Research Article

Reproductive Responses of Northern Goshawks to Variable Prey Populations

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ABSTRACT Developing comprehensive conservation strategies requires knowledge of factors influencing population growth and persistence. Although variable prey resources are often associated with fluctuations in raptor demographic parameters, the mechanisms of food limitation are poorly understood, especially for a generalist predator like the northern goshawk (*Accipiter gentilis*). To determine the reproductive responses of goshawks to variable prey populations, we evaluated 823 goshawk breeding opportunities on the Kaibab Plateau, Arizona, USA, during 1994–2002. Concurrently, density was estimated for 4 prey species (2 avian, 2 mammalian). We explored the relationship between goshawk reproduction and prey density at one temporal scale (year) and 2 spatial scales (study area, forest type). Prey density for all 4 species combined accounted for 89% of the variation in goshawk reproduction within the entire study area ($P < 0.001$), 74% in mixed conifer forest ($P = 0.003$) and 85% in ponderosa pine (*Pinus ponderosa*) forest ($P < 0.001$). We found that an incremental increase in prey density resulted in a greater increase in goshawk reproduction in ponderosa pine forest than in mixed conifer forest, suggesting that the denser structural conditions of mixed conifer forest may have reduced prey availability. Red squirrel (*Tamiasciurus hudsonicus*) density explained more annual variation in goshawk reproduction within the study area ($r^2 = 0.87$, $P < 0.001$), mixed conifer forest ($r^2 = 0.80$, $P = 0.001$), and ponderosa pine forest ($r^2 = 0.85$, $P < 0.001$) than did any other individual species. Although certain prey species were more strongly correlated with fluctuations in goshawk reproduction than were others, the high model selection uncertainty and the strong relationship between total prey density and number of goshawk fledglings produced indicated that alternate prey species were readily substituted for one another. Therefore, conservation strategies concerned with the status of goshawk populations should incorporate forest management practices that increase the abundance, diversity, and availability of prey resources. (JOURNAL OF WILDLIFE MANAGEMENT 71(7):2274–2283; 2007)

Recently, concern has developed that northern goshawk (*Accipiter gentilis*) populations are declining due to reduced habitat quality and increased habitat loss and fragmentation (Speiser and Bosakowski 1984, Reynolds et al. 1992, Widén 1997). The goshawk is a large raptor (mass: F, 860–1,364 g; M, 631–1,099 g) that occupies forested habitat throughout the Holarctic (Squires and Reynolds 1997). Although goshawks are habitat generalists that use a variety of forest types, ages, structural conditions, and successional stages (Squires and Reynolds 1997), they tend to nest and hunt in mature and old forests with sufficient space beneath the forest canopy to enable flight and access to prey (for review see Reynolds et al. 2006). As a result, goshawk habitat requirements potentially conflict with forest management practices such as timber harvests and fire suppression that alter forest compositional and structural conditions beneficial to goshawks and their prey species. In an attempt to prevent population declines, 3 petitions were filed during the 1990s with the United States Fish and Wildlife Service to list the northern goshawk as threatened under the Endangered Species Act (U.S. Fish and Wildlife Service 1998), but each petition was denied due to insufficient data

on the status of goshawk populations. The status of goshawk populations continues to be the focus of considerable conservation interest (Andersen et al. 2004). An effective conservation strategy for the goshawk requires an understanding of the processes that limit population dynamics, especially how these processes vary over space and time.

Reproductive rates are an essential component of population growth and persistence (Sæther and Bakke 2000). Potential factors limiting reproductive output include the availability of nest sites, food resources, and predation rates (Newton 1979, Reynolds et al. 2006). Food supply is often recognized as the ultimate limiting factor of reproduction because variation in the abundance of food may determine nest-site quality, the ability of females to produce eggs, the number of eggs produced, and nestling survival rates (Newton 1998). Several studies have established a close association between food abundance and measures of goshawk reproduction (Wikman and Lindén 1981, Doyle and Smith 2001, Salafsky et al. 2005, Keane et al. 2006, Wiens et al. 2006). Further, experimental manipulations of goshawk food supply (Ward and Kennedy 1996, Dewey and Kennedy 2001) found that supplemental food may have reduced predation rates on nestlings by enabling adults to spend more time in defense of the nest, particularly when background prey levels were low. Thus, the abundance of food may determine the number of young contributed to future populations. Ultimately, fewer fledglings are pro-

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duced during periods of low food resources (Doyle and Smith 2001, Salafsky et al. 2005, Keane et al. 2006), suggesting that food is an important factor regulating goshawk populations.

Much of our current knowledge on the relationship between food supply and raptor demographic parameters is from information on species with specialized diets (Newton 1998). Identifying the responses of goshawks to variation in food resources will improve our understanding of food limitation in a generalist predator (Rutz and Bijlsma 2006, Squires and Kennedy 2006). Evidence suggests that relative consistency in the abundance of important prey species may stabilize reproductive rates of predators; species dependent on cyclical prey tend to exhibit greater fluctuations in reproduction than species with stable prey populations (Korpimäki 1988, Doyle and Smith 2001, Krüger and Lindström 2001). However, the magnitude of effects from a reduced prey base may be mitigated by a diverse diet. Fourteen species of birds and mammals regularly contribute to goshawk diets in the southwestern United States (Boal and Mannan 1994, Reynolds et al. 1994). Reynolds et al. (1992) hypothesized that this diverse diet may stabilize goshawk reproductive rates. If populations of primary prey species vary asynchronously, goshawks may obtain adequate food for reproduction by switching to more abundant prey species. Further, because the abundances of alternate prey species vary by habitat, variation in predator reproductive rates is often associated with the spatial distribution of prey resources (Newton 1998). Spatial variation in prey resources is a function of prey abundance and accessibility, and prey accessibility ultimately depends on detection and capture probabilities, which vary with foraging habitat characteristics. Thus, if environmental conditions such as forest composition and structure influence prey accessibility, then prey resources within each forest type may limit goshawk reproduction.

