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PREY AND WEATHER FACTORS ASSOCIATED WITH TEMPORAL VARIATION IN NORTHERN GOSHAWK REPRODUCTION IN THE SIERRA NEVADA, CALIFORNIA

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Abstract. We studied the association between Northern Goshawk (*Accipiter gentilis*) reproduction and annual variation in prey and weather factors in the Lake Tahoe region of the Sierra Nevada, California, during 1992–1995. The proportion of Northern Goshawk breeding territories occupied varied between years although differences were not statistically significant. However, annual variation was observed in the proportion of Northern Goshawk territories with active nests, successful nests, and in the number of young produced per successful nest. Annual variation in reproduction was associated with variation in late-winter and early-spring temperatures and Douglas squirrel (*Tamiasciurus douglasii*) abundance (February–April). Douglas squirrel abundance, and their frequency and biomass in diets of Northern Goshawks during the breeding period, varied annually in concordance with cone crop production. Northern Goshawk reproduction was greatest in 1992 following both abundant late-winter and early-spring Douglas squirrel populations, which resulted from high cone crop production the previous autumn, and mild late-winter and early-spring temperatures. These results are consistent with the prediction that carnivorous birds require increased energy before breeding in order to reproduce successfully. In the high elevations of the Sierra Nevada, prey availability is reduced during the late winter and early spring because of the migration and hibernation patterns of important prey species and temperatures are near or below the lower critical temperature for Northern Goshawks during this period. In contrast to other prey species, Douglas squirrels are active throughout the year and are available during this period. Thus, our results suggest that forest management and restoration strategies adopted to enhance Northern Goshawk foraging areas should consider management of conifer tree size distributions and species compositions to enhance seed production in terms of frequency over time, number of seeds per crop, and energetic value of seeds by tree species, as these are important habitat elements and ecological processes influencing Douglas squirrel populations. Autecological studies of focal species of concern such as the Northern Goshawk are necessary to provide the basic ecological knowledge required to integrate species level concerns with landscape and ecosystem management perspectives to advance conservation science and improve land management.

Key Words: *Accipiter gentilis,* California, cone-crop production, diet, Douglas squirrel, Northern Goshawk, reproductive success, Sierra Nevada, *Tamiasciurus douglasii,* weather.

PRESA Y FACTORES DEL CLIMA ASOCIADOS CON LA VARIACIÓN TEMPORAL EN LA REPRODUCCIÓN DEL GAVILÁN AZOR EN LA SIERRA NEVADA, CALIFORNIA

Resumen. Estudiamos la asociación entre la reproducción y la variación anual en la presa, así como los factores del clima del Gavilán Azor (*Accipiter gentilis*), en la región de Lake Tahoe de la Sierra Nevada, en California, durante 1992–1995. La proporción ocupada de territorios de reproducción del Gavilán Azor varió entre los años, a pesar de que las diferencias no fueron estadísticamente significantes. Sin embargo, la variación anual fue observada en la proporción de territorios del Gavilán Azor con nidos activos, nidos exitosos, y en el número de juveniles producidos por nido exitosos. La variación anual en la reproducción estuvo asociada con la variación en temperaturas al final del invierno y al principio de la primavera, y con la abundancia de la ardilla de Douglas (*Tamiasciurus douglasii*), febrero–abril. La abundancia de la ardilla de Douglas, y la frecuencia y biomasa en las dietas de los Gavilanes Azor durante el período reproductivo, varió anualmente de acuerdo a la producción de la cosecha de conos. La reproducción del Gavilán Azor en 1992 fue mayor, seguida de poblaciones abundantes de ardillas de Douglas durante el final del invierno y el principio de la primavera, lo cual resultó de una alta producción en la cosecha de conos durante el otoño anterior y las temperaturas blandas durante el final del invierno y el principio de la primavera. Dichos resultados son consistentes con la predicción de que las aves carnívoras requieren un incremento en la energía antes de reproducirse, con el fin de reproducirse exitosamente. En las altas elevaciones de la Sierra Nevada, la disponibilidad de la presa es reducida durante el final del invierno y el principio de la primavera, debido a los patrones de migración e hibernación de especies importantes de presas, y ya que las temperaturas durante este período se acercan o están por debajo de la temperatura crítica de los Gavilanes Azor. En contraste a otras especies de presas, las ardillas de Douglas son activas durante todo el año, y están disponibles durante este período. Es por esto que nuestros resultados sugieren que el manejo forestal y las estrategias de restauración adoptadas para mejorar las áreas de forrajeo del Gavilán Azor, deberían considerar el manejo de las distribuciones en el tamaño de árboles de coníferas, así como la composición de las especies, para mejorar la producción de la semilla en términos de frecuencia a través del tiempo, número de semillas por cosecha y valor energético de las semillas por especie de árbol; ya que estos son elementos importantes del hábitat, así como procesos ecológicos, los cuales influyen las poblaciones de la ardilla de Douglas. Estudios Auto ecológicos de especies focales de interés, tales como los del Gavilán Azor, son necesarios para proveer el conocimiento ecológico básico requerido para integrar las preocupaciones del nivel de especies, con el paisaje y el manejo del ecosistema, con el fin de avanzar en la ciencia de la conservación y de mejorar el manejo de la tierra.

The Northern Goshawk (*Accipiter gentilis*) has been of conservation concern recently in North America due to uncertainty regarding population trends and potential impacts of forest management practices on habitat (Block et al. 1994, Kennedy 1997, DeStefano 1998, Andersen et al. 2004). Northern Goshawks are distributed throughout forests and woodlands of the Holarctic (Brown and Amadon 1968). In North America, Northern Goshawks are found in forested vegetation types ranging across the boreal forest and extending south through the western mountains into Mexico and, in the East, south through the mixed conifer-hardwood forest to approximately New York and New Jersey (Palmer 1988, Squires and Reynolds 1997; Bosakowski and Smith, *this volume*). Conservation strategies for Northern Goshawks will need to be developed at appropriate ecological scales to account for variability in vegetation, climate, diet, and prey dynamics across the broad geographic range of the species (Reynolds et al. 1992, Keane and Morrison 1994, Andersen et al. 2004).

The influence of biotic and abiotic factors on population dynamics has been of fundamental interest to ecologists (Andrewartha and Birch 1954, Lack 1966, Newton 1998). Food and weather are primary limiting factors for raptor populations (Newton 1979a). Studies of Northern Goshawk populations in boreal forests of both the Nearctic and Paleoarctic have demonstrated that annual variation in their reproduction, as well as migration patterns, are associated with cyclic population dynamics of galliformes or lagomorphs, their primary prey in those regions (McGowan 1975, Doyle and Smith 1994, Sulkava et al. 1994, Erdman et al. 1998). Weather factors, specifically temperature and precipitation, are also associated with annual variation in Northern Goshawk reproduction (Kostrzewa and Kostrzewa 1990, Sulkava et al. 1994). Like populations in boreal forests, populations of Northern Goshawks in temperate North American forests also exhibit high variation in reproduction between years (Bloom et al. 1986, Reynolds et al. 1994, Kennedy 1997). Although breeding season diets have been described for a number of Northern Goshawk populations in these temperate forest systems (Andersen et al. 2004), the data are generally reported as overall summaries of frequency and biomass pooled over multiple years of the study. We are unaware of any studies that have attempted to quantify annual variation in diets, prey abundance, and weather factors associated with annual variation in reproduction.

