WILDLIFE
MONOGRAPHS

Vol. 197, May 2017

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Supplement to The Journal of Wildlife Management

WILDLIFE MONOGRAPHS

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Funding was provided by

USDA Forest Service, Southwestern Region
USDA Forest Service, Rocky Mountain Research Station
Joint Fire Science Program
Arizona Game and Fish Department

Publication costs were provided by

USDA Forest Service, Rocky Mountain Research Station

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Cover Image: Adult female (band code R6) northern goshawk (*Accipiter gentilis*), one of the longer-lived and more reproductive females on the Kaibab Plateau, Arizona, USA. R6 was banded on the Kaibab Plateau as a nestling in 1998 and recruited into the local breeding population in 2000. She was unusual in that she nested in 4 different territories (the great majority of Kaibab goshawks nested on 1 territory only), had 5 sequentially different mates (the majority of females had 1 or 2 lifetime mates), and laid eggs in 9 years. However, 5 of her 9 nest attempts failed. Still she produced 7 fledglings, a lifetime reproduction in the 70th percentile of 250 breeding females on the Kaibab Plateau.
Photo by Christie Van Cleave.

Wildlife Monographs 197:1–40; 2017; DOI: 10.1002/wmon.1023

Long-Term Demography of the Northern Goshawk in a Variable Environment

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ABSTRACT The Nearctic northern goshawk (*Accipiter gentilis atricapillis*) is a resident of conifer, broadleaf, and mixed forests from the boreal to the southwestern montane regions of North America. We report on a 20-year mark-recapture investigation (1991–2010) of the distribution and density of breeders, temporal and spatial variability in breeding, nestling sex ratios, local versus immigrant recruitment of breeders, breeding age structure, age-specific survival rates, and rate of population change (λ) of this species on the Kaibab Plateau, a forested sky island in northern Arizona, USA. We used an information-theoretic approach to rank models representing alternative hypotheses about the influence of annual fluctuations in precipitation on the annual frequency of goshawk breeding and fledgling production. We studied 125 goshawk breeding territories, representing approximately 87% of an estimated 144 total territories based on a mean distance of 3.8 km between territory centers in a 1,728-km^2 study area. The salient demographic feature of the population was extensive annual variation in breeding, which manifested as large inter-annual variation in proportions of pairs laying eggs, brood sizes, nest failure rates, and fledgling production. The percent of territories known in a prior year in which eggs were laid in a current year ranged from 8% to 86% ($\bar{x} = 37\%$, SE = 4.51), annual mean nest failure rate (active nests that failed) ranged from 12% to 48% (overall $\bar{x} = 23\%$, SE = 2.48), and mean annual brood size of successful nests (fledged ≥1 fledgling) ranged from 1.5 young to 2.5 young (overall $\bar{x} = 2.0$ young, SE = 0.03). Inter-annual variation in reproduction closely tracked inter-annual variation in precipitation, which we hypothesize influenced primary forest productivity and bird and mammal prey abundance. The best breeding years (1992–1993, 77–87% of pairs laid eggs) were coincident with a record-long El Niño-Southern Oscillation (ENSO) wet period and the worst breeding year (2003; 8% of pairs laid eggs) was the last of a 3-year record drought. Overall breeding success was 83% with most failures occurring during incubation; once eggs hatched, goshawks tended to fledge young. The pooled 20-year nestling sex ratio did not differ from unity (53% M; $n = 410$ M, 366 F) but was significantly male-biased in 2 years and female-biased in 1 year. Nonetheless, the overall greater production of male fledglings followed a strong trend of greater male production in other goshawk populations, suggesting that breeders might have been adaptively adjusting their offspring sex ratio, perhaps to produce more of the rarer (male) sex. Annual recruitment of new individuals into the breeding population averaged 43% during the study. Study area recruitment rate of hawks locally born (*in situ*) and banded was 0.12. Both sexes had equal tendencies to return to the Kaibab Plateau to breed (no differences in philopatry) and there were no differences in natal dispersal distances (natal to first breeding site) between the sexes. During the final years of study (1999–2010), an estimated 46% of breeding recruits were locally born and 54% were immigrants from distant forests. Minimum age at first breeding was 2 years and mean age at first breeding by known-age hawks (banded as nestlings or aged on plumage at first breeding) was 3.7 years for males and 3.5 years for females. Mean lifespan (yr from first banding as nestling to last resighting) of known-age goshawks was 6.9 years for both sexes. Mean minimum apparent lifespan of breeders aged ≥4 years based on plumage at first capture was 6.5 years for both sexes. Average age of goshawks at their first detection was 3.9 years old, at which time apparent survival was estimated at 0.77 for both sexes, which was just slightly less than the peak survival of 0.78 as a function of age. Age-specific survival estimates showed a steady decline after 9 years old and approached 0 at 20 years of age. Estimates of λ for breeding adults (M, 0.94, SE = 0.037; F, 0.98, SE = 0.038) provided only weak evidence for a population decline during the study. Although sex was not in the top survival model, models including age + sex were competitive, evidencing lower male than female survival, a finding corroborated by the occurrence of sex

Received: 6 May 2015; Accepted: 20 December 2016

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effects in the top λ model. Lower male survival may result from higher mortality associated with hunting agile prey in vegetation-filled environments during long breeding seasons when they are the primary forager. Lower survival may be compensated by the more frequent production (53%) of male fledglings. High-severity crown fire was an existential threat to the population. In addition to 4 large high-severity fires that burned roughly 3,770 ha (equal to 3 goshawk territories) in the 30 years preceding 1991, 6 high-severity fires burned another 30,945 ha during our study and killed most (>64%) of the forests in 8 known territories and possibly another 2 that were burned before we completed surveys.

Based on a lack of any recent demographic perturbations in age structure, a relatively high and time-constant annual adult survival rate, confidence intervals around adult λ estimates overlapping 1.0, and a study area saturated with territories, we surmise that the goshawk population on the Kaibab Plateau was stable during the 20-year study. Nonetheless, uncertainty remains regarding the population's future status because of a declining trend in breeding frequency, uncertain status (dead, alive, emigrated) of non-breeding adults, extensive temporal and spatial variation in breeding, and high frequency of immigrant recruits to the breeding population on the Kaibab Plateau. If the century-long decline in precipitation persists, especially at the increased rate seen since 1980, and manifests as deeper droughts, diminished wet periods, and weaker pulses in forest productivity, then the Kaibab Plateau goshawk population would be expected to show unambiguous evidence of decline. Evidence would include reduced local and regional goshawk reproduction and survival, reduced frequency of immigration, and further habitat loss to catastrophic fire.

KEY WORDS *Accipiter gentilis*, age structure, Arizona, brood sex ratio, demography, immigration, Kaibab Plateau, lambda, precipitation, recruitment, reproduction, survival.

Demografía a Largo Plazo del Azor Común en un Ambiente Variable

RESUMEN El azor común (*Accipiter gentilis atricapillis*) es un residente de bosques de coníferas de hoja ancha y mixtos de las regiones boreales al suroeste de América del Norte. Durante 20 años recapturando aves marcadas (1991–2010) se investigó la distribución y densidad de parejas reproductoras, la variabilidad temporal y espacial de crías, las proporciones en el sexo de los polluelos, el reclutamiento de aves reproductoras locales versus inmigrantes, las tasas de supervivencia específicas por edad y el cambio de la tasa poblacional (λ) de esta especie en la meseta de Kaibab, una montaña aislada parte de las islas del cielo (sky islands) en el norte de Arizona, EE.UU. Mediante un enfoque teórico, utilizamos la información para clasificar los modelos sugiriendo hipótesis alternativas de la influencia de fluctuaciones en la precipitación anual sobre la frecuencia anual en la reproducción de azores y la producción de volantones. Se estudiaron 125 territorios reproductivos de azores, representando aproximadamente el 87% de un total de 144 territorios, basados en una distancia media de 3.8 km entre centros territoriales en un área de estudio de 1,728 km^2. La característica demográfica más destacada fue una amplia variación anual en la población reproductiva que se manifestó en grandes variaciones interanuales en las proporciones de parejas que ponían huevos, el tamaño de las crías, las tasas de fracaso de los nidos y la producción total de polluelos. El porcentaje de territorios conocidos en un año anterior en el que los huevos fueron puestos en un año corriente osciló entre el 8% y el 86% ($\bar{x} = 37\%$, SE = 4.51), la tasa anual de fracaso del nido (nidos activos que fallaron) osciló entre 12 y 48% (en general $\bar{x} = 23\%$, SE = 2.48), y el tamaño medio anual de la nidada en nidos exitosos (plumado ≥ 1 polluelo) osciló entre 1.5 y 2.5 crías (en general $\bar{x} = 2.0$ crías, SE = 0.03). La variación interanual en la reproducción siguió de cerca la variación interanual en la precipitación, lo que suponemos influenció la productividad del bosque primario y la abundancia de presas de aves y mamíferos. Los mejores años de cría (1992–1993, 77–87% de huevos puestos por parejas) coincidieron con un período récord de El Niño Oscilación del Sur (ENOS) y el peor año de reproducción (2003, 8% de huevos puestos por parejas) siguió una sequía récord de tres años. El éxito nido en general fue del 83% y la mayoría de los fracasos ocurrieron durante la incubación; una vez salían del cascarón, los polluelos tendían a volar. La proporción de sexos en un combinado de 20 años no difirió de la unidad (53% M; $n = 410$ M, 366 H), pero hubo un sesgo de machos significativo de 2 años y un sesgo de hembras de 1 año. Sin embargo, la mayor producción de volantones macho siguió a una fuerte tendencia de mayor producción de machos registrado en otras poblaciones de azores, lo que sugiere que las parejas reproductoras podrían haber ajustado de forma adaptativa la proporción sexual de sus descendientes, tal vez para aumentar la producción del sexo más raro (machos). El reclutamiento anual de nuevos individuos en la población reproductora promedió 43% durante el estudio. La tasa de reclutamiento en el área de estudio de los azores nacidos localmente (*in situ*) y anillados fue de 0.12. Aves de ambos sexos tuvieron la tendencia de regresar a la meseta de Kaibab para reproducirse

(sin diferencias en la filopatía) y no hubo diferencias en las distancias de dispersión natal (natal al primer lugar de reproducción) entre los repatriados. Durante los últimos años de estudio (1999–2010), aproximadamente el 46% de los reclutas reproductivos fue de origen local y el 54% eran inmigrantes de bosques lejanos. La edad mínima en la primera reproducción fue 2 años y la edad media en la primera reproducción de azores conocidos (anillados como polluelos o cuya edad fue determinada por su plumaje en su primera reproducción) fue de 3.7 años para los machos y 3.5 años para las hembras. El tiempo de vida promedio (año desde el primer anillamiento como polluelo hasta el último avistamiento) de los azores de edad conocida fue de 6.9 años para ambos sexos. El tiempo de vida promedio mínimo aparente de aves reproductoras de ≥ 4 años en base a las características del plumaje en la primera captura fue de 6.5 años para ambos sexos. La edad promedio de los azores en su primera detección fue de 3.9 años de edad, en la que la supervivencia aparente se estimó en 0.77 para ambos sexos, lo cual fue sólo ligeramente menor que el pico de supervivencia de 0.78 en función de la edad. El estimado de supervivencia específico a la edad mostró una disminución constante después de los 9 años de edad y se aproximó a 0 a los 20 años de edad. Estimados de lambda (λ) para los adultos reproductores (M, 0.94, SE = 0.037; H, 0.98, SE = 0.038) sólo proporcionaron una evidencia débil de una disminución poblacional durante el estudio. Aunque el sexo no estaba en los principales modelos de supervivencia, los modelos incluyendo la edad + sexo fueron competitivos, evidenciando una menor supervivencia de machos que de hembras, un hallazgo corroborado por la ocurrencia de efectos en el sexo en el principal modelo de lambda. La menor supervivencia de machos puede ser el resultado de una mayor mortalidad asociada con la caza de presas ágiles en ambientes llenos de vegetación durante las extensas temporadas de reproducción, cuando estos son los cazadores principales. La menor supervivencia puede ser compensada por la producción más frecuente (53%) de polluelos macho. El fuego de copa de alta severidad fue una amenaza existencial para la población. Además de cuatro grandes incendios de alta severidad que quemaron un total de ~3,770 hs (igual a 3 territorios de azor) en los 30 años anteriores a 1991, 6 incendios de alta severidad quemaron otras 30,945 hs durante nuestro estudio que mató a la mayor parte (64%) de los bosques en 8 territorios conocidos y posiblemente otros 2 que fueron quemados antes de que se completaran las mediciones.

En base a la ausencia de perturbaciones demográficas recientes en la estructura de edades, una tasa de supervivencia anual relativamente alta y temporalmente constante, intervalos de confianza de estimados de lambda para adultos que se aproximan 1,0, y de un área de estudio saturada de territorios, estimamos que la población de azor en la meseta de Kaibab fue estable durante los 20 años de estudio. No obstante, sigue habiendo incertidumbre sobre el estado futuro de la población debido a una tendencia decreciente en la frecuencia de reproducción, el estado incierto (muerto, vivo, emigrado) de adultos no reproductores, una extensa variación temporal y espacial en la reproducción y una alta frecuencia de reclutas inmigrantes a la población reproducción en la meseta de Kaibab. Si el descenso en precipitación ya cercano a un siglo persiste, sobre todo a la alta razón observada desde 1980, y se manifiesta como sequías más profundas, disminución de los períodos húmedos y pulsos más débiles en la productividad forestal, se espera que la población de azores en la meseta de Kaibab muestre evidencia inequívoca de disminución. La evidencia incluiría una reducción en la reproducción y supervivencia de los azores locales y regionales, la reducción de la frecuencia de la inmigración y la pérdida adicional de hábitat ante incendios catastróficos.

Démographie à Long Terme de l'Autour des Palombes dans un Environnement Variable

RÉSUMÉ L'autour des palombe néarctique (*Accipiter gentilis atricapillis*) réside dans les forêts de conifères, de feuillus, ainsi que dans les forêts mixtes de la région boréale au sud-ouest de l'Amérique du Nord. Nous produisons un rapport sur une investigation d'une période de 20 ans (1991 à 2010) de marquage/recapture portant sur la répartition et la densité de reproducteurs, la variabilité temporelle et spatiale au niveau de la reproduction, la répartition des sexes chez les oisillons, le recrutement local versus celui provenant de l'immigration chez les reproducteurs, la structure d'âge en lien avec la reproduction, les taux de survie selon l'âge et le taux de changement de population (λ) de cette espèce sur le plateau de Kaibab, un massif de montagne forestier dans le nord de l'Arizona, aux États-Unis. Nous avons utilisé une approche de théorie de l'information pour classer les modèles représentant des hypothèses alternatives sur l'influence des fluctuations annuelles des précipitations sur la fréquence annuelle de reproduction chez les autours de palombes et sur la production d'oisillons. Nous avons étudié 125 territoires de reproduction d'autours de palombes, représentant approximativement 87% d'un total estimé de 144 territoires, basé sur une distance moyenne de 3,8 km entre les centres territoriaux, dans une zone d'étude de 1 728 km carrés. La caractéristique démographique saillante de la population était une variation annuelle importante de la reproduction, qui se manifestait sous la forme de grandes variations interannuelles des proportions de couples pondant des œufs, de la taille des couvées, des échecs de nidification et de la production totale de naissances. Le pourcentage de territoires connus lors d'une année antérieure, où des œufs ont été pondus au cours de l'année en cours, variait entre

8% et 86% ($\bar{x} = 37\%$, SE = 4,51), le taux annuel moyen d'échec de nidification (échec de nids actifs) variait de 12 à 48% (moyenne globale $\bar{x} = 23\%$, SE = 2.48), et la taille de couvée annuelle moyenne pour les nids productifs (production $\geq$1 naissance) variait de 1.5 à 2.5 petits (moyenne globale $\bar{x} = 2.0$ petits, SE = 0.03). La variation interannuelle au niveau de la reproduction suivait de près la variation interannuelle au niveau des précipitations, ce qui selon notre hypothèse a influencé la productivité de la forêt primaire, ainsi que l'abondance de proies d'espèces mammifères et oiseaux. Les meilleures années reproductrices (1992–1993, 77–87% des couples ont pondu de œufs) ont coïncidé avec une période humide record d'oscillation australe El Niño (ENSO) et la pire année de reproduction (2003; 8% des couples ont pondu des œufs) était la dernière d'une sécheresse record de 3 ans. Le succès de nid global a été de 83%, le plus grand nombre d'échecs s'étant produits pendant l'incubation; une fois les œufs éclos, les autours des palombes s'envolent généralement du nid assez jeunes. Le ratio combiné de sexe sur la période de 20 ans n'a pas différé de l'unité (53% M; $n = 410$ M, 366 F) mais a été biaisé de façon significative pendant deux années au niveau des mâles, et au cours d'une année chez les femelles. Néanmoins, la plus grande production de mâles a suivi une forte tendance de production accrue de mâles dans les autres populations d'autours des palombes, suggérant que les reproducteurs pourraient avoir ajusté de façon adaptative le ratio de leur progéniture, possiblement pour produire une plus grande quantité du sexe le plus rare (mâle). Le recrutement annuel de nouveaux individus dans la population reproductive a atteint une moyenne de 43% pendant 1'étude. Le taux de recrutement dans la zone de l'étude d'autours nés localement (*in situ*) et bagués a été de 0.12. Les deux sexes ont présenté une égale tendance à retourner dans le plateau de Kaibab pour se reproduire (aucune différence de philopatrie) et il n'y a eu aucune différence dans les distances de dissémination natale (naissance dans le premier site de reproduction) parmi les oiseaux ayant effectué un retour. Pendant les dernières années de l'étude (1999–2010), un pourcentage estimé de 46% des recrues à la reproduction était né localement, et 54% avait immigré de forêts distantes. L'âge minimal lors de la première reproduction était de 2 ans, et l'âge moyen de la première reproduction par les autours dont l'âge était connu (baguées comme des oisillons ou âge selon la plumage à première reproduction) était de 3.7 ans pour les mâles, et de 3.5 ans pour les femelles. La durée de vie moyenne (année du premier baguage comme un oisillon jusqu'à la dernière relocalisation) des autours de palombes d'âge connu était de 6.9 ans pour les deux sexes. La durée de vie minimale moyenne apparente des reproducteurs âgés de plus de 4 ans, en se basant sur le plumage lors de la première capture était de 6.5 ans pour les deux sexes. L'âge moyen de la première détection des autours de palombes était de 3.9 ans, âge auquel le taux de survie apparent était estimé à 0.77 pour les deux sexes, ce qui étaient juste au-dessous du sommet de taux de survie de 0.78 en fonction de l'âge. Les estimés de taux de survie spécifiques à l'âge ont présenté un déclin stable après 9 ans, et approchait de 0 à 20 ans. Les estimés lambda (λ) pour les adultes reproducteurs (M, 0.94, SE = 0.037; F, 0.98, SE = 0.038) ont fourni seulement de faibles preuves d'un déclin de population pendant l'étude. Même si le sexe n'était pas dans le principal modèle de survie, les modèles incluant l'âge et le sexe étaient concurrentiels, démontrant une plus faible survie des mâles que des femelles, un découverte corroborée par l'occurrence des effets du sexe dans le modèle lambda principal. Le plus bas taux de survie des mâles pourrait résulter d'une mortalité plus élevée associée à la chasse de proies agiles dans des environnements densément peuplés de végétation pendant les longues saisons de reproduction, alors qu'ils sont les principaux fourrageurs. Le plus bas taux de survie pourrait être compensé par une production plus fréquente (53%) d'oisillons mâles. Les feux de cimes de grande ampleur ont aussi été un risque existentiel pour la population. En plus de 4 feux de cime d'envergure ayant brÛlé approximativement 3,770 hectares (équivalant à 3 territoires d'autours des palombes) dans les 30 années précédant 1991, 6 feux de grande ampleur ont aussi brÛlé un autre 30,945 ha pendant notre étude, et brÛlé la plupart des forêts (>64%) dans les 8 territoires connus et possiblement 2 autres qui ont brÛlé avant que les études ne se terminent.

En se basant sur l'absence de perturbations démographiques au niveau de la structure d'âge, d'un taux de survie adulte relativement élevé et stable au fil du temps, d'intervalles de confiance relatifs aux estimés de l'adulte lambda cumulant 1,0, et une zone d'étude saturée de territoires, nous supposons que la population d'autours de palombes sur le plateau de Kaibab a été stable au cours de l'étude. Néanmoins, de l'incertitude demeure à propos de l'état futur de la population en raison de la tendance de déclin au niveau de la fréquence de reproduction, de l'état incertain (mort, vivant ou ayant émigré) d'adultes sans progéniture, des variations importantes temporelles et spatiales au niveau de la reproduction, et de la présence élevée de recrues immigrantes dans la population reproductive sur le plateau de Kaibab. Si le déclin des précipitations perdurant depuis plus d'un siècle se poursuit, dont le rythme est accru depuis les années 1980, et fait apparaître des sécheresses plus intenses, une diminution des périodes humides et des niveaux plus faibles de productivité des forêts, alors il serait attendu que la population d'autours des palombes du Plateau de Kaibab présente des signes évidents de déclin. Ces signes incluraient un taux local et régional de reproduction et de survie des autours de palombes en baisse, une fréquence réduite de l'immigration, et une disparition d'habitat accrue en raison d'incendies catastrophiques.