The purpose of this study was to ascertain how goshawk prey abundance varies with forest type and how changes in the abundance of prey populations influence goshawk reproduction. Given the main objective of the study, we first estimated how the abundance of goshawk prey species varied annually between forest types. Second, we explored the extent to which goshawk reproduction covaried with annual and forest type changes in prey abundance. Third, we explored the contribution of individual prey species and groups of prey species to determine which species are most highly correlated with variation in goshawk reproduction. We distinguished 2 hypotheses associated with 2 potential outcomes: 1) goshawk reproduction is prey-species specific as indicated by a close relationship between goshawk reproduction and a single prey-species predictor variable; or 2) goshawk reproduction is limited by populations of alternate prey species that can be readily substituted for one another, as indicated by the close relationship between goshawk reproduction and the total-prey predictor variable.

STUDY AREA

The 1,285-km² study area included the North Kaibab Ranger District of the Kaibab National Forest above 2,182 m elevation on the Kaibab Plateau in northern Arizona, USA. The Kaibab Plateau was a forested island surrounded by shrub-steppe desert (Rasmussen 1941). The eastern, southern, and western edges of the plateau were formed by steep escarpments, which created distinct boundaries between the shrub-steppe desert and the forested study area. In contrast, gradual slopes formed the northern edge of the plateau, creating an indistinct boundary. Mixed conifer (*Pinus ponderosa*, *Abies concolor*, *Pseudotsuga menziesii*, *Populus tremuloides*) forests occupied 275 km² at the highest elevations of the study area, which gradually transitioned to 714 km² of ponderosa pine (*Pinus ponderosa*) forests, and 106 km² of pinyon–juniper (*Pinus edulis–Juniperus* spp.) woodlands with descending elevation. Of the dominant forest classes on the plateau, mixed conifer forest covered approximately 21% and ponderosa pine forest covered approximately 56% of the study area (Joy 2002). Quaking aspen (*Populus tremuloides*) forests and pinyon–juniper woodlands each comprised <10% of the study area so they were not considered dominant vegetation classes. See Reynolds et al. (1994, 2005) for further detail on the study area and its management history.

METHODS

Goshawk Reproduction

To determine annual goshawk reproductive rates, we conducted nest visits during 1994–2002. Because goshawks may use >1 nest within a territory among breeding years (Reynolds et al. 1994, Reynolds and Joy 2006), we visited all nest structures annually in spring to determine the territory occupancy status. A territory is the area (approx. 11 km²) defended by a pair of goshawks during the breeding season (Reynolds et al. 1994). If we did not locate an active nest (nest containing eggs or young) within an existing territory, systematic foot searches and broadcast surveys were conducted until we found an active nest or thoroughly searched the entire territory (Joy et al. 1994, Reynolds et al. 2004, Reynolds and Joy 2006). We also conducted systematic foot searches during May through August to locate new territories. Because we located new territories each year, the number of territories under study increased annually (Reynolds and Joy 2006). To ensure equal detection of breeding attempts and an unbiased count of fledglings produced per nest, we only used goshawk territories that were monitored for the entire breeding season in our analyses. To determine nest status and goshawk reproduction, we visited all active nests weekly throughout the breeding season. We counted goshawk offspring in the nest 7–10 days prior to fledging or from the ground after fledging. We estimated goshawk productivity annually as the mean number of fledglings produced per territory under study.

Prey Sampling

Count-indices.—We conducted annual count-indices of prey species from 1994 through 2002. Count-indices (counts) were tallies of prey species seen or heard while observers walked meandering transects within the study

area. For analyses, we pooled counts over observers and stratified the counts by forest type. Observers conducted counts on random days throughout the goshawk breeding season. Counts were initiated at different times throughout the day and conducted for variable amounts of time. To account for differences in the duration and number of counts conducted per year, we standardized the number of individuals counted for each prey species by the amount of time spent counting, resulting in estimated indices of prey abundance. Observers conducted counts simultaneously with activities such as goshawk nest searching, and ceased counting during inclement weather. All individuals seen or heard during counts were identified and recorded by species, but the observers did not estimate detection distances. We collected count data on a subset of common goshawk prey species, the 2 avian and 6 mammalian species that comprised the majority of goshawk diets on the Kaibab Plateau during 1990–1992 (Boal and Mannan 1994, Reynolds et al. 1994).

Distance sampling.—To estimate prey abundance, the same observer (Salafsky) conducted distance sampling along line transects (Buckland et al. 1993) from 1999 through 2002. We placed 60 500-m transects randomly in the study area within a priori identified vegetation-based strata. We partitioned strata by dominant forest types (mixed conifer or ponderosa pine) and classified sites based on elevation in addition to tree species composition and density. To estimate prey abundance by stratum, 30 transects were randomly established within each forest type and encompassed similar structural elements and silvicultural treatments. Salafsky sampled transects in groups of 4 per day and the sampling order of the groups was determined randomly. Daily sampling began 0.5 hours after sunrise and was completed within 3 hours. Salafsky did not conduct sampling during inclement weather (rain, winds >24 km/hr) due to reduced probability of prey detection. Prey seen or heard during sampling were identified to species and Salafsky measured the perpendicular distance from the detected animal to the transect line with a laser rangefinder (accurate to ±1 m). We collected data on the same prey species from the counts, which included black-tailed jackrabbit (*Lepus californicus*), cottontail rabbit (*Sylvilagus* spp.), golden-mantled ground squirrel (*Spermophilus lateralis*), Kaibab squirrel (*Sciurus aberti kaibabensis*), northern flicker (*Colaptes auratus*), red squirrel (*Tamiasciurus hudsonicus*), rock squirrel (*Spermophilus variegatus*), and Steller's jay (*Cyanocitta stelleri*).

