawks ate mostly Belding's ground squirrels (*Spermophilus beldingi*) (Fig. 1). Ground squirrels were delivered by males on 24 of the 51 observed prey deliveries. We did not collect prey remains from plucking posts because goshawks were found to pluck birds and not ground squirrels. Instead, ground squirrels were brought directly to the nest. Mean rate of prey delivery was 0.31 prey item per hour. This was comparable to delivery rates reported by Boal and Mannan (*this volume*). As the nesting season progressed and ground squirrels began to estivate, we observed a shift in the types of prey that were delivered. After 1 July, males began to bring in more birds such as American Robins (*Turdus migratorius*) and Northern Flickers (*Colaptes auratus*) (Fig. 2).

DISCUSSION

In high-elevation shrubsteppe habitats, goshawks nest in small, widely-spaced stands of mature aspen trees that grow along creeks and drainages. These aspen stands are located primarily on north or east-facing slopes. The tree in which

the nest is built averages 60 years of age. The canopy is mostly closed and the understory is open with little cover. Understory cover is probably limited by livestock that use the stands for grazing and shading during the hot summer months.

Helicopter surveys were effective in surveying this type of habitat for nesting goshawks. These surveys are best conducted when the ground is snow-covered and prior to aspen catkin emergence. Lack of snow and early catkin emergence made survey conditions less favorable in 1992. As a result, the number of adults seen in the vicinity of nests was reduced from ten in 1991 to six in 1992. Also, the lack of contrasting snow cover lowered the visibility of nest structures in trees.

Nest observations indicated that female goshawks remained almost continuously in the vicinity of nests, even when young approached fledging age. Male goshawks did almost all the hunting. Many authors state that the female begins to hunt as the young get older (Palmer 1988, Johnsgard 1990). We did not observe this. Females were never seen to leave the immediate vicinity of the nest, even when the young were near fledging.

In 1992, 11 of 22 breeding females were in "sub-adult" plumage of 2-year-old birds (Bent 1937, Johnsgard 1990). We expected to find subadult females less successful than older females in rearing young, but found no difference. No females in 1-year-old plumage bred in 1992, but 5 of 14 breeding females observed in 1991 were in first-year plumage. In Alaska, younger birds bred during years of increasing prey abundance that follow a sharp decline in both prey and goshawk numbers (McGowan 1975). Apparently it is when populations of their preferred food, snowshoe hares (*Lepus americanus*), are increasing that younger females are recruited into the breeding population. A similar increase in the population of the preferred food of goshawks in northern Nevada may have accounted for the large number of one-year-old females that bred in 1991.

Our results indicated that the collection of prey remains from plucking posts to determine goshawk diets may be highly biased when they are feeding on mammals as opposed to birds. We observed that males delivering ground squirrels to nests brought them in unplucked. They did, however, pluck birds at plucking posts. This indicates that, in places where goshawks feed heavily on small mammals, dietary studies must focus on both prey at nests and plucking posts to develop an unbiased estimate of the diets of these birds.

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

FRANK I. DOYLE AND JAMES M. N. SMITH

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 km^2 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 km^2 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 km^2) 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 "kak-king" 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 km^2), 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 km^2). 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-

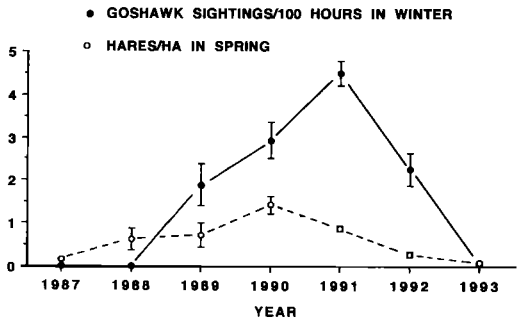

FIGURE 1. Mean number of goshawks sighted per month in winter (November to March), in relation to mean numbers of snowshoe hares live-trapped in spring (mean of two to three plots) at Kluane, Yukon. The bars represent one standard error.

