

DISSERTATION

REPRODUCTIVE RESPONSES OF AN APEX PREDATOR TO CHANGING CLIMATIC
CONDITIONS IN A VARIABLE FOREST ENVIRONMENT

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Susan Rebecca Salafsky

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Doctoral Committee:

Advisor: Ruth Hufbauer

Alan Franklin

Richard Reynolds

Julie Savidge

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ABSTRACT

REPRODUCTIVE RESPONSES OF AN APEX PREDATOR TO CHANGING CLIMATIC CONDITIONS IN A VARIABLE FOREST ENVIRONMENT

Apex predators are ideal subjects for evaluating the effects of changing climatic conditions on the productivity of forested landscapes, because the quality of their breeding habitat depends primarily on the availability of resources at lower trophic levels. Identifying the environmental factors that influence the reproductive output of apex predators can, therefore, enhance our understanding of the ecological relationships that provide the foundation for effective forest management strategies in a variable environment. To identify the determinants of breeding-habitat quality for an apex predator in a forest food web, I investigated the relationships between site-specific environmental attributes and the reproductive probabilities of northern goshawks (*Accipiter gentilis*) on the Kaibab Plateau, Arizona during 1999-2004.

I used dynamic multistate site occupancy models to quantify annual breeding probabilities (eggs laid) and successful reproduction probabilities (≥ 1 young fledged) relative to temporal and spatial variation in climatic conditions (precipitation and temperature), vegetation attributes (forest composition, structure, and productivity), and prey resources (abundances of 5 mammal and bird species). Climatic conditions during the study period varied extensively, and included extreme drought in 2003 and record-high precipitation in 2004. There was also substantial variation in the amount and distribution of 4 forest cover types among 102 goshawk territories within the 1,285-km² study area. The abundance of most prey species, especially mammals, also varied considerably among years, cover types, and goshawk territories. I

identified the environmental components that best explained spatiotemporal variation in goshawk reproductive parameters using an information-theoretic approach to evaluate the relative weight of evidence for each model.

Out of 62 potential models representing how the distribution of territories with breeding goshawks varied among years and across the landscape, the model with the most evidence indicated that breeding attempts depended on the interaction between the current-year conditions and the site-specific attributes of territories, whereas fledgling production only varied among years. The best-supported model containing variables for climatic conditions included the effects of average annual precipitation and ambient temperature prior to egg-laying on breeding probabilities, and cumulative precipitation during the first 3 weeks post-hatching on successful reproduction probabilities. The best-supported model incorporating vegetation attributes included year-specific effects of forest cover type on breeding probabilities, and conifer cone production on successful reproduction probabilities. Of the prey models I considered, the best-supported model included the effects of the abundance of prey species with distinct ecological niches on both breeding and successful reproduction probabilities. Overall, a habitat model representing food resource availability was the most parsimonious explanation of variation in goshawk reproduction, because it incorporated the effects of temporal variation in climatic conditions and spatial variation in vegetation attributes on the abundance and distribution of prey species with different functional traits. I found that greater heterogeneity in habitat attributes mitigated the effects of changing climatic conditions on reproductive probabilities, because more diverse prey communities increased the abundance of food resources for goshawks during and following drought. Based on the environmental factors that had the greatest influence on reproductive output of an apex predator, I identified management actions designed to enhance

the diversity of niches at a landscape scale and reduce the effects of climatic extremes on the productivity of forest food webs.

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INTRODUCTION

The rate and magnitude of changes in climate, land cover, and disturbance regimes are increasing, largely as a consequence of human impacts on the composition, structure, and dynamics of ecosystems (Melillo et al. 2014). Changes in the frequency, duration, and intensity of droughts combined with timber harvests and fire suppression have extensively altered forest ecosystems and the population dynamics of species that depend on them (May et al. 1997, Sanderson et al. 2002, Joyce et al. 2014). Given the alarming rate of species extinctions (Pimm et al. 2008), it is critical to understand how changes in the compositional and structural attributes of forested landscapes affect population persistence, species richness, and habitat quality. Assessing the effects of variation in abiotic and biotic factors on the abundance and distribution of species, however, is inherently difficult due to the complexity of ecological interactions within forest ecosystems. Therefore, our ability to identify and maintain a landscape configuration that enhances the resilience of forests to changing climatic conditions requires detailed information on the processes influencing ecological relationships over a range of temporal and spatial scales.

Apex predators are ideal subjects for evaluating the ramifications of environmental variation on the integrity of forested landscapes because their population dynamics are primarily influenced by the availability of resources at lower trophic levels (Fuller et al. 1996). Adequate food supplies are necessary for individuals to survive and reproduce, so the persistence of apex predator populations ultimately depends on the environmental factors controlling the abundance and accessibility of prey resources. The combination of inherently low population densities and low reproductive rates coupled with extensive area requirements makes most apex predators reliant on a wide range of resources and sensitive to changes in habitat conditions (Ripple et al.

2014). Moreover, because of their top-down influence on lower trophic levels, apex predators may have a disproportionately large influence on ecosystem function (Estes et al. 2011).

Consequently, understanding how temporal and spatial variation in the population dynamics of apex predators relate to site-specific environmental conditions can provide insights into the factors affecting changes in the integrity of forest ecosystems over time and space.

Habitat and habitat quality have been defined in various ways in the ecological literature (Hall et al. 1997, Morrison and Hall 2002, Johnson 2007). Following the recommendations of Hall et al. (1997), I define “habitat” as the combination of abiotic and biotic factors that allow organisms to survive and reproduce within specific areas. In the formal sense, I consider “habitat quality” to represent the availability of environmental resources that influence the lifetime reproductive success of individuals and their contribution to population growth rates (Fretwell and Lucas 1970, Wiens 1989, Franklin et al. 2000). As Van Horne (1983) illustrated, information on site-specific measures of survival and reproduction are necessary for accurate assessments of habitat quality. However, if the failure to produce viable offspring is widespread and repeated, population growth rates will eventually decline even when survival rates are high (Stearns 1992, Newton 1998). Because it takes more resources to reproduce than to survive, the reliability of habitat assessments can be enhanced by quantifying factors hypothesized to control the availability of resources necessary for individuals to successfully reproduce in a variable environment. Thus, identifying temporal and spatial variation in the reproductive parameters of apex predators relative to the environmental factors that influence habitat quality can enhance our understanding of ecological relationships.

Climate, vegetation, and prey represent three primary sources of environmental variation that influence habitat quality and the reproductive rates of apex predators in terrestrial

ecosystems (Newton 1998). Climatic conditions can affect reproductive performance directly, through the impact of weather extremes on the physical condition and energetic demands of individuals, and indirectly, by influencing the abundance of food resources for prey species. Vegetation composition and structure influences the extent and configuration of breeding habitat and, consequently, the density and accessibility of prey items within foraging areas. The abundance and distribution of prey species influences the availability of food resources required to meet the energetic constraints of reproduction and survival. Thus, quantifying how temporal variation in climatic conditions and spatial variation in landscape characteristics interact to influence reproductive probabilities is necessary to assess habitat quality in a variable environment. Herein, I evaluate how temporal and spatial variation in climatic conditions, vegetation attributes, and prey abundance individually and collectively affect the site-specific reproductive performance of an apex predator in a complex food web to identify the determinants of high-quality habitat within forested landscapes (Fig. 1).

The northern goshawk (*Accipiter gentilis*) is an apex predator that inhabits most forests throughout the Holarctic (Squires and Reynolds 1997). It is an opportunistic predator that consumes a wide variety of mammalian and avian prey species (Marti et al. 1993). Goshawk diet composition varies with the local prey base but regularly includes a broad diversity of prey, including: rabbits, hares, tree squirrels, ground squirrels, large passerines, woodpeckers, corvids, and gallinaceous birds (Squires and Reynolds 1997). Given the distinct niches of these prey taxa, the effects of environmental variation on the density and distribution of prey varies among species. As a consequence, goshawk diet composition varies considerably with temporal and spatial variation in the abundance of prey resources (Squires and Kennedy 2006). In a variable environment, goshawks can theoretically obtain sufficient food resources for the energetic

demands of reproduction by maximizing foraging efficiency through increased encounter rates with prey species that are more consistently available over time, or by switching among alternate prey species with annual abundances that vary asynchronously. Because we lack a clear understanding of the connections between goshawk diet composition and the availability of food resources, any assumptions regarding the importance of prey species and the characteristics of optimal foraging habitat may be unwarranted without further empirical study (Rosenberg and Cooper 1990).

Temporal and spatial variation in environmental factors such as climate, vegetation, and prey can influence the frequency and extent of goshawk reproduction. Exposure of vulnerable eggs or nestlings to severe weather (e.g., cold temperatures, torrential rain) is associated with increased nest-failure rates (Kostrzewa and Kostrzewa 1990, Boal et al. 2005). Greater canopy cover, higher densities of mature trees, and sparse ground cover within breeding habitat appears to be related to increases in goshawk nesting rates and productivity (Reynolds et al. 1982, Woodbridge and Detrich 1994, Keane 1999, Finn et al. 2002). Variation in the abundance of prey is associated with fluctuations in the proportion of goshawk pairs breeding, nest success, and number of young produced (Doyle and Smith 1994, Keane et al. 2006, Salafsky et al. 2007). However, because these environmental factors interact in complex ways, their combined impact on goshawk reproduction may be greater than the sum of their individual effects (Reynolds et al. 2006a). For example, prolonged droughts decrease the abundance of seeds, fungi, and other important food resources for prey species and, consequently, the abundance of prey items (Smith 1968, Newton 1998, Brown and Ernest 2002). Based on goshawk morphology and foraging strategies, interactions between vegetation characteristics and prey abundance are hypothesized to influence goshawk foraging success and the likelihood of obtaining sufficient resources for

reproduction, but these relationships have not been thoroughly studied (Reynolds et al. 1992, Squires and Kennedy 2006). Lower foraging rates may also reduce goshawk productivity when adult females are forced to spend more time foraging and less time brooding or defending their young from predators (Ward and Kennedy 1996, Dewey and Kennedy 2001). However, the strength of these interactions likely depends on factors such as temporal variation in climatic conditions, spatial variation in forest attributes, and the degree of synchrony in fluctuations among populations of prey species.

During 1999-2004, I conducted an empirical study of goshawk-habitat relationships on the Kaibab Plateau in northern Arizona to assess the effects of environmental variation on goshawk reproduction. My overall goal was to integrate a wide range of ecological information to determine how temporal and spatial variation in environmental components influences the quality of goshawk breeding habitat. An evaluation of habitat quality for an apex predator provides a critical link between forest attributes and the productivity of the landscape, but our current knowledge is restricted by a lack of detailed information on the spatiotemporal dynamics of goshawk reproduction. Within habitat that is considered suitable for reproduction there may be substantial variation in conditions due to differences in geomorphology, land-use practices, and environmental factors such as the availability of food resources. As a result, some breeding sites likely confer greater reproductive advantages to goshawks than others.

To identify the relationship between factors influencing quality of breeding habitat and goshawk reproductive rates, I addressed two primary questions: 1) How do temporal and spatial variation in environmental components influence goshawk reproduction? 2) What habitat attributes are associated with increased probabilities of producing offspring under changing climatic conditions? I examined these questions by quantifying temporal and spatial variation in

goshawk reproductive parameters, climatic conditions, vegetation characteristics, food resources for prey species, and prey abundance (Fig. 1). Because food supply ultimately limits avian populations (Lack 1966, Newton 1998), I predicted habitat characteristics that reduce temporal variation in the availability of prey resources enhance goshawk reproductive output. Herein, I evaluate the individual and combined effects of environmental factors on goshawk reproduction to identify the characteristics of high-quality habitat that can inform forest management strategies and provide targets for maximizing the productivity of forest food webs in a variable environment.

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 (Fig. 2). The Kaibab Plateau is a large (95 km x 55 km) forested island surrounded by shrub-steppe desert. With the exception of the south rim of Grand Canyon National Park 18 km to the south, the nearest forests and geographically distinct goshawk populations are 80-250 km from the Kaibab Plateau (Bayard de Volo et al. 2005). The eastern, southern, and western edges of the limestone-capped plateau are formed by steep escarpments, which create distinct boundaries between the shrub-steppe desert at 1,750 m elevation and the forested plateau (maximum elevation 2,800 m). In contrast, the gradual slopes that form the northern edge of the plateau create a broad ecotone between the forests and lower elevation woodlands.

Approximately 275 km² of mixed conifer forests occupy the highest elevations of the study area, transitioning with descending elevation to 714 km² of ponderosa pine (*Pinus ponderosa*) forests and 106 km² of pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodlands (Reich et al. 2004). Interspersed among the other forest types are areas dominated by quaking aspen (*Populus tremuloides*) or Gambel oak (*Quercus gambelii*), which occupy approximately 112 km² of the study area. There are several long narrow meadows that intersect the mixed conifer forest in the southern half of the study area.

Mature mixed conifer forest on the Kaibab Plateau is characterized by high tree species diversity, closed canopies, and low to intermediate understory density (Rasmussen 1941, White and Vankat 1993). The dominant tree species are white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), ponderosa pine, Engelmann spruce (*Picea engelmannii*), subalpine fir

(*Abies lasiocarpa*), and quaking aspen. The most common understory plants include grasses (*Bromus* spp., *Poa* spp.), sedges (*Carex* spp.), forbs (*Antennaria* spp., *Fragaria* spp., *Lotus wrightii*), and shrubs (*Berberis repens*, *Juniperus communis*). In contrast to mixed conifer forest, mature ponderosa pine forest on the Kaibab Plateau has low tree species diversity, open canopies, and patchy understories of grasses and forbs in between tree clumps (Rasmussen 1941, White and Vankat 1993). Common understory plants include grasses (*Muhlenbergia montana*, *Poa* spp., *Sitanion hystrix*), sedges (*Carex* spp.), forbs (*Antennaria* spp., *Eriogonum* spp., *Lotus wrightii*, *Lupinus* spp., *Solidago* spp.), and few shrubs with limited distributions (*Berberis repens*, *Ceanothus fendleri*).

Due to its relative isolation, the Kaibab Plateau was less subjected to the large-scale intensive logging common to other forests in the southwestern United States prior to 1948 (Pearson 1950, Sesnie and Bailey 2003). However, land-management practices including timber harvest, grazing, and fire suppression have altered forest composition and structure. Within the North Kaibab Ranger District, silvicultural practices included single-tree or group-selection harvests (the removal of individual large-diameter trees), extensive seed-tree or shelterwood harvests (the removal of most of the large trees), and small clearcuts (the removal of most of the standing biomass in a few ca. 0.1 km² areas; Nyland 1996). The more intensive silvicultural treatments began in 1982 and continued until 1991, after which harvesting levels declined in response to public concern and lawsuits from environmental organizations (Sesnie and Bailey 2003). The implementation of fire suppression during 1920-1995 altered the historic fire regime and greatly reduced the natural frequency of low-intensity surface fires on the Kaibab Plateau (Mitchell and Freeman 1993, Wolf and Mast 1998, Fulé 2003). Lack of frequent fires resulted in extensive regeneration of fir and other shade-tolerant tree species under forest canopies (Smith et

al. 1997). Fewer fires also increased the accumulation of heavy fuel loads and, consequently, the likelihood of catastrophic fires. More recently, forest management within the study area has included thinning and prescribed burning to reduce tree density and fuel loads.

The climate of the Kaibab Plateau is characterized by cold and snowy winters and cool summers (White and Vankat 1993). Most of the precipitation accumulates as snow from December to March and rain during monsoonal thunderstorms in July and August. On the southern tip of the Kaibab Plateau during 1925-2004, mean monthly temperatures \pm SE ranged from a maximum of 25.3 ± 0.2 °C in July to a minimum of -8.8 ± 0.4 °C in January (Bright Angel Ranger Station, Arizona, Western Regional Climate Center, <http://www.wrcc.dri.edu>, accessed 07 May 2013). Mean annual precipitation \pm SE during April-March for the same weather station and 80-year period of record was 61 ± 3 cm.

During my study period (1999-2004), mean temperatures ranged from a maximum of 26.9 ± 0.9 °C in July to a minimum of -8.2 ± 0.7 °C in January (Western Regional Climate Center). Mean July temperatures for four of the six years of the study period were at least 2.1 °C warmer than the 80-year average, and 2003 was the warmest on record at 29.3 °C. Mean annual precipitation during 1999-2004 was 63 ± 14 cm. Although cumulative precipitation was slightly higher than average during the study period, it was also more variable. During the 80-year period of record, 2004 was the wettest year with 130 cm of precipitation, and 2001 was the third driest, with only 29 cm of precipitation (Western Regional Climate Center). Warmer temperatures and extended precipitation deficits resulted in extreme drought; 2003 had the lowest Palmer Drought Severity Index value (-4.46) for northern Arizona since 1903 (Fig. 3; NOAA, National Climatic Data Center, <http://lwf.ncdc.noaa.gov>, accessed 07 May 2013).

METHODS

Identifying the reproductive responses of specific birds to environmental factors generally requires information from marked individuals, which can be difficult to obtain for goshawks. Thus, I considered reproduction as a population-level response and focused on how the reproductive state of goshawk territories changed over time relative to variation in environmental factors hypothesized to influence the quality of breeding sites. An advantage of this approach is that individual goshawks do not need to be identified to determine the annual reproductive probabilities for each potential breeding site within the study area (MacKenzie et al. 2010). Recently developed extensions of occupancy modeling by Nichols et al. (2007) and MacKenzie et al. (2010) enable classification of sites by different categories or states while accounting for imperfect detection and misclassification errors. Identification of detection and classification probabilities is critical to accurately determine reproductive probabilities, especially when individuals that do not breed are difficult to detect. Multistate dynamic occupancy modeling provides a framework for estimating landscape-level population parameters and the degree of variation in these parameters relative to environmental factors (MacKenzie et al. 2009). By incorporating the reproductive state of potential nesting territories, this method provided a useful framework for identifying the effects of territory-specific environmental attributes on goshawk demographic parameters.

Demographic studies of the goshawk population on the Kaibab Plateau likely included >80% of all possible breeding sites (121 of 150 estimated territories) where the identities of breeding goshawks and their annual reproductive output have been documented during 12 years of research (1991-2002; Reynolds et al. 2005). My evaluation of the relationships among site-

specific environmental characteristics and reproductive probabilities for an apex predator was particularly well-suited for this study population for several reasons. First, a high density of evenly distributed territories (Fig. 2), a delayed age at first breeding (median = 3 yr), and a high adult site-fidelity rate ($\geq 94\%$) suggested that all available breeding habitat on the Kaibab Plateau was occupied by territorial goshawks (Reich et al. 2004, Wiens and Reynolds 2005, Reynolds and Joy 2006). Thus, the density and distribution of breeding sites within the study area appeared to be relatively consistent over time, whereas there was considerable variation in annual reproductive output among goshawk territories (Reynolds et al. 2005). Second, a reproductive state could usually be established for each territory within the study area with high confidence, but there was greater uncertainty regarding the identity of territorial goshawks because the elusive behavior of the adults often made it difficult to detect them. Finally, a putative high level of competition for a limited number of breeding sites on the Kaibab Plateau likely resulted in continuous occupancy of most territories by ≥ 1 adult goshawk. Hence, the reproductive state of each territory could be more reliably assessed, even when the identity of the goshawks occupying the territory was unknown. Thus, I focused on estimating patterns of temporal and spatial variation in the external conditions that may regulate goshawk reproduction to determine the physiographic characteristics of territories that enhance reproductive output under a range of environmental conditions.

Data Collection and Preparation

Goshawk reproduction.— From 1999-2004, 102 goshawk nesting territories were monitored during the breeding season (April-August) of each year (Fig. 2). I used data from ≤ 4 surveys per breeding season to identify the annual reproductive state of each goshawk territory.

The surveys were completed using a combination of nest-visit, foot-search, and call-broadcast methods following protocols described by Reynolds et al. (1994) and Reynolds et al. (2005). The initial survey for each territory was conducted during April or May, after egg-laying and before most nest failures occurred. If breeding goshawks were not detected during the first survey, the territory was surveyed again up to two more times until evidence of nesting was observed (e.g., nest construction or maintenance, incubating bird, eggs or young in nest). Following the removal design for occupancy estimation (Mackenzie et al. 2006), territories were excluded from searches for evidence of nesting once the presence of breeding goshawks was confirmed.

All territories with breeding goshawks were visited weekly to assess nesting status and fledgling production. Then, late in the breeding season, these territories were surveyed again to determine whether the breeding attempt had failed (i.e., no fledglings produced) or was successful (i.e., produced ≥ 1 fledgling). Nests used for a breeding attempt (i.e., eggs laid) that failed to produce ≥ 1 fledgling were checked for the presence of unhatched eggs or other evidence of a failed nesting attempt (e.g., dead young). I used the number of young present in the nest 7-10 days prior to fledging or in the nest area during the first 3 weeks of the post-fledging dependency period to estimate fledgling production per territory.

Goshawk diets.— During 1999-2004, diet composition was assessed annually using prey remains (pelage, plumage, skeletal parts) found within goshawk territories. During weekly visits to territories with a breeding attempt, the 12-ha area surrounding the nest was thoroughly searched. Prey remains were collected from under nest trees, plucking perches, or from the nest and categorized by territory, date collected, and location recovered (i.e., distance and azimuth to the nest).

All prey remains were identified to species or the most specific taxon possible. The age and sex of prey items were established using the methods of Bielefeldt et al. (1992) and Gilbert (1993). Components of remains were pooled by territory, species, and collection date and evaluated to assess the minimum number of individuals consumed (Reynolds and Meslow 1984). Only one individual of each species was counted unless there was unambiguous evidence for >1 individual.

All methods for quantifying raptor diets have inherent biases (Marti 1987). However, Kennedy (1991) reported that estimates of diet composition for goshawks in New Mexico were similar among samples collected using prey-remain, pellet, and direct-observation methods. I used prey remains to estimate the biomass of prey items consumed. Prey items that could not be identified to genus or species were excluded from diet calculations. Remains were primarily collected from goshawk territories with a breeding attempt, so there were insufficient data to identify variation in diet composition among goshawk territories with and without breeding adults. As a result, I pooled the annual samples of prey remains over all goshawk territories and calculated the biomass contribution of each prey species to annual diets of goshawks.

The biomass contribution of species i in the diet sample for year t was calculated by multiplying the number of individuals of species i by the mean mass of species i (avian mass based on Dunning 1993; mammalian mass based on Hall 1981, Boal 1993, or Wilson and Ruff 1999; Appendix A). The masses of fledglings and of juvenile mammals were calculated as two-thirds of the mean adult weight (Rutz 2003). I estimated total biomass as the summed biomass of all prey items in the annual diet sample pooled over territories. In addition, I separately estimated annual biomass contribution for black-tailed jackrabbit (*Lepus californicus*), cottontail rabbit (*Sylvilagus* spp.), Kaibab squirrel (*Sciurus aberti kaibabensis*), red squirrel (*Tamiasciurus*

hudsonicus), northern flicker (*Colaptes auratus*), and Steller's jay (*Cyanocitta stelleri*) because these six species each contributed $\geq 4\%$ of total biomass to goshawk diets during the study period (Appendix A).

Space use.— As territorial breeders, goshawks maintain an exclusive area with ≥ 1 nest site and foraging area. Given the difficulties associated with observing highly-mobile birds over long distances in dense forests, I did not identify the specific foraging areas used by breeding goshawks within each territory. However, if choice of prey items and foraging areas is a function of proximity to nest site, as has been suggested for central-place foragers (Orians and Pearson 1979), breeding goshawks will be less likely to exploit resources that are further from the nest (Rosenberg and McKelvey 1999). Therefore, I delineated each goshawk territory based on the spatial configuration of nests within territories and of neighboring territories using Euclidean distance allocation (R. J. Davis and J. Hobson, USDA Forest Service, personal communication; Fig. 4). First, I identified the mean center of each territory by averaging the Universal Transverse Mercator (UTM) coordinates for all nests within a territory, weighted by the number of years each nest was used (Reynolds and Joy 2006). Next, I used the territory centers to estimate the mean nearest-neighbor distance (2.39 km) among 102 goshawk territories within the study area. I then used one-half the mean nearest-neighbor distance (1.20 km) to define the maximum distance to allocate around each nest within each territory. In areas where the distance between nests in adjacent territories was less than the maximum allocation distance, the midpoint between neighbors marked the territory boundary. The resulting dimensions of each territory were assumed to approximate the exclusive area occupied by breeding goshawks during 1991-2004. The mean territory size was 578 ha (SE = 16 ha, range = 335-1047 ha).

Climatic conditions.— I obtained high-resolution (4 km²) spatially explicit monthly precipitation and temperature data for the conterminous United States from the PRISM Climate Group (<http://www.prism.oregonstate.edu>, created 7 April 2011). Estimates of climatic elements from PRISM data sets are based on the physiographic similarity of digital elevation model grid cells and weather stations in terms of location, elevation, coastal proximity, topographic aspect, slope position, vertical atmospheric layer, and orographic effectiveness of the terrain (Daly et al. 2008). I converted the PRISM ASCII files into ArcInfo grids for analyses. Weather data included mean monthly maximum temperature (°C) and total monthly precipitation (mm). Although a standardized measure for quantitatively estimating errors in spatial weather data was not available for these maps, accuracy assessments indicated these maps provide reasonable estimates of the spatial distribution, patterns, and range of values in weather variables for the western United States (Daly 2006). I used a geographic information system (GIS: ArcGIS, Version 10.1, Environmental Systems Research Institute, Inc., Redlands, CA) to extract annual weather variables for each goshawk territory and to compute the average value of the raster cells.

I quantified temporal and spatial variation in climatic conditions among goshawk territories during 1999-2004 that I hypothesized might influence energetic constraints, prey species, or foraging rates of goshawks and, consequently, the ability of the adults to obtain sufficient food resources necessary to produce offspring. Colder ambient temperatures increase the energetic demands of thermoregulation for goshawks, whereas the amount of precipitation can affect the availability of prey items by influencing the abundance of food resources for prey species and prey activity levels. Thus, I characterized temperature and precipitation data for critical time periods that coincide with the period of increased energetic demands prior to egg-laying (March-April). To account for the influence of precipitation on the production of food

resources for prey species, I summed monthly precipitation data over annual time intervals (April-March) that correspond to the phenology of cone-crop cycles for conifer species on the Kaibab Plateau. Engelmann spruce, white fir, and subalpine fir cones develop and mature during one season (Alexander et al. 1990, Alexander and Shepperd 1990, Laacke 1990); Douglas fir cone production depends on the abortion rate of primorida in the preceding year (Hermann and Lavender 1990); and the development of ponderosa pine seed-bearing cones takes 27 months (Krannitz and Duralia 2004). To account for these patterns and to investigate their influence on goshawk reproduction, I used territory-specific measures of annual precipitation for the current year, previous year, and 2-year average prior to the current breeding season. Due to the length and intensity of dry conditions during 1999-2004 (Fig. 3), I also incorporated annual covariates based on Palmer Drought Severity index values for northern Arizona.

I also quantified weather variables that may influence nesting success (i.e., ≥ 1 young fledged). As in other bird species, inclement weather during any stage of the goshawk breeding cycle can increase mortality rates of eggs or nestlings and lower overall reproductive success (Newton 1998). However, the first 2-3 weeks post-hatching are especially critical for goshawks because recently hatched nestlings are highly dependent on parental care and need to be fed and warmed by the adults to survive (Boal 1994, Squires and Reynolds 1997). Consequently, hatchlings may be more vulnerable to weather extremes prior to developing feathers, especially during periods of food scarcity when the adult female must spend more time foraging and less time brooding (Ward and Kennedy 1996, Dewey and Kennedy 2001). To examine how inclement weather influenced site-specific goshawk productivity, I compiled maximum temperature and precipitation data for the entire breeding season (April-August) and monthly time periods that approximated 30-d incubation (Reynolds and Wight 1978) or 24-d brooding

(Boal 1994) stages of the annual breeding cycle. If the brooding or incubation stage overlapped two months, I averaged data from both months. I quantified weather variables for each nesting stage based on the estimated hatching date for each territory calculated from the mean age of young 7-10 d prior to fledging.

Vegetation composition and structure.— I quantified spatial variation in vegetation characteristics for goshawk territories using GIS. My vegetation data for the study area were based on 10-m² resolution raster maps created from the interpretation of 1997 Landsat TM imagery and concurrent field sampling (Reich et al. 2004). Structural data included in my analyses were: percent canopy cover, basal area (m²/ha), and proportion of the total basal area classified as ponderosa pine (% ponderosa pine) or mixed conifer (% mixed conifer). The predictive performance of the vegetation structure models was evaluated by Joy (2002) using stratified 11-fold cross-validation. Accuracy of the models of forest structure was 95% for canopy cover, 96% for total basal area, 93% for % ponderosa pine, and 90% for % mixed conifer. Elevation data for the study area were based on a digital elevation model (1:24000 scale, 30-m spatial resolution, U.S. Geological Survey) and used to distinguish the boundaries between forest types (2250 m for pinyon-juniper and ponderosa pine, 2550 m for ponderosa pine and mixed conifer; Reich et al. 2004). I used Resource Information System data obtained from the North Kaibab Ranger District of the Kaibab National Forest to identify the dimensions and distribution of silvicultural management units within the study area (Joy et al. 2003; Fig. 2).

I used vegetation data from the Reich et al. (2004) maps to categorize the amount and distribution of the dominant forest cover types within the study area (Appendix B). First, I extracted meadows, areas of windthrow, and pure aspen stands (>0.99 aspen basal area) and reclassified them as a non-dominant vegetation type. Then I used the Jenks natural breaks

method (Jenks 1967) to identify the break points for dividing the continuous vegetation data into discrete classes. Based on the predominance of tree species, I divided the % mixed conifer data into two categories representing ponderosa pine ($\leq 14\%$ mixed conifer) or mixed conifer ($> 14\%$ mixed conifer) forest types. Next, to categorize the structural attributes of the dominant silvicultural treatments within the study area, I divided the basal area data into two classes per forest type representing the density of mature trees in lightly-harvested or intensively-harvested areas with break points of $87 \text{ m}^2/\text{ha}$ for ponderosa pine and $112 \text{ m}^2/\text{ha}$ for mixed conifer (Fig. B-1). Then I used these attributes to classify the cover type of each 10-m^2 raster cell within the study area as high-density ponderosa pine ($\leq 14\%$ mixed conifer and $> 87 \text{ m}^2/\text{ha}$ basal area), low-density ponderosa pine ($\leq 14\%$ mixed conifer and $\leq 87 \text{ m}^2/\text{ha}$ basal area), high-density mixed conifer ($> 14\%$ mixed conifer and $> 112 \text{ m}^2/\text{ha}$ basal area), low-density mixed conifer ($\leq 14\%$ mixed conifer and $\leq 112 \text{ m}^2/\text{ha}$ basal), or a non-dominant cover type (Fig. B-2). Thus, I used the cover type classifications to represent the structural characteristics of conifer forests associated with either a high density of mature trees or a low density of mature trees and small openings. Overall accuracy of my reclassified cover type map was 95% based on ground assessments completed at 60 study plots (Table B-1). I used the reclassified map to derive landscape metrics for the study area including the amount, distribution, and mean patch size of each forest cover type (Fig. 5).

For each goshawk territory, I quantified vegetation attributes that influence the structural complexity of goshawk foraging habitat and, consequently, the abundance and distribution of prey species with distinct ecological niches. Because goshawks are opportunistic predators that consume a wide variety of prey types with different habitat requirements (e.g., tree and ground squirrels, rabbits, birds), the vegetation composition and structure within foraging habitat

influences their access to diverse prey communities and species that are habitat specialists. For example, Kaibab squirrel habitat is characterized as mature ponderosa pine stands with interlocking crowns, small openings interspersed among clumps of trees, and variable stem densities and tree age classes (Rasmussen 1941, Patton 1984). Red squirrel habitat is characterized by multi-storied stands of mixed conifer with high densities of mature trees, high canopy cover, snags, and downed logs that provide important foods and appropriate conditions for food storage in middens (Hoffmeister 1986, Patton and Vahle 1986). Ground squirrel and lagomorph habitat on the Kaibab Plateau encompasses ponderosa pine and mixed conifer forests with well-developed herbaceous understories as these habitats contain greater amounts of important food resources for ground-dwelling prey (McKeever 1964, Cayot 1978, Hoffmeister 1986). Therefore, I used the proportion of 4 forest cover types (high-density pine, low-density pine, high-density mix, low-density mix), maximum patch size of harvested management units, mean patch size of high-density forest (high-density pine + high-density mix), and distance between each territory center and the nearest boundary between forest types (pinyon-juniper/ponderosa pine or ponderosa pine/mixed conifer) to quantify differences in the composition and configuration of prey habitats among goshawk territories and, ultimately, the availability of species in the prey community.

Tree density, canopy cover, aspect, and habitat fragmentation (i.e., patch size) influence the microclimate of goshawk nest areas (Reynolds et al. 1992) and, potentially, the abundance and proximity of great horned owls and other predators that occupy more open forest habitats (Crocker-Bedford 1990, LaSorte et al. 2004). Thus, goshawk nesting success may be affected by vegetation structural attributes that increase solar insolation, edge effects, the visibility of the nest, and the abundances of goshawk predator and prey species (U.S. Fish and Wildlife Service

1998), especially during periods of food scarcity when the adult female must spend more time foraging and less time brooding or defending the nest (Ward and Kennedy 1996, Dewey and Kennedy 2001). I used percent canopy cover, mean patch size of high-density forest, proportion of low-density forest (low-density pine + low-density mix), and abundance of food resources for prey species (see below) to quantify differences in vegetation structural attributes among goshawk territories that may influence the number of young fledged per breeding attempt.