Consideration of avian ecological energetics provides a foundation for framing questions related to the role of biotic and abiotic environmental factors on annual variation in Northern Goshawk reproduction. Weathers and Sullivan (1993) reviewed the avian ecological energetics literature and suggested that diet is a factor that determines which of two competing hypotheses regarding seasonal energetic patterns applies to species in seasonal environments. Omnivorous or granivorous species follow a reallocation-pattern hypothesis whereby overall energetic requirements are similar between seasons and individuals reallocate energy from thermoregulation in winter to reproductive needs in spring and summer. Carnivorous or insectivorous species follow an increased demand hypothesis, whereby individuals have increased energy demands in the breeding season (Weathers and Sullivan 1993). For example, field metabolic rates of Long-eared Owls (*Asio otus*) increased by 42% (Wijandts 1984), and male Eurasian Kestrels (*Falco tinnunculus*) by 48% during the breeding season as compared to the winter (Masman et al. 1988).

Female raptors require a significant increase in energy intake to acquire the substantial body reserves necessary before egg laying (Hirons 1985). The amount of food required to attain these body reserves is potentially much greater than the food required solely for egg production in large raptors (Newton 1993). Females that do not accumulate these reserves do not lay eggs. Typically, females do not actively hunt during the pre-laying period and the majority of food is provided by the male. Therefore, whether a pair will breed successfully depends on the ability of the male to provide extra food in the early spring which is affected by a number of potential factors that include the individual hunting prowess of the male, prey abundance and availability, and thermal stress induced by weather conditions (Newton 1993).

Our goal was to study the ecology of Northern Goshawks in the Sierra Nevada of California to investigate annual variation in reproduction and its relationship to prey and weather factors. Our specific objectives were to investigate annual variation in: (1) the proportion of Northern Goshawk territories occupied, active, and successfully producing young, (2) the frequency and biomass of each prey species in Northern Goshawk diets during the breeding period, (3) the relative abundance of key prey species, (4) factors affecting the abundance of key prey species, and (5) relationships between weather and reproduction. An understanding of these relationships is necessary to develop an effective conservation strategy for Northern Goshawks and to provide a basis for integrating a single-species perspective with broader ecosystem perspectives to advance conservation and land management in the Sierra Nevada.

STUDY AREA

Our study was conducted within an approximately 950 km^2 area in the Lake Tahoe region (39º00', 120º00') of the Sierra Nevada range of California. Geologically, the region is dominated by the Lake Tahoe Basin, a fault block that has sunk between the uplifted Sierra Nevada and Carson Range fault blocks with Lake Tahoe having formed as a result of volcanic and glacial processes (Whitney 1979). Elevation in the study area ranged from 1,800–2,450 m. The Sierra Nevada is characterized by a Mediterranean climate with hot, dry summers and cool, wet winters (Schoenherr 1992). Average summer and winter temperatures were 14.8 C and -0.8 C, respectively, and total annual precipitation (1 July–30 June) ranged from 41.1–155.5 cm during the study between 1991–1995 (Western Regional Climate Center, Reno, NV, unpubl. data). Primary forest types in the study area consisted of mixed-conifer (ponderosa pine [*Pinus ponderosa*], Jeffrey pine [*Pinus jeffreyi*], white fir [*Abies concolor*], red fir [*Abie magnifica*], and incense cedar [*Libocedrus decurrens*]), red fir, eastside pine (Jeffrey-ponderosa), and lodgepole pine (*Pinus contorta*). Other prominent vegetation types present were montane chaparral (*Arctostaphylus-Quercus-Ceanothus*), riparian, and montane meadow.

METHODS

Northern Goshawk Reproduction

We surveyed for Northern Goshawk territories using two survey techniques to meet two objectives during March–September 1991–1995. We used broadcast surveys to inventory and document the location of Northern Goshawk breeding territories across the study area. We used status surveys to monitor occupancy and reproductive status at known Northern Goshawk territories.

Broadcast surveys were conducted by systematically traversing each survey area and broadcasting conspecific calls from sample points at approximately every 200 m (Kennedy and Stahlecker 1993, Joy et al. 1994). Each point was surveyed for approximately 10 min by alternating broadcast calling with silent observation. Territorial alarm calls were used during the incubation and nestling periods and a combination of wailing and territorial alarm calls were used during the fledgling dependency period (Kennedy and Stahlecker 1993). All watersheds in the northern, western, and southern regions of the Lake Tahoe Basin were surveyed. We also surveyed select areas to the north and west of the basin proper that had historic records of nesting activity with no current information on occupancy status or where observations of birds suggested the potential location of Northern Goshawk breeding territories. All areas were surveyed with broadcast surveys a minimum of two times each year. Broadcast surveys were conducted during the nestling and fledgling dependency periods of the breeding season when these methods are most effective (Kennedy and Stahlecker 1993). We also conducted at least one status survey per year in each of the historic sites using a combination of intensive stand searches and broadcast surveys described below.

We considered an area a Northern Goshawk territory if an active nest (i.e., adult incubating, nestlings, or fledglings) was found in any one year of nest monitoring. Thus, we excluded areas where we found old nests but did not detect adult birds or nest attempts during the study as we had no information on when the territory may have been last occupied. Each year we monitored all known nesting areas to document occupancy and reproductive status. Intensive stand searches were used in April–June to determine territory occupancy, estimate laying dates, and nest locations within 0.8 km of known nest trees; each known site was visited two–three times. Intensive stand searches at this time of the breeding period consisted of one or two observers silently traversing the survey area searching for nests or sign (feathers, prey remains, and/or whitewash). If we did not locate an active nest with the early season intensive stand searches, we conducted broadcast surveys and repeated intensive stand searches during the nestling and fledgling dependency periods of the nest cycle to determine territory status. The area within 1.6 km of known nest trees was surveyed a minimum of five times using a combination of broadcast surveys and intensive stand searches. One or two observers systematically traversed the area along transects spaced at approximately 50 m apart visually searching for nests and sign, and broadcast conspecific calls approximately every 150 m to illicit territorial responses. Territorial alarm calls were used during the incubation and nestling periods and a combination of wailing and territorial alarm calls were used during the fledgling dependency period (Kennedy and Stahlecker 1993).

A nest area was classified as occupied if adult birds were detected one or more times within the 1.6 km survey area around known nest locations (February–September). A nest site was considered active in any one year if a nest with an incubating adult or nestlings, or fledglings in the immediate nest area were detected. A nest site was also considered active in that year if a failed nest with either fresh greenery, whitewash at the base of the tree, fresh prey remains, or fresh down on the nest rim was observed indicating that pairs had initiated nest building and egg-laying before abandoning the nest attempt. A nest site was classified as successful if fledglings successfully dispersed from the area. Nest sites were considered inactive if neither adult birds nor an active nest were located. Given that we conducted surveys throughout the entire breeding period and that fledglings are highly vocal and thus detectable during the fledgling dependency period, and remain in the nest area for 4–6 wk after fledgling (J. Keane, unpubl. data), it is likely we would have detected most successful nest attempts. However, we may not have detected pairs that had moved farther than 1.6 km among alternate nest locations between years. Woodbridge and Detrich (1994) reported that known alternate nest sites were within 0.7 km for 85% of 28 pairs in northern California. Reynolds and Joy (1998) reported that >95% of alternate nests were located within 1.6 km of each other. We used chi-square analysis (Sokal and Rohlf 1981) to separately test for differences in the proportion of territories occupied, active, and successful between years, and the proportion of active nests that were successful between years. Only data from known territories were used in these analyses. Data from the initial year in which a territory was located were not used in the analysis. This was done to eliminate potential bias resulting from including only new territories with active nests because search efforts are likely biased towards locating new territories when they have active nests versus when they are unoccupied or occupied but non-nesting. We used one-way analysis of variance (ANOVA; Sokal and Rolhf 1981) to compare the number of young produced per territory and per successful nest among years. Data from all successful nests, including new nests located within each year, were used in the comparison of young produced per successful nest in this analysis.