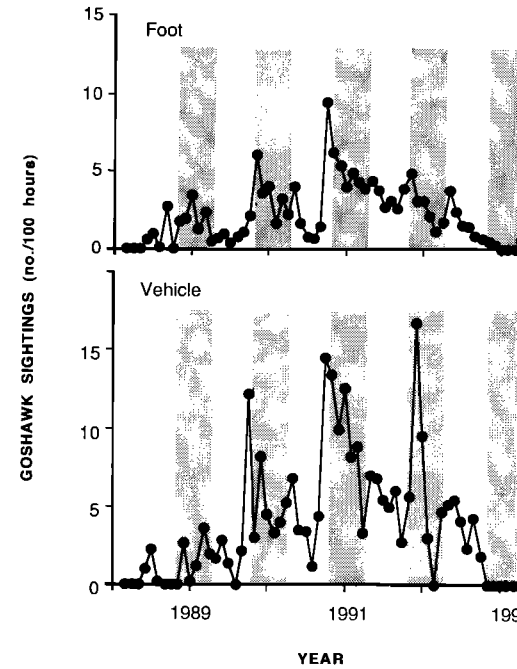

FIGURE 2. Monthly index of sightings (per 100 hours) of Northern Goshawks by observers on foot, and observers in vehicles. Shaded areas display the five winter months (November to March).

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)

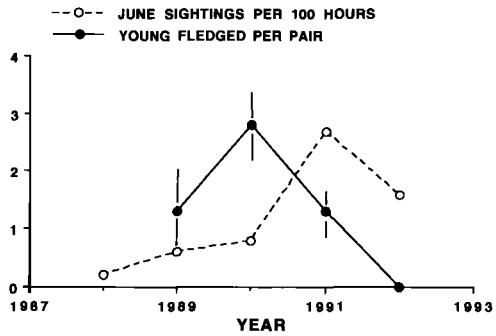

FIGURE 3. Breeding success of Northern Goshawks at Kluane, Yukon (mean number of young fledged per territorial pair), in relation to an index of abundance of goshawks during the breeding season. The bars are one standard error. No data are plotted for 1988, as no breeding pairs of goshawks were detected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

ACKNOWLEDGMENTS

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TERRITORY FIDELITY, MATE FIDELITY, AND MOVEMENTS OF COLOR-MARKED NORTHERN GOSHAWKS IN THE SOUTHERN CASCADES OF CALIFORNIA

PHILLIP J. DETRICH AND BRIAN WOODBRIDGE

Abstract. Eighty adult Northern Goshawks (*Accipiter gentilis*) were marked with color bands during a 9-year period in northern California, and 119 nestlings were banded. Observations in subsequent years located 47% of the adult females and 40% of the adult males. Seventy-two percent of the adults located in consecutive years retained the mate from the previous year. There was no significant difference in mate retention among sexes. Males were significantly more likely to remain in the same territory from year to year than were females. Among hawks located in years subsequent to marking, 18.2% of the females and 23.1% of the males were found breeding in other territories 4–13 km from the location of marking. Two banded nestlings (1.7%) were recaptured as adult female breeders at distances of 16 and 24 km from their natal sites.

Key Words: *Accipiter gentilis*; color-marking; movements; Northern Goshawk; site and mate fidelity.

Since 1983, Northern Goshawks (*Accipiter gentilis*) have been marked on three USDA Forest Service ranger districts (RD) in northern California: the McCloud RD on the Shasta–Trinity National Forest (1983–1989), the Goosenest RD on the Klamath National Forest (1985–1993), and the Devil's Garden RD on the Modoc National Forest (1988–1992). The objectives of this marking were to evaluate mate fidelity and site fidelity, turnover of adults at territories, and movements among territories.