Food resources for prey.— Conifer cones are important food resources for many goshawk prey species, particularly Kaibab squirrels and red squirrels (Hall 1981, Hoffmeister 1986). I used cone production to estimate annual variation in the abundance of food resources for prey species among goshawk territories. During 1999-2004, I sampled cone crops annually during the latter half of July and the first half of August from a fixed set of 960 trees. Individual live trees used to sample cone crops were randomly selected based on the closest large (≥ 30 cm diameter at breast height) tree within each quadrant (NE, SE, SW, NW) of 4 sampling sites established along prey transects (see below). Sampling sites were centered on 4 stakes randomly selected from the 9 stakes that marked 50-m intervals of each transect ($n = 240$). For ponderosa pine, Douglas fir, and Engelmann spruce trees, I sampled cone crops by counting the number of new cones on the ground within a 1-m² frame that was placed under the crown of the tree at each cardinal direction (N, NE, E, SE, S, SW, W, NW). For species such as white fir and subalpine fir that do not accumulate cones on the ground, I counted the number of cones visible in the canopy.

I estimated annual cone production for all tree species combined (Engelmann spruce, Douglas fir, ponderosa pine, subalpine fir, white fir) and also individually for ponderosa pine (Appendix C). Average cone production per forest cover type (high-density pine, low-density pine, high-density mix, low-density mix) was calculated by summing the annual cone counts for

all 15 transects per cover type, and then dividing the total by the number of live trees with ≥ 1 cone counted. I standardized the annual counts using the number of live trees to avoid artificially reducing cone production over time due to mortality in the fixed sample of trees during the study period. Variation in cone production per tree may result from differences in site-specific landscape characteristics (e.g., elevation, topographic aspect, slope position), so I used a random sample of trees that were widely distributed across the entire study area within each forest cover type to incorporate spatial variation in cone crops. I quantified variation in conifer cone crops among goshawk territories by multiplying the proportion of each forest cover type within the territory by the corresponding annual estimate of cone production and summing the resulting quantities.

Prey abundance.— From 1999-2004, I collected data on 17 prey species that are common in goshawk diets on the Kaibab Plateau and considered important components of goshawk diets in the southwestern United States (Reynolds et al. 1992, Salafsky et al. 2005). Avian prey included: American robin (*Turdus migratorius*), blue grouse (*Dendragapus obscurus obscurus*), band-tailed pigeon (*Columba fasciata*), Clark's nutcracker (*Nucifraga columbiana*), hairy woodpecker (*Picoides villosus*), mourning dove (*Zenaida macroura*), northern flicker, red-naped sapsucker (*Sphyrapicus nuchalis*), Steller's jay, and Williamson's sapsucker (*Sphyrapicus thyroideus*). Mammalian prey included: black-tailed jackrabbit, chipmunk (*Tamias* spp.), cottontail rabbit, golden-mantled ground squirrel (*Callospermophilus lateralis*), Kaibab squirrel, red squirrel, and rock squirrel (*Spermophilus variegatus*).

To estimate prey abundance for this diverse group of species, I conducted distance sampling along 500-m line transects using a stratified random sampling design based on forest cover type (Buckland et al. 2001). I used natural color aerial photographs (1:12000; USDA

Forest Service, North Kaibab Ranger District, Fredonia, Arizona) to identify areas of the four dominant cover types in my study area (high-density pine, low-density pine, high-density mix, low-density mix). Initially, potential sampling locations were randomly placed throughout areas of each cover type. To account for management treatments that occurred subsequent to the 1991 aerial photography, I conducted ground assessments of potential transects to visually classify the current cover type. I selected transects for sampling that exemplified the dominant characteristics of each forest and management type in terms of overstory diversity, understory coverage, and tree density and closely adhered to the assumptions of distance sampling (Thomas et al. 2010). I established 15 transects per cover type ($n = 60$).

During 1999-2004, each transect was sampled three times per year during time periods that corresponded with the stages of goshawk reproduction on the Kaibab Plateau: incubation/hatching stage (28 May-24 June), nestling stage (25 June-22 July), and fledging stage (23 July-14 August). One observer (Salafsky) completed all of the prey sampling to eliminate the potential confounding effects of different observers. Transects were sampled in groups of four per day and the sampling order of groups was randomized within time periods. Daily sampling began 0.5 h after sunrise and was completed within 3 h. Sampling was not conducted during inclement weather (rain, winds >24 km/h) due to reduced probability of prey detection. Prey seen or heard during sampling were identified to species and the perpendicular distance from the detected prey item to the transect line was estimated with a laser rangefinder.

I used program Distance (Version 6.0, Release 2, Research Unit for Wildlife Population Assessment, St. Andrews, UK) to estimate annual densities of goshawk prey species. A small number of observations of individuals precluded estimating prey density per transect, so I used data from all 15 transects to quantify annual prey density per cover type for lightly-harvested

ponderosa pine, intensively-harvested ponderosa pine, lightly-harvested mixed conifer, and intensively-harvested mixed conifer. Because many species only contributed a few prey items to goshawk diets (Appendix A), I wanted to estimate the densities of the six species that together contributed >79% of all prey items and >86% of total biomass to goshawk diets during my study period: cottontail rabbit, black-tailed jackrabbit, Kaibab squirrel, red squirrel, northern flicker, and Steller's jay. However, small sample sizes precluded estimation of cottontail rabbit and black-tailed jackrabbit density per cover type per year, both individually and pooled between species. Because cottontail rabbits, black-tailed jackrabbits, and golden-mantled ground squirrels are ground-dwelling prey items with similar habitats and primary food resources, these species may have corresponding functional roles within the goshawk food web. Moreover, the dependence of lagomorphs and ground squirrels on grasses and forbs suggests annual variation in their abundance is more likely to be synchronized. Consequently, since I could not estimate the abundance of lagomorph species, I used golden-mantled ground squirrel density estimates to approximate the abundance of all ground-dwelling prey.

I truncated the distance data for each species following the recommendations of Thomas et al. (2010) to make the data easier to model and improve the precision of the density estimates. I used the multiple-covariate analysis engine (MCDS) in program Distance so I could include both temporal and spatial covariates (i.e., year, cover type) in the estimation of detection probabilities. Use of the MCDS algorithm allowed an estimate of prey density per cover type per year for each prey species even if there were too few observations to fit a separate detection function to each subset of the data. For each prey species, I fit four models with different detection function covariates (none, year, cover type, or year+cover type) to the distance sampling data. The best approximating models were selected based on histogram and quantile-

quantile plots, χ^2 goodness-of-fit statistics, and Akaike's Information Criterion (AIC_c) values (Thomas et al. 2010). For each species, only the top model in the set had substantial support in the data; all other models had little to no support ($\Delta AIC_c > 8$). The best approximating model for Kaibab squirrel and golden-mantled ground squirrel density included no detection function covariates. The best approximating model for red squirrel, northern flicker, and Steller's jay density included additive effects of year and cover type covariates. I used the density estimates from the model with the smallest AIC_c in each set to quantify prey resources (Appendix D).

For each goshawk territory, I estimated the annual abundance of prey items per species by multiplying the area of each forest cover type within the territory by the corresponding annual density estimate and summing the resulting quantities. However, in some years, a small number of detections of mammal prey species precluded accurate annual density estimates per cover type (see Appendix D mixed conifer estimates for Kaibab squirrels in 2000). As a result, in calculations of the abundance of prey items per goshawk territory, I approximated annual density per cover type for prey species with ≤ 2 individuals detected as 0.001 individuals per ha (i.e., the smallest value possible) instead of using the larger density estimate from program Distance. In addition to estimating the abundance of Kaibab squirrels, red squirrels, golden-mantled ground squirrels, northern flickers, and Steller's jays, I also estimated prey abundance for categorical groupings of species that represent distinct functional groups. The arboreal grouping included two species of tree squirrels (Kaibab squirrel and red squirrel), and the aerial grouping included two bird species (northern flicker and Steller's jay). The mammal grouping consisted of tree squirrels and golden-mantled ground squirrel, and total prey abundance included all species in the mammal and aerial groupings. To account for differences in the detection probabilities of

prey species among the forest cover types, I calculated the density of each functional group per cover type per year by summing the individual density estimates for the species in the group.

Data Analysis

Estimation of reproduction with dynamic multistate occupancy models.— I used the dynamic multistate site occupancy model described by MacKenzie et al. (2009) to assess how temporal and spatial variation in climatic conditions, vegetation attributes, and prey abundance influenced the distribution of breeding goshawks. Using information from repeated surveys, this modeling framework allowed me to estimate annual changes in reproductive probabilities while accounting for imperfect detection of breeding goshawks. On each survey occasion, each goshawk territory under study was classified as being in one of three reproductive states: unoccupied by breeding adults (state 0 = no reproduction), occupied with reproduction but no fledglings produced (state 1 = eggs laid), or occupied with successful reproduction (state 2 = ≥ 1 young fledged). Because fledging does not occur until late in the breeding season, the reproductive state of territories may change within a season, so the annual state classification of each territory was based on the reproductive state at the end of each breeding season. The observed reproductive states are hierarchical in uncertainty regarding the true state of the territory, so the highest observed state (≥ 1 young fledged) has no ambiguity and the lowest observed state (no reproduction) has the greatest ambiguity about the true state (MacKenzie et al. 2009). For example, if evidence of ≥ 1 young fledged (state 2) was observed then the true state of the territory at the end of the breeding season cannot be state 1 or state 0. However, because goshawks that do not breed are difficult to detect, the true state of a territory classified as having no reproduction (state 0) could be unoccupied, occupied by one adult, occupied by two adults

without a breeding attempt, or a misclassified reproductive state if evidence of occupancy by breeding goshawks was missed. To estimate the transition probabilities for reproductive states among years, I used the conditional binomial parameterization of the dynamic multistate model $\Psi_t^{[m]} R_t^{[m]}$, where both the probability of transitioning to an egg-laying state ($\Psi_t^{[m]}$) and the probability of reproducing successfully ($R_t^{[m]}$) in year t depend on state m of the territory in the previous year (MacKenzie et al. 2009). For example, the probability of a territory transitioning between state 0 (no reproduction) in year $t-1$ to state 2 (≥ 1 young fledged) in year t is $\Psi_t^{[0]} R_t^{[0]}$, the product of the probability that eggs were laid in year t and the probability that young were fledged in year t given no reproduction in year $t-1$ and eggs were laid in year t .

I used the repeated surveys conducted over the course of the breeding season within each goshawk territory to estimate detection probabilities for each reproductive state. Detection probabilities were parameterized as $p^{[1]}(t, i)$, defined as the probability of detecting a breeding attempt (eggs laid) in year t during survey i , and $p^{[2]}(t, i)$, defined as the probability of detecting a successful breeding attempt (≥ 1 young fledged) in year t during survey i . I allowed the detection probabilities to vary over reproductive states, years, and surveys within years. Classification probabilities were parameterized as $\delta(t, i)$, defined as the probability of correctly identifying a successful breeding attempt during survey i , given eggs were laid in year t (MacKenzie et al. 2009). As in other studies that used dynamic multistate models to assess reproductive probabilities of raptors (e.g., Martin et al. 2009, MacKenzie et al. 2010), it was not possible to identify a successful breeding attempt (≥ 1 young fledged) early in the breeding season so I fixed δ to 0 for survey occasions 1-3. In my study, once the presence of breeding goshawks was confirmed, the site was checked weekly to determine nesting status, and the territory was surveyed again late in the breeding season to count the number of fledglings. Because the fourth

survey was only completed for territories with a breeding attempt at a known nest site, there was virtually no possibility of not detecting or misclassifying successful reproduction, which allowed me to fix the detection probabilities (p) and classification probabilities (δ) for the final survey occasion of each breeding season to 1.0.

Model development and selection.— Unbiased estimates of reproduction probabilities relative to site-specific environmental conditions are necessary to identify the factors influencing the reproductive responses of goshawks in a variable environment. Without accounting for imperfect detection of breeding goshawks, inferences regarding ecological dynamics may be misleading or inaccurate (MacKenzie et al. 2009). Thus, prior to modeling environmental covariates, I performed model selection on the set of models developed to describe temporal and spatial variation in the detection history data for goshawk territories (see below). Initially, I evaluated models that incorporated various constraints on detection parameters (p) as a function of year and survey occasion, and included models that were time-dependent or constant over time and dependent or independent of survey period. Then, using the best supported model structure for p , I evaluated models involving various constraints on the dynamic reproductive parameters $\Psi_t^{[m]}$ and $R_t^{[m]}$ that represent different hypotheses regarding how the distribution of territories with a breeding attempt and territories with ≥ 1 young fledged varied over time and space. For example, model $\{\Psi_{(.)} R_{(.)}\}$ assumed constant reproduction probabilities among years and territories, model $\{\Psi_{(\text{year})} R_{(\text{year})}\}$ assumed only annual variation in reproduction probabilities, whereas model $\{\Psi_{(\text{state+year})} R_{(\text{state+year})}\}$ assumed annual variation in reproduction probabilities was consistent among territories but varied over years, and model $\{\Psi_{(\text{state*year})} R_{(\text{state*year})}\}$ assumed annual variation in reproduction probabilities depended on the site-specific attributes of territories (i.e., reproductive state in the prior year, $t-1$). Because the

probability of producing ≥ 1 fledgling is conditional on eggs being laid, I considered models with only two states in year $t-1$ (state 0: no reproduction, state 1: 0 or ≥ 1 young fledged) in addition to models with three states in year $t-1$ (state 0: no reproduction, state 1: eggs laid, state 2: young fledged).

Using the structure from the best model without environmental covariates, I then evaluated how well models incorporating climatic conditions, vegetation attributes, prey abundance, or habitat attributes explained temporal and spatial variation in goshawk reproduction. Reproductive probabilities were modeled as logit functions of annual, site-specific covariates. The effects of environmental variables were assumed to be consistent regardless of reproductive state in the previous year and constraints on reproductive parameters were not applied to the probabilities associated with the first year of the study (MacKenzie et al. 2009). To evaluate the relative influence of environmental components on goshawk reproduction, I compared the weight of evidence, based on Akaike weights, for each of the top climate, vegetation, and prey models and the best supported model without environmental covariates (see below).

I used a four-step strategy to model the hypothesized effects of climatic conditions, vegetation attributes, prey resources, and the combined effects of these environmental attributes on the reproductive parameters of goshawks (Table 1). First, I explored the relationships between annual climatic conditions and goshawk reproduction with models incorporating different combinations of site-specific covariates for ambient temperature and precipitation. I hypothesized that annual reproduction probabilities increase with temperate and mesic conditions that 1) reduce the energetic demands of thermoregulation for adult and nestling goshawks, and 2) increase the production of food resources for prey species and, consequently, the abundance of

prey items. Thus, for probabilities of transitioning to an egg-laying state $\Psi_t^{[m]}$, I predicted positive effects of warmer temperatures and high annual precipitation prior to egg-laying that enhance the ability of adult goshawks to meet energetic constraints for thermoregulation and egg production. For successful reproduction probabilities $R_t^{[m]}$, I predicted positive effects of warm temperatures that reduce the energetic demands of thermoregulation for nestlings and greater amounts of precipitation during the breeding season that increase the abundance of prey resources and, consequently, the more consistent presence of the adult female at the nest.

Second, I explored relationships between vegetation attributes and goshawk reproduction with models incorporating different combinations of site-specific covariates for canopy cover, conifer cone production, proportion of forest cover types, mean patch size of high-density cover types, and maximum patch size of intensive silvicultural treatments. Because most vegetation attributes were fixed for the duration of the study period, I also incorporated models that allowed the effects of forest structural components to vary annually. In addition, I also used covariates for the dimensions and vegetation composition of goshawk territories including territory size and distance to the nearest boundary between forest types. I hypothesized that annual reproductive probabilities should be higher for goshawks with territories that have greater amounts of vegetation attributes that enhance the availability of food resources by influencing the abundance and distribution of prey species with distinct ecological niches. Thus, for the probability of transitioning to an egg-laying state $\Psi_t^{[m]}$, I predicted positive effects of higher canopy closure, larger cone crops, more diverse forest cover types, larger areas with a high-density of mature trees, and smaller patches of extensive timber harvests. I hypothesized that the likelihood of producing ≥ 1 fledgling per breeding attempt increases with vegetation attributes that enhance the abundance of food resources for prey species and prey populations and those that reduce edge

effects or the abundance of nest predators. Thus, for successful reproduction probabilities $R_t^{[m]}$, I predicted positive effects of higher canopy closure, greater cone production, and larger areas of high-density cover types and negative effects of greater proportions of low-density cover types (i.e., predator habitat).

Third, I explored the relationships between prey resources and goshawk reproduction with models incorporating different combinations of covariates for the abundance of prey species. I compared models that included individual and additive effects of prey on goshawk reproduction, but I primarily used combinations of covariates for species with distinct ecological niches. I hypothesized that annual reproduction probabilities would be higher for territories with more abundant prey resources that enhance goshawk encounter rates with prey items. Thus, for reproduction probabilities $\Psi_t^{[m]}$ and $R_t^{[m]}$, I predicted positive effects of more abundant prey items per species (i.e., number of individuals) and species with diverse functional traits.

Finally, I compared the top-ranked model with environmental covariates from each model set (climate, vegetation, and prey) and models containing variables for the effects of prey biomass or covariates for habitat attributes that incorporate variation in the availability of environmental resources among goshawk territories to assess the weight of evidence for hypotheses regarding goshawk-habitat relationships. Specifically, I compared models that incorporated the additive effects of: 1) climatic conditions and vegetation attributes, 2) climatic conditions and prey resources, and 3) vegetation attributes and prey resources on goshawk reproduction. For models that incorporated the effects of climate and vegetation, I hypothesized that annual reproduction probabilities should be higher for goshawk territories with greater amounts of vegetation attributes that ameliorate the effects of drought and increase the abundance and diversity prey species. Thus, for egg-laying ($\Psi_t^{[m]}$) and successful reproduction

($R_t^{[m]}$) probabilities, I predicted positive effects of vegetation attributes (e.g., larger patches of high-density cover, more diverse forest types) that reduce evaporation of soil moisture, enhance the production of food resources for prey species with distinct ecological niches, and, consequently, increase the abundance of prey items during and preceding drought. For the model that incorporated the effects of weather and prey on goshawk reproduction, I hypothesized that more abundant and diverse prey resources within goshawk territories enhance the likelihood of the adults obtaining sufficient food to meet the energetic demands of thermoregulation and reproduction, especially when climatic conditions are harsh. Here, I predicted positive effects of warm ambient temperatures and more abundant prey items on goshawk reproduction probabilities $\Psi_t^{[m]}$ and $R_t^{[m]}$. For the model that incorporated the effects of vegetation and prey on goshawk reproduction, I hypothesized annual reproduction probabilities are higher for territories with more abundant food resources for prey species and more diverse prey communities that increase the availability of prey items necessary for goshawks to produce eggs and fledglings when environmental resources are limited. As a consequence, I predicted positive effects of high cone production and more abundant prey species with distinct functional traits on $\Psi_t^{[m]}$ and $R_t^{[m]}$. For the model that incorporated covariates for the biomass contribution of prey species to goshawk diets, I hypothesized that greater proportions of large prey species (e.g., cottontail rabbit, black-tailed jackrabbit) enhance the production of eggs and fledglings by increasing the ability of adult goshawks to meet energetic constraints of reproduction, especially when food resources are limited. In this case, I predicted positive effects of goshawk diets containing greater proportions of lagomorphs and larger squirrels on annual reproductive probabilities $\Psi_t^{[m]}$ and $R_t^{[m]}$.

Since producing ≥ 1 fledgling depends on eggs being laid, I first evaluated models incorporating the effects of environmental components on breeding probabilities with successful reproduction constant among years and territories. Then after identifying environmental covariates that had the greatest effect on variation in breeding probabilities, I evaluated the effects of additional environmental attributes on successful reproduction probabilities. I used Program MARK (Version 7.1, G. C. White, Colorado State University, Fort Collins, CO) to estimate the parameters of the dynamic multistate occupancy models and conduct model selection using maximum likelihood techniques. I used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to objectively rank, compare, and select the best approximating model during each stage of my analysis (Burnham and Anderson 2002). To assess the competitiveness of ranked models, I used renormalized AIC_c weights (Burnham and Anderson 2002). I also determined the size and direction of covariate effects on goshawk reproductive parameters based on the sign of the beta estimates and the degree to which 95% confidence intervals overlapped zero (Graybill and Iyer 1994). I report all estimates \pm SE unless stated otherwise. Currently, there is no goodness-of-fit test available for dynamic multistate occupancy models (G. C. White and L. L. Bailey, Colorado State University, personal communication). However, there is no reason to suspect a lack of fit due to a violation of model assumptions (i.e., independence among sites or closure to changes in reproductive status among years) because goshawks are a territorial species with high site-fidelity ($\geq 94\%$) among breeding seasons (Reynolds et al. 2005). As a result, I compared models that represent hypotheses regarding the influence of habitat attributes on the reproductive responses of goshawks, to evaluate which environmental components were the most parsimonious explanation of temporal and spatial variation in goshawk reproduction given the data.

RESULTS

Goshawk Reproduction

Annual variation.— Goshawk reproduction during 1999-2004 was highly variable among years (Table 2). The coefficient of variation (CV) was 56% for number of breeding attempts (eggs laid), 71% for successful breeding attempts (≥ 1 young fledged), and 83% for total number of young fledged per year. In contrast, the mean number of young fledged per successful breeding attempt was less variable among years (CV = 22%) and was higher in 1999, 2000, and 2004 than in 2001-2003.

Spatial distribution.— Although the spatial arrangement of all 102 goshawk territories was evenly distributed throughout the Kaibab Plateau study area (Fig. 6), the annual distribution of goshawk territories with a breeding attempt varied among years and across the study area during 1999-2004. In 1999 and 2000, 53 and 61 goshawk territories with a breeding attempt were evenly dispersed throughout the study area within both ponderosa pine and mixed conifer forest (Fig. 7 and 8). In 2001, during the first year of drought, 28 goshawk territories with a breeding attempt were primarily located within ponderosa pine forest and the northern two-thirds of the study area where the size of intensively-harvested management units was smaller (Fig. 2 and 9). In 2002, during the second year of drought, 19 territories with a breeding attempt were primarily located in the middle of the study area and predominantly consisted of lightly-harvested ponderosa pine and mixed conifer cover types with a high-density of mature trees (Fig. 10). In 2003, during extreme drought, the few territories with a breeding attempt ($n = 10$) contained primarily ponderosa pine cover types and most territories were located in the northern two-thirds of the study area and in close proximity to the study area boundary and alternate cover types at

lower elevations (e.g., pinyon-juniper; Fig. 11). In 2004, when annual precipitation was above average, the 41 goshawk territories with a breeding attempt were once again more evenly distributed throughout the study area and among the forest cover types (Fig. 12).

Over the 6-year study period, 73 of 102 territories had ≥ 1 observed breeding attempt. The number of annual breeding attempts per territory ranged from 0 attempts ($n = 29$ territories) to 6 attempts ($n = 1$ territory) in 6 years. Rates of successful breeding attempts ranged from 0% ($n = 2$ territories) to 100% for ≥ 1 breeding attempt ($n = 37$ territories). For territories with ≥ 1 successful breeding attempt, the mean number of young fledged per territory per year during 1999-2004 ranged from 0.17 ($n = 5$ territories) to 2.00 ($n = 1$ territory). Over the 6-year study period, ≥ 1 fledgling was produced per year on 30 of 102 goshawk territories.

Reproduction model results.— Model selection results ($\Delta AIC_c > 2$) for detection probabilities indicated that detection rates of breeding attempts and successful reproduction were similar [$p^{[1]}(t, i) = p^{[2]}(t, i)$], but varied among years and surveys $\{p(\text{year, survey})\}$ with equivalent detection probabilities for surveys 1-3 and a different detection probability for survey 4. In 1999-2003, 86-95% of breeding attempts were detected during the first survey, whereas only 66% of breeding attempts were detected in 2004 (Table 2). In contrast, in 1999-2003, 0-10% of breeding attempts were detected during the third survey, whereas 29% were detected in 2004. Consequently, estimates of annual detection probabilities were generally high during 1999-2003 and ranged from 0.81 ± 0.08 to 0.95 ± 0.05 . However, after 3 years of drought when fewer goshawks attempted to breed annually, the probability of detecting a breeding attempt was only 0.40 ± 0.12 in 2004.

Out of 62 models incorporating effects of current year conditions and territory reproductive state in the prior year on goshawk reproduction, the best supported model

$\{\Psi(\text{state2}*\text{year}) R(\text{year})\}$ indicated variation in the probability of transitioning to an egg-laying state depended on within-year variation in the site-specific attributes of each territory, whereas the probability of producing ≥ 1 fledgling only varied among years (Table 3, Appendix E). Models that incorporated only reproductive state, year, or additive effects of state and year on Ψ were not supported in the data, indicating that egg-laying probabilities were not consistent among years, territories, or territories within years. The top ranked model $\{\Psi(\text{state2}*\text{year}) R(\text{year})\}$ accounted for 56% of the model Akaike weights. Since an additional covariate for reproductive state in the second-ranked model $\{\Psi(\text{state2}*\text{year}) R(\text{state2}+\text{year})\}$ did not add additional information (based on little change in $-2l$ values), I used the structure of the top model without environmental covariates in subsequent analyses to evaluate the relative effects of each environmental component (climate, vegetation, prey, habitat) on goshawk reproduction.

Annual variation in goshawk reproduction.— Under the best supported model, annual probabilities of transitioning to egg-laying state during the study period ranged from 0.02 (SE = 0.02, 95% CI = 0.00, 0.16) in 2001 to 0.51 (SE = 0.11, 95% CI = 0.30, 0.72) in 2004 for territories with no reproduction in the previous year and from 0.16 (SE = 0.08, 95% CI = 0.05, 0.39) in 2003 to 0.90 (SE = 0.04, 95% CI = 0.79, 0.95) in 2000 for all territories with a breeding attempt in the previous year regardless of the number of young fledged (i.e., 0-4 fledglings; Appendix F). In contrast, annual probabilities of successful reproduction (≥ 1 young fledged) ranged from 0.53 (SE = 0.11, 95% CI = 0.31, 0.73) in 2002 to 0.89 (SE = 0.04, 95% CI = 0.78, 0.94) in 2000. Overall, year-specific probabilities of producing ≥ 1 fledgling were much less variable over time (CV = 22%) than annual egg-laying probabilities for territories with a successful (CV = 60%) or failed (CV = 97%) breeding attempt in the prior year.

Influence of Climatic Conditions

Temporal variation in climatic conditions.— Climatic conditions varied extensively during 1999-2004 due to an extended drought during 2001-2003 and record high annual precipitation in 2004. Mean annual (April-March) precipitation averaged over all territories varied among years (CV = 37%) and ranged from 37.2 ± 0.3 cm in 2001 to 92.9 ± 1.0 cm in 2004 (Fig. 13). Mean ambient temperature prior to egg laying during March-April was less variable among years (CV = 13%); ranging from 9.4 ± 0.1 °C in 2003 to 13.2 ± 0.2 °C in 2004. Mean ambient temperature during the breeding season (April-August) was the least variable among years (CV = 7%) and ranged from 18.4 ± 0.1 °C in 1999 to 22.4 ± 0.1 °C in 2002.

Spatial variation in climatic conditions.— Relative to annual variation in mean precipitation and maximum temperature among years, most climatic covariates were less variable among goshawk territories over the 6-yr study period. During 1999-2004, mean annual precipitation varied the most among territories (CV = 10%) and ranged from 45.4 ± 6.9 cm to 70.0 ± 11.4 cm, whereas mean temperatures prior to the egg-laying period (March-April) were less variable (CV = 9%) and ranged from 9.6 ± 0.7 °C to 13.1 ± 0.5 °C. Mean temperatures during the breeding season (April-August) were the least variable among territories (CV = 7%) and ranged from 17.8 ± 0.6 °C to 23.6 ± 0.6 °C.

Climate model results.— The model without environmental covariates, $\{\Psi(\text{state} \times \text{year}) R(\text{year})\}$, accounted for 100% of the AIC_c model weight and explained more variation in goshawk reproduction than any models that incorporated climatic covariates (Table 4). Because the top model without environmental covariates contained an interaction between territory reproductive state and year for egg-laying probabilities, it incorporated the effects of both spatial and temporal variation on the distribution of goshawk territories with reproduction. In contrast,

models with climatic covariates primarily incorporated effects of temporal variation in environmental attributes on reproductive parameters due to greater among-year variation in regional climatic conditions relative to among-territory variation in precipitation and ambient temperature during the study period. Consequently, variation in climatic conditions explained less spatial variation in goshawk reproduction than the top model without environmental covariates.

Of models incorporating climatic covariates, $\{\Psi(\text{RAIN}_{2\text{avg}}*\text{TEMP}_{\text{egg}}) R(\text{RAIN}_{\text{hatch}})\}$ had the most support in the goshawk reproductive data. This model included an interaction between 2-yr average annual precipitation prior to the current breeding season and average ambient temperature during March-April on egg-laying probabilities and effects of precipitation during the 3-weeks post-hatching on successful reproduction probabilities (Table 4). The top ranked model incorporating climatic covariates indicated that breeding probabilities increased in years with higher annual precipitation and warmer temperatures prior to egg-laying ($\beta_{\text{RAIN}_{2\text{avg}}*\text{TEMP}_{\text{egg}}} = 0.005$, SE = 0.002, 95% CI = 0.002, 0.008). The high ranking of models incorporating an interaction between ambient temperature and annual precipitation and the larger effect of temperature ($\beta_{\text{TEMP}_{\text{egg}}} = -2.11$, SE = 0.80, 95% CI = -3.86, -0.54) relative to precipitation ($\beta_{\text{RAIN}_{2\text{avg}}} = -0.05$, SE = 0.02, 95% CI = -0.09, -0.02) on egg-laying probabilities supported my hypothesis that energetic constraints of thermoregulation limited egg production, especially during drought. More precipitation during the 24-day brooding period had a positive effect on annual probabilities of producing ≥ 1 fledgling ($\beta_{\text{RAIN}_{\text{hatch}}} = 0.12$, SE = 0.04, 95% CI = 0.05, 0.20) and supported the hypothesis that the effect of precipitation on the abundance of food resources influences nest attendance by the adult female and, therefore, goshawk reproductive success. Based on estimates of egg-laying probabilities from the best supported model in the

climate model set (Table 4), warmer ambient temperatures regardless of 2-yr average precipitation (2000, 2004) were more productive than cool and wet conditions in 2001, whereas cool and wet conditions in 2001 were more productive than warmer and drier conditions in 2002, and cold and dry conditions in 2003 were the least productive (Fig. 14).

Influence of Vegetation Composition and Structure

Spatial variation in vegetation attributes.— There were substantial differences in vegetation attributes among goshawk territories (Fig. 15). The proportion of forest cover types within each territory ranged from 0.01 to 0.71 for lightly-harvested ponderosa pine (high-density pine), from 0.01 to 0.70 for both intensively-harvested ponderosa pine (low-density pine) and lightly-harvested mixed conifer (high-density mix), and from 0 to 0.49 for intensively-harvested mixed conifer (low-density mix). The coefficient of variation for the proportion of each cover type among goshawk territories was higher for low-density mix (111%) and high-density mix (108%) than for low-density pine (71%) or high-density pine (53%). Overall, 57% of territories were predominantly (>75%) ponderosa pine, whereas only 24% of goshawk territories were primarily mixed conifer forest. In addition, only 10% of territories contained >75% of high-density cover types (ponderosa pine, mixed conifer) and no territories contained >75% low-density cover. Although patch size varied extensively among territories for area of high-density cover (CV = 125%) and extensive timber harvests (CV = 124%), territory size was much less variable among sites (CV = 27%). Mean cone production per tree was the most consistent vegetation attribute among territories during the 6-year study period (CV = 5%) and ranged from 21.12 ± 3.23 to 25.16 ± 9.11 cones per tree for all species.

Temporal variation in vegetation attributes.— Most vegetation covariates were fixed over the 6-yr study period, so only the abundance of food resources for prey species varied among years. Mean cone production per tree for all conifer species was more variable among years than among territories (CV = 29%) and ranged from a high of 31.4 ± 0.33 cones in 2000 to a low of 12.2 ± 0.02 cones in 2002. Overall, food resources for prey species were less abundant during drought years (2001-2003).

Vegetation model results.— The model without environmental covariates, $\{\Psi(\text{state} \cdot \text{year}) R(\text{year})\}$, accounted for 84% of the AIC_c model weight and explained more variation in goshawk reproduction than any of the models that included vegetation covariates (Table 5). However, the best-ranked model incorporating vegetation $\{\Psi(\text{tPINEhigh} + \text{tMIXhigh} + \text{tPINElow} + \text{tMIXlow}) R(\text{CONEall})\}$ also had some support in the data with 14% of the weight of evidence. This model contained time-dependent effects of all 4 cover types (high-density pine, high-density mix, low-density pine, low-density mix) on egg-laying probabilities and the effects of conifer cone production on successful reproduction probabilities. All other models incorporating vegetation covariates had no support in goshawk reproduction data. As expected, larger cone crops for all conifer species had a positive effect on fledgling production ($\beta_{\text{CONEall}} = 0.07$, SE = 0.02, 95% CI = 0.02, 0.11) and suggested more abundant food resources for prey may have enhanced the ability of adults to provision nestlings and to defend the nest from predators. Although I found no clear relationships between annual egg-laying probabilities and time-dependent effects of forest cover type, models that allowed the effect of each cover type to vary over time were consistently ranked higher than the same models with cover types fixed over time (Table 5). This indicated that the effect of forest cover type on egg-laying probabilities varied among years. Moreover, when I compared forest composition averaged over annual samples of goshawk

territories with a breeding attempt relative to mean proportions of cover types averaged over all 102 territories, I found that in non-drought years (2000, 2004) the composition of cover types was similar among all territories (Fig. 16). In contrast, during drought, the forest composition of territories with reproduction varied among years and differed from the mean proportions of cover types for all territories regardless of reproductive state. In 2001 and 2003, most territories with a breeding attempt were primarily composed of ponderosa pine cover types (high-density and low-density), whereas in 2002 they predominantly consisted of high-density cover types (ponderosa pine and mixed conifer). This suggested that when water resources were limited, the availability of resources necessary for goshawks to reproduce were restricted to fewer cover types. Consequently, goshawks occupying territories with heterogeneous forest composition were more likely to produce eggs during drought. Because high-density pine, high-density mix, and low-density pine encompass the habitat attributes of Kaibab squirrels, red squirrels, and golden-mantled ground squirrels, respectively, territories with greater proportions of all forest cover types may have increased access to alternate prey species. Overall, these results provide support for the hypothesis that a greater diversity of ecological niches increased egg-laying probabilities by enhancing the availability of food resources necessary for goshawks to reproduce, especially during drought.