Data Analysis

We based goshawk productivity on the number of fledglings produced per territory under study. We classified territories based on ≥1 breeding attempt on the territory, the identity of the adult birds, and the mean interterritory distance (3.8 km; Reynolds et al. 2005). A high density of territories, a tendency for individuals to retain the same territory for life, and a delayed age at first breeding (Wiens and Reynolds 2005) suggests that the breeding habitat on the Kaibab Plateau was saturated. Further, given infrequent breeding attempts on low-quality territories and the difficulties

associated with locating nonbreeding goshawks, intensive searches over many consecutive years were needed in saturated breeding habitats to categorize territories unequivocally as unoccupied by goshawks (Reynolds et al. 2005). By including all territories instead of only those that were confirmed active or occupied, we accounted for all potential breeding opportunities and the full range of variability in the reproductive qualities of goshawk territories. To determine goshawk productivity by forest type, we classified goshawk territories as either mixed conifer or ponderosa pine based on the proportional predominance of each forest type within an 11-km^2 area around the territory center. We determined forest types from a grid model of dominant vegetation types that was created from the interpretation of 1997 Landsat TM imagery and concurrent field sampling (Joy 2002). We determined territory centers based on the mean distance between nests within a territory, weighted by the total number of years each nest within the territory was active (Joy 2002). We determined goshawk productivity for each forest by dividing the total number fledglings produced per forest type by the number of territories assigned to each forest type.

We analyzed distance sampling data using program DISTANCE, Version 3.5 (Thomas et al. 1998). Reliable estimates of density from distance sampling data depend on 3 critical assumptions: 1) all individuals on the transect line were detected, 2) all individuals were detected at their initial location, and 3) all distances were measured accurately (Buckland et al. 1993). We designed data collection methods to meet these assumptions.

We used data collected with both sampling methods during 1999–2002 to estimate the empirical relationship between distance-based density estimates and relative abundances from the counts. Because variable distance sampling estimates a detection function that compensates for differences in detection probabilities among species, forest types, and distances from transects (Buckland et al. 1993), density estimates based on distance data are not confounded by factors affecting detectability and thus are representative of the true population size. In contrast, prey abundance indices are unreliable as estimates of abundance because count methodology does not account for differences in detection probabilities (Rosenstock et al. 2002). Therefore, to obtain the most accurate estimates of prey abundance, we regressed the square roots of the annual count data on concurrent density estimates from the distance sampling data to develop a calibration equation for each prey species by forest type (PROC REG, SAS Institute 1999). We applied the square root transformation to the count data to correct for heterogeneity of variance, which also improved the fit to a linear model. After preliminary examination of the data, we excluded the counts conducted in 2000 from the subsequent calibration analyses because few counts were conducted in this year so the prey abundance indices from 2000 were not comparable to the other years. We predicted individual prey-density estimates for mixed conifer and ponderosa pine forest annually from
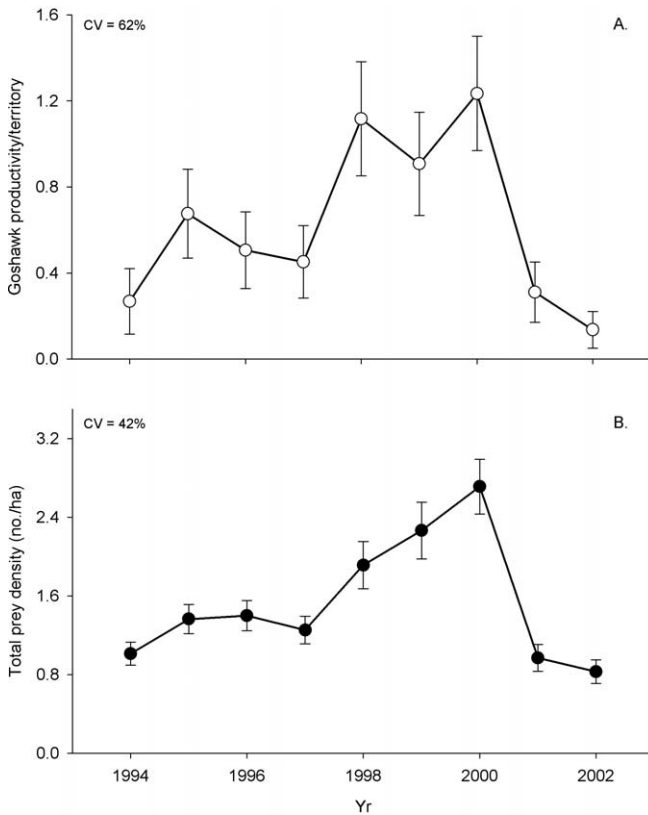
Figure 1. Annual variation in (A) mean number of northern goshawk young produced per territory under study and (B) total prey density on the Kaibab Plateau, Arizona, USA, 1994–2002. Error bars represent ±95% confidence intervals.

the calibration for 1994–1998 using linear regression (PROC REG, SAS Institute 1999). We used mixed conifer and ponderosa pine density estimates from program DISTANCE for 1999–2002. To obtain annual estimates of prey abundance for the entire study area, we weighted the individual prey species density estimates for mixed conifer and ponderosa pine forest by the area occupied by each forest type to account for proportional predominance of ponderosa pine within the study area. We calculated total prey density as the sum of the individual prey densities for species with a sufficient number of detections.