Northern Goshawk Diet

Northern Goshawk diets were determined by collecting prey remains (i.e., feathers, fur, skin, and skeletal parts) and pellets found in the nest area during the nesting period by systematically searching the entire area within approximately 150-m radius circle centered on each active nest. All methods used to quantify raptor diets have associated biases (Marti 1987). Boal and Mannan (1994) reported that estimates based on collections of prey remains are biased towards conspicuous prey species, e.g., mammals, as compared to direct observations of prey delivered to nests. Their observations suggest that mammals may constitute a larger portion of the diet then our data might indicate. However, we think that our estimates of relative annual variation in diet provide a comparative measure of prey species in the diet among years because Collopy (1983) reported that remains analysis, pellet analysis, and direct observation yielded similar rankings of prey taxons for Golden Eagles (*Aquila chrysaetos*) and Northern Goshawks. Prey items were categorized to species based on comparisons with specimens in the bird and mammal collection in the Department of Wildlife, Fisheries and Conservation Biology at the University of California, Davis. Some items were identified only to genus due to difficulty in identifying species (e.g., *Spermophilus* and *Tamias*). Biomass was estimated by calculating mean weights for adult mammal species based on values obtained from museum specimens and mean values reported in Jameson and Peeters (1988). We used adult weights for calculating mammal biomass and used an average weight for all species in a genus for those species identified to genus. Mean values reported in Dunning (1984) were used to calculate biomass for avian species. Following Reynolds and Meslow (1984), we used one half of the adult weight as an estimate of fledgling and sub-adult weights for birds.

We calculated the frequency and biomass contribution of each prey species by year and created eight subgroups of species or taxonomic groups for analysis based on sample size (individual species comprised >5% of total prey by frequency or biomass in most years, or they were grouped into general class of birds or mammals) and identification criteria (pooled *Spermophilus* and *Tamias*).

Douglas squirrel (*Tamiasciurus douglasii*), American Robin (*Turdus migratorius*), Steller's Jay (*Cyanocitta stelleri*), and Northern Flicker (*Colaptes auratus*) were the most frequently recorded prey species and were analyzed as individual species. Additional, infrequently recorded bird species were lumped into the taxonomic group labeled other birds for analysis. Golden-mantled ground squirrel (*Spermophilus lateralis*), Belding ground squirrel (*Spermophilus beldingi*), and California ground squirrel (*Spermophilus beecheyi*) were lumped into the taxonomic group *Spermophilus* for analysis based on the difficulty of identifying prey remains to species. Shadow chipmunk (*Tamias senex*), long-eared chipmunk (*Tamias quadrimaculatus*), lodgepole chipmunk (*Tamias speciosus*) , and yellow-pine chipmunk (*Tamias amoenus*) occurred in the study area and were lumped into the taxonomic group *Tamias* for analysis due to difficulty in identifying prey remains to species. Additional, infrequently recorded mammal species were lumped in the species group labeled other mammals for analysis. We used chi-square analysis (Sokal and Rohlf 1981) to compare the frequency and biomass of each species or taxonomic group in the diet between years.

Prey Abundance

Point counts (Verner 1985) were used to estimate an index of abundance for bird prey species and Douglas squirrels from autumn 1991 through spring 1994. A total of 312 sample points were established and distributed in grids across Donner Memorial, Burton Creek, Sugar Pine Point, D.L. Bliss, Emerald Bay, and Washoe Meadows California state parks, and across the Angora Creek watershed in the southwestern corner of the Lake Tahoe Basin on land administered by the USDA Forest Service. From a random starting location, each grid was laid out with count points at 300 m intervals along cardinal compass directions. The nearest tree, defined as >2 m in height and >5 cm diameter at breast height (dbh) served as the center of the sample point. Grids were located to provide complete coverage of the watershed or park and Northern Goshawk nesting territories were located within each of the watersheds where prey sampling was conducted. The grids were distributed north to south across the entire study area, with approximately 33 km^2 covered by the prey sampling grids, to provide estimates of prey abundance across the study area.

A random sample of 205 count points was selected from the 312 total points across the study sites for monthly point count sampling to assess the relative abundance of prey species. We attempted to conduct monthly counts at the same 205 points from November 1991 through April 1994. A 7-min point count was conducted at each point count within which the observer recorded all birds and Douglas squirrels heard or seen within distance bands of 0–30 m, 31–60 m, 61–100 m, and >100 m. All counts were conducted within 4 hr after dawn. Approximately 10–15 points were counted per sample day. A total of six observers collected data during the study, with three observers the same throughout the study. All observers were experienced with bird identification and had extensive training on identification and count methods to minimize potential observer bias. Not all points could be counted in each month, largely due to inclement winter weather. Although point-count sampling ended in spring 1994 due to funding constraints, an estimate of Douglas squirrel abundance for spring 1995 was obtained from similar point count sampling conducted at 160 points in six watersheds within the study area, four of which were the same watersheds where we conducted point counts (P. Manley, USDA Forest Service, unpubl. data).

Monthly counts were grouped into four seasonal groups for statistical analysis (autumn = September–November; winter = December–February; spring = March–May; summer = June–August). We calculated an index of abundance defined as the total number of detections per 100 points. We used ANOVA (Sokal and Rohlf 1981) to compare the abundance of each species within each season between years. Lack of data for all four seasons across all 4 yr, and likely differences in detectability among seasons, precluded use of a factorial ANOVA to assess interactions between seasons and years. Scheffe's test was used for multiple comparisons to assess between group differences when ANOVAs indicated significant differences. Only results for species which comprised at least 5% of Northern Goshawk prey items across years are included.

Relationships with Cone Crop Production

Cone crop production was qualitatively assessed during autumn of each year based on a visual assessment of each of the conifer tree species across the study area (Petty et al. 1995). Cone crop production in the study area was classified subjectively based on an index score relative to the maximum cone production observed in autumn 1991. An extra large crop of cones was produced in autumn 1991 on both ponderosa and Jeffrey pines and white and red fir. Cone production was qualitatively scored in each year relative to this baseline with a score ranging from 0–3 (0 = no cone production observed on any conifer species; 1 = low cone production [cone production observed on one conifer species—individual trees producing small number of cones]; 2 = medium cone production [large numbers of cones within one conifer species or small numbers of cones produced across two or more conifer species]; 3 = high cone production [large numbers of cones across two or more conifer species]).

Based on the observed patterns between Northern Goshawk reproduction, frequency and biomass of Douglas squirrel in the diet, and the relative abundance of Douglas squirrels across the 4 yr of the study, we assessed the relationship of these variables to cone crop production measures. We used simple linear regression analysis (Sokal and Rohlf 1981) to assess the relationship between cone crop production and spring Douglas squirrel abundance, and the proportion of Douglas squirrels in the Northern Goshawk diet for both frequency and biomass across years. We used simple linear regression analysis to assess the relationship between the proportion of Northern Goshawk territories successful and spring Douglas squirrel abundance, and the frequency and biomass of Douglas squirrel in the diet across years.