Influence of Prey Abundance

Temporal variation in prey resources.— In 1999-2004, the estimated number of prey items per goshawk territory varied extensively among years for most species (Fig. 17). Overall, prey abundance was higher in 1999 and 2000 prior to drought and lower in 2001-2003 during the drought. Following drought, the abundance of most species increased in 2004. However, Kaibab

squirrels, red squirrels, northern flickers, and Steller's jays were less abundant in 2004 than prior to drought in 2000. In contrast, the abundance of golden-mantled ground squirrels was highest in 2004 during a wet year proceeding drought. Although annual abundances of each prey species varied among years, the magnitude of fluctuations in abundance was much larger for some species. The among-year coefficient of variation was 36% for Steller's jay, 55% for northern flicker, 60% for Kaibab squirrel, 85% for golden-mantled ground squirrel, and 105% for red squirrel. Overall, annual variation in the abundance of prey items per territory was greater for mammals than for birds, especially red squirrels.

Spatial variation in prey resources.— Over the 6-yr study period, the estimated abundance and distribution of prey items among goshawk territories varied by species. During 1999-2004, the mean number of prey items per territory was 89 ± 4 for Kaibab squirrel, 272 ± 7 for Steller's jay, 424 ± 14 for northern flicker, 705 ± 57 for red squirrel, and 998 ± 34 for golden-mantled ground squirrel. Moreover, the distribution of prey species within goshawk territories varied among forest cover types (Fig. 18). Kaibab squirrels were more abundant in high-density pine, red squirrels were more abundant in high-density mix, and golden-mantled ground squirrels were more abundant in low-density cover types, especially ponderosa pine. In contrast, northern flicker abundance was similar among the cover types, whereas Steller's jays were more abundant in ponderosa pine than in mixed conifer. The coefficient of variation among cover types was 121% for Kaibab squirrel, 114% for red squirrel, 105% for golden-mantled ground squirrel, 50% for Steller's jay, and 17% for northern flicker. Together, these differences in the distribution of prey species among cover types indicated that mammal species were more habitat specialists relative to the bird species. In addition, the distribution of species also varied among goshawk territories during 1999-2004. The among-territory coefficient of variation was 27% for Steller's

jay, 33% for northern flicker, 34% for golden-mantled ground squirrel, 45% for Kaibab squirrel, and 82% for red squirrel. Thus, bird and ground squirrel prey items were more evenly distributed throughout the study area, whereas tree squirrels were restricted to fewer goshawk territories.

Prey model results.— In contrast to models incorporating variables for climatic conditions or vegetation attributes, models containing covariates for prey abundance accounted for considerably more variation in goshawk reproduction than the top-ranked model without environmental covariates ($\Delta AIC_c = 12.9$; Table 6). The model with the most support in the goshawk reproductive data, $\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}) R(\text{Kaibab}+\text{Flicker})\}$, had 36% of the weight of evidence. This model incorporated the effects of the abundance of Kaibab squirrels, red squirrels, and golden-mantled ground squirrels on egg-laying probabilities, and the effects of the abundance of Kaibab squirrels and northern flickers on successful reproduction probabilities. As predicted, the best-supported model incorporating prey covariates indicated that goshawk reproductive probabilities were higher in years and on territories with more abundant populations of alternate prey resources. Annual egg-laying probabilities were positively associated with greater numbers of prey items per territory for Kaibab squirrels ($\beta_{\text{Kaibab}} = 0.052$, SE = 0.011, 95% CI = 0.031, 0.073), red squirrels ($\beta_{\text{Red}} = 0.004$, SE = 0.001, 95% CI = 0.002, 0.005), and golden-mantled ground squirrels ($\beta_{\text{Ground}} = 0.005$, SE = 0.001, 95% CI = 0.002, 0.007). In contrast, there was no clear relationship between annual fledging probabilities and the abundance of Kaibab squirrels ($\beta_{\text{Kaibab}} = 0.029$, SE = 0.016, 95% CI = -0.003, 0.062) or northern flickers ($\beta_{\text{Flicker}} = 0.006$, SE 0.004, 95% CI = -0.002, 0.013). The high ranking of the model containing individual covariates for all three mammal species relative to the model containing one covariate for all mammals ($\Delta AIC_c = 30.31$) or the model incorporating additive effects of all five prey species ($\Delta AIC_c = 8.54$), indicated that the abundance of species with distinct ecological niches explained

more temporal and spatial variation in goshawk egg-laying probabilities than the abundance of all prey items per se. Moreover, the effects of mammal species were year-specific (Fig. 19). All goshawk territories regardless of reproductive state contained more Kaibab squirrels, red squirrels, and golden-mantled ground squirrels in non-drought years than in drought years. However, during drought, most territories with reproduction contained only more Kaibab squirrels and ground squirrels in 2001 and 2003 or only more red squirrels in 2002. Consequently, within- year variation in the abundance of mammal species among territories had the greatest influence on goshawk breeding probabilities and provided support for the hypothesis that the abundance of prey species with distinct ecological niches enhances the availability of prey items necessary for reproduction in a variable environment.

Influence of Habitat

Spatiotemporal variation in the abundance of environmental resources.— Relative to mean annual precipitation during 1925-2004 (61 ± 3 cm; Fig. 13), cumulative precipitation within the study area was above average in 1997 (73.5 ± 0.8), below average in 1998 (53.3 ± 0.4), average in 1999 (62 ± 0.05 cm), below average in 2000 (49 ± 0.04 cm), 2001 (37 ± 0.03 cm), 2002 (48 ± 0.04 cm) and 2003 (41 ± 0.03 cm), and much higher than average in 2004 (93 ± 0.08). Thus, years with greater annual precipitation in the prior and/or current year resulted in increased water availability in 1999, 2000, and 2004 relative to 2001, 2002 and 2003 when precipitation in both years was below average. Moreover, variation in the amount of annual precipitation influenced the production of conifer cones among forest cover types. Annual precipitation was highly and positively correlated with ponderosa cone production in both high-density ($n = 6, r = 0.93, P < 0.01$) and low-density ($n = 6, r = 0.86, P = 0.03$) mixed conifer,

whereas there was no correlation with cone production in high-density ($n = 6$, $r = -0.27$, $P = 0.60$) or low-density ponderosa pine ($n = 6$, $r = 0.16$, $P = 0.77$). Prior to drought, ponderosa pine cone crops were higher in pine cover types, but subsequent to consecutive years with below-average precipitation, ponderosa pine trees in mixed conifer cover types produced as many or more cones than trees in ponderosa pine cover types in 2002-2004 (Fig. 20). Differences in ponderosa cone production among the forest cover types suggested an influence of landscape characteristics (e.g., elevation, aspect, slope) and vegetation attributes (e.g., density of mature trees, understory vegetation) on soil moisture. As a result, the forest cover types with more abundant food resources for prey species likely varied among years.

The rate at which the abundance of prey items changed over time within and among forest cover types varied among species (Fig. 21). The abundance of golden-mantled ground squirrels was relatively constant within cover types among years during 1999-2003, but in a year with record-high precipitation (2004), their abundance increased in all cover types including in high-density mix, a cover type they had been previously absent from. In contrast, red squirrels were more abundant within all cover types in 1999 and 2000, but during drought they were less abundant in high-density mix than in most alternate cover types prior to drought and all other cover types only contained few individuals. Following drought, despite increases in the number of prey items per cover type, red squirrel abundance remained well below pre-drought levels. Overall, Kaibab squirrels were most abundant in high-density pine, but after two years with below-average precipitation, they were more evenly distributed among all cover types when ponderosa pine cone production was more consistent across the study area (Fig. 20). As a result, the abundance and distribution of each mammal species varied among years and cover types.

During the 6-year study period, cottontail rabbits contributed the largest proportion of total biomass to goshawk diets every year of the study except in 2003, at the height of the extended drought, when black-tailed jackrabbits contributed >52% of total biomass (Fig. 22). Despite increases in the abundances of most prey species between 2003 and 2004, goshawk diets primarily consisted of cottontail rabbits (64%) in 2004. However, in years when the abundances of most prey species was high (e.g., 2000), the contribution of each species to annual goshawk diets was more evenly distributed among all prey species. Moreover, species that composed <4% of the total dietary biomass during the study period contributed twice as many individuals (25%) to annual goshawk diets in 2000 than in any other year. Consequently, the diversity of annual goshawk diets was greater in years when the abundance of all food resources was higher.

The biomass contribution of each prey species to annual goshawk diets also varied among years (Fig. 22). The biomass contribution of Kaibab squirrels to annual goshawk diets was 1% in 1999, 10-18% in 2000-2002, and $\leq 3\%$ in 2003 and 2004. The biomass contribution of red squirrels to annual diets was 8-12% in 1999-2000 and $\leq 3\%$ in 2001-2004. The biomass contribution of golden-mantled ground squirrels was $\leq 1\%$ in 1999-2001 and 2004, whereas no individuals were identified in annual samples of goshawk diets in 2002 and 2003. The biomass contribution of northern flickers to annual diets was 6-10% in 1999-2002 and <2% in 2003-2004. In contrast, the biomass contribution of Steller's jays to annual goshawk diets was relatively constant over time (2-6%). Most diet samples were obtained from goshawk territories with a breeding attempt, and because the abundance and distribution of mammal prey species varied among years and forest cover types, annual differences in the species composition of goshawk diets reflect variation in the abundance of prey resources among goshawk breeding sites.

Habitat model results.— The model incorporating covariates for variation in the food resources of prey species and the diversity of the prey community had more support in the goshawk reproductive data than the top-ranked model in each of the climate, vegetation, and prey model sets (Table 7). Model $\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}+\text{CONEpine}) R(\text{CONEpine})\}$ accounted for 74% of the weight of evidence and incorporated the effects of ponderosa pine cone production and the abundance of Kaibab squirrels, red squirrels, and golden-mantled squirrels on annual egg-laying probabilities, and the effects of ponderosa pine cone crops on successful reproduction probabilities. Moreover, only models containing functional attributes of goshawk breeding habitat had some support in the data. Overall, these model selection results provided evidence that variation in goshawk reproduction was primarily a function of temporal variation in the abundance of prey items and spatial variation in the distribution of prey species that influences the availability of food resources necessary for goshawks to reproduce. Consequently, variation in the abundance of mammal prey species among goshawk territories can be used to identify the attributes of high-quality breeding habitat under changing climatic conditions.

Reproductive responses of goshawks.— Based on estimates from best supported model incorporating habitat attributes, annual probabilities of transitioning to egg-laying state were lowest in 2003 and highest in 2004 and ranged from 0.06 ± 0.01 to 0.47 ± 0.09 for territories with no reproduction in the previous year and from 0.31 ± 0.05 to 0.85 ± 0.06 for all territories with a breeding attempt in the previous year regardless of the number of young fledged (i.e., 0-4 fledglings; Fig. 23). Annual egg-laying probabilities were higher for territories with consecutive breeding attempts (consistent reproduction) than those with no reproduction in the prior year (intermittent reproduction). In contrast, annual probabilities of producing ≥ 1 fledgling did not depend on the site-specific attributes of territories. Successful reproduction probabilities ranged

from a low of 0.56 ± 0.08 in 2002 to a high of 0.82 ± 0.04 in 2004 (Fig. 23). As a result, annual egg-laying probabilities varied among years for both territories with intermittent reproduction (CV = 91%) or consistent reproduction (CV = 41%) and declined significantly during drought, whereas successful reproduction probabilities were relatively constant among territories and less variable over time (CV = 15%). This suggested that within-year variation in the abundance of mammal prey species among territories primarily affected goshawk reproduction by influencing the availability of food resources necessary to meet the energetic constraints of egg production during drought. Moreover, because the habitat model with the most support in the goshawk reproductive data incorporated covariates for prey species with distinct ecological niches, I used differences in three functional traits of the mammal prey species to identify how the attributes of breeding habitat influenced the egg-laying probabilities of goshawks under changing climatic conditions.

First, I considered the magnitude and frequency of fluctuations in the annual abundances of mammal species. The abundances of all mammal prey varied among years, but the rate and magnitude of fluctuations in abundance varied by species (Fig. 17). Kaibab squirrels were likely a more consistent food resource due to reduced fluctuations in their abundance over the 6-yr study period. In contrast, red squirrels were a more variable food resource among years due to the magnitude of annual fluctuations in their abundance during and preceding drought. Although the abundance of golden-mantled ground squirrels was relatively constant among years prior to and during drought, the number of individuals per goshawk territory was much higher in the year after drought. Consequently, among-year variation in the abundance of prey items for each mammal species was associated with the frequency of annual breeding attempts for goshawks on the Kaibab Plateau (Fig. 24). Goshawk territories without a breeding attempt in

consecutive years contained fewer Kaibab squirrel and red squirrel prey items. However, both territories with intermittent or consecutive breeding attempts contained equivalent numbers of Kaibab squirrels, whereas most territories with consecutive breeding attempts contained more red squirrel prey items than territories with intermittent breeding attempts. In contrast, territories with no reproduction or consecutive breeding attempts had fewer golden-mantled ground squirrels than territories with intermittent breeding attempts. This suggested that annual variation in the abundances of each mammal species among goshawk territories influenced the frequency of breeding attempts during and following drought.

Next, I considered differences in the primary habitats of the mammal prey species. Over the 6-yr study period, Kaibab squirrels were most abundant in high-density ponderosa pine, red squirrels were most abundant in high-density mixed conifer, and golden-mantled ground squirrels were more abundant in low-density cover types, especially ponderosa pine (Fig. 18). As a result, differences in the distribution of prey species with distinct functional traits among years and territories suggested that greater heterogeneity of forest compositional attributes enhanced goshawk reproductive output by increasing the diversity of the prey community and reducing annual variation in the abundance of food resources.

Finally I considered differences in individual prey items among the mammal species. Given variation in the average biomass of mammal species (Appendix A), larger prey items may have enhanced energy gained per unit effort, especially when the abundances of most prey species were reduced which decreased the likelihood of goshawks encountering additional prey items. Thus, although increased breeding probabilities of goshawks were associated with higher estimated abundances of all mammals per territory, the relationship varied by species (Fig. 25). The annual abundance of Kaibab squirrels ($r^2 = 0.83$, $P = 0.03$) accounted for the most variation

in reproduction probabilities for goshawk territories with consecutive breeding attempts in the prior and current year, followed by red squirrels ($r^2 = 0.55$, $P = 0.15$), and golden-mantled ground squirrels ($r^2 = 0.50$, $P = 0.18$). In most years of the study, the incremental increase in egg-laying probabilities per individual prey item was greater for larger prey such as Kaibab squirrels (697 g) relative to red squirrels (212 g) and golden-mantled ground squirrels (195 g). This suggested that heavier prey items had a greater influence on the availability of food biomass necessary for the energetic constraints of egg production, especially during drought when declines in the abundances of most mammal species reduced the number of all potential prey items within goshawk breeding habitat.

I further explored the effects of habitat attributes on the reproductive responses of goshawks by comparing the diversity of prey resources within each territory. Annual variation in the distributions of mammal species among the forest cover types influenced the abundance of alternate prey populations within each goshawk territory, especially during drought when there were fewer individuals of most prey species in their primary cover types (Fig. 21). Consequently, the frequency of annual breeding attempts among goshawk territories was associated with the abundances of different mammal species with distinct ecological niches (Fig. 24). Goshawk territories with consecutive breeding attempts contained greater numbers of drought-resistant prey species like Kaibab squirrels; species with food resources that enable them to withstand short-term declines in annual precipitation due to longer cone production cycles (>2-yr) and greater year-round availability (e.g., cambium from subterminal twigs). Goshawk territories with intermittent breeding attempts contained more prey items of drought-resilient species like golden-mantled ground squirrels; species with food resources that increase more rapidly following severe drought due to shorter vegetation growth cycles (e.g., grasses and forbs). In

contrast, due to seasonal food caches and shorter cone production cycles (<1-yr), red squirrels have food resources that enable them to withstand short-term droughts and respond more quickly to annual variation in precipitation. Thus, both goshawk territories with consecutive or intermittent breeding attempts contained greater numbers of red squirrel prey items. Because prey species differed in availability (Fig. 17), habitat (Fig. 18), and efficiency (Fig. 25), goshawk territories that contained a greater diversity of prey species with distinct functional traits were associated with higher annual egg-laying probabilities for territories with intermittent or consistent breeding attempts (Fig. 26). This indicated that breeding habitat that contained heterogenous compositional and structural attributes enhanced the reproductive output of goshawks by mitigating the effects of changing climatic conditions on the availability of food resources during and following drought.

DISCUSSION

Although my study period for this research was only six years (1999-2004), it included both extreme drought and record high annual precipitation. These extreme climatic conditions enhanced the identification of the thresholds for goshawk reproduction. Furthermore, the geographically isolated, 1,285-km² forested study area included a variety of different forest cover types used by breeding goshawks. Because I incorporated year- and site-specific information on the environmental components for all goshawk territories within the study area regardless of the number of breeding attempts, I was able to identify the reproductive responses of goshawks to changing climatic conditions in a variable environment and, consequently, the attributes of high-quality breeding habitat for an apex predator in a forest food web.

Goshawk Reproduction

Because territorial goshawks use a defined space, detection probabilities of breeding attempts are enhanced and facilitate understanding of the factors influencing reproduction. The high breeding-site fidelity of individual goshawks in some populations (Reynolds and Joy 2006) makes it possible to assess how reproductive parameters are affected by temporal and spatial variation in environmental resources among territories. The effects of habitat conditions on population dynamics most often occur when high quality sites are selected before low quality sites (Pulliam and Danielson 1991) and goshawks may follow this territory settlement pattern (Krüger and Lindström 2001, Squires and Kennedy 2006). Thus, when local breeding areas are saturated, some individuals may be forced into progressively poorer habitats or non-breeding status, which can be associated with decreased overall reproductive rates (Newton 1998).

Consequently, higher quality territories (i.e., territories that produce more fledglings) are more likely to be consistently occupied by breeding goshawks, whereas fewer breeding attempts (eggs laid) occur on lower quality territories, suggesting a non-random use of breeding sites among years (Kostrzewa 1996, Krüger and Lindström 2001).

Reproductive probabilities for the goshawk population on the Kaibab Plateau were highly variable among years and territories during the 6-year study period. Because the best supported model without environmental covariates incorporated an interaction between year and reproductive state of the territory in the previous year, the annual probability of transitioning to an egg-laying state was year- and territory-specific. This suggested that within-year differences among the environmental conditions of territories influenced the reproductive output of goshawks. Moreover, annual egg-laying probabilities were higher for goshawk territories with consecutive breeding attempts (Appendix F), so territories with reduced among-year variation in the availability of resources necessary for egg production contained higher-quality breeding habitat. In addition, because most breeding attempts were successful and the probability of producing ≥ 1 fledgling did not depend on the site-specific attributes of each territory, goshawks that reproduced more often had a greater likelihood of contributing to future generations. Thus, the habitat attributes of territories primarily influenced goshawk reproduction by reducing annual variation in availability of environmental resources necessary for egg production.

Relationship with Climatic Conditions

Annual precipitation varied extensively among years but was relatively constant among goshawk territories on the Kaibab Plateau during 1999-2004. In contrast, ambient temperatures were less variable than precipitation among years and territories. Based on the best supported

model incorporating climatic covariates, the interaction between average annual precipitation during the two years prior to the current breeding season and mean ambient temperature during March-April had the greatest effect on egg-laying probabilities, whereas cumulative precipitation during the first three weeks post-hatching had the greatest effect on successful reproduction probabilities. Although ambient temperature had a larger influence on egg-laying probabilities relative to the lag effect of precipitation, the effect of ambient temperatures on goshawk reproduction varied with average annual precipitation (Fig. 14). As a result, colder temperatures had a greater impact on goshawk egg production during drought (2001-2003). Ultimately, larger fluctuations in regional precipitation among years relative to variation in ambient temperatures suggested that annual egg-laying probabilities for goshawks on the Kaibab Plateau were primarily influenced by the magnitude of variation in cumulative precipitation.

In a semi-arid environment, like in northern Arizona, water limits the productivity of habitats. Forests initially respond to drought conditions with a reduction in water use and net primary productivity (Dale et al. 2001). Because greater amounts of precipitation increases the production of seeds, fungi, grasses and other food resources for prey species, it enhances the reproductive output of prey species by allowing more offspring to be produced per breeding attempt and more breeding attempts per season in years with above average precipitation (Crick 2004, Halupka et al. 2008, Lehikoinen 2009). Like other birds, goshawks with greater access to abundant prey resources prior to egg-laying are better able to meet the energetic demands of thermoregulation and egg production and, therefore, are more likely to have sufficient energy reserves for reproduction when ambient temperatures are low (Martin 1987). Because annual variation in regional precipitation influences the productivity of the entire landscape, abundant prey populations are more widespread among goshawk territories in years with normal to above

average precipitation. However, in years with below average precipitation, the abundance of prey items is reduced and fewer territories contain sufficient food resources necessary for goshawks to meet the energetic constraints of reproduction.

Inclement weather has been associated with delayed egg laying, abandonment of reproductive attempts, retarded development of nestlings, reduced brood size, and lower survival of nestlings (Zachel 1985, Kostrzewa and Kostrzewa 1990, Bloxton 2002, Boal et al. 2005). Of the studies that addressed the relationships between climatic conditions and goshawk productivity, only some found that ambient temperatures influenced reproduction. For those that did, warmer temperatures early in the breeding season were correlated with increased reproductive output (Kostrzewa and Kostrzewa 1990, Ingraldi 1999, Fairhurst and Bechard 2005). In contrast, the amount of precipitation in late winter and spring was more consistently associated with the number of breeding attempts (eggs laid), successful nests (≥ 1 young fledged), and young fledged (Kostrzewa and Kostrzewa 1990, Penteriani 1997, Ingraldi 1999, Doyle 2000, Fairhurst and Bechard 2005). Some of these studies, however, found that increased precipitation early in the breeding season negatively affected reproductive output (Kostrzewa and Kostrzewa 1990, Penteriani 1997, Ingraldi 1999), whereas others found evidence of a positive relationship (Doyle 2000, Fairhurst and Bechard 2005).

Differences observed in the effects of precipitation on goshawk reproduction may be related to the abundance of prey resources prior to egg-laying. Bird species (pigeons, jays) were identified as the dominant prey items in the two European studies that documented negative relationships between measures of goshawk reproduction and increased precipitation during March-May (Kostrzewa and Kostrzewa 1990, Penteriani 1997). Conversely, in studies that documented positive relationships between goshawk reproduction and increased precipitation in

April and May (Doyle 2000, Fairhurst and Bechard 2005), goshawks primarily consumed ground-dwelling mammals (hares or squirrels). Precipitation in early spring is more likely to have a positive effect on goshawk reproduction when it increases the abundance of food resources (i.e., grasses and forbs) that influence litter size and date of emergence for ground-dwelling mammals and, subsequently, the availability of prey items during an energetically stressful time for goshawks. Because goshawks have difficulty meeting their energy demands when food supplies are restricted, climatic conditions may be a more important factor regulating goshawk reproduction when prey are less abundant and metabolic costs are higher. Thus, it is the indirect effects of prolonged and severe climatic conditions (e.g., droughts, long cold winters) on the abundance of prey resources that likely has a greater influence on goshawk reproduction.

The indirect effects of annual climatic conditions on measures of goshawk reproduction have received little attention. Most other goshawk studies used monthly time periods to quantify climatic conditions so only the direct effects of weather on the breeding condition of adults, viability of eggs, and survival of nestlings could be identified. Whereas these studies found a high correlation among short-term climatic conditions and annual goshawk reproduction (Kostrzewa and Kostrzewa 1990, Penteriani 1997, Ingraldi 1999, Doyle 2000, Fairhurst and Bechard 2005), my study found that ambient temperature and a lag effect of annual precipitation prior to egg-laying accounted for less variation in goshawk reproductive probabilities than a year-specific effect (i.e., annual variation). Because previous studies compared landscape-scale weather variables to annual measures of reproduction, they could only account for temporal variation in goshawk reproduction. Although I compared year- and territory-specific climatic covariates, I found that models incorporating only climatic conditions explained less variation in goshawk reproduction because they did not account for the combined effects of annual variation

in precipitation and spatial variation in vegetation attributes on the productivity of goshawk breeding habitat.

Relationship with Vegetation

Vegetation attributes varied extensively among goshawk territories across the study area and resulted in annual differences in the compositional and structural attributes of sites with a breeding attempt. The best supported model incorporating vegetation covariates included year-specific effects of all forest cover types on egg-laying probabilities. However, the proportion of high-density pine was relatively constant among years during the study period, whereas the amount of low-density pine and high-density mix varied among years during drought (Fig. 16). Because tree canopies increase the amount of water available to plants by modifying soil temperature, moisture, and evaporation rates (Breshears et al. 1998), the density of trees enhances soil water retention when cumulative precipitation is reduced, especially if the substrate is porous (e.g., Kaibab limestone). Since even slight differences in soil moisture can have disproportionately large effects on annual vegetation growth, forests with denser canopies may be more productive during extended drought (Lauenroth et al. 1987, Kljun et al. 2006). However, since competition for limited water resources is greater with higher densities of trees, forests with lower densities or more patchy distributions of mature trees may be more productive in the first year of drought.

Cone crops for all tree species were reduced during drought. However, relative to species with shorter cone production cycles (≤ 1 year), the lag effect of short-term decreases in soil moisture on ponderosa pine cone production is reduced because the development of seed-bearing cones occurs over 27 months (Krannitz and Duralia 2004). Given a gradient of differences in the

phenology of cone production cycles among tree species, ponderosa pine occurs at the long-term end of the spectrum with reduced annual fluctuations in cone crops (Fig. 27). Greater consistency in food resources for prey species among years translates into more stable prey populations over time and, potentially, more abundant prey resources in ponderosa pine during drought.

Moreover, the widespread distribution of ponderosa pine throughout the study area, including in areas of mixed conifer forests, increases the diversity of niches and prey communities within goshawk territories. Although Kaibab squirrels are ponderosa pine obligates, I observed them in mixed conifer forests with large ($\geq 30 \text{ m}^2$) patches of ponderosa pine. Thus, the distinct temporal scales and prey species associated with ponderosa pine may enhance the diversity of food resources available over time and space and, therefore, the ability of goshawks to reproduce under a wider variety of climatic conditions.

Despite extensive annual variation in the reproductive rates of goshawks within populations, no other studies assessed year-specific effects of vegetation attributes on goshawk reproduction. Previous studies only compared spatial variation in mean vegetation attributes among all breeding sites. These studies found that breeding habitats characterized by high densities of large trees ($29\text{-}54 \text{ m}^2 \text{ ha}^{-1}$) and greater canopy cover ($50\text{-}95\%$) were associated with increased goshawk nesting rates and productivity (Hayward and Escano 1989, Siders and Kennedy 1996, Finn et al. 2002, McGrath et al. 2003, Morrison et al. 2011). However, the extent to which goshawks require these vegetation characteristics for nesting is unclear, as some goshawks continue to use the same breeding sites despite reductions in tree density and canopy cover from timber harvests or natural disturbances (Penteriani and Faivre 2001, Penteriani et al. 2002, Mahon and Doyle 2005, Moser and Garton 2009). This apparent tolerance of habitat alteration may be a consequence of the strong site fidelity of goshawks, which can arise through

high competition for a limited number of territories in saturated breeding habitats. For example, the number of breeding attempts declined on Canadian islands in areas with more than 30% of mature forests harvested, but on mainland Canada, where the density of territories was approximately twice as high, similar levels of harvesting were not associated with reduced breeding success (Doyle 2006). Further, despite the presence of suitable nest sites and abundant prey populations, goshawks rarely nest in the Coast Ranges of Oregon (DeStefano and McCloskey 1997). Reynolds et al. (1982) hypothesized that the dense brushy understories of these forests conflicted with the hunting strategies of goshawks and precluded them from breeding in the Coast Ranges. Thus, although goshawks demonstrate considerable specificity in choice of structural conditions for nesting, foraging habitat may ultimately have a greater effect on reproduction because it influences the abundance and availability of food resources that are necessary for goshawks to reproduce (Widén 1989, Reynolds et al. 2006a).

Goshawks forage in a wide variety of cover types, but overall they appear to select areas within forest cover types that contain higher densities of large trees, greater canopy cover, and relatively open understories when they are available (Beier and Drennan 1997, Finn et al. 2002, reviewed in Squires and Kennedy 2006). Goshawk breeding sites with these structural attributes have been associated with higher occupancy and nesting rates (Finn et al. 2002, Joy 2002, Desimone and DeStefano 2005, Morrison et al. 2011). Since trees modify their surrounding environment (Breshears et al. 1998, Barr et al. 2007), forest cover types with greater structural complexity may be more productive during extended periods of reduced precipitation than cover types that have more homogenous structural conditions (e.g., intensively-harvested mature forests). Thus, forests with lower harvest intensities and more patchy distributions of mature trees may provide more stable food resources for a greater variety of goshawk prey species

during drought. However, because differences in elevation, topography, soil characteristics, and vegetation composition and structure influence primary production in forests (Kljun et al. 2006), the forest cover type with the most abundant food resources for prey species can vary among years with changes in climatic conditions.

In the absence of large-scale disturbances, vegetation composition and structure are relatively constant over short time periods, so mean values of forest structural components may adequately capture temporal and spatial variation in vegetation attributes. However, information on nesting or foraging habitat characteristics pooled over years does not account for the effects of dynamic environmental conditions on goshawks' use of specific forest attributes. Because other studies pooled information over years instead of assessing annual variation in goshawk habitat use, they may have failed to identify selection for specific cover types. For example, during my study period, goshawk territories with a breeding attempt contained similar proportions of all four cover types in 2000 and 2004 (Fig. 16). In contrast, during drought, territories with a breeding attempt contained more high-density pine ($\geq 4\%$) and low-density pine (9%) in 2001, more high-density mix (5%) in 2002, and more low density pine (9%) in 2003. Moreover, because most previous goshawk studies did not consider variables representing annual variation in the productivity of habitats, the mechanisms that influence the relationship between forest attributes and goshawk reproduction could not be identified. I compared year- and territory-specific variables and found that vegetation composition and structure explained less variation in goshawk reproduction because it does not incorporate the combined effects of temporal variation in precipitation and spatial variation in the productivity of forest cover types on the abundance of prey resources.

Relationship with Prey

The abundances of most goshawk prey species were highly variable among years, forest cover types, and territories on the Kaibab Plateau during 1999-2004. Of the three mammal prey species, the annual abundance of Kaibab squirrels was the most constant over time (Fig. 17). Given the year-round availability of cambium from subterminal twigs and a >2-year productivity cycle for ponderosa ovulate cones, Kaibab squirrels are subject to less annual variation in primary food resources (Hall 1981). Thus, Kaibab squirrels may be the most reliable food resource for goshawks on the Kaibab Plateau because their dependence on ponderosa pine reduces the magnitude of annual fluctuations in their abundance. In contrast, the production of conifer seeds that are the year-round dietary staple of red squirrels is more variable among years and tree species (Hoffmeister 1986). Because mixed conifer contains a greater diversity of tree species with shorter cone crop cycles (3-18 months) than ponderosa pine, cone production of mixed conifer can respond more quickly and intensely to increases in annual precipitation. In years with high cone production, red squirrels in Arizona can have up to 2 litters of 2-5 young, which may result in greater increases in goshawk food resources in mixed conifer (Hoffmeister 1986). However, given the greater average mass of Kaibab squirrels, red squirrels need to be over three times more abundant than Kaibab squirrels to provide a comparable food resource, assuming equal capture rates among the prey species. In 2000, when the mean number of individuals per territory for tree squirrels was highest, red squirrels were nine times more abundant than Kaibab squirrels, but in 2003 when their abundance was lowest, there were only twice as many red squirrels (Fig. 17). Thus, the importance of red squirrels as a food resource for goshawks on the Kaibab Plateau may be more variable over time due to much larger annual fluctuations in available biomass relative to Kaibab squirrels. Despite severe drought, the

abundance of golden-mantled ground squirrels was relatively constant during the study period except in 2004 when average annual precipitation was the highest in an 80-year period of record (Fig. 13). Thus, as a smaller prey item with infrequent periods of high abundance, the importance of golden-mantled ground squirrels as a food resource for goshawks likely depends on their availability relative to the abundance of other larger prey items such as arboreal squirrels and lagomorphs.