METHODS

Adult Northern Goshawks were captured at nest sites using the dho-gaza with a live Great Horned Owl (*Bubo virginianus*) as a lure (Bloom 1987, Bloom et al. 1992). Adult goshawks were banded with U.S. Fish and Wildlife Service (USFWS) aluminum bands on one leg, and with colored plastic bands with contrasting numerals on the other leg. Goshawks were identified in subsequent years either by re-trapping or by reading color bands with binoculars or spotting scope. The degree of annual follow-up effort varied considerably because of variation in personnel and funding. Typically, each year several hours were spent during the nestling period searching for nests and hawks in each area where nesting had been recorded in the past. In later years, taped goshawk calls were used to locate nests. On the Goosenest RD, standardized belt transects were employed to locate sites, and blinds were built to facilitate reading color bands. Climbers banded nestling goshawks with USFWS bands; nestlings were not marked with color bands. Most nests were climbed while the adult female was held hooded.

We did not reliably locate marked goshawks that did not nest or that failed during incubation, because early in the nesting season access was limited by snow and the goshawks were secretive. Because we were most successful in finding nests and trapping and identifying adults during the nestling period, this study was limited primarily to goshawks that were successful in hatching young.

We used the term "occupancy" to include any year in which a marked adult was found in a territory (including the year of marking). Goshawks that had not yet ended a period of occupancy were not included in calculations of duration of occupancy. We used the term "fidelity" to refer to consecutive years of occupancy or mate retention by marked individuals. A territory was defined as a cluster of nest sites with >1 year of recorded use (Woodbridge and Detrich *this volume*). Occasionally, marked adults were located in a territory even though the nest was not found. Because these adults demonstrated site fidelity, they were included in the analysis. Significance of proportional differences in fidelity to mate and site were analyzed using the log-likelihood ratio (Zar 1984:52).

RESULTS AND DISCUSSION

Through the 1991 season, we color-banded 47 adult females and 33 adult males, and banded 119 nestlings. Results include re-sightings through the 1992 season. Twenty-two females and 13 males were found in years following marking. Thus, 53% of the females and 60% of the males either died or were not found in subsequent years. Two goshawks banded as nestlings were located as breeders in subsequent years. One marked goshawk was found dead. At least one adult was marked in 46 territories. We attempted to locate marked birds in 194 territory-years (i.e., a year subsequent to marking during which searches or observations took place in the territory). Marked females were located in 98 (51%) of these opportunities, and marked males were located in 60 (31%).

OCCUPANCY AND FIDELITY TO MATES AND NEST TERRITORY

Territory occupancy by females ranged from 1 to 7 years, and averaged 1.8 years (SD = 1.3, N = 40). Because of the difficulty of finding nests

TABLE 1. SITE AND MATE FIDELITY AMONG MARKED REPRODUCTIVELY SUCCESSFUL NORTHERN GOSHAWKS IN SUCCESSIVE YEARS IN NORTHERN CALIFORNIA

Pattern	% males (N)	% females (N)	Overall (N)
Same mate	75.0 (12)	69.2 (13)	72.0 (25)
Same nest area	76.5 (17)*	71.4 (49)	73.1 (66)

* Significant difference between sexes (G = 5.2, df = 1, P < 0.025).

TABLE 2. MATE FIDELITY AMONG MARKED REPRODUCTIVELY SUCCESSFUL NORTHERN GOSHAWKS IN SUCCESSIVE YEARS IN THE SAME BREEDING TERRITORY IN NORTHERN CALIFORNIA

Pattern	% males (N)	% females (N)	Overall (N)
Same mate	80.0 (10)	69.2 (13)	73.9 (23)
Different mate	20.0	30.8	26.1

in consecutive years (Woodbridge and Detrich *this volume*), the observed mean occupancy was probably less than the actual.

Territory occupancy by males ranged from 1 to 3 years, and averaged 1.3 years (SD = 0.54, N = 27). The observed occupancy by males was also believed to be lower than the actual rate and cannot be directly compared with that of females because of the greater difficulty in trapping and observing males.