Relationships with Weather

We obtained weather data collected from a monitoring station in the study area near Tahoe City, California, operated by the Western Regional Climate Center. Simple linear regression analysis (Sokal and Rohlf 1981) was used to assess the relationships of the proportion of active and successful goshawk territories, and the number of young produced per successful nest, with three measures of weather across years—total precipitation, number of days with recorded precipitation, and mean temperature. The relationships between reproductive and weather variables were examined across the late-winter and early-spring period (February–April). This timeframe corresponded to the pre-laying period of the reproductive cycle when radio telemetry indicated that females began to reduce their ranging behavior and center their activity within or near their nest stands (Keane 1999).

RESULTS

Northern Goshawk Reproduction

Northern Goshawk reproduction was monitored on 17–24 nest sites each year of the study (Table 1). The proportion of territories occupied varied across years, ranging from 82–100%, although differences were not statistically significant ($\chi^2 = 3.16$, df = 3, P = 0.37). Both the proportion of territories with active nests ($\chi^2 = 12.70$, df = 3, P = 0.01) and successful nests ($\chi^2 = 8.22$, df = 3, P = 0.04) differed significantly between years. The proportion of territories with successful nests was greatest in 1992 (82%), declined to 47% in 1993 and 37% in 1994, and increased to 58% in 1995 (Table 1).

The proportion of active nests that were successful did not differ significantly between years ($\chi^2 = 2.29$, df = 3, P = 0.51), but nonetheless ranged from a low of 62% in 1993 to a high of 82% in 1992. Of the total 13 nest failures recorded over the 4-yr study period, nine attempts failed during the incubation period from undocumented causes. In each of these cases a previously active nest was abandoned during one of the approximately weekly monitoring visits (two failed nests in 1992, 1993, and 1994; three failed nests in 1995). One nest failed during the nestling period, apparently due to Great Horned Owl (*Bubo virginianus*) depredation. One nesting attempt

Table 1. Results of chi-square analysis of annual variation in the proportion of Northern Goshawk nest sites occupied, and with active and successful nests, in the Lake Tahoe region, California, 1992–1995.

Variable	1992	1993	1994	1995	Total	P
N territories	17	17	19	24	77	
N occupied	17	14	16	21	68	0.368
Percent occupied	100	82.4	84.2	87.5	88.3	
N active nests	17	13	9	17	56	0.005
Percent occupied	100	76.5	47.4	70.8	72.7	
N successful nests	14	8	7	14	43	0.042
Percent occupied	82.4	47.1	36.8	58.3	55.8	

TABLE 2. RESULTS OF ANOVA FOR ANNUAL VARIATION IN THE NUMBER OF YOUNG PRODUCED PER TERRITORY AND PER SUCCESSFUL NEST (MEAN ± SD) FOR NORTHERN GOSHAWKS IN THE LAKE TAHOE REGION, CALIFORNIA, 1992–1995.

Variable	1992	1993	1994	1995	P
N young/ Territory [a]	2.0 ± 1.22 A	0.8 ± 0.90 B	0.7 ± 1.00 B	1.0 ± 0.93 B	<0.001
N young/ Successful nest [a]	2.4 ± 0.85 A	1.7 ± 0.50 AB	1.9 ± 0.76 AB	1.6 ± 0.51 B	0.005

[a] Numbers with different letters are significantly different (P <0.05) based on multiple comparisons using Scheffe's test.

failed during the early fledging period in 1994 when the single fledgling disappeared from the nest area 5–10 d after fledging. We observed two females during 1993 incubating eggs for approximately 62–65 d. Each of their clutches contained two eggs, from which we collected a total of three eggs. All three eggs were infertile, suggesting that the females may not have attained a sufficient energetic condition to produce viable eggs (Keane 1999).

The number of young produced per territory (F = 6.28, df = 3, P <0.001) and per successful nest (F = 4.53, df = 3, P = 0.01) differed significantly among years (Table 2). More young were fledged per territory in 1992 than the other 3 yr. The number of young per successful nest differed between 1992 and 1995. We documented one incidence of nestling mortality during the nestling period in addition to the nest predation event described above. The remains of two young from a nest containing three young approximately 4 wk old were found at the base of the nest tree during June of 1992 following an overnight snowstorm with 6 cm of snow. The proximate cause of death could not be determined.

Incubation was initiated in mid-April in 1992, the first week of May in 1993, the fourth week of April in 1994, and the first week of May in 1995. The number of young fledged per successful nest was associated with both the earliest laying date (adj. $r^2 = 0.92$, df = 3, P = 0.03) and the proportion of successful nests fledging three young (adj. $r^2 = 0.96$, df = 3, P = 0.01). Nine of fourteen successful nests (64%) fledged three young in 1992 whereas one of seven (14%) did in 1994. None of the successful nests fledged three young in 1993 or 1995 (Fig. 1). Thus, the number of young per successful nest was greatest in years when breeding was initiated earlier in the spring.

NORTHERN GOSHAWK DIET

A total of 1,058 individual prey items comprised of 12 mammal and 22 bird species were identified (Keane 1999). Mammals comprised 49% by frequency and 58% by biomass of the prey items identified, whereas birds comprised 51% by frequency and 42% by biomass (Tables 3 and 4). The frequency ($\chi^2 = 39.602$, df = 3, P <0.001) and biomass ($\chi^2 = 7.87$,

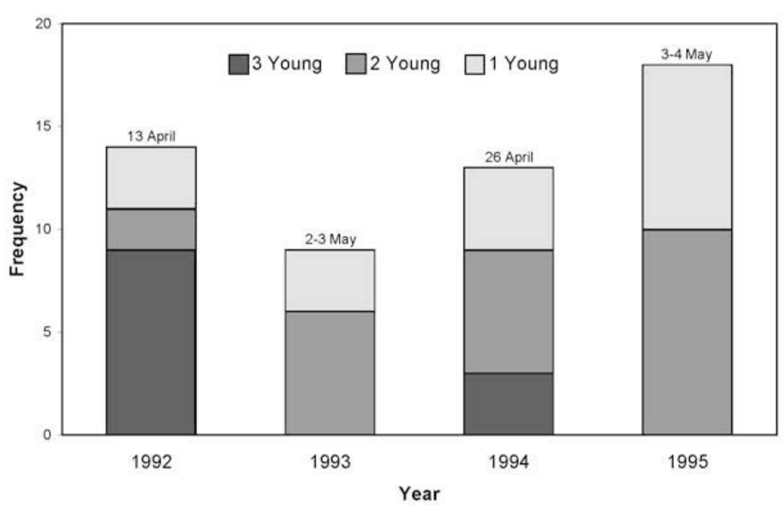

FIGURE 1. Frequency of the number of young produced per nest for successful Northern Goshawk nests in the Lake Tahoe region, California, 1992–1995. Dates indicate initiation of incubation.

TABLE 3. FREQUENCY AND PERCENT OCCURRENCE OF SELECTED SPECIES AND SPECIES GROUPS IDENTIFIED IN PREY REMAINS COLLECTED AT NORTHERN GOSHAWK NESTS IN THE LAKE TAHOE REGION, CALIFORNIA, 1992–1995.

