**THESIS**

**COVARIATION BETWEEN PREY ABUNDANCE AND NORTHERN**

**GOSHAWK FECUNDITY ON THE KAIBAB PLATEAU, ARIZONA**

Submitted by

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Graduate Degree Program in Ecology

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY SUSAN REBECCA SALAFSKY ENTITLED COVARIATION BETWEEN PREY ABUNDANCE AND NORTHERN GOSHAWK FECUNDITY ON THE KAIBAB PLATEAU, ARIZONA BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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**ABSTRACT OF THESIS**

COVARIATION BETWEEN PREY ABUNDANCE AND NORTHERN GOSHAWK

FECUNDITY ON THE KAIBAB PLATEAU, ARIZONA

Knowledge of factors limiting population growth and persistence is necessary to develop comprehensive conservation strategies. Although variable prey resources are often associated with fluctuations in raptor demographic rates, the mechanisms of food limitation are poorly understood especially for an opportunistic predator like the northern goshawk (*Accipiter gentilis*). To determine the reproductive responses of goshawks to variable prey populations, I evaluated the number of young produced from 823 goshawk breeding-opportunities on the Kaibab Plateau, Arizona from 1994-2002. Concurrently, abundance was calculated for five prey species (3 mammal, 2 bird). I explored the relationship between goshawk reproduction and prey abundance at one temporal (year) and two spatial (study area, forest type) scales. I also analyzed the relative contribution of individual prey species to goshawk reproduction. Goshawk reproduction showed significant annual variation within the entire study area, mixed conifer forest, and ponderosa pine forest. However, reproduction did not vary between forest types. Abundance of all prey species combined accounted for 88% of the variation in goshawk reproduction within the study area, 72% in mixed conifer forest, and 85% in ponderosa pine forest. Red

squirrel (*Tamiasciurus hudsonicus*) density explained more annual variation in

goshawk reproduction in the study area (88%), mixed conifer forest (73%), and

ponderosa pine forest (89%) than any other species.  However, I could not

determine whether the abundance of individual prey species or total prey

abundance was more important to goshawk reproduction because most prey

species populations fluctuated in phase.  These results suggest that goshawk

population dynamics are strongly associated with prey abundance and the

importance of each prey species is likely dependent on the abundance, quality,

and availability of alternate prey.  Thus, appropriate conservation strategies for

forest-dependent predators such as goshawks should emphasize forest

management practices that benefit prey resources.

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## INTRODUCTION

Effective conservation strategies require an understanding of the
processes that influence population growth and persistence. Although birth,
death, immigration, and emigration rates influence population dynamics,
immigration and emigration rates are often ignored in population models (Gotelli
1998). However, the movement of individuals among populations may provide a
fundamental component to the persistence and survival of populations within the
larger population or metapopulation (Levin 1976). Furthermore, some local
populations may contribute more individuals to the metapopulation than others
through emigration or dispersal. Populations with a positive intrinsic growth rate,
more births than deaths and higher emigration than immigration, are considered
source populations (Pulliam 1988) and the dynamics of source populations may
determine the persistence of other populations and ultimately the stability of the
regional population.

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: female 860-1364 g, male
631-1099 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 old or mature forests with sufficient space beneath the forest canopy to enable flight and access to prey. As a result, goshawk habitat requirements potentially conflict with forest management practices such as timber harvests and fire suppression that alter forest composition and structure. In an attempt to prevent population declines, three 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. Thus, more information is needed on the demographic rates of individual populations, especially source populations, and how these rates vary over space and time.

In 1991, a goshawk demographic study was initiated on the Kaibab Plateau in northern Arizona. After more than 12 years of research, evidence suggests that this goshawk population may be a source population. Long-term population stability and a surplus of individuals characterize source populations (Pulliam 1988). In territorial species, such as goshawks, the number of potential territories within a given area remains relatively constant (Hanski 2001) and the rate of territory occupancy provides an indicator of population stability. On the Kaibab Plateau, the breeding habitat appears saturated due to the high density of territories, the tendency of individuals to retain the same territory for life, and the delayed age at first breeding (Reynolds et al. 1994, Wiens and Reynolds 2004). Further, high territory occupancy rates create few opportunities to secure vacant territories and individuals without territories may be forced to disperse. On the

Kaibab Plateau, emigration of adult goshawks (age >2 yr) appeared to be low due to high territory fidelity and low breeding dispersal rates (R. T. Reynolds, Rocky Mountain Research Station, unpublished data).  Thus, if the Kaibab goshawk population is a source population, then the juvenile goshawks may be the main source of dispersing individuals.  Wiens (2004) found that most juvenile goshawks from the Kaibab Plateau dispersed beyond the bounds of the study area in their first year.  If these juveniles are able to secure breeding territories in other areas, they may contribute to the persistence of other goshawk populations.  Further, because fluctuations in the annual number of juvenile goshawks produced may ultimately influence the availability of potential breeders, and thus the stability of the regional population, it is important to determine the factors influencing goshawk reproduction on the Kaibab Plateau.

Two key factors likely to affect the reproductive output of raptors are availability of nest sites and food resources (Newton 1979).  Although either of these resources may limit reproduction at a particular point in time, annual reproductive output should fluctuate in response to variation in the resource with the greatest influence on reproduction.  Food-supply is often recognized as the ultimate limiting factor of reproduction, because variation in the abundance of food may determine nesting habitat quality, the ability of females to produce eggs, the number of eggs produced, and nestling survival rates (Lack 1954, Newton 1998).  Experimental manipulations of goshawk food-supply (Ward and Kennedy 1996, Dewey and Kennedy 2001) suggest that supplemental food may reduce nestling predation rates by enabling adults to spend more time in defense

of the nest, particularly when background prey levels are assumed to be low. Thus, *when* food resources are available may be as important as the amount of food available.  The abundance and availability of food is particularly critical during two stages in the breeding cycle when most breeding failures occur: prior to egg-laying/incubation when the female needs to accumulate sufficient energy reserves to produce and incubate eggs, and the early nestling period when the male provides most of the food for the female and nestlings (Newton 1979). Thus, temporal variation in the abundance and availability of food may ultimately influence the number of young contributed to future breeding populations.

If food-supply is limiting goshawk reproduction, then fluctuations in goshawk productivity (number of young produced) should be associated with changes in prey abundance.  Furthermore, if the quantity, quality, or availability of prey is inadequate, goshawk productivity may be reduced.  Circumstantial evidence suggests that the relative consistency in the abundance of prey species may stabilize reproductive rates of predators, since species dependent on cyclical prey tend to exhibit greater fluctuations in reproduction then species with stable prey populations (Korpimäki 1988, Doyle and Smith 1994, Newton 1998). 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; southwestern goshawks may achieve adequate food for

reproduction by switching to more abundant alternate prey species. However, if there is a difference in the quality of individual prey species, goshawk reproductive rates may fluctuate with the abundance of alternate prey species. Because prey species vary by habitat, variation in reproductive rates is often associated with spatial variation in prey resources (Netwon 1998). Thus, if environmental conditions such as forest composition and structure influence prey accessibility, then goshawk reproduction may be limited by prey availability as well as prey abundance.