Annual variations in predator reproductive rates are greatest among species with restricted diets dominated by cyclic prey (Korpimäki 1988, Newton 1998). In the Yukon, goshawks fledged 2.8 young per nest in years when the abundance of snowshoe hares (*Lepus americanus*) was high, whereas apparently no fledglings were produced when hare populations were low (Doyle and Smith 1994). In Wisconsin, Erdman et al. (1998) found the productivity of goshawks fluctuated with abundance of snowshoe hares and ruffed grouse (*Bonasa umbellus*). Thus, the sensitivity of goshawk reproduction to changes in the abundance of specific prey species may be related to differences among species in terms of caloric content or availability to goshawks during critical periods in the breeding cycle. In northern Arizona, only the proportion of red squirrel in the diet had a significant and positive relationship with the number of goshawk fledglings produced annually during 1999-2002 despite the greater contribution of other prey species to goshawk diets in terms of frequency and biomass (Salafsky et al. 2005). Both Maurer (2000) and Keane et al. (2006) found that, although goshawks in California consumed a wide range of prey species, reproduction was most strongly influenced by the abundance of Douglas' squirrels (*Tamiasciurus douglasii*) in spring. Although several studies have illustrated disproportionately strong relationships between goshawk reproduction and the abundance of one

or more key prey species, synchronous declines in prey abundance can make it difficult to determine the influence of each species on goshawk reproductive performance.

Some studies have documented the effects of temporal variation in prey abundance on goshawk reproduction, but few have explored the effects of spatial variation in the abundance of prey species. In this study, estimated abundances of all three mammal prey species varied extensively among forest cover types, but the abundances of red squirrels and Kaibab squirrels were more variable among goshawk territories than the abundance of golden-mantled ground squirrels. Because I used territory-specific proportions of forest cover types to estimate the annual abundance of mammal prey species, there was greater uncertainty regarding the number of prey items per territory, especially in years when too few individuals were detected to accurately estimate the density of habitat specialists in alternate cover types (Appendix D). However, since Kaibab squirrels, red squirrels, and golden-mantled ground squirrels have distinct ecological niches and were most abundant in different forest cover types (Fig. 18), together the three mammal prey species incorporated spatial variation in the availability of prey resources among goshawk territories.

Given large differences in the densities of individual prey species among forest cover types, the lack of a spatial dimension in previous studies may have resulted in inaccurate conclusions regarding the prey resources that primarily influence goshawk reproduction (Byholm 2005). For example, in this study, the model that contained the additive effects of Kaibab squirrel, red squirrel, and golden-mantled ground squirrel abundance explained more variation in goshawk reproduction than the same model with the covariate that incorporated the combined abundances of all three mammal species ($\Delta AIC_c = 25.7$; Table 6). Summing the number of individuals per territory over species with distinct ecological niches reduced spatial variation in

the annual abundance of prey resources among goshawk territories. Consequently, models with covariates pooled over species explained less year- and territory-specific variation in goshawk reproduction than models with separate covariates for each species. Because the ability of goshawks to switch among alternate prey species increases their opportunities to obtain sufficient food resources for reproduction, the importance of each species may ultimately depend on their availability in time and space relative to each other.

By comparing year- and territory-specific variables, I found the model incorporating the additive effects of prey species with distinct ecological niches explained more variation in goshawk reproduction because it accounts for temporal variation in the abundance of prey items among years and spatial variation in the distribution of prey species among goshawk territories. Overall, annual probabilities of producing eggs or ≥ 1 fledgling were higher in years and on goshawk territories with more abundant prey items. Reduced fluctuations in the abundance of prey resources over time translate into greater food stability for goshawks. However, the abundance of mammal species such as Kaibab squirrels, red squirrels, and golden-mantled ground squirrels may have had a greater effect on goshawk reproduction probabilities than birds (northern flicker and Steller's jay) because mammals are efficient prey items. Lagomorphs and arboreal squirrels were the heaviest prey items most frequently consumed by goshawks on the Kaibab Plateau (Appendix A). Larger prey species potentially enhance goshawk foraging efficiency by increasing net energy gained per individual prey item, whereas multiple captures are necessary to obtain the equivalent biomass from smaller prey. However, smaller prey items may be more profitable if goshawks expend less energy per successful foraging attempt to capture them. Net energy gain per unit time (i.e., foraging rate) potentially increases with encounter rates, so the abundance of prey items can influence goshawk foraging efficiency (Pyke

et al. 1977). Less energy expended to obtain critical food resources results in more energy available for the energetic demands of reproduction (Martin 1987). Thus, goshawk reproductive probabilities are enhanced with more reliable access to abundant prey resources.

Relationship with Habitat

Because many species use a variety of cover types, I considered “habitat” to be the combination of different compositional, structural, and functional attributes of landscapes that allow wildlife populations to persist under changing climatic conditions. Out of all models incorporating the effects of these environmental attributes on goshawk reproduction probabilities, those that included the abundances of prey species with distinct ecological niches received the most support from the data. Because the abundance of individual prey species within each goshawk territory is a function of temporal variation in climatic conditions and spatial variation in vegetation attributes, the diversity of the prey community effectively captured the influence of environmental variation on the spatiotemporal dynamics of goshawk reproduction. Thus, the model containing the additive effects of the abundance of mammal prey species with distinct functional traits and annual variation in ponderosa cone production among cover types explained more year- and territory-specific variation in goshawk reproduction because it incorporated the cumulative effects of climatic conditions, vegetation attributes, habitat productivity, prey populations and, consequently, the factors and processes influencing the availability of food resources necessary for goshawks to reproduce (Fig. 1).

In a semi-arid environment, water is the limiting factor of habitat productivity. Because the amount of water influences plant primary productivity, temporal variation in annual precipitation determines the length of moisture deficit periods and the cumulative effects of

drought on the productivity of vegetation (Krishnan 2006). However, the response of conifers to climatic variability and drought varies among species and sites (Babst et al. 2013, Lévesque et al. 2014). In this study, annual differences in ponderosa pine cone production among forest cover types suggested that interactions among landscape characteristics (e.g., elevation, aspect, slope) and the attributes of forests (e.g., density of mature trees, canopy closure, understory density) in mixed conifer forests may have mitigated the effects of reduced precipitation on cone production by reducing evaporative demand and enhancing soil water retention during drought. Since seeds, vegetation, and fungi are important components of the diets of many prey species, drought-induced declines in these food resources can drastically reduce prey abundance. However, given the dependence of Kaibab squirrel and red squirrels on tree species with different temporal scales of seed production, the amplitude and frequency of annual fluctuations in prey abundance varies among species.

Differences in the phenology of vegetation growth cycles relative to annual variation in precipitation influenced how the abundance of each prey species varied over time. Thus, I conceptualized goshawk prey species as either “constant” or “rapid” responders. “Constant responders” are prey species with less temporal variation in abundance because they depend on food resources that are more consistent among years. “Rapid responders” are prey species with greater fluctuations in abundance over time because they depend on food resources that are more variable among years due to shorter (<1 yr) growth cycles. As a constant responder, Kaibab squirrels are a more consistent food resource for goshawks because large fluctuations in their abundance only occur under extended periods (≥ 2 yr) of drought (Fig. 17). As rapid responders, the abundance of cottontail rabbits, black-tailed jackrabbits, golden-mantled ground squirrels, and red squirrels can fluctuate extensively among years, so these species may provide a more

intermittent food resource for goshawks. Although goshawks with territories that contain abundant Kaibab squirrels may breed more often, goshawks with access to rapid responders may be more productive in specific years when greater numbers of red squirrels, golden-mantled ground squirrels, and lagomorphs can increase the available prey biomass by an order of magnitude. However, goshawks that have access to both types of prey are more likely to reproduce annually because the abundances of species with distinct functional traits are less likely to be synchronized and thereby increase the availability of food resources in a variable environment (Newton 1979). Thus, goshawks with access to prey species with diverse ecological niches are better able to compensate for variation in environmental factors (e.g., extreme weather) that increase energy demands and affect their physiological condition, given greater probabilities of obtaining sufficient food resources when the abundance of one or more prey species is reduced.

Differences in the ecological niches of mammal species relative to spatial variation in vegetation compositional and structural attributes influenced how the distribution of prey items varied across the landscape. As a habitat specialist of ponderosa pine, the abundance of Kaibab squirrels was most variable among forest cover types (Fig. 18). In contrast, due to greater abundance in both low-density ponderosa pine and low-density mixed conifer, golden-mantled ground squirrels were more widely distributed among forest cover types and goshawk territories. Although the abundance of red squirrels varied less among forest cover types than Kaibab squirrels, small-scale differences in forest structural conditions that influence cone production and create appropriate conditions for food storage in middens may have resulted in greater spatial variation in red squirrel abundance among goshawk territories, especially during drought. Because each mammal species has distinct functional traits that are uniquely adapted to an

ecological niche, the abundance of specific food resources influenced the distribution of prey items among the forest cover types. Thus, the availability of each prey species was much higher within primary cover types in years when their food resources were abundant (Fig. 21).

However, during drought, when primary productivity was reduced, the number of prey items per species was more evenly distributed among all cover types. Consequently, spatial heterogeneity in the vegetation attributes of forested landscapes relative to climatic conditions defined the environmental conditions that enhanced the abundance of all species and the diversity of the prey community among forest cover types.

As an apex predator in a complex food web, goshawks have one of the most diverse diets of any North American raptor (Marti et al. 1993). In this study, 34 species contributed one or more prey items to goshawk diets on the Kaibab Plateau during 1999-2004, but only 6 species (cottontail rabbit, black-tailed jackrabbit, Kaibab squirrel, red squirrel, northern flicker, and Steller's jay) each contributed $\geq 4\%$ of the total biomass to annual goshawk diets (Appendix A). Although golden-mantled ground squirrels were the most abundant prey species in 2004 (Fig. 17), they contributed fewer prey items and less biomass to goshawk diets than each of the 6 dominant prey species. Despite a large increase in their abundance in 2004, golden-mantled ground squirrels only contributed a small proportion ($< 1\%$) of total biomass to goshawk diets relative to cottontail rabbits (64%). Thus, the effects of the abundance of golden-mantled ground squirrels likely encompassed the functional role of ground-dwelling prey in the goshawk food web, and suggested that these squirrels were an appropriate surrogate for the effects of lagomorphs on goshawk reproduction. In addition, although golden-mantled ground squirrels contributed $< 4\%$ of the total dietary biomass to goshawk diets, their abundance accounted for more variation in goshawk reproduction probabilities than the abundances of northern flickers

and Steller's jays, species that were more evenly distributed among the forest cover types (Table 6, Fig. 18). As a result, together the abundances of three squirrel species with different primary cover types explained more variation in goshawk reproduction than the abundance of mammals or all prey items. Therefore, variation in the abundance of Kaibab squirrels, red squirrels, and golden-mantled ground squirrels likely incorporated the availability of all prey species with similar ecological niches within high-density ponderosa pine, high-density mixed conifer, and low-density forest, respectively. This indicated that the habitat model representing food resource availability was the most parsimonious explanation of spatiotemporal variation in goshawk reproduction because it incorporated the effects of temporal variation in climatic conditions and spatial variation in vegetation attributes on the annual abundance of all species within the prey community for each goshawk territory.

During the 6-yr study period, annual probabilities of producing eggs or ≥ 1 fledgling were higher in years with more abundant prey items and on goshawk territories containing more heterogeneous ecological niches. Because the abundance of prey species within forest cover types depended on temporal and spatial variation in specific environmental resources, vegetation attributes that reduced annual fluctuations in the abundance of all prey items per territory may have enhanced goshawk foraging efficiency. Foraging efficiency is ultimately a function of energy gained per unit effort. Thus, optimal foraging theory predicts that reducing energy expenditure is more efficient when abundant food resources increase encounter rates with prey items, whereas maximizing energy gain per effort is more efficient when all food resources are scarce and there is greater uncertainty in encountering additional prey items (Pyke et al. 1977). In this study, when most prey species were abundant in 2000, goshawks diet composition was more diverse and contained greater amounts of smaller prey items (Fig. 22, Appendix A). In

contrast, during drought when the annual abundance of prey items was lowest in 2003, goshawk diets were almost entirely composed of larger prey species and primarily black-tailed jackrabbits. Thus, territories that encompassed more heterogeneous vegetation attributes may have influenced the foraging efficiency of goshawks by increasing the availability of alternate prey items with distinct ecological traits. This suggested that greater compositional and configurational heterogeneity in forest cover types within territories enhanced the ability of goshawks to obtain sufficient food resources for the energetic demands of reproduction and, ultimately, the quality of their breeding habitat under changing climatic conditions.

Declines in prey resources are typically associated with reductions in the annual proportion of goshawk pairs breeding and number of fledglings produced. In years with abundant prey resources, goshawks attempt to breed on most territories, whereas in years with scarce prey resources, few pairs attempt to breed and individual goshawks are rarely detected on low-quality territories (Doyle and Smith 1994, Rutz and Bijlsma 2006, Salafsky et al. 2007). In this study, lower annual probabilities of transitioning to an egg-laying state for all goshawk territories during 2001-2003 suggested that sufficient prey resources for egg production were restricted to fewer territories during drought. Because egg-laying probabilities depended on the interaction between annual climatic conditions and the site-specific attributes of territories and were associated with the annual abundances of species in the prey community, goshawks occupying territories with habitat attributes that reduced among-year variation in prey resources had higher reproductive probabilities. Thus, greater heterogeneity of foraging areas within territories mitigated the effects of changing climatic conditions on goshawk reproduction by maintaining the abundance of all food resources during and following drought.

Goshawks territories that encompass heterogeneous habitat characteristics have been associated with higher occupancy and reproductive rates. For example, Kostrzewa (1996) found that goshawks with territories that encompassed both woodland and open areas had the highest reproductive output and Morrison et al. (2011) found that territories with more mixed conifer forest than Jeffrey pine forest were occupied more often. Hargis et al. (1994) found home ranges of breeding goshawks were typically located in areas with high vegetative and seral diversity. Moreover, forests encompassing varied tree composition and structural attributes generally support more wildlife than managed, monotypic forests (Newton 1979, Reynolds et al 1992, Reynolds et al. 2013). In this study, the relationships between goshawk reproduction and the attributes of breeding habitat indicated that territories containing a greater diversity of ecological niches confer greater reproductive advantages to breeding goshawks by reducing temporal variation in the abundance of prey items during and following drought. Thus, if annual variation in the availability of food resources within each territory determines the reproductive responses of goshawks to changing climatic conditions, then how often individuals reproduce and how many fledglings they produce is ultimately a function of the heterogeneity of their breeding habitat.

CONCLUSIONS

Our ability to predict ecological responses to system dynamics depends on the relationship between temporal and spatial scales of variation (Wiens 1989). Thus, it is critical to establish the context of variation in time and space to identify ecological patterns and the processes that cause them. The context of this study was the population of breeding goshawks within the Kaibab National Forest on the Kaibab Plateau, Arizona during 1999-2004, and spatiotemporal variation in goshawk reproduction was most reliably predicted by the annual abundances of three mammal species with distinct ecological traits. Together, these species accounted for more variation in the temporal and spatial scales of environmental components because they are most abundant in different forest cover types with varied responses to temporal variation in annual climatic conditions. This suggests that the degree of heterogeneity in vegetation attributes and growth cycles of forest biota relative to variation in abiotic conditions determine the frequency and magnitude of goshawk reproduction within ponderosa pine and mixed conifer forests on the Kaibab Plateau and, consequently, the quality of breeding habitat (Fig. 24). As an apex predator in a complex food web, goshawks ultimately depend on the productivity of all lower trophic levels in the system. As such, their reproductive performance aggregates the effects of variation in environmental components over time and space. Thus, greater habitat complexity may be associated with increased goshawk reproduction because it incorporates a greater diversity of niches and prey resources and, consequently, encompasses a greater variety of responses to changing climatic conditions.

All environments vary over time and space at multiple scales. However, temporal and spatial scales of resolution influence our perception of the frequency and magnitude of

environmental variation (Chase and Knight 2013). Thus, it is important to standardize the scale of environmental relationships to biological populations that incorporate long temporal scales and broad spatial scales to accurately identify the context of environmental variation and the ability of individuals to adapt to changing conditions (Wisz et al. 2013). Greater temporal variation in climatic conditions increases the likelihood of crossing critical thresholds for environmental variables thereby reducing population persistence, whereas increased spatial variation in habitat attributes enhances the probability of population persistence in a variable environment (White 2000). Variation that influences the population persistence of apex predators is of the greatest concern because changes in their population dynamics integrate the effects of environmental variation on all biotic components of the food web. Therefore, forest management should focus on enhancing the heterogeneity of functional attributes of landscapes for goshawks and other apex predators to allow for a greater diversity of responses to temporal variation in annual climatic conditions.

MANAGEMENT IMPLICATIONS

Managed forests that are ecologically sustainable contain heterogeneous compositional, structural, and functional elements over a range of spatial scales (Lindenmayer et al. 2000). For any species in the goshawk food web, forests can be mapped as a mosaic of patches ranging from unsuitable to highly suitable based on the functional attributes of the forest compositional and structural elements. However, because goshawks are opportunistic predators with diverse diets, not all prey species are dependent on the same environmental resources. Consequently, differences in the resource dependencies of representative prey species can be used to quantify the functional heterogeneity of landscapes and the desired forest conditions for goshawk habitat. Based on the forest management recommendations for goshawks in the Southwestern United States, important habitat elements for goshawks and their prey species in ponderosa pine and dry mixed conifer forests include higher densities of mature large trees, snags, interlocking tree crowns, open understories, downed logs, woody debris, and dispersed small openings with well-developed grass/forb/shrub vegetation (Reynolds et al. 1992, Reynolds et al. 2006b, Reynolds et al. 2013). Given these diverse habitat attributes, maintaining a landscape configuration that promotes viable populations of multiple species requires managing for the environmental factors that affect the productivity of all forest cover types over a range of temporal and spatial scales. Thus, forest management may be most effective when it is focused on reducing the severity of droughts and other disturbance events that are associated with dynamic landscapes (reviewed in Reynolds et al. 2013). Although fluctuations in abiotic factors or stochastic events cannot be feasibly controlled or predicted, it may be possible to increase the resilience of forest ecosystems

to changing climatic conditions by managing forest structural attributes to mitigate the effects of climatic extremes.

Increases in the frequency and magnitude of droughts for many regions, including the southwestern United States, are predicted to occur with global climate change (Parry et al. 2007, Grant et al. 2013, Melillo et al. 2014). Most tree species and all major forest types exhibit vulnerability to drought that manifest in declines in the productivity of forests (Choat et al. 2012). In addition, increased drought conditions can enhance the susceptibility of forest vegetation to insect outbreaks, diseases, and catastrophic fires (Negron 1998, Dale et al. 2001, Raffa et al. 2008). Consequently, to reduce the effects of drought, forest management should focus on enhancing water retention attributes of landscapes by manipulating the size, orientation, spatial pattern, and density of forest openings. For example, large patches of residual trees in addition to smaller dimensions and a north-south orientation of more intensive timber harvests may reduce evaporation by enhancing the extent of shade across openings (Marenholtz et al. 2010, Grant et al. 2013). Smaller management units and irregular tree patterns also influences snow retention and understory plant abundance (Moore et al. 2006, Varhola et al. 2010). Ultimately, the negative impacts of human-induced habitat alteration may be reduced if managed areas more closely resemble historic stand conditions of mature forests that are the result of long-term processes and natural disturbances. By using the fine-scale mosaic of the compositional and structural attributes of mature forests as a template for desired forest conditions, it may be possible to enhance the ability of forests to withstand temporal variation in annual climatic conditions by increasing the water retention capabilities of forests (Allen et al. 2002, Binkley et al. 2007).

Increasing the resilience of forest ecosystems has become a primary objective of management due to the alarming rate of human-induced habitat alteration and the projected effects of climate change (May et al. 1997, Joyce et al. 2009). Evidence suggests that spatial heterogeneity in vegetation composition and structure over multiple scales is a critical factor influencing the effect of changing climatic conditions and disturbance on the integrity of forest ecosystems (Churchill et al. 2013). Thus, effective management strategies for enhancing the resilience of forest ecosystems must maintain greater habitat complexity over a range of spatial scales. Habitat complexity ultimately requires a landscape-level approach, but developing and maintaining a landscape configuration that incorporates heterogeneous biotic components can be difficult to conceptualize and implement. However, greater spatial heterogeneity within forested landscapes can be achieved by using goshawk territories to identify the extent of management areas and the distinct ecological niches of representative prey species to define the size and composition of habitat patches within each territory. Structural complexity of habitats can be enhanced by increasing variation in the dimensions, spatial patterns, and harvesting intensities of strategically placed management units. For example, locating irregular or amorphous-shaped harvests of different intensities relative to the breeding sites of neighboring goshawks, increases habitat heterogeneity within and among goshawk territories. In addition, creating multiple sizes of openings with different densities of mature trees may provide habitat for species that specialize on early-seral forests and grass/forb/shrub habitat, reduce barriers to dispersal, facilitate tree regeneration, and increase the diversity of understory plants (Boyden et al. 2005, Reynolds et al. 2006b). Moreover, heterogeneous structural conditions can potentially reduce the extent and intensity of disturbance processes such as catastrophic fire and epidemic insect outbreaks (Beatty and Taylor 2007, Fettig et al. 2007).

Increased structural complexity of forested habitat encompasses more distinct niches and, consequently, greater biodiversity. More heterogeneous biota incorporates a wider range of temporal and spatial scales and, therefore, a greater diversity of responses to extreme climatic conditions and disturbances. Because change is constant and climatic extremes are inevitable, management strategies that increase the structural complexity of landscapes ultimately enhance the integrity and quality of forested habitats in a dynamic environment.

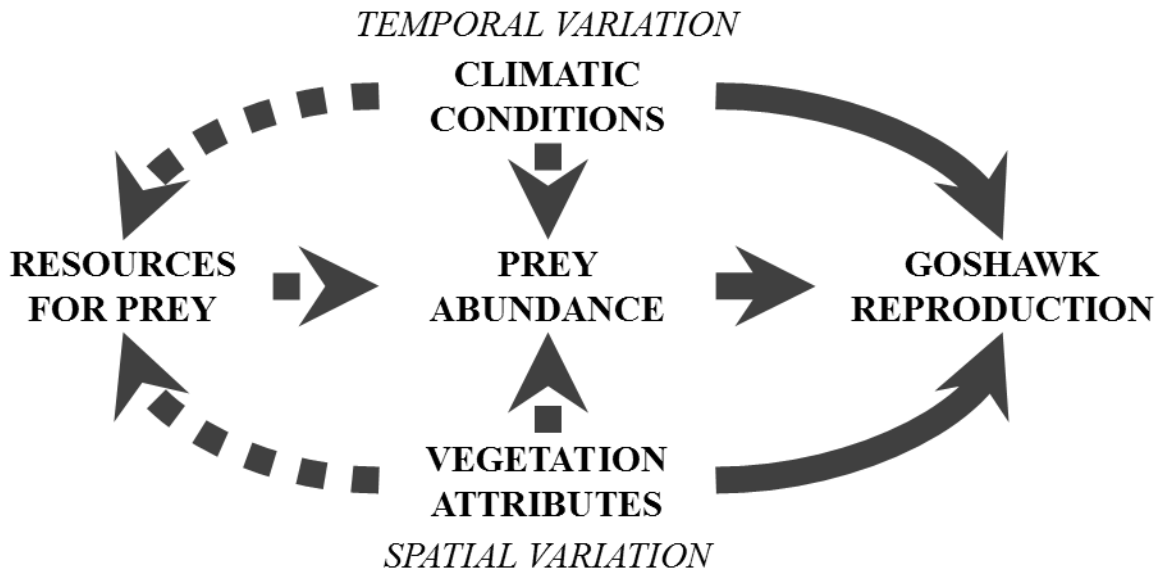


Figure 1. Schematic diagram representing hypothesized effects of environmental components on the reproductive output of an apex predator (northern goshawk). Solid lines represent direct effects and dashed lines represent indirect effects of environmental attributes on reproduction. Variation in the availability of food resources necessary for goshawks to reproduce is a function of the combined effects of annual variation in climatic conditions and site-specific variation in vegetation attributes on food resources for prey species and the abundance of prey items.

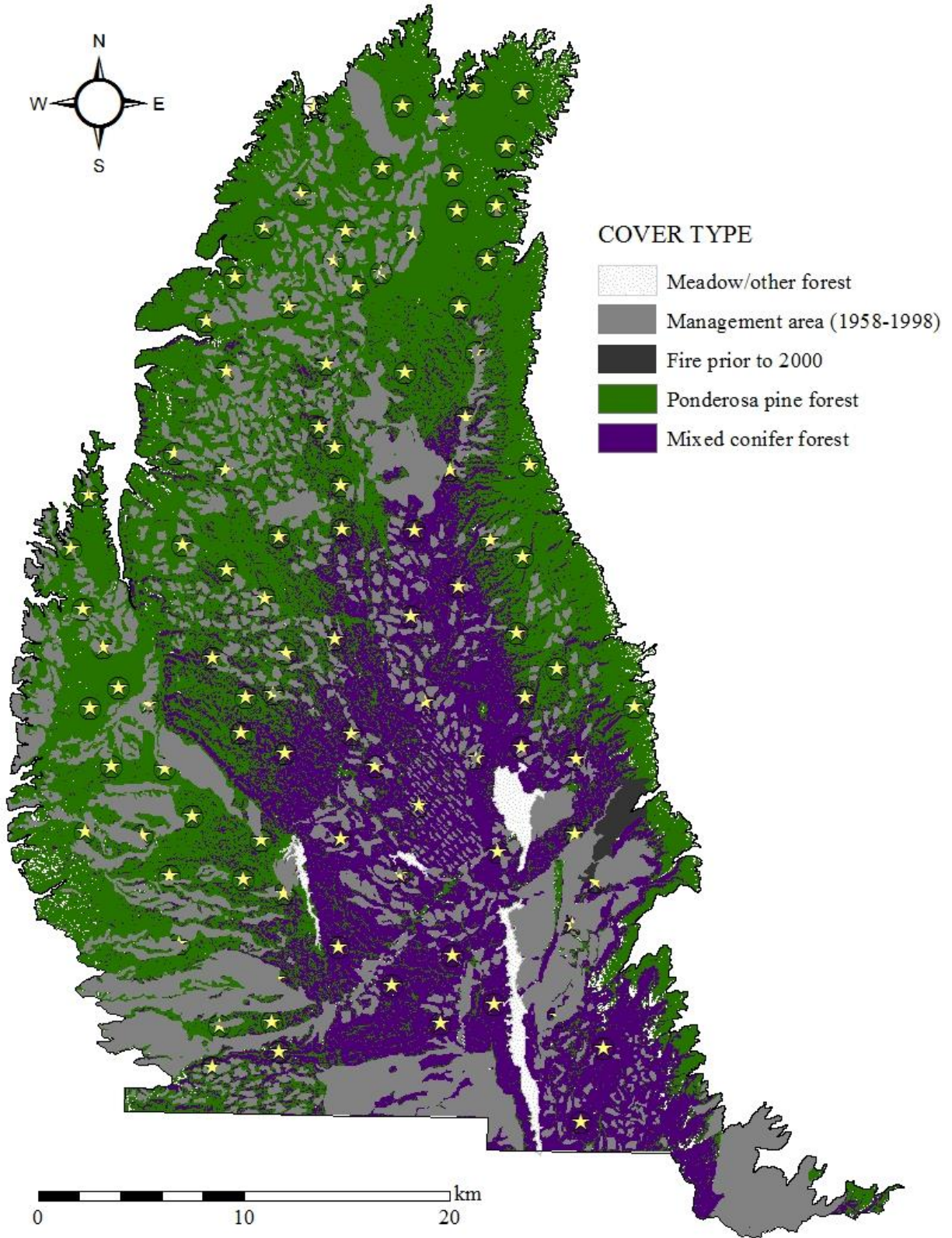


Figure 2. Distribution of goshawk territories ($n = 102$), forest types, management areas, and historic fires within the study area on the Kaibab Plateau, Arizona.

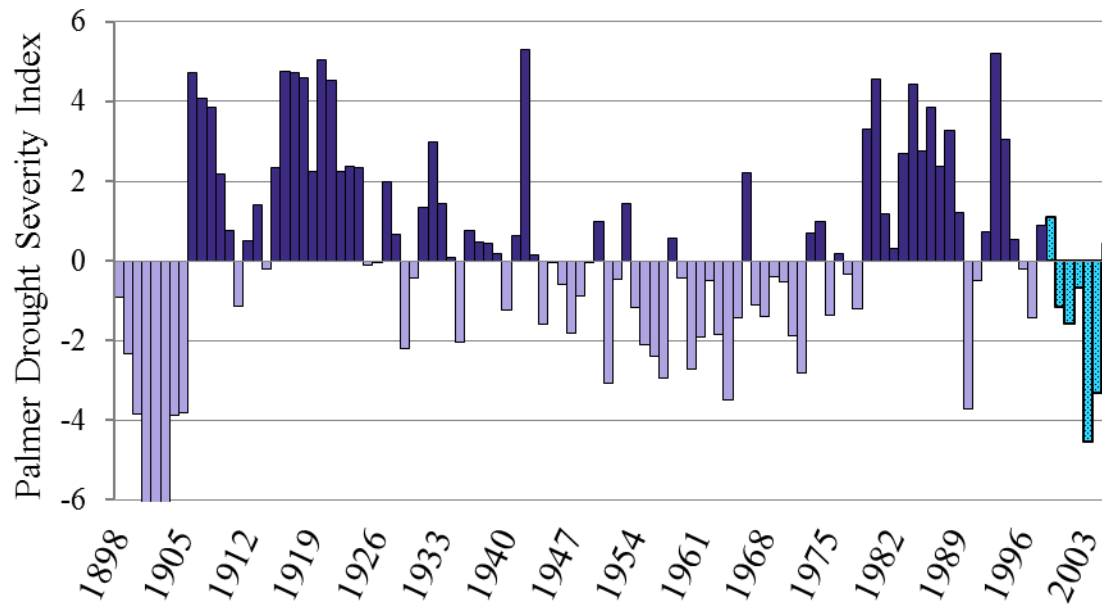


Figure 3. Palmer Drought Severity Index values for northern Arizona during 1898-2005. Blue bars denote annual values for the study period (1999-2004). Index values are derived from recent air temperature, precipitation, and local soil moisture data. Values less than -4 indicate extreme drought, values between -2 and 2 encompass normal variation in climatic conditions, and values more than 4 indicate extreme wet conditions.

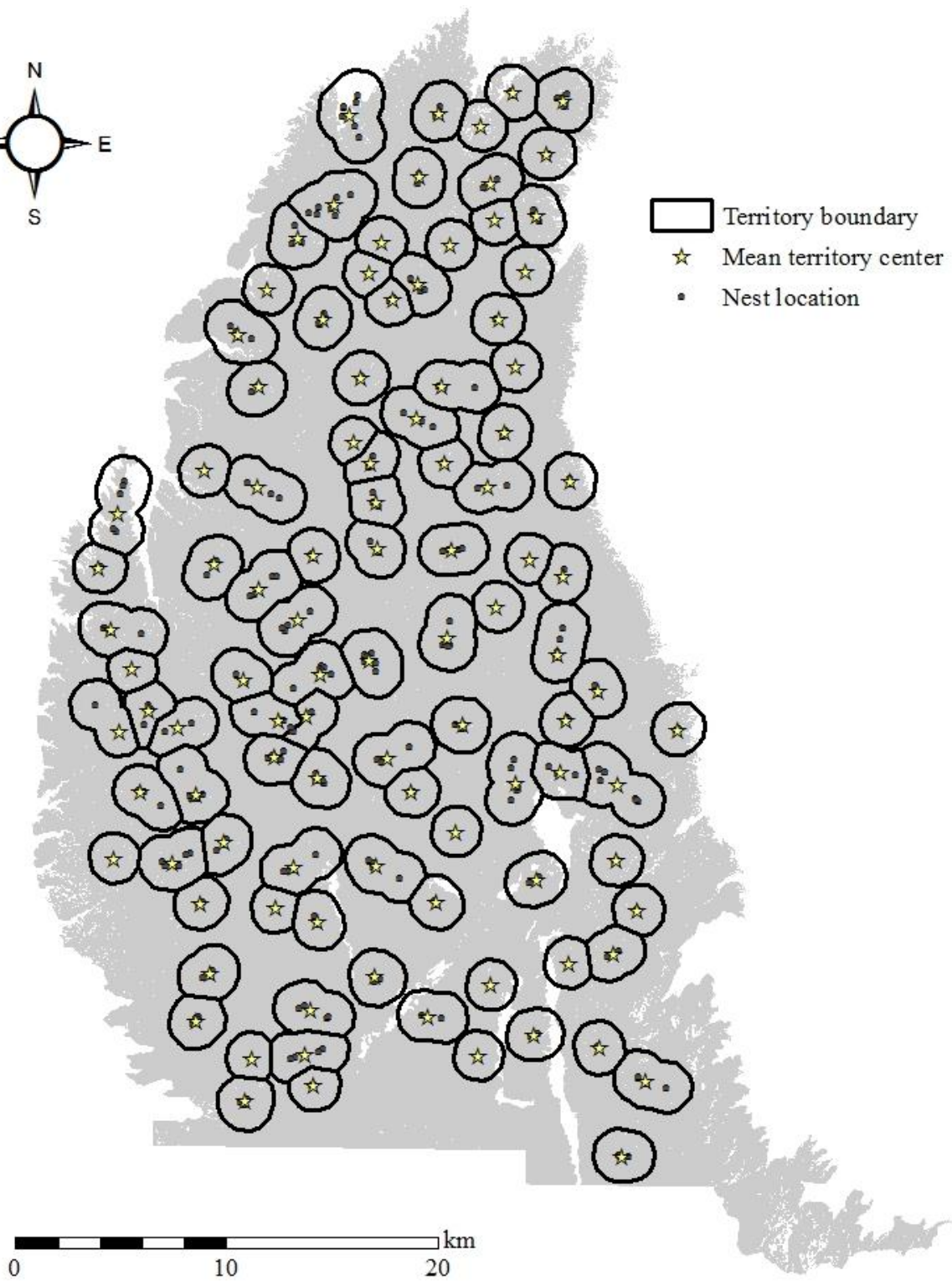
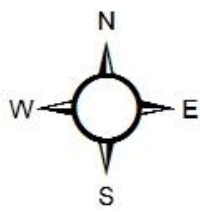


Figure 4. Distribution of nests and mean territory centers of 102 goshawk territories on the Kaibab Plateau, Arizona. Territory boundaries were delineated based on the spatial configuration of nests within territories and the proximity of neighboring territories using Euclidean distances. The dimensions of each territory were assumed to approximate the exclusive area occupied by breeding goshawks during 1991-2004.

