Appendix AAC

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POPULATION ECOLOGY, DEMOGRAPHICS, HABITAT, AND GENETICS OF THE NORTHERN GOSHAWK ON THE KAIBAB PLATEAU, ARIZONA.

Progress Report 2002

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INTRODUCTION

The northern goshawk (*Accipiter gentilis*) has been at the center of controversy over management of its habitat in the western United States for over 3 decades. Logging, fire suppression, and grazing in forests are thought to have changed the composition and structure of forest habitats used by goshawks, thereby causing declines in their populations. In 1991, we began intensive studies into the ecology, demography, habitat, and genetics of a large, isolated population of goshawks on the Kaibab Plateau in northern Arizona. The large study area (1,735 km^2) comprises the North Kaibab Ranger District (NKRD) and the Grand Canyon National Park-North Rim (GCNP) above 2,195 m elevation. Our studies have identified 121 of an estimated 145 territories of breeding goshawks on the study area. All breeding goshawks were uniquely color-banded and capture-recapture methods were used to estimate their vital demographic rates. Vital rates and the ecology of juvenile goshawks were also studied with capture-recapture methods and radio-telemetry. The importance of food abundance in the life history of goshawks has been studied since 1994 when we began annual counts of goshawk prey species by forest type and silvicultural treatment on the Kaibab Plateau. Our habitat studies have focused on habitat conditions within goshawk territories and the long-term demographic performance of goshawks on those territories with the objective of identifying the vegetation correlates of habitat quality. Understanding habitat quality is important because species typically occupy a range of habitats differing in the resources necessary for survival and reproduction. Habitat management plans for a species must unequivocally include higher quality habitats where a species' improved survival and reproduction result in abundant offspring that can then emigrate to occupy lesser quality habitats where reproduction is often insufficient to balance local mortality.

The focus of the Kaibab Plateau goshawk studies is to investigate the effects of forest management on the ecology and demography of the goshawk population, prey populations, and the abundances of predators and competitors. Our research design compares the long-term demographic performance of goshawk pairs on territories heavily changed to territories more lightly changed by past (pre-1991) management. We are also taking advantage of the extraordinary opportunity to compare the vital rates of goshawks, as well as prey abundances, in the NKRD and GCNP -- two areas where existing forest structures are quite different due to different resource management histories. In addition, we are studying the effects of current (post-1991) management by measuring changes in goshawk vital rates, and prey, predator, and competitor populations as the goshawk habitat management recommendations and fire fuels reductions are implemented. Finally, we are investigating the role of weather (i.e., wet vs. dry periods) on forest productivity and prey populations on the observed large inter-annual variations in goshawk fecundity. Documenting the effects of natural variation is a prerequisite for identifying the effects of forest management on goshawk fecundity.

OBJECTIVES

1. Identify the distribution, density, vital rates, habitat, and the genetic structure of the northern goshawk population on the Kaibab Plateau.

2. Identify factors such as habitat, food, predators, competitors, and short- and long-term weather patterns, and interactions among these factors, that are limiting the population of goshawks on the Kaibab Plateau.

3. Identify the effects of forest management on both the vital rates of the Kaibab Plateau goshawk population and each of their population limiting factors.

4. Identify habitat elements that differentiate high quality from low quality habitat by investigating the relationship between the long-term demographic performance of individual goshawks and the landscape-level composition and structure of the habitat within their territories.

5. Investigate the forensic use of DNA from molted feathers for identification of individual goshawks in capture-recapture studies. Determine the population genetic and evolutionary relationships among North American goshawk populations, including the putative subspecies *A. g. apache* and *A. g. laingi*.

Density and Distribution of Territories.-- Occupancy of territories by breeding adult goshawks as well as their reproduction were determined on 121 territories on the Kaibab Plateau in 2002; 104 of these territories were in the NKRD and 17 were in the GCNP (Fig. 1). Using half the mean distance between territory centers (3.8 km; Theissen polygon method) as a radius for estimating the "exclusive area" for each territory, we estimated that there is room on the Kaibab study area for 140-145 territories. If this proves true, then we have located about 85% of the total possible territories on the Plateau. Based on the spacing of known territories, most of the territories yet to be located are within the GCNP.