In 18 of 25 instances when mates were identified in consecutive years, the mate from the previous year was retained (Table 1). Mate retention did not differ significantly between sexes (G = 0.8, df = 1, P < 0.40). In 48 of the 66 instances in which adults in a territory were identified in consecutive years, marked adults remained in the territory. Males were significantly more likely to remain in the same territory from year to year than were females (G = 5.2, df = 1, P < 0.025).

Among the 23 adults that remained on the same territory in consecutive years and whose mate was known in those years (Table 2), there was no significant difference in mate retention between sexes (G = 3.6, df = 1) at P < 0.05, but at P < 0.10, males were more likely to retain the same mates than were females, suggesting a tendency in this regard.

Considerable variation was observed among adults that did not retain mates in consecutive years. For instance, in three territories observed for five-year periods, two males and two females bred in three different combinations. Another male bred with three different females in the same territory during a six-year period; one of these females was present in three non-consecutive years.

We remain uncertain as to the effects of our activities on site occupancy and fidelity. Among 17 occupied nests where no trapping or banding occurred, only two were occupied in the following year, indicating a high degree of movement in the undisturbed population. However, because these adults were not marked, fidelity patterns in the undisturbed population could not be determined for comparison.

MOVEMENTS

Among the 22 females located in years subsequent to marking, four (18.2%) were found breeding at a second territory. These movements ranged from 5.5 to 12.9 km (mean = 9.8 km, SD = 2.7). One of these females later returned to the territory where she had been marked; that territory had been occupied by another female during the interim. Among the 13 males located in years subsequent to marking, three (23.1%) were found breeding at a second territory. Their movements ranged from 4.2 to 10.3 km (mean = 6.5 km, SD = 2.7).

The distances to the nearest neighboring territory for most of the adults that moved were not reliably known. However, nearest-neighbor distances in intensively surveyed portions of the study area ranged from 1.3 to 6.1 km (mean = 3.3 km, SD = 0.3) (Woodbridge and Detrich *this volume*). All adult movements among territories were more than two standard deviations greater than the mean nearest-neighbor distance, and thus, it appears that few were likely to involve movements to neighboring territories.

Two of the 119 nestlings banded (1.7%) were recaptured as adult female breeders at distances of 16.1 and 24.2 km from their natal sites. One was captured in the fifth year following banding, the other in the seventh year following banding.

TURNOVER IN TERRITORIES

Analysis of turnover was problematic because of the high rate of attrition of territories (Woodbridge and Detrich *this volume*), movement among territories by both sexes, intermittent use of territories by individuals, and the need for more years for observations of hawks marked in recent years.

In 27 territories occupied in the year following marking of adults, eight (30%) were occupied by new females and six (23%) were occupied by new males. Among the 43 territories with marked females, 16 were occupied by different females during different years. One was occupied by three different females in a 6-year period, and another by four different females in an 8-year period.

Among the 34 territories with marked males, 13 were occupied by different males in different years; one was occupied by three males in an 8-year period.

To our knowledge, there are no published data on Northern Goshawks for comparison with the results of this study. Our data indicate that some previous assumptions about mate fidelity need re-examination, for instance statements by Jones (1979) and Palmer (1988) that goshawks probably mate for life.

Site fidelity reported for the congeneric European Sparrowhawk (*Accipiter nisus*) (Newton and Wyllie 1992) was similar to that found in our study in that about 70–75% of hawks found in successive years were on the same territory. Northern Goshawks on our study area retained mates more frequently than European Sparrowhawks (Newton and Marquiss 1982), which might be partially explained by a presumably higher mortality rate among the smaller sparrowhawks. Movements by male sparrowhawks were often to a neighboring territory, whereas females typically moved further (Newton and Wyllie 1992).

Our data provide only a partial understanding of tendencies and variation within the population studied, despite a substantial sustained effort in the field. Our experience indicates that obtaining complete demographic data for Northern Goshawks will demand efforts far exceeding those expended in the last 10 years on the Northern Spotted Owl (*Strix occidentalis caurina*) (Thomas et al. 1990). Researchers contemplating marking studies of Northern Goshawks must be committed to intensive long-term efforts to obtain adequate data.