Contents

INTRODUCTION

A species' demography reflects the multiple trade-offs that individuals make among life-history traits such as site fidelity versus emigration, increased survival versus reduced reproduction, or a preference for one habitat over another. Demography is therefore a basis for estimating fitness of individuals occupying different habitats. The influence of biotic and abiotic factors on demography has been of interest to ecologists and it has been demonstrated that vegetation composition and structure, food, and weather are primary limiting factors for many species (Doyle and Smith 1994, Newton 1998*a*, Rutz et al. 2006, Salafsky et al. 2007, Penteriani et al. 2013). Because apex predators occupying forests are often sensitive to changes in their habitats (Belovsky 1987, Melián and Bascompte 2002), scientists have aspired to identify the abiotic and biotic determinants of habitat quality by investigating relationships between the vital rates of individuals within populations and the composition and structure of occupied habitats. Because raptors are relatively long-lived and survival and reproduction vary among individuals (e.g., aging effects, variable reproductive lifespans), documenting a species' demography requires long-term studies that exceed multiple lifespans, especially in variable environments where the periodicity of variation may never be experienced by many individuals in their lifetimes.

Northern goshawks (*Accipiter gentilis*) are the largest North American species in the genus *Accipiter* and typically occupy mature temperate and boreal woodlands and forests throughout their Nearctic range. They hunt a variety of birds from passerines to grouse (*Dendragapus* spp.) and mammals from tree (*Tamiasciurus* spp., *Sciurus* spp.) and ground squirrels (*Callospermophilus* spp., *Urocitellis* spp., *Otospermophilus* spp.) to rabbits (*Sylvilagus* spp.) and hares (*Lepus* spp.; diets reviewed in Squires and Reynolds 1997, Squires and Kennedy 2006). Goshawks are socially monogamous and territorial, lay a single clutch per year, are moderately dimorphic (M body mass about 71% of F mass; Reynolds et al. 1994), and have different sex roles during breeding. Females do much of the incubation and brooding and are therefore in the nest area through most of the 6-month breeding season beginning in March and ending in August. Males provide most of the food from before egg-laying until the end of a 2-month post-fledging dependency period on our study area (Wiens et al. 2006). In good prey years, females may not assist males in foraging until after fledging, whereas in poor prey years females may leave nestlings unattended to hunt (Squires and Reynolds 1997).

The effects of forest management on habitats and populations of northern goshawks has been a focus of conservation across its Holarctic distribution for several decades (Kenward and Widén 1989, Reynolds et al. 1992, Penteriani and Faivre 2001, Kudo et al. 2005, Rutz et al. 2006). Crocker-Bedford (1990), for example, reported the effects of tree cutting on goshawks in a 3-year study (1985–1987) on the North Kaibab Ranger District (NKRD) portion of the Kaibab Plateau in northern Arizona, USA. He compared territory occupancy in treatment areas (partially harvested before 1985 where 33% of trees from 80% of stands were removed) to control areas (forests that had light selection harvesting in the 1950s and 1960s) and reported 75–80% declines in occupancy and 94% declines in reproduction in the treatment areas despite nests being protected by uncut forest buffers of 1.2–200 ha. Crocker-Bedford (1990), using the ratio of occupied nests to numbers of known nest structures and the spacing among occupied nests, estimated that there were 260 breeding pairs on the NKRD before the initiation of tree harvests in the 1950s. He further posited that light harvesting in the 1950s and 1960s and partial harvesting in the 1980s reduced the population to 60 pairs by the late 1980s. Citing Crocker-Bedford (1990), environmental groups filed numerous lawsuits to protect goshawk habitat and submitted petitions to list the goshawk as endangered under the Endangered Species Act (Squires and Kennedy 2006). Subsequent to these lawsuits and petitions, the number of goshawk habitat studies throughout North America rapidly increased.

Estimating the effects of forest management on goshawk demography and population viability has proven difficult because of their relatively low population densities, elusive behaviors, structurally complex forest habitats, and variable year-to-year breeding rates (Doyle and Smith 1994, Risch et al. 2004, Krüger 2005, Reynolds et al. 2005, Bechard et al. 2006). As a result, many studies of tree-cutting effects on goshawk populations have been equivocal because they had insufficient within-year sampling or were conducted over too few years to distinguish environmental variation from forest management effects on vital rates (Reynolds et al. 2005). Goshawk populations, especially in western North America, are particularly difficult to enumerate and monitor because of the hawk's propensity to skip breeding years (Ingraldi 2005, Reynolds et al. 2005, Keane et al. 2006, Reynolds and Joy 2006). The ability of a population estimate to represent the true status of a population depends on errors associated with the estimate (Thompson et al. 1998). Incomplete year-to-year counts of breeding goshawks introduce a non-trivial source of error due to low detection probabilities (see below), a consequence of their elusive behavior, structurally complex habitats, and frequent use of alternative nests (Reynolds et al. 2005).

Detectability of goshawks is seasonally variable (Joy et al. 1994, Squires and Ruggiero 1995, Squires and Reynolds 1997, Sonsthagen et al. 2006), being highest during breeding as a result of their aggressive nest defense, vocalizations, molted feathers, feces, and prey remains in nest areas (nest tree and surrounding forest containing roosts, prey handling sites). Detectability is generally lowest during non-breeding when the hawks are dispersed in their home ranges or wandering over longer distances. Breeding females have greater detectability (easier to trap and resight) than males because females are more often near the nest and are strongly defensive (Reynolds and Joy 2006). When pairs fail to produce eggs or when nests fail early in breeding, adult detectability declines rapidly because they quickly abandon nest areas. Year-to-year detectability of territorial adults can be highly variable because of extensive temporal variation in proportion of pairs laying eggs and frequent year-to-year movements of pairs among alternate nests within their territories (Reynolds et al. 2005).

We studied a population of goshawks on the Kaibab Plateau in northern Arizona, USA. Our study included, but was not limited to, an area studied by Crocker-Bedford (1990), and was incentivized by lawsuits and legal actions based on contentions that forest management practices (i.e., tree cutting) were affecting goshawk habitat quality and were motivated by controversial aspects of Crocker-Bedford (1990) as discussed in Crocker-Bedford (1998), Kennedy (1998), and Smallwood (1998). We monitored goshawks on as many as 125 breeding territories in a 20-year (1991–2010) mark-recapture study on 2 differently managed landscapes, one with tree harvests (NKRD) and one without harvests (Grand Canyon National Park; GCNP), using intensive and extensive sampling designed to maximize detectability of breeding hawks and minimize the likelihood of missing nests (Reynolds et al. 2005). Our objectives were to 1) document the dispersion of breeding pairs of northern goshawks on these differently managed landscapes, 2) determine the annual variation in reproduction and identify environmental sources of variation, 3) measure annual brood sex ratios and age structures of breeders, 4) determine rates of turnover of breeders and estimate the proportion of recruits that were local-born (*in situ*) versus immigrants, 5) estimate sex- and age-specific survival and investigate whether survival varied by reproductive effort, and 6) estimate the annual rate of population growth.

The data compiled to address these objectives allowed us to test a number of hypotheses about important factors driving variation in goshawk demography during our study. First, breeding in highly variable systems has been observed to track resource pulses that are often initiated by climatic events leading to brief periods of reproductive increases (Yang et al. 2008). Furthermore, goshawks in western North America are known to skip breeding for periods of years (Ingraldi 2005, Reynolds et al. 2005, Bechard et al. 2006, Keane et al. 2006). We hypothesized that temporal and spatial process variation in goshawk breeding in our study area was driven by environmental variation resulting from wet and dry precipitation periods associated with El Niño Southern Oscillation (ENSO). We conjectured an association between annual variation in precipitation and goshawk reproduction resulting from precipitation-induced pulses of primary forest productivity. We further supposed that these pulses, leading to annual variation in food abundance within and among forest types, cascaded up through food webs, manifesting as temporal (annually variable numbers of breeders) and spatial variation (annually variable breeder abundances among forest types) in goshawk reproduction.

Secondly, we explored a number of competing hypotheses about the drivers of skewed brood sex ratios in goshawks. Brood sex ratios in raptors vary according to sex-specific recruitment patterns and variable environmental conditions. The seasonal sex-specific recruitment hypothesis states that the sex whose age at first breeding is more strongly accelerated by an early birth (sufficient maturation time) should be produced earliest in a breeding season (Pen et al. 1999). This hypothesis has been supported in a number of studies (Dijkstra et al. 1990, Daan et al. 1996, Tella et al. 1996, Smallwood and Smallwood 1998, Arroyo 2002) but not in others (Byholm et al. 2002, Hipkiss and Hornfeldt 2004, Laaksonen et al. 2004). Nonetheless, we investigated whether a particular sex in our study was produced more often in early-season broods under the expectation that there would be more females in early broods because more goshawk females than males breed as 1-year-olds (Daan et al. 1996).

The local resource competition hypothesis (Gowaty 1993, Taylor 1994) posits that if dispersal is sex-biased, and offspring of the less-dispersing sex potentially compete among themselves and with their parents, it may be advantageous to produce more of the less-dispersing sex (F in goshawks; Byholm et al. 2003, Wiens 2006) in good habitats (i.e., where resources are abundant). Julliard (2000) modeled habitat-dependent sex ratios in species with sex-specific dispersal and predicted that in environments with spatially varying habitat quality and reproductive success, brood sex ratios should indeed be skewed toward the less-dispersing sex in high-quality habitats and toward the more-dispersing sex in low-quality habitats (but see Leturque and Rousset 2003). This hypothesis was supported in several species including warblers and goshawks

(Komdeur et al. 1997, Julliard 2000, Rutz 2012). We investigated whether male sex ratio in our study varied as predicted in higher-quality habitats.

Finally, the variation in reproductive value hypothesis states that if the reproductive value of sons and daughters differ, parents should adjust offspring sex accordingly to maximize their own fitness (Trivers and Willard 1973, Frank 1990). Although mechanisms of sex allocation in birds remains a puzzle, there is increasing empirical evidence supporting the idea that parents can manipulate their offspring sex ratio according to environmental conditions (Hasselquist and Kempenaers 2002, Byholm 2005). Theory states that a minority sex has higher fitness than a majority sex because the majority sex may often not breed because of the lack of potential mates (Hardy 2002, Durell 2006). Although documenting unbalanced sex ratios within a population of breeders is problematic, departures from 1:1 can result from differential survival of the sexes in either the juvenile and adult stages. Lower survival of males has been demonstrated in demographic studies of goshawks and other raptors with large sexual-size dimorphism (Newton et al. 1983, DeStefano et al. 1994, Kenward et al. 1999, Reynolds and Joy 2006, Krüger 2007). Consistent lower survival of adult males in goshawk populations could result in males being the rarer sex and breeders that produced more males would have higher fitness because more of their offspring could breed. We conjectured that if male survival is consistently lower than females in goshawks, then breeders could be adaptively adjusting sex ratios of their brood to favor males.

Based on our 20-year demographic findings, we close with an evaluation of the current status of goshawks on the Kaibab Plateau and then considered our findings within the context of future threats from forest management prescriptions and climate change to goshawks and their habitats. We offer recommendations for managing ponderosa pine and mixed-conifer forests that not only restore habitat diversity in these highly altered ecosystems but also create forest conditions that were historically resilient to fire.

STUDY AREA

The 1,728-km^2 study area included the entire Kaibab Plateau in Arizona above the 2,182 m asl (above sea level) elevation contour (Fig. 1). The Kaibab Plateau is a high-elevation plateau that rises from a Great Basin desert scrub plain (Turner 1994) at 1,750 m to its highest point at 2,800 m. Surface weathering produced gentle drainages and moderately sloping valleys on the Plateau, which is bounded by escarpments of the Grand Canyon of the Colorado River on its south side, by steep slopes on its east, and by gentle slopes on the north and west sides that descend to the desert scrub plain. The southern portion of the study area included the GCNP North Rim (443 km^2) and the northern portion included the NKRD (1,285 km^2) of the Kaibab National Forest (KNF). Forests on the Kaibab Plateau are isolated from other forest areas by varying expanses of desert scrub vegetation. Distances to the nearest forest areas were 97 km to the north (Dixie National Forest), 250 km to the east (Chuska Mountains), 80 km to the west (Mount Trumbull), and 89 km to the south (Coconino National Forest; except for a small area of ponderosa pine forest in the GCNP South Rim at 18 km).

Spruce- and fir-dominated mixed-conifer forests (~360 km^2) occurred at the highest elevations (>2,600 m) on the study area

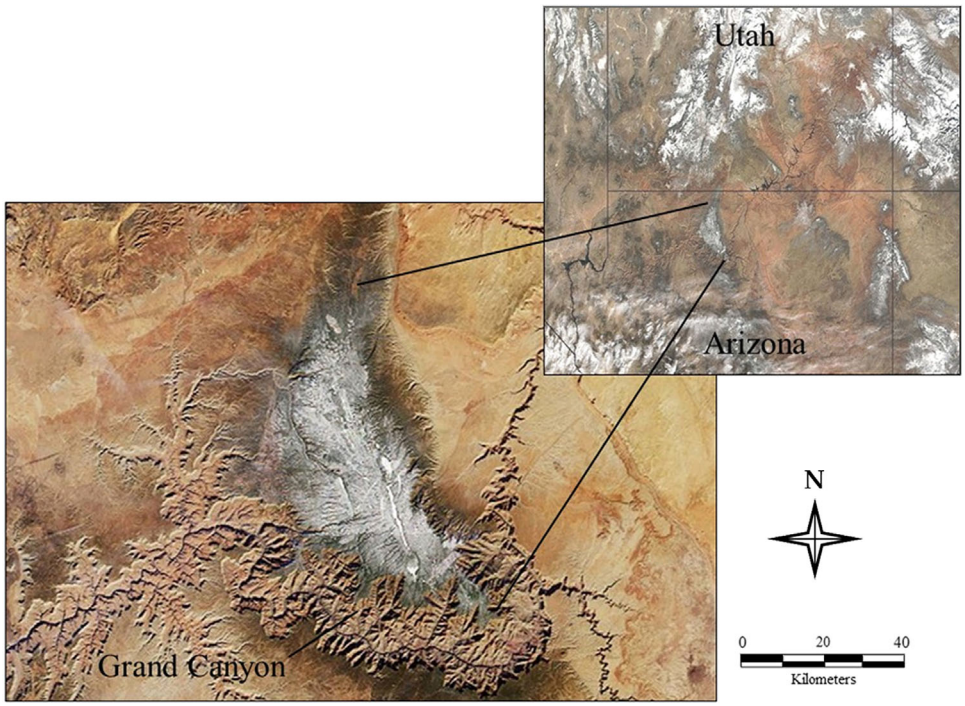

Figure 1. The Kaibab Plateau study area and its setting in northern Arizona, USA. The white area was snow-covered ponderosa pine and mixed-conifer forest. Snow cover extended down to about 2,190 m above sea level and almost exactly defined the boundary of the study area. Dark areas below snow were pinyon-juniper woodlands and brown areas were Great Basin desert scrub vegetation. Shown are portions of the Grand Canyon of the Colorado River. Photograph was taken in 2002, before the 2006 Warm Fire.

nd were dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), but ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) occurred on ridge tops and south-facing slopes. Mixed-conifer forests ($\sim$516 km^2), consisting of ponderosa pine, Douglas-fir, white fir (*Abies concolor*), blue spruce (*Picea pungens*), and quaking aspen (*Populus tremuloides*) occurred between 2,450 m and 2,650 m elevation. Quaking aspen was commonly mixed with conifers above 2,500 m elevation. Forests of nearly pure ponderosa pine ($\sim$122.4 km^2) occurred between 2,075 m and 2,450 m elevation, but quaking aspen, Douglas-fir, and blue spruce occurred locally in ravines and on north-facing slopes throughout this zone (Rasmussen 1941). At lower elevations, ponderosa pine was typically mixed with Rocky Mountain pinyon (*Pinus edulis*), Utah pinyon (*P. osteosperma*), Gambel oak (*Quercus gambelii*), New Mexican locust (*Robinia neomexicana*), and rabbit brush (*Chrysothamnus viscidiflorus*; Rasmussen 1941, White and Vankat 1993, Weng and Jackson 1999). Pinyon (*Pinus* spp.)-juniper (*Juniperus monosperma*) woodlands, often mixed with Gamble oak, cliff rose (*Purshia mexicana*), rabbit brush, and sagebrush (*Artemisia* spp.), occurred below the study area between 1,700–2,075 m elevation. However, pinyon-juniper woodlands occasionally extended up into low-elevation ponderosa pine forests on south-facing slopes, whereas stringers of ponderosa pine extended down drainages into pinyon-juniper woodlands. Desert scrubland occurred below 1,700 m elevation. With the exception of several narrow (<1 km) meadows, some areas burned by high-severity wildfire, and small tree harvest areas (see below), forests on the study area were contiguous (Reynolds et al. 1994, Joy et al. 2003; Fig. 2).

Average annual precipitation (1925–1977) at the GCNP North Rim weather station (elevation 2,560 m) was 642 mm, of which most occurred in winter as snow, and temperatures ranged from an average July maximum of 26° C to an average January minimum of −8° C (White and Vankat 1993). Winters had high snowfall and cold temperatures, and summers were cool. Precipitation was bimodal with a peak occurring in November to March followed by a drought period from May through June, then monsoonal rains from thunderstorms resulting in a lesser peak in July and August (White and Vankat 1993).

Because of its isolation by the Grand Canyon, the Kaibab Plateau was spared the intensive railroad logging that occurred over much of the western United States in the late 1800s (Burnett 1991). Nonetheless, in the late nineteenth century, various land use practices altered the composition and structure of forests on the Kaibab Plateau. In a 1909 survey of forests on the Kaibab Plateau, Lang and Stewart (1910:6) reported forests to be practically an "unbroken body of mature timber." Livestock grazing began in the 1880s and continued until the mid-1900s, except in the GCNP where grazing ceased when GCNP lands were fenced in the 1930s (Verkamp 1940, Rasmussen 1941, Merkle 1962, Fulé et al. 2002). Reductions in herbaceous fuels by livestock grazing, reduction in continuity of fuels by road construction, and initiation of active fire suppression in the early 1900s reduced the frequency of low-severity surface fire that historically burned on the Plateau (Lang and Stewart 1910, White and Vankat 1993, Fulé et al. 2002). Early reports and restoration studies showed that both mixed-conifer forest types on the Kaibab Plateau had a mixed-severity fire regime (a mix of surface- and stand-replacing fires) that resulted in groups and patches of trees of different ages and sizes (Lang and Stewart 1910, Grissimo-Mayer et al. 1995, Wolf and Mast 1998, Fulé et al. 2003).

Organized tree harvests on the NKRD began in the early 1920s and were primarily limited to cutting dead and dying trees (sanitation cuts) during which an average of 8.7 m^3/ha (1,500 board feet per acre) was removed (Garrett et al. 1997, Sesnie and Bailey 2003). Small (2–3 ha) patch cuts in mixed-conifer forests in the south-central portion of the Kaibab Plateau began in the late 1960s but were discontinued in the early 1970s (total patch cut area = 922 ha). Intensive stand management using even-aged management systems began in 1984 with shelterwood and seed-tree harvests in ponderosa and mixed-conifer forests until 1991 (Sesnie and Bailey 2003). From 1984 to 1991, the average volume of wood removed from treated units (4–24 ha) was 20.4 m^3/ha (3,500 board feet/acre; Garrett et al. 1997, Sesnie and Bailey 2003). Although the pre-1960s sanitation cuts occurred over much of the NKRD, shelterwood and seed-tree harvests occurred on 12,632 ha in scattered blocks of 8–17 ha (Burnett 1991, Sesnie and Bailey 2003). As a result of a reduction in fire frequency and tree cutting, forests on the NKRD during our study were denser (except in intensively managed areas) and younger than historical conditions, whereas forests in the GCNP (where no tree cutting has occurred) were also dense because of fire suppression, extensive regeneration, and no tree harvests (Lang and Stewart 1910, Wolf and Mast 1998, Fulé et al. 2003).

Four high-severity fires burned in the study area (1960 Saddle, 2,065 ha; 1974 Moquitch, 451 ha; 1977 DeMotte, 438 ha; 1987 Willis Fire, 817 ha) before our work (Meigs 2005; Fig. 2). During our study, these burns remained mostly open with scattered young ponderosa pine trees or had dense young stands of pine mixed with quaking aspen or dense brush (*Quercus* sp., *Robinia* sp.). Also during our study, 6 fires each burned $\geq$500 ha (an area about half the size a goshawk territory) at high-severity in ponderosa pine and/or mixed-conifer forests: 1993 Northwest, 504 ha; 1993 Point, 500 ha; 1996 Bridger, 5,156 ha; 2000 Outlet, 5,036 ha; 2003 Poplar, 4,709 ha; and 2006 Warm, 15,040 ha (Meigs 2005, U.S. Department of Agriculture Forest Service 2007). Thus, over the past 55 years, >347 km^2 (equivalent to about 30 goshawk territories) of forests on the 1,728-km^2 study area were burned by high-severity fire.