We used the Tukey–Kramer adjustment for multiple comparisons of means to test for differences in goshawk productivity among years (PROC GLM, SAS Institute 1999). We tested differences in mean prey densities among years and forest types with Z-statistics (Buckland et al. 1993). To control for Type I error associated with multiple comparisons, we only tested for differences in prey density between a few specific pairwise comparisons (e.g., mixed conifer and ponderosa pine forest). We assessed annual differences in density by the degree of overlap among the 95% confidence intervals. We used Pearson's correlation coefficient (r) to characterize the strength of the relationship between individual prey species. To determine covariation between prey abundance and goshawk reproduction we used linear regression (PROC REG, SAS Institute 1999) with annual goshawk productivity averaged over all territories as

the dependent variable and density estimates for individual prey species and summed over prey species as independent variables. We used an information-theoretic approach (Burnham and Anderson 2002) to identify the prey variables that resulted in the most parsimonious explanation of annual variation in goshawk productivity per territory for the entire study area and by each forest type. We developed candidate models a priori to depict the potential effects of prey density on goshawk productivity. Food supply is an important and ubiquitous factor limiting goshawk reproduction (Reynolds et al. 2006), so the relationship between prey density and goshawk productivity should be strongest for the prey species or group of prey species that contributed the most to goshawk reproduction. We ranked competing models by their adequacy in explaining variation in the data using Akaike's Information Criterion (PROC MIXED, SAS Institute 1999). We explored model fit to the data based on an examination of the standardized residual plots for lack of normality. To compare the relative importance of each prey species, we used cumulative Akaike weights (Burnham and Anderson 2002), which were calculated by summing the weights across all models that incorporated the prey variable.

RESULTS

Variation in Goshawk Productivity

The number of goshawk territories used to estimate productivity increased from 71 in 1994 to 103 in 2002 and resulted in a total of 823 breeding opportunities. Goshawk productivity for the study area varied annually ($F_{8,814} = 15.21$, $P < 0.001$). Annual productivity ($\bar{x} \pm$ SE) ranged from 1.23 ± 0.14 young produced per territory in 2000 to 0.14 ± 0.04 young produced per territory in 2002 (Fig. 1A). The degree of overlap in the confidence intervals indicates that there were 3 distinct periods in goshawk productivity: 1994–1997, 1998–2000, and 2001–2002. There was also a 75% decline in goshawk productivity ($F_{1,199} = 37.15$, $P < 0.001$) between 2000 ($\bar{x} = 1.23$, SE = 0.14, $n = 98$) and 2001 ($\bar{x} = 0.31$, SE = 0.07, $n = 103$).

We excluded 3 territories each year from the analyses by forest type because there was no predominant forest type within these territories. In contrast to productivity at the study area scale, the mean number of young produced per territory did not differ significantly ($F_{1,794} = 0.79$, $P = 0.375$) between mixed conifer ($\bar{x} = 0.57$, SE = 0.07, $n = 195$) and ponderosa pine ($\bar{x} = 0.65$, SE = 0.04, $n = 601$) forest. However, within forest type, goshawk productivity varied annually for both mixed conifer ($F_{8,186} = 3.12$, $P = 0.003$) and ponderosa pine ($F_{8,592} = 11.91$, $P < 0.001$) forest. Annual productivity in mixed conifer forest ($\bar{x} \pm$ SE) ranged from 0.96 ± 0.24 young produced per territory in 2000 to 0.13 ± 0.09 young produced per territory in 2001 (Fig. 2). Annual productivity in ponderosa pine forest ($\bar{x} \pm$ SE) ranged from 1.34 ± 0.17 young produced per territory in 2000 to 0.13 ± 0.05 young produced per territory in 2002 (Fig. 2).

Variation in Prey Abundance

Although we collected data on 8 prey species with both sampling methods, only 4 species had a sufficient number of
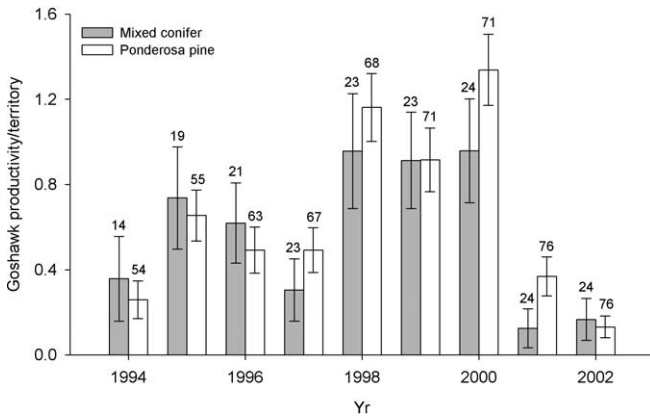
Figure 2. Mean number of northern goshawk young produced per territory for mixed conifer and ponderosa pine forest on the Kaibab Plateau, Arizona, USA, 1994–2002. Error bars represent standard errors. Numbers above error bars indicate the total number of territories used to calculate the means.

Figure 3. Annual northern goshawk prey density estimates (no./ha) for Kaibab squirrel, northern flicker, red squirrel, and Steller's jay on the Kaibab Plateau, Arizona, USA, 1994–2002. Error bars represent standard errors.

detections for accurate density estimates. Together, these 4 species contributed >60% of individual prey items ($n =$ 1,305) to goshawk diets on the Kaibab Plateau during 1994–2002 (S. R. Salafsky, United States Department of Agriculture Forest Service, unpublished data). Unfortunately, we were unable to estimate densities for important prey species such as black-tailed jackrabbit, cottontail rabbit, and golden-mantled ground squirrel. We explored the relationship between count and distance sampling data by forest type for Kaibab squirrel, northern flicker, red squirrel, and Steller's jay. Kaibab squirrels were rarely observed in mixed conifer, so we were unable to accurately estimate the density of these squirrels in this forest type. Therefore, we excluded Kaibab squirrels from mixed conifer forest analyses. In mixed conifer forest the percentage of variance in prey density that was explained by the calibrated counts was 90% for northern flicker ($P = 0.053$), 95% for red squirrel ($P = 0.025$), and 76% for Steller's jay ($P = 0.128$). In ponderosa pine forests, calibrated counts of prey accounted for 95% of the variability in Kaibab squirrel density ($P = 0.026$), 99% of the variability in northern flicker density ($P = 0.004$), 94% of the variability in red squirrel density ($P = 0.031$), and 96% of the variability in Steller's jay density ($P = 0.021$).