	1992		1993		1994		1995		Total	
Species	N	%	N	%	N	%	N	%	N	%
Douglas squirrel	70	32.6	24	14.3	59	14.1	90	34.9	243	23.0
Spermophilus spp.	40	18.6	40	23.8	44	10.6	27	10.5	151	14.3
Tamias spp.	8	3.7	13	7.7	38	9.1	35	13.6	94	8.9
Other mammals	1	0.5	8	4.8	14	3.4	3	1.2	26	2.4
American Robin	11	5.1	12	7.1	70	16.8	3	1.2	96	9.1
Northern Flicker	26	12.1	25	14.9	77	18.5	30	11.6	158	14.9
Steller's Jay	45	20.9	32	19.0	74	17.7	49	19.0	200	18.9
Other birds	14	6.5	14	8.3	41	9.8	21	8.1	90	8.5
Total mammals	119	55.3	85	50.6	155	37.2	155	60.1	514	48.6
Total birds	96	44.7	83	49.4	262	62.8	103	39.3	544	51.4
Total prey items	215	20.3	168	15.9	417	39.4	258	24.4	1,058	100.0

TABLE 4. BIOMASS OF SELECTED SPECIES AND SPECIES GROUPS IDENTIFIED IN PREY REMAINS COLLECTED AT NORTHERN GOSHAWK NESTS IN THE LAKE TAHOE REGION, CALIFORNIA, 1992–1995.

	1992		1993		1994		1995		Total	
Species	Kg.	%	Kg.	%	Kg.	%	Kg.	%	Kg.	%
Douglas squirrel	16.34	44.6	5.60	19.2	13.77	21.3	21.01	49.9	56.72	32.9
Spermophilus spp.	8.19	22.3	7.70	26.3	9.82	15.2	5.24	12.5	30.95	17.9
Tamias spp.	0.48	1.3	0.79	2.7	2.30	3.6	2.11	5.0	5.68	3.3
Other mammals	0.17	0.4	2.82	9.6	3.42	5.3	0.50	1.2	6.91	4.0
Northern Flicker	3.69	10.1	3.48	11.9	10.93	17.0	4.26	10.1	22.37	13.0
Steller's Jay	3.87	10.6	3.07	10.5	7.47	11.6	5.04	12.0	19.45	11.3
American Robin	0.77	2.1	0.89	3.0	5.26	8.2	0.23	0.6	7.15	4.1
Other birds	3.14	8.6	4.89	16.7	11.54	17.9	3.69	8.7	23.26	13.5
Total mammals	25.18	68.7	16.91	57.8	29.31	45.4	28.86	68.6	100.26	58.1
Total birds	11.48	31.3	12.33	42.2	35.20	54.6	13.22	31.4	72.23	41.9
Total biomass	36.66	21.2	29.24	17.0	64.51	37.4	42.08	24.4	172.49	100.0

df = 3, 0.02 < P < 0.050) of birds and mammals in Northern Goshawk diets varied among years. The frequency of mammals ranged from 60% in 1995 to 37% in 1994 (Table 3). The biomass of mammals in the prey items ranged from highs of 69% in 1992 and 1995 to a low of 45% in 1994 (Table 4).

Overall the Douglas squirrel was the most frequently recorded species, followed by Steller's Jay, Northern Flicker, and *Spermophilus* spp. (Table 3). Douglas squirrel also contributed the most to total biomass, followed by *Spermophilus* spp., other birds, Northern Flicker, and Steller's Jay (Table 4).

The frequency (χ^2 = 58.035, df = 3, P <0.001) and biomass (χ^2 = 14.20, df = 3, P < 0.01) of Douglas squirrel in the diet varied among years, with both being greater in 1992 and 1995 than in 1993 and 1994 (Tables 3 and 4). The frequency of *Spermophilus* spp. (χ^2 = 23.31, df = 3, P < 0.001), *Tamias spp*. (χ^2 = 14.36, df = 3, P = 0.002), other mammals (χ^2 = 10.49, df = 3, P = 0.015), and American Robins (χ^2 = 54.48, df = 3, P <0.001) in Northern Goshawk prey remains varied in a statistically significant manner among years (Table 3). Other than Douglas squirrel, no significant annual differences were found in the proportion of biomass contributions by the other species or species groups.

Prey Abundance

Overall, populations of primary prey species exhibited significant differences in relative abundance and high degrees of variation within and among years (Table 5). Douglas squirrel abundance differed significantly among years during all four seasons based on point counts. Squirrel numbers during autumn were greater in 1992 than in 1993, which in turn were greater than in 1991. During winter, squirrel numbers were greater in winter 1991–1992 than in 1992–1993 or 1993–1994. Similarly, spring squirrel numbers were greater in 1992 than in 1993 or 1994. Squirrel numbers were greater in summer 1992 versus 1993. Squirrel numbers were high in spring 1995 with a relative abundance estimate of 114.4 individuals/100 count points and where detected at 64% of the count points (frequency of detection of 0.64; P. Manley, unpubl. data). Over the 4-yr study, spring Douglas squirrel numbers were high in 1992 and 1995 and low in 1993 and 1994.

Steller's Jay abundance differed significantly among years during each of the four seasons (Table 5). During autumn, Steller's Jay numbers were greater in 1993 than in 1994. Steller's Jay numbers were greater in winter 1991–1992 than during 1992–1993 and 1993–1994. Steller's Jay numbers were greater in spring 1993 than in 1992 or 1994 and greater in summer 1992 than summer 1993. Northern Flicker abundance differed significantly among years during autumn, winter, and summer (Table 5). Northern Flicker numbers were greater in autumn 1991 and 1992 versus 1993, greater in winter 1991–1992 versus 1992–93 and 1993–1994, and greater in summer 1992 versus 1993 (Table 5). American Robin abundance differed significantly among years only during the spring (Table 5). American Robin numbers in spring 1994 were lower than in 1992.

Relationships with Cone Crop Production

High cone crop production (score = 3) was recorded in autumn 1991 and autumn 1994 when ponderosa, Jeffrey, and sugar pines, and white and red firs produced large numbers of cones. No cone crop production (score = 0) was noted in autumn 1992. Cone crop production was low (score = 1) in autumn 1993 when only a low proportion of white fir produced low numbers of cones.

The proportion of territories with successful nests, the number of young per territory, the frequency and biomass of Douglas squirrel in the diet, the winter and spring abundance of Douglas squirrel, and cone production varied in a similar pattern with one another over the four years of the study (Fig. 2). The overall pattern was that each of the aforementioned variables was relatively high in 1992, declined in 1993 and 1994, and then increased again in 1995. The frequency (adj. r^2 = 0.89, df = 3, P =0.04) and biomass (adj. r^2 = 0.85, df = 3, P = 0.05) of Douglas squirrel in the diet varied with spring Douglas squirrel abundance. Spring Douglas squirrel abundance (adj. r^2 = 0.89, df = 3, P = 0.04), and the frequency (adj. r^2 = 0.87, df = 3, P = 0.04) and biomass (adj. r^2 = 0.90, df = 3, P = 0.03) of Douglas squirrels in the Northern Goshawk diet, varied in concordance with cone crop production. Spring Douglas squirrel abundance accounted for a high proportion of the variation observed in the proportion of territories with successful nests between years, although the relationship was not statistically significant (adj. r^2 = 0.71, df = 3, P = 0.10).