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SURVIVAL OF NORTHERN GOSHAWKS IN THE SOUTHERN CASCADES OF CALIFORNIA

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Abstract. From 1983 to 1992, 95 Northern Goshawks (*Accipiter gentilis*) were marked with numbered, colored leg bands in northern California. We used capture-recapture techniques to estimate survival and resighting (or recapture) rates. Low sample size of marked birds and low resighting rates contributed to lack of fit of these data to the capture-recapture model. Survival estimates were generated, but variance was high. There were indications, however, that survival in goshawks varied among years, and survival of females was higher than males. We suggest that researchers interested in estimating survivorship of raptors strive for large numbers of marked birds, high resighting rates, and at least 5 years of data. These recommendations necessitate large study areas, large field crews, and careful consideration of model assumptions and raptor biology.

Key Words: *Accipiter gentilis*; California; capture-recapture; Northern Goshawk; survival.

In many wildlife studies, the presence of animals in certain habitats is often thought to be an indication of the quality of those habitats. Presence of individuals and estimates of relative densities among different habitats, however, may not be adequate to assess habitat quality (Van Horne 1983, Vickery et al. 1992). Other demographic parameters, such as reproductive success and survival, perhaps in conjunction with density, may be important indicators of habitat quality or "habitat fitness" (i.e., the capacity of a habitat to support optimum fecundity and high survival).

Much of the research conducted on Northern Goshawks (*Accipiter gentilis*) has focused on habitat use during the breeding season, often with some associated measure of reproductive success (Reynolds and Wight 1978, Crocker-Bedford 1990). Estimates of survival, however, are difficult to obtain for most species and involve some degree of uncertainty because absence of a marked individual does not necessarily indicate mortality. This is particularly true for studies of marked goshawks because of their low densities, large home ranges, high mobility, and secretive behavior.

Capture-recapture methodology (Cormack 1964, Jolly 1965, Seber 1965) conducted over long periods of time with an adequate sample of marked individuals, each of which has a high probability of being resighted ("visually recaptured"), can overcome these challenges. Capture-recapture models have been developed to account for the uncertainty inherent in survival estimation.

We used capture-recapture techniques to (1) explore the feasibility of calculating survival estimates for goshawks, (2) calculate point estimations and variances of survival, and (3) examine the yearly variation in survivorship and sex-related differences in goshawks. We then make recommendations for studies designed to estimate survival and suggest a cautious approach to interpretation of the results.

STUDY AREA AND METHODS

Northern Goshawks were captured on the Goosenest Ranger District of the Klamath National Forest and adjacent lands on the Shasta–Trinity and Modoc National Forests in the southern Cascades of northern California. The area was dominated by Sierra montane and upper montane forests. The former was comprised of Douglas-fir (*Pseudotsuga menziesii*), incense-cedar (*Calocedrus decurrens*), red fir (*Abies magnifica*), white fir (*A. concolor*), and ponderosa pine (*Pinus ponderosa*), and was interspersed with permanent streams and wet meadows with stands of lodgepole pine (*P. contorta*) and trembling aspen (*Populus tremuloides*). Upper montane forests consisted of pure stands of red fir, white fir, and lodgepole pine with some ponderosa pine. Stream drainages were few and typically dry. Forest seral stages were characterized by small patches of unmanaged mature forest interspersed among varying degrees of managed forest. Dominant silvicultural systems included thinning, shelterwood cuts, and small clearcuts.

Surveys for nests were conducted on 10,440 and 10,230 ha blocks in Sierra montane and upper montane forest types, respectively. We used conspecific alarm and begging tapes to elicit responses from adult and fledgling goshawks and visual clues (feathers, prey remains, nest structures, whitewash) to locate nests (Kimmel and Yahner 1990, Kennedy and Stahlecker 1993). In addition, about 20 nests outside of the study blocks were monitored. Adult goshawks were captured at nests with dho-gaza sets with a live Great Horned Owl (*Bubo virginianus*) as a decoy (Bloom et al. 1992). Adults were marked with uniquely numbered plastic colored leg bands and U.S. Fish and Wildlife Service aluminum leg bands. We used camouflaged blinds and spotting scopes to observe marked adults at nests in subsequent years; some bands were read when adults were re-trapped in subsequent years.