Little is known about how goshawk prey abundance and availability varies with forest composition and how changes in the abundance of prey populations affect southwestern goshawk populations. Given that the abundance of prey species may be influenced by habitat composition and structure, one objective of this study was to estimate how the abundance of goshawk prey species varied annually between forest types. In addition, because food abundance may limit raptor reproduction, a second objective was to determine the extent of covariation between goshawk reproduction and prey abundance. If the abundance of individual prey species fluctuates independently, the relative importance of prey to goshawk reproduction should vary by species. Therefore, the third objective was to determine which prey species were most highly correlated with annual variation in goshawk reproduction.

## STUDY AREA

The 1,285-km$^2$ 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 (Fig. 1).  The Kaibab Plateau is a forested island surrounded by shrub-steppe desert (Rasmussen 1941).  The eastern, southern, and western edges of the plateau are formed by steep escarpments, which create distinct boundaries between the shrub-steppe desert and the forested study area.  In contrast, gradual slopes that form the northern edge of the plateau create an indistinct boundary.  Mixed conifer (*Pinus ponderosa*, *Abies concolor*, *Pseudotsuga menziesii*) forest occupy 275 km$^2$ at the highest elevations of the study area, which gradually transition to 714 km$^2$ of ponderosa pine (*Pinus ponderosa)* forest, and 106 km$^2$ of pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodland with descending elevation.  Of the dominant forest classes on the plateau, mixed conifer forest covers approximately 21% and ponderosa pine forest covers approximately 56% of the study area (Joy 2002).  Quaking aspen (*Populus tremuloides*) forest and pinyon-juniper woodland each comprise less than 10% of the study area, and thus were not considered as dominant vegetation classes.

Due to its relative isolation, the Kaibab Plateau was not subjected to large-scale clear-cut timber harvesting methods (Pearson 1950).  Instead, single-tree harvests, the removal of individual large-diameter trees (Nyland 1996), were implemented on the study area in 1923 and were conducted over most of the plateau (Burnett 1991).  Seed-tree harvests, an intensive tree-harvesting method

that removes most of the large trees (Nyland 1996), began in the mid-1980s and continued until 1990 (Reynolds et al. 1992). Beginning in the 1940s, implementation of fire suppression greatly reduced the natural frequency of low-intensity ground fires (Rassmussen 1941). Lack of frequent fires resulted in extensive regeneration of pine and shade-tolerant tree species under forest canopies, altered vegetation from historical species composition and structure, and increased the accumulation of heavy fuel loads, which escalated the likelihood of catastrophic fires (Smith et al. 1997). Since 1992, forest management on the study area shifted to include prescribed burning, reduction of fire fuels, and thinning of small diameter trees to simulate natural ecological processes and create forest composition and structure beneficial to goshawks and their prey (Reynolds et al. 1992).

## METHODS

**Goshawk Reproduction**

To determine annual goshawk reproductive rates, nest visits were conducted from 1994-2002. Because goshawks may use more than one nest within a territory among breeding years (Reynolds et al. 1994, Reynolds and Joy 1998), all nest structures were visited annually in spring to determine the territory occupancy status. A territory is the area (approximately 11 km$^2$) used by a pair of goshawks during the breeding season (Reynolds et al. 1994). Footsearch and broadcast surveys were conducted May through August to locate new nests and territories (Joy et al. 1994, Reynolds and Joy 1998). Because new territories

were located each year, the number of territories under study increased annually (Reynolds and Joy 1998). To insure equal detection of breeding attempts and an unbiased count of young produced per nest, I only used territories that were monitored for an entire breeding season, thus I determined annual goshawk reproduction for the cohort of territories from the previous year (Table 1). To determine nest status and goshawk reproduction, all active nests (nests containing eggs or young) were visited weekly throughout the breeding season. Goshawk reproduction was estimated annually with productivity, the mean number of young produced per territory (Table 1). To determine goshawk productivity by forest type, goshawk territories were classified as either mixed conifer or ponderosa pine based on the proportional predominance of each forest type within a territory-sized area around the territory center. Territory centers were determined 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). Goshawk productivity for each forest type was determined by dividing the total number of young produced per forest type by the number of territories assigned to each forest type (Table 1).

**Prey Sampling**

Goshawks in the southwestern United States consume a variety of birds and mammals including large passerines, woodpeckers, gamebirds, corvids, rabbits, and ground and tree squirrels (Squires and Reynolds 1997). Such diverse diets require sampling methods capable of estimating bird and diurnally-

active mammal populations simultaneously. Traditional sampling methods such as mark-recapture typically sample only one vertebrate class at a time, require a large investment of time, are labor intensive, and sample areas usually <10 ha (Morrison and Kennedy 1989). To overcome these limitations, I used two sampling methods to estimate prey abundance: distance sampling (counts on line transects with distance estimates) and count-indices (index counts of detections).

*Distance Sampling.* – To estimate prey abundance, distance sampling along line transects (Buckland et al. 1993) was conducted from 1999-2002. Sixty, 500-m transects were placed randomly in the study area within a priori identified habitat strata, and sampled by the same observer (Salafsky) for the four years. Habitat strata were partitioned by forest type (mixed conifer or ponderosa pine) and classified based on elevation and tree species composition. To estimate prey abundance by habitat, 30 transects were randomly established within each forest type. Transects were sampled in groups of four per day and the sampling order of groups was determined randomly. Daily sampling began 0.5 h after sunrise and was completed within 3 h. Sampling was not conducted during inclement weather (rain, winds >15 mph) due to reduced probability of prey detection. Prey seen or heard during sampling were identified to species and the perpendicular distance from the detected animal to the transect line was measured with a laser rangefinder (accurate to ±1 m). Data were collected on eleven bird and six mammal species (Appendix 1) that comprised the majority of

goshawk diets on the Kaibab Plateau (Boal and Mannan 1994, Reynolds et al. 1994).

Count-indices. – Annual count-indices of prey species were conducted from 1994-2002.  Count-indices (hereafter counts) were tallies of prey species seen or heard while observers walked meandering transects within the study area.  For analyses, counts were pooled over observers and stratified by forest type.  Counts were conducted on randomly selected days throughout the goshawk breeding season.  Counts were initiated at random 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, the total number of individuals counted was standardized by the amount of time spent counting for each prey species and resulted in indices of prey abundance.  Counts were conducted simultaneously with activities such as goshawk nest searching, and ceased during inclement weather.  All individuals seen or heard during counts were identified and recorded by species, but no detection distances were estimated.  Count data were collected on a subset of prey species, the two bird and six mammal species (Appendix 1) that occurred most frequently in goshawk diets on the Kaibab Plateau during 1991-1992 (Reynolds et al. 1994).


**Data Analysis**

Distance sampling data were analyzed using program DISTANCE (Version 3.5; Thomas et al. 1998).  Reliable estimates of density from distance sampling data depend on three 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). Data collection methods were designed to meet these assumptions.  Annual density estimates were determined for only those species with sufficient sample sizes (>80 detections).