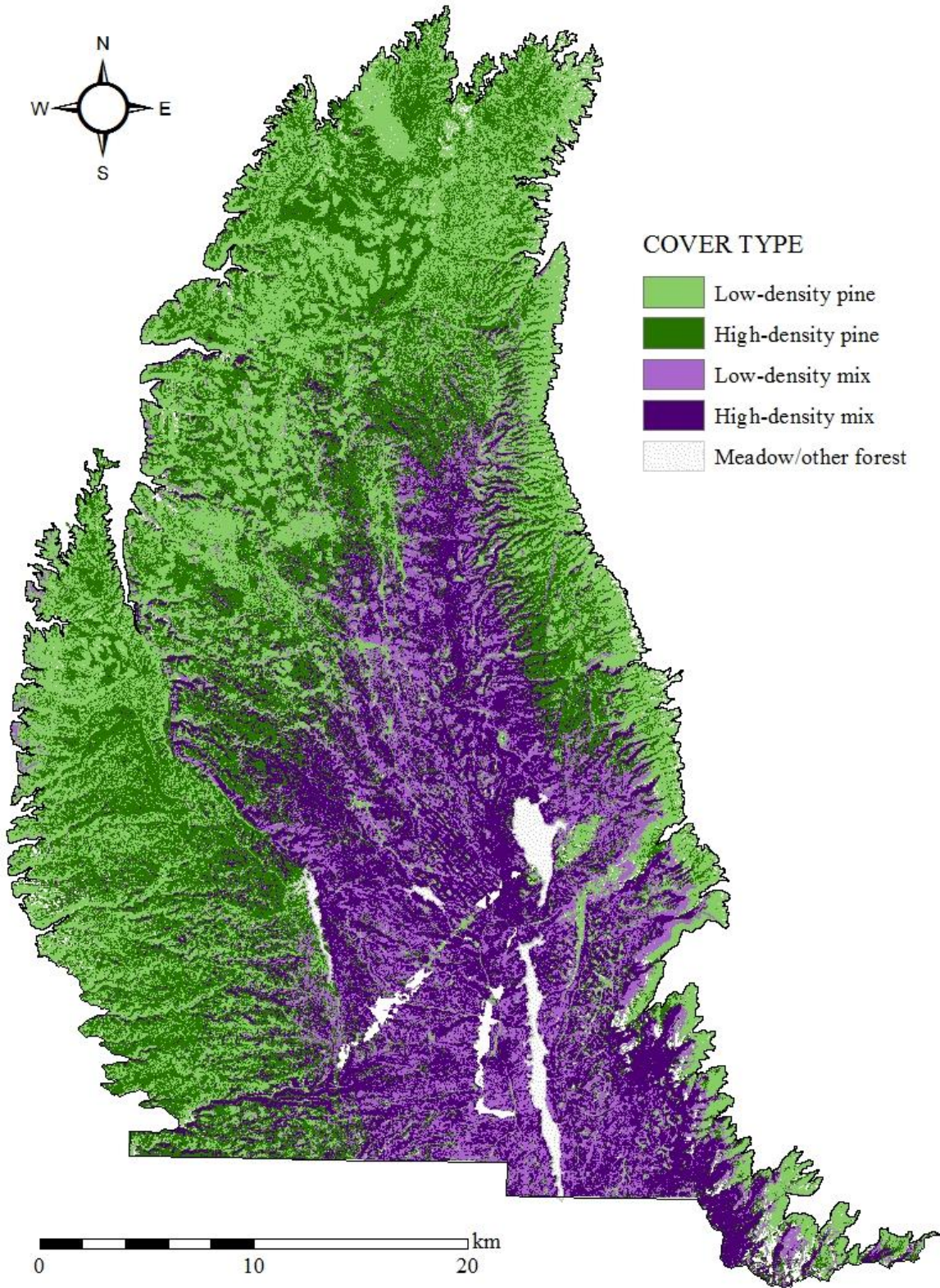


Figure 5. Distribution of the 4 dominant cover types for the study area within the Kaibab National Forest on the Kaibab Plateau, Arizona. Classifications of the cover types were based on the dominant species and density of mature trees in lightly harvested (high-density) or more intensively harvested (low-density) ponderosa pine (pine) or mixed conifer (mix) forest.

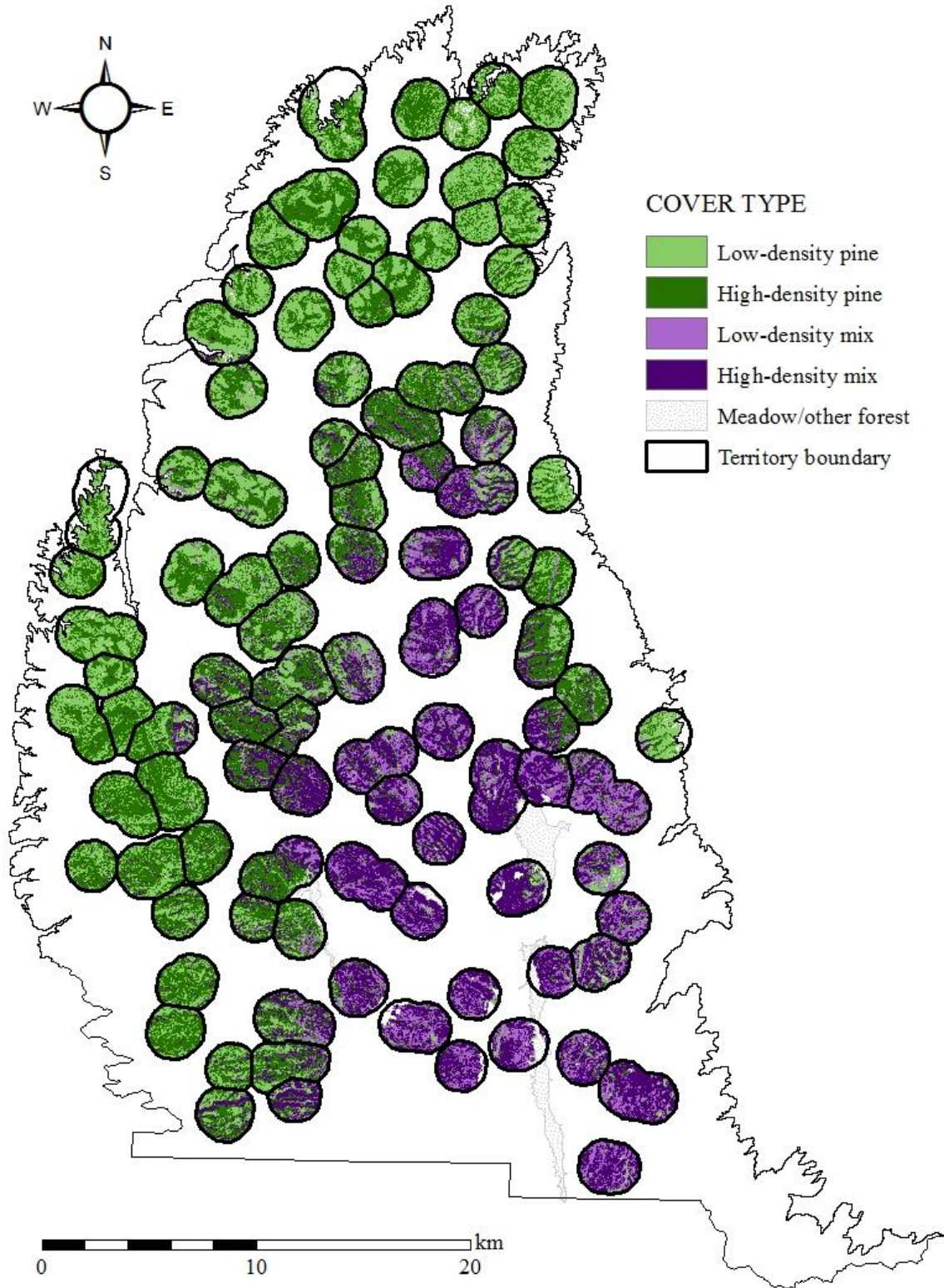


Figure 6. Forest cover type composition and distribution of 102 goshawk territories within the 1,285-km² study area on the Kaibab Plateau, Arizona during 1999-2004. Classifications of cover types were fixed over time and based on the dominant species and density of mature trees in lightly harvested (high-density) and more intensively harvested (low-density) mixed conifer (mix) or ponderosa pine (pine) forest.

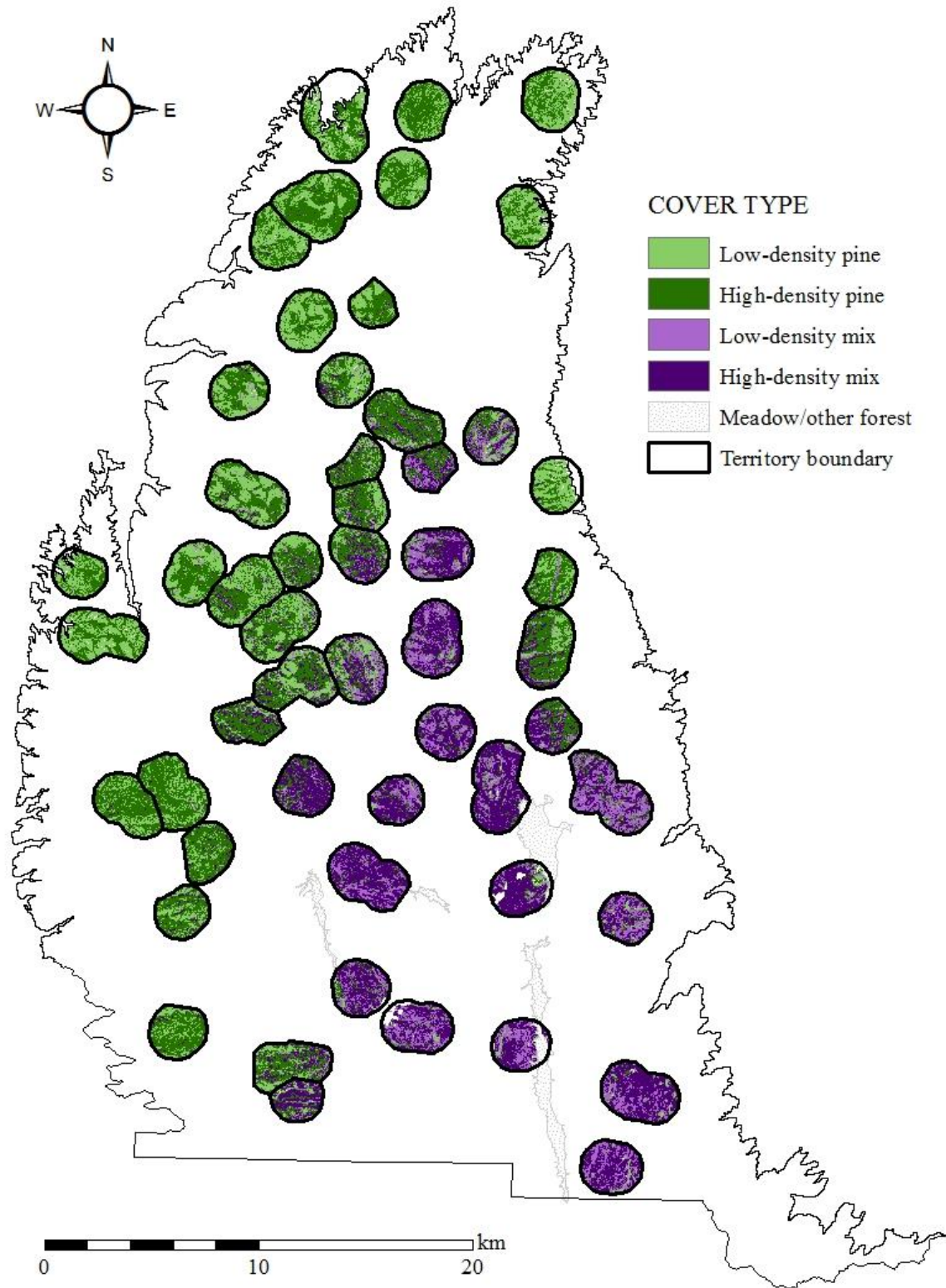


Figure 7. Distribution of 4 forest cover types within the 53 goshawk territories with a breeding attempt (eggs laid) in 1999 on the Kaibab Plateau, Arizona. Classifications of cover types were fixed over time and based on the dominant species and density of mature trees in lightly harvested (high-density) and more intensively harvested (low-density) mixed conifer (mix) or ponderosa pine (pine) forest.

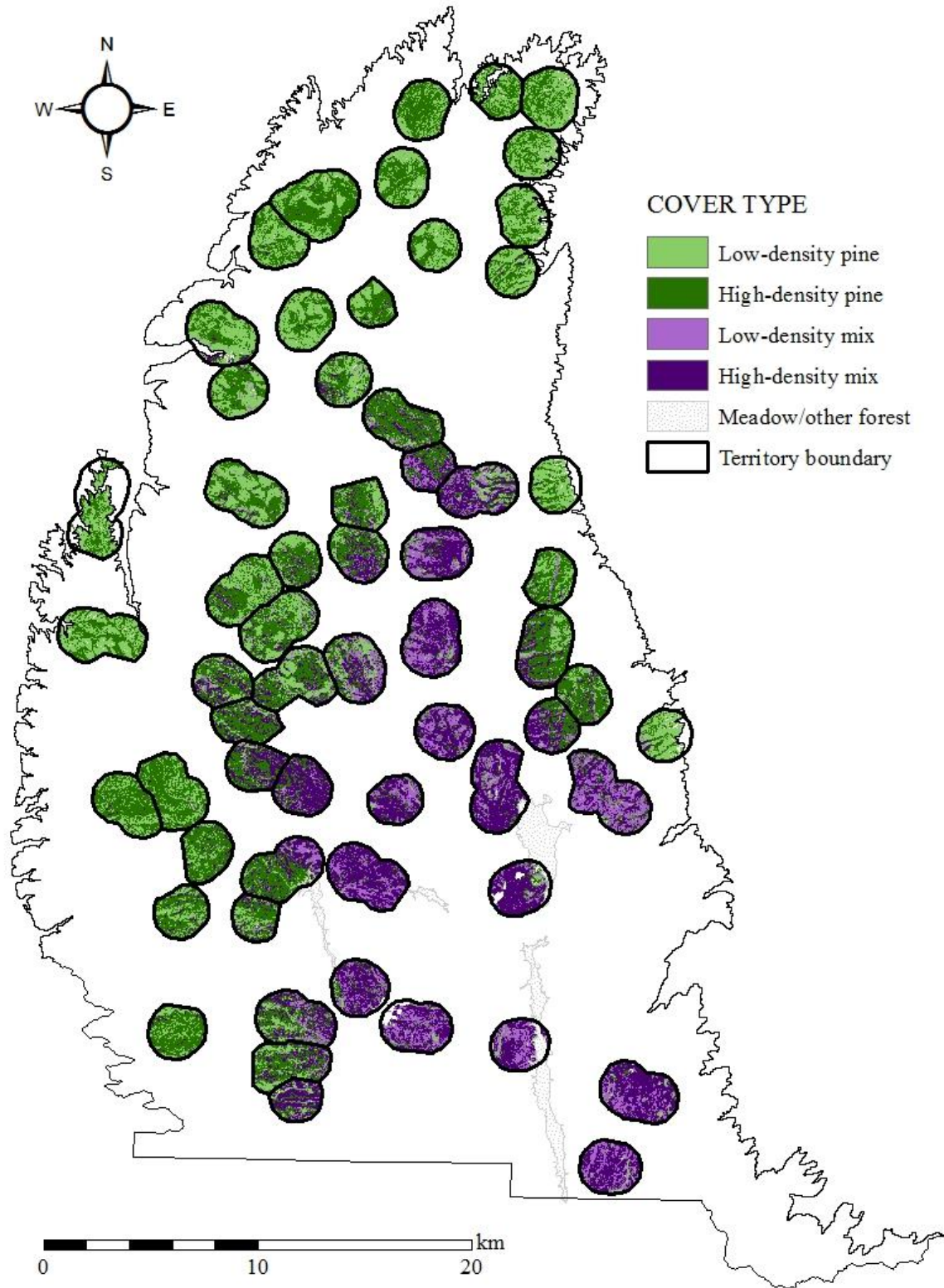


Figure 8. Distribution of 4 forest cover types within the 61 goshawk territories with a breeding attempt (eggs laid) in 2000 on the Kaibab Plateau, Arizona. Classifications of cover types were fixed over time and based on the dominant species and density of mature trees in lightly harvested (high-density) and more intensively harvested (low-density) mixed conifer (mix) or ponderosa pine (pine) forest.

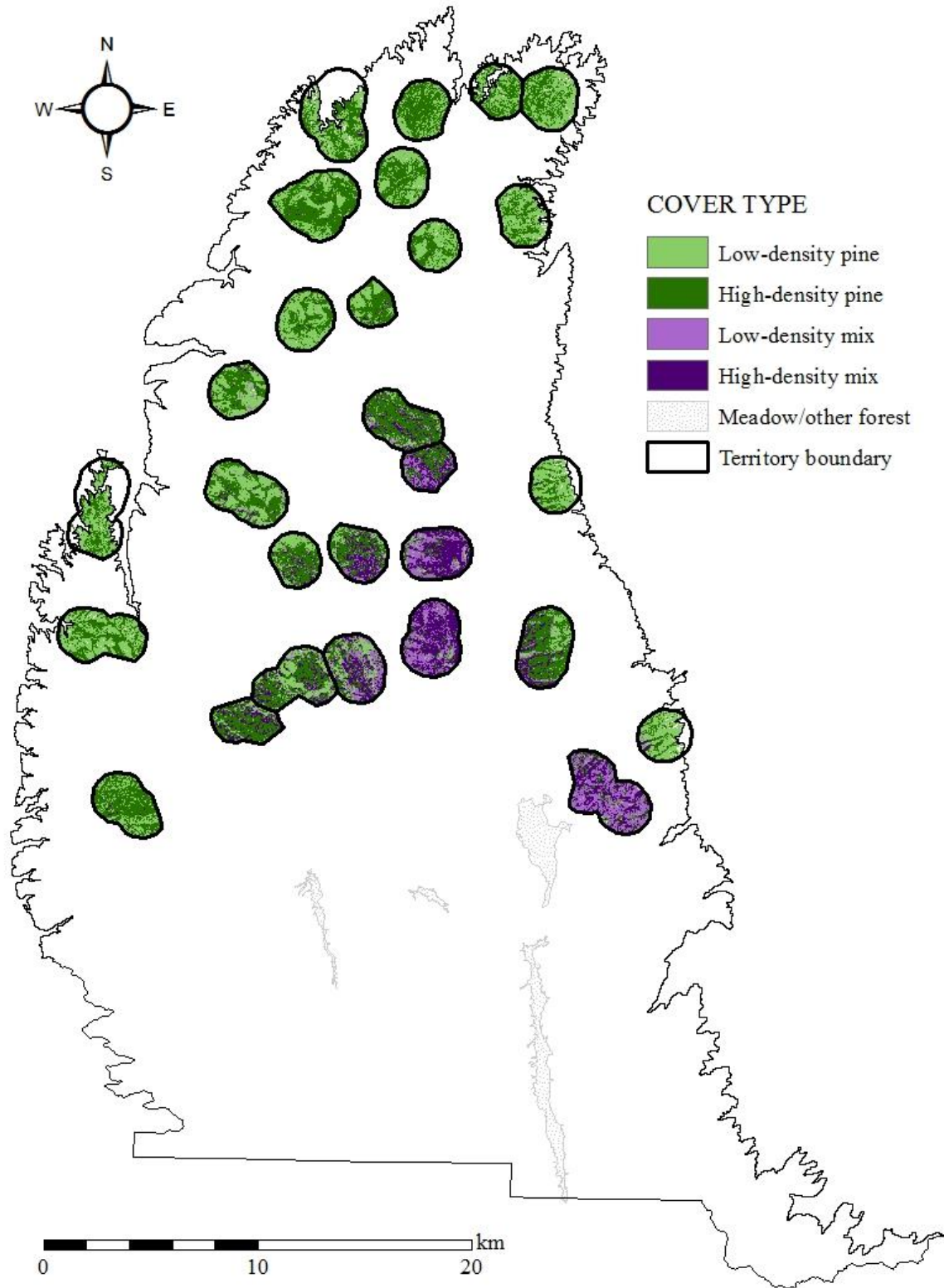


Figure 9. Distribution of 4 forest cover types within the 28 goshawk territories with a breeding attempt (eggs laid) in 2001 on the Kaibab Plateau, Arizona. Classifications of cover types were fixed over time and based on the dominant species and density of mature trees in lightly harvested (high-density) and more intensively harvested (low-density) mixed conifer (mix) or ponderosa pine (pine) forest.

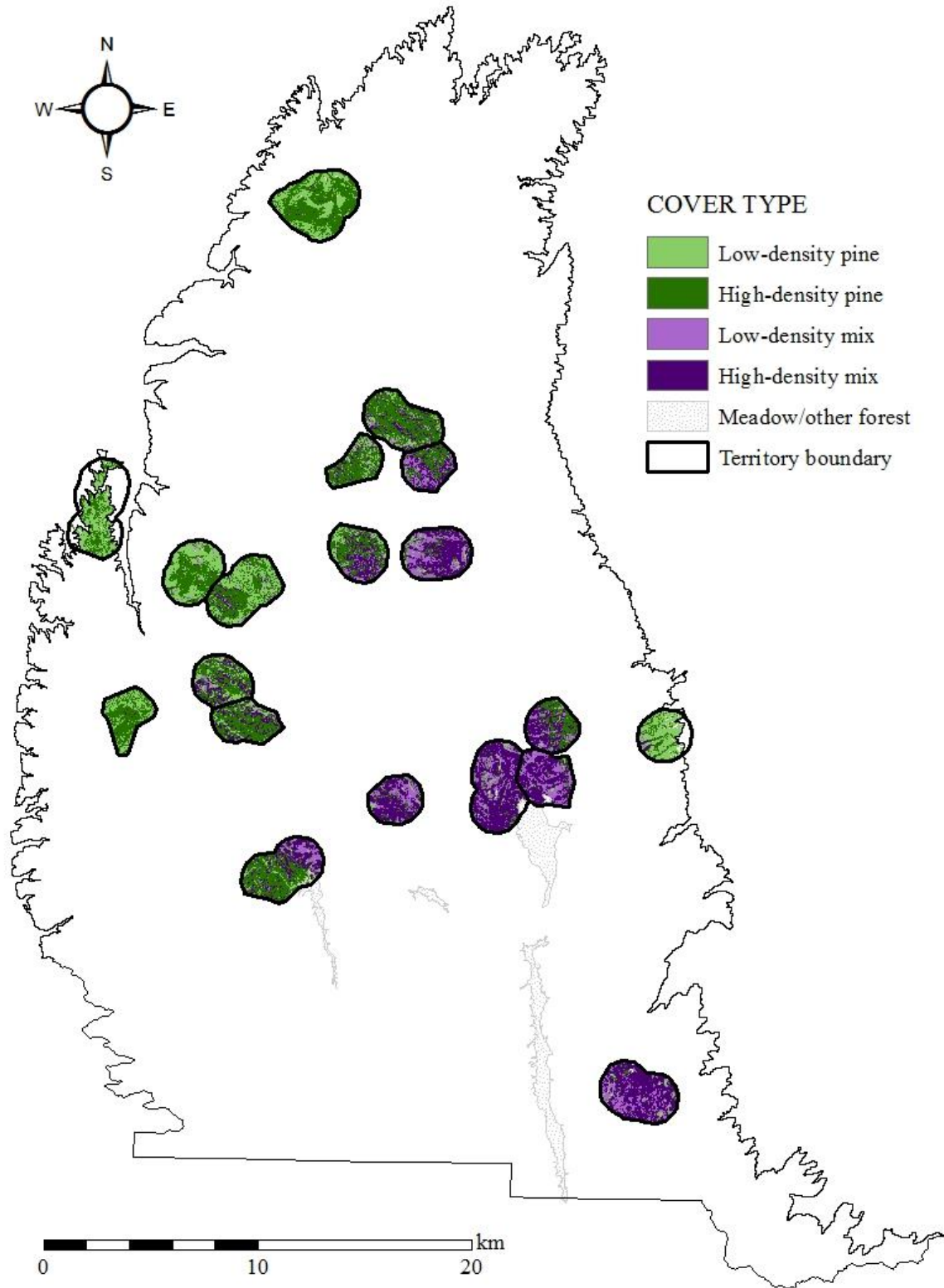


Figure 10. Distribution of 4 forest cover types within the 19 goshawk territories with a breeding attempt (eggs laid) in 2002 on the Kaibab Plateau, Arizona. Classifications of cover types were fixed over time and based on the dominant species and density of mature trees in lightly harvested (high-density) and more intensively harvested (low-density) mixed conifer (mix) or ponderosa pine (pine) forest.

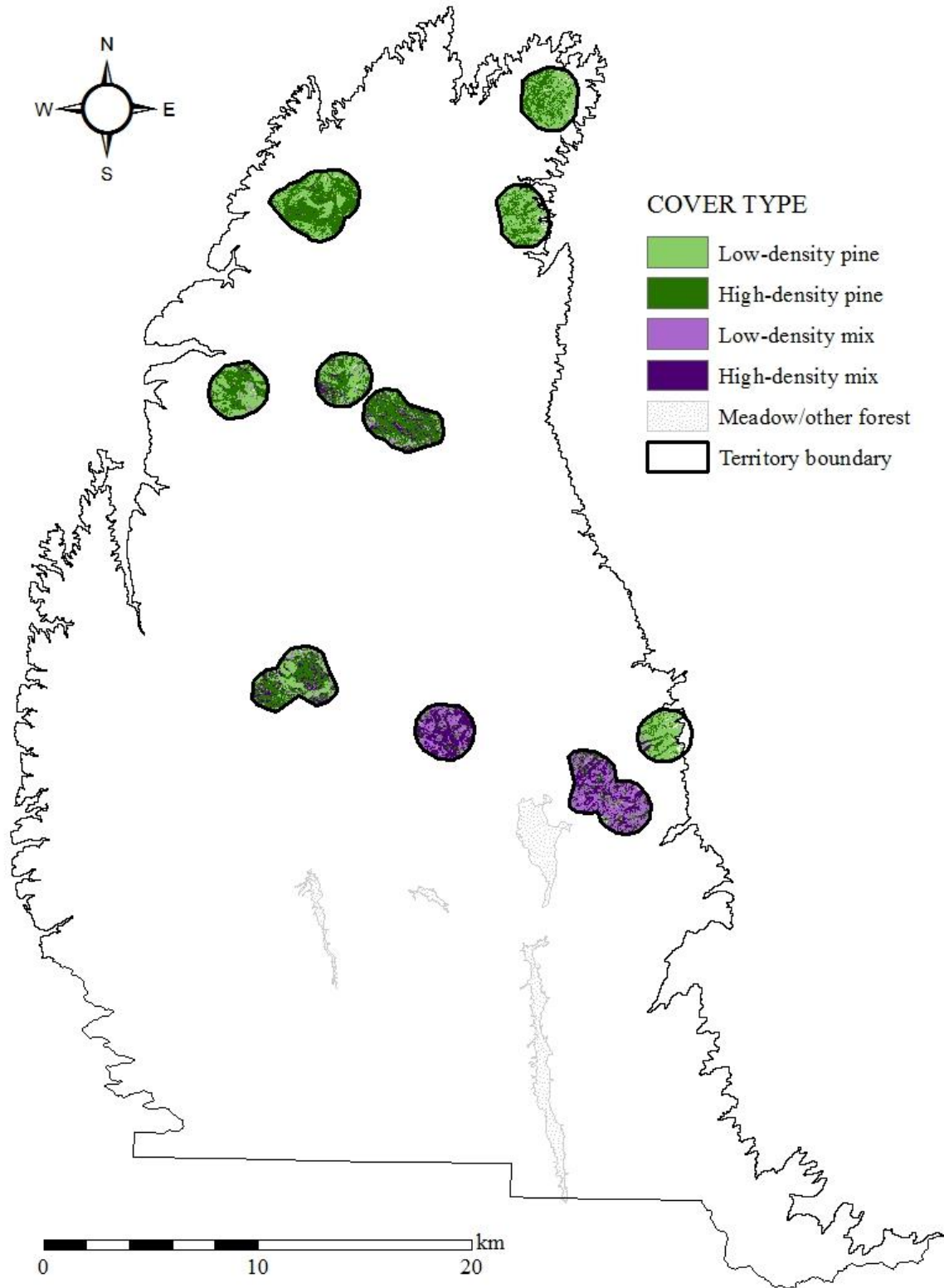


Figure 11. Distribution of 4 forest cover types within the 10 goshawk territories with a breeding attempt (eggs laid) in 2003 on the Kaibab Plateau, Arizona. Classifications of cover types were fixed over time and based on the dominant species and density of mature trees in lightly harvested (high-density) and more intensively harvested (low-density) mixed conifer (mix) or ponderosa pine (pine) forest.

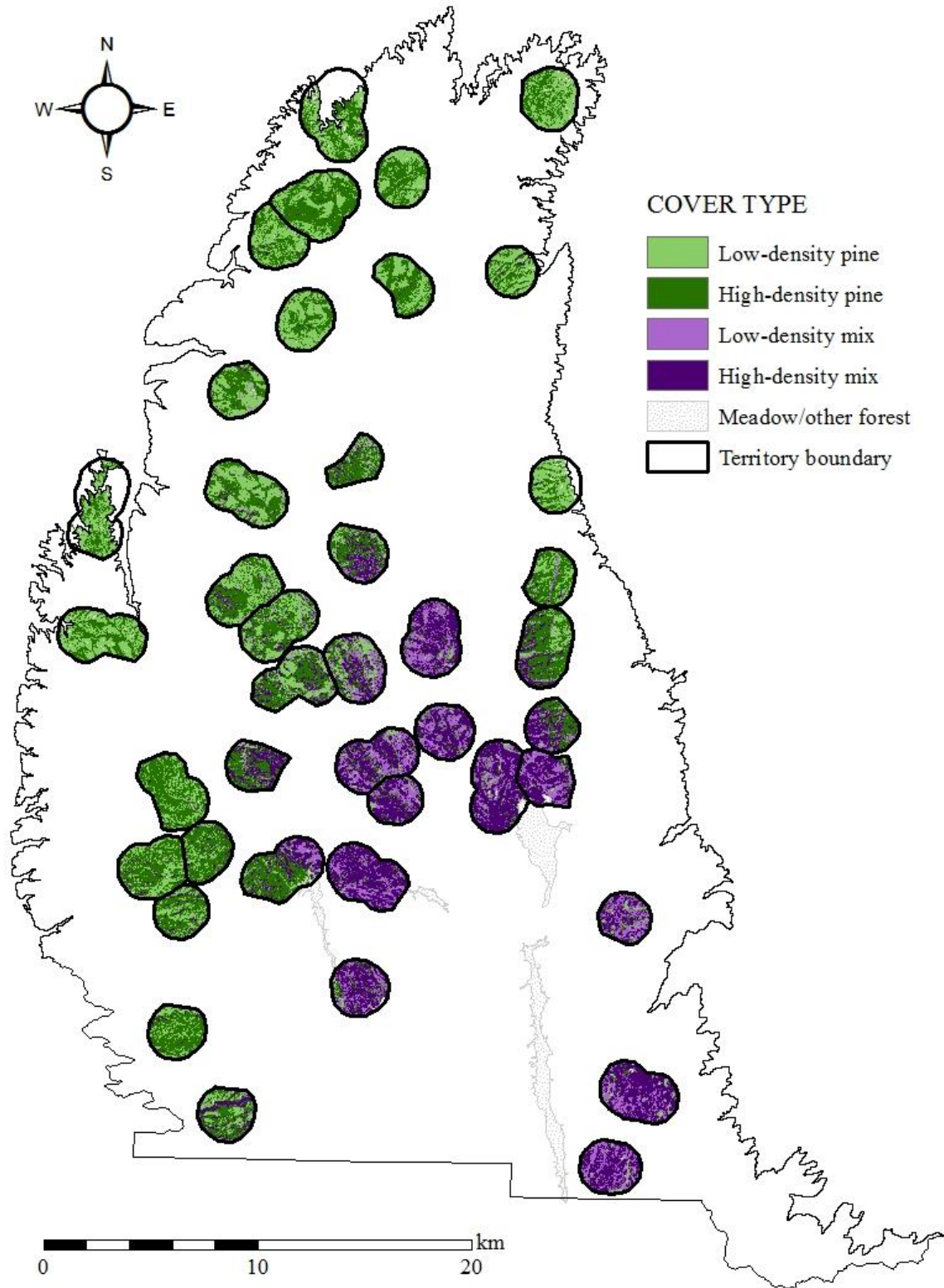


Figure 12. Distribution of 4 forest cover types within the 41 goshawk territories with a breeding attempt (eggs laid) in 2004 on the Kaibab Plateau, Arizona. Classifications of cover types were fixed over time and based on the dominant species and density of mature trees in lightly harvested (high-density) and more intensively harvested (low-density) mixed conifer (mix) or ponderosa pine (pine) forest.