Total prey density ($\bar{x} \pm$ SE) for the study area varied annually ($Z = 48.45$, $P < 0.001$), ranging from 2.71 ± 0.14 individuals/ha in 2000 to 0.83 ± 0.06 individuals/ha in 2002 (Fig. 1B). Like goshawk productivity, total prey density exhibited 3 distinct periods: 1994–1997, 1998–2000, and 2001–2002. The annual densities of individual prey species were highly variable; the coefficient of variation was 46% for Kaibab squirrel, 37% for northern flicker, and 67% for red squirrel, compared to only 17% for Steller's jay. All prey species exhibited a decline in density between 2000 and 2001, but only red squirrel density decreased by an order of magnitude (Fig. 3). Further, red squirrel density was highly correlated with the densities of Kaibab squirrel ($r = 0.72$, $n = 9$, $P = 0.029$) and northern flicker ($r = 0.77$, $n = 9$,
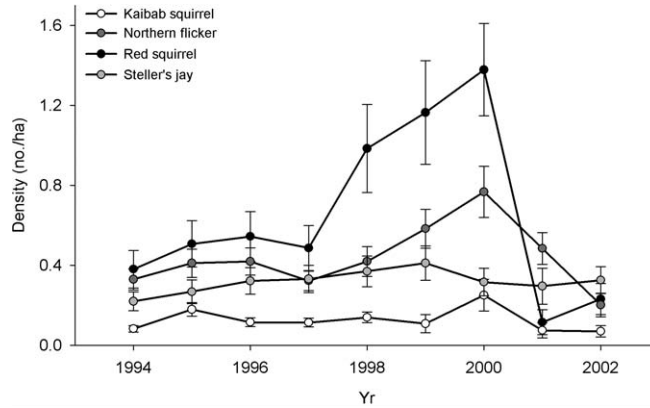
$P = 0.015$), and relatively uncorrelated with Steller's jay density ($r = 0.54$, $n = 9$, $P = 0.131$). Although the magnitude of variation in density differed for each prey species, the relationships among prey species suggests there were synchronous fluctuations in the densities of most prey species (Fig. 3).

Total prey density ($\bar{x} \pm$ SE) for all years combined was twice as high in mixed conifer forest with 22.46 ± 0.23 individuals/ha than in ponderosa pine forest with 10.35 ± 0.10 individuals/ha ($Z = 48.45$, $P < 0.001$). Northern flicker ($Z = 9.28$, $P < 0.001$) and red squirrel ($Z = 29.68$, $P < 0.001$) exhibited higher densities in mixed conifer than in ponderosa pine forest (Fig. 4). In contrast, Kaibab squirrel ($Z = -22.74$, $P < 0.001$) and Steller's jay ($Z = -4.89$, $P < 0.001$) had higher densities in ponderosa pine forest (Fig. 4).

Covariation Between Prey Abundance and Goshawk Productivity

There was a strong positive relationship ($r^2 = 0.89$, $P < 0.001$) between total prey density and goshawk productivity over 1994–2002 (Fig. 5). Based on individual prey-species regression models, red squirrel ($r^2 = 0.87$, $P < 0.001$) explained the most variation in goshawk productivity, followed by Kaibab squirrel ($r^2 = 0.64$, $P = 0.010$), northern flicker ($r^2 = 0.60$, $P = 0.014$), and Steller's jay ($r^2 = 0.24$, $P = 0.180$). The strong positive relationship between total prey density and annual goshawk productivity varied by forest type (Fig. 5); total prey density explained less of the variation in goshawk productivity in mixed conifer ($r^2 = 0.74$, $P = 0.003$) than in ponderosa pine ($r^2 = 0.85$, $P < 0.001$) forest. In mixed conifer forest, red squirrel density ($r^2 = 0.80$, $P = 0.001$) was most strongly correlated with goshawk productivity, followed by northern flicker ($r^2 = 0.22$, $P = 0.206$) and Steller's jay ($r^2 = 0.17$, $P = 0.265$). Within ponderosa pine forest, red squirrel ($r^2 = 0.85$, $P < 0.001$) also explained more variation in goshawk productivity than Kaibab squirrel ($r^2 = 0.62$, $P = 0.012$), northern flicker ($r^2 = 0.60$, $P = 0.014$), or Steller's jay ($r^2 = 0.25$, $P = 0.172$).