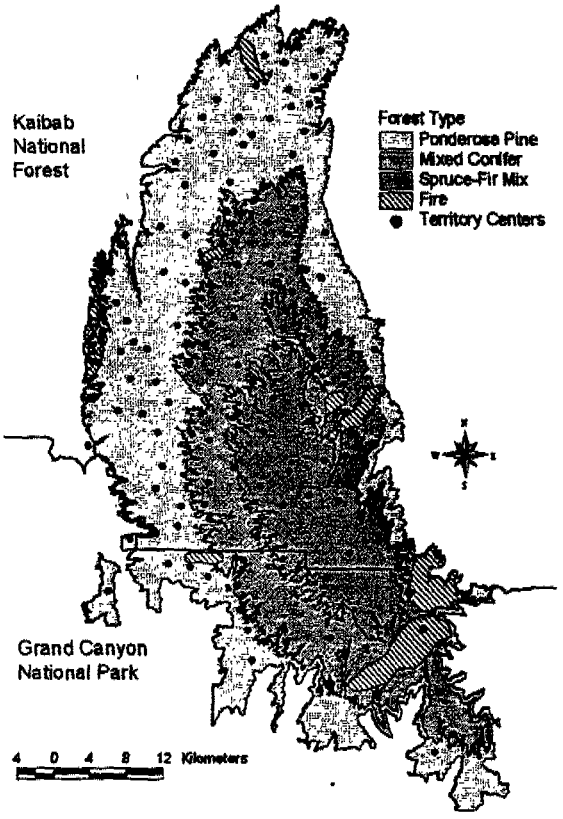

Figure 1. Northern goshawk territory centers on the Kaibab Plateau study area.

Goshawk Fecundity.-- Over the 12-year study the annual proportion of territories on which goshawks laid eggs was highly variable, with high proportions laying in 1992-93,

intermediate proportions in 1995 and 1998-2000, and low proportions in 1994, 1997, and 2001-2002 (Fig. 1). The lowest proportion (17%) of pairs laying eggs occurred in 2002 during perhaps the worst drought year on record. Coincident with this was the highest proportion (47%) of nest failures (eggs laid, no young fledged) in 2002, which was preceded by the second highest nest failure year (2001). Prior to 2001 the proportion of active nests (those with eggs) that failed had been relatively low and somewhat stable (7-26%) among years (Fig. 2). High nest failure rates in 2001-2002 were also likely to be related to the drought and low prey abundance (see below).

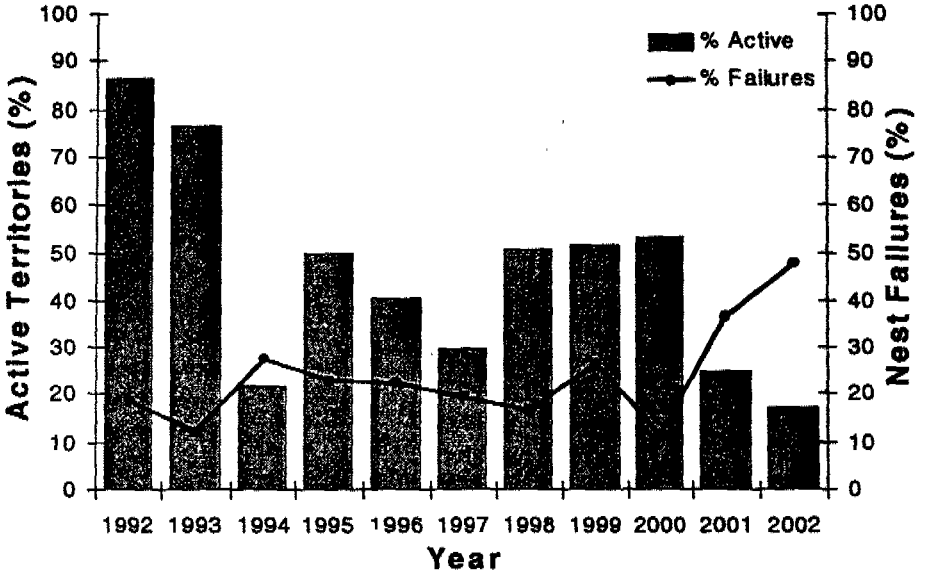

Figure 2. The annual proportion of territories with active nests (eggs laid) and the proportion of active nests that failed (no young fledged) on the Kaibab Plateau, 1992-2002.