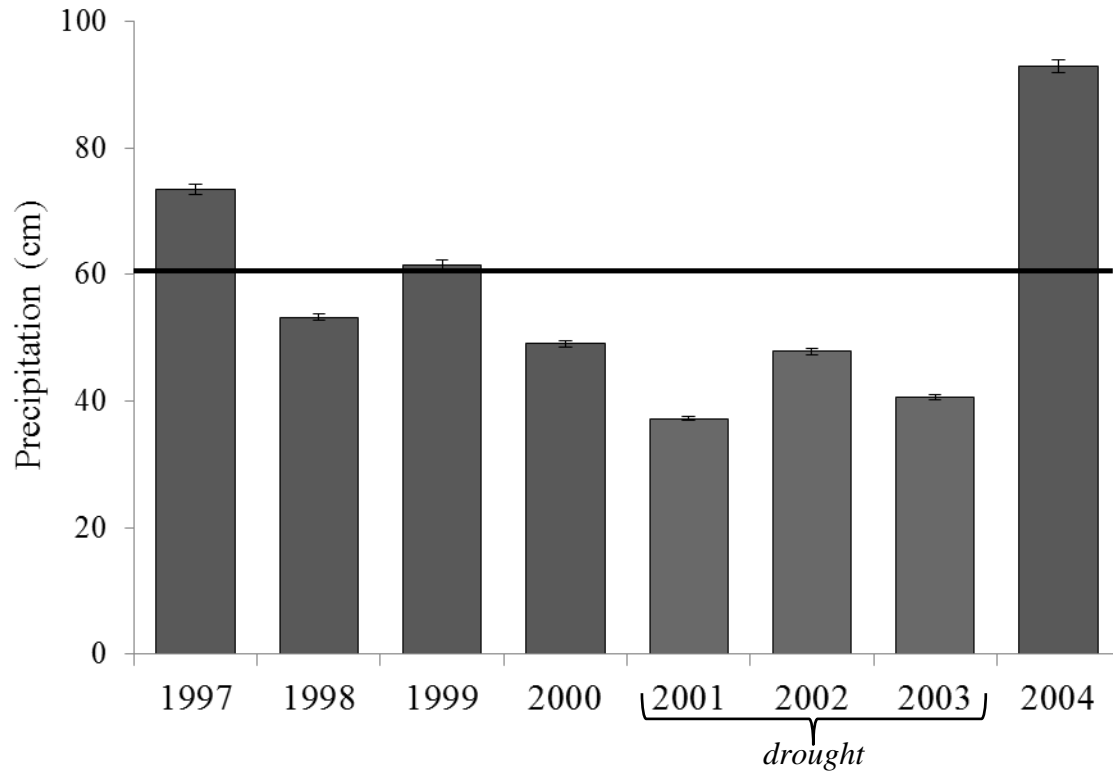


Figure 13. Mean cumulative (April-March) precipitation (\pm SE) per year for 102 goshawk territories on the Kaibab Plateau, Arizona during 1997-2004. The black line represents average annual precipitation during 1925-2004 for the Bright Angel Ranger Station, Arizona located on the southern tip of the Kaibab Plateau. Years with below-average precipitation (<61 cm) in the current and prior year were considered drought years.

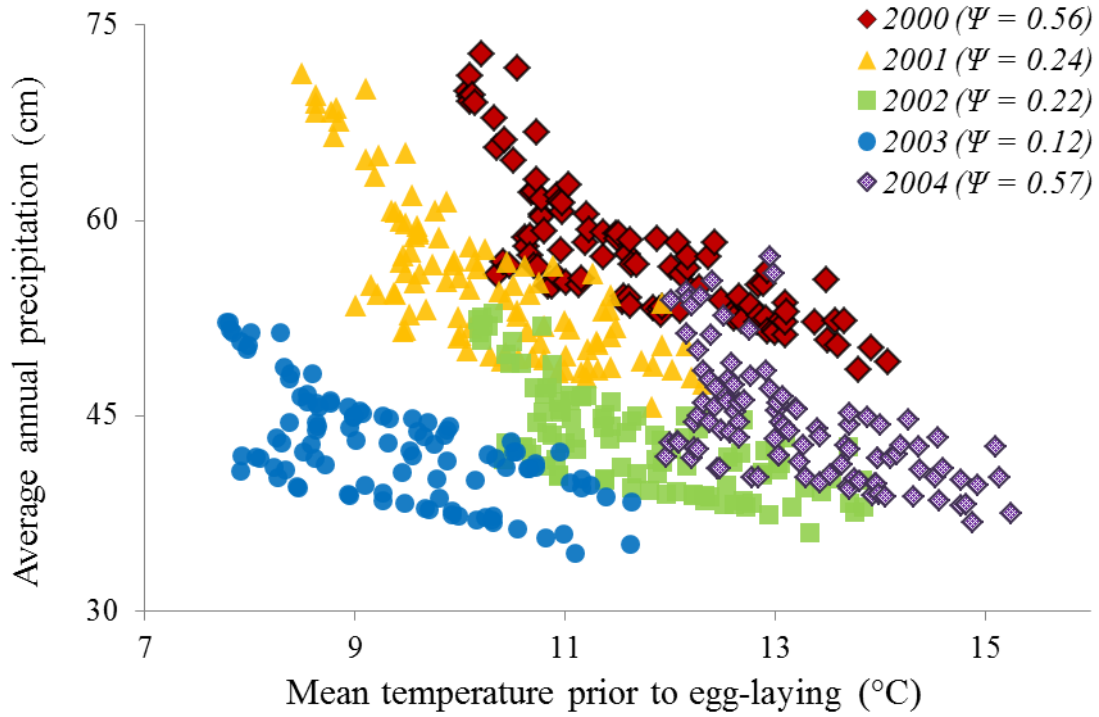


Figure 14. Relationship between 2-yr average annual precipitation (April-March) prior to the breeding season and mean temperature during the 2 months prior to egg laying (March-April) per territory ($n = 102$) per year relative to mean annual egg-laying probabilities (Ψ) for all goshawk territories on the Kaibab Plateau, Arizona during 2000-2004. Estimates of Ψ were obtained from the climate model with the most support in the goshawk reproduction data (Table 4). Warmer temperatures were associated with higher breeding probabilities, whereas colder temperatures were associated with the lowest egg-laying probabilities, especially during drought (2001-2003).

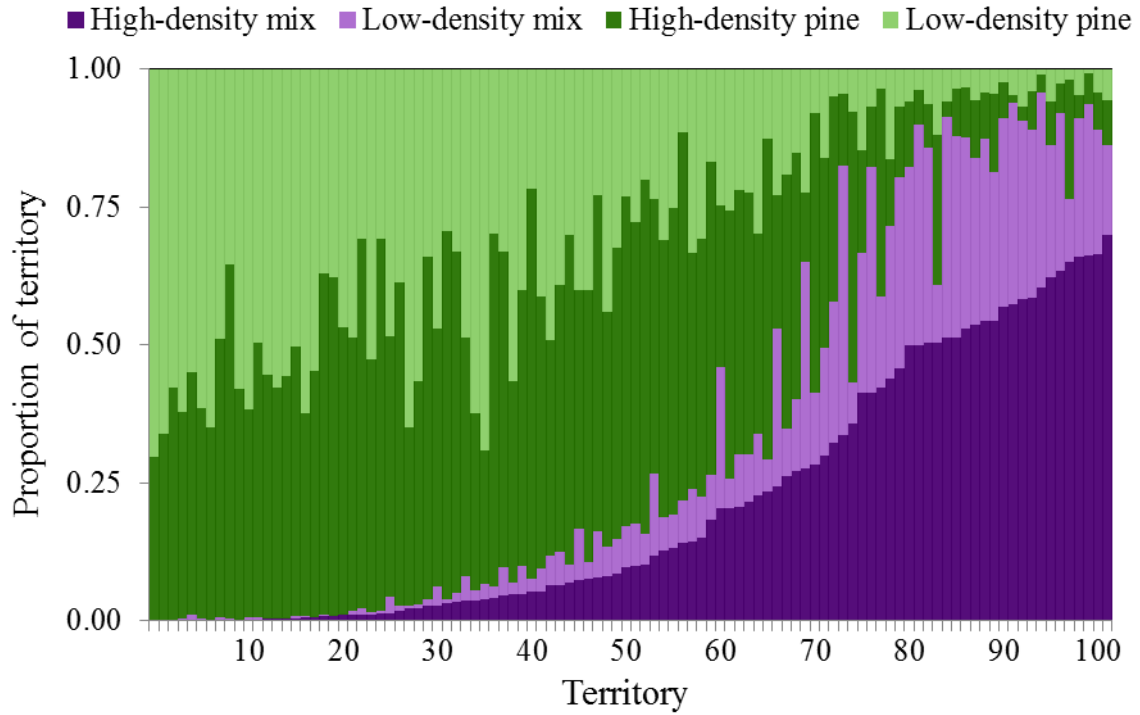


Figure 15. Composition of forest cover types within each goshawk territory ($n = 102$) on the Kaibab Plateau, Arizona during 1999-2004. Classifications of cover types were fixed over time and based on the dominant species and density of mature trees in lightly harvested (high-density) and more intensively harvested (low-density) mixed conifer (mix) or ponderosa pine (pine) forest.

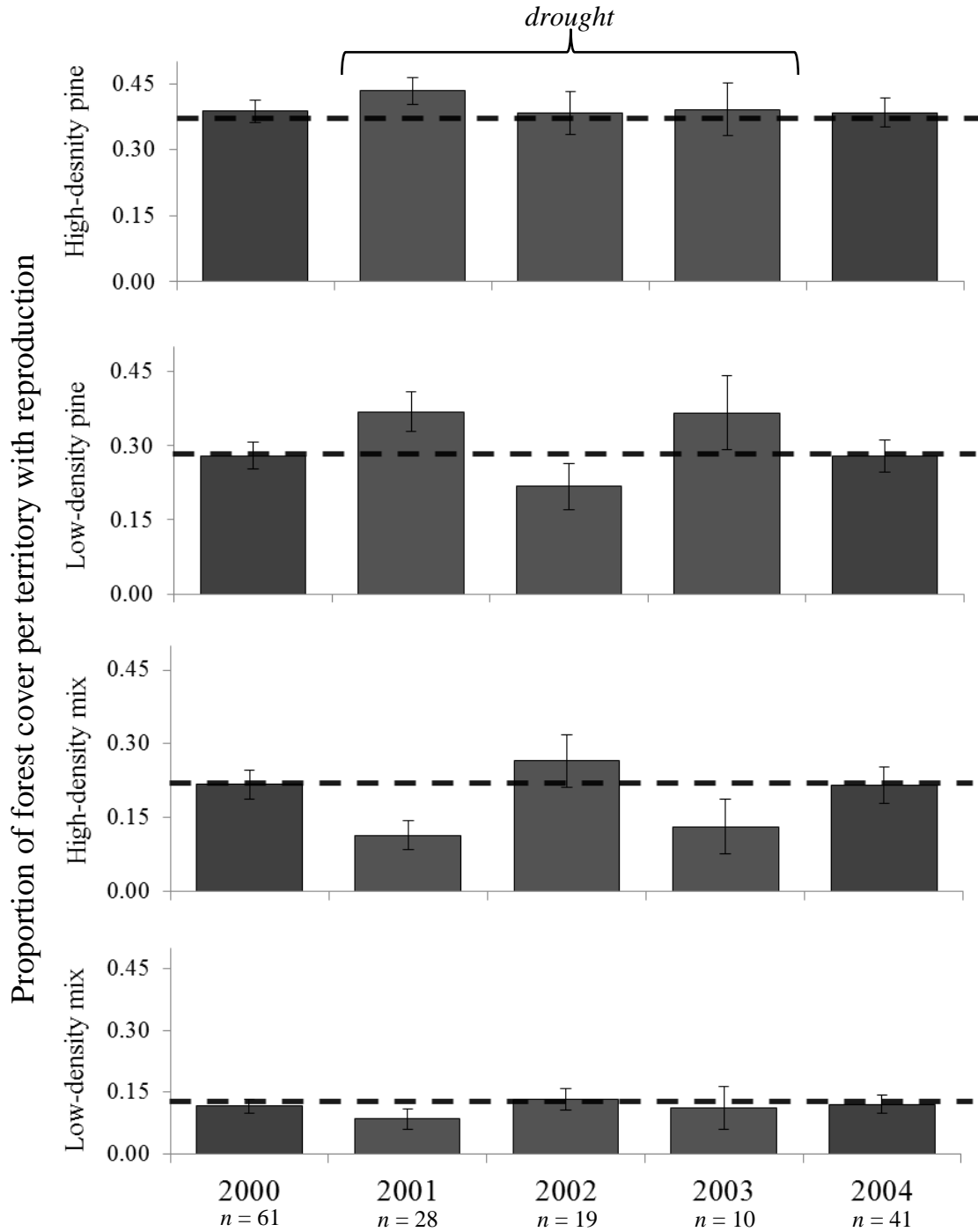


Figure 16. Comparison of mean coniferous forest composition averaged over annual samples of goshawk territories with a breeding attempt (n) on the Kaibab Plateau, Arizona during 2000-2004. Cover-type proportions (\pm SE) were estimated for lightly-harvested ponderosa pine (high-density pine), intensively-harvested ponderosa pine (low-density pine), lightly-harvested mixed conifer (high-density mix), and intensively-harvested mixed conifer (low-density mix). Dashed lines represent mean proportions averaged over all territories within the study area ($n = 102$). In non-drought years (2000, 2004), forest composition of territories with reproduction was similar to the average proportion for all 102 territories. In contrast, during drought (2001-2003), there was greater variation in the forest composition of territories among years, especially in the amount of low-density pine and high-density mix.

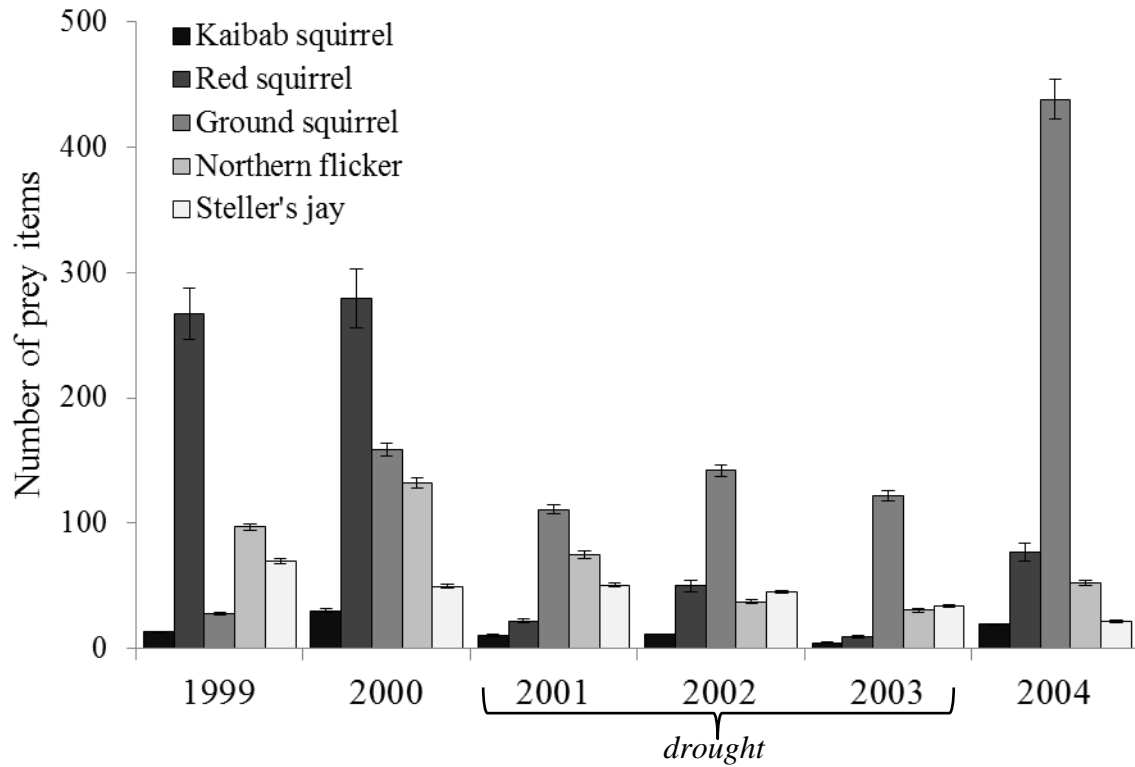


Figure 17. Estimated mean number of prey items (\pm SE) per territory per year for 5 primary prey species of goshawks on the Kaibab Plateau, Arizona during 1999-2004. Years with below-average precipitation in the current and prior year were considered drought years (Fig. 13).

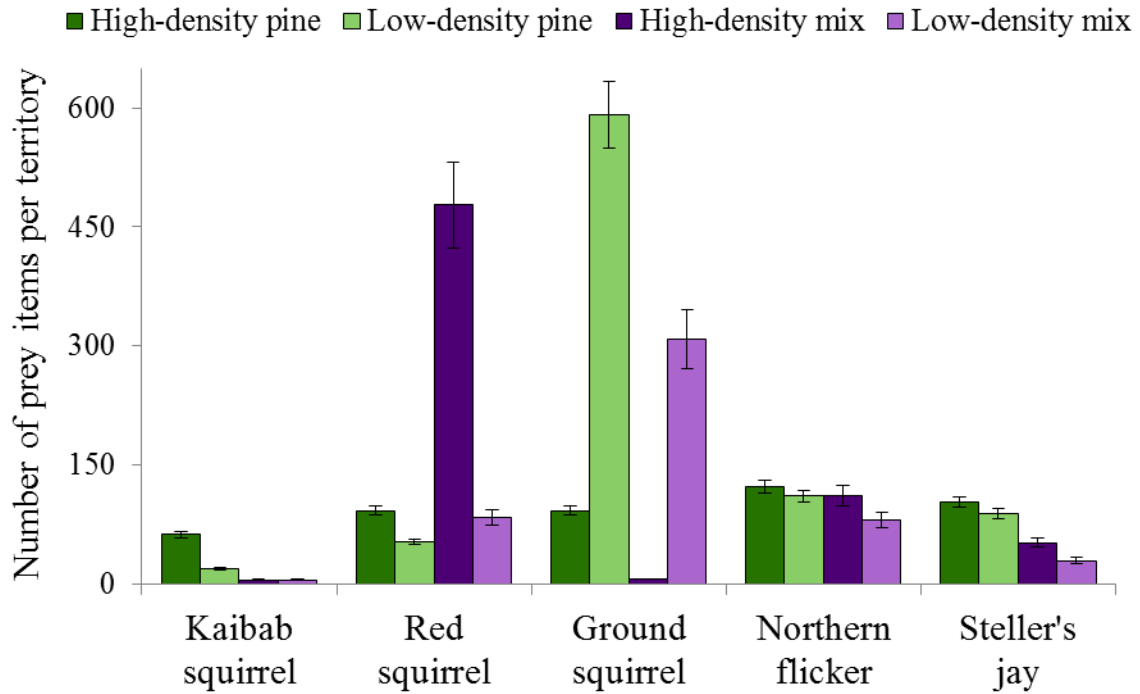


Figure 18. Comparison of the estimated mean number of prey items (\pm SE) per forest cover type within 102 goshawk territories on the Kaibab Plateau, Arizona during 1999-2004. Cover types included lightly-harvested ponderosa pine (high-density pine), intensively-harvested ponderosa pine (low-density pine), lightly-harvested mixed conifer (high-density mix), and intensively harvested mixed conifer (low-density mix).

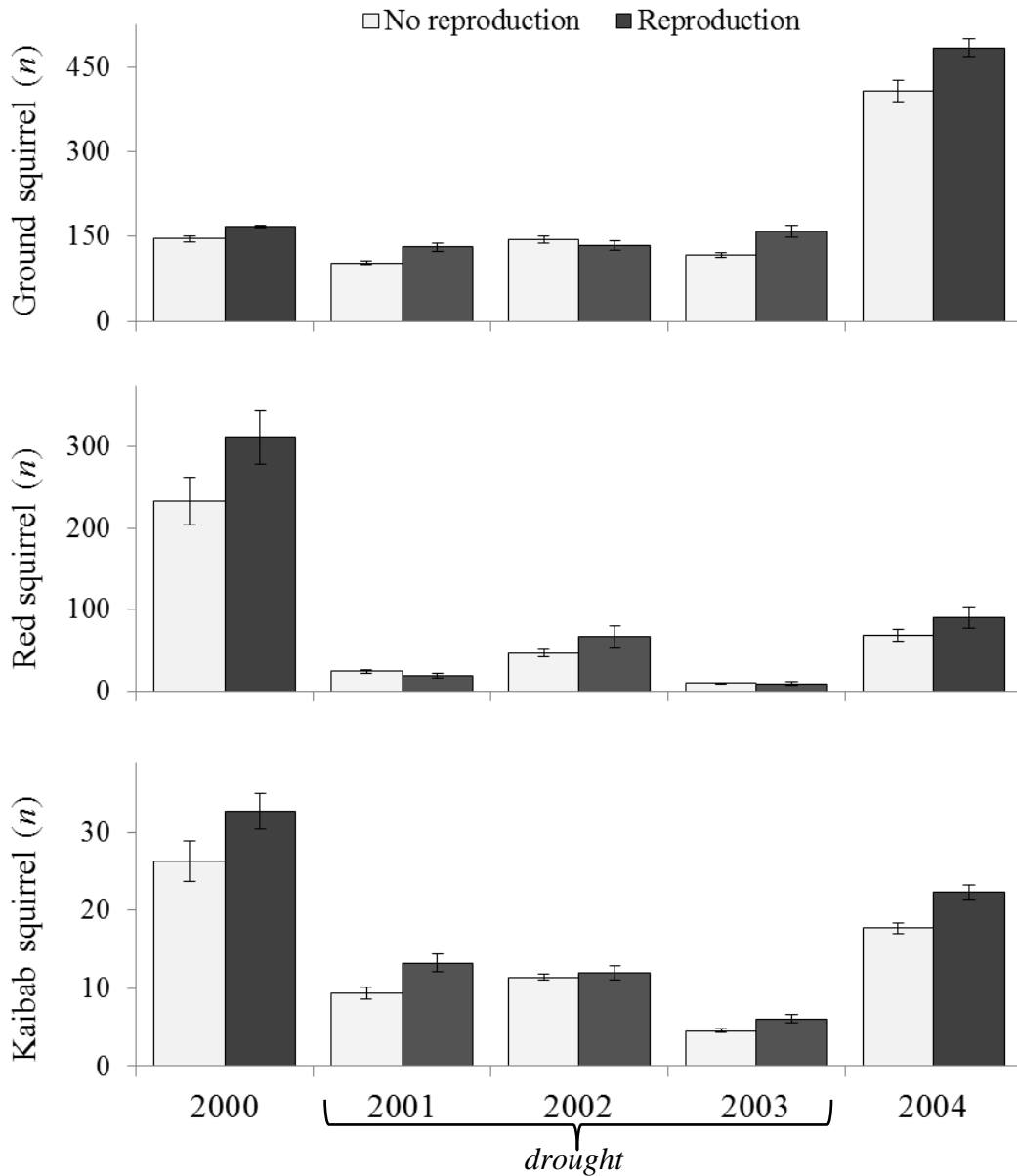


Figure 19. Comparison of the estimated mean number of mammal prey items (\pm SE) per species among 102 goshawk territories categorized annually by reproductive state for sites without a breeding attempt (no reproduction) or sites with eggs or ≥ 1 fledgling produced (reproduction) on the Kaibab Plateau, Arizona during 2000-2004. Years with below-average precipitation in the current and prior year were considered drought years (Fig. 13). All territories regardless of reproductive state contained more Kaibab squirrels, red squirrels and ground squirrels in non-drought years than in drought years. However, during drought, most territories with reproduction contained only more Kaibab squirrels and ground squirrels in 2001 and 2003 or only more red squirrels in 2002.

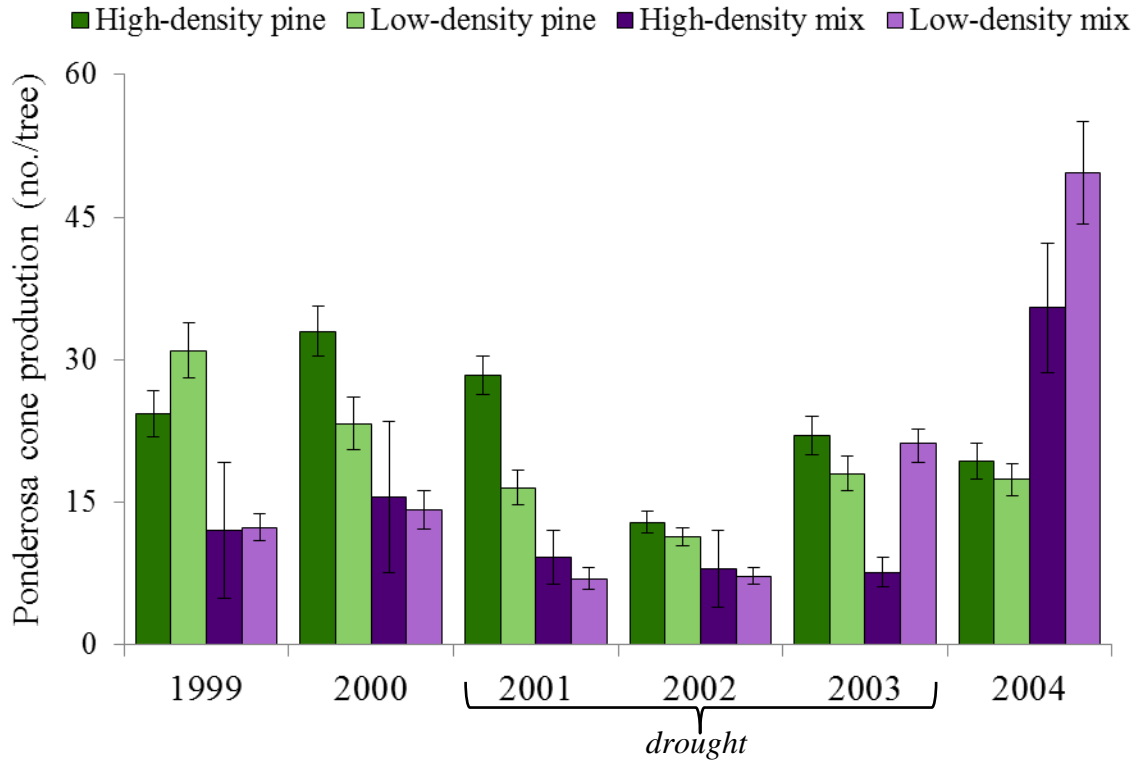


Figure 20. Among- and within-year variation in mean cone production (\pm SE) per forest cover type for ponderosa pine trees on the Kaibab Plateau, Arizona during 2000-2004. Cover types included: lightly-harvested ponderosa pine (high-density pine), intensively-harvested ponderosa pine (low-density pine), lightly-harvested mixed conifer (high-density mix), and intensively-harvested mixed conifer (low-density mix). Years with below-average precipitation in the current and prior year were considered drought years (Fig. 13).

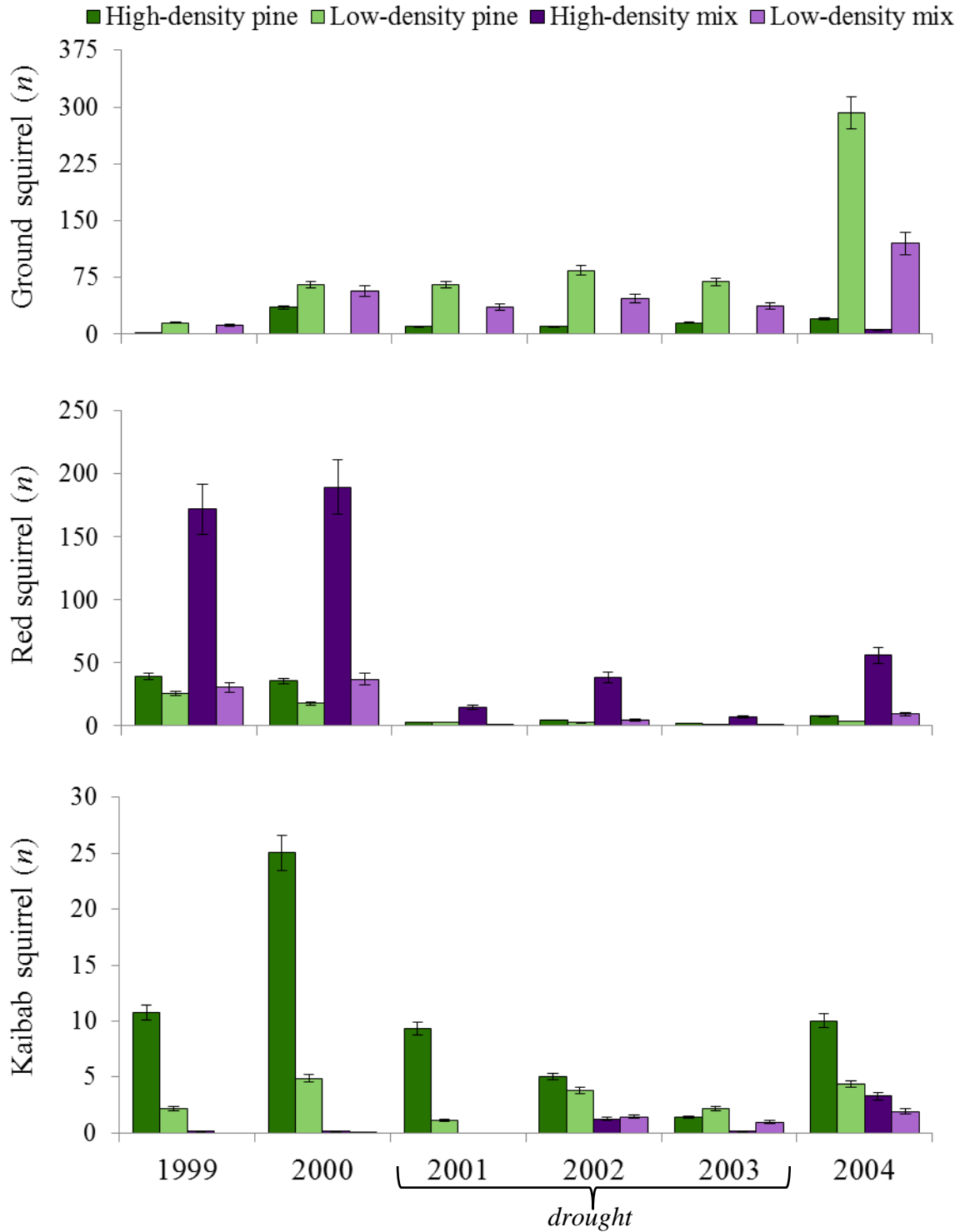


Figure 21. Estimated mean number of prey items (\pm SE) per forest cover type per year for mammal prey species within 102 goshawk territories on the Kaibab Plateau, Arizona during 1999-2004. Cover types included: lightly-harvested ponderosa pine (high-density pine), intensively-harvested ponderosa pine (low-density pine), lightly-harvested mixed conifer (high-density mix), and intensively-harvested mixed conifer (low-density mix). Years with below-average precipitation in the current and prior year were considered drought years (Fig. 13).

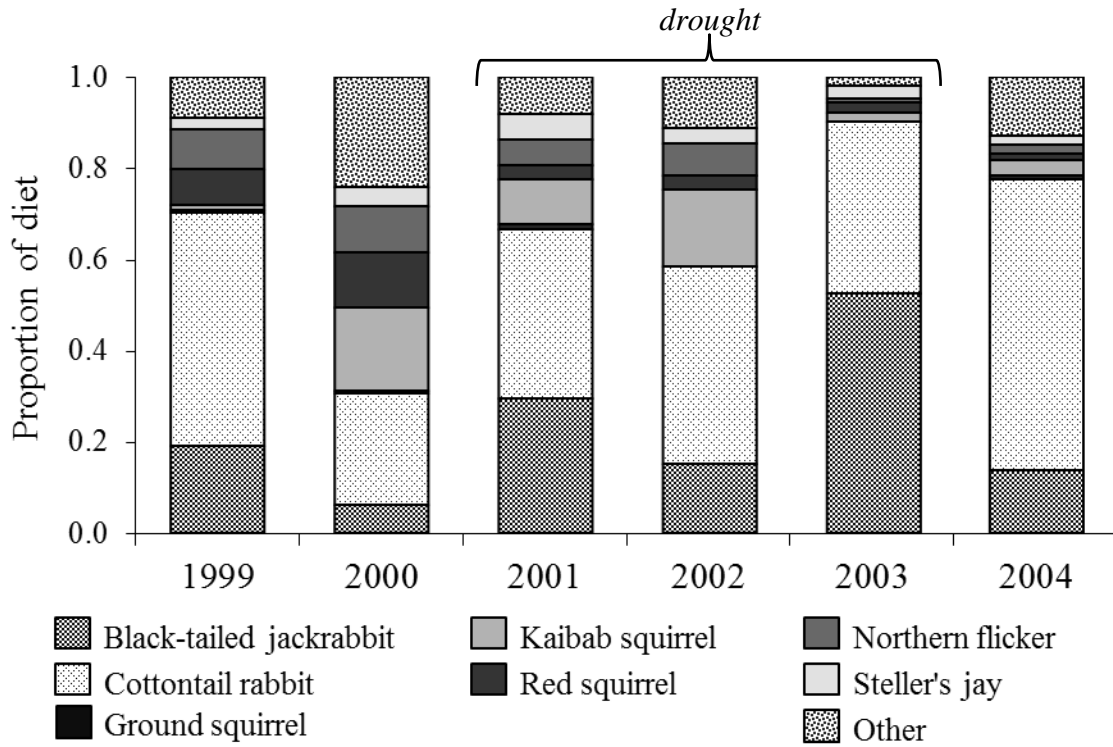


Figure 22. Biomass contribution of primary prey species to the annual diets of goshawks on the Kaibab Plateau, Arizona during 1999-2004. "Other" included all prey species that each contributed <4% of total biomass to goshawk diets during the study period. Years with below-average precipitation in the current and prior year were considered drought years (Fig. 13).