Based on model selection results for the entire study area, the best model included red squirrel and Kaibab squirrel
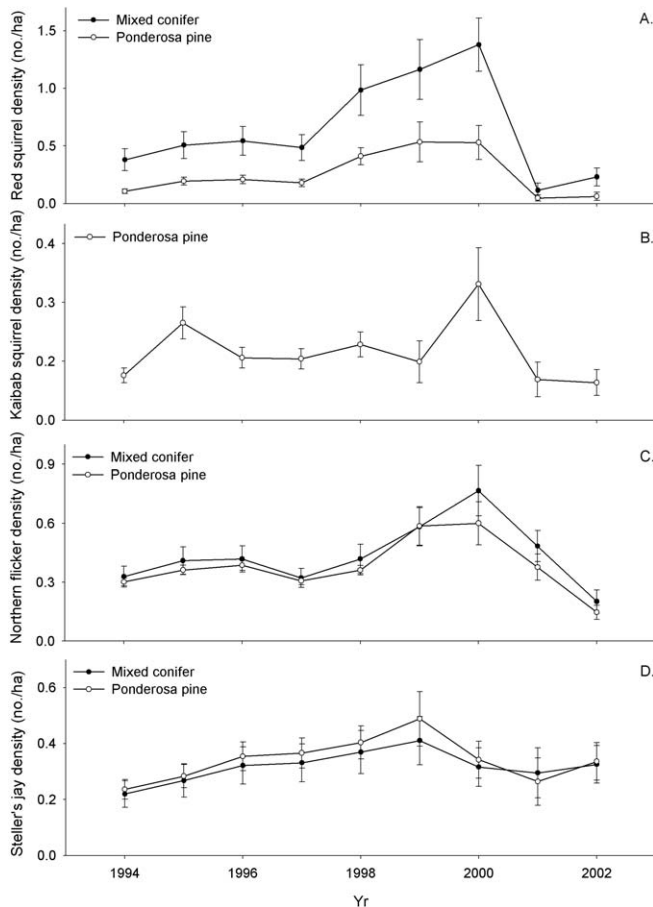
Figure 4. Annual northern goshawk prey density estimates (no./ha) by forest type for (A) red squirrel, (B) Kaibab squirrel, (C) northern flicker, and (D) Steller's jay on the Kaibab Plateau, Arizona, USA, 1994–2002. Error bars represent standard errors.

Table 1. Ranking of models relating prey density variables to mean number of northern goshawk young produced per territory ($n = 823$) for the entire study area on the Kaibab Plateau, Arizona, USA, 1994–2002.[a]

Model	AIC	K	ΔAIC	w_i
Red squirrel, Kaibab squirrel	2,299.1	4	0.0	0.30
Red squirrel, Kaibab squirrel, Steller's jay	2,300.1	5	1.0	0.18
Red squirrel	2,300.4	3	1.3	0.15
Red squirrel, Kaibab squirrel, northern flicker	2,301.1	5	2.0	0.11
Red squirrel, northern flicker	2,301.6	4	2.5	0.08
Red squirrel, Kaibab squirrel, northern flicker, Steller's jay	2,302.0	6	2.9	0.07
Red squirrel, Steller's jay	2,302.3	4	3.2	0.06
Red squirrel, northern flicker, Steller's jay	2,303.6	5	4.5	0.03
Kaibab squirrel, northern flicker, Steller's jay	2,306.6	5	7.5	0.01
Kaibab squirrel, Steller's jay	2,306.6	4	7.5	0.01
Kaibab squirrel, northern flicker	2,321.8	4	22.7	0.00
Northern flicker, Steller's jay	2,325.5	4	26.4	0.00
Kaibab squirrel	2,328.2	3	29.1	0.00
Northern flicker	2,333.2	3	34.1	0.00
Steller's jay	2,376.6	3	77.5	0.00

[a] Model rankings based on Akaike's Information Criterion (AIC) and include model covariates, no. of parameters (K), AIC differences (ΔAIC), and Akaike wt (w_i).

densities (Table 1). Due to high model selection uncertainty, there was little evidence to infer a single best model because the top 3 models had substantial support in the data (Table 1). The top 3 models contained over half of the weight of evidence (0.63). However, red squirrel density was included in all of the top models and the model with red
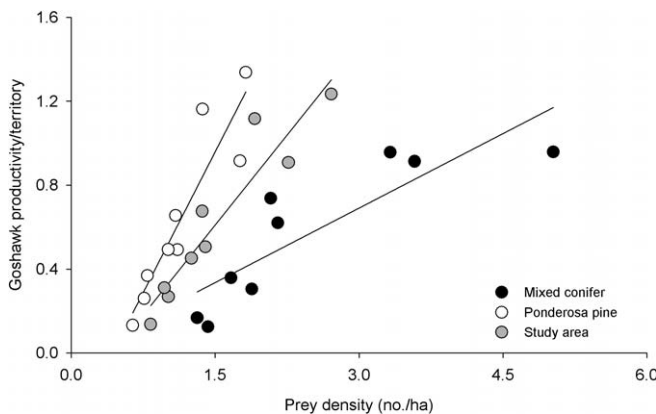

Figure 5. The relationship between total prey density (no./ha) and mean number of northern goshawk young produced per territory for mixed conifer forest, ponderosa pine forest, and the entire study area on the Kaibab Plateau, Arizona, USA, 1994–2002.

squirrel was the only single-species model with some weight of evidence. All other models based on individual prey species had minimal support and failed to explain variation in goshawk productivity (Table 1). Across all models, red squirrel had the highest cumulative Akaike weight (0.99) compared to Kaibab squirrel (0.67), Steller's jay (0.35), and northern flicker (0.30). Thus, Kaibab squirrels and red squirrels appeared to be important prey species to goshawk productivity for the entire study area.

In mixed conifer forest, the model with red squirrel density was selected as the top model (Table 2). However, the top 3 models had substantial support in the data and contained most of the weight of evidence (0.91). There was little difference between the top model with only red squirrel density and those models with additional prey densities (covariates) in the model (Table 2). The 95% confidence interval on the regression coefficients for additional covariates included zero, so there was no evidence that the density of northern flickers or Steller's jays had an effect on variation in goshawk productivity. Thus, the high ranking of models with additional covariates was due mostly to the inclusion of the red squirrel variable in the models, suggesting that red squirrel density had the greatest influence on goshawk productivity in mixed conifer forest.