METHODS

Hawk Surveys and Monitoring

We defined a goshawk breeding territory as an area exclusively occupied by a pair of goshawks during a breeding season (Reynolds et al. 2005). We assumed that goshawks defended territories and that the observed dispersion and density of breeders on the Kaibab Plateau was constrained by territoriality. We estimated territory size as a circular area centered on a nest or the geometric center of a cluster of alternate nests (nests used by territorial hawks over years) with a radius of half the mean distance among neighboring pairs. We assigned alternate nests to

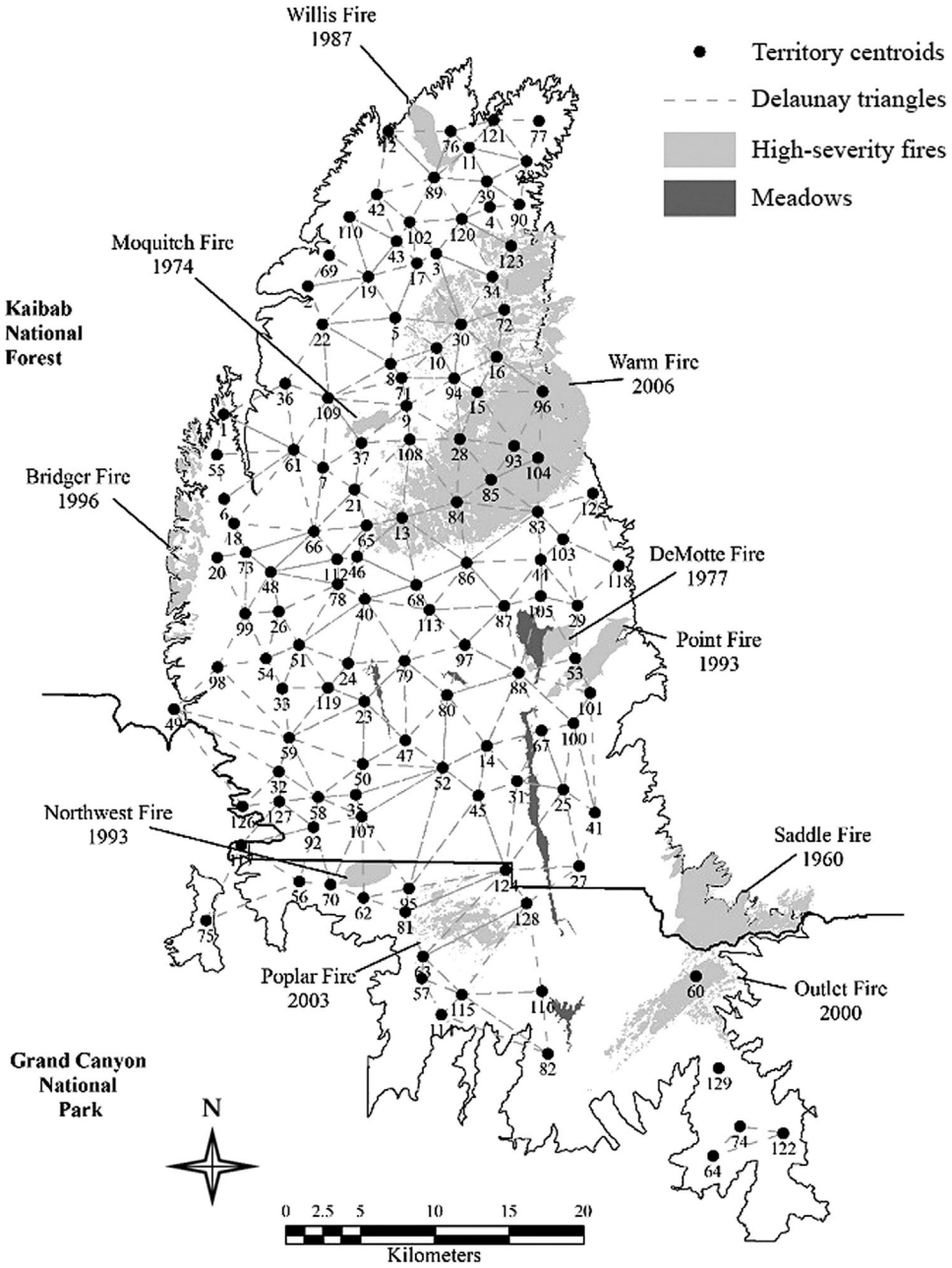

Figure 2. The 1,728-km^2 Kaibab Plateau study area, which included all of the Kaibab Plateau above 2,182 m above sea level, northern Arizona, USA. Shown are natural meadows, high-severity fires, and Delaunay triangles used to determine first-order nearest neighbor distance between 124 goshawk breeding territory centroids (1 territory excluded). Not shown are tree harvest areas. The southern portion of the study area included the Grand Canyon National Park North Rim and the northern portion included the North Kaibab Ranger District of the Kaibab National Forest.

a territory based on the identities of banded goshawks. We identified adjacent territories as distinct only when both were occupied by egg-laying goshawks in the same year. Resighting of banded goshawks showed that all but a few breeding adults had lifetime fidelity to their territories (R. T. Reynolds, Rocky Mountain Research Station, unpublished data).

We initially located breeding goshawks using combinations of systematic foot-searches and broadcasts of goshawk vocalizations from transects systematically arranged in large (35–45 km^2) forested areas (Kennedy and Stahlecker 1991, Joy et al. 1994, Reynolds et al. 2005). We identified a new territory when 1) we observed a nest with an incubating or brooding adult, eggs, nestlings, or fledglings; or 2) when adults that failed to lay (occupied-only territories) were subsequently observed on $\geq$2 separate visits to a nest area outside of a known territory. Occupied-only territories typically contained breeding goshawks in subsequent years. We were unable to completely search the study area for breeding goshawks in a single year because of its size. Thus, we expanded nest searches into unsearched portions of the study area each year. Expanded searches resulted in large increases in numbers of known territories until most of the study area had been searched by the end of the third year (1993). After 1993, a small annual increase in numbers of known territories resulted from annual revisits to areas suspected of having

breeding goshawks based on nest spacing (Reynolds et al. 1994, 2005).

Each year, 55–76% of goshawks moved as far as 2.4 km to lay eggs in an alternate nest within their territories (Reynolds et al. 2005). To account for these movements within identified territories, we used a within-territory multiple-step nest searching protocol. First, an initial visit involved checking all known nest structures within territories during the egg-laying period (Apr–May). We conducted searches for goshawk feces, molted feathers, or nests refurbished with green twigs within 100 m of all previously used alternate nests and all suitably sized nest structures found over years. Second, if none of the nests or nest structures were occupied by goshawks within a territory, we conducted foot searches within a 500-m-radius area centered on a territory's centroid (geometric means of coordinates of known alternate nests weighted by numbers of years each was used during the study; Reynolds et al. 2005). Foot searches involved systematically walking the 500-m-radius circle looking for goshawks and examining all trees for nests during the 2 weeks before egg laying to 3 weeks after hatching. Third, if we did not find a nest during foot searches, we conducted broadcast searches in 1,600-m-radius circles also centered on a territory's centroid. We conducted broadcasts from stations on transects arranged as in Joy et al. (1994); broadcasts occurred from >10 days post-hatch to the end of the post-fledging dependency period (late Aug or early Sep). Territories received 3 classifications: active if we observed females in incubation posture, eggs, egg fragments, nestlings, or fledglings; occupied-only when we observed goshawks or their molted feathers in a nest area on ≥2 occasions in a season but did not observe eggs; or unknown if none of the above were met. We recorded the coordinates of alternate nests and other suspicious nest structures found during searches with a global positioning system.

We visited active nests weekly to determine their status, count young, and estimate the timing and causes of nest failures. We banded nestlings in the 10 days before fledging and used the counts of nestlings at banding as the number of young fledged. We captured breeding adults with dho-gaza nets in their nest areas using live great horned owls (*Bubo virginianus*) from 10 days after egg-hatch to 10 days post-fledging (Reynolds et al. 1994). We determined sex of breeding adults based on behavior, body mass, tarsus–metatarsus length, and toe-pad length, which is the maximally stretched distance between the junction of the toe-pad with the hallux talon and junction of the toe-pad with the third digit talon (Bednarz 1987). If not banded as nestlings (ages known), we assigned breeding goshawks to 1 of 4 age classes (assuming a 1 Jun birth date) based on plumage characteristics and eye color at first capture: 1 year old (juvenal plumage, gray to yellow eyes), 2-year-old subadult (juvenal mixed with adult plumage, yellow eyes), 3-year-old subadult (predominantly adult plumage, scattered juvenal feathers, upper breast with coarse streaking and barring, orange eyes), and ≥4-year-old adult (full adult plumage, breast with fine vertical streaking throughout, orange-red to red eyes). These plumage age classes matched the ages of 2-year-old to 4-year-old breeding hawks that had been banded as nestlings.

All goshawks received a United States Geological Survey (USGS) leg band and a colored aluminum band with unique alpha-numeric codes readable from 80 m with 40–60× telescopes (Reynolds et al. 1994). Nestlings received green or orange color bands, adult males received blue bands, and adult females received black bands. If reading an alpha-numeric code was ambiguous during resighting (e.g., because of wear), we recaptured hawks, identified them by USGS band, and gave them a new band. We replaced bands (green, orange) on nestlings with sex-specific colored bands when we recaptured them as breeders. Application of 2 bands showed no cases of band loss among individuals resighted or recaptured over the 20 years. Annual field efforts of crews consisting of 15–23 persons were focused on finding new territories, visiting nests, capturing, banding, and resighting breeding goshawks, and banding nestlings. Capturing and marking of birds were conducted under United States Fish and Wildlife Service Banding and Auxiliary Marking permit (#21294), United States Geological Service Scientific Collecting permit (#MB044583-0), Arizona Fish and Game Department Scientific Collecting permit (#SP708255), Grand Canyon National Park Scientific Research and Collecting permit (#GRCA-2014-SCI-0025), and Colorado State University Animal Care and Use Committee permit (#05-086A-01). All research activities were consistent with American Ornithologists Union guidelines for capturing and handling birds.

We used Dirichlet tessellation and Delauney triangulation to estimate distances between first-order neighboring territory centroids. We estimated the potential number of breeding territories on the study area by assigning an exclusive circular area to each pair of goshawks using half the mean distance between neighboring territory centroids as the radius of the exclusive area (1,134 ha) and dividing the study area (163,225 ha; excludes 5,750 ha of natural openings and 3,771 ha burned by moderate- and high-severity fires pre-1991) by the exclusive area (Reynolds et al. 2005). We think our estimation of number of territories is reasonable because of regular territory spacing in a study area of nearly contiguous forests (Reynolds et al. 2005).

Reproduction

Temporal and spatial variation.—We characterized temporal variation in reproduction as the annual proportions of territories on which eggs were laid and as annual numbers of fledglings produced per active (eggs laid) nest. Numbers of known territories increased over years as a result of expanding nest searches, especially in the first 3 years, and we annually repeated searches in areas suspected of having breeding goshawks. We therefore report the proportions of territories with breeders in a year as a fraction of the prior-year's $(t-1)$ cohort of known territories. Thus, we used only territories receiving monitoring from early in a year's breeding cycle to determine the proportion of territories with breeding and final production of fledglings, which minimized biases associated with missed early-season nestling losses or nest failures. We also report the variation in duration (defined as numbers of consecutive years) of breeding and nonbreeding bouts among territories.

Because the probability of territory discovery was conditional on frequency of breeding, we investigated whether territories discovered early in the study were discovered first because they were of higher quality than those discovered late and were therefore not representative of the population of territories on the study area. We used a hurdle model

(Greene 2003; Proc NLMIXED in SAS 9.3; SAS Institute, Cary, NC, USA) to conditionally model the number of young fledged given that eggs were laid on territories within cohort groups (territories discovered in 1991 vs. those discovered in 1992–2008, 1991–1992 vs. 1993–2008. 1991–1993 vs. 1994–2008, and so on). We modeled egg-laying as a binomial probability and the number of young fledged as a truncated Poisson count. We evaluated the null hypothesis that annual probability of egg-laying and reproduction given egg-laying were not different among cohorts (i.e., that there were no differences in average territory or individual quality among cohorts) and that therefore any inter-annual variation in frequency of egg-laying and fledgling production in territories likely reflected inter-annual variation in environmental resources.

Goshawks are highly territorial and long-lived, making it difficult to distinguish spatial variation (among territory) effects from individual effects. We estimated the proportion of total variability that could be explained by temporal (yr-to-yr) and spatial (territory + individual) variation in a variance components analysis. We used a linear mixed model and a normal distribution of young fledged by breeding females and males as they aged. We included female and male ages and a linear temporal trend as fixed effects, and estimated random effects as spatial (territory + individual) and temporal (yr-to-yr). The sampling unit was a breeding attempt. We used the normal rather than the Poisson distribution because Poisson regression does not partition variance suited to a variance components analysis. Forsman et al. (2011) used the normal distribution in a similar variance components analysis of reproduction by spotted owls (*Strix occidentalis*). We used a Poisson distribution of fledgling counts for hypothesis testing and predictive modeling.

Fire, forest type, and management effects.—During our study, 6 large wildfires burned 30,945 ha at high-severity (crown fire; canopy trees killed, extensive below and above ground fuel and soil organic layer consumed; Keeley 2009) and about 8,450 ha at low-severity (surface fire; canopy trees not killed, surface litter consumed, soil organics largely intact; Keeley 2009) in ponderosa pine and mixed-conifer forests on the Kaibab Plateau. Moderate-severity (some canopy trees killed, understory plants charred or consumed, soil organic layer largely consumed; Keeley 2009) and high-severity fire affected all or proportions of forests in 8 goshawk territories and low-severity fires burned all or portions of 20 territories that were under study when burned. We continued monitoring these territories and documented the post-fire frequency of breeding and fledgling production by territory, and proportion of territory burned at high- and low-severity. We also monitored 7 territories with active nest areas burned by low-severity surface fire. We documented nest success and fledgling production in the year of the burns.

Spatial variation in reproduction may manifest as annual differences in densities of breeders among forest types. We used a quasi-Poisson generalized linear model to model the number of active (eggs laid) territories by forest type and quality of year for breeding, defined as good (>45% of territories active), moderate (24–45% active), and poor (<24% active). Forest type and quality of year were categorical predictors and we used an offset of the amount of area of ponderosa pine, mixed-conifer, and spruce-fir dominated mixed-conifer forests in the study area. We limited the data used in this analysis to the annual occurrence of egg laying on 89 NKRD territories during the final 16 years (1995–2010) of our study because by 1995 we had a near census of NKRD territories and could therefore determine the annual densities of breeding pairs by forest type (we did not include the GCNP because a census of breeding pairs was not attained). We obtained the area of each NKRD forest type from Joy (2002) and Joy et al. (2003), and adjusted the area of each type in 2007 to account for forest losses in the high-severity 2006 Warm Fire. To investigate the possibility of an interaction between forest type and the quality of breeding year, we initially included an interaction term but removed the term in a reanalysis because of its insignificance.

To appraise the effects of tree harvest on density of territories, occupancy of territories by breeders, and fledgling production by goshawks in the NKRD, we first compared territory spacing in the GCNP (no harvests) to the NKRD (with tree harvests) with a 2-sample *t*-test using the first-order neighborhood triangle leg lengths from the Delaunay triangulation described above. Second, we compared annual occupancy (proportions of territories with active nests) on the 2 areas with logistic regression using categorical year (1993–2010; 1992 occupancy could not be estimated in GCNP) and NKRD and GCNP as source factors. Third, we compared mean numbers of fledglings produced per active nest in the 2 areas in those years ($n = 13$) that had a minimum of 3 active nests in each area (excluded 1991, 1994, 1997, 2001–2003, 2009) with a paired *t*-test. We determined borderline significance to be $\alpha = 0.1$ and significance to be $\alpha = 0.05$.

Precipitation effects.—To explore relationships between inter-annual variation in precipitation and inter-annual variation in fledgling production, we derived annual precipitation estimates for the Kaibab Plateau from monthly totals measured at the Fort Valley Experimental Forest (FVEF) weather station (Menne et al. 2011), 12 km northwest of Flagstaff, Arizona (latitude 35.2681, longitude 111.7428). The FVEF was at 2,239 m elevation in ponderosa pine forests similar to the forests on Kaibab Plateau, 115 km to the northwest. Although actual precipitation amounts at FVEF and Kaibab Plateau likely differed, we assumed that year-to-year variation in precipitation was similar at the 2 locations because of the documented region-wide nature of wet and dry periods in the Southwest that are linked to the ENSO. Regional synchrony of wet and dry periods is demonstrated by the temporally consistent variability in annual precipitation at 97 long-term weather stations situated across the entire Colorado Plateau (Hereford et al. 2002). Consistent variability is corroborated by the synchronous years in which forest fires occurred over 2 centuries (1700–1900), reflecting the regional to subcontinental scales of Southwest wet and dry periods (Swetnam and Betancourt 1998).

We modeled the effects of annual precipitation on goshawk reproduction during a 12-month goshawk breeding cycle that begins and ends with the month when fledging occurs (1 Jul–30 Jun; Fig. 3). Because important phenological events that affect vegetation resource production in support of goshawk prey species occur within a given breeding cycle and up to 2 years prior to a particular fledging event, we

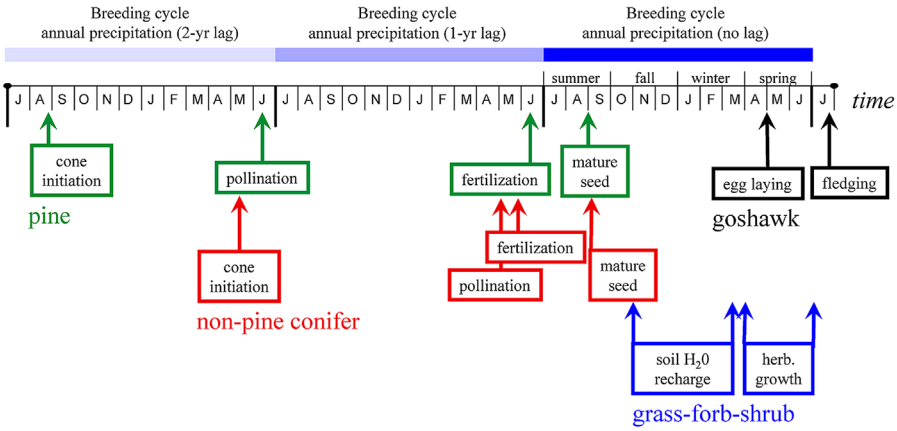

Figure 3. Inclusive months of the goshawk annual breeding cycle, the timing of precipitation (2-year lag, 1-year lag, and no lag), and the phenology of forest overstory and understory vegetation production of food resources for bird and mammal prey used in modeling effects of precipitation on goshawk reproduction.

investigated the effects of precipitation on the number of goshawk young fledged (Y) using a 2-year lag, a 1-year lag, and a current year (no lag) estimate of the annual breeding cycle precipitation (Fig. 3). We estimated total annual fledgling production for the entire study area (assuming 144 territories on the Kaibab Plateau, see below) with a negative binomial generalized linear model with an offset specified as the log-proportion of the 144 territories studied in a given year to account for the increasing effective sample through time as we discovered more territories. We used the information-theoretic framework to compare 8 models (all combinations of the 3 annual precipitation variables and an intercept-only model) of Kaibab-wide goshawk production using the MASS package (Venables and Ripley 2002) in R (R Development Core Team 2014). We ranked models based on corrected Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002). Final predictions of annual goshawk productivity were based on ensemble model averaging using individual model i weights (w_i) in the averaging process. The ensemble prediction was derived from a subset of models (i.e., the confident set) defined by those with $\Delta AIC_c \leq 2$ using the MuMIn package in R (Barton 2014). We report the root mean square errors and the mean absolute errors of the observed versus predicted values for all 8 competed models and the averaged model to further evaluate the goodness of fit. We used the Durbin–Watson (D–W) statistic for detecting autocorrelation between values separated from each other by time lags in the deviance residuals in all models (Durbin and Watson 1950, 1951).

Sex Ratio and Age Structure

We determined brood sex ratios at nests in which we identified the sex of all nestlings. We sexed nestlings based on body mass, tarsus–metatarsus length, and toe-pad length. This procedure misclassified only 2 of 104 (1.9%) banded nestlings that we subsequently retrapped or resighted as breeders; both were initially classified as females but recaptured as breeding males. We used a chi-square analysis to test whether nestling sex ratio differed from 1:1. We tested whether nestling sex ratio varied seasonally (i.e., more F produced in early broods as in Daan et al. 1996) using the mean hatch dates of broods by back-calculating from the mean age of brood members estimated with a photographic guide in Boal (1994) to determine annual variation in egg-laying dates. We calculated a mean Julian hatch-date for each year (1994–2010) and recorded individual brood hatch dates as deviations in days from the year's mean Julian hatch data. We considered broods that hatched before the year's mean Julian hatch date as early season broods and broods that hatched after the year's mean Julian hatch date as late season broods. We used a t-test of equal means and F-test of equal variances to investigate seasonal differences in nestling sex ratios.

We investigated whether nestling sex ratios varied between high- and low-quality habitats (McPeek and Holt 1992, Julliard 2000, Leturque and Rousset 2003) by regressing the proportion of territories occupied in a year by breeders (a surrogate for prey abundance) against the proportion of males in broods in that year. We ranked habitat (territory) quality based on the incidence of breeding such that territories more often occupied by breeders were assumed to be of higher quality than less frequently occupied territories, a well-supported assumption (Ferrer and Donázar 1996, Kostrzewa 1996, Linkhart and Reynolds 1997, Sergio and Newton 2003). We recognize that habitat quality can be confounded by individual quality, especially in long-lived species with high site fidelity (Sæther 1990, Goodburn 1991, Forslund and Pärt 1995, Sergio et al. 2009). However, we think our ranking of territories based on occupancy by breeders and total reproduction reflected differences in habitat quality because goshawks appeared to follow the ideal-despotic model of habitat choice (Fretwell and Lucas 1970) based on their strong fidelity to exclusive territories and the progressive occupation of infrequently occupied territories as annual breeding density increased on our study area. Thus, as predicted by the despotic model, the most-fit goshawks preemptively select the best habitats, relegating lower-quality individuals to lower-quality habitats where occupancy and reproduction were less frequent (Fretwell and Lucas 1970, Petersen and Best 1987, Sherry and Holmes 1989, Rodenhouse et al. 1997). Furthermore, occupancy has been shown to be tightly correlated to other measures of habitat quality such as survival and quantity and quality of resources (Sergio and Newton 2003).