Food Abundance. -- In 1994, after noting a dramatic decline from previous years in red squirrels (an important goshawk prey) and numbers of goshawks that laid eggs, we began counts of bird and mammal prey of goshawks. Our objectives were to investigate the relationships between inter-annual variations of food abundance and goshawk reproduction in order to partition the importance of natural environmental variation in food abundance from the effects of forest management on goshawk reproduction. Prey counts were conducted on the Kaibab Plateau in each breeding season from 1994-2002. Plots of total (all species combined) prey density and the proportion of total goshawk pairs laying eggs each year showed a very close association between the inter-annual variation in prey abundance and the proportions of goshawk pairs nesting (Fig. 3).

We believe the relationship between prey abundance and the proportion of goshawks breeding stems from the following. Goshawks surviving the winter return to their nest areas in early spring to breed. Some of these hawks appear to be unmated, having lost their mates from the previous year. While a rare few unmated hawks leave their territories to pair with hawks on near-by territories, most wait on their territories for new mates.

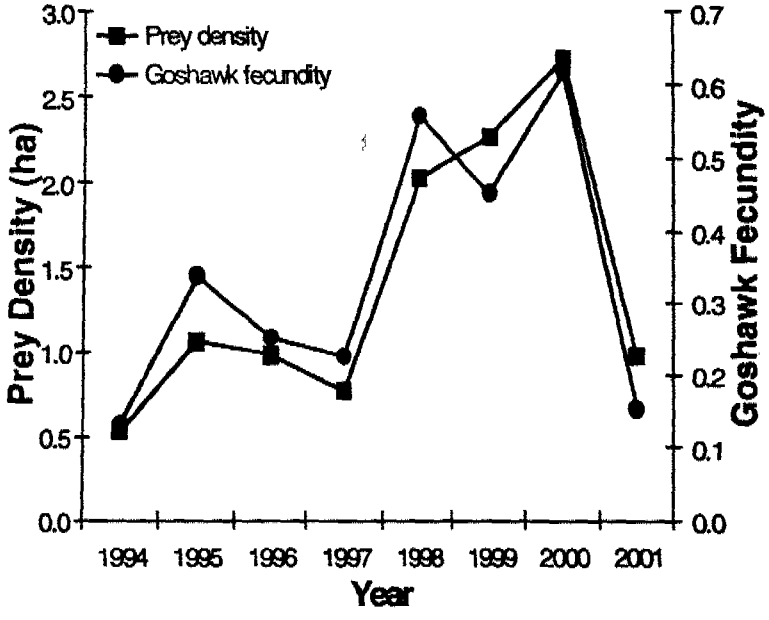

Figure 3. Association between inter-annual variation in total prey density and inter-annual variation in goshawk fecundity on the Kaibab Plateau, 1994-2001.

Whether or not pairs lay eggs in a given year probably depends on the physical condition of the female, which partly depends on the previous winter's food availability and the male's ability to provide enough food to them during the spring courtship period. In years when prey is abundant (e.g., 1998-2000) most females enter the courtship period in improved condition and are easily supplied with enough food by their mates during to lay eggs. In years of low prey abundance (e.g., 1994, 2001-2002), however, more females enter the courtship period in poorer condition and their mates are unable to find enough food to supply the necessary energy for egg laying. In good prey years, the number of breeding pairs is probably augmented by the increased over-winter survival of young birds, providing more individuals to replace the mortalities of breeders. For example, radio telemetry research on juvenile goshawks during 1998-2001 has shown that pre-dispersal survival is positively associated with prey abundance, particularly in the first few weeks after the young have fledged (Fig. 4).

Abundance of bird and mammal prey of goshawks is affected by the conditions of their habitats. We are testing the hypothesis that increased primary forest productivity during wet years (El Niño) results in abundant foods (seed masts, bumper cone crops, insects) and increased populations of birds and mammals. In dry years (La Niña), goshawk food populations decline due to declining forest productivity. For example, the years 1991-1993 were associated with an unusual 3-year-long El Niño event (1990-92) that coincided with the highest proportion of goshawk pairs laying eggs in our 12-year study (1992-93) (Fig. 2). In contrast, 1994 was a relative weak El Niño year and prey populations and goshawk reproduction were both low. The winter of 1997-98 was a also and El Niño year and coincided with both increased prey populations and goshawk reproduction in 1998-2000.