Relationship with Weather

Total precipitation recorded during late-winter and early-spring differed by a factor of about four among years (Table 6). Total precipitation was lower during 1992 and 1994, about 50% greater in 1993, and about 300% greater in 1995. In addition

TABLE 5. RELATIVE ABUNDANCE (N/100 COUNT POINTS) AND FREQUENCY OF OCCURRENCE OF SELECTED NORTHERN GOSHAWK PREY SPECIES ESTIMATED FROM POINT COUNTS IN THE LAKE TAHOE REGION, CALIFORNIA, FALL 1991 THROUGH SPRING 1994. ANOVA WAS USED TO TEST FOR ANNUAL VARIATION IN SPECIES RELATIVE ABUNDANCE WITHIN SEASONS AMONG YEARS

Species	1991–92			1992–93			1993–94			
Season	Mean[a]	SE	Frequency	Mean	SE	Frequency	Mean	SE	Frequency	P
Douglas Squirrel										
Fall	147.4 A	10.88	0.78	386.1 B	8.03	0.95	272.6 C	7.37	0.91	<0.0001
Winter	125.8 A	5.13	0.69	61.2 B	5.51	0.44	84.1 B	6.68	0.47	<0.0001
Spring	132.9 A	4.63	0.74	48.9 B	3.13	0.36	55.1 B	4.72	0.43	<0.0001
Summer	292.7	6.78	0.94	156.8	5.57	0.73		--[b]		<0.0001
Steller's Jay										
Fall	137.7 AB	9.84	0.76	165.9 A	7.16	0.71	112.6 B	6.48	0.53	<0.0001
Winter	74.4 A	5.03	0.43	30.5 B	6.73	0.20	10.5 B	2.91	0.07	<0.0001
Spring	162.4 A	5.89	0.75	200.0 B	8.01	0.73	132.4 A	9.73	0.56	<0.0001
Summer	165.0	5.72	0.79	126.7	4.82	0.68		--		<0.0001
Northern Flicker										
Fall	42.1 A	5.70	0.37	30.5 A	2.41	0.24	20.6 B	1.96	0.18	<0.0001
Winter	11.5 A	1.58	0.10	0.9 B	0.62	0.01	1.4 B	0.83	0.01	<0.0001
Spring	44.0	2.48	0.39	38.4	2.66	0.31	36.7	4.38	0.27	0.1933
Summer	46.7	3.36	0.36	28.9	2.36	0.23		--		<0.0001
American Robin										
Fall	33.3	8.69	0.20	20.7	6.49	0.09	23.6	2.85	0.16	0.5933
Winter	2.9	1.10	0.02	0.9	0.62	0.01	0.7	0.48	0.01	0.1878
Spring	79.2 A	5.25	0.49	64.3 AB	6.29	0.38	53.5 B	5.45	0.34	0.0227
Summer	47.8	3.06	0.36	52.5	3.40	0.37		--		0.3024

[a] Numbers with different letters are significantly different ($P < 0.05$) based on multiple comparisons using Scheffe's test.
[b] Data not available for this sample period.

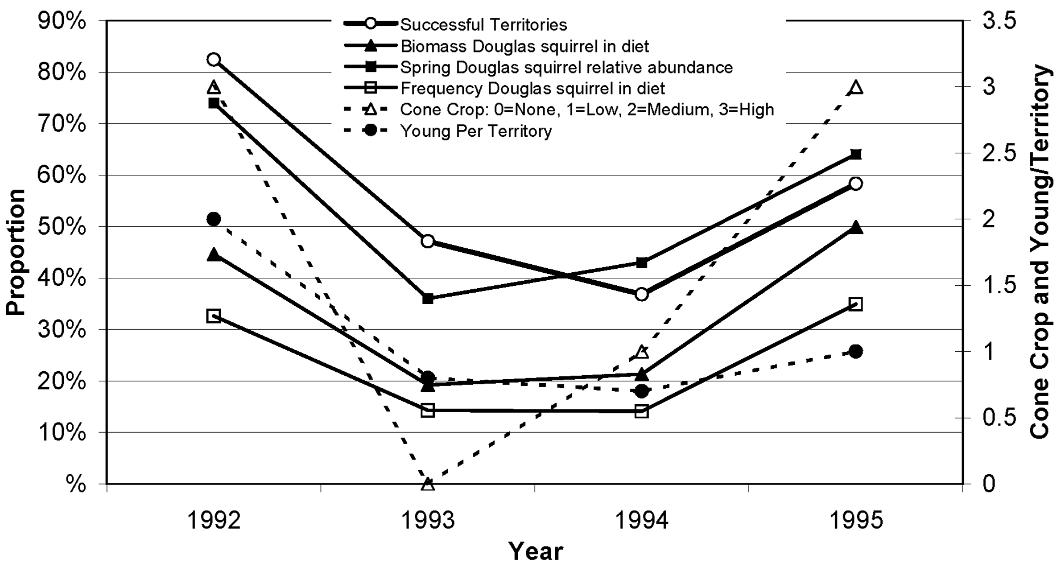

FIGURE 2. Relationship among percent nest success, number of young fledged per territory, percent Douglas squirrel recorded in Northern Goshawk diets by frequency and biomass, spring Douglas squirrel abundance based on percent of counts where squirrels were recorded, and an index of cone crop production for northern goshawks in the Lake Tahoe region, California, 1992–1995.

TABLE 6. TEMPERATURE AND PRECIPITATION RECORDED DURING THE PRE-INCUBATION PERIOD (FEBRUARY–APRIL) FOR NORTHERN GOSHAWKS IN THE LAKE TAHOE REGION, CALIFORNIA, 1992–1995.

	Year			
Variable	1992	1993	1994	1995
Mean temperature (°C)	4.4	1.7	2.6	1.3
Total precipitation (cm)	18.7	33.0	20.7	66.2
Days with precipitation (≥0.025 cm)	22	28	24	33

to high total amounts, snow and rain storms continued through May and mid-June in 1995 (J. Keane, pers. obs.). Late-winter and early-spring mean temperatures were higher in 1992 than in the other three years (Table 6). The number of young produced per successful nest was positively associated with warmer late-winter and early-spring mean temperature (adj. $r^2 = 0.999$, df = 3, P = <0.001; Table 7).

DISCUSSION

Northern Goshawks in our study area exhibited significant annual variation in reproduction. We propose that this annual variation was the result of both prey and weather factors that determined whether Northern Goshawks were able to attain the necessary energetic condition required for successful

TABLE 7. RESULTS OF REGRESSION ANALYSES OF THE PROPORTION OF NORTHERN GOSHAWK TERRITORIES WITH ACTIVE AND SUCCESSFUL NESTS, AND THE NUMBER OF YOUNG PER SUCCESSFUL NEST, AGAINST TEMPERATURE AND PRECIPITATION VARIABLES RECORDED DURING THE PRE-INCUBATION PERIOD (FEBRUARY–APRIL) IN THE LAKE TAHOE REGION, CALIFORNIA, 1992–1995.

	Proportion of territories active		Proportion of territories successful		Young/successful nest	
Weather variables	adj. r^2	P	adj. r^2	P	adj. r^2	P
Mean temperature	-0.060	0.459	0.131	0.351	0.999	<0.001
Total precipitation	-0.484	0.895	-0.496	0.949	0.320	0.261
Days with precipitation	-0.432	0.786	-0.411	0.757	0.662	0.120

reproduction. More specifically, annual variation in Northern Goshawk reproduction in the study area was associated with variation in both Douglas squirrel abundance and late-winter and early-spring temperature. In turn, annual variation in Douglas squirrel abundance was associated with cone crop production patterns.

Northern Goshawk reproduction was greatest in terms of both the proportion of territories with successful nests and number of young produced per successful nest in 1992. The success of 1992 was associated with high cone crop production in autumn 1991 and increased relative abundance of Douglas squirrels during winter and spring. The abundance of Douglas squirrels was manifest through greater frequency and biomass of squirrels in Northern Goshawk diets. Warmer temperatures in late winter and early spring were also positively associated with nesting success. Northern Goshawk reproduction was lower in both 1993 and 1994, with each of these breeding seasons preceded by low cone crop production and lower winter and spring Douglas squirrel abundance relative to 1992. Late-winter and early-spring mean temperatures preceding each of these breeding seasons were also lower relative to 1992.