We input capture-resighting data as a capture history matrix, and used program RELEASE for data summarization and goodness-of-fit tests (Burnham et al.

TABLE 1. NUMBER OF FEMALE AND MALE NORTHERN GOSHAWKS BANDED IN THE SOUTHERN CASCADE RANGE, CALIFORNIA, 1983–1992

Year	Female	Male
1983	0	3
1984	2	2
1985	2	6
1986	2	6
1987	8	7
1988	6	6
1989	4	4
1990	2	6
1991	4	2
1992	10	13
Totals	40	55

1987). Goodness-of-fit tests examine the data with a series of χ^2 contingency tables to determine if the data fit the capture-recapture model. In RELEASE, goodness-of-fit has two components that look for differences in survival and recapture rates among cohorts (groups rereleased on different occasions; TEST 2) and subcohorts (individuals with different capture histories; TEST 3). Differences, shown by low P-values, among cohorts or subcohorts indicate lack of fit. We used program SURGE (Lebreton et al. 1992) to derive point estimates and variances of survival. Models used for estimation of survival were based on the Cormack-Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) model $\{\phi, p\}$, where ϕ = survival and p = probability of resighting.

We examined eight models, where ϕ and p were assumed to vary among years (subscript t) and between sexes (subscripts F for female and M for male). Twelve models were used to evaluate the interaction between time and sex. We used Akaike's Information Criteria (AIC), which is a numerical measure based on the deviance and the number of parameters in a model, and the principle of parsimony to select the model that best fit the data with the fewest number of parameters, and was still biologically reasonable (i.e., the "best" model) (Burnham et al. 1987, Lebreton et al. 1992).

RESULTS

We marked 95 adult goshawks with color bands and collected resightings of these marked birds from 1983 to 1992 (Tables 1, 2). For all goshawks (i.e., females and males combined) goodness-of-fit tests indicated that there was a definite lack of fit of the data to the capture-recapture model at the cohort and subcohort levels (χ^2 = 12.9, df = 7, P = 0.07 and χ^2 = 16.6, df = 12, P = 0.16 for TESTS 2 and 3, respectively), and overall fit of the data to the model was inadequate (χ^2 = 29.6, df = 19, P = 0.06 for TEST 2 + TEST 3; Burnham et al. 1987:71–77).

We first examined two sets of nested models to estimate survival (Table 3). Time-specific models revealed that there may be yearly differences in survival of goshawks, as model $\{\phi_t, p\}$ had the lowest AIC value, with $\{\phi_t, p_t\}$ as a competitive model (Likelihood ratio test, χ^2 = 4.67, df = 7, P = 0.70). The model with no time specificity ($\{\phi, p\}$) was not competitive (χ^2 = 30.6, df = 8, P = 0.0002). Survival rates were not estimable in some years because of low sample sizes (Table 4). According to our analysis, survival and resighting probabilities were higher for females than for males, but wide confidence intervals, due mainly to low sample sizes, precluded us from demonstrating a statistical difference (Table 4).

We then examined 12 models where the parameters ϕ and p were allowed to vary as an interaction between time (years) and sex (Table 3). The model $\{\phi_{Ft}, \phi_{Mt}, p\}$ had the lowest AIC value, which indicated that survival varied among years and between sexes (Table 4).