Changes in a stable age distribution can occur if 1) survival in at least 1 age interval changes, 2) fecundity rate for 1 or more ages changes, or 3) both survival and fecundity rates change (Caughley 1978). We determined breeder age structure as counts of known-age individuals in yearly age classes during each of the final 11 years (2000–2010) of the study. We used age structure data from only the final 11 years to allow sufficient time for numbers of known-age breeders to equilibrate across age classes. To investigate whether age structures were stable year to year, we used a general linear mixed model (GLIMIX) with a log link function where the count of breeders at each age was the response variable and the response distribution was negative binominal. Age, sex, and year and interactions between sex and age, sex and year, and age and year were fixed effects we assessed using PROC GLIMMIX in SAS 9.4. We used least-square means from the model to compare counts of individuals among all main effects and their interactions.

Turnover, Recruitment, and Immigration

We defined a turnover as a replacement of a known (observed in a prior year, unbanded or banded) breeder on a territory by another breeder (a banded breeder replacing an unbanded or banded breeder or unbanded breeder replacing a banded breeder) in subsequent years. We report turnovers in consecutive years and in cases following 1–7-year breaks in breeding on territories. We defined recruitment as the addition of a new breeder to the local population and determined recruitment rate as the ratio of numbers of new breeders (unbanded or banded) to numbers of known prior breeders. We tallied hawks changing breeding territories (breeding dispersals) as turnovers on their new territory but not as recruits. We could determine the year of turnovers and recruitments only when breeding occurred in consecutive years on territories. We otherwise assumed the year a turnover or recruitment occurred was the year in which we first detected the new hawk or recruit as a breeder. Because of high inter-annual variation in proportion of territories with breeding and equally variable opportunities to detect recruitment (only breeders could be resighted), we smoothed out year-to-year fluctuations in recruitment by using 7-year moving averages. We used a 7-year average because 6.9 years was the mean lifespan of both goshawk sexes on our study area (R. T. Reynolds, unpublished data).

We estimated the geographic source of recruits (locally born vs. immigrants) by comparing annual proportions of banded (locally born) to unbanded recruits on all territories during the final 13 years (1998–2010) of the study because the ratio of banded to unbanded recruits reached an asymptote (equilibrated) in 1998. We were unable to band all nestlings at some nests because of unsafe tree climbing conditions (e.g., snags), late discovery of nests (e.g., just before or after fledgling), or logistical constraints in years with many active nests. Nonetheless, we tallied fledglings produced at all unclimbed nests and recorded the sum as the number of unbanded fledglings (N_{uf}). We derived estimates for the number of unbanded locally born fledglings that were expected to recruit and the proportion of immigrant recruits using the following procedure. First, we estimated the proportion of banded locally born recruits (P_{blr}) at time $t+2$ as

$$P_{blr}(t+2) = \frac{\#\ banded\ fledglings\ that\ recruited\ at\ time\ (t+2)}{\#\ of\ banded\ fledglings\ at\ time\ t},$$

where the numerator accounted for a minimum 2-year age at recruitment. Second, we estimated the number of unbanded locally born recruits (N_{ulr}) at time $t+2$ as

$$N_{ulr}(t+2) = P_{blr}(t+2) \times N_{uf}(t),$$

under the assumption that unbanded fledglings recruited at the same rate at banded fledglings. Third, we estimated the total number of locally born recruits ($N_{tot,lr}$) at time $t+2$ as

$$N_{tot,lr}(t+2) = (\#\ banded\ fledglings\ that\ recruited\ at\ time\ [t+2]) + N_{ulr}(t+2).$$

Finally, we estimated the proportion of immigrant recruits (P_{ir}) at time $t+2$ as

$$P_{ir} = 1 - \left(\frac{N_{tot,lr}\ [t+2]}{\#\ of\ total\ recruits\ at\ time\ [t+2]}\right).$$

We determined proportions of local versus immigrant recruits annually because numbers of territories studied changed as we found new territories and lost others to fire during the 13-year period.

We evaluated sex bias in philopatry (tendency to return to the Kaibab Plateau) in a chi-square 2×2 contingency table comparison of proportions of locally born and banded males to locally born and banded females that eventually recruited as breeders on our study area. We tested for equality in local (*in situ*) natal dispersal distance (map distance between natal nest and first breeding nest) for males and females with a 2-tailed t-test assuming equal variances. We evaluated age differences between males and females at recruitment (age at first breeding attempt) with a Pearson's chi-square test where age classes were 2, 3, 4, 5, 6, and 7+.

Adult Survival

To estimate apparent survival of breeding adults, we pooled individuals captured, marked, and resighted each breeding season (Mar–Sep) and considered each year a separate encounter occasion, resulting in 20 marking (1991–2010) and 19 resighting occasions. In capture–recapture studies, mortality cannot be distinguished from emigration from a study area. Survival probabilities are therefore the product of true survival and fidelity to the study area, and apparent survival is less than true survival when study area fidelity <1. Temporary or permanent emigration by breeding goshawks from our study area could thus result in underestimates of true survival. However, emigration by breeders was likely rare because of lifetime fidelity to territories displayed by most goshawks. The few observed breeding dispersals were rarely beyond 5 territories (R. T. Reynolds, unpublished data), a fraction of the number of territories a disperser could move and still remain on the study area. Because our study area was a forested sky island (Fig. 1), breeders emigrating from our study area would have to cross long distances of desert scrublands to settle in other suitable forests, which they were certainly capable

of doing. Because male goshawks were particularly difficult to trap and resight, we were unable to resight some banded males and a few females in one or more breeding years, especially when breeding attempts failed before a year's trapping or resighting was completed. In these cases, we assumed the same known (banded) male or female was breeding in a missed year only when a single missed year was bracketed by resights of the same individual.

We estimated annual recapture probabilities (p) and apparent survival probabilities (φ) of breeding adults using Cormack–Jolly–Seber (CJS) open-population live-recapture models (Cormack 1964, Jolly 1965, Seber 1965) in Program MARK (White and Burnham 1999). Because of delayed age of first breeding (R. T. Reynolds, unpublished data) and permanent emigration of most juveniles (Wiens et al. 2006), resighting rates of goshawks in their first and second calendar years were insufficient to estimate the probabilities of juvenile survival. We defined recapture probabilities as the probability a goshawk in year $t+1$ was recaptured, given it was alive and on the study area at the beginning of year t. We defined apparent survival as the probability a goshawk survived and stayed on the study area from t to $t+1$, given it was alive at the beginning of t. The yearly estimate of apparent survival was approximately 15 June in year t to 14 June in year $t+1$, the approximate mid-point of the annual field season for the demographic study (from mid-Apr to mid-Aug).

We examined factors affecting apparent survival by developing a set of *a priori* models for analysis based on biological hypotheses. Specifically, we tested whether 1) survival differed between the sexes as a result of different mortality rates associated with different breeding sex roles; 2) survival differed by age, reflecting an initial increase in survival with life experience followed by senescence; and 3) survival differed with mean fledgling production/year, reflecting a cost of reproduction on survival. We then represented these *a priori* models with statistical models in Program MARK (White and Burnham 1999). We evaluated goodness of fit and estimated an overdispersion parameter (c) for the data set and estimated recapture probabilities and apparent survival with the *a priori* models in Program MARK. If needed, we adjusted the covariance matrices and AIC_c values with $\hat{c}$ to obtain $QAIC_c$ values for model selection and to inflate variances of parameter estimates, and then selected the most parsimonious model for inference based on $QAIC_c$ (Burnham and Anderson 2002).

We modeled the effect of age on apparent survival of banded adult male and female goshawks as an individual covariate with the CJS data type in Program MARK (White and Burnham 1999). We included the mean number of young produced per successful (fledged $\geq$1 young) nest per year (fledgling rate) by banded males and females as a temporal covariate, and used analysis of deviance to assess the amount of deviance explained by this covariate. We considered 5 combinations of sex (s) and time (t) covariates (., s, t, s + t, and s × t) for models of apparent survival (φ) and detection probability (p), resulting in 25 models, with model-naming conventions following Lebreton et al. (1992). We used AIC_c (Burnham and Anderson 2002) to select the top 2 models, and then added the age effect on φ to each model using a logit link function, first as a linear effect, and then as a quadratic effect. We evaluated goodness of fit to estimate overdispersion (c) with the goodness-of-fit tests in Program RELEASE (Burnham et al. 1987) and the median $\hat{c}$ procedure in MARK.

Rate of Population Change

We estimated the population rate of change for each year for banded adult males and females with the Pradel seniority (γ) data type (parameters for φ, p, and γ) of breeders (Pradel 1996) in Program MARK (White and Burnham 1999). We considered 5 combinations of sex (s) and time (t) covariates (., s, t, s + t, and s × t) for models of apparent survival (φ), detection probability (p), and seniority (γ), resulting in 128 models, with model naming conventions following (Lebreton et al. 1992). Additionally, we included a temporal covariate of fledging rate to model φ and γ. We estimated the rate of annual population change (λ) as a derived parameter, $\lambda_i = \varphi_i/\gamma_{i+1}$. Two important assumptions of Pradel (1996) are that study-area size and survey effort were annually constant; that is, hawks were not gained or lost because of changes in a study area or survey effort. If new individuals are added in subsequent years because of study area expansion, or if some individuals are missed in the first years of the study (e.g., because of low detection of non-breeders), estimates of λ from early years may be biased high. Thus, we used only λ values for 1994 and after in the analyses because the size of our study area increased in the years 1991–1993 as we identified new territories and hawks. By the end of the 1993 breeding season, we had searched the majority of the study area at least once for breeding goshawks. We used AIC_c (Burnham and Anderson 2002) to rank models (Burnham and Anderson 2002).

We used maximum likelihood estimates of $\log(\lambda)$ in the random effects procedure of Program MARK (White et al. 2001) to obtain shrinkage estimates [$\log(\tilde{\lambda})$]. We used the minimum AIC_c model without fledging rate, so the values of λ used in the analysis were not a function of fledging rate. We then used these shrunk estimates to determine the probability of population change over a 20-year period by randomly selecting 20 values with replacement from the set of $\log(\tilde{\lambda})$ and summing the 20 values to determine population level at the end of the 20-year period (Burnham and Anderson 2002, White et al. 2002). We repeated this process 10,000,000 times to obtain a distribution of 20-year trends, from which we tabulated percentiles to assess population rate of change. We evaluated goodness of fit to estimate overdispersion (c) with the goodness-of-fit tests in Program RELEASE (Burnham et al. 1987) and the median $\hat{c}$ procedure in MARK using the CJS data type that conditions on first capture. The CJS data type is appropriate for evaluating goodness of fit of the Pradel data types because all lack of fit in the model can occur only in the recaptures, not with initial captures.

RESULTS

Territory Dispersion

Numbers of goshawk territories under study increased from 37 in 1991 to 125 in 2010, with rapid increases in the first 3 years ($n = 82$ in 1993) and gradual increases thereafter (Table 1). Initial increases mostly resulted from annual expansions of nest searches that began in the northwest of the study area and generally expanded to the north, east, and south. At the close of the 1993 breeding season, nearly all of the NKRD and about 70% of the GCNP had received initial searches. Post-1993 increases in territory numbers resulted from nests discovered in repeated searches in areas likely to have nests based on nest spacing. The

Table 1. Number of territories under study, numbers of active (eggs laid) goshawk nests, number and percent of non-active (no eggs laid) territories that were occupied by breeders, number and percent of non-active territories with unknown occupancy status, and mean and standard error of fledglings per active nests and per successful nests per year on the Kaibab Plateau, Arizona, 1991–2010.

	Year																			$\bar{x}$
	1991	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	
Territories	37	64	82	88	99	105	106	109	113	120	120	121	121	121	121	123	123	124	124	125	107.3
Active nests	36	59	67	21	53	46	31	58	57	66	30	21	10	51	46	62	33	29	28	42	42.3
Successful nests	34	49	58	16	43	35	25	49	42	59	19	11	6	41	36	52	21	16	24	34	33.5
Territories occupied-only	1	2	6	25	21	23	27	5	10	8	19	30	18	5	5	4	19	12	18	6	13.2
(%)	(0)	(3)	(7)	(28)	(21)	(22)	(25)	(5)	(9)	(7)	(16)	(25)	(15)	(4)	(4)	(3)	(15)	(10)	(15)	(5)	(12.3)
Territories unknown status	0	3	9	42	25	36	48	46	46	46	71	70	93	65	70	57	71	83	78	77	51.8
(%)[a]	(0)	(5)	(11)	(48)	(25)	(34)	(45)	(42)	(41)	(38)	(59)	(58)	(77)	(54)	(58)	(46)	(57)	(67)	(63)	(62)	(48.3)
Fledglings	72	107	115	27	69	59	45	119	96	139	35	16	9	84	66	105	38	24	38	58	66.0
Fledglings/active nest	2.0	1.8	1.7	1.3	1.3	1.3	1.5	2.1	1.7	2.1	1.2	0.8	0.9	1.6	1.4	1.7	1.2	0.8	1.4	1.4	1.6
(SE)	(0.13)	(0.14)	(0.12)	(0.20)	(0.12)	(0.13)	(0.15)	(0.14)	(0.16)	(0.13)	(0.19)	(0.18)	(0.28)	(0.15)	(0.14)	(0.13)	(0.17)	(0.16)	(0.14)	(0.14)	(0.04)
Fledglings/successful nest	2.1	2.2	2.0	1.7	1.6	1.7	1.8	2.4	2.3	2.4	1.8	1.5	1.5	2.0	1.8	2.0	1.8	1.5	1.6	1.7	2.0
(SE)	(0.11)	(0.10)	(0.10)	(0.15)	(0.11)	(0.10)	(0.10)	(0.10)	(0.11)	(0.10)	(0.16)	(0.16)	(0.22)	(0.11)	(0.10)	(0.10)	(0.11)	(0.13)	(0.10)	(0.11)	(0.03)

[a] Insufficient observations of adult goshawks and their sign in a territory to meet occupied-only status.

success of repeated nest searches both reflected and characterized extensive temporal variation of breeding on territories; we searched potential areas as many as 4–5 years before we found active nests (see below). Access and logistical constraints prevented nest searches in the east-central portion of the GCNP; about 25% of the GCNP remained unsearched through the study, enough area for about 19 territories.

The centroids of 124 territories (territory GCNP-60 excluded because of incomplete nest searching in surrounding area) were spaced at a mean distance of 3.8 km (SE = 0.08 km, range = 1.2–8.4 km, $n = 588$ first-order neighbor triangle leg distances; Fig. 2). The mean number of used alternate nests in 122 territories (eggs never laid in 3 territories) was 3.6 (SE = 0.17, median = 4 alternates; range = 1–10 alternates) and the median distance from territory centroids to alternates (not including 18 territories with <2 nests) was 306 m ($\bar{x} = 413$ m, SE = 16 m, range = 6–1,614 m, $n = 415$ alternates). The 20-year movements of banded goshawks among alternate nests suggested that territories were spatially stable. We estimated territory size as 11.3 km^2. Dividing the study area by 11.3 km^2 produced an estimate of about 144 territories in the study area. Thus, the 125 monitored territories comprised about 87% of potential territories. Because we completely searched the NKRD portion of the study area and it appeared saturated with territories, most of the undiscovered territories (about 18–20) were likely in the GCNP.

Reproduction

Of 846 active nests in the full sample of territories (those known from prior yr + newly discovered territories; Table 1), 21% (176) failed and 79% (670) fledged ≥1 young and produced 1,321 fledglings. Of 734 active nests in a prior-year's cohort of territories (Table 2), 23% (167) failed and 77% (567) fledged ≥1 young and produced 1,127 fledglings, demonstrating that a sample of territories monitored from early in a breeding season yields a higher failure rate. Mean brood size of successful nests was 2.0 (SE = 0.03 nestlings, range = 1–4 nestlings; Table 2); 153 (27%) broods had 1 young, 272 (48%) had 2, 138 (24%) had 3, and 4 (1%) had 4 young. Of the failures in prior-year's cohort of territories, 104 (62%) occurred during incubation and 63 (38%) occurred during the nestling period. Number of fledglings produced by active and successful nests in our full sample of territories ($\bar{x} = 1.6$ fledglings/active nest, SE = 0.04; $\bar{x} = 2.0$ fledglings/successful nests, SE = 0.03; Table 1) were the same or nearly the same as produced in prior-year's cohort of territories ($\bar{x} = 1.5$ fledglings/active nest, SE = 0.04; $\bar{x} = 2.0$ fledglings/successful nests, SE = 0.03; Table 2).

Temporal and spatial variation.—Temporal variation in breeding within and among territories was extensive (Appendix A). For 121 territories with ≥9 years of monitoring (excluding 4 territories discovered after 2002), breeding occurred in only 40% of the years (SE = 1.97, median = 45%, range = 8–86%; 841 breeding-yr in 2,098 territory-monitoring-yr). Breeding was never observed on 3 territories (1 in NKRD, 2 in GCNP), although each of the 3 had an occupied-only status in ≥1 year, and only 3 territories had breeding in excess of 80% of years. A weak bimodal distribution of breeding frequency on the 121 territories partitioned them into 2 groups: 1 with breeding

Table 2. Prior-year's cohort (territories active in year t that were under study in year $t-1$), numbers of active (eggs laid) nests in prior year's cohort, proportion of prior year's cohort that was active, and mean and standard error of fledglings per active nests, nest failures, and fledglings (brood size) per successful nests in each prior year's cohort of goshawk territories on the Kaibab Plateau, 1991–2010.

	Year																			$\bar{x}$
	1991	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	
Territories	37	64	82	88	99	105	106	109	113	120	119[a]	120	120	120	120	122	115[b]	116	116	117	105.4
Active nests in prior year cohort		32	49	18	44	40	31	55	56	60	30	21	10	51	46	60	33	29	28	41	38.6
(%)		(86)	(77)	(22)	(50)	(40)	(30)	(52)	(51)	(53)	(25)	(18)	(8)	(43)	(38)	(50)	(27)	(25)	(24)	(35)	(37)
Fledglings		65	88	21	56	51	45	112	94	128	35	16	9	84	66	101	38	24	38	56	59.3
Fledglings/active nest		2.0	1.8	1.2	1.3	1.3	1.5	2.0	1.7	2.1	1.2	0.8	0.9	1.7	1.4	1.7	1.2	0.8	1.4	1.4	1.5
(SE)		(0.20)	(0.15)	(0.22)	(0.14)	(0.14)	(0.15)	(0.15)	(0.16)	(0.14)	(0.19)	(0.18)	(0.28)	(0.15)	(0.14)	(0.13)	(0.17)	(0.16)	(0.14)	(0.14)	(0.04)
Failed nests		6	7	5	10	10	6	9	15	7	11	10	4	10	10	10	12	13	4	8	8.8
(%)		(18.8)	(14.3)	(27.8)	(22.7)	(25.0)	(19.4)	(16.4)	(26.8)	(11.7)	(36.7)	(47.6)	(40.0)	(19.6)	(21.7)	(16.7)	(36.4)	(44.8)	(14.3)	(19.5)	(22.7)
Brood size/successful nest		2.5	2.1	1.6	1.7	1.8	1.8	2.4	2.3	2.4	1.8	1.5	1.5	2.1	1.8	2.0	1.8	1.5	1.6	1.7	2.0
(SE)		(0.11)	(0.12)	(0.18)	(0.12)	(0.11)	(0.10)	(0.11)	(0.12)	(0.11)	(0.16)	(0.16)	(0.22)	(0.11)	(0.10)	(0.10)	(0.11)	(0.13)	(0.10)	(0.11)	(0.03)

[a] One territory burned in 2000 Outlet Fire.
[b] Seven territories >64% burned in 2006 Warm Fire.

in <40% of years and the other >40% of years (Fig. 4A). The bimodal distribution was more obvious when we excluded the initial 3 survey years (1991–1993) to guard against inflated breeding frequency resulting from the way territories were identified (they had to be initially active; Fig. 4B). The removal of the 3 initial study years provided a truer reflection of the underlying distribution of breeding frequency (annual mean of territories with breeding = 36%, SE = 2.0, median = 36%, range = 8–53%, 679 breeding yr in 1,916 territory-monitoring-yr) and showed that changes in the breeding status of territories occurred most often in less frequently used territories as breeding conditions changed. By the end of our study in 2010, territory density on the NKRD was 8.4 territories/100 km^2 ($n = 108$) and annual densities of active nests in the years 1995–2010 ranged from 0.8 to 4.8 nests/100 km^2 ($\bar{x} = 2.9$ nests/100 km^2, median = 3.1 nests/100 km^2).