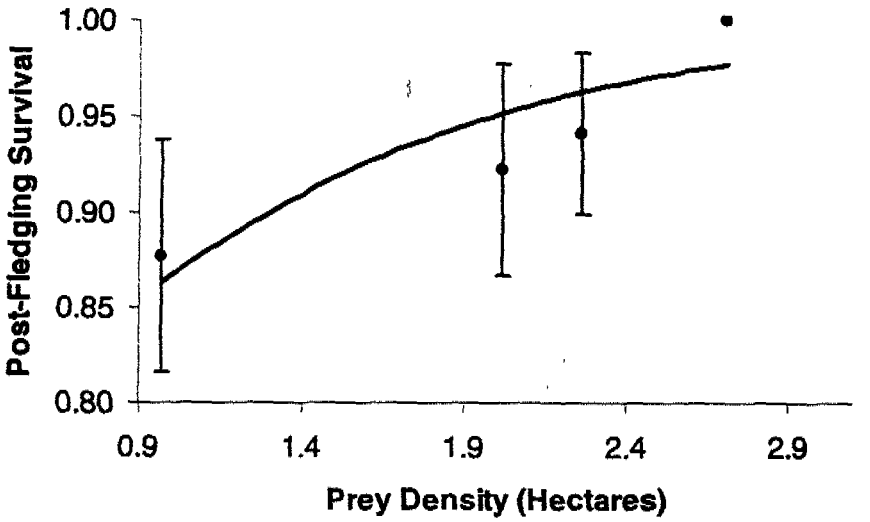

Figure 4. Relationship between juvenile goshawk survival during the post-fledging dependency period and density of four major prey species on the Kaibab Plateau, 1998-2001. Error bars represent ±1 SE (the estimate of survival in 2000 was at the boundary of 1.0, and a realistic variance could not be estimated).

An extended dry period (La Niña), beginning in 1999 and culminating in the worst drought in memory in 2002, was associated with the very low prey populations in 2001-02 and the lowest goshawk reproduction noted in our study in 2002. Current weather forecasts show a developing, but weaker than normal, El Niño for the winter of 2002-03. We are currently extending studies of the effects of local (Kaibab Plateau) inter-annual variations in winter/summer precipitation on forest productivity, prey populations, and goshawk fecundity.

In addition to weather patterns and forest productivity, bird and mammal prey can be affected by the changes in the composition and structure of their forest habitats caused by management activities. We are investigating the effects of management practices on bird and mammal communities on 75, 500-m transects in areas with single-tree and seed-tree harvests, as well as in areas with no tree harvests (GCNP). We are also investigating the cumulative effects of tree harvests and fires within goshawk territories on the frequency of reproduction of the resident pairs of goshawks.

Adult Survival and Territory Fidelity. -- Goshawks on the Kaibab Plateau showed very high annual fidelity to their territories; only 24 cases (5.7 % of 419 opportunities) of breeding dispersal (change of breeding territory) were detected. Overall 95% of males and 94% of females remained on their original territories from one year to the next. Mate fidelity on the Kaibab Plateau was also high; only three divorces were detected. Given an annual adult survival rate of 0.75 (SE = 0.02, 95% C.I. = 0.71, 0.78) for both males and females, the observed year-to-year mate retention rate of 0.56 was the same as the probability (0.56) of remaining together from one year to the next given the annual survival rate of both sexes (0.75 x 0.75 = 0.56). The lifetime fidelity of Kaibab goshawks to their

territories enables us to determine the relationship between a breeding goshawk's long-term demographic performance and the composition and structure of the habitat within their territories.

Failure of a nest attempt in a previous year had little influence on either territory or mate fidelity. The great majority of goshawks whose nests failed continued to occupy their territories, often missing one or more breeding seasons, and typically reusing their former nests in a subsequent breeding year. Other than the three divorce cases of dispersal, all dispersals were associated with disappearance of a mate. Because none of these mates were ever seen again, we assumed that their disappearances were due to mortality. Dispersing males moved a median of 2.1 km (0 =2.3 km) and no farther than to adjacent territories, while females moved a median of 4.3 km (0 = 6.2 km) and no further than five territories (max=18.8 km) distant.