In ponderosa pine forest, the best model included red squirrel and Kaibab squirrel densities (Table 3). Due to high model selection uncertainty, there was little evidence for a single best model. The top 4 models all had a ΔAIC <2, indicating that all 4 models had substantial support as the best approximating model for goshawk productivity in ponderosa pine forest (Table 3). Across all models, red squirrel had the highest cumulative Akaike weight (0.99) compared to Kaibab squirrel (0.61), Steller's jay (0.54), and northern flicker (0.31). Thus, red squirrels, Kaibab squirrels,

Table 2. Ranking of models relating prey density variables to mean number of northern goshawk young produced per territory ($n = 195$) for mixed conifer forest on the Kaibab Plateau, Arizona, USA, 1994–2002.[a]

Model	AIC	K	ΔAIC	w_i
Red squirrel	523.5	3	0.0	0.5
Red squirrel, northern flicker	525.2	4	1.7	0.22
Red squirrel, Steller's jay	525.4	4	1.9	0.19
Red squirrel, northern flicker, Steller's jay	527.2	5	3.7	0.08
Northern flicker, Steller's jay	532.1	4	8.6	0.01
Steller's jay	537.7	3	14.2	0.00
Northern flicker	538.5	3	15.0	0.00

[a] Model rankings based on Akaike's Information Criterion (AIC) and include model covariates, no. of parameters (K), AIC differences (ΔAIC), and Akaike wt (w_i).

Table 3. Ranking of models relating prey density variables to mean number of northern goshawk young produced per territory ($n = 601$) for ponderosa pine forest on the Kaibab Plateau, Arizona, USA, 1994–2002.[a]

Model	AIC	K	ΔAIC	w_i
Red squirrel, Kaibab squirrel	1,707.1	4	0.0	0.29
Red squirrel, Steller's jay	1,707.7	4	0.6	0.21
Red squirrel, Kaibab squirrel, Steller's jay	1,708.5	5	1.4	0.14
Red squirrel, northern flicker, Steller's jay	1,708.9	5	1.8	0.12
Red squirrel, Kaibab squirrel, northern flicker	1,709.1	5	2.0	0.11
Red squirrel, Kaibab squirrel, northern flicker, Steller's jay	1,710.1	6	3.0	0.06
Red squirrel	1,710.8	3	3.7	0.05
Red squirrel, northern flicker	1,712.7	4	5.6	0.02
Kaibab squirrel, northern flicker, Steller's jay	1,715.2	5	8.1	0.01
Kaibab squirrel, Steller's jay	1,716.9	4	9.8	0.00
Kaibab squirrel, northern flicker	1,720.1	4	13.0	0.00
Kaibab squirrel	1,730.5	3	23.4	0.00
Northern flicker, Steller's jay	1,733.1	4	26.0	0.00
Northern flicker	1,733.8	3	26.7	0.00
Steller's jay	1,766.5	3	59.4	0.00

[a] Model rankings based on Akaike's Information Criterion (AIC) and include model covariates, no. of parameters (K), AIC differences (ΔAIC), and Akaike wt (w_i).

and to some extent Steller's jays appeared to be important prey species to goshawk productivity within ponderosa pine forests.

DISCUSSION

Goshawk reproduction was strongly related to total prey abundance. Goshawk productivity was ≥2 times higher in the period from 1998 to 2000, when the density of prey items was highest (>1.5 individuals/ha), suggesting that greater numbers of potential prey items result in more goshawk fledglings. However, this is assuming that more abundant prey increase goshawk encounter and capture rates, which translates into greater adult fitness and improved nestling survival. This relationship is supported by several other goshawk studies that identified a close association between prey abundance and measures of goshawk productivity (McGowan 1975, Huhtala and Sulkava 1981, Doyle and Smith 1994, Salafsky et al. 2005, Keane et al. 2006). Goshawks apparently adjust their reproductive efforts in response to prey abundance. In years of high prey resources, goshawks attempt to breed on most territories compared to low prey resource years, when few pairs attempt to breed and individual goshawks are rarely detected on low-quality territories (Doyle and Smith 1994, Reynolds et al. 2005, Salafsky et al. 2005, Rutz and Bijlsma 2006). On the Kaibab Plateau, fluctuations in goshawk productivity corresponded to interannual variation in total prey resources. Predators that depend on variable prey populations often exhibit more variation in population parameters, such as birth rates, than do predators that are dependent on relatively stable prey populations (Korpimäki 1988, Newton 1998). Although the abundance of all prey species on the Kaibab Plateau varied annually, the magnitude of fluctuations was much greater for red squirrels, Kaibab squirrels, and northern flickers than for Steller's jays. The considerable interannual variation in goshawk productivity was likely in response to the large fluctuations in the densities of most prey species. In contrast, Krüger and Lindström (2001) found that prey abundance did not appear to limit goshawk reproduction due to the relative stability of a diverse prey base (>60 prey species).

Stability in breeding rates is often associated with diversity of diet because a greater number of prey species increases the opportunities to obtain sufficient food resources (Newton 1979). However, the benefits of a diverse diet are reduced if the abundances of most prey species decline simultaneously. On the Kaibab Plateau all 4 prey species exhibited a decline in density between 2000 and 2001, as did goshawk productivity. These synchronous fluctuations make it difficult to determine the importance of individual prey species to goshawk reproduction. In this study, red squirrel density explained more variation in goshawk productivity than any other prey species. Red squirrel was also the only species to have a significant and positive relationship with goshawk productivity on the Kaibab Plateau in terms of density and percentage of diet during 1999–2002 (Salafsky et al. 2005). However, in this study, the strong relationship between total prey density and goshawk productivity and the high model selection uncertainty suggest that alternate prey species were readily substituted for one another. Goshawks are opportunistic predators, so the contribution of prey species to goshawk diets likely varies with their abundance (Tornberg 1997). Boal and Mannan (1994) found the predation rate of golden-mantled ground squirrels on the Kaibab Plateau was >2:1 over any other prey species. In contrast, Reynolds et al. (1994) found that although golden-mantled ground squirrels were an important component of goshawk diets on the Kaibab Plateau, Steller's jays, cottontail rabbits, northern flickers, Kaibab squirrels, Williamson's sapsuckers (*Sphyrapicus thyroideus*), black-tailed jackrabbits, and red squirrels each contributed twice as many individuals to goshawk diets. The discrepancy between the 2 studies was likely reflective of a potentially greater abundance of golden-mantled ground squirrels during Boal and Mannan's study, the methodology used to quantify goshawk diets, and the forest types incorporated within each study. Thus, the reproductive responses of goshawks to changes in prey

abundance may ultimately depend on the distribution of prey species among habitats.