Breeding on territories occurred either in single-year bouts or in bouts of consecutive years of various lengths separated by a single year or consecutive years of non-breeding. Breeding bouts occurred most commonly as single-year bouts (41% of 378 bouts) and as the consecutive-year length of bouts increased, their frequency declined (Fig. 5). Non-breeding bouts showed a similar steep decline, the most frequent being single-year bouts followed by decreasing frequencies of bouts with increasing consecutive years of non-breeding. The maximum non-breeding bout of 20 years reflected the 3 territories on which egg-laying never occurred.

Box plots from the hurdle model of the probability of egg-laying and counts of numbers of fledglings produced given egg-laying in each year's cohort of territories showed no evidence of among-cohort heterogeneity in predicted probability of egg laying or predicted count of fledglings given egg-laying in years following discovery (95% CIs for predicted probability of egg-laying for all cohorts overlapped and 95% CIs of predicted differences in count of fledglings overlapped 0; Fig. 6A,B). Thus, there were no differences in means and variances in reproduction among cohorts of territories, and, by extension, no differences in average quality (measured by probability of egg-laying and productivity) of territories among cohorts whether discovered early or late in the study. Lack of heterogeneity supported our approach to use the prior-year cohort of territories to estimate the relative quality of a breeding year based on the population-wide egg-laying and productivity rates.

The exceptional breeding years of 1992 and 1993 had breeding rates of 86% and 77% of prior-year cohorts of territories, respectively, well above the next highest year (2000) when breeding occurred on 53% of territories (Table 2, Fig. 7). In contrast, 2002 and 2003 were the poorest breeding years when only 18% and 8%, respectively, of territories had breeding. All other years had variable but intermediate percentages of territories (22–53%) with breeders. Annual brood sizes and nest failure rates varied in concert with proportions of territories with breeding goshawks; in good breeding years, brood sizes tended to be large and nest failures low, whereas in poor breeding years, brood sizes were small and nest failures more frequent (Figs. 7 and 8A,B). Based on a mean brood size of 2.0 nestlings (Table 2) and only 2 (5%) of the 36 active nests failing, 1991 appeared to be as good a breeding year as 1992 and 1993 (Fig. 7). A variance

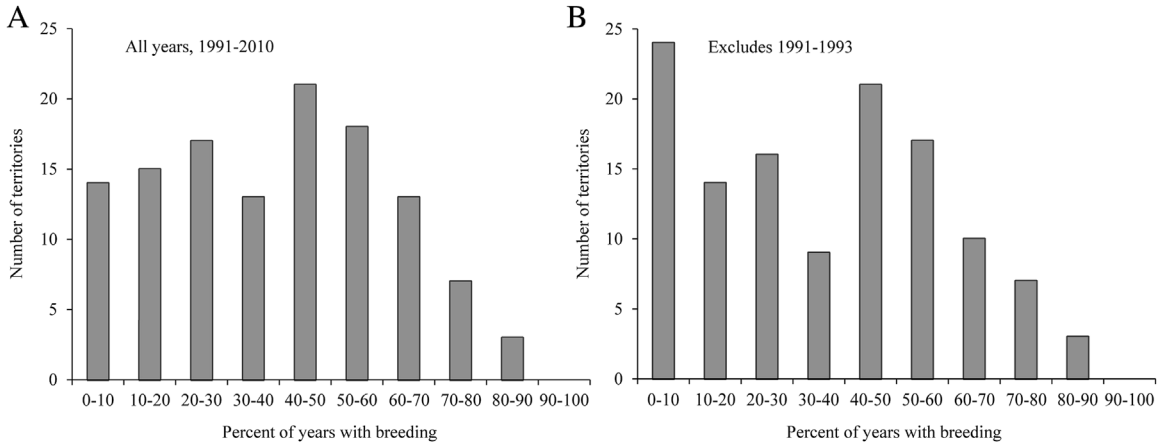

Figure 4. Percent of years with breeding on territories (number of years of egg-laying on a territory divided by numbers of years each was studied) for territories studied ≥9 years ($n = 121$), from 1991 to 2010 (A) and percent of years with breeding on the same territories excluding the exceptional breeding years of 1991–1993 (B) on the Kaibab Plateau, Arizona, USA.

components analysis of spatial variation in annual reproduction, which reflected both territory and individual variation, showed that spatial variation was somewhat less than temporal variation, but both sources of variation were small relative to total variance (spatial estimate = 0.05, % total variance = 4.8; temporal estimate = 0.08, % total variance = 8.3; residual estimate 0.86, % total variance = 86.8; total estimate = 0.99).

Fire effects.—We were unaware if any goshawk nests occurred within 4 large, high-severity fires that burned in the 30 years preceding our study (Fig. 2). Although none of these burned areas contained active goshawk nests during our study, each had active nests within 500 m of their perimeters. During our study, 6 large moderate- to high-severity fires burned 30,945 ha of ponderosa pine and mixed-conifer forests. Only the Outlet and Warm fires killed all or most of the tree canopies in goshawk territories (1.9-km radius) monitored during our study. The Outlet Fire burned an entire goshawk territory (GCNP-60) at high-severity but was large enough to have burned another 2 potential territories at high-severity before nest searches were completed. Territory GCNP-60 was never reoccupied after the Outlet Fire. Prescribed or natural low-severity surface fires burned through 7 active nest areas during incubation and nestling periods. All but 1 of the 7 nests fledged young ($\bar{x} = 2$ fledglings, SE = 0.37, range = 1–3, $n = 6$ nests). The exception failed well after the fire, likely because of an exceptionally long (10-day) period of rain when a number of other nests in unburned forests also failed.

The Warm Fire (8 Jun–4 Jul 2006) burned all or portions of forests in 20 territories (Table 3, Fig. 2). During its initial 18 days, this lightning-initiated fire burned about 7,700 ha as a low-intensity surface fire with little overstory tree mortality. On 25 June, high winds caused the fire to enter the overstory canopy and it burned about 15,040 ha, mostly at high-severity but with some moderate-severity fire on the burn's edges. Moderate and high-severity fire killed tree canopies in ≥64% of the territory area (including nest areas) within 7 of the 20 territories, 50–64% of canopies within 5 territories, 25–50% of canopies within 3 territories, and 0–25% of canopies within 5 territories. None of the 7 territories losing tree canopies in >64% of the territory to moderate and high-severity burn in the Warm Fire were re-occupied by breeding goshawks in any of the 4 post-fire study years. Three of the 5 (60%) Warm Fire territories that lost canopies in 50–64% of their area to high-severity fire had active nests in the 4 post-fire study years (Table 3). Two pairs that laid eggs in post-fire years used nest areas that were partially burned by high-severity fire, and another 2 pairs moved 849 m and 1,740 m from burned portions of their territory to lay eggs in new unburned nest areas. Three of 3 (100%) territories that lost between 20–50% of their forests to moderate and high-severity fire had active nests in post-fire study years, and 3 of 5 (60%) territories that lost <20% of forests to moderate and high-severity fire, including various percentages of low-severity surface fire, had active nests in post-fire years (Table 3). We did not know if any breeding adult goshawks were killed by high-severity fire, but none of 3 banded breeders at 2 nests that were active during the Warm

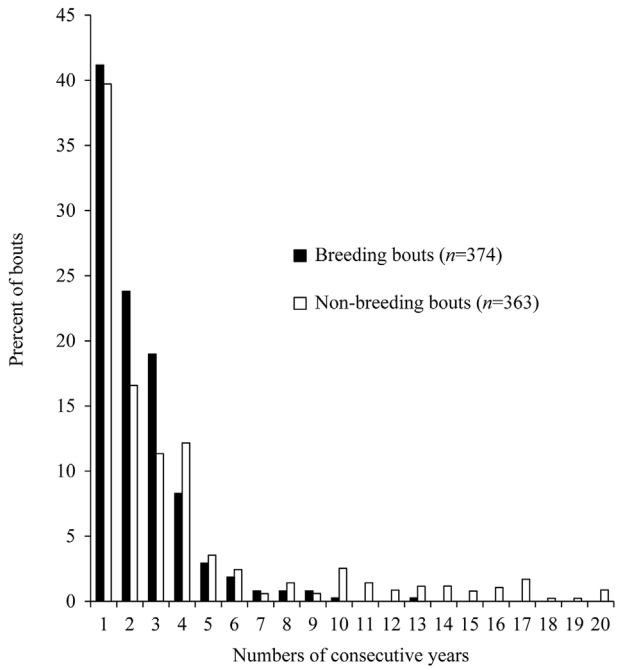

Figure 5. Percent of breeding and non-breeding bouts lasting a single year or various numbers of consecutive years on 124 goshawk territories (1 territory with 1 year of study not included), Kaibab Plateau, Arizona, USA, 1991–2010.

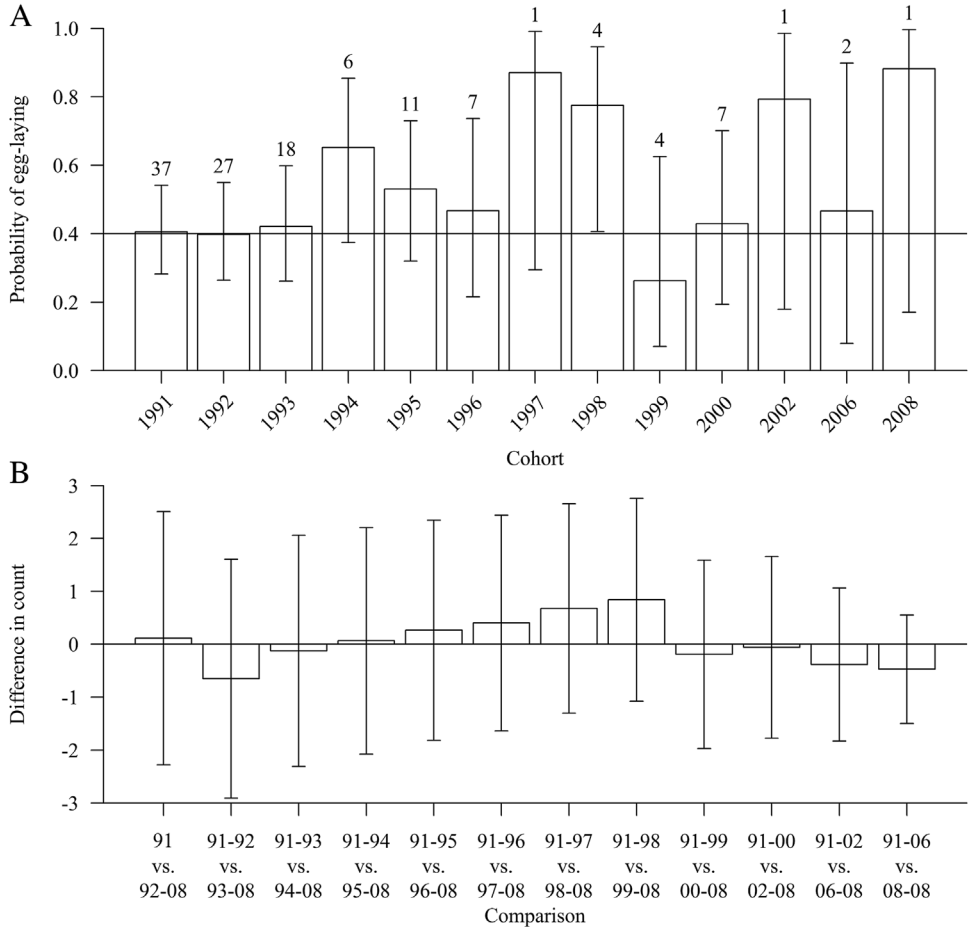

Figure 6. Hurdle model tests for differences in future probability of egg-laying and production of fledglings given egg-laying among cohorts of territories of goshawks discovered in succeeding years on the Kaibab Plateau, Arizona, USA. We did not include a 1-territory cohort discovered in 2010 because 2010 was the terminal study year and no new territories (cohorts) were discovered in 2001, 2003–2005, or 2007. A) Predicted probability of egg-laying on territories in each cohort subsequent to year of discovery (1991 cohort, probability of eggs in 1992–2010; 1992 cohort, probability of eggs 1993–2010; 1993 cohort, probability of eggs 1994–2010; and so on). Bars (and 95% CI) are predicted probabilities of egg laying. Numbers above cohort are numbers of territories in cohort. Horizontal line is the observed overall mean (0.40) portion of years with egg-laying on territories. B) Predicted differences in counts of fledglings produced by cohort comparison group (Poisson portion of hurdle model): 1991 versus 1992–2008; 1991–92 versus 1993–2008; 1991–93 versus 1994–2008, and so on. Bars (and 95% CI) are predicted differences in counts of fledglings.

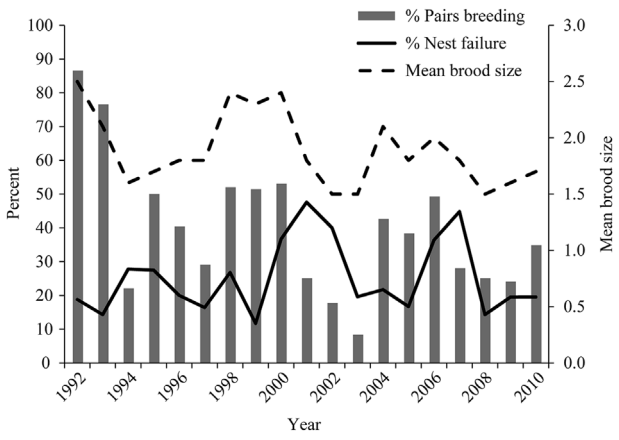

Figure 7. Temporal variation in percentage of goshawk territories in prior-year's cohort with breeding, mean brood size (count of nestlings at banding age), and percent of active nests failing to fledge ≥1 young on Kaibab Plateau, Arizona, 1992–2010.

Fire and lost >64% of their canopies were resighted in any post-fire year. Of 6 banded goshawks on 4 territories with active nests at the time of the Warm Fire that lost 20–64% of their canopies to high-severity fire, 3 were resighted as breeders in post-fire years, all but 1 on their same (pre-fire) territory. The overall post-fire breeding rate (35%, 18 of 52 years) on the 13 territories losing <64% of their canopies to high-severity fire was only slightly less than the overall 40% annual breeding rate on 121 territories monitored ≥9 years (see above). As an indicator of continued post-fire suitability of some territories for breeding not attributable to the fidelity of original breeders, recruitment of new breeders (turnovers) in the post-fire years occurred on 4 of the 6 territories that lost 39–58% of their canopies.

Forest type and management effects.—Our comparison of the density of breeding goshawks in the 3 forest types (ponderosa pine, mixed-conifer, spruce-fir dominated mixed-conifer) over 16 years (1995–2010) showed that the mean annual density of breeders was significantly higher in ponderosa pine ($Z = -3.82$, $P < 0.001$) and mixed-conifer ($Z = -4.37$, $P < 0.001$) than in spruce-fir dominated mixed-conifer, but there were no differences in the mean densities of breeders in ponderosa pine and mixed-conifer

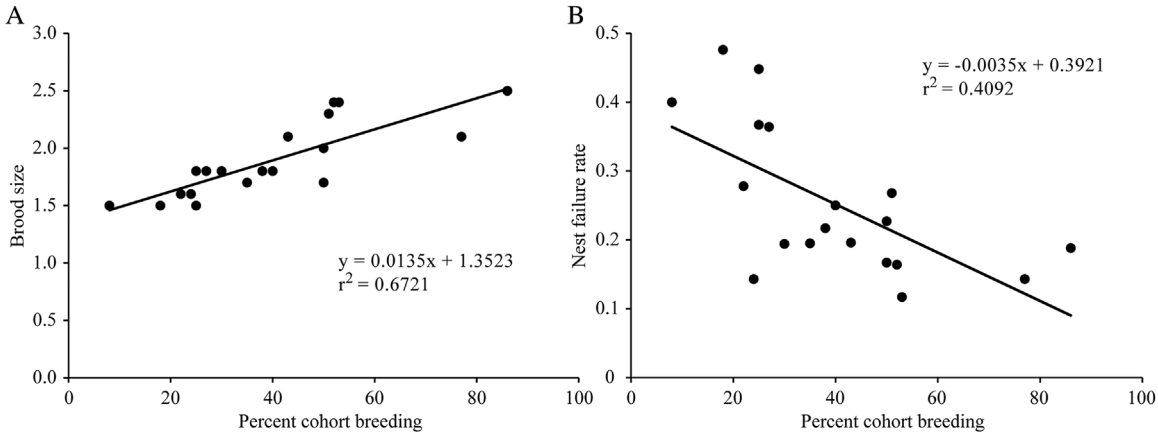

Figure 8. Co-variation of goshawk annual brood size (A) and annual nest failure rate (B) with percent of territories in prior-year's cohort breeding, Kaibab Plateau, Arizona, USA, 1992–2010.

($Z = 1.68$, $P = 0.21$; Fig. 9). Comparisons of the mean annual densities of breeders among the categories of breeding year quality were all significantly different (moderate to good, $Z = -4.61$, $P < 0.001$; poor to good, $Z = -8.80$, $P < 0.001$; poor to moderate, $Z = -4.95$, $P < 0.001$).

Although the range (min., max.) of distances between territory centroids was nearly identical in the differently managed NKRD and the GCNP, the mean distance between centroids was significantly less in the NKRD ($\bar{x} = 3.7$ km, SE = 0.07, median = 3.6, range = 1.2–8.2, $n = 107$ territories, 275 triangle legs) than in the GCNP ($\bar{x} = 4.5$ km, SE = 0.04, median = 4.2, range = 1.5–8.0, $n = 17$ territories, 29 triangle legs; $t = 3.63$, $P < 0.001$). The logistic regression model for comparing occupancy and productivity of territories in differently managed landscapes (NKRD and GCNP) was significant ($P = 0.007$), with territories in the NKRD having about 1.5 times the odds of being active compared to the GCNP. However, the difference in mean fledglings per active nests in 13 years in which there were ≥3 active nests in either area in a year ($n = 13$ yr; exclusive of 1991, 1994, 1997, 2001–2003, 2009) was not different in the 2 landscapes (NKRD, $\bar{x} = 1.6$ fledglings, SE = 0.04, $n = 767$ active nests; GCNP, $\bar{x} = 1.4$ fledglings, SE = 0.11, $n = 72$ active nests; $t = -1.36$, $P = 0.175$).

Table 3. Territory number, percent of territory burned by high-severity and low-severity fire, pre- and post-fire breeding status, and number of fledglings post-fire produced on 20 goshawk territories burned in the 8 June–4 July 2006 Warm Fire on the Kaibab Plateau, Arizona, USA.

			Warm Fire severity (% area)		2006		2007		2008		2009		2010	
Territory	Yr active pre-fire	Last yr active pre-fire	% high[a]	% low	Status	Fledged	Status	Fledged	Status	Fledged	Status	Fledged	Status	Fledged
93	1	1995[b]	100	0										
104	7	2006	100	0	active[c]	2								
85	1	1994[b]	99	0.6										
84	8	2005	96	0.9										
96	8	2006	94	3	active	1								
28	12	2005	75	7										
72	1	1993[b]	64	5										
13	10	2006	63	14	active	1			active	0[d]	occ[e]			
16	9	1999	59	9			occ							
30	9	2006	58	4	active	2	active	3	active	1				
123	3	2005	53	2							active	1		
34	3	1993[b]	52	5										
15	3	2000	49	23							active	1	active	1
83	9	2006	49	0	active	3			active	1	active	0	active	1
10	9	2006	39	16	active	1					active	2	occ	
65	11	2006	19	6	active	1	active	2	active	1	active	1	active	2
86	8	2005	13	15			active	0					active	2
94	8	2002	12	48										
108	8	2006	10	50	active	3	occ		active	0	occ		active	1
37	11	2006	0	51	active	3								

[a] Combination of high and moderate fire type and area.
[b] Territories last active >10 years before Warm Fire.
[c] Active nest (eggs laid).
[d] Nest failed, no young fledged.
[e] Occupied only (no eggs laid).

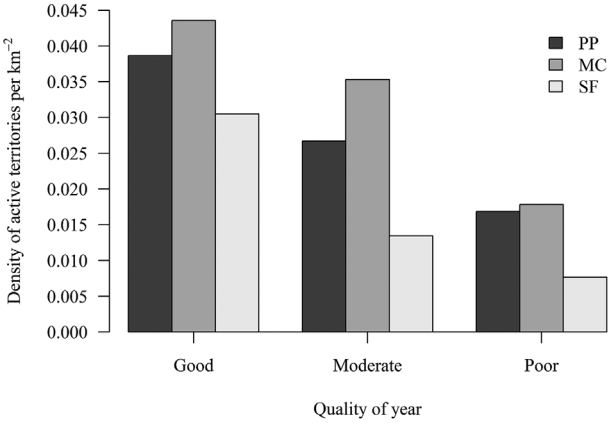

Figure 9. Density of active (eggs laid) goshawk territories in ponderosa pine (PP), mixed-conifer (MC), and spruce-fir dominated mixed-conifer (SF) forests in good (≥50% territories active), moderate (28–49% active), and poor (≤27% active) breeding years on the North Kaibab Ranger District, Arizona, USA, 1995–2010.

Precipitation effects.—The minimum AIC_c model relating precipitation to (Kaibab-wide) annual fledgling production included the breeding cycle (1 Jul–30 Jun) precipitation with a no-year lag and a 1-year lag (Table 4). Durbin–Watson statistics for all but the intercept-only model showed no autocorrelation ($P = 0.08$–0.97; null model $P = 0.05$), indicating a repeated-measures design was unnecessary. Given the model set considered, the top model had only modest evidence ($w_1 = 0.35$) supporting its use as the best approximating model. There were 3 models (out of the 8 candidate models considered) that defined our confidence set that best captured the goshawk productivity process. The ensemble prediction from this confidence set provided evidence ($\sum_{i=1}^{3} w_i = 0.73$) that precipitation in all 3 years (no lag, 1-yr lag, 2-yr lag) was associated with goshawk reproduction—although the evidence supporting inclusion of a 2-year lag was weaker compared to evidence in support of a 1-year lag effect.