TABLE 2. MARK-RECAPTURE DATA ARRAY FOR NORTHERN GOSHAWKS IN THE SOUTHERN CASCADES, CALIFORNIA, 1983–1992. R_i IS THE NUMBER OF GOSHAWKS MARKED AND RELEASED ON THE iTH OCCASION (OR YEAR OF STUDY), M_{ij} THE NUMBER OF GOSHAWKS MARKED AND RELEASED ON OCCASION i THAT WERE RECAPTURED OR RESIGHTED ON OCCASION J, AND R_i THE TOTAL NUMBER OF GOSHAWKS MARKED AND RELEASED ON OCCASION i THAT WERE LATER RECAPTURED (= ΣM_{ij})

		m_{ij} for j =									
i	R_i	2	3	4	5	6	7	8	9	10	r_i
1	3	1	1	0	0	0	0	0	1	0	3
2	5		1	1	1	1	0	0	0	0	4
3	10			6	3	1	0	0	0	0	10
4	15				9	0	0	0	0	0	9
5	28					13	1	0	0	0	14
6	27						7	1	0	0	8
7	16							5	0	0	5
8	14								4	2	6
9	11									3	3

TABLE 3. CAPTURE-RECAPTURE MODELS, WHERE ϕ IS SURVIVAL RATE AND p IS RECAPTURE RATE, USED TO ESTIMATE SURVIVAL IN NORTHERN GOSHAWKS IN THE SOUTHERN CASCADES OF CALIFORNIA, 1983–1992. ASSOCIATED AKAIKE'S INFORMATION CRITERIA (AIC = [2 × NO. OF PARAMETERS] + DEVIANCE) IS USED TO EVALUATE RELATED MODELS; LOWEST AIC VALUE INDICATES THE BEST MODEL (I.E., THE MODEL WITH THE FEWEST PARAMETERS AND FITS THE DATA AND IS BIOLOGICALLY REASONABLE). SUBSCRIPT T INDICATES TIME (I.E., SURVIVAL AND RECAPTURE RATES ESTIMATED FOR EACH YEAR, 1983–1990); SUBSCRIPTS F AND M INDICATE FEMALES AND MALES, RESPECTIVELY

Model	No. of parameters	Deviance	AIC
Time-specific models			
$\{\phi_t, p_t\}$	17	236.53	270.53
$\{\phi_t, p\}$	10	241.20	261.20
$\{\phi, p_t\}$	10	258.08	278.08
$\{\phi, p\}$	2	271.82	275.82
Sex-specific models			
$\{\phi_F, \phi_M, p_F, p_M\}$	4	268.77	276.77
$\{\phi_F, \phi_M, p_{F+M}\}$	3	269.51	275.51
$\{\phi_{F+M}, p_F, p_M\}$	3	269.43	275.43
$\{\phi_{F+M}, p_{F+M}\}$	2	271.82	275.82
Time- and sex-specific models			
$\{\phi_{Ft}, \phi_{Mt}, p_{Ft}, p_{Mt}\}$	34	223.21	291.21
$\{\phi_{Ft}, \phi_{Mt}, p_{Ft}, p_M\}$	27	231.69	285.69
$\{\phi_{Ft}, \phi_{Mt}, p_F, p_{Mt}\}$	27	227.40	281.40
$\{\phi_{Ft}, \phi_{Mt}, p_F, p_M\}$	20	235.88	275.88
$\{\phi_{Ft}, \phi_M, p_{Ft}, p_{Mt}\}$	27	234.86	288.86
$\{\phi_F, \phi_{Mt}, p_{Ft}, p_{Mt}\}$	27	236.70	290.70
$\{\phi_F, \phi_M, p_{Ft}, p_{Mt}\}$	20	248.31	288.31
$\{\phi_{Ft}, \phi_M, p_{Ft}, p_M\}$	19	243.81	281.81
$\{\phi_F, \phi_{Mt}, p_F, p_{Mt}\}$	19	248.21	286.21
$\{\phi_{Ft}, \phi_M, p_F, p_{Mt}\}$	20	239.05	279.05
$\{\phi_F, \phi_{Mt}, p_{Ft}, p_M\}$	20	245.14	285.14
$\{\phi_{Ft}, \phi_{Mt}, p\}$	19	236.50	274.50