The proportion of territories with successfully reproducing pairs increased in 1995 following high cone crop production in autumn 1994, increased relative abundance of Douglas squirrels in spring 1995 and increased frequency and biomass of squirrels in the diet. However, relative to 1992, the proportion of successful pairs was lower, fewer young were produced, and birds initiated laying 3 wk later in 1995. We think that these differences were a result of low late-winter and early-spring temperatures in 1995. Mean temperatures in late winter and early spring 1995 were the lowest that occurred during the study. Additionally, total precipitation during the preceding winter and spring was 300% greater, and high amounts of precipitation occurred in March and April during 1995 relative to 1992. Thus, we hypothesize that weather factors may have interacted to moderate the effect of cone crop production on Northern Goshawk reproduction in 1995 relative to 1992. We conclude that annual variation in Northern Goshawk reproduction during our study in this region of the Sierra Nevada was a result of an interaction between food and weather. Reproduction was greatest in years following high cone crop production, which positively affected Douglas squirrel abundance, and mild late winter and early springs with higher temperatures and low total precipitation.

The high rates of annual variation in reproduction we observed are similar to those reported from other studies (McGowan 1975, Bloom et al. 1986, DeStefano et al. 1994a, Doyle and Smith 1994, Sulkava et al. 1994, Erdman et al. 1998), indicating that high rates of annual variation in Northern Goshawk reproduction is a consistent pattern across their range. Studies from northern forest systems have demonstrated that annual variation in Northern Goshawk reproduction is linked with cycles in key prey species (snowshoe hare and galliformes) occurring at periodic intervals (McGowan 1975, Doyle and Smith 1994, Sulkava et al. 1994, Erdman et al. 1998). Weather factors have also been shown to affect Northern Goshawk reproduction. Kostrzewa and Kostrzewa (1990) reported a negative correlation between the proportion of pairs laying eggs and March–April precipitation, while the number of fledglings per successful nest was positively correlated with April–May temperature and negatively correlated with the number of days with precipitation in May for a Northern Goshawk population in Germany. Sulkava et al. (1994) reported a negative correlation between the initiation of nest building and February–March temperature for Northern Goshawks in western Finland. Northern Goshawk populations in temperate western North American forests also exhibit high rates of annual variation in reproduction. Bloom et al. (1986) reported that the proportion of territories active in a year ranged from 27–86% during 1981–1983 based on a sample of monitored territories throughout the Sierra Nevada and White Mountains in California. Similarly, the proportion of territorial pairs laying eggs varied from 22–86% on the Kaibab Plateau in Arizona during the 1990s (Reynolds and Joy 1998). However, to date no studies have directly addressed both the biotic and abiotic environmental factors associated with documented patterns of annual variation in Northern Goshawk reproduction in these systems. Our results indicate that both biotic and abiotic factors are associated with annual variation in Northern Goshawk reproduction and that interactions among multiple factors likely determine whether individuals can successfully reproduce.

Northern Goshawks are resident in the Lake Tahoe region, exhibiting increases in home range sizes by a factor of three-four during winter relative to the breeding season, and appear to initiate breeding in February when females concentrate their activity in the nest stand (Keane 1999). Initiation of egg-laying varied over approximately a 3-wk period ranging from mid-April in 1992 to early-May in 1993 and 1995. It is during this late-winter and early-spring period before egg-laying that females must accumulate sufficient body reserves to reproduce successfully. The accumulation of body reserves is affected by both the energetic condition of the birds at the end of winter as they initiate breeding and their ability to acquire needed reserves prior to laying (Newton 1993). Mean low temperatures during this period ranged from -2.2–4.0 C. Results from laboratory studies of Northern Goshawk basal metabolic rates indicate that they have a lower critical temperature of approximately 1.7 C (J. Keane, unpubl. data). Thus, at this time of year goshawks may be experiencing increased energetic demands for thermal requirements in addition to the needed reserves to produce eggs successfully. We suggest that consideration of the timing of these increased energy requirements in conjunction with the natural history of key prey species explains the patterns we detected between Northern Goshawk reproduction, diet, prey abundance, cone crop production and temperature.

Of the prey species comprising at least 5% of prey items or biomass in most years of the study, American Robins and Northern Flickers are facultative migrants at high elevations in the Sierra Nevada and in the study area (Grinnell and Miller 1944, Beedy and Granholm 1985, Gaines 1988, Keane 1999). Both species forage to a large extent on the ground and hence most individuals emigrate from the higher elevations and apparently move up or down in altitude and north or south in response to snow cover, with large numbers of individuals of both species present in the lower elevation oak woodlands during winter (Block 1989, J. Keane, pers. obs.). Steller's Jays apparently are partial migrants at higher elevations in the Sierra Nevada, with some segment of the population emigrating in the winter and others being resident (Grinnell and Miller 1944). Golden-mantled and Belding ground squirrels hibernate during winter, with their active period being later in the year with increasing elevation in the Sierra Nevada (Bronson 1979). Golden-mantled ground squirrels became active in mid-March following the mild winter and early meltout in 1992. Conversely, they did not appear to become active till mid- to late-April in years following heavy snow and lingering snowpacks (J. Keane, pers. obs.).

In contrast to breeding season studies of Northern Goshawk diets in other North American forest systems (Boal and Mannan 1994, Doyle and Smith 1994, Reynolds et al. 1994, Erdman et al. 1998, Andersen et al. 2004), galliformes or lagomorphs did not constitute a significant proportion of the breeding period diet in our study area. Since male goshawks are the primary prey providers during the breeding period, perhaps during winter, when the larger females are foraging, galliformes and lagomorphs comprise a larger proportion of the diet. On one occasion we flushed an adult female off of a snowshoe hare kill during January (J. Keane, pers.obs.). The Lake Tahoe race of the snowshoe hare (*Lepus americanus tahoensis*) was the only lagomorph in the study area and is listed as a mammalian subspecies of special concern in California (Williams 1986). Little information exists regarding their distribution and abundance, although they appear to be relatively uncommon (Williams 1986). Additionally, Blue Grouse (*Dendragapus obscurus*) abundance appeared to be low based on our point count sampling (Keane 1999). Thus, the apparent low abundance of galliformes and lagomorphs in our study area may be the reason why these two prey species groups were not associated with annual variation in reproduction or frequently recorded in the diet in our study area.

Douglas squirrels are resident and active year round (Ingles 1965, Smith 1968), and are available during the late-winter and early-spring period when Northern Goshawks experience increased energy demands necessary for successful reproduction. Douglas squirrels feed primarily on seeds and fungi, and their populations vary annually in response to cone crop production, as manifested through increased over-winter survival and both earlier and greater reproduction in springs following years of high cone crop production (Smith 1968, Sullivan and Sullivan 1982). Our data indicate that Northern Goshawks respond functionally, as evidenced through increased frequency and biomass of squirrels in the diet, and numerically, as evidenced by higher reproduction, to increased Douglas squirrel populations following high cone crop production. This relationship in turn appears to be affected by an interaction with temperature. Colder temperatures, as well as greater precipitation, during late winter and early spring likely affect Northern Goshawk energetic dynamics through increased energetic stress, and may influence prey availability by reducing hunting success or by directly affecting the migration, hibernation, and abundance of prey. Thus, considering the energetic strategy of raptors, our observations on diet, prey abundance, and weather, the data suggested that Northern Goshawk reproduction during our study was associated with both specific prey (Douglas squirrel) and temperature factors. If true, Northern Goshawk reproduction in this region of the Sierra Nevada should be greatest, in terms of the proportion of territories with successful nests and young produced per successful nest, in years following high cone crop production and mild late-winter and early-spring weather, such as we observed in 1992. Our observational study was conducted over a 4-yr period that included annual variation in prey, weather, and cone crop production, along with various combinations of each of the factors. We recommend that observations be continued over longer time periods and in other study areas to assess if the patterns regarding the importance of specific prey species and weather factors during the pre-laying period are generally supported. Additionally, carefully crafted experimental studies might be used to assess the degree to which Northern Goshawks are energy limited during the pre-laying period.