Delayed acquisition of territories by young goshawks [mean age of banded recruits at first breeding was 2.7 years (range = 2 - 4years) for males and 4.1 years (range = 2 - 8 years) for females], relatively high annual survival of breeders (0.77), strong territory fidelity (0.95), and high density of territories on the Kaibab Plateau (8.4 territories/100km^2) suggests that there may be intense competition for territories. When a mate did not return in the spring, a goshawk's options were to (1) stay in its territory and wait for a new mate, (2) forgo breeding if a new mate is not found, or (3) seek a unpaired mate in another territory. Possibly to avoid losing a territory, widowed goshawks appeared to wait for new mates on their original territories while making home-based visits to nearby territories to prospect for unpaired goshawks. The importance of guarding a territory is suggested by the fact that 76 percent of goshawks whose mates did not return in the spring stayed in their original territories, many not breeding for one or more subsequent years.
Strong territory fidelity may "trap" goshawks in territories even as habitat changes accrue through anthropogenic and natural disturbances, resulting in reproduction declines. As a result, existing habitat conditions within territories are not necessarily indicative of conditions that were originally chosen by settling goshawks, and attempts to use existing habitats to determine habitat "value," without referencing existing habitats to long-term demographic parameters of resident goshawks, could be misleading.

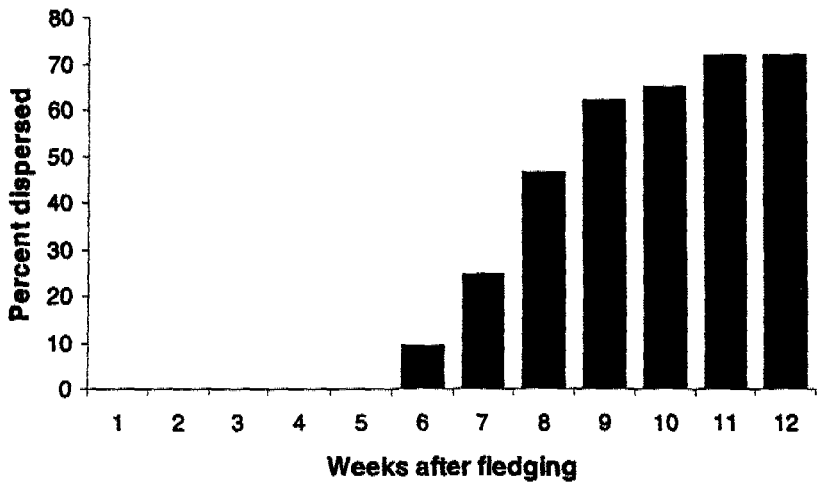

Figure 5. Percentage of radio-marked juveniles dispersing beyond the Kaibab study area in relation to weeks after fledging, 1998-2001 (n=71). By the 12th week after fledging, 71% of marked juveniles had left the Kaibab Plateau.

Juvenile Survival and Dispersal. – We found that juvenile survival prior to dispersal from natal areas was high ($\hat{S}$ = 0.98; 95% C.I. = 0.96, 0.99) yet varied annually coinciding with fluctuations in prey abundance (Fig. 4). Radio telemetry research suggests that a high proportion of juveniles produced in a given year disperse beyond the study area region within the first few months after leaving their natal territories (Fig. 5). These data, when coupled with estimates of adult survival, fidelity, and dispersal, suggest that competition for breeding territories on the Kaibab may be high as a direct result of a saturated breeding population.

Goshawk Habitat Quality. – Since 1991, we have been investigating the quality of goshawk habitat at a variety of spatial scales. One of our objectives is to predict the location of active goshawk nests in a given year; a difficult task due to the reclusive behavior of goshawks, their propensity for not nesting every year, and the long distances between alternate nests. We simulated the spatial interaction of goshawk pairs and the forest environment using a Gibbsian pairwise potential model. Models based on multi-way, dynamic relationships are integral to understanding how populations respond to changes in habitat. Our dynamic modeling effort, or dynamic spatial simulation, is unique in its approach in that it incorporates the goshawk's territorial behavior and habitat conditions interactively to simulate the spatial distribution of nests and to investigate whether the availability of nest habitat limits, or otherwise affects, the distribution and abundance of goshawks. Using logistic regression, we then model the probability of an occurrence of an active nest within a 10-m x 10-m area. By correlating the location of known nests with habitat variables that account for the large-grain variability in the landscape, we were able to identify habitat that is more likely to contain active nests (Fig. 6).