Goodness-of-fit statistics provided further evidence supporting lagged precipitation effects. Root mean squared errors and mean absolute errors of the observed versus predicted values were lowest for the full model and the averaged model (Table 4). Plots of the predicted numbers of fledglings produced across the study area from the best and averaged models compared to the observed numbers of fledglings produced showed a good fit for most years (Fig. 10). The 1992 poor fit likely reflected an extrapolation error to the number of offspring for the entire breeding population from a sample of only 37 territories (35% of 144 territories) in the 1991 cohort. Lesser model fit in 1994, 2000, and 2008 may have resulted from local differences in precipitation at Fort Valley Experimental Forest and on the Kaibab Plateau or from variables not measured in this study (e.g., seasonal patterns of precipitation, incidence of prey epidemics).

Table 4. Model selection results for evaluating effects of total precipitation during the annual breeding cycle (ppt_l), where l indicates the annual lag, on the Kaibab-wide estimated young fledged (Y) by goshawks on the Kaibab Plateau, Arizona, USA. Models are ranked by corrected Akaike's Information Criterion (AIC_c). We also present the change (ΔAIC_c) in a model's AIC_c from the top model, the weight (w_i) of model i, and its number of parameters (K). The intercept-only $Y(.)$ and the ensemble prediction (model average) across the confidence model set (models 1–3) are shown for comparison.

					Model prediction error[a]	
Model[b]	AIC_c	ΔAIC_c	w_i	K	RMSE	MAE
1. $Y(ppt_0 + ppt_1)$	191.99	0.00	0.35	4	32.41	25.44
2. $Y(ppt_1)$	192.81	0.82	0.23	3	34.43	26.11
3. $Y(ppt_0 + ppt_1 + ppt_2)$	193.62	1.63	0.15	5	30.08	22.08
4. $Y(ppt_1 + ppt_2)$	194.47	2.48	0.10	4	34.73	27.53
5. $Y(ppt_0)$	194.92	2.92	0.08	3	36.35	31.29
6. $Y(ppt_0 + ppt_2)$	196.16	4.17	0.04	4	33.27	30.13
7. $Y(.)$	196.65	4.66	0.03	2	38.47	33.81
8. $Y(ppt_2)$	198.26	6.26	0.02	3	36.47	32.57
9. Model average[c]			0.73		30.49	23.72

[a] Root mean square error (RMSE) and mean absolute error (MAE) of model-predicted numbers of goshawk fledglings produced in all study area territories, using the log-proportion of known (i.e., studied) territories out of an estimated 144 total territories Kaibab-wide as an offset to account for annual variation in the number of known territories.

[b] Models are based on the aggregated 12-month total precipitation during the goshawk breeding season, 1 July–30 June, specified with current year (ppt_0), 1-year lag (ppt_1), and 2-year lag (ppt_2) effects.

[c] Model averaging over the full set of 8 models (Burnham and Anderson 2002).

Population Structure

We determined sex ratios for 772 nestlings from 376 broods in which all brood members were sexed at banding. The nestling sex ratio summed over 20 years (53% M; 410 M, 366 F) was not different from unity ($\chi^2 = 2.63$, $P = 2.49$). However, there were significant departures from unity in 3 of the 20 years; twice as many females as males were produced in 1996, whereas twice as many males were produced in 1999 and 2010 (Table 5). There was no evidence ($F_{11} = 0.82$, $P = 0.37$; 2-tailed $t_{22} = -0.29$, $P = 0.77$) that nestling sex ratio varied seasonally (e.g., more produced in early broods) and no relationship between sex ratio and food-rich versus food-poor habitats, which we estimated as good versus poor breeding years ($r^2 = 0.018$, $P = 0.58$).

Results of the GLIMMIX analysis into the year-to-year stability of age structures of 98 known age male and female breeding goshawks in each of the final 11 years of the study (2000–2010) showed that mean counts of individuals varied by

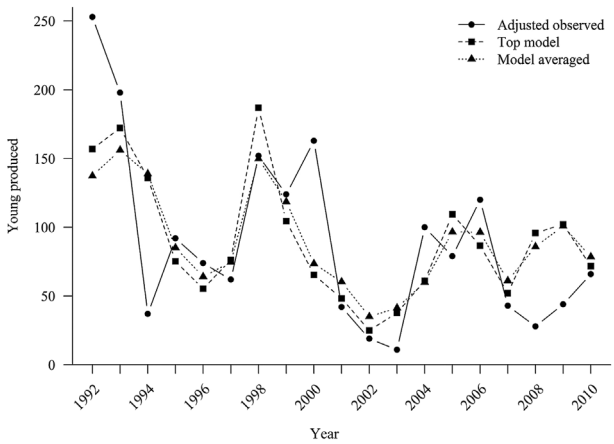

Figure 10. Comparison of number of adjusted observed goshawks fledged (observed + offset to account for the increasing effective sample through time) and total predicted young fledged from the fitted top model, which included current year precipitation and 1-year lag precipitation, and the model-averaged predicted young fledged on the Kaibab Plateau, Arizona, USA, 1992–2010.

Table 5. Sex ratio of goshawk nestlings at banding in 376 goshawk broods in which all brood members were sexed, Kaibab Plateau, Arizona, USA, 1991–2010. Asterisks indicate significant chi-square difference from unity with a female bias in 1996 and male bias in 1999 and 2010.

Yr	Broods	Nestlings	F	M	Ratio (proportion M)	Chi-square
1991	19	40	23	17	0.43	0.90
1992	7	19	10	9	0.47	0.05
1993	26	56	27	29	0.52	0.07
1994	12	18	9	9	0.50	0.00
1995	28	48	26	22	0.46	0.33
1996	23	39	26	13	0.33	4.33*
1997	19	35	15	20	0.57	0.71
1998	28	68	35	33	0.49	0.06
1999	27	65	23	42	0.65	5.55*
2000	38	91	41	50	0.55	0.89
2001	15	28	14	14	0.50	0.00
2002	9	13	4	9	0.69	1.92
2003	5	8	3	5	0.63	0.50
2004	18	42	19	23	0.55	0.38
2005	22	44	18	26	0.59	1.45
2006	32	71	36	35	0.49	0.01
2007	18	34	13	21	0.62	1.88
2008	8	14	8	6	0.43	0.29
2009	2	4	3	1	0.25	1.00
2010	20	39	13	26	0.67	4.33*
Total	376	776	366	410	0.53	2.49

age, sex, and year (main effects; $P \leq 0.002$). However, there were no significant interactions ($P \geq 0.81$) between sex and age, sex and year, and age and year (Table 6). Lack of an interaction between age and year ($P = 0.98$) indicated age distribution stability across years. Thus, we found no evidence that the predicted mean count of individuals by age varied over the 11 years (Fig. 11). Of the 98 known-age hawks, only a fraction (~18%; Table 2) breed in any given year.

Turnover, Recruitment, and Immigration

Of 1,321 opportunities (instances in which we observed breeders as an original or new breeder) to detect turnovers during 1992–2010, we recorded 265 (20%) turnovers (Table 7). As expected, the fewest turnovers occurred from 1 year to the next during consecutive years of egg-laying (18%; 108 turnovers in 609 opportunities) with female turnovers (18%; 64 of 364 opportunities) matching that of males (18% M; 44 of 245 opportunities). The frequency of turnovers increased with increasing consecutive years of non-breeding on territories. Turnover was 40% (23 of 57 opportunities) for males and 49% (41 of 83 opportunities) for females following a 1-year gap in breeding and 83% (10 of 12 opportunities) for males and 79% (19 of 24 opportunities) for females after 2-year gaps. Combined male and female turnovers following 3- and 4-year gaps was 69% (29 of 42 opportunities) and 91% (10 of 11 opportunities), respectively. Only 2 original breeders (1 M, 1 F on different territories) were the same following 5 consecutive years of non-breeding. A total of 57 (14 M, 36 F; 6 hawks moved ≥2 times) turnovers resulted from breeding dispersals of hawks banded on their original territories. Because of low detectability of non-breeders, we tallied turnovers in the year the new hawks were first detected as breeders. Nonetheless, new goshawks were occasionally observed in nest areas in the year before they first laid eggs. Despite our efforts, we missed 456 (26%; 456/1,777) opportunities (314 M, 142 F) to detect whether a turnover had occurred. Missed opportunities resulted from early nest failures (failed before resighting was completed), difficult-to-resight males, and a few nest discoveries at or after fledgling (too late to resight breeders).

On initial capture or resighting we considered all breeding goshawks, whether unbanded or banded as nestlings, to be recruits to local breeding population. The minimum age of recruitment for 146 (58 M, 88 F) known-age hawks was 2 years and there were no significant differences in ages of males and females at recruitment ($\chi^2_5 = 4.49$, $P = 0.48$). Of 447 recruits, 195 (44%) were male and 252 (56%) were female. Mean age at first breeding was 3.7 years for males (SE = 0.23, range = 2–9 yr, $n = 58$) and 3.5 years for females (SE = 0.17, range = 2–9 yr, $n = 88$). Fewer detections of male than female recruits was likely an artifact of lower detection probabilities of males versus females; mean annual probability of detection ($\hat{p}$) was 0.45 (range = 0.10–0.83) for males and 0.55 (range = 0.15–0.89) for females over 19 trapping occasions (see below). Interestingly, although the number of recruits detected in a year was constrained by the number of territories with breeders in that year (see below), the mean proportion of breeders that were new recruits tended to be relatively low in all but the best of breeding years (defined here as ≥50 active nests [see Table 1]) that followed poor breeding years (<50 active nests). In good breeding years, the proportion of breeders that were recruits was higher ($\bar{x} = 65\%$ recruits, range = 60–75%) than in poor years ($\bar{x} = 34\%$ recruits, range = 10–52; Fig. 12), most likely because of a progressive filling of vacancies in unoccupied territories by new breeders as breeding conditions improved. Of the 447 recruits we detected, 104 (23%) had been banded as nestlings on the study area and

Table 6. Fixed effects in general linear mixed model for testing stable age distributions of male and female goshawk breeders during the final 11 years (2000–2010) of the study on the Kaibab Plateau, Arizona, USA.

Effect	Treatment DF	Error DF	*F* value	*P* > *F*
Age	13	130	14.11	<0.001
Year	10	130	2.92	0.003
Sex	1	130	11.96	<0.001
Sex × age	13	130	0.64	0.81
Sex × year	10	130	0.40	0.95
Age × year	130	130	0.81	0.89

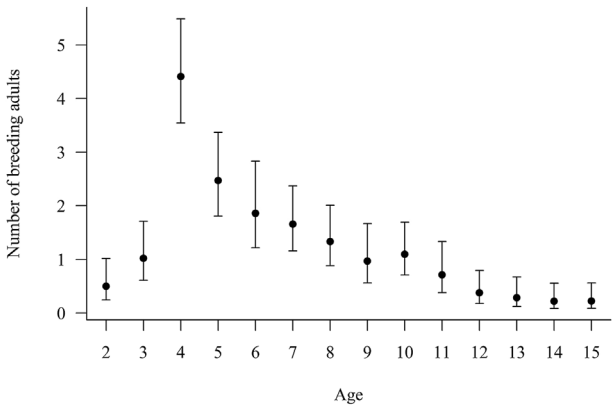

Figure 11. Predicted (least square means and 95% CI) average annual age distribution of 146 know-age goshawks (sexes combined) observed breeding on 308 occasions during the final 11 years (2000–2010) of study on the Kaibab Plateau, Arizona, USA.

Table 7. Number (%) of turnovers (replacements of prior breeders by new breeders) of goshawk males and females combined (tallied individually, not as pairs) and by sex between 2 consecutive years of breeding and following 1- to >6-year gaps in breeding on territories, Kaibab Plateau, Arizona, 1991–2010. Opportunities are numbers of occasions for each breeding sequence in which the identity (unbanded or banded) of prior hawks and their replacements were known.

			M		F		
Breeding sequence	**No. (%) occupied by same individual**	**No. (%) turnovers**	**No. (%) same**	**No. (%) turnovers**	**No. (%) same**	**No. (%) turnovers**	**Opportunities to detect turnover**
Consecutive yr	501 (82)	108 (18)	201 (40)	44 (41)	300 (60)	64 (59)	609
1-yr gap	76 (54)	64 (46)	34 (45)	23 (36)	42 (55)	41 (64)	140
2-yr gap	7 (19)	29 (81)	2 (29)	10 (34)	5 (71)	19 (66)	36
3-yr gap	13 (31)	29 (69)	5 (38)	12 (41)	8 (62)	17 (59)	42
4-yr gap	1 (9)	10 (91)	0 (0)	2 (20)	1 (100)	8 (80)	11
5-yr gap	2 (18)	9 (82)	1 (50)	4 (38)	1 (50)	5 (63)	11
>6-yr gap	0 (0)	16 (100)	0 (0)	5 (31)	0 (0)	11 (69)	16

343 (77%) were unbanded at first breeding. Thus, of 862 nestlings (M, 52%; F, 48%) banded in 1991–2008 (nestlings banded in 2009–2010 not included because of 2-yr-old minimum age of first breeding), the overall recruitment rate (104/862) was 0.12 (M = 0.05, $n = 45$; F = 0.07, $n = 59$). As expected, the number of detected recruits from each birth year was strongly related to the number of breeding pairs in that year (Fig. 13).

After adjusting for differences in detection probabilities, the numbers of *in situ* recruitments of locally born and banded male and female goshawks showed no differences between the sexes (M, 22%; 100 recruited, 350 not recruited; F, 26%, 107 recruited, 305 not recruited; $\chi^2_1 = 1.66$, $P = 0.198$). The unadjusted difference (M = 10%, 45 recruited; F = 14%, 59 recruited) was only marginally significant ($\chi^2_1 = 3.78$, $P = 0.052$). Thus, locally born males and females were equally philopatric to the Kaibab. Further, for locally born hawks there was no difference in natal dispersal distance (distance from natal nest to first breeding nest) of males ($\bar{x} = 16$ km, SE = 1.51, medium = 13.7, range 3–58, $n = 45$) and females ($\bar{x} = 18$ km, SE = 1.35, medium = 16.9, range 0.1–46, $n = 59$; $t = 0.99$, $P = 0.32$). Interestingly, 1 female settled in her natal territory and bred with an unrelated male.

The ratio of banded (locally born) recruits to unbanded recruits, some assumed to be immigrants, increased to an asymptote circa 1998 (Fig. 14). We estimated immigration rate using the ratio of the number of locally born recruits (banded + estimate of numbers of locally born unbanded hawks that recruited) to unbanded recruits each year during 1998–2010. From 1998 to 2010, we detected 235 recruits (39% M, 61% F), including 138 (59%) unbanded (36% M, 64% F) and 97 (41%) banded recruits (43% M, 57% F). Because of the 2-year minimum age of recruitment, we estimated the annual number of local-born hawks available for recruitment in 1998–2010 as the number of locally born fledglings produced at studied territories in 1996–2008 to account for the 2 years between fledgling and recruitment (first breeding). Thus, of 835 fledglings produced at studied nests from 1996 to 2008, 643 (77%) were banded and 192 (23%) were unbanded (Table 8). Of the 643 banded nestlings, 81 were recruited in 1998–2010 at a mean annual recruitment rate of 0.126 (range = 0–0.278; Table 7). Thus, an estimated 26 of 192 unbanded fledglings from missed nests were likely to have recruited at a mean rate of 2.0 recruits/year (SE = 0.08, range = 0–6 recruits, $n = 13$ yr). We estimated 107 locally born recruits (26 unbanded + 81 banded), which indicated that about 46% (107/235) of recruits were locally born and 54% were immigrants (Table 8).

Adult Survival

We trapped 447 breeding goshawks during our 20-year study, of which 104 (45 M, 59 F) had been locally banded as nestlings (known-age hawks) and recruited. Of the 104 recruits, 23 (8 M, 15 F) were 2 years old, 22 (11 M, 11 F) were 3 years old, and 59 (26 M, 33 F) were ≥4 years old on first capture as breeders. In addition, 42 trapped breeders (initially unbanded) were aged on first capture as 2-year-old (20; 7 M, 13 F) and 3-year-old (22; 6 M, 16 F) subadults on the basis of their plumage characteristics.

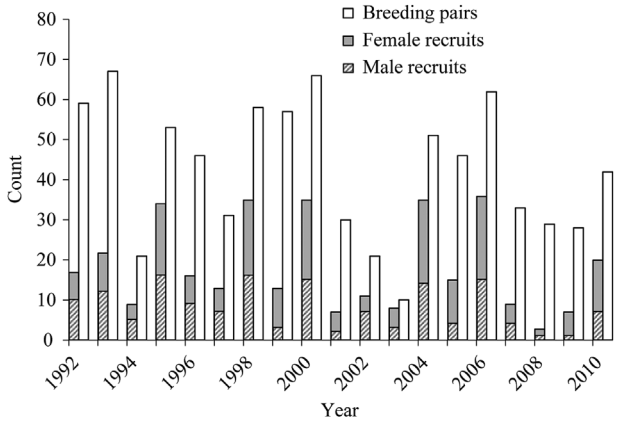

Figure 12. Annual count of territories with breeding goshawks and counts of male and female recruits on the Kaibab Plateau, Arizona, USA, 1992–2010.

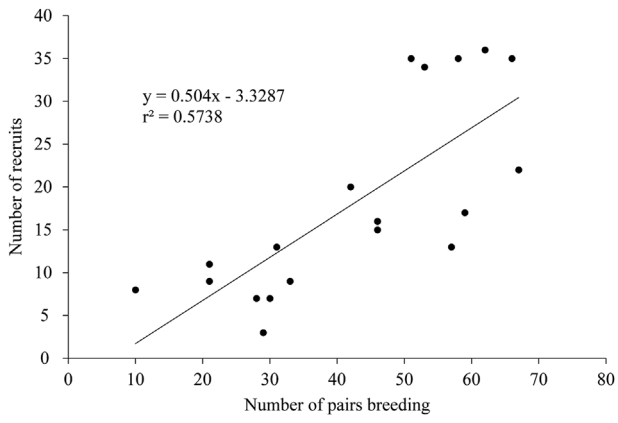

Figure 13. Linear relationship between numbers of territories with breeding goshawks in a year and numbers of new recruits on the Kaibab Plateau, Arizona, USA, 1992–2010.

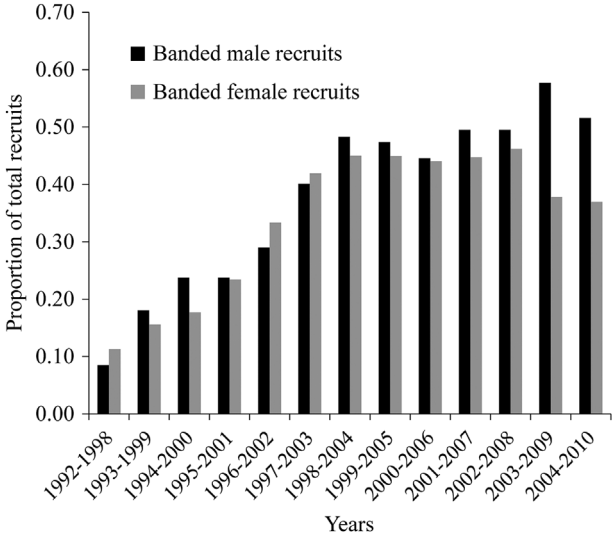

Figure 14. Moving window averages (7-yr) of annual proportions of locally born and banded male and female recruits to the breeding population of goshawks on the Kaibab Plateau, Arizona, USA, 1992–2010.

The remainder, 301 (139 M, 162 F) were unbanded, in full-adult plumage, and aged as ≥4 years old. We recorded 678 recaptures (including resightings) of the 447 breeders, approximately 1.5 times the number of initial captures. Mean lifespan of known-age hawks was 6.9 years for both sexes (M, SE = 0.38, range = 2–13 yr, $n = 58$; F, SE = 0.30, range = 3–13 yr, $n = 88$) and mean minimum lifespan of breeders aged ≥4 years based on plumage was 6.5 years for both sexes (males, SE = 0.21, range 4–15 yr, $n = 137$; females, SE = 0.19, range 4–15 yr, $n = 162$).