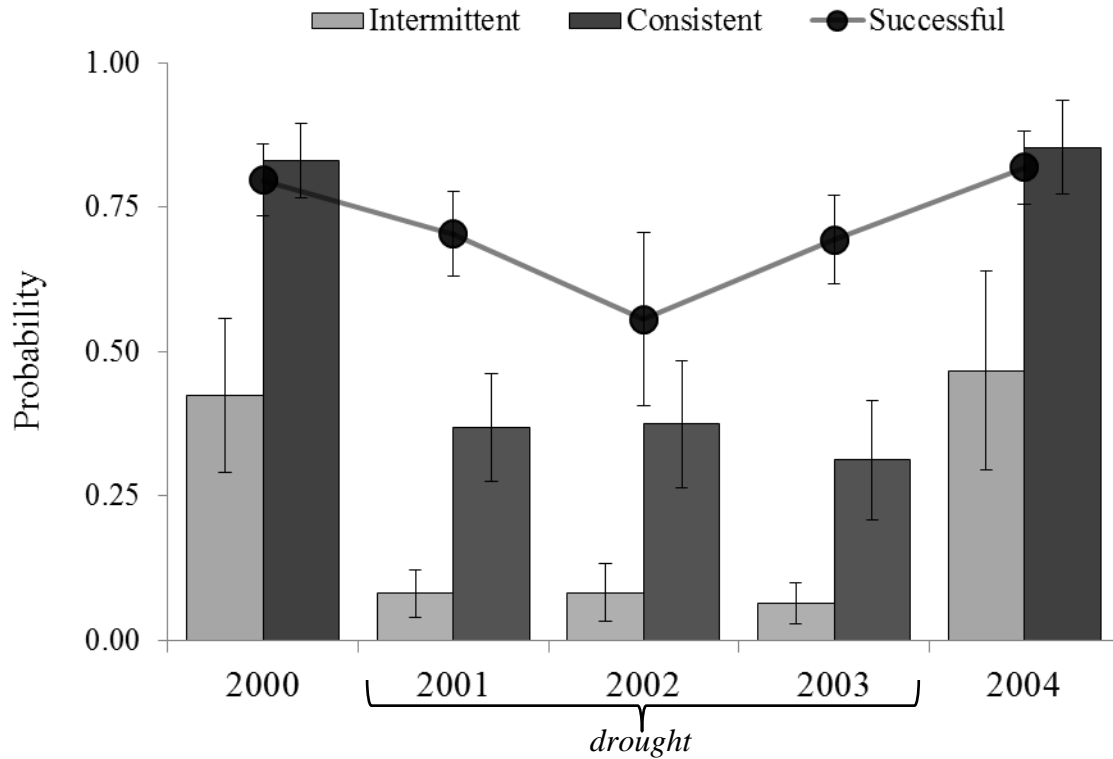


Figure 23. Comparison of annual egg-laying probabilities and 95% confidence intervals among goshawk territories with consecutive breeding attempts in the current and prior year (consistent reproduction) and territories without a breeding attempt in the prior year (intermittent reproduction) on the Kaibab Plateau, Arizona during 2000-2004. Also shown are annual probabilities of producing ≥ 1 fledgling (successful reproduction) and 95% confidence intervals for all territories regardless of nesting status in the prior year. Estimates of reproductive probabilities were obtained from the habitat model with the most support in the data (Table 7). Years with below-average precipitation in the current and previous year were considered drought years (Fig. 13).

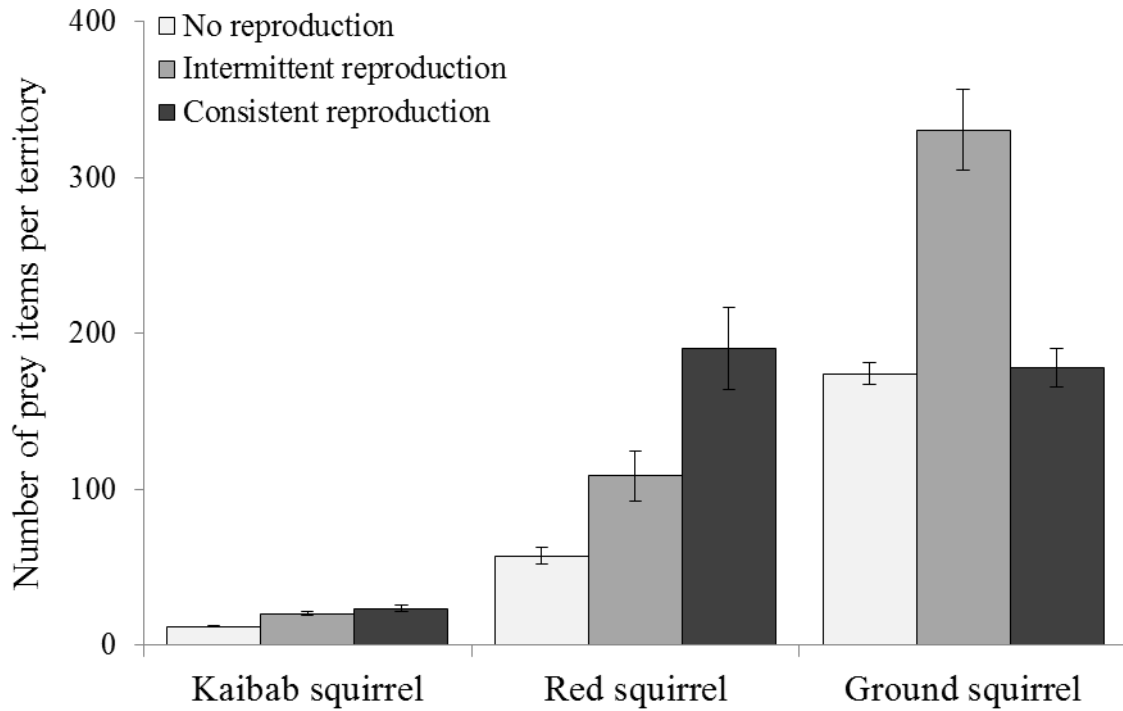


Figure 24. Comparison of the estimated mean number of prey items per mammal species (\pm SE) among goshawk territories with consecutive breeding attempts in the prior and current year (consistent reproduction), territories with a breeding attempt only in the current year (intermittent reproduction), and territories without breeding attempt in the prior or current year (no reproduction) on the Kaibab Plateau, Arizona during 2000-2004.

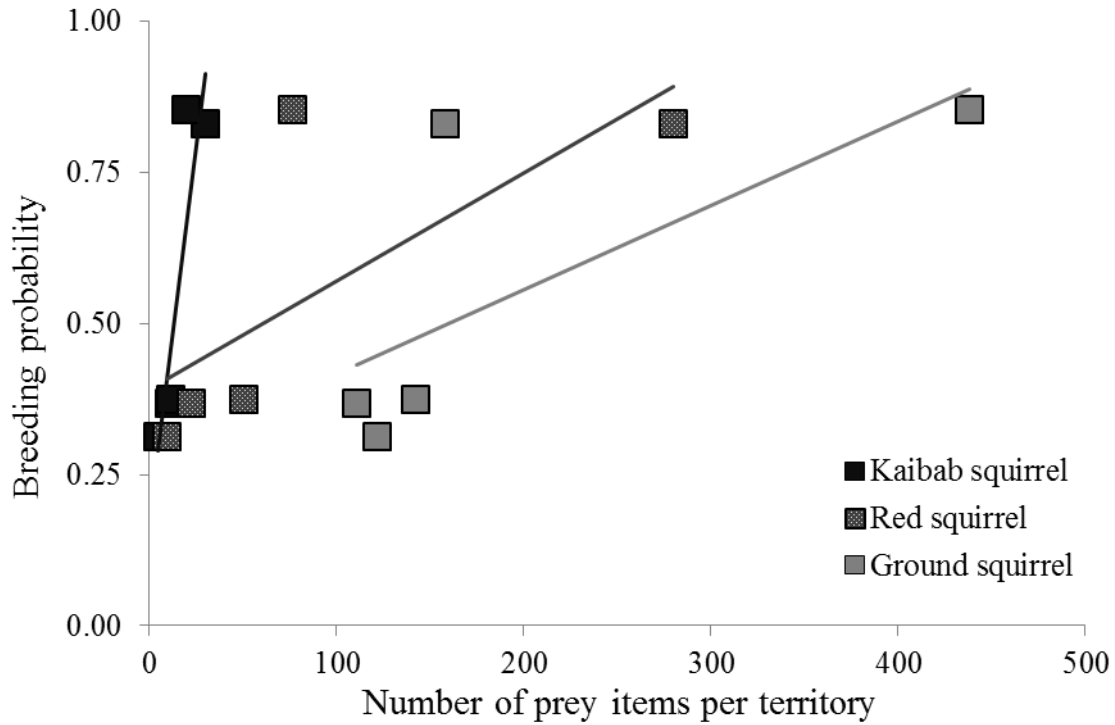


Figure 25. Relationships between the estimated mean number of mammal prey items and annual egg-laying probabilities for goshawk territories with consecutive breeding attempts in the current and prior year (i.e., consistent reproduction) on the Kaibab Plateau, Arizona during 2000-2004. Prediction lines are from the habitat model with the most support in the goshawk reproduction data (Table 7), which included the additive effects of all three mammal prey species (Kaibab squirrel, red squirrel, and golden-mantled ground squirrel).

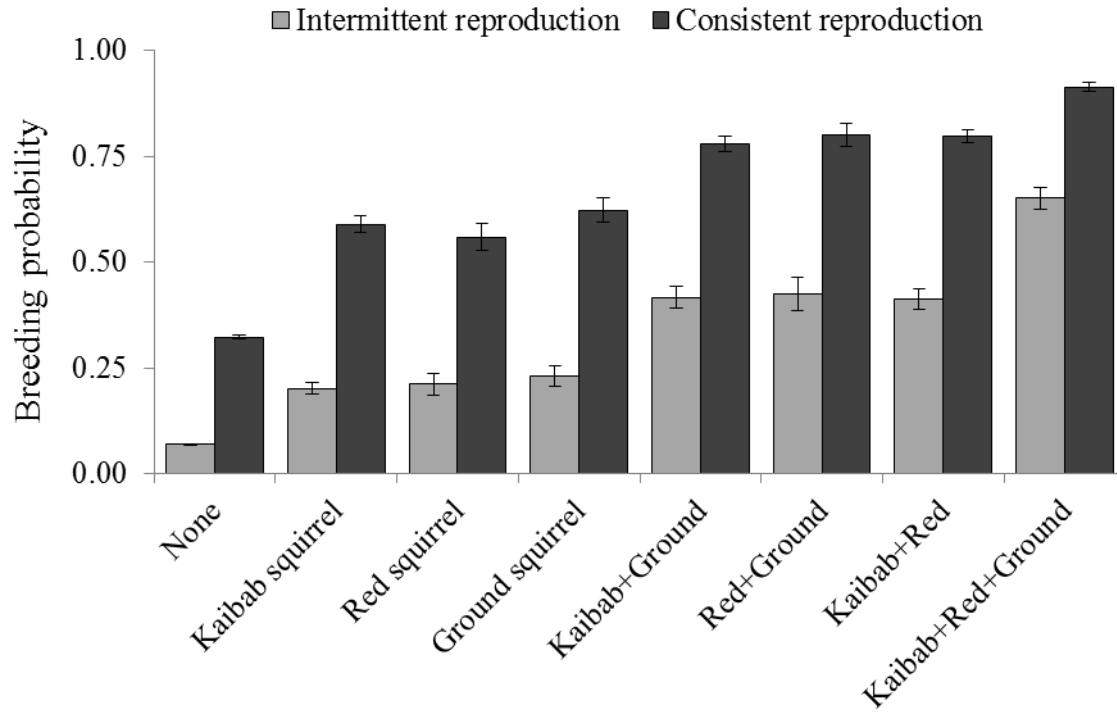


Figure 26. Comparison of mean annual breeding probabilities (\pm SE) among goshawk territories with food resources dominated by ≥ 1 mammal prey species on the Kaibab Plateau, Arizona during 2000-2004. Estimates of breeding probabilities per territory with consecutive breeding attempts in the prior or current year (consistent reproduction) or only a breeding attempt in the current year (intermittent reproduction) were obtained from the habitat model with the most support in the goshawk reproductive data (Table 7).

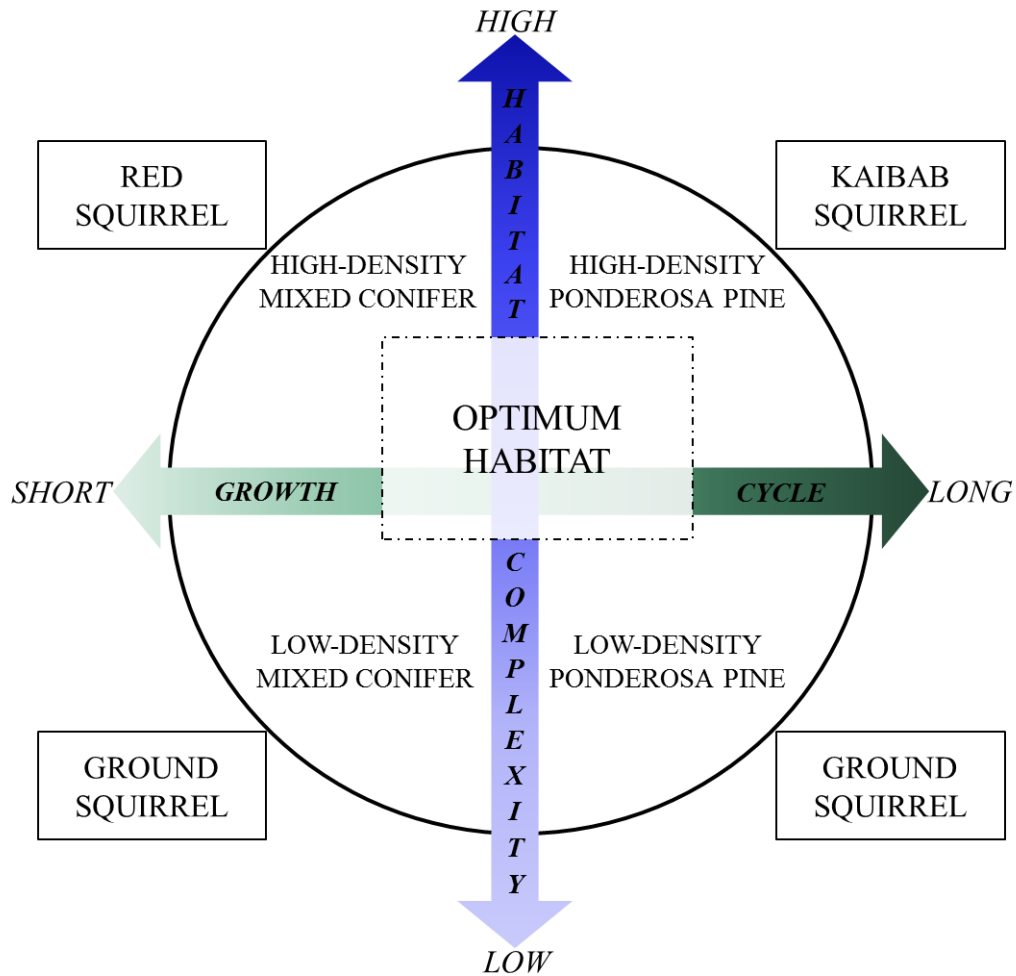


Figure 27. Schematic diagram representing the spectrum of variation in goshawk habitat characteristics on the Kaibab Plateau, Arizona. Forest cover types include: lightly-harvested (high-density) or intensively-harvested (low-density) mixed conifer and ponderosa pine forest. Prey species indicate forest cover type associated with the highest abundance of each species. The productivity of each cover type is influenced by length of growth cycle and heterogeneity of structural attributes (habitat complexity) relative to temporal and spatial variation in annual climatic conditions. Longer growth cycles and greater habitat complexity maximize the overall productivity of forested landscapes by reducing the effects of drought on forest biota. Optimum goshawk habitat incorporates more forest types and alternate prey communities that enhance the diversity of responses to dynamic climatic conditions.

Table 1. Variables used in dynamic multistate site occupancy models to assess how temporal and spatial variation in climatic conditions, vegetation attributes, and prey abundance influences goshawk reproduction probabilities on the Kaibab Plateau, Arizona during 1999-2004.

Variable	Definition	Covariate type
State	Territory reproductive state in the prior year: 3 states (no reproduction, eggs laid, ≥ 1 fledged) or 2 states (no reproduction/breeding attempted)	Territory-specific
Year	Annual variation	Annual
Temperature	Mean monthly maximum temperature ($^{\circ}\text{C}$)	Time-varying site-specific
Precipitation	Cumulative precipitation (cm)	Time-varying site-specific
Drought	Palmer Drought Severity Index value for northern Arizona	Annual
Canopy	Mean canopy cover (%)	Territory-specific
Forest cover	Proportion of territory for each cover type: selectively-harvested ponderosa pine (high-density pine) or mixed conifer (high-density mix), extensively-harvested ponderosa pine (low-density pine) or mixed conifer (low-density mix)	Territory-specific
Contagion	Mean patch size of high-density forest (ha)	Territory-specific
Management	Maximum patch size of extensive timber harvests (ha)	Territory-specific
Forest edge	Distance between territory center and nearest boundary between forest types (m)	Territory-specific
Cone crop	Mean number cone per tree for all mixed conifer species or only ponderosa pine	Time-varying site-specific
Prey	Number per territory for Kaibab squirrel, red squirrel, golden-mantled ground squirrel, northern flicker, or Steller's jay	Time-varying site-specific
Biomass	Proportion each species contributed to annual diet for cottontail rabbit, black-tailed jackrabbit, Kaibab squirrel, red squirrel, northern flicker, or Steller's jay	Annual

Table 2. Number of goshawk territories surveyed, proportion of territories searched with evidence of a breeding attempt for survey periods 1-3, and number of breeding attempts, successful breeding attempts (≥ 1 young fledged), fledged, and fledged per successful breeding attempt per year on the Kaibab Plateau, Arizona during 1999-2004.

Year	Surveyed	Survey 1	Survey 2	Survey 3	Attempt	Success	Fledged	Fledge/Success
1999	97	0.89	0.06	0.06	53	40	91	2.28
2000	102	0.89	0.02	0.10	61	54	129	2.39
2001	102	0.86	0.11	0.04	28	17	31	1.82
2002	102	0.95	0.05	0.00	19	10	14	1.40
2003	102	0.90	0.00	0.10	10	6	9	1.50
2004	102	0.66	0.05	0.29	41	32	69	2.16

Table 3. Ranking of the top 10 dynamic multistate site occupancy models, without environmental covariates, used to examine variation in annual probabilities of producing eggs (Ψ) or ≥ 1 fledgling (R) among goshawk territories on the Kaibab Plateau, Arizona during 1999-2004. The same structure was used for the detection and classification components of all models in the model set. See Appendix E for the ranking of all 62 models without environmental covariates.

Model ^a	AIC _c	Δ AIC _c	w	K	$-2l$
Ψ (state2*year) R (year)	1079.42	0.00	0.56	23	1031.5
Ψ (state2*year) R (state2+year)	1081.04	1.62	0.25	24	1031.0
Ψ (state2*year) R (state3+year)	1083.21	3.79	0.08	25	1031.0
Ψ (state2*year) R (state2*year)	1085.13	5.71	0.03	28	1026.3
Ψ (state3*year) R (year)	1086.04	6.62	0.02	28	1027.2
Ψ (state2*year) R (.)	1086.29	6.87	0.02	19	1047.0
Ψ (state3*year) R (state2+year)	1087.66	8.24	0.01	29	1026.6
Ψ (state2*year) R (state2)	1088.42	9.00	0.01	20	1047.0
Ψ (state3*year) R (state3+year)	1089.87	10.45	0.00	30	1026.6
Ψ (state2+year) R (year)	1090.29	10.87	0.00	19	1051.0

Model selection notation: Akaike's Information Criterion corrected for small sample size (AIC_c), relative difference (Δ AIC_c), model weight (w), number of parameters (K), and twice the negative log-likelihood ($-2l$).

^aConstraints on reproductive parameters: constant over time (.), annual variation (year), dependent on reproductive state of the territory in the previous year for 2 states (state2: no reproduction, breeding attempted) or 3 states (state3: no reproduction, 0 young fledged, ≥ 1 young fledged), additive effects of state and year (state+year), or an interaction between state and year (state*year).

Table 4. Ranking of dynamic multistate site occupancy models used to characterize effects of variation in climatic conditions on annual probabilities of producing eggs (Ψ) or ≥ 1 fledgling (R) among goshawk territories on the Kaibab Plateau, Arizona during 1999-2004. The model without environmental covariates $\{\Psi(\text{state*year}) R(\text{year})\}$ was included to evaluate the relative effects of climatic conditions on goshawk reproduction. All models in the set incorporated a covariate for territory reproductive state in the prior year (state) and the same structure for the detection and classification components of the model.

Model ^a	AIC _c	Δ AIC _c	w	K	$-2l$
$\{\Psi(\text{state*year}) R(\text{year})\}$	1079.42	0.00	1.00	23	1031.52
$\{\Psi(\text{RAIN2avg*TEMPegg}) R(\text{RAINhatch})\}$	1092.66	13.24	0.00	15	1061.85
$\{\Psi(\text{RAIN2avg*TEMPegg}) R(.)\}$	1103.01	23.59	0.00	14	1074.30
$\{\Psi(\text{RAIN2avg*TEMPegg}) R(\text{TEMPhatch})\}$	1103.23	23.81	0.00	15	1072.42
$\{\Psi(\text{RAIN2avg*TEMPegg}) R(\text{RAINsit})\}$	1104.09	24.67	0.00	15	1073.27
$\{\Psi(\text{RAINegg}+(\text{RAIN2avg*TEMPegg})) R(.)\}$	1104.64	25.22	0.00	15	1073.82
$\{\Psi(\text{RAIN2avg*TEMPegg}) R(\text{RAINbreed})\}$	1104.76	25.35	0.00	15	1073.95
$\{\Psi(\text{RAIN2avg*TEMPegg}) R(\text{TEMPbreed})\}$	1104.92	25.50	0.00	15	1074.10
$\{\Psi(\text{RAIN2avg*TEMPegg}) R(\text{TEMPsit})\}$	1105.05	25.63	0.00	15	1074.23
$\{\Psi(\text{RAIN1pre*TEMPegg}) R(.)\}$	1107.31	27.89	0.00	14	1078.60
$\{\Psi(\text{RAIN1pre}+\text{TEMPegg}) R(.)\}$	1121.76	42.34	0.00	13	1095.14
$\{\Psi(\text{drought}) R(.)\}$	1126.59	47.17	0.00	12	1102.06
$\{\Psi(\text{RAIN2avg}+\text{TEMPegg}) R(.)\}$	1127.15	47.73	0.00	13	1100.54
$\{\Psi(\text{drought*TEMPegg}) R(.)\}$	1127.66	48.24	0.00	14	1098.95
$\{\Psi(\text{RAINegg*TEMPegg}) R(.)\}$	1128.27	48.85	0.00	14	1099.56
$\{\Psi(\text{RAINegg}+\text{TEMPegg}) R(.)\}$	1134.13	54.71	0.00	13	1107.51
$\{\Psi(\text{TEMPegg}) R(.)\}$	1134.37	54.95	0.00	12	1109.85
$\{\Psi(\text{RAIN1pre}) R(.)\}$	1134.62	55.20	0.00	12	1110.09
$\{\Psi(\text{RAINegg}) R(.)\}$	1141.92	62.50	0.00	12	1117.40
$\{\Psi(\text{RAIN2avg}) R(.)\}$	1142.07	62.65	0.00	12	1117.55

Model selection notation: Akaike's Information Criterion corrected for small sample size (AIC_c), relative difference (Δ AIC_c), model weight (w), number of parameters (K), and twice the negative log-likelihood ($-2l$).

^aModel covariates: constant effect among years and territories (.), annual variation (year), site-specific variation (state); total precipitation based on 2-yr average prior to the current breeding season (RAIN2avg) or accumulated during the previous year (RAIN1pre), 2 months prior to egg laying (RAINegg), 30-day incubation period (RAINsit), 24-day brooding period (RAINhatch) or 5-month breeding season (RAINbreed); annual Palmer Drought Severity Index value (drought); and mean maximum temperature for 2 months prior to egg laying (TEMPegg), 30 day incubation period (TEMPsit), 24 day brooding period (TEMPhatch) or 5 month breeding season (TEMPbreed).

Table 5. Ranking of dynamic multistate site occupancy models used to characterize effects of variation in forest attributes on annual probabilities of producing eggs (Ψ) or ≥ 1 fledgling (R) among goshawk territories on the Kaibab Plateau, Arizona during 1999-2004. The model without environmental covariates $\{\Psi(\text{state}*\text{year}) R(\text{year})\}$ was included to evaluate the relative effects of vegetation attributes on goshawk reproduction. All models in the set incorporated a covariate for territory reproductive state in the prior year (state) and the same structure for the detection and classification components of the model.

Model ^a	AIC _c	Δ AIC _c	w	K	$-2l$
$\{\Psi(\text{state}*\text{year}) R(\text{year})\}$	1079.42	0.00	0.84	23	1031.52
$\{\Psi(\text{tPINEhigh}+\text{tMIXhigh}+\text{tPINElow}+\text{tMIXlow}) R(\text{CONEall})\}$	1082.94	3.52	0.15	32	1015.26
$\{\Psi(\text{tPINEhigh}+\text{tMIXhigh}+\text{tPINElow}+\text{tMIXlow}) R(.)\}$	1090.75	11.34	0.00	31	1025.30
$\{\Psi(\text{tPINEhigh}+\text{tMIXhigh}+\text{tPINElow}+\text{tMIXlow}) R(\text{PATCHhigh})\}$	1091.52	12.10	0.00	32	1023.84
$\{\Psi(\text{tPINEhigh}+\text{tMIXhigh}+\text{tPINElow}+\text{tMIXlow}) R(\text{canopy})\}$	1091.65	12.23	0.00	32	1023.97
$\{\Psi(\text{tPINEhigh}+\text{tMIXhigh}+\text{tPINElow}+\text{tMIXlow}+\text{harvest}) R(.)\}$	1092.42	13.01	0.00	32	1024.74
$\{\Psi(\text{tPINEhigh}+\text{tMIXhigh}+\text{tPINElow}+\text{tMIXlow}+\text{PATCHhigh}) R(.)\}$	1092.50	13.08	0.00	32	1024.82
$\{\Psi(\text{tPINEhigh}+\text{tMIXhigh}+\text{tPINElow}+\text{tMIXlow}) R(\%low)\}$	1092.96	13.54	0.00	32	1025.28
$\{\Psi(\text{tPINEhigh}+\text{tMIXhigh}) R(.)\}$	1096.12	16.71	0.00	21	1052.55
$\{\Psi(\text{tMIXhigh}+\text{tMIXlow}) R(.)\}$	1100.97	21.56	0.00	21	1057.39
$\{\Psi(\text{tMIXhigh}) R(.)\}$	1101.02	21.60	0.00	16	1068.10
$\{\Psi(\text{PINEhigh}+\text{MIXhigh}+\text{PINElow}+\text{MIXlow}+\text{year}) R(.)\}$	1103.78	24.37	0.00	19	1064.49
$\{\Psi(\text{PATCHhigh}) R(.)\}$	1103.95	24.53	0.00	12	1079.43
$\{\Psi(\text{CONEall}) R(.)\}$	1106.54	27.12	0.00	12	1082.01
$\{\Psi(\text{tPINEhigh}+\text{tPINElow}) R(.)\}$	1107.44	28.02	0.00	21	1063.86
$\{\Psi(\text{tMIXlow}) R(.)\}$	1112.08	32.67	0.00	16	1079.16
$\{\Psi(\text{tPINEhigh}) R(.)\}$	1112.29	32.87	0.00	16	1079.37
$\{\Psi(\text{tPINElow}) R(.)\}$	1116.05	36.63	0.00	16	1083.13
$\{\Psi(\text{size}) R(.)\}$	1117.02	37.60	0.00	12	1092.49
$\{\Psi(\text{harvest}) R(.)\}$	1141.22	61.80	0.00	12	1116.69
$\{\Psi(\text{PINEhigh}) R(.)\}$	1141.27	61.85	0.00	12	1116.74
$\{\Psi(\text{canopy}) R(.)\}$	1141.33	61.91	0.00	12	1116.80
$\{\Psi(\text{MIXlow}) R(.)\}$	1141.87	62.45	0.00	12	1117.34
$\{\Psi(\text{PINElow}) R(.)\}$	1141.93	62.51	0.00	12	1117.41
$\{\Psi(\text{MIXhigh}) R(.)\}$	1142.09	62.67	0.00	12	1117.56
$\{\Psi(\text{PINEhigh}+\text{MIXhigh}+\text{PINElow}+\text{MIXlow}) R(.)\}$	1146.38	66.96	0.00	15	1115.57

Model selection notation: Akaike's Information Criterion corrected for small sample size (AIC_c), relative difference (Δ AIC_c), model weight (w), number of parameters (K), and twice the negative log-likelihood ($-2l$).

^aModel covariates: constant effect among years and territories (.), annual variation (year), site-specific variation (state); time-dependent effects (t); proportion of high-density ponderosa pine (PINEhigh), high-density mixed conifer (MIXhigh), low-density ponderosa pine (PINElow) or low-density mixed conifer (MIXlow) cover type; proportion of low-density cover types (%low); mean patch size of high-density cover types (PATCHhigh); maximum patch size of extensive timber harvest (harvest); size of territory (size); percent canopy cover (canopy); and mean annual cone production per tree for all conifer species (CONEall).

Table 6. Ranking of dynamic multistate site occupancy models used to characterize effects of variation in the abundance of prey species on annual probabilities of producing eggs (Ψ) or ≥ 1 fledgling (R) among goshawk territories on the Kaibab Plateau, Arizona during 1999-2004. The model without environmental covariates $\{\Psi(\text{state}*\text{year}) R(\text{year})\}$ was included to evaluate the relative effects of prey abundance on goshawk reproduction. All models in the set incorporated a covariate for territory reproductive state in the prior year (state) and the same structure for the detection and classification components of the model.

Model ^a	AIC _c	Δ AIC _c	<i>w</i>	<i>K</i>	-2 <i>l</i>
$\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}) R(\text{Kaibab}+\text{Flicker})\}$	1066.51	0.00	0.36	16	1033.59
$\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}) R(\text{Kaibab})\}$	1066.80	0.28	0.32	15	1035.98
$\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}) R(\text{Flicker})\}$	1067.83	1.31	0.19	15	1037.02
$\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}) R(.)\}$	1071.13	4.62	0.04	14	1042.42
$\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}) R(\text{Red})\}$	1071.20	4.69	0.03	15	1040.39
$\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}) R(\text{Jay})\}$	1072.83	6.31	0.02	15	1042.01
$\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}+\text{Jay}) R(.)\}$	1072.95	6.44	0.01	15	1042.14
$\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}+\text{Flicker}) R(.)\}$	1073.09	6.58	0.01	15	1042.28
$\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}) R(\text{Ground})\}$	1073.22	6.71	0.01	15	1042.41
$\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}+\text{Flicker}+\text{Jay}) R(.)\}$	1075.06	8.54	0.01	16	1042.14
$\{\Psi(\text{state}*\text{year}) R(\text{year})\}$	1079.42	12.90	0.00	23	1031.52
$\{\Psi(\text{Kaibab}+\text{Red}+\text{Flicker}+\text{Jay}) R(.)\}$	1084.60	18.08	0.00	15	1053.78
$\{\Psi(\text{Flicker}+\text{Jay}) R(.)\}$	1093.40	26.89	0.00	13	1066.79
$\{\Psi(\text{Kaibab}+\text{Ground}+\text{Flicker}) R(.)\}$	1095.93	29.41	0.00	14	1067.22
$\{\Psi(\text{all}) R(.)\}$	1096.27	29.76	0.00	12	1071.75
$\{\Psi(\text{mammal}) R(.)\}$	1096.83	30.31	0.00	12	1072.30
$\{\Psi(\text{Kaibab}+\text{Ground}) R(.)\}$	1097.46	30.95	0.00	13	1070.85
$\{\Psi(\text{Kaibab}+\text{Red}) R(.)\}$	1097.86	31.35	0.00	13	1071.25
$\{\Psi(\text{bird}) R(.)\}$	1098.41	31.89	0.00	12	1073.88
$\{\Psi(\text{Red}+\text{Ground}) R(.)\}$	1099.27	32.75	0.00	13	1072.65
$\{\Psi(\text{Kaibab}+\text{Flicker}) R(.)\}$	1100.02	33.50	0.00	13	1073.40
$\{\Psi(\text{Kaibab}) R(.)\}$	1100.32	33.80	0.00	12	1075.79
$\{\Psi(\text{Flicker}) R(.)\}$	1101.53	35.02	0.00	12	1077.01
$\{\Psi(\text{tree}) R(.)\}$	1102.88	36.36	0.00	12	1078.35
$\{\Psi(\text{Red}) R(.)\}$	1103.94	37.43	0.00	12	1079.42
$\{\Psi(\text{Ground}) R(.)\}$	1104.33	37.81	0.00	12	1079.80
$\{\Psi(\text{Jay}) R(.)\}$	1141.64	75.12	0.00	12	1117.11

Model selection notation: Akaike's Information Criterion corrected for small sample size (AIC_c), relative difference (Δ AIC_c), model weight (*w*), number of parameters (*K*), and twice the negative log-likelihood (-2*l*).