Conservation Implications for Northern Goshawk Management in the Sierra Nevada

Prey abundance is a primary environmental limiting factor influencing raptor populations such that densities can vary in concordance with variation in prey abundance across landscapes (Newton 1986). Managing forests to provide prey is recognized as a primary need for managing habitat for Northern Goshawks (Kenward and Widén 1989, Reynolds et al. 1992, Widén 1997). Reynolds et al. (1992) recommended managing forests in the southwestern US as interspersed mosaics of structural stages with the goal to provide for a diversity of habitat for Northern Goshawk prey. Although we recorded a total of 22 bird and 12 mammal species in the diets of Northern Goshawks in our study area, our results suggest that the Douglas squirrel may be a particularly important prey species associated with annual variation in Northern Goshawk reproduction. This evidence suggests that management of Northern Goshawk foraging habitat in this study area, while needing to consider the habitat requirements of the full suite of other prey species, might be weighted towards managing habitat for Douglas squirrels. This would seem to be an appropriate additional focus for management because it targets factors that directly affect Northern Goshawk fitness. Further information on Northern Goshawk habitat and prey use patterns, and their demographic response, both in reproduction and survival, to variation in forest structure and composition is needed to assess conservation strategies.

Observational and experimental studies have demonstrated that Douglas squirrel, as well as the closely related red squirrel (*Tamiasciurus hudsonicus*), populations vary in concordance with cone crop production (Smith 1968, 1970, Kemp and Keith 1970, Sullivan and Sullivan 1982, Buchanan et al. 1990, Sullivan 1990). A greater proportion of females breed, litter sizes are larger, and over-winter survival is greater in response to cone crop production (Smith 1968, Sullivan and Sullivan 1982). Douglas squirrels are territorial with territory size inversely related to food availability (Smith 1968). Territories are a critical resource in that they provide the mechanism for squirrels to survive over the winter by caching food (cones and fungi) and squirrels without a territory experience high mortality (Smith 1968). Kemp and Keith (1970) proposed that red squirrel territories differ in quality across a continuum, with high-quality territories occupied year-round and able to provide sufficient food sources for individuals to survive through intervals between cone crops. They noted that high-quality territories encompassed mature conifer trees capable of cone production. These observations suggest that one goal of Douglas squirrel habitat management in the Sierra Nevada should be to target vegetative structure and composition that can provide high quality squirrel habitat as measured by survival and fecundity. Currently no data are available relating habitat structure and composition to habitat quality for Douglas squirrels in the Sierra Nevada.

Factors related to cone crop production dynamics should be a management focus when considering management of habitat for Douglas squirrels. Cone crop production differs in both magnitude and frequency across tree-size classes and between conifer species (Fowells and Schubert 1956, Burns and Honkala 1990). Cone production is greater by mature conifers in terms of both magnitude (number of cones per tree) and frequency (periodicity of cone production) relative to younger, smaller conifers. Further, seeds from different tree species differ in their caloric value (Smith 1968). Therefore, changes in tree size distributions and species composition may affect cone crop production dynamics and related trophic dynamics. We hypothesize that cone crop production by ponderosa and Jeffrey pines, because of the large size of their seeds, may be particularly important in influencing the absolute amounts of primary productivity generated through cone crop production in the forests in our study area.

Northern Goshawks are distributed across a wide elevational gradient and across several forest vegetation types in the Sierra Nevada (Zeiner et al. 1990). Further work is needed to determine the degree to which the results of our study are applicable across the full range of the species in the Sierra Nevada. Specifically, comparable studies are needed to assess ecological relationships in west side mixed conifer forests between 750–1,500 m elevation and in eastside pine forests. Both of these forest types have been highly affected by human management activities (Franklin and Fites-Kaufmann 1996). Douglas squirrels reach the edge of their distribution in the eastern Sierra Nevada and work is needed to assess their importance to Northern Goshawks in the relatively drier forests of the eastside in order to improve our ability to manage for prey habitat requirements. In west side mixed-conifer forests, presumably, winters would be relatively less severe but perhaps more variable at lower elevations and snow melt should occur earlier in the spring. This would make prey species affected by snow cover (American Robins, Northern Flickers, and golden-mantled and Belding ground squirrels) more available. Further, additional species (e.g., western gray squirrel [*Sciurus griseus*] and brush rabbit [*Sylvilagus bachmani*]) may be available to Northern Goshawks at these elevations, although the ability of male Northern Goshawks to regularly capture adult gray squirrels because of their large size has been questioned (Kenward 1996).

Increasing emphasis has been focused on the need to link species-based perspectives with ecosystem and landscape level perspectives that consider ecological processes in order to advance conservation science and improve ecological understanding (Karr et al. 1992, Noss et al. 1997, Thomas 1999). Seed production has been demonstrated to affect numerous species and ecological interactions in forest systems (Smith 1970, Smith and Balda 1979, Mattson et al. 1992, Benkman 1993, Pucek et al. 1993, Ostfeld et al. 1996, Wolff 1996, this study). Thus, cone crop production might be viewed as an important bottom-up trophic effect in forested systems that generates pulses of primary productivity at irregular intervals into these systems. In turn these pulses of primary productivity may affect species populations throughout forest communities through both direct and indirect interactions. Understanding factors that generate population dynamics for species in fluctuating or periodic environments have implications for population viability assessments (Beissinger 1995).

The structure and composition of forests in the Sierra Nevada have been significantly modified as a result of human management activities in the past 150 yr. Timber harvest and fire suppression practices have resulted in a reduction in the proportion of late-seral and old-growth forests, reduced the number of large trees, and reduced the pine component and increased the fir component throughout the range (McKelvey and Johnston 1992, Franklin and Fites-Kaufmann 1996). Given that the magnitude and frequency of cone production increases with increasing conifer size and that the energy value of seeds differs between tree species, changes in the distribution, abundance, and species composition of large trees and mature and old-growth vegetation classes would be predicted to affect cone crop production dynamics. These changes may have implications for a number of additional species and interspecific interactions in these systems (Bock and Lepthien 1976, Zielinski et al. 1983, Spencer 1987, Benkman 1993, Reitsma et al. 1990, Darveau et al. 1997, Ruggerio et al. 1998). Ecologists have recognized the increasing need to meld single-species conservation approaches with ecosystem- and landscape-scale perspectives in order to more effectively address conservation issues (Franklin 1993, Harris et al. 1996, Noss et al. 1997). Detailed autecological studies of focal species of concern, such as the Northern Goshawk, are essential and can begin to provide an understanding of environmental factors relevant to the conservation of both the species and the structure and function of the system (Woolfenden and Fitzpatrick 1991, James et al. 1997, Derrickson et al. 1998).

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