Individual and total prey density varied by forest type. Specific habitat preferences of prey species (Rasmussen 1941, Hoffmeister 1986, Reynolds et al. 1992) generally corresponded to the differences we detected in prey densities between forest types on the Kaibab Plateau. Mixed conifer forest has been identified as the preferred habitat for northern flickers and red squirrels (Reynolds et al. 1992); this is the forest type in which we recorded the highest densities for these species. Although others rarely reported red squirrels in pure ponderosa pine stands (Rasmussen 1941, Hoffmeister 1986), in this study the density of red squirrels in ponderosa pine forest during 1998–2000 was greater than or equal to the density of red squirrels in mixed conifer forest during 1994–1997 and 2001–2002. This suggests that red squirrels expanded into ponderosa pine forest during periods of high abundance (1998–2000) and were mostly restricted to mixed conifer forest only when abundance was low. We found Kaibab squirrels to be primarily restricted to ponderosa pine–dominated forest, as did Rasmussen (1941). Kaibab squirrel detections in mixed conifer forest were so low that we could not estimate their density for that forest type. In fact, the few Kaibab squirrels observed in mixed conifer forest were usually located within patches of ponderosa pine (S. R. Salafsky, unpublished data).

The distribution of prey species varies by forest type, so variation in goshawk reproduction should be highly correlated with spatial variation in prey resources. Prey species that are more abundant and widely distributed should be more important to goshawk productivity at the landscape scale. The consistent high ranking of models incorporating red squirrel abundance across all forest types may be related to the distribution of red squirrels across the entire study area, especially in years of high abundance (Hoffmeister 1986). In contrast, although Kaibab squirrels have a greater average mass than red squirrels (Kaibab squirrel, 795 g; red squirrel, 196 g) and potentially contribute more biomass to goshawk diets, they are almost exclusively limited to ponderosa pine forest (Hoffmeister 1986). Further, the density of red squirrels had a greater influence on goshawk productivity in mixed conifer than in ponderosa pine forest, suggesting that goshawk prey choice varies with the density and distribution of each prey species. On the Kaibab Plateau, goshawks with lower elevation territories consume more rabbits than goshawks with territories at higher elevations that lack preferred rabbit habitats (S. R. Salafsky, unpublished data). Apparently, rabbits are an important resource for breeding goshawks on some territories, but their limited distribution precluded our ability to detect their influence on goshawk productivity at the landscape scale.

Although the relationship between annual prey abundance and goshawk productivity was consistent across the entire study area and within each forest type, it was not consistent between mixed conifer and ponderosa pine forest. Total prey density was approximately 2 times higher in mixed conifer than in ponderosa pine forest, but goshawk productivity did not differ significantly by forest type. Thus, an incremental increase in prey density resulted in a greater increase in goshawk productivity in ponderosa pine than in mixed conifer forest. This suggests that other factors might be influencing the spatial correlations between goshawk reproduction and prey abundance by forest type. The relationship between prey density and goshawk prey choice ultimately depends on the forest conditions that influence goshawks' access to prey items. Ponderosa pine forests on the Kaibab Plateau are characterized as open with widely spaced trees and understories free from shrubs, smaller trees, and logs (Rasmussen 1941). In contrast, mixed conifer forests on the Kaibab differ greatly in appearance from ponderosa pine because the trees are closely spaced and the understory is dense with shrubs and woody debris (Rasmussen 1941). Dense forests make it difficult for goshawks to detect, pursue, and capture prey because of the reduced line of sight, increased risk of injury while maneuvering through tight spaces, and greater amounts of escape cover for prey. Because greater vegetation density may reduce prey availability, the more open forest structure of ponderosa pine likely ameliorated the affects of lower prey density in that forest type. Evidence suggests that the availability of food resources, as determined by the vegetation structure of foraging habitat, affects goshawk reproduction (Widén 1989, Andersen et al. 2004). However, given the limitations of our data we are unable to determine the influence of forest habitat elements on prey availability and goshawk productivity. Ultimately, because the interannual fluctuations in prey abundance were consistent between forest types, exogenous factors acting at broad spatial scales, such as climate, may have directly or indirectly affected the annual abundance of prey populations. Thus, goshawk productivity is probably affected more by broad-scale changes in prey abundance and factors limiting prey abundance and availability rather than forest type per se. More research is needed to determine the factors influencing prey density and distribution, goshawk prey choice, and habitat-specific foraging rates to understand the synergistic effects of prey populations and forest structural conditions on goshawk reproductive rates.

MANAGEMENT IMPLICATIONS

The close association between goshawk productivity and total prey abundance suggests that goshawks respond to variable prey populations with fluctuating reproductive rates. Thus, forest management strategies concerned with the status of goshawk populations should focus on providing habitat elements necessary to maintain abundant populations of diverse prey species. Richer prey communities allow goshawks to exploit alternate prey species when preferred prey items (e.g., red squirrels) are scarce, which may ultimately favor goshawk population persistence. However, the benefits of an abundant and diverse prey base are reduced when forest composition and structure limits the

accessibility of prey. Because forest management has altered stand structure and tree species composition (Köchli and Brang 2005), it is imperative that we determine how prey populations and goshawk foraging efficiency are impacted by these changes in forest characteristics (Squires and Kennedy 2006). Determining important prey species, prey–habitat relationships, and prey availability will improve our understanding of the critical habitat elements necessary to maintain abundant populations of diverse prey species, appropriate foraging habitat, and ultimately viable goshawk populations.

ACKNOWLEDGMENTS

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