^aModel covariates: constant effect among years and territories (.), annual variation (year), site-specific variation (state) and estimated abundance per species for Kaibab squirrel (Kaibab), red squirrel (Red), golden-mantled ground squirrel (Ground), northern flicker (Flicker), Steller's jay (Jay), arboreal prey (tree), aerial prey (bird), mammal prey (mammal) and all species (all).

Table 7. Ranking of dynamic multistate site occupancy models used to characterize effects of variation in habitat attributes on annual probabilities of producing eggs (Ψ) or ≥ 1 fledgling (R) among goshawk territories on the Kaibab Plateau, Arizona during 1999-2004. The model without environmental covariates $\{\Psi(\text{state}*\text{year}) R(\text{year})\}$ was included to evaluate the relative effects of habitat components on goshawk reproduction. All models in the set incorporated a covariate for territory reproductive state in the prior year (state) and the same structure for the detection and classification components of the model.

Model ^a	AIC _c	Δ AIC _c	w	K	$-2l$
$\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}+\text{CONEpine}) R(\text{CONEpine})\}$	1063.4	0.0	0.74	16	1030
$\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}) R(\text{Kaibab}+\text{Flicker})\}$	1066.5	3.2	0.15	16	1034
$\{\Psi(\text{Kaibab}+\text{Red}+\text{Ground}+\text{TEMPegg}) R(\text{Kaibab}+\text{Flicker})\}$	1068.6	5.3	0.05	17	1034
$\{\Psi(\text{RAIN2avg}*\text{TEMPegg}+\text{PATCHhigh}+\text{EDGE}) R(\text{RAINhatch}+\text{CONEpine})\}$	1070.1	6.8	0.03	22	1024
$\{\Psi(\text{RAIN2avg}*\text{TEMPegg}+\text{PATCHhigh}+\text{harvest}) R(\text{RAINhatch}+\text{CONEpine})\}$	1070.2	6.9	0.02	22	1025
$\{\Psi(\text{state}*\text{year}) R(\text{year})\}$	1079.4	16.1	0.00	23	1032
$\{\Psi(\text{tPINEhigh}+\text{tMIXhigh}+\text{tPINElow}+\text{tMIXlow}) R(\text{CONEall})\}$	1082.9	19.6	0.00	32	1015
$\{\Psi(\text{MASS}_{\text{Kaibab}+\text{Red}+\text{Rabbit}+\text{Hare}}) R(\text{MASS}_{\text{Kaibab}+\text{Red}+\text{Rabbit}+\text{Hare}})\}$	1090.3	26.9	0.00	19	1051
$\{\Psi(\text{RAIN2avg}*\text{TEMPegg}) R(\text{RAINhatch})\}$	1092.7	29.3	0.00	15	1062

Model selection notation: Akaike's Information Criterion corrected for small sample size (AIC_c), relative difference (Δ AIC_c), model weight (w), number of parameters (K), and twice the negative log-likelihood ($-2l$).

^aModel covariates: annual variation (year) or site-specific variation (state); biomass contribution (MASS) or annual abundance of Kaibab squirrel (Kaibab), red squirrel (Red), golden-mantled ground squirrel (Ground), northern flicker (Flicker), Steller's jay (Jay), cottontail rabbit (Rabbit), and black-tailed jackrabbit (Hare); total precipitation based on 2-yr average prior to the current breeding season (RAIN2avg) or accumulated during the 24-day brooding period (RAINhatch); mean maximum temperature for 2 months prior to egg laying (TEMPegg); time-dependent effects (t); proportion of high-density ponderosa pine (PINEhigh), high-density mixed conifer (MIXhigh), low-density ponderosa pine (PINElow) or low-density mixed conifer (MIXlow) cover type; mean patch size of high-density cover types (PATCHhigh); maximum patch size of extensive timber harvests (harvest); distance to the nearest boundary between forest types (EDGE); and mean annual cone production per tree for ponderosa pine (CONEpine).

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APPENDICES

Appendix A. Number, adult mean mass, and biomass contribution of prey species in the diets of breeding goshawks on the Kaibab Plateau, Arizona during 1999-2004.

Prey species	No.	Mass(g)	Source ^a	% of diet
Birds				
American coot (<i>Fulica americana</i>)	1	642	1	<0.01
American kestrel (<i>Falco sparverius</i>)	1	116	1	<0.01
American robin (<i>Turdus migratorius</i>)	8	77	1	<0.01
Audubon's warbler (<i>Dendroica coronata</i>)	1	12	1	<0.01
Band-tailed pigeon (<i>Columba fasciata</i>)	1	343	1	<0.01
Blue grouse (<i>Dendragapus obscurus</i>)	8	1040	1	0.03
Clark's nutcracker (<i>Nucifraga columbiana</i>)	38	135	1	0.01
Common poorwill (<i>Phalaenoptilus nuttallii</i>)	1	52	1	<0.01
Common raven (<i>Corvus corax</i>)	5	1199	1	0.01
Cooper's hawk (<i>Accipiter cooperii</i>)	3	439	1	<0.01
Great horned owl (<i>Bubo virginianus</i>)	1	1309	1	<0.01
Hairy woodpecker (<i>Picoides villosus</i>)	1	66	1	<0.01
Hermit thrush (<i>Catharus guttatus</i>)	3	31	1	<0.01
Long-eared owl (<i>Asio otus</i>)	10	262	1	0.01
Mallard (<i>Anas platyrhynchos</i>)	1	1082	1	<0.01
Mourning dove (<i>Zenaida macroura</i>)	19	119	1	0.01
Northern flicker (<i>Colaptes auratus</i>)	145	142	1	0.06
Northern goshawk (<i>Accipiter gentilis</i>)	1	1025	1	<0.01
Northern saw-whet owl (<i>Aegolius acadicus</i>)	2	83	1	<0.01
Pinyon jay (<i>Gymnorhinus cyanocephalus</i>)	3	103	1	<0.01
Sharp-shinned hawk (<i>Accipiter striatus</i>)	2	139	1	<0.01
Steller's Jay (<i>Cyanocitta stelleri</i>)	101	128	1	0.04
Western bluebird (<i>Sialia mexicana</i>)	15	28	1	<0.01
White-breasted nuthatch (<i>Sitta carolinensis</i>)	1	21	1	<0.01
Wild turkey (<i>Meleagris gallopavo</i>)	1	5811	1	0.02
Williamson's sapsucker (<i>Sphyrapicus thyroideus</i>)	8	48	1	<0.01
Mammals				
Black-tailed jackrabbit (<i>Lepus californicus</i>)	42	2100	2	0.19
Chipmunk (<i>Tamias</i> spp.)	5	58	2	<0.01
Cottontail rabbit (<i>Sylvilagus</i> spp.)	215	718	2	0.44
Golden-mantled ground squirrel (<i>Spermophilus lateralis</i>)	12	195	2	0.01
Kaibab squirrel (<i>Sciurus aberti kaibabensis</i>)	42	697	3	0.08
Pocket gopher (<i>Thomomys</i> spp.)	1	137	4	<0.01
Red squirrel (<i>Tamiasciurus hudsonicus</i>)	91	212	2	0.06
Rock squirrel (<i>Spermophilus variegatus</i>)	13	617	2	0.02

^aMass estimate source: 1 = Dunning 1993; 2 = Boal 1993; 3 = Hall 1981; 4 = Wilson and Ruff 1999.

Appendix B. Development of vegetation maps representing primary forest cover types within the study area on the Kaibab Plateau, Arizona.

Classification of forest cover types

I used vegetation data that were derived from the interpretation of 1997 Landsat TM imagery and concurrent field sampling (Reich et al. 2004) to identify the amount and distribution of 2 forest types and 2 silvicultural treatments within the study area (Fig. B-1). First I extracted meadows, blowdowns, and pure aspen stands (>0.99 aspen basal area) and reclassified them as non-dominant cover types. Then I used the Jenks natural breaks method (Jenks 1967) to divide the continuous vegetation data into discrete classes. To classify forest type, I divided the mixed conifer basal area data into 2 categories representing areas dominated by mixed conifer species ($>14\%$ mixed conifer) or ponderosa pine ($\leq 14\%$ mixed conifer). To classify the dominant silvicultural treatments, I divided the total basal area data into 2 categories per forest type. I used a break value of $112 \text{ m}^2/\text{ha}$ for mixed conifer and $87 \text{ m}^2/\text{ha}$ for ponderosa pine to account for differences in the density of mature trees resulting from selective (single-tree) or extensive (seed-tree) timber harvests. Then I used this information to classify the cover type of each 10-m^2 raster cell within the study area as lightly-harvested mixed conifer (high-density mix), intensively harvested mixed conifer (low-density mix), lightly-harvested ponderosa pine (high-density pine), intensively-harvested ponderosa pine (low-density pine), or meadow/other forest (Fig. B-2).

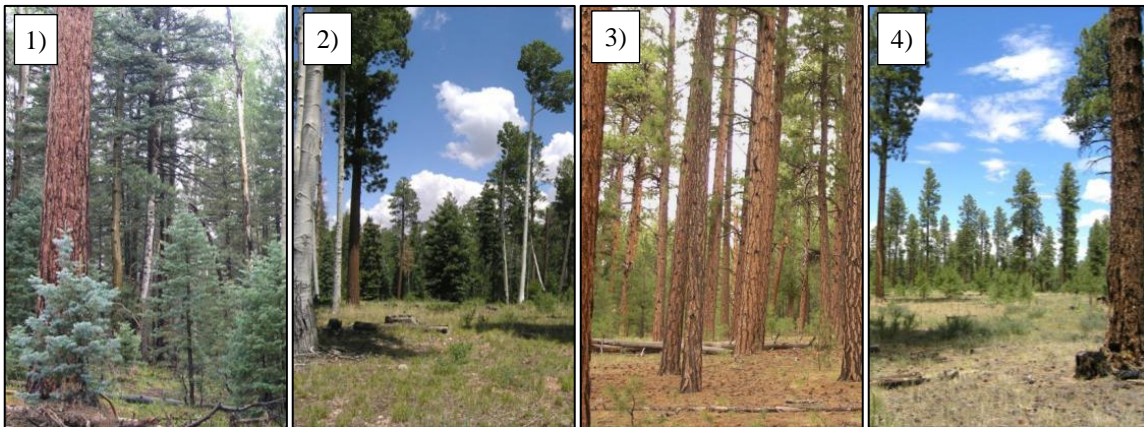


Figure B-1. Examples of the dominant forest types and silvicultural treatments within the study area on the Kaibab Plateau, Arizona: 1) lightly-harvested mixed conifer; 2) intensively-harvested mixed conifer; 3) lightly-harvested ponderosa pine; 4) intensively-harvested ponderosa pine.

Accuracy assessment

Accuracy of the classified cover type map was assessed by comparing observed and predicted vegetation characteristics at 60 plots used to sample prey abundance within the analysis region. The observed vegetation composition and structure of each plot (15 per cover type) exemplified the dominant characteristics of the cover type in terms of overstory diversity, understory coverage, and density of mature trees. The predicted cover type of each plot was assessed within a $500 \times 300 \text{ m}$ rectangle because this area encompassed the location of $>99\%$ of all prey items observed. I used a geographic information system to identify the majority and median cover type for each plot on the map. I estimated the accuracy of the image classification for cover type by comparing site-specific predicted and observed vegetation conditions using a standard error matrix (Congalton and Green 2009; Table B-1).

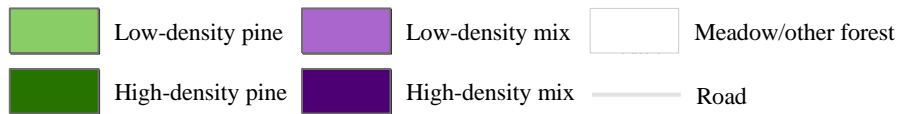
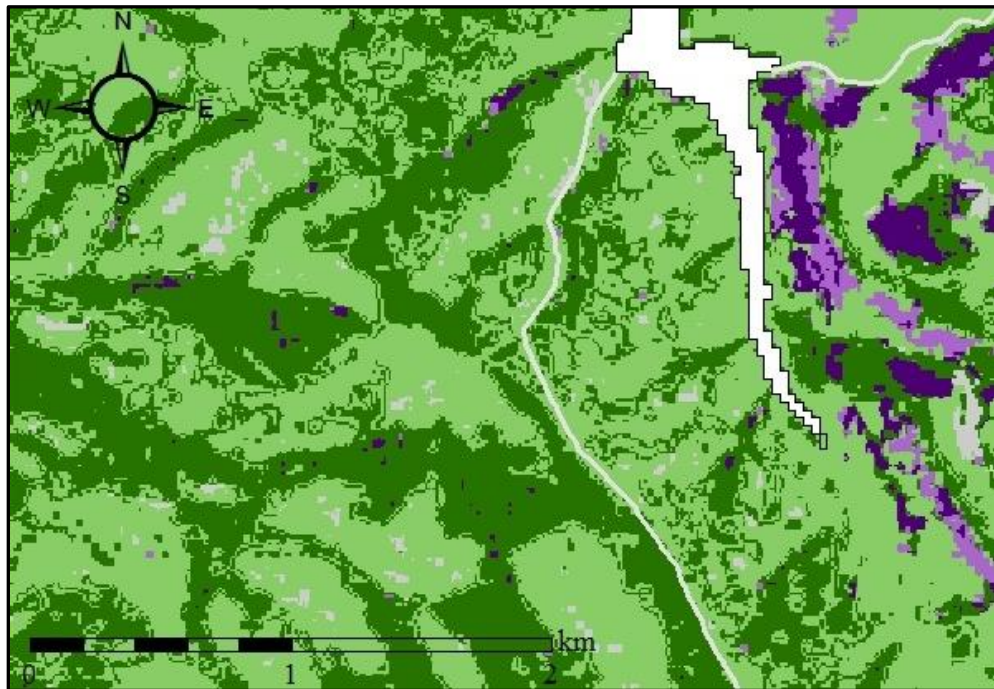


Figure B-2. A section of the 1,285 km² study area on the Kaibab Plateau, Arizona from an aerial photograph circa 1992 (upper) and a geographic information system map of the dominant forest cover types (lower). Each 10-m² raster cell within the study area was classified as 1 of 5 cover types: lightly-harvested ponderosa pine (high-density pine), intensively-harvested ponderosa pine (low-density pine), lightly-harvested mixed conifer (high-density mix), intensively-harvested mixed conifer (low-density mix), or a non-dominant cover type (meadow/other forest). White indicates areas below 2,182 m elevation that were excluded from the study area.

Table B-1. Error matrix of class-specific prediction accuracies of the cover type map based on observed vegetation characteristics at 60 plots. Reference plots with the majority and/or median cover type classified correctly fall along the diagonal in grey.

Predicted cover	Observed cover ^a				Total	User's (%) ^b
	High-density mix	Low-density mix	High-density pine	Low-density pine		
High-density mix	15	1	1		17	88
Low-density mix		13			13	100
High-density pine		1	14		15	93
Low-density pine				15	15	100
Total	15	15	15	15	60	
Producer's(%) ^c	100	87	93	100		95

^aCover descriptions: lightly-harvested mixed conifer (high-density mix), intensively-harvested mixed conifer (low-density mix), lightly-harvested ponderosa pine (high-density pine), and intensively-harvested ponderosa pine (low-density pine).

^bUser's accuracy measures the error of inclusion.

^cProducer's accuracy measures the error of exclusion.

Appendix C. Mean annual cone crop estimates (no./tree) and standard errors (SE) per forest cover type used to quantify variation in the abundance of food resources for prey species among goshawk territories on the Kaibab Plateau, Arizona during 1999-2004.

Year	Cover type ^b	All conifer species ^a		Ponderosa pine	
		Mean	SE	Mean	SE
1999	High-density mix	15.97	2.29	12.00	7.14
	Low-density mix	12.08	1.21	12.34	1.42
	High-density pine	24.30	2.44	24.30	2.44
	Low-density pine	31.09	2.83	30.98	2.86
2000	High-density mix	45.60	9.59	15.57	8.01
	Low-density mix	20.63	4.09	14.21	2.03
	High-density pine	33.01	2.60	33.01	2.60
	Low-density pine	23.51	2.75	23.29	2.78
2001	High-density mix	15.00	2.25	9.21	2.87
	Low-density mix	8.49	1.29	6.97	1.12
	High-density pine	28.41	2.03	28.41	2.03
	Low-density pine	17.61	1.96	16.56	1.79
2002	High-density mix	12.08	2.01	8.00	4.06
	Low-density mix	11.66	2.58	7.26	0.88
	High-density pine	12.92	1.19	12.92	1.19
	Low-density pine	11.61	0.96	11.35	0.96
2003	High-density mix	28.59	4.50	7.64	1.55
	Low-density mix	23.16	1.95	21.17	2.01
	High-density pine	22.03	2.03	22.01	2.04
	Low-density pine	19.00	1.84	18.02	1.80
2004	High-density mix	39.81	5.30	35.47	6.78
	Low-density mix	63.11	8.00	49.64	5.35
	High-density pine	19.38	1.88	19.38	1.88
	Low-density pine	18.22	1.74	17.42	1.70

^aAll species include: ponderosa pine, Douglas fir, Engelmann spruce, white fir, and subalpine fir.

^bCover type descriptions: lightly-harvested mixed conifer (high-density mix), intensively-harvested mixed conifer (low-density mix), lightly-harvested ponderosa pine (high-density pine), and intensively-harvested ponderosa pine (low-density pine).

Appendix D. Annual density estimates (no./ha) and standard errors (SE) per forest cover type used to quantify prey abundance within each goshawk territory on the Kaibab Plateau, Arizona during 1999-2004.

Year	Cover type ^a	Kaibab squirrel		Red squirrel		Ground squirrel		Northern flicker		Steller's jay	
		Density	SE	Density	SE	Density	SE	Density	SE	Density	SE
1999	Low-density pine	0.014	0.007	0.161	0.041	0.097	0.060	0.202	0.027	0.187	0.025
1999	High-density pine	0.051	0.015	0.187	0.046	0.024 ^c	0.024	0.164	0.023	0.133	0.027
1999	Low-density mix	0.000		0.438	0.052	0.169	0.094	0.219	0.033	0.066	0.019
1999	High-density mix	0.003 ^c	0.003	1.435	0.138	0.000		0.125	0.026	0.063	0.019
2000	Low-density pine	0.031	0.012	0.111	0.032	0.411	0.126	0.204	0.025	0.076	0.020
2000	High-density pine	0.119	0.028	0.169	0.047	0.169	0.073	0.200	0.030	0.116	0.027
2000	Low-density mix	0.007 ^c	0.007	0.529	0.074	0.821	0.307	0.347	0.053	0.050	0.016
2000	High-density mix	0.003 ^c	0.003	1.581	0.161	0.000		0.279	0.050	0.081	0.030
2001	Low-density pine	0.007	0.005	0.019	0.009	0.411	0.130	0.136	0.025	0.093	0.021
2001	High-density pine	0.044	0.015	0.015	0.009	0.048	0.034	0.069	0.019	0.076	0.018
2001	Low-density mix	0.000		0.015	0.012	0.507	0.183	0.233	0.036	0.117	0.033
2001	High-density mix	0.000		0.125	0.040	0.000		0.184	0.040	0.098	0.028
2002	Low-density pine	0.024	0.009	0.016	0.010	0.531	0.160	0.052	0.012	0.092	0.022
2002	High-density pine	0.024	0.012	0.022	0.012	0.048	0.034	0.037	0.011	0.071	0.022
2002	Low-density mix	0.020	0.009	0.067	0.020	0.676	0.202	0.096	0.017	0.085	0.023
2002	High-density mix	0.010	0.006	0.322	0.060	0.000		0.122	0.030	0.084	0.025
2003	Low-density pine	0.014	0.007	0.004 ^c	0.004	0.435	0.168	0.039	0.008	0.073	0.016
2003	High-density pine	0.007	0.005	0.009	0.007	0.072	0.042	0.037	0.010	0.042	0.012
2003	Low-density mix	0.014	0.007	0.009 ^c	0.010	0.531	0.233	0.095	0.018	0.082	0.026
2003	High-density mix	0.007 ^c	0.007	0.059	0.023	0.000		0.083	0.022	0.067	0.027
2004	Low-density pine	0.027	0.013	0.024	0.011	1.836	0.449	0.061	0.014	0.036	0.012
2004	High-density pine	0.048	0.012	0.036	0.015	0.097	0.049	0.074	0.015	0.051	0.019
2004	Low-density mix	0.027	0.010	0.135	0.034	1.715	0.540	0.153	0.029	0.016	0.009
2004	High-density mix	0.027	0.011	0.466	0.067	0.048	0.034	0.137	0.025	0.035	0.017

^aCover type descriptions: lightly-harvested mixed conifer (high-density mix), intensively-harvested mixed conifer (low-density mix), lightly-harvested ponderosa pine (high-density pine), and intensively-harvested ponderosa pine (low-density pine).

^bToo few individuals (≤ 2) detected to accurately estimate density, so density was approximated as 0.001 individuals per ha in calculations for quantifying prey abundance per goshawk territory.

Appendix E. Ranking of dynamic multistate site occupancy models without environmental covariates representing different hypotheses regarding the distribution of goshawk territories with reproduction on the Kaibab Plateau, Arizona during 1999-2004. Ψ denotes the probability of transitioning to an egg-laying state and R denotes the probability of reproducing successfully (≥ 1 young fledged) in year t conditional on the reproductive state of the territory in year $t-1$ for 2 states (no reproduction, breeding attempted) or 3 states (no reproduction, 0 young fledged, ≥ 1 young fledged). For example, model $\{\Psi_{(.)} R_{(.)}\}$ assumed constant reproduction probabilities among years and territories, model $\{\Psi_{(year)} R_{(year)}\}$ assumed only annual variation in reproduction probabilities, whereas model $\{\Psi_{(state+year)} R_{(state+year)}\}$ assumed annual variation in reproduction probabilities was consistent among territories (i.e., independent of territory reproductive state in year $t-1$), and model $\{\Psi_{(state*year)} R_{(state*year)}\}$ assumed variation in reproduction probabilities depended on site-specific attributes of territories within years. For all models, the same structure was maintained for the detection (p) and classification (δ) components of the models.

Model ^a	AIC _c	Δ AIC _c	w	K	$-2l$
Ψ (state2*year) R (year)	1079.42	0.00	0.56	23	1031.5
Ψ (state2*year) R (state2+year)	1081.04	1.62	0.25	24	1031.0
Ψ (state2*year) R (state3+year)	1083.21	3.79	0.08	25	1031.0
Ψ (state2*year) R (state2*year)	1085.13	5.71	0.03	28	1026.3
Ψ (state3*year) R (year)	1086.04	6.62	0.02	28	1027.2
Ψ (state2*year) R (.)	1086.29	6.87	0.02	19	1047.0
Ψ (state3*year) R (state2+year)	1087.66	8.24	0.01	29	1026.6
Ψ (state2*year) R (state2)	1088.42	9.00	0.01	20	1047.0
Ψ (state3*year) R (state3+year)	1089.87	10.45	0.00	30	1026.6
Ψ (state2+year) R (year)	1090.29	10.87	0.00	19	1051.0
Ψ (state2*year) R (state3)	1090.52	11.10	0.00	21	1046.9
Ψ (state3+year) R (year)	1091.33	11.91	0.00	20	1049.9
Ψ (state2+year) R (state2+year)	1091.84	12.43	0.00	20	1050.4
Ψ (state3*year) R (state2*year)	1091.90	12.48	0.00	33	1022.0
Ψ (state3*year) R (.)	1092.74	13.33	0.00	24	1042.7
Ψ (state3+year) R (state2+year)	1092.88	13.46	0.00	21	1049.3
Ψ (state2*year) R (state3*year)	1092.93	13.51	0.00	33	1023.0
Ψ (state2+year) R (state3+year)	1093.99	14.57	0.00	21	1050.4
Ψ (state3*year) R (state2)	1094.93	15.51	0.00	25	1042.7
Ψ (state3+year) R (state3+year)	1095.03	15.61	0.00	22	1049.3
Ψ (state2+year) R (state2*year)	1095.60	16.18	0.00	24	1045.5
Ψ (state3+year) R (state2*year)	1096.71	17.29	0.00	25	1044.5
Ψ (state3*year) R (state3)	1097.06	17.64	0.00	26	1042.6
Ψ (state2+year) R (.)	1097.28	17.86	0.00	15	1066.5
Ψ (state3+year) R (.)	1098.29	18.87	0.00	16	1065.4
Ψ (state2+year) R (state2)	1099.36	19.95	0.00	16	1066.4

Appendix E (continued).

$\Psi(\text{state3*year}) R(\text{state3*year})$	1099.91	20.49	0.00	38	1018.7
$\Psi(\text{state3+year}) R(\text{state2})$	1100.38	20.96	0.00	17	1065.3
$\Psi(\text{state2+year}) R(\text{state3})$	1101.43	22.02	0.00	17	1066.4
$\Psi(\text{state3+year}) R(\text{state3})$	1102.46	23.04	0.00	18	1065.3
$\Psi(\text{state2+year}) R(\text{state3*year})$	1103.23	23.81	0.00	29	1042.2
$\Psi(\text{state3+year}) R(\text{state3*year})$	1104.38	24.96	0.00	30	1041.1
$\Psi(\text{state2}) R(\text{year})$	1132.92	53.50	0.00	15	1102.1
$\Psi(\text{state3}) R(\text{year})$	1135.01	55.59	0.00	16	1102.1
$\Psi(\text{state3}) R(\text{state2+year})$	1137.04	57.62	0.00	17	1102.0
$\Psi(\text{state2}) R(\text{state2*year})$	1139.03	59.61	0.00	20	1097.6
$\Psi(\text{state3}) R(\text{state3+year})$	1139.16	59.74	0.00	18	1102.0
$\Psi(\text{state2}) R(.)$	1140.02	60.61	0.00	11	1117.6
$\Psi(\text{state3}) R(\text{state2*year})$	1141.16	61.74	0.00	21	1097.6
$\Psi(\text{state2}) R(\text{state2})$	1141.93	62.52	0.00	12	1117.4
$\Psi(\text{state3}) R(.)$	1142.01	62.60	0.00	12	1117.5
$\Psi(\text{state2}) R(\text{state3})$	1143.98	64.56	0.00	13	1117.4
$\Psi(\text{state3}) R(\text{state3})$	1145.99	66.57	0.00	14	1117.3
$\Psi(\text{state2}) R(\text{state3*year})$	1146.12	66.70	0.00	25	1093.9
$\Psi(\text{state3}) R(\text{state2})$	1148.04	68.62	0.00	13	1121.4
$\Psi(\text{state3}) R(\text{state3*year})$	1148.24	68.82	0.00	26	1093.8
$\Psi(\text{year}) R(\text{year})$	1149.43	70.01	0.00	18	1112.3
$\Psi(\text{year}) R(\text{state2+year})$	1150.85	71.44	0.00	19	1111.6
$\Psi(\text{year}) R(\text{state3+year})$	1152.99	73.57	0.00	20	1111.6
$\Psi(\text{year}) R(\text{state2*year})$	1154.46	75.04	0.00	23	1106.6
$\Psi(\text{year}) R(.)$	1156.45	77.03	0.00	14	1127.7
$\Psi(\text{year}) R(\text{state2})$	1158.49	79.07	0.00	15	1127.7
$\Psi(\text{year}) R(\text{state3})$	1160.55	81.13	0.00	16	1127.6
$\Psi(\text{year}) R(\text{state3*year})$	1162.07	82.65	0.00	28	1103.3
$\Psi(.) R(\text{year})$	1195.28	115.86	0.00	14	1166.6
$\Psi(.) R(\text{state2+year})$	1196.87	117.45	0.00	15	1166.1
$\Psi(.) R(\text{state3+year})$	1198.98	119.56	0.00	16	1166.1
$\Psi(.) R(\text{state2*year})$	1200.22	120.80	0.00	19	1160.9
$\Psi(.) R(.)$	1204.12	124.70	0.00	10	1183.8
$\Psi(.) R(\text{state2})$	1204.48	125.07	0.00	11	1182.0
$\Psi(.) R(\text{state3})$	1206.52	127.10	0.00	12	1182.0
$\Psi(.) R(\text{state3*year})$	1207.80	128.38	0.00	24	1157.7

Model selection notation: Akaike's Information Criterion corrected for small sample size (AIC_c), relative difference (ΔAIC_c), model weight (w), number of parameters (K), and twice the negative log-likelihood ($-2l$).

^aConstraints on reproductive parameters: constant over time ($.$), annual variation (year), dependent on the reproductive state of the territory in the previous year for 2 states (state2) or 3 states (state3).

Appendix F. Annual parameter estimates for the probability of transitioning to an egg-laying state (Ψ), fledging ≥ 1 young (R), detecting a breeding attempt (p), and correctly classifying successful breeding attempts (δ) from the multistate site occupancy model without environmental covariates $\{\Psi(\text{state} \times \text{year}) R(\text{year}) p(\text{year}, \text{survey}) \delta(\text{survey})\}^a$ with the most support in the goshawk reproduction data from the Kaibab Plateau, Arizona during 1999-2004 (Appendix E). Annual probabilities of transitioning to an egg-laying state were different for territories without a breeding attempt ($\Psi[0]$) and territories with an unsuccessful (0 young fledged) or a successful (≥ 1 young fledged) breeding attempt ($\Psi[1]$) in the prior year.

Parameter	Estimate	SE	Lower	Upper
$\Psi(1999)$	0.56	0.05	0.46	0.66
$R(1999)$	0.75	0.06	0.62	0.85
$\Psi[0](2000)$	0.22	0.06	0.12	0.37
$\Psi[0](2001)$	0.02	0.02	0.00	0.16
$\Psi[0](2002)$	0.15	0.04	0.08	0.25
$\Psi[0](2003)$	0.09	0.03	0.04	0.17
$\Psi[0](2004)$	0.51	0.11	0.30	0.72
$\Psi[1](2000)$	0.90	0.04	0.79	0.95
$\Psi[1](2001)$	0.46	0.07	0.33	0.59
$\Psi[1](2002)$	0.28	0.08	0.15	0.47
$\Psi[1](2003)$	0.16	0.08	0.05	0.39
$\Psi[1](2004)$	0.64	0.23	0.20	0.92
$R(2000)$	0.89	0.04	0.78	0.94
$R(2001)$	0.61	0.09	0.42	0.77
$R(2002)$	0.53	0.11	0.31	0.73
$R(2003)$	0.60	0.15	0.30	0.84
$R(2004)$	0.78	0.06	0.63	0.88
$p(1999, \text{survey } 1)$	0.88	0.05	0.76	0.94
$p(1999, \text{survey } 2)$	0.88	0.05	0.76	0.94
$p(1999, \text{survey } 3)$	0.88	0.05	0.76	0.94
$p(1999, \text{survey } 4) \text{ fixed}$	1.00	0.00	1.00	1.00
$p(2000, \text{survey } 1)$	0.94	0.03	0.84	0.98
$p(2000, \text{survey } 2)$	0.94	0.03	0.84	0.98
$p(2000, \text{survey } 3)$	0.94	0.03	0.84	0.98
$p(2000, \text{survey } 4) \text{ fixed}$	1.00	0.00	1.00	1.00
$p(2001, \text{survey } 1)$	0.81	0.08	0.60	0.93
$p(2001, \text{survey } 2)$	0.81	0.08	0.60	0.93
$p(2001, \text{survey } 3)$	0.81	0.08	0.60	0.93
$p(2001, \text{survey } 4) \text{ fixed}$	1.00	0.00	1.00	1.00

Appendix F (continued).

p (2002, survey 1)	0.95	0.05	0.71	0.99
p (2002, survey 2)	0.95	0.05	0.71	0.99
p (2002, survey 3)	0.95	0.05	0.71	0.99
p (2002, survey 4) fixed	1.00	0.00	1.00	1.00
p (2003, survey 1)	0.82	0.13	0.46	0.96
p (2003, survey 2)	0.82	0.13	0.46	0.96
p (2003, survey 3)	0.82	0.13	0.46	0.96
p (2003, survey 4) fixed	1.00	0.00	1.00	1.00
p (2004, survey 1)	0.40	0.12	0.20	0.65
p (2004, survey 2)	0.40	0.12	0.20	0.65
p (2004, survey 3)	0.40	0.12	0.20	0.65
p (2004, survey 4) fixed	1.00	0.00	1.00	1.00
δ (survey 1) fixed	0.00	0.00	0.00	0.00
δ (survey 2) fixed	0.00	0.00	0.00	0.00
δ (survey 3) fixed	0.00	0.00	0.00	0.00
δ (survey 4) fixed	1.00	0.00	1.00	1.00

^aConstraints on parameters: dependent on the interaction of reproductive state of the territory in the previous year and current-year conditions (state*year), dependent on only current-year conditions (year), year- and survey-specific (year, survey), and only specific to survey (survey).