I used data collected with both sampling methods in 1999-2002 to estimate the empirical relationship between distance-based density estimates and the counts.  Because variable distance sampling estimates a detection function that compensates for differences in detection probabilities among species, habitats, and distances from transects (Emlen 1971, Buckland et al. 1993), density estimates based on distance data are not confounded by factors affecting detectability and thus are more likely to represent the true population size.  In contrast, prey counts are not reliable 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, annual count data were regressed on concurrent density estimates (1999-2002) from distance sampling to develop a calibration equation for each prey species by forest type (PROC REG, SAS Institute 1999).  I used a square root transformation of the count data to improve the fit to a linear model and meet assumptions of normality.  After preliminary examination of the data, I excluded the counts conducted in 2000 from the subsequent calibration analyses because prey abundance indices from this year were not comparable to the other years due to the low number of counts conducted in 2000.  I explored the

relationship between count and distance sampling data for five prey species common to both sampling methods and with sufficient detections; golden-mantled ground squirrel (*Spermophilus lateralis*), Kaibab squirrel (*Sciurus aberti kaibabensis*), northern flicker (*Colaptes auratus*), red squirrel (*Tamiasciurus hudsonicus*), and Steller's jay (*Cyanocitta stelleri*). The abundance of individual prey species in mixed conifer and ponderosa pine forest were predicted annually for 1994-2002 using linear regression (PROC REG, SAS Institute 1999). To obtain annual estimates of prey abundance for the entire study area, I 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.

Differences in mean prey densities among years and forest types were tested with z-statistics (Buckland et al. 1993). To control for Type I error associated with multiple comparisons, I only tested for differences in density between a few specific pairwise comparisons (e.g., between mixed conifer and ponderosa pine forest). The Tukey-Kramer adjustment for multiple comparisons of means was used to test for differences in goshawk productivity among years (PROC GLM, SAS Institute 1999). To determine covariation between prey abundance and goshawk reproduction, I used linear regression (PROC REG, SAS Institute 1999) with annual goshawk productivity averaged over all breeding opportunities as the dependent variable and density estimates for individual prey species and summed over prey species as independent variables. I used an information-theoretic approach (Burnham and Anderson 2002) to identify the

prey variables that explained the most annual variation in goshawk productivity

per breeding opportunity for the entire study area and by each forest type. A

priori candidate models were developed to depict the potential effects of prey

density on goshawk productivity. If goshawk reproduction is food limited then the

relationship between prey density and goshawk productivity should be strongest

for the prey species that contributed the most to goshawk reproduction.

Competing models were ranked by their adequacy in explaining variation in the

data using Akaike's Information Criterion (AIC; PROC MIXED, SAS Institute

1999). I examined model fit to the data based on a visual inspection of the

standardized residual plots for lack of normality. Models were compared using

the difference between AIC for the best approximating model and all other

models ($\Delta$AIC). AIC weights ($w_i$) were used to evaluate the prey density models.

To compare the relative importance of each prey species, I used cumulative

Akaike weights (Burnham and Anderson 2002), which were calculated by

summing the weights across all models that incorporated the prey variable of

interest. The relevance of additional covariates in each model was assessed

based on the degree to which 95% confidence intervals on the regression

coefficients overlapped zero (Graybill and Iyer 1994).


## RESULTS

### Variation in Goshawk Productivity

The number of goshawk territories used to estimate productivity increased

from 71 in 1994 to 103 in 2002 (n = 823). Goshawk productivity for the study

area showed significant annual variation ($F_{8, 814}$ = 15.21, $P < 0.001$). Annual

productivity ($\bar{x} \pm$ SE) ranged from 0.14 $\pm$ 0.04 young produced per territory in

2002 to 1.23 $\pm$ 0.14 young produced per territory in 2000 (Table 1). There was a

significant decline in goshawk productivity ($F_{1, 199}$ = 37.15, $P < 0.001$) between

2000 and 2001 (Table 1).

In contrast, the mean number of young produced per breeding opportunity

did not significantly differ ($F_{1, 794}$ = 0.79, $P = 0.375$) between mixed conifer ($\bar{x}$ =

0.57, SE = 0.07) and ponderosa pine ($\bar{x}$ = 0.65, SE = 0.04) 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

(Table 1). The number of goshawk territories used to estimate productivity in

mixed conifer forest increased from 14 in 1994 to 24 in 2002 (n = 195). Annual

productivity in mixed conifer forest ($\bar{x} \pm$ SE) ranged from 0.13 $\pm$ 0.09 young

produced per territory in 2001 to 0.96 $\pm$ 0.24 young produced per territory in

2000. In contrast, the number of goshawk territories used to estimate

productivity in ponderosa pine forest increased from 54 in 1994 to 76 in 2002 (n =

601). Annual productivity in ponderosa pine forest ($\bar{x} \pm$ SE) ranged from 0.13 $\pm$

0.05 young produced per territory in 2002 to 1.34 $\pm$ 0.17 young produced per

territory in 2000. There was a significant decline in goshawk productivity

between 2000 and 2001 for both mixed conifer ($F_{1, 46}$ = 10.20, $P = 0.003$) and

ponderosa pine ($F_{1, 145}$ = 26.97, $P < 0.001$) forest (Table 1).

**Variation in Prey Abundance**

   Data were collected on eight prey species with both sampling methods, but only five of these species had a sufficient number of detections for accurate density estimates. Therefore, I was unable to estimate densities of some important prey species such as black-tailed jackrabbits (*Lepus californicus*) and cottontail rabbits (*Sylvilagus* spp.) that contributed a large proportion of biomass to goshawk diets on the Kaibab Plateau (Reynolds et al. 1994). Explained variance ($r^2$) from the calibration regressions for mixed conifer forest were 0.26 for golden-mantled ground squirrel, < 0.01 for Kaibab squirrel, 0.90 for northern flicker, 0.95 for red squirrel, and 0.76 for Steller's jay. Explained variance ($r^2$) from the calibration regressions for ponderosa pine forest were 0.87 for golden-mantled ground squirrel, 0.95 for Kaibab squirrel, 0.99 for northern flicker, 0.94 for red squirrel, and 0.96 for Steller's jay. Golden-mantled ground squirrel density was omitted from further analyses due to inadequate sampling effort in the count and distance sampling methods for two of the four years used in the calibration regressions for this species.

   Total prey density ($\bar{x} \pm$ SE) for the study area varied annually, ranging from $0.86 \pm 0.06$ individuals ha$^{-1}$ in 2002 to $2.72 \pm 0.14$ individuals ha$^{-1}$ in 2000 ($z$ = 12.14, $P$ < 0.001). For the majority of individual prey species, 2002 was a low-density year and 2000 was a high-density year (Fig. 2). Further, the density of most prey species decline between 2000 and 2001. Although Kaibab squirrels ($z$ = 2.42, $P$ = 0.008), northern flickers ($z$ = 2.55, $P$ = 0.005), and red squirrels ($z$ =

4.55, $P < 0.001$) declined significantly between 2000 and 2001, only red squirrel

density decreased by an order of magnitude (Fig. 2).