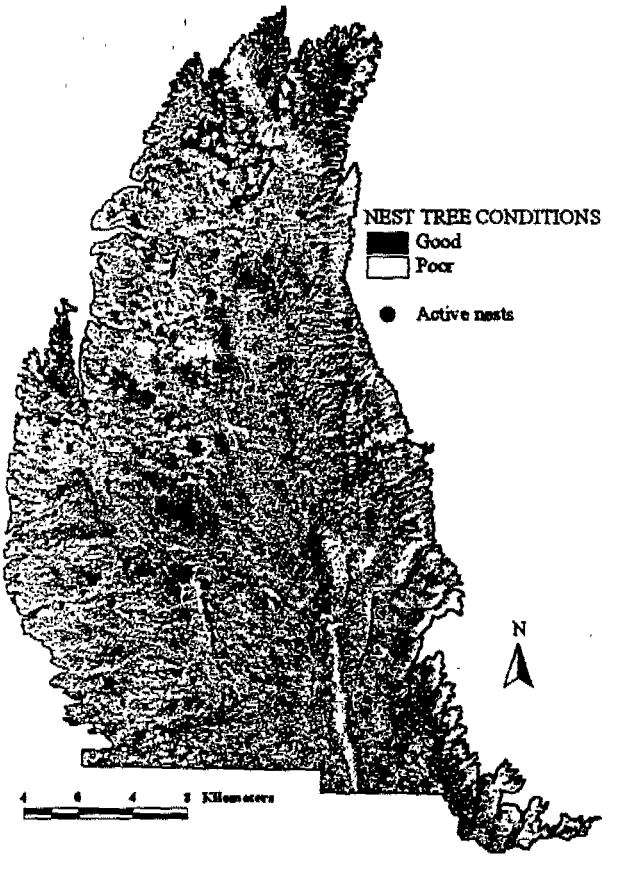

Figure 6. Spatial distribution of "good" and "poor" habitats for goshawk nests on the North Kaibab Ranger District and all active nests in 1991-1998. "Good" habitats have higher probabilities of containing an active nest (probability of finding an active nest is higher). However, goshawks do not necessarily have increased reproduction on those sites.

Areas with potential nest habitat were abundant and

randomly distributed, suggesting that the availability of quality nest areas is not limiting the Kaibab goshawk population. Qualitative differences between "high" and "low" quality goshawk territories and random locations were assessed by comparing vegetative characteristics among random plots and nest plots on goshawk territories with higher and lower reproductive performance. Differences in territory quality were distinguished by differences in the annual rate of egg laying and total fledglings produced between 1991 and 2000. Habitat characteristics (proportion plots in pinyon-juniper, ponderosa pine, mixed conifer, spruce- and deciduous-dominated mixes, openings, and vegetative diversity) were characterized at five spatial scales within non-overlapping concentric circular plots around goshawk nests and random sampling points.

On higher quality territories, the amount of deciduous vegetation and forest openings increased with distance for circle plots; whereas, proportions of these habitats decreased with distance from random locations (Fig. 7). Differences in these relationships were significant up to 0.60 km from the sample plots for deciduous vegetation ($P < 0.06$) and openings ($P < 0.02$). The proportion of openings at distances of up to 0.60 km was also important ($P < 0.05$) in distinguishing lower quality territories from random locations. As circle size increased, the difference between main effects in the models became smaller due to overlap in the measurement of habitat variables. These distances incorporated the nest area (NA) and post-fledging family (PFA) areas within a goshawk's home range. The NA provides critical habitat for nests, and may include more than one nest. The PFA, in addition to providing a staging ground for young goshawks to learn to hunt while still receiving food from their parents also provides food and cover for a number of the goshawk's prey species.