Using these capture–recapture data, the goodness-of-fit tests in Program RELEASE (Burnham et al. 1987) in the global model $\{\varphi(s \times t)\ p(s \times t)\}$ suggested no overdispersion ($\chi^2_{98} = 75.5$, $P = 0.955$, $\hat{c} = 0.771$), and the median $\hat{c}$ procedure in MARK used with the minimum AIC_c model that did not include age produced 3 estimates of $\hat{c} = 0.980$, 0.992, and 0.906. Thus, we concluded that there was no detectable lack of fit or extra-binomial variation present for analyses. Our estimation of apparent survival tested *a priori* hypotheses that survival differed between sexes, differed with age (i.e., initial increase followed by senescence), and differed with fledgling rate (i.e., reproduction lowers survival). Initial model selection results supported models $\{\varphi(.)\ p(s + t)\}$ and $\{\varphi(s)\ p(s + t)\}$ as the minimum AIC_c models (Table 9; models 12 and 13). We then added age and fledging rate to these 2 models. The model with the sex effect on φ received less weight than the model without sex effect, and the model with an interaction between sex and age $\{\varphi(s \times age^2)\ p(s + t)\}$ (model 7) was 2.117 AIC_c units larger than a model without the interaction (model 3; Table 9). Thus, there was only weak evidence for a difference in survival by sex or a difference in how survival changes with age for the 2 sexes. Because models with age incorporated as a quadratic effect produced smaller AIC_c values than models with age as only a linear effect, only model $\{\varphi(age^2)\ p(s + t)\}$ (model 3) was further considered. Average age of goshawks at first detection was 3.9 years old when apparent survival was estimated at 0.77 for both sexes. This rate was just slightly less than the peak survival of 0.78 at age 5, after which survival declined steadily to 0.69 by age 10, and reached an estimable survival of 0.34 at age 15, the oldest age reached by hawks of both sexes (Fig. 15).

Detection rates for females (0.55) were on average 0.10 greater than those for males (0.45; log-odds ratio of female p from the minimum AIC_c model = 1.631, SE = 0.274). Mean annual fledging rate did not improve age-specific survival models with age^2 in them but did explain 17.4% ($P = 0.086$) of the deviance in

Table 8. Proportion of recruits (replacement of a breeding goshawk on a territory by another) that were either immigrants or born on the study area in 1998–2010 on the Kaibab Plateau, Arizona, USA. A known number of fledglings were not banded (missed) because of logistical constraints. To account for locally born but unbanded (missed) recruits, we adjusted counts of banded recruits detected on studied territories upward by an estimated annual number of missed fledglings that likely recruited based on the proportion of banded fledglings that recruited. We estimated 46% (107/235) of recruits on studied territories were locally born and 54% were immigrants.

Year	Fledglings banded on study area in yr t	Banded fledglings eventually recruited	Proportion of banded fledglings recruited	Fledglings from studied territories not banded[a]	Estimated unbanded fledglings recruited in yr $t + 2$[b]	Estimated total fledglings recruited from studied territories[c]	Observed total banded and unbanded recruits on studied territories
1996	41	1	0.024	18			
1997	36	10	0.28	9			
1998	85	14	0.165	34	0.44	1.44	35
1999	76	16	0.21	20	2.50	12.50	13
2000	111	15	0.14	28	5.60	19.60	34
2001	31	1	0.03	4	4.21	20.21	7
2002	16	0	0.00	0	3.78	18.78	11
2003	9	1	0.11	0	0.13	1.13	8
2004	52	9	0.17	32	0.00	0.00	38
2005	53	7	0.13	13	0.00	1.00	15
2006	78	4	0.05	27	5.54	14.54	37
2007	36	2	0.06	2	1.72	8.72	7
2008	19	1	0.05	5	1.38	5.38	3
2009					0.11	2.11	7
2010					0.26	1.26	20
Total	643	81		192	25.67	107	235

[a] Number of fledglings produced and counted on studied territories in year t but not banded because of several constraints.
[b] Estimated number of locally born (in year t) but unbanded fledglings recruited (in year $t + 2$ because of minimum 2-yr age of recruitment) into the breeding population.
[c] Sum of banded fledglings in year t that eventually recruited plus the estimated number of unbanded fledglings that recruited from studied territories.

Table 9. Model selection results for evaluating age effects on survival with Cormack–Jolly–Seber models for male and female goshawks on the Kaibab Plateau, Arizona, 1991–2010. Model naming conventions follow Lebreton et al. (1992), where φ is survival, t is time, s is sex, and p is detection probability. Models are ranked by minimum corrected Akaike's Information Criterion (AIC_c) values (Burnham and Anderson 2002). Also reported are changes (ΔAIC_c) in AIC_c from the top model, the weight (w_i) of model i, the number of parameters (K) in the model, and the model's likelihood (L).

Model	AIC_c	ΔAIC_c	w_i	K	−2log(L)
1. {φ(age^2) p(s + t)}	2,218.13	0.00	0.226	23	2,170.98
2. {φ(age^2 + fledge rate) p(s + t)}	2,218.28	0.15	0.210	24	2,169.02
3. {φ(s + age^2) p(s + t)}	2,218.62	0.48	0.178	24	2,169.36
4. {φ(s + age^2 + fledge rate) p(s + t)}	2,218.74	0.61	0.167	25	2,167.38
5. {φ(s + age + fledge rate) p(s + t)}	2,220.37	2.23	0.074	24	2,171.11
6. {φ(s + age) p(s + t)}	2,220.38	2.25	0.074	23	2,173.23
7. {φ(s × age^2) p(s + t)}	2,220.73	2.60	0.062	26	2,167.26
8. {φ(age) p(s + t)}	2,224.82	6.68	0.008	22	2,179.76
9. {φ(fledge rate) p(s + t)}	2,234.62	16.48	0.000	22	2,189.56
10. {φ(s + fledge rate) p(s + t)}	2,234.79	16.65	0.000	23	2,187.63
11. {φ(s × fledge rate) p(s + t)}	2,236.82	18.68	0.000	24	2,187.56
12. {φ(.) p(s + t)}	2,236.88	18.75	0.000	21	2,193.92
13. {φ(s) p(s + t)}	2,237.05	18.91	0.000	22	2,191.99
14. {φ(s) p(t)}	2,240.55	22.42	0.000	21	2,197.59
15. {φ(.) p(t)}	2,242.51	24.38	0.000	20	2,201.64
16. {φ(t) p(s + t)}	2,247.96	29.83	0.000	38	2,168.81
17. {φ(s + t) p(s + t)}	2,247.99	29.86	0.000	39	2,166.67
18. {φ(s + t) p(t)}	2,251.49	33.36	0.000	38	2,172.34
19. {φ(t) p(t)}	2,253.57	35.43	0.000	37	2,176.58
20. {φ(.) p(s × t)}	2,259.34	41.21	0.000	39	2,178.02
21. {φ(s) p(s × t)}	2,260.01	41.88	0.000	40	2,176.52
22. {φ(t) p(s × t)}	2,271.57	53.44	0.000	56	2,152.65
23. {φ(s + t) p(s × t)}	2,271.72	53.58	0.000	57	2,150.54
24. {φ(age^2) p(s + fledge rate)}	2,272.59	54.46	0.000	6	2,260.51
25. {φ(s × t) p(s + t)}	2,275.15	57.02	0.000	57	2,153.97
26. {φ(s × t) p(t)}	2,276.04	57.90	0.000	56	2,157.11
27. {φ(.) p(s + fledge rate)}	2,288.56	70.43	0.000	4	2,280.52
28. {φ(fledge rate) p(s + fledge rate)}	2,289.89	71.75	0.000	5	2,279.83
29. {φ(s × t) p(s × t)}	2,299.82	81.69	0.000	74	2,139.54
30. {φ(s + t) p(s)}	2,400.02	181.88	0.000	22	2,354.96
31. {φ(t) p(s)}	2,400.68	182.54	0.000	21	2,357.71
32. {φ(s + t) p(.)}	2,402.16	184.03	0.000	21	2,359.20
33. {φ(t) p(.)}	2,405.11	186.98	0.000	20	2,364.24
34. {φ(s) p(s)}	2,419.09	200.96	0.000	4	2,411.05
35. {φ(.) p(s)}	2,419.32	201.18	0.000	3	2,413.29
36. {φ(s) p(.)}	2,420.95	202.82	0.000	3	2,414.93
37. {φ(.) p(.)}	2,423.36	205.23	0.000	2	2,419.35
38. {φ(s × t) p(s)}	2,427.10	208.97	0.000	40	2,343.60
39. {φ(s × t) p(.)}	2,427.62	209.48	0.000	39	2,346.29

survival explained by time (Table 10). Nonetheless, as expected, fledging rate did explain a significant proportion of the temporal variation in p (60.5%, $P < 0.001$; Table 11) given the global model φ(.) p(s + t). However, AIC_c was minimized in the p(s + t) models versus the p(s + fledge rate) models, suggesting that important time variation in detection probability was not explained by fledging rate.

Rate of Population Change

The minimum AIC_c model from the initial set of 128 considered was {φ(s) p(s + t) γ(t)}, with 43% of the overall model weight. When we added fledging rate to this model, the model improved by 2.30 AIC_c units, with fledging rate explaining 17.6% ($P = 0.083$; Tables 12 and 13) of the temporal deviance in φ given the p(s + t) γ(t) model. In contrast, the model {φ(s) p(s + t) γ(fledge rate)} was 1.769 AIC_c units larger than the {φ(s) p(s + t) γ(.)} model, demonstrating that fledging rate did not improve estimates of λ (Appendix B). Because the estimates of λ were almost identical between the top models, we used the $\log(\hat{\lambda})$ from model {φ(s) p(s + t) γ(t)} in the random effects analysis. We analyzed the $\log(\hat{\lambda})$ sequence for females and males separately for this model because the φ(s) effect causes the values of $\log(\hat{\lambda})$ to differ by a constant on the logit scale for the 2 sexes. Thus, male and female estimates were not independent. We estimated the mean $\log(\hat{\lambda})$ as −0.0410 (SE = 0.0429) for females and −0.0811 (SE = 0.0436) for males, giving annual λ values of 0.960 (SE = 0.041) and 0.922 (SE = 0.040) for females and males, respectively. Both sequences of $\log(\hat{\lambda})$ gave identical estimates of the process standard deviation as 0.162 (95% CI = 0.110–0.267), which is expected given that the difference between the 2 sequences is just an additive constant on the logit scale of survival. The 16 $\log(\hat{\lambda})$ values for the males and females each (Table 14) produced contrasting results when sampled with replacement to produce 20-year trajectories (Fig. 16). Females have a 13.4% chance of the population growing when projected for 20 years, whereas males have only a 1.0% chance.

DISCUSSION

Our long-term study, which incorporated intensive monitoring at the nest-, territory-, and landscape-scales combined with mark–recapture of multiple goshawk generations, produced the

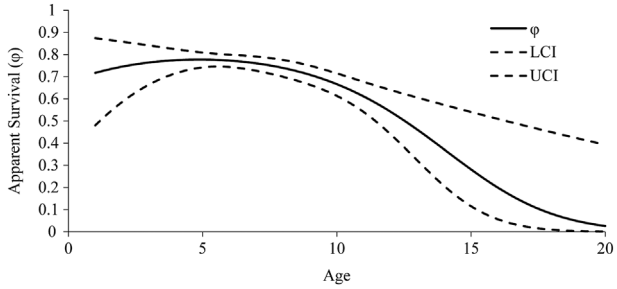

Figure 15. Apparent survival (φ) with lower (LCI) and upper (UCI) 95% confidence intervals versus age for goshawks (sexes combined) on the Kaibab Plateau, Arizona, USA, 1991–2010. We estimated apparent survival of goshawks with a Cormack–Jolly–Seber model that modeled survival as a quadratic effect of age and detection probability as linear effect of sex and time with a logit link function.

most robust and reliable estimates of goshawk vital rates yet published for the species. From a demography perspective, our study benefited by the inclusion of all tall-conifer forest habitat (exclude some pinyon-juniper woodlands) on the Kaibab Plateau, a large forested island surrounded by desert scrubland. Benefits included study boundaries defined by biological criteria where edge-mediated habitat effects such as a species' abundance and productivity near natural edges can be studied; reduction of confounding interactions of individuals across study boundaries as may occur in studies embedded in continuous forest; and an ability to assess long-distance (i.e., patch to patch) immigration on a species' demography. Application of our methods in a near-census (87%) of a population in an insular habitat allowed estimation of immigrant recruitment and documentation of the effects of low- and high-severity fire on territory occupancy and reproduction by goshawks. It also provided unique opportunities to evaluate long-term effects of forest management on the demography of a large breeding population of goshawks. We specifically documented the distribution, territory occupancy, and productivity of breeding goshawks in 2 differently managed landscapes, one with century-long suppression of fire (GCNP) and the other with a similar period of fire suppression combined with more than a half-century of tree harvests (NKRD). Finally, because our long-term study included multiple ENSO El Niño–La Niña precipitation cycles, we could investigate relationships between inter-annual variations in precipitation and goshawk reproduction.

Given that forest types on the Kaibab Plateau represent a restricted range of the forest types occupied by goshawks in North America and that forests there were under strong ENSO influences, we caution that statistical inferences drawn from our study can be made only to the sample of marked and recaptured individuals on the Kaibab Plateau. Nonetheless, because of similar vegetation composition and structure, faunal communities, and food webs (Reynolds et al. 2006), we believe our results are generalizable to other ponderosa pine and mixed-conifer forests throughout the Southwestern United States.

Table 10. Analysis of deviance table for the temporal covariate, fledging rate, used to model apparent survival (φ) of goshawks on the Kaibab Plateau, Arizona, 1991–2010. The global model used in the survival analysis was $\{\varphi(t)\ p(s+t)\}$, the constant model was $\{\varphi(.)\ p(s+t)\}$, and the covariate model was $\{\varphi(\text{fledge rate})\ p(s+t)\}$, where φ is survival, t is time, s is sex, and p is detection probability. Fledging rate explained 17.4% (4.358/25.109) of the temporal deviance in φ given the $p(s+t)$ model.

Source	Df	Deviance	$\bar{x}$ deviance	F	P
Uncorrected total	38	2,193.915			
Grand mean	21	2,168.806			
Corrected total	17	25.109			
Total covariate	1	4.358	4.358	3.3604	0.0855
Error	16	20.751	1.297		

Table 11. Analysis of deviance table for the temporal covariate, fledging rate, used to model detection probability (p) of goshawks on the Kaibab Plateau, Arizona, 1991–2010. The global model used in this analysis was $\{\varphi(.)\ p(s+t)\}$, the constant model was $\{\varphi(.)\ p(s)\}$, and the covariate model was $\{\varphi(.)\ p(s+\text{Fledge rate})\}$, where φ is survival, t is time, s is sex, and p is detection probability. Fledging rate explained 60.5% (132.771/219.376) of the temporal deviance in p given the φ(.) model.

Source	Df	Deviance	$\bar{x}$ deviance	F	P
Uncorrected total	21	2,413.291			
Grand mean	3	2,193.915			
Corrected total	18	219.376			
Total covariate	1	132.771	132.771	26.0622	<0.0001
Error	17	86.605	5.094		

Reproduction

Temporal and spatial variation.—The predominant demographic feature of the goshawk population on the Kaibab Plateau was large temporal variation in reproduction (e.g., 8–87% of territories with breeders in a year). Interannual variation in frequency of egg-laying on the Kaibab Plateau was associated with interannual variation in goshawk prey abundance (Salafsky et al. 2005, 2007); in years of low prey abundance, few pairs laid eggs, broods were smaller, and nest failures were more frequent than in years with high prey abundance and when more pairs laid eggs. Clutch sizes increasing with high, and decreasing with low, food availability has been reported in other goshawk populations (Kenward 2006) and in birds in general (Newton 1998*b*). On the Kaibab Plateau, the annual coefficient of variation in proportions of territories with eggs (CV = 49.6) exceeded the coefficients of variation in percent of nest failures (CV = 42.5) and brood sizes (CV = 17.2), suggesting food availability to meet the energetic demands for breeding had a greater limiting effect on a hawk's ability (or decision) to produce a clutch than to raise a brood once

Table 12. Top 8 models accounting for at least 1% of corrected Akaike's Information Criterion (AIC_c) weights (w_i) from Pradel (1996) seniority models for 5 combinations (., s, t, s + t, and s × t) of sex (s) and time (t) for models of apparent survival (φ), detection probability (p), and seniority (γ) for breeding male and female goshawks on the Kaibab Plateau, Arizona, USA, 1991–2010. We examined the effect of fledging rate (fledge rate) in 3 models (2 with apparent survival; 1 with seniority). Models are ranked by minimum AIC_c values (Burnham and Anderson 2002) across 128 models. Also reported are changes (ΔAIC_c) in AIC_c from the top model, the weight (w_i) of model i, the number of parameters (K) in the model, and the model's likelihood (L). Full list of model selection results are presented in Appendix B.

Model	AIC_c	ΔAIC_c	w_i	K	−2log(L)
1. $\{\varphi(s+\text{fledge rate})\ p(s+t)\ \gamma(t)\}$	4,761.00	0.00	0.553	42	4,673.311
2. $\{\varphi(s)\ p(s+t)\ \gamma(t)\}$	4,763.30	2.30	0.175	41	4,677.787
3. $\{\varphi(s)\ p(s+t)\ \gamma(s+t)\}$	4,765.08	4.08	0.072	42	4,677.388
4. $\{\varphi(s)\ p(t)\ \gamma(t)\}$	4,765.79	4.79	0.050	40	4,682.450
5. $\{\varphi(.)\ p(s+t)\ \gamma(s+t)\}$	4,766.09	5.09	0.043	41	4,680.574
6. $\{\varphi(\text{fledge rate})\ p(s+t)\ \gamma(t)\}$	4,766.27	5.27	0.040	41	4,680.760
7. $\{\varphi(s)\ p(t)\ \gamma(s+t)\}$	4,766.30	5.30	0.039	41	4,680.788
8. $\{\varphi(.)\ p(s+t)\ \gamma(t)\}$	4,768.41	7.41	0.014	40	4,685.063

Table 13. Analysis of deviance table for the temporal covariate, fledging rate, used to model apparent survival (φ) in the Pradel analysis of goshawks on the Kaibab Plateau, Arizona, 1991–2010. The global model used in the Pradel was $\{\varphi(s+t)\ p(s+t)\ \gamma(t)\}$, the constant model was $\{\varphi(s)\ p(s+t)\ \gamma(t)\}$, and the covariate model was $\{\varphi(s+\text{fledge rate})\ p(s+t)\ \gamma(t)\}$, where φ is survival, t is time, s is sex, p is detection probability, and γ is seniority. Fledging rate explained 17.6% (4.477/25.385) of the temporal deviance in φ given the $p(s+t)\ \gamma(t)$ model.

Source	Df	Deviance	$\bar{x}$ deviance	*F*	*P*
Uncorrected total	58	838.200			
Grand mean	41	812.815			
Corrected total	17	25.385			
Total covariate	1	4.477	4.477	3.4258	0.0827
Error	16	20.908	1.307		

Table 14. Maximum likelihood and shrunk estimates of log(λ) (where λ is the annual rate of population change) for male and female goshawks on the Kaibab Plateau, Arizona, 1994–2009. Maximum likelihood estimates are denoted with carets, whereas the shrunk estimates from the random effects analysis are denoted with tildes.

Sex	Yr	$\log(\hat{\lambda})$	SE $[\log(\hat{\lambda})]$	$\log(\tilde{\lambda})$	SE $[\log(\tilde{\lambda})]$
F	1994	0.125	0.249	0.043	0.160
	1995	−0.286	0.018	−0.279	0.019
	1996	−0.245	0.116	−0.192	0.106
	1997	0.094	0.099	0.066	0.087
	1998	−0.149	0.058	−0.133	0.056
	1999	0.191	0.078	0.168	0.074
	2000	−0.149	0.079	−0.121	0.075
	2001	0.117	0.160	0.097	0.109
	2002	0.085	0.294	0.084	0.123
	2003	0.091	0.269	0.086	0.119
	2004	−0.286	0.018	−0.279	0.019
	2005	0.233	0.101	0.195	0.092
	2006	−0.137	0.083	−0.111	0.077
	2007	−0.286	0.018	−0.279	0.019
	2008	−0.034	0.130	−0.020	0.098
	2009	0.080	0.149	0.054	0.110
M	1994	0.084	0.249	0.003	0.160
	1995	−0.326	0.020	−0.319	0.021
	1996	−0.286	0.117	−0.232	0.106
	1997	0.054	0.099	0.026	0.087
	1998	−0.189	0.058	−0.173	0.056
	1999	0.151	0.078	0.128	0.074
	2000	−0.189	0.079	−0.162	0.075
	2001	0.077	0.160	0.057	0.109
	2002	0.045	0.294	0.044	0.123
	2003	0.051	0.269	0.046	0.119
	2004	−0.326	0.020	−0.319	0.021
	2005	0.192	0.101	0.155	0.092
	2006	−0.177	0.084	−0.151	0.078
	2007	−0.326	0.020	−0.319	0.021
	2008	−0.074	0.131	−0.060	0.098
	2009	0.040	0.150	0.014	0.110

eggs were laid. Insufficient food in the pre-lay period may prevent females from attaining physiological conditions necessary for clutch production and, by forcing males to hunt more, reducing opportunities for fertilizing eggs. If food deprivation continues, females may interrupt incubation to hunt. Tellingly, the majority of nest failures in our study occurred during incubation and many nests, especially failed nests, commonly had infertile eggs or eggs with dead embryos.

Extensive temporal variation in breeding led to variable year-to-year detection probabilities (probability of capture and resight) of breeding goshawks because we were unable to capture or resight non-breeders. Detectability was also reduced by frequent year-to-year movements of breeders among alternate nests, requiring additional survey effort. Annually, 50–75% of egg-laying goshawks had moved to alternate nests, some of which were widely dispersed (max. inter-nest distance = 2,426 m) within a territory (Reynolds et al. 2005).