TABLE 4. MAXIMUM LIKELIHOOD ESTIMATES OF SURVIVAL (ϕ) AND PROBABILITY OF RESIGHTING (P) FOR NORTHERN GOSHAWKS IN THE SOUTHERN CASCADE RANGE, CALIFORNIA, 1983–1992, BASED ON CAPTURE-RECAPTURE TECHNIQUES. NUMBERED SUBSCRIPTS INDICATE THE YEAR FOR WHICH SURVIVAL IS ESTIMATED; SUBSCRIPTS F INDICATE SURVIVAL ESTIMATES FOR FEMALES, M FOR MALES. ESTIMATES ARE SHOWN FOR MODELS WITH THE LOWEST AIC VALUES (SEE TEXT FOR FURTHER EXPLANATION)

Model	Parameter	ϕ	SE(ϕ)	P	SE (P)
$\{\phi_t, p\}$	ϕ_{83}	Inest.[1]	Inest.	0.54	0.06
	ϕ_{84}	0.91	0.15		
	ϕ_{85}	Inest.	Inest.		
	ϕ_{86}	0.94	0.12		
	ϕ_{87}	0.71	0.14		
	ϕ_{88}	0.39	0.11		
	ϕ_{89}	0.43	0.14		
	ϕ_{90}	0.58	0.19		
$\{\phi_{Ft}, \phi_{Mt}, p\}$	ϕ_{F83}	Inest.	Inest.	0.54	0.07
	ϕ_{F84}	0.85	0.19		
	ϕ_{F85}	Inest.	Inest.		
	ϕ_{F86}	0.93	0.15		
	ϕ_{F87}	0.80	0.18		
	ϕ_{F88}	0.44	0.15		
	ϕ_{F89}	0.35	0.17		
	ϕ_{F90}	0.81	0.27		
	ϕ_{M83}	Inest.	Inest.		
	ϕ_{M84}	Inest.	Inest.		
	ϕ_{M85}	Inest.	Inest.		
	ϕ_{M86}	0.94	0.30		
	ϕ_{M87}	0.57	0.22		
	ϕ_{M88}	0.31	0.16		
	ϕ_{M89}	0.60	0.31		
	ϕ_{M90}	0.20	0.19		

[1] Parameter inestimable.

DISCUSSION

Much interest has been generated by the estimates of survival and associated population rate of change (λ) generated for the federally listed Northern Spotted Owl (*Strix occidentalis caurina*) (Anderson and Burnham 1992). We were able to calculate survival estimates for goshawks using the same capture-recapture methodology, but these estimates were imprecise due to small samples of marked birds and low resighting rates. In addition, the estimates that were produced were likely biased low because some marked goshawks emigrated off of the study area, and only birds that were associated with successful nests were resighted. These problems contributed to the lack of fit of the data to the capture-recapture model, resulting in low resighting probabilities and biased parameter estimates. However, empirical estimates of survival for goshawks in Arizona by Leslie et al. (pers. comm.) showed that survival may indeed be higher than our estimates, but their data did support the conclusion that female survival is higher than male survival.

We recommend to researchers wishing to estimate ϕ and λ that they strive for large numbers of banded birds, the highest resighting rates possible, and > 5 years of data collected over a broad geographic area. Opportunities to coordinate banding and resighting efforts with adjacently located studies should be considered and encouraged. In addition, we recommend that researchers become familiar with all the assumptions of capture-recapture models when planning their study (see Burnham et al. 1987:51–54). Capture and recapture episodes are assumed to be instantaneous, an obviously unrealistic requirement. Confining banding and resighting efforts to as short a time period as possible, however, would move toward fulfilling this assumption. A 1-month capture and resighting period may be realistic for field conditions. Another important

assumption is that marks not be lost or misread. Color band loss over time and error in identifying bands needs to be assessed.

Studies such as these will require large field crews and will be expensive. We strongly suggest that the biology of Northern Goshawks, such as their wide-ranging habits and mobility, be considered carefully when designing a study and interpreting results of survival estimation. We believe that these recommendations will be helpful in survival studies of other raptor species as well.

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