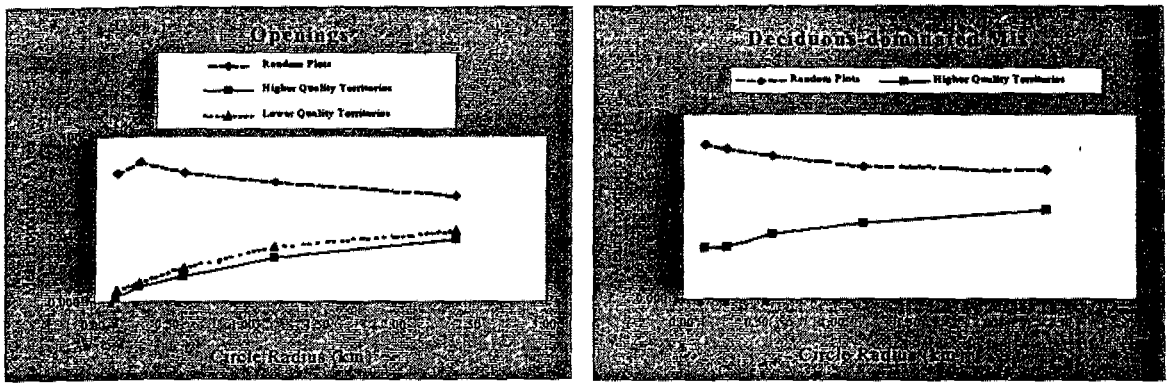

Figure 7. Relationships among the proportions of habitat components around nests in high and low quality goshawk territories and random plots on the North Kaibab Ranger District. Habitat proportions were measured at 5 spatial scales (0.15, 0.30, 0.60, 1.20, and 2.4 km radii) in concentric, overlapping circles around sample plots. Territory quality was based on the annual rate of egg laying and number of young produced in territories between 1991-2000. Asterisks indicate significant differences in landscape scales (distances) between main effects.

Less deciduous-dominated habitat was found at higher and lower quality territories than at random plots. Although goshawks will nest in aspen trees, aspen crowns provide less protection from predators and greater exposure to inclement weather. Aspen stands also

provide less concealment while hunting, but are good trees for cavity excavation by hole-nesting prey such as woodpeckers.

Large openings are poor habitat for red and Kaibab squirrels, both of which are important prey in goshawk diets, and, while openings are important for prey such as rabbits and ground squirrels, even small openings may diminish the concealment of goshawk nests. The number and size of forest openings within a goshawk's territory and foraging range are therefore important to the goshawk's reproductive success. The occurrence of smaller and fewer openings on higher and lower quality territories than on random plots illustrates this point. Openings on the study area ranged from 100 m^2 to 2.15 km^2.

Goshawk Genetics. -- Genetic research on the Kaibab Plateau involves two separate investigations. The first is a forensic investigation in which we hope to use molted feathers, collected at nests sites, as a source of DNA to genetically identify individual goshawks whose color-coded bands cannot be resighted in a given year (for example, in cases where a nest attempt fails before the goshawk's bands can be resighted). Being able to identify all individuals alive in the population in each year greatly increases the precision of adult goshawk survival estimates.

The second genetic investigation involves a comparison of the genetic structure of the population of goshawks on the Kaibab Plateau to other North American goshawk populations. Our objectives are to determine the extent to which gene flow occurs among populations and if, and where, there are geographic barriers to gene flow (immigration, emigration). This knowledge is important in identifying "evolutionary significant units" for management (e.g., the question of the validity of the sub-species *A. g. apache* and *A. g. laingi* and other Fish and Wildlife Service's "listable entities").

RECOMMENDATIONS

This study has identified large inter-annual variations in goshawk fecundity and has shown that much of the inter-annual variation is associated with large inter-annual variations in prey abundances. The evidence is mounting that prey abundance varies in response to variations in forest productivity (e.g., cone crops, understory plant production) and short- and long-term weather patterns (wet vs. dry periods). Goshawk fecundity in the last two years (2001-2002) was the lowest in the 12 years of study and this low coincided with the worst drought in many years. The promise of at least a moderate wet period (El Niño) in the Southwest in 2002-2003 offers a further opportunity to increase our confidence in the hypothesized relationship between weather, forest productivity, prey abundance, and goshawk fecundity. Understanding this relationship is a prerequisite for distinguishing weather-caused variation in goshawk fecundity from habitat-related reductions in their fecundity. Therefore, we recommend that the study continue until goshawk fecundity returns to the 50-60% level (see Fig. 2).