Total prey density ($\bar{x} \pm$ SE) for all years combined was higher in mixed

conifer forest with $22.73 \pm 0.24$ individuals ha$^{-1}$ than in ponderosa pine forest with

$10.41 \pm 0.08$ individuals ha$^{-1}$ ($z = 49.13$, $P < 0.001$). Northern flicker ($z = 8.12$, $P$

$< 0.001$) and red squirrel ($z = 30.85$, $P < 0.001$) exhibited higher densities in

mixed conifer than in ponderosa pine forest (Table 2). In contrast, Kaibab

squirrel ($z = -19.91$, $P < 0.001$) and Steller's jay ($z = -5.33$, $P < 0.001$) had higher

densities in ponderosa pine forest (Table 2). Between 2000 and 2001, northern

flicker ($z = 3.32$, $P < 0.001$) and red squirrel ($z = 7.72$, $P < 0.001$) densities

declined significantly in mixed conifer forest (Table 2). In ponderosa pine forest,

Kaibab squirrel ($z = 2.82$, $P = 0.003$) and northern flicker ($z = 2.21$, $P = 0.014$)

densities declined significantly between 2000 and 2001 (Table 2).


**Covariation Between Prey Abundance and Goshawk Productivity**

There was a strong positive relationship ($r^2 = 0.88$) between total prey

density and goshawk productivity for the entire study area from 1994-2002 (Fig.

3). Based on individual prey species regression models, red squirrel ($r^2 = 0.88$)

explained the most variation in goshawk productivity, followed by Kaibab squirrel

($r^2 = 0.70$), northern flicker ($r^2 = 0.67$), and Steller's jay ($r^2 = 0.45$). Mammal prey

species ($r^2 = 0.90$) explained more of the variation in goshawk productivity than

did avian prey species ($r^2 = 0.72$).

The strong positive relationship between total prey density and annual

goshawk productivity varied by forest type (Fig. 3); total prey density explained

less of the variation in goshawk productivity in mixed conifer ($r^2$ = 0.72) than in

ponderosa pine ($r^2$ = 0.85) forests.  In mixed conifer forest, red squirrel density ($r^2$

= 0.73) was most strongly correlated with goshawk productivity, followed by

Steller's jay ($r^2$r2 = 0.52), and northern flicker ($r^2$ = 0.52).  Within ponderosa pine

forest, red squirrel ($r^2$ = 0.89) also explained more variation in goshawk

productivity than Kaibab squirrel ($r^2$ = 0.69), northern flicker ($r^2$ = 0.63), or

Steller's jay ($r^2$ = 0.38).  For both forest types, mammal prey density (mixed

conifer: $r^2$ = 0.72; ponderosa pine: $r^2$ = 0.94) was more strongly correlated with

goshawk productivity than avian prey density (mixed conifer: $r^2$ = 0.60;

ponderosa pine: $r^2$ = 0.62).

Based on model selection results for the entire study area, the best model

included Kaibab squirrel, red squirrel, and Steller's jay densities (Table 3).  Due

to model selection uncertainty, there was little evidence to infer a single best

model because the top three models had substantial support in the data (Table

3).  The top three models contained most of the weight of evidence (0.70) and

each model incorporated both Kaibab squirrel and red squirrel densities.

However, red squirrel density was included in eight of the top ten models (more

top models than any other variable) and the model with red squirrel density 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 some

of the variation in goshawk productivity (Table 3).  Across all models, red squirrel

had the highest cumulative Akaike weight (0.95) compared to Kaibab squirrel (0.81), Steller's jay (0.68), and northern flicker (0.36).  In addition, the cumulative Akaike weight for mammals (0.76) was much higher than for avian prey species (0.27).  Thus, Kaibab squirrels, red squirrels, and to some extent Steller's jays appeared to be important prey species to goshawk productivity for the entire study area.

In mixed conifer forest, the top two models had approximately equal support in the data (Table 4).  Red squirrel density was included in all four of the top models and there was little difference between the top model with only red squirrel density and those models with additional prey density covariates (Table 4).  The 95% confidence interval of the regression coefficients for additional avian covariates included zero, so there was no evidence that the abundance of northern flickers or Steller's jays had a significant affect on variation in goshawk productivity.  Thus, the high ranking of models with additional covariates were due mostly to the presence of the red squirrel variable in these models, suggesting that red squirrel abundance had the greatest influence on goshawk productivity in mixed conifer forest.

In ponderosa pine forest, the best model included Kaibab squirrel, northern flicker, and red squirrel densities (Table 5).  Due to model selection uncertainty, there was little evidence for a single best model because the top three models had a $\Delta AIC \leq 2$ indicating that all three models had substantial support as the best approximating model for goshawk productivity in ponderosa pine forest (Table 5).  However, Kaibab squirrel and red squirrel densities were

included in the top three models, and because the 95% confidence intervals for northern flicker and Steller's jay included zero, these covariates failed to explain some substantial variation in goshawk productivity.  In addition, the cumulative Akaike weight for mammals (0.85) was much higher compared to the cumulative weight for avian prey species (0.18).  Therefore, it is reasonable to infer that mammal prey abundance was an important resource for goshawk productivity in ponderosa pine forest.

## DISCUSSION

Observational studies do not provide a strong basis for estimating the causal relationship between prey abundance and goshawk reproduction because observational studies cannot isolate the effects of each factor on goshawk reproduction.  Fluctuations in other factors, such as climate, may have coincided with changes in prey abundance, so the mechanisms ultimately responsible for annual variation in goshawk productivity may be difficult to identify in an observational study.  Further, the importance of individual prey species to goshawk reproduction cannot be determined without examining goshawk diets for the proportion of each prey species consumed.  Thus, only an association between the abundance of prey species and goshawk reproduction can be established.  However, it seems reasonable to infer that prey abundance influences goshawk reproductive rates if the patterns observed between prey density and goshawk productivity are consistent across all temporal and spatial

scales, and if the conclusions of supplemental food experiments and food limitation theory support the observed relationship.

The abundance, quality, and availability of each prey species likely determine the contribution of individual prey species to goshawk reproduction. The abundance of prey populations fluctuates with changes in the survival and reproductive rates of each prey species. Predators that depend on relatively stable prey populations often exhibit less variation in survival and reproduction than predators that are dependent on variable prey populations (Korpimäki 1988, Newton 1998). Although the annual abundance of all prey species within the study area on the Kaibab Plateau varied significantly, the magnitude of fluctuations was relatively greater for red squirrels and northern flickers compared to Kaibab squirrels and Steller's jays. Thus, some alternate prey species such as Kaibab squirrels may have provided a more consistent food resource for goshawk reproduction than others. 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 abundance of most prey species decline simultaneously. On the Kaibab Plateau, most prey species appeared to vary in phase, which resulted in years of "poor" and "good" prey resources. Goshawk productivity increased in good prey years and decreased in poor prey years. Thus, the interannual fluctuations in goshawk reproduction appeared to be closely associated with variations in prey abundance. Because goshawks are opportunistic predators, the potential contribution of prey to

goshawk reproduction varied by species.  However, the consistent high-ranking of the model incorporating all prey species for which I had data indicated that each species was an important component of the prey resources available to goshawks within the study area.  The results of this study are similar to other observational goshawk studies that explored the relationship between goshawk reproduction and prey abundance.  For example, in Alaska goshawks prey on relatively few species with snowshoe hares (*Lepus americanus*) contributing the greatest percent biomass to their diets, and high numbers of snowshoe hares were associated with increased goshawk productivity (McGowan 1975, Doyle and Smith 1994).  In addition, experimental goshawk studies that manipulated food-supply found that additional food during the incubation and nestling stages may have influenced the number of young produced by increasing nestling survival when prey abundance was presumed to be low (Ward and Kennedy 1996, Dewey and Kennedy 2001).  Thus, the reproductive responses of goshawks to changes in prey abundance may ultimately depend on the abundance of prey during critical stages in the goshawk breeding cycle.

Prey abundance may influence the ability of females to produce eggs, the number of eggs produced, or juvenile survival rates (Newton 1998), so the interaction between stage-specific food requirements and seasonal changes in prey abundance may affect goshawk breeding rates.  Results from observational and experimental studies suggest that food resources during the early stages of the breeding cycle influences egg-laying date and clutch size, with early clutches producing more fledglings than later ones (Korpimäki 1987*a, b*).  This indicates

that prey abundance prior to egg-laying is an important determinant of annual

goshawk reproduction.  Further, spring prey abundance was highly correlated

with annual goshawk productivity in the Sierra Nevada of California (Keane 1999)

and on the Kaibab Plateau, Arizona (Salafsky et al. 2004), so the seasonal

abundance of prey may ultimately determine annual goshawk reproductive rates.

Seasonal variation in prey abundance depends on the timing of migration,

hibernation, survival, and reproduction for each prey species (Newton 1979).

Resident prey species that are active year round may provide a more reliable

food resource, so these species may be critically important to goshawk

reproduction.  Thus, the high correlation between goshawk productivity and red

squirrel abundance on the Kaibab Plateau may be related to the availability of

red squirrels throughout the year (Hoffmeister 1986).  In contrast, golden-mantled

ground squirrels hibernate (Hoffmeister 1986) reducing their importance to

goshawks from fall to early spring.  Reynolds et al. (1994) found that although

golden-mantled ground squirrels were an important component of goshawk diets

during the breeding season on the Kaibab Plateau, rabbits and red squirrels

contributed more to goshawk diets.  In contrast, Boal and Mannan (1994) found

that golden-mantled ground squirrels contributed more to goshawk diets on the

Kaibab Plateau then both rabbits and red squirrels.  However, the discrepancy

between the two studies may reflect a difference in the abundance of golden-mantled

ground squirrels during the two studies, the methods used to quantify

goshawk diets (observation of prey deliveries versus collecting prey remains),

and the forest types (ponderosa pine versus mixed conifer/ponderosa pine) incorporated within each study.

Individual and total prey density varied annually and by forest type. Habitat preferences of each prey species (Rasmussen 1941, Hoffmeister 1986, Reynolds et al. 1992) corresponded to differences detected in prey densities between forest types on the Kaibab Plateau. Mixed conifer forest is identified as the preferred habitat for northern flickers and red squirrels (Reynolds et al. 1992); the forest type in which I found these species to be most abundant. Red squirrels were rarely reported in pure ponderosa pine stands (Rasmussen 1941, Hoffmeister 1986); however, in this study red squirrel density was not significantly different in ponderosa pine forest in 1999 and 2000 than in mixed conifer forest in 2001. This suggests that during periods of high abundance, red squirrels expanded into ponderosa pine forest and were mostly restricted to mixed conifer forest during periods of low abundance. Similar to Rasmussen (1941), I found Kaibab squirrels to be primarily restricted to ponderosa pine dominated forest. Kaibab squirrels detections in mixed conifer forest were so low that their density could not be estimated for that forest type. Further, the few Kaibab squirrels observed in mixed conifer forest were usually located within patches of ponderosa pine.

The importance of individual prey species to goshawk reproduction within different forest types is likely dependent on the abundance of each prey species within each forest type. Because the distribution of prey species varies by forest type, goshawk reproduction should be highly correlated with spatial variation in

prey resources.  Prey species that are more abundant in mixed conifer forest should be more important to goshawk productivity in that forest type.  Therefore, the consistent high ranking of models incorporating red squirrel abundance across all forest types may be related to the relatively widespread 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 thus may contribute a greater percentage of biomass to goshawk diets, they are almost exclusively limited to ponderosa pine forest (Hoffmeister 1986).  However, the high ranking of models including Kaibab squirrel density indicates that this species was an important food resource for goshawks in ponderosa pine forest.

While 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 almost two times higher in mixed conifer than in ponderosa pine forest, but goshawk productivity did not significantly differ by forest type.  Thus, there was a greater increase in goshawk productivity in ponderosa pine than in mixed conifer forest for an incremental increase in prey density.  This suggests that other factors might be influencing the spatial correlations between goshawk reproduction and prey abundance by forest type. Greater vegetation density may reduce prey availability, so the more open forest structure of ponderosa pine might ameliorate the affects of lower prey density in that forest type.  Further, the exclusion of important prey species that mainly

occur in ponderosa pine habitat, such as rabbits (Hoffmeister 1986), might have resulted in an underestimate of prey density in ponderosa pine forest.  Research is needed on goshawk diets and prey density by forest type to ascertain the affects of prey availability and habitat quality on 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.


## MANAGEMENT IMPLICATIONS

The close association between goshawk productivity and prey abundance suggests that goshawks respond to variable prey populations with fluctuating reproductive rates.  As an opportunistic predator, goshawks in the southwestern United States consume a wide variety of prey species.  Thus, the collective abundance of species within the entire prey community may be the factor limiting goshawk reproduction on the Kaibab Plateau.  Further, the contribution of each prey species likely fluctuates with the abundance, quality, and availability of alternate prey species, so the importance of individual prey species to goshawk reproduction may depend on the alternate prey populations.  Although certain prey, such as red squirrels, were more strongly correlated with fluctuations in goshawk productivity than other species, most prey populations varied in phase

so it is unclear whether the abundance of a particular prey species or total prey abundance limits goshawk productivity. Ultimately, because goshawks rely on a variety of prey species, comprehensive conservation plans for the goshawk should incorporate a multi-species approach to sustain diverse prey populations.

The relationship between prey density and goshawk productivity varied by habitat and was probably associated with prey species distributions, habitat preferences, and habitat-specific availability to goshawks. Further, at some spatial scale(s) the habitat requirements of each prey species clearly differs. As a result, managing for goshawk prey necessitates managing for a suite of habitat characteristics at multiple spatial scales. Thus, forest management strategies for goshawk habitat should include an interspersed mosaic of desired forest conditions to provide the habitat resources necessary to maintain populations of goshawks and their diverse prey base.

Although prey abundance appears to be an important limiting factor, goshawk reproduction may be limited by other biotic and abiotic factors. Because unfavorable weather conditions may have a greater effect on goshawk reproduction when prey populations are low, it is important to study the relationship between goshawk productivity and prey resources over long time periods and variable environmental conditions. Furthermore, environmental factors such as climate and forest productivity are probably limiting prey populations. Because goshawks in the southwestern United States rely on prey populations that fluctuate by habitat, season, and year, future research should focus on identifying potential limiting factors of prey populations and the temporal

and spatial scales over which these influences operate. Determining the

important limiting factors of goshawk and prey populations will improve habitat

management strategies for the goshawk and provide a multi-species approach to

forest management that will ultimately protect biological diversity and the

fundamental processes of forest systems.


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Table 1.  Number of northern goshawk territories in each cohort, number of young produced, and mean number of young produced per territory and standard errors for mixed conifer forest (MC), ponderosa pine forest (PP), and the study area (Total) on the Kaibab Plateau, Arizona, 1994-2002.

| Year | Territories in Cohort | | | Total No. Young | | | Mean No. Young (SE) | | |
|------|------|------|-------|------|------|-------|-------------|-------------|-------------|
|      | MC   | PP   | Total | MC   | PP   | Total | MC          | PP          | Total       |
| 1994 | 14   | 54   | 71    | 5    | 14   | 19    | 0.36 (0.20) | 0.26 (0.09) | 0.27 (0.08) |
| 1995 | 19   | 55   | 77    | 14   | 36   | 52    | 0.74 (0.24) | 0.65 (0.12) | 0.68 (0.11) |
| 1996 | 21   | 63   | 87    | 13   | 31   | 44    | 0.62 (0.19) | 0.49 (0.11) | 0.51 (0.09) |
| 1997 | 23   | 67   | 93    | 7    | 33   | 42    | 0.30 (0.15) | 0.49 (0.10) | 0.45 (0.09) |
| 1998 | 23   | 68   | 94    | 22   | 79   | 105   | 0.96 (0.27) | 1.16 (0.16) | 1.12 (0.14) |
| 1999 | 23   | 71   | 97    | 21   | 65   | 88    | 0.91 (0.23) | 0.92 (0.15) | 0.91 (0.12) |
| 2000 | 24   | 71   | 98    | 23   | 95   | 121   | 0.96 (0.24) | 1.34 (0.17) | 1.23 (0.14) |
| 2001 | 24   | 76   | 103   | 3    | 28   | 32    | 0.13 (0.09) | 0.37 (0.09) | 0.31 0.07)  |
| 2002 | 24   | 76   | 103   | 4    | 10   | 14    | 0.17 (0.10) | 0.13 (0.05) | 0.14 (0.04) |

Table 2. Annual northern goshawk prey density estimates (ha$^{-1}$) and standard errors for Kaibab squirrel (KASQ), northern flicker (NOFL), red squirrel (RESQ), and Steller's jay (STJA) in mixed conifer forest (MC) and ponderosa pine forest (PP) within the study area on the Kaibab Plateau, Arizona, 1994-2002.

| Year | KASQ MC | KASQ PP | NOFL MC | NOFL PP | RESQ MC | RESQ PP | STJA MC | STJA PP |
|------|------|------|------|------|------|------|------|------|
| 1994 | * | 0.11 (0.02) | 0.40 (0.10) | 0.30 (0.02) | 1.09 (0.18) | 0.11 (0.02) | 0.18 (0.07) | 0.24 (0.03) |
| 1995 | * | 0.25 (0.04) | 0.53 (0.13) | 0.36 (0.02) | 1.32 (0.21) | 0.20 (0.03) | 0.23 (0.09) | 0.28 (0.04) |
| 1996 | * | 0.16 (0.03) | 0.50 (0.12) | 0.39 (0.03) | 1.41 (0.23) | 0.21 (0.04) | 0.24 (0.09) | 0.35 (0.05) |
| 1997 | * | 0.16 (0.03) | 0.36 (0.09) | 0.31 (0.02) | 1.28 (0.21) | 0.18 (0.03) | 0.24 (0.10) | 0.37 (0.05) |
| 1998 | * | 0.19 (0.03) | 0.57 (0.14) | 0.36 (0.02) | 2.47 (0.40) | 0.41 (0.07) | 0.28 (0.11) | 0.40 (0.06) |
| 1999 | * | 0.17 (0.03) | 0.77 (0.18) | 0.58 (0.04) | 2.50 (0.40) | 0.49 (0.09) | 0.36 (0.14) | 0.50 (0.07) |
| 2000 | * | 0.35 (0.09) | 1.20 (0.16) | 0.60 (0.11) | 3.58 (0.37) | 0.53 (0.15) | 0.25 (0.07) | 0.34 (0.07) |
| 2001 | * | 0.08 (0.01) | 0.52 (0.12) | 0.35 (0.02) | 0.63 (0.10) | 0.17 (0.03) | 0.21 (0.08) | 0.32 (0.05) |
| 2002 | * | 0.06 (0.01) | 0.26 (0.06) | 0.21 (0.01) | 1.13 (0.18) | 0.10 (0.02) | 0.18 (0.07) | 0.22 (0.03) |
| Total | * | 1.53 (0.06) | 5.10 (0.19) | 3.46 (0.07) | 15.41 (0.41) | 2.39 (0.10) | 2.16 (0.14) | 3.03 (0.08) |

* = too few observations to accurately estimate density

Table 3.  Ranking of models relating prey density variables to mean number of northern goshawk young produced per breeding opportunity (n = 823) for the study area on the Kaibab Plateau, Arizona, 1994-2002.  Model ranking based on Akaike's Information Criteria (AIC) and include model covariates, number of parameters (K), AIC differences ($\Delta$AIC), and Akaike weights ($w_i$).

| Model | AIC | K | $\Delta$AIC | $w_i$ |
|---|---|---|---|---|
| Kaibab squirrel, Red squirrel, Steller's jay | 2297.7 | 5 | 0.0 | 0.32 |
| Kaibab squirrel, Red squirrel, Steller's jay, Northern flicker | 2298.3 | 6 | 0.6 | 0.24 |
| Kaibab squirrel, Red squirrel | 2299.3 | 4 | 1.6 | 0.14 |
| Red squirrel | 2300.4 | 3 | 2.7 | 0.08 |
| Kaibab squirrel, Red squirrel, Northern flicker | 2301.0 | 5 | 3.3 | 0.06 |
| Red squirrel, Steller's jay | 2301.2 | 4 | 3.5 | 0.06 |
| Kaibab squirrel, Steller's jay | 2302.1 | 4 | 4.4 | 0.04 |
| Red squirrel, Northern flicker | 2302.4 | 4 | 4.7 | 0.03 |
| Red squirrel, Steller's jay, Northern flicker | 2303.2 | 5 | 5.5 | 0.02 |
| Kaibab squirrel, Steller's jay, Northern flicker | 2304.1 | 5 | 6.4 | 0.01 |
| Kaibab squirrel, Northern flicker | 2315.0 | 4 | 17.3 | 0.00 |
| Kaibab squirrel | 2320.5 | 3 | 22.8 | 0.00 |
| Steller's jay, Northern flicker, | 2321.2 | 4 | 23.5 | 0.00 |
| Northern flicker | 2324.3 | 3 | 26.6 | 0.00 |
| Steller's jay | 2351.9 | 3 | 54.2 | 0.00 |

Table 4.  Ranking of models relating prey density variables to mean number of northern goshawk young produced per breeding opportunity (n = 195) for mixed conifer forest within the study area on the Kaibab Plateau, Arizona, 1994-2002. Model ranking based on Akaike's Information Criteria (AIC) and include model covariates, number of parameters (K), AIC differences ($\Delta$AIC), and Akaike weights ($w_i$).

| Model | AIC | K | $\Delta$AIC | $w_i$ |
|---|---|---|---|---|
| Red squirrel | 525.5 | 3 | 0.0 | 0.34 |
| Red squirrel, Steller's jay | 525.7 | 4 | 0.2 | 0.30 |
| Red squirrel, Northern flicker, | 527.5 | 4 | 2.0 | 0.12 |
| Red squirrel, Steller's jay, Northern flicker | 527.7 | 5 | 2.2 | 0.11 |
| Steller's jay, Northern flicker, | 528.4 | 4 | 2.9 | 0.08 |
| Steller's jay | 530.8 | 3 | 5.3 | 0.02 |
| Northern flicker | 531.1 | 3 | 5.6 | 0.02 |

Table 5.  Ranking of models relating prey density variables to mean number of northern goshawk young produced per breeding opportunity (n = 601) for ponderosa pine forest within the study area on the Kaibab Plateau, Arizona, 1994-2002.  Model ranking based on Akaike's Information Criteria (AIC) and include model covariates, number of parameters (K), AIC differences (ΔAIC), and Akaike weights ($w_i$).

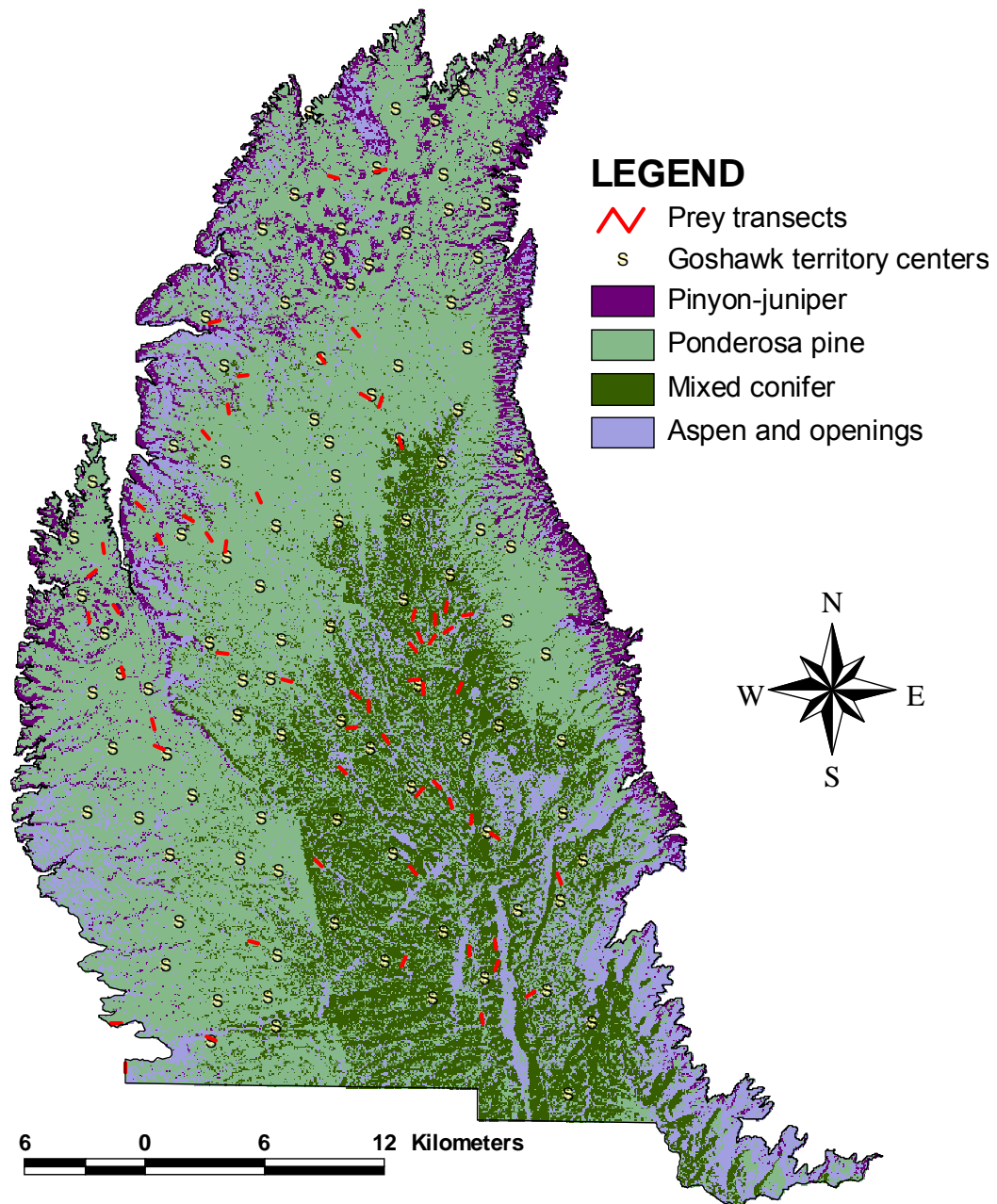| Model | AIC | K | ΔAIC | $w_i$ |
|---|---|---|---|---|
| Kaibab squirrel, Red squirrel, Northern flicker | 1703.0 | 5 | 0.0 | 0.42 |
| Kaibab squirrel, Red squirrel | 1704.1 | 4 | 1.1 | 0.24 |
| Kaibab squirrel, Red squirrel, Steller's jay, Northern flicker | 1704.8 | 6 | 1.8 | 0.17 |
| Red squirrel | 1707.0 | 3 | 4.0 | 0.06 |
| Red squirrel, Northern flicker | 1707.6 | 4 | 4.6 | 0.04 |
| Red squirrel, Steller's jay | 1707.9 | 4 | 4.9 | 0.04 |
| Red squirrel, Steller's jay, Northern flicker | 1708.6 | 5 | 5.6 | 0.03 |
| Kaibab squirrel, Steller's jay | 1712.2 | 4 | 9.2 | 0.00 |
| Kaibab squirrel, Steller's jay, Northern flicker | 1714.2 | 5 | 11.2 | 0.00 |
| Kaibab squirrel, Northern flicker | 1719.2 | 4 | 16.2 | 0.00 |
| Kaibab squirrel | 1723.8 | 3 | 20.8 | 0.00 |
| Northern flicker | 1731.2 | 3 | 28.2 | 0.00 |
| Steller's jay, Northern flicker | 1732.4 | 4 | 29.4 | 0.00 |
| Steller's jay | 1753.9 | 3 | 50.9 | 0.00 |

Fig. 1. Dominant forest classes, northern goshawk territory centers, and distance sampling transects for prey within the study area on the Kaibab Plateau, Arizona, 1994-2002.
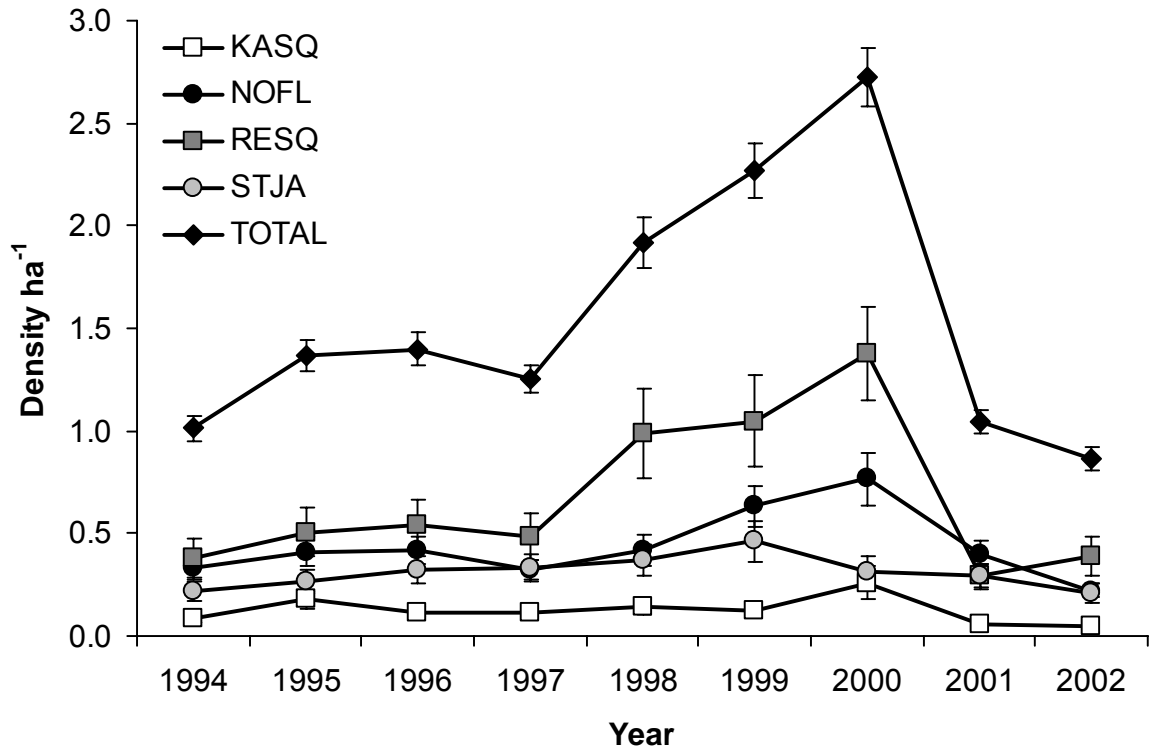
Fig. 2. Annual northern goshawk prey density estimates (ha$^{-1}$) and standard errors for Kaibab squirrel (KASQ), northern flicker (NOFL), red squirrel (RESQ), Steller's jay (STJA), and all prey species combined (TOTAL) within the study area on the Kaibab Plateau, Arizona, 1994-2002.
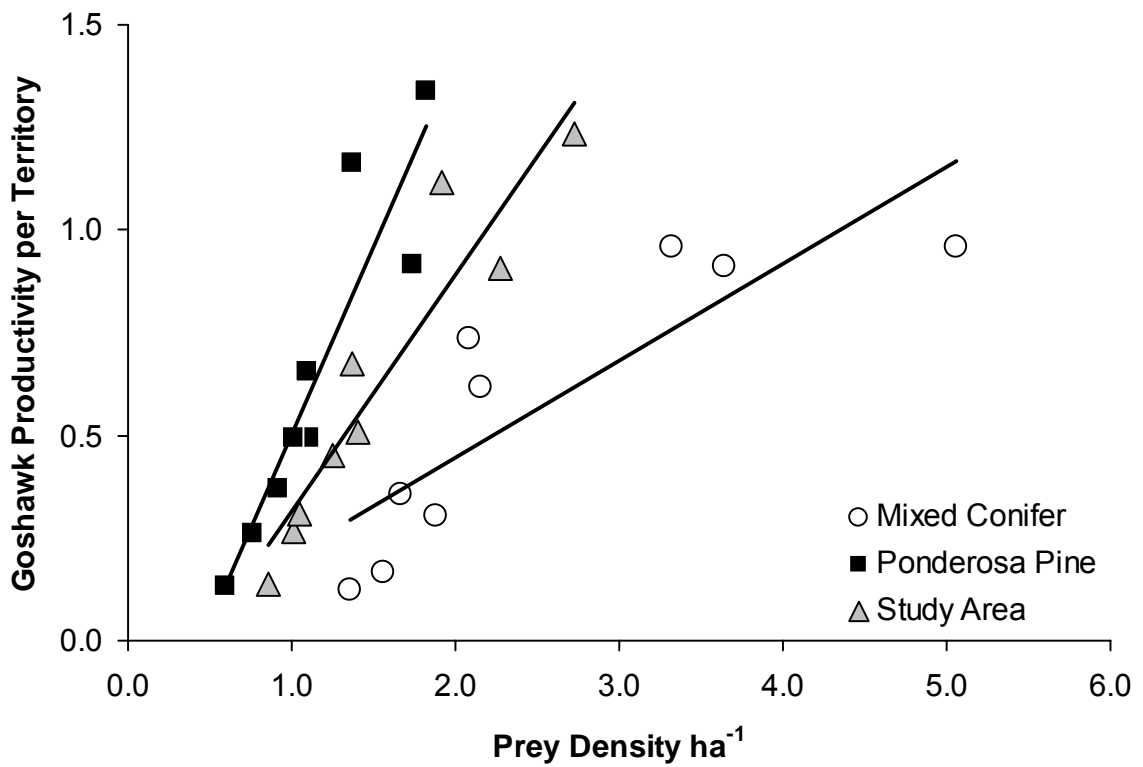
Fig. 3. Regressions of total prey density (ha$^{-1}$) and mean number of northern goshawk young produced per year for mixed conifer forest, ponderosa pine forest, and the study area on the Kaibab Plateau, Arizona, 1994-2002. Lines of best fit determined by linear regression (mixed conifer: $\hat{y} = -0.02 + 0.23x$; ponderosa pine: $\hat{y} = -0.41 + 0.92x$; study area: $\hat{y} = -0.26 + 0.58x$)

APPENDIX 1.  Scientific name, common name (abbreviation code), and sampling method (D = distance sampling, C = count) for northern goshawk prey species on the Kaibab Plateau, Arizona.

| Scientific name | Common name (abbreviation) | Method |
| --- | --- | --- |
| *Turdus migratorius* | American robin (AMRO) | D |
| *Columba fasciata* | Band-tailed pigeon (BTPI) | D |
| *Lepus californicus* | Black-tailed jackrabbit (BTJA) | D, C |
| *Dendragapus obscurus* | Blue grouse (BLGR) | D |
| *Nucifraga columbiana* | Clark's nutcracker (CLNU) | D |
| *Sylvilagus* spp. | Cottontail rabbit (CORA) | D, C |
| *Picoides pubescens* | Downy woodpecker (DOWO) | D |
| *Spermophilus lateralis* | Golden-mantled ground squirrel (GMSQ) | D, C |
| *Picoides villosus* | Hairy woodpecker (HAWO) | D |
| *Sciurus aberti kaibabensis* | Kaibab squirrel (KASQ) | D, C |
| *Zenaida macroura* | Mourning dove (MODO) | D |
| *Colaptes auratus* | Northern flicker (NOFL) | D, C |
| *Tamiasciurus hudsonicus* | Red squirrel (RESQ) | D, C |
| *Spermophilus variegatus* | Rock squirrel (ROSQ) | D, C |
| *Cyanocitta stelleri* | Steller's jay (STJA) | D, C |
| *Picoides tridactylus* | Three-toed woodpecker (TTWO) | D |
| *Sphyrapicus thyroideus* | Williamson's sapsucker (WISA) | D |