Final density of breeding territories on the NKRD (8.4/100 km^2) always exceeded the annual density of active nests (range = 0.8–4.8 nests/100 km^2), representing a 6-fold variation in density. Although the mean annual density of NKRD active nests (2.9 breeders/100 km^2) was within the range of mean densities of active nests reported for goshawks across North America, the median annual density of breeders (3.1/100 km^2) was somewhat lower than the among-study median density of breeders (3.4/100 km^2) in both America and Europe (Kenward 2006). Spatial variation in breeding manifested as differences in fledgling production territory to territory and in densities of breeders among forest types. Goshawks are long-lived and the majority of males and females showed lifetime fidelity to their territories. As a consequence, it was difficult to partition spatial from individual effects (R. T. Reynolds, unpublished data). Nevertheless, temporal variation explained more of total variation than did territory-to-territory variation, but these sources combined explained only 13% of total variation.

Fire, forest type, and management effects.—The effects of high-severity, crown-killing fire on goshawk reproduction depended on the proportion of a territory that burned. Territories losing ≥64% of forest cover to moderate- and high-severity fire were not re-occupied by breeders during our study, whereas territories losing <64% of forest cover to fire had similar post-fire productivity as unburned territories. Post-fire breeder re-occupancy of partially burned territories appeared dependent on whether at least 1 alternate nest area within the territory escaped high-severity fire; some pairs reused unburned or partially burned nest areas while others moved up to 1.7 km to unburned nest areas. The long-term effects of these high-severity fires on territory occupancy and reproduction by goshawks were unknown. Prey counts conducted for 4 years post-Warm Fire showed that northern flickers (*Colaptes auratus*), hairy woodpeckers (*Picoides villosus*), and chipmunks (*Tamias* spp.) were as or more abundant in burned areas compared to areas not burned. These species may have been important in goshawk breeding energetics in areas burned by high-severity fire, but the extent to which goshawks hunted in killed forests was unknown (Lambert 2015). Low-severity surface fire in territories and in active nest areas had no detectable effect on reproduction in the year of the fire or in subsequent study years.

Annual densities of breeders were consistently higher in ponderosa pine and mixed-conifer than in spruce-fir dominated mixed-conifer forests, regardless of breeding-season quality. Different breeding densities likely reflected changing species composition and abundance (available biomass) in suites of prey as the composition of vegetation and tree densities changed with increasing elevation. Lagomorphs (hares, rabbits), ground squirrel, and gallinaceous birds are linked to herbaceous and shrub communities, which are typically more ubiquitous and productive in more open (lower elevation) forests. Consequently, the combined abundance of these larger more profitable prey was likely greater in ponderosa pine and mixed-conifer forests

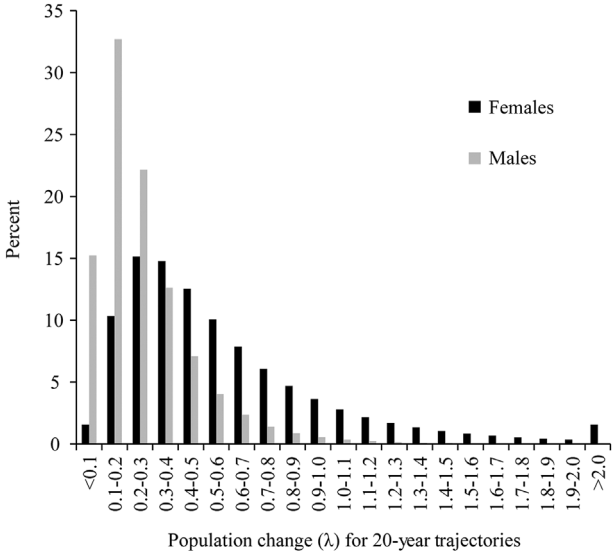

Figure 16. Distribution of population change (λ) over a hypothetical 20-year period for breeding male and female goshawks on the Kaibab Plateau, Arizona, USA, 1991–2010. We derived the distribution of λ separately for males and females from maximum likelihood estimates of log (λ) in the random effects procedure of Program MARK. We then used shrunk estimates in 10,000,000 iterations of randomly selecting (with replacement) 20 values from the set of $log(\hat{\lambda})$ and summing the 20 values to obtain the population level at the end of the 20-year period. We converted the frequency, by sex, of binned λ values to percent of 10,000,000 realizations.

and least common in spruce-fir dominated forests. Added to these species is the Kaibab squirrel (*Sciurus aberti kaibabensis*), a large tree squirrel whose ecology is closely tied to ponderosa pine and whose density decreases with decreasing preponderance of ponderosa pine trees with increasing elevation within the mixed-conifer type (Hall 1981, Dodd et al. 2003). Interestingly, the red squirrel (*Tamiasciurus hudsonicus*), which occurs rarely in ponderosa pine forests but is typically abundant in mixed-conifer forests, adds an additional tree squirrel to the suite of prey in this forest type. The combination of these 2 tree squirrels plus other large-bodied herbaceous and shrub-occupying prey likely accounts for the consistently higher breeding density of Kaibab goshawks in the mixed-conifer type through poor to good breeding years (Fig. 9).

The effects of tree cutting on goshawk populations have been a conservation concern across the species' Holarctic range for decades (Reynolds et al. 1982, Kenward and Widén 1989, Crocker-Bedford 1990, Widén 1997, Rutz et al. 2006). Numerous studies described forest structure in goshawk nest areas, but only a few documented the effects of tree harvests or catastrophic tree-felling events in nest areas on goshawk breeding (Penteriani and Faivre 2001, Penteriani et al. 2002, Mahon and Doyle 2005). Fewer yet studied tree harvest effects at the home range scale on goshawk vital rates in a quasi-experimental or experimental framework (Squires and Kennedy 2006). Our investigation of the effects of tree cutting on goshawks in differently managed landscapes, one with (NKRD) and one without (GCNP) tree harvests, showed differences in territory spacing and frequency of reproduction. Although minimum and maximum distances between territory centers in the 2 areas were nearly identical, the mean distance between centers was significantly less in the NKRD than in the GCNP. Also, NKRD territories had about 1.5 times the odds of being active compared to GCNP territories and there were no differences in mean fledglings per active nests in the 2 areas. Although we think that differences in territory spacing was a consequence of the small sample of GCNP territories, differences in frequency of reproduction may reflect different tree densities in the 2 areas. Decades of anthropogenic suppression of naturally occurring low-severity surface fires in both the GCNP and NKRD permitted tree densities to increase, a spreading of trees into small natural openings, and, because of increased tree shading, a reduction in the amount and productivity of grass-forb vegetation. In the NKRD, tree harvests countered these changes by maintaining more open forest conditions and a retention of much of the naturally occurring grass-forb habitats. On the other hand, lack of tree harvests in the GCNP resulted in considerably denser forests there than in the NKRD. Increased forest cover and a concomitant reduction in distribution, abundance, and productivity of grass-forb habitats likely resulted in a lowered diversity and abundance of important large prey (i.e., lagomorphs, ground squirrels, and gallinaceous birds) and less frequent goshawk reproduction in the GCNP.

One quasi-experimental short-term study (3 yr, 1985–1987) of tree harvest effects on goshawks compared breeding-pair occupancy (had active nests) and reproduction in control (forests that received light selection harvests in the 1950s and 1960s) and treatment (more intensive partial harvests during 1960–1985) territories on the NKRD (Crocker-Bedford 1990). This study reported that occupancy varied from 63–79% on control territories compared to 17–25% on treatment territories. Furthermore, when goshawk nests were monitored more intensively (i.e., 1987), Crocker-Bedford (1990) reported that reproduction across treatment territories was 94% lower than control territories. The effect size (a 77% reduction in territory density) attributable to timber harvesting by Crocker-Bedford (1990) conflicts with our finding of higher territory density on the more heavily managed NKRD compared to the minimally managed GCNP. To examine this contrast, we compared goshawk occupancy and reproduction in territories monitored during our study to occupancy and reproduction in the same full list of territories studied by Crocker-Bedford (1990; territory and reproductive data on file at U.S. Forest Service, Southwestern Region Office, Albuquerque, NM, USA). During our study, Crocker-Bedford's (1990) control territories were occupied 42% of 419 territory study years, fledged a mean of 1.6 fledglings/active nest (SE = 0.10), and produced 274 total fledglings, while his treatment territories were occupied 35% of 444 territory study years, fledged a mean of 1.7 fledglings/active nest (SE = 0.10), and produced 268 total fledglings. Thus, contrary to the extensive differences in occupancy and reproduction in control versus treatment territories reported in Crocker-Bedford (1990), there was little difference in these metrics in the same control and treatment territories during our 20-year study. We believe the differences between the 3-year Crocker-Bedford (1990) study versus our 20-year study demonstrates the inadequacy of short-term studies of a long-lived bird in a highly variable environment.

Precipitation effects.—Model results of associations between precipitation and goshawk reproduction supported our *a priori* hypothesis that inter-annual variation in precipitation associated with ENSO influenced goshawk reproduction in combinations of same-year effect, a 1-year lag effect, and a weaker 2-year lag effect (Table 4). Thus, our confidence set of models indicated that precipitation across 3 breeding years should be considered when anticipating goshawk productivity. Hypothesized lags were based on different precipitation-induced phenological responses in net primary productivity (NPP) of the different tree species and understory grass, forb, and shrub species in our study area (Fig. 3). The weaker 2-year lag effect probably reflected a 26–27 month period between ovulate cone initiation and production of mature seed in *Pinus* species (Williams 2009). Precipitation effects on the initiation of cone production and masting (synchronous production of large seed crops) in *Pinus* has been documented in several studies (Burns and Honkala 1990, Krannitz and Duralia 2004, Shepperd et al. 2006, Zlotin and Parmenter 2008, Mooney et al. 2011). A 1-year lag reflected a 12–14-month interval between ovulate cone initiation and seed maturation in non-*Pinus* conifers (Williams 2009). Although precipitation effects on masting in non-*Pinus* conifers are less well understood, soil moisture enhances seed production in these conifers, especially in water-limited environments (Forcella 1981, Shea 1987, Stromberg and Patten 1993). A no-lag model reflected an almost immediate response of the grass, forb, and shrub understory species to a breeding year's precipitation (Fig. 3), including summer and fall understory production, carry-over seed banks, plant cover (Polis et al. 1996, 1997), recharging of deep soil moisture by spring snow melt, and follow-up spring grass, forb, shrub production of foliage, flowers, fruits, and seeds (Ehleringer et al. 1991, Riegel et al. 1992, Ernest et al. 2000, Ogle and Reynolds 2004, Moore et al. 2006, Hernandez et al. 2011).

These productivity responses likely affected goshawk reproduction via the production of resource pulses (strong in a series of wet yr, weak in dry yr) that cascaded up through primary and secondary consumers (prey) to goshawks. Such pulses were hypothesized to affect reproduction, recruitment, and over-winter survival of goshawk prey. In wet years, increased prey abundance in fall, winter, and early spring improved the physiological conditioning of female goshawks emerging from winter, resulting in more egg-laying pairs, larger clutches, and larger broods. In dry years, lower primary productivity and decreased prey abundance resulted in poorer goshawk physiological condition, fewer egg-laying pairs, smaller clutches, and smaller broods. A same-year (0-lag) reproductive response by goshawks was possible because of fall and winter abundance of understory-dependent prey, whose reproduction and survival were driven by the understory's quick productivity response to the year's summer and fall precipitation. Prey abundance prior to spring egg-laying by goshawks apparently determines whether territorial females can or cannot produce a clutch. The same-year effect may be enhanced by the ability of species such as red squirrels, a 1-year lag species, to anticipate resource pulses by increasing their reproductive output prior to a masting event (Dolbeer 1973; Gurnell 1983, 1984; Ernest et al. 2000; Boutin et al. 2006; Bergeron et al. 2011).

The ENSO occurs at an average episodic periodicity of 3–4 years and usually lasts only 1 year (Milne et al. 2003). Thus, the co-occurrence of conifer masting with a wet year's understory resource pulse would be rare, and the consequence of rarity would be an annual norm of 35–45% of goshawk territories with breeding (Table 2). However, in a 3-year wet period, sequential years of understory production, carry-over seed banks, and plant covers combined with pine and non-pine conifer masting would produce cumulative prey population expansions over 3 years. Cumulative increases in prey abundance would support monotonic increases in goshawk reproduction and increases in territory occupancy through recruitment from expanding pools of immigrant and locally produced floaters. Multiple-year precipitation-driven resource pulse events clearly manifested in 2 extreme weather events during our study; a record 4-year wet El Niño event in 1991–1993 (Trenberth and Hoar 1996, Polis et al. 1997) coincided with the best of breeding years, and a record 4-year drought in 1999–2003 (Svoboda et al. 2002) coincided with the poorest of breeding years (Fig. 17). Qualitative prey abundance assessments in 1991–1993 (R. T. Reynolds, personal observation) indicated higher abundance of rabbits, hares, ground squirrels, and red squirrels by an order of magnitude than in any subsequent year of prey counts (Salafsky et al. 2007, Lambert 2015, Salafsky 2015).

High interannual variation in territory occupancy by breeding goshawks coincident with inter-annual variations in prey abundance have been reported in other goshawk populations (McGowan 1975, Lindén and Wikman 1983, Doyle and Smith 1994, Tornberg et al. 2005, Bechard et al. 2006) and in other raptor species with year-round fidelity to territories (Southern 1970, Adamcik et al. 1978, Village 1981, Steenhof et al. 1997). On the Kaibab Plateau, Salafsky et al. (2005, 2007) reported that densities of red squirrel, Kaibab squirrel, northern flicker, and Steller's jay (*Cyanocitta stelleri*) explained 89% of the inter-annual variation in goshawk reproduction from 1994 to 2002. Had lagomorph density been estimated, it is likely that a larger percentage of temporal variation in goshawk breeding would have been explained, as lagomorphs contributed more biomass to goshawk diets than most other species combined (Salafsky 2015).

We contend that interannual variation in prey abundance resulted in similarly variable goshawk body condition that manifested as annually variable clutch and brood sizes, nest failure rates, and fledgling production. Indeed, the tendency for goshawks on the Kaibab Plateau to have a wide range of annual territory occupancy rates, nest failure rates, and annual productivities compared to other populations suggested that the Kaibab breeding environment was more variable. The mean annual rate (37%) and range of occupancy (8%–86%; Table 2) of territories by breeders on the Kaibab Plateau was lower and greater, respectively, than in 3 other long-term goshawk studies in Finland ($\bar{x} = 45\%$, range = 37–58%, Hakkarainen et al. 2004; $\bar{x} = 43\%$, range = 36–55%, Tornberg et al. 2005; $\bar{x} = 68\%$, range = 32–86%, Lindén and Wikman 1983). Overall nest failure ($\bar{x} = 25.5\%$, annual range = 12–48%) on the Kaibab Plateau was also typically higher than reported for other North American goshawk populations (range of among-study means = 5–23%; reviewed in Squires and Reynolds 1997, Boal et al. 2005) and in Europe (range of means = 0.15–24%; reviewed in Kenward 2006, Byholm and Nikula 2007). At the same time, overall mean productivity per active ($\bar{x} = 1.5$ fledglings, range of annual

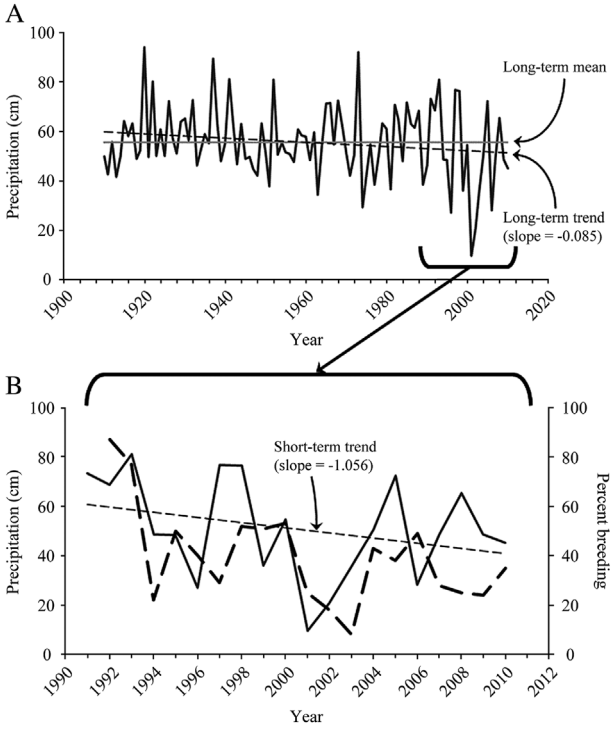

Figure 17. A) Precipitation (solid black line) during the goshawk breeding cycle (Jul–Jun) over 101 years (1909–2010) at Fort Valley Experimental Forest, Arizona, USA (latitude 35.2681, longitude 111.7428, elevation, 2,239 m; 114 km south of the Kaibab Plateau). Included are the long-term mean (solid gray line) and long-term trend (dashed black line) in precipitation at Fort Valley. B) Study period (1991–2010) breeding-cycle precipitation (solid line) with a no-year lag and the percent of prior-year's cohort of territories with breeding (dashed line) on the Kaibab Plateau, Arizona, USA.

means = 0.8–2.1; Table 2) and per successful nest ($\bar{x}$ = 2.0 fledglings, range of annual means = 1.5–2.4; Table 2) on the Kaibab tended to be lower but generally covered the range of the mean equivalent productivities per nest in North America (among study means = 0.94–2.0 fledglings/active nest and 1.4–3.9 fledglings/successful nest; reviewed in Boal et al. 2005). Interestingly, North American goshawks were typically less productive than in Europe (Kenward 2006).

Population Structure

Although the pooled brood sex ratio on the Kaibab Plateau did not differ from unity, males significantly outnumbered females in 2 years and females outnumbered males in 1 year. Significantly alternating sex ratios in goshawks have been noted by others. Byholm et al. (2002) reported more males in broods in good prey years (more woodland grouse) when the goshawks also had larger broods, whereas more females were produced in poor grouse years when broods were smaller. Rutz (2012) noted that broods became more male-biased as the proportion of feral pigeons (*Columba livia*) in the diet increased. Daan et al. (1996) found that in goshawks and other size-dimorphic raptors, more females were produced in early broods and more males in late broods. Wikman (1976), Dijkstra et al. (1990), and Kenward et al. (1993) showed that as brood size increased, sex ratios became more male-biased. Observations of varying sex ratios raised the possibility that goshawks were adaptively adjusting brood sex ratios to varying environmental conditions and several authors proposed hypotheses to explain such phenomenon (see Introduction). We found no evidence supporting the seasonal sex-specific recruitment hypothesis (Daan et al. 1996) that brood sex ratios on the Kaibab Plateau varied between early broods (more females) versus late broods (more males), nor supporting the local resource competition hypothesis (Gowaty 1993, Byholm et al. 2002, Rutz 2012) that brood sex ratios varied between food-rich (more males) versus food-poor habitats (more females).

The greater overall production of males in nearly all reports of goshawk brood sex ratios was compelling. Despite no significant difference in overall brood sex ratios on the Kaibab Plateau, the more frequent production of males (53% M) was in the same direction as in a preponderance of goshawk studies, including Arizona (64% M; Ingraldi 2005), the Swedish island of Gotland (51–55% M; Penteriani et al. 2013), Netherlands (53% M; Bijlsma 1993), Finland (52.3% M; Wikman 1976), and 14 of 17 other European studies ($\bar{x}$ = 54% M, SD = 0.3, range = 51–60% M) summarized by Rutz (2012).

Given the preponderance of goshawk studies showing male-biased broods, reports of lower survival of juvenile and adult males relative to females (Kenward et al. 1999; this study [Table 12]), and a female-bias among potential breeding adults (Kenward et al. 1999), we submit that breeding goshawks adaptively adjust their brood sex ratios to produce more of the rarer (male) sex (the variation in reproductive value hypothesis; Trivers and Willard 1973). Higher adult male mortality may stem from their food provisioning role during the long breeding season and increased exposure to accidents while pursuing agile prey in vegetation-filled environments. Lower male survival in goshawks was also reported in California, USA (DeStefano et al. 1994) and Gotland, Sweden (Kenward et al. 1999). In Gotland, male survival in their first 2 years was estimated at 0.49–0.54 and 0.54, respectively, whereas female survival was 0.69–0.71 in the first and 0.71 in their second year; thereafter, survival rates for both sexes were 0.79. In the same study, Kenward et al. (1999) estimated an adult population sex ratio of 1.0 M:1.78 F with only 40% of females breeding annually compared to 71% of males, and speculated that different mortalities of the sexes in the first 2 years resulted from lower abundance of suitably sized prey for males. Although more males (52%) hatched, the difference was not significant (Kenward et al. 1993, 1999). In Scotland, male sparrowhawks (*A. nisus*), a forest-dwelling goshawk congener with even greater size dimorphism, also had lower adult (2- to 9-yr-old) survival (0.462) than females (0.635), and the adult male:female sex ratio was 1:1.86, with many adult females not breeding because of either a lack of mates or poor food conditions (Newton et al. 1983). Again, although not significant, more males fledged (51%; Newton and Marquiss 1979). Finally, in Cooper's hawks (*A. cooperii*), another forest-dwelling and strongly dimorphic congener, brood sex ratios were reported to be male-biased at conception (53%), as nestlings (54%), and as fledglings (60%) in Wisconsin (Rosenfield et al. 1996).

Recruitment, Adult Survival, and Population Change

Annual recruitment rates of local-banded nestling goshawks used to estimate immigration to our study area may have slightly underestimated true local recruitment (and overestimated immigration) because a few banded hawks delayed recruitment as much as 9 years. Nonetheless, the estimated 13-year rate of immigration (