The goshawk makes much of its living in the forest sub-canopy space. Therefore, we hypothesize that the goshawk needs tall forests with lifted canopies with a minimum of

understory trees and woody debris filling the sub-canopy space. Due to the prohibitive costs of quantifying the vertical structure of forests in the landscape, much of our current landscape habitat data is reflective of a horizontal variation in forest structure. While we detected differences in horizontal habitat structure in goshawk territories and non-territory plots, we were unable to fully detect horizontal habitat differences in high versus low quality territories. LiDAR is a relatively new aircraft- or space-borne radar technology that can rapidly and inexpensively measure the vertical structure of forest canopies (e.g., canopy profiles) in large landscapes. Due to the hypothesized importance of the role of vertical structure of forests in variations of goshawk habitat quality, we recommend attaining LiDAR coverage of forests on the Kaibab Plateau. The availability LiDAR will also benefit forest resources and fire fuels assessments on the NKRD and the GCNP.

RESEARCH PRODUCTS

Manuscripts Published

Reynolds, R. T., S. M. Joy, and D. G. Leslie. 1994. Nest productivity, fidelity, and spacing of northern goshawks in Arizona. Studies in Avian Biol. 16:106-113.

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Reynolds, R. T., S. M. Joy, J. D. Wiens, S. R. Salafsky, and J. C. Seyfried. Territory and mate fidelity and breeding dispersal in the northern goshawk. Condor.

Reich, R. M., S. M. Joy, and R. T. Reynolds. Predicting the location of northern goshawk nests: modeling the spatial dependency between nest locations and forest structure. Ecological Modeling.

Manuscripts in Preparation

Joy, S. M., R. T. Reynolds, and R. M. Reich. Northern goshawk habitat: distinguishing high quality territories from random locations.

Reynolds, R. T., S. M. Joy, and R. M. Reich. Effects of anthropogenic and natural disturbances on frequency of breeding by goshawks on the Kaibab Plateau.

Salafsky, S. R., R. T. Reynolds, and B. R. Noon. Influence of annual and seasonal variation in prey abundance on goshawk fecundity.

Salafsky, S. R., R. T. Reynolds, and B. R. Noon. Influence of forest composition and structure on prey abundance and northern goshawk fecundity.

Bayard de Volo, S, M. F. Antolin, and R. T. Reynolds. Recovering DNA from molted raptor feathers for use in sexing, genotyping and mark/recapture analysis: a work in progress.

Bayard de Volo, S, M. F. Antolin, and R. T. Reynolds. Detecting population genetic structure in the northern goshawks of the Kaibab Plateau, Arizona.

Wiens, J.D., R.T. Reynolds, and B.R. Noon. Factors influencing post-fledgling survival, length of the dependency period, and timing of dispersal in juvenile northern goshawks in Arizona.

Wiens, J.D., R.T. Reynolds, and B.R. Noon. Landscape structure and composition of northern goshawk natal areas.

Dissertations and Theses

Miller, R. S. 2001. Determining differences in the spatial distribution of forest structure on the Kaibab Plateau: implications for forest management and the northern goshawk. M.S. Thesis, Colorado State University, Colorado State University, Fort Collins, CO.

Joy, S. M. 2002. Northern goshawk habitat on the Kaibab National Forest in Arizona: factors affecting nest locations and territory quality. Ph.D. Dissertation, Colorado State University, Fort Collins, CO.

Salafsky, S.R. In prep. Co-variation between prey abundance and northern goshawk fecundity on the Kaibab Plateau, Arizona. M.S. Thesis, Colorado State University, Colorado State University, Fort Collins, CO.

Wiens, J.D. In prep. Post-fledgling movement, habitat use, survival, and dispersal of juvenile northern goshawks in Arizona. M.S. Thesis, Colorado State University, Fort Collins, CO.

Bayard de Volo, S. In prep. Recovering DNA from molted raptor feathers for use in sexing, genotyping and mark/recapture analysis. M.S. Thesis, Colorado State University, Fort Collins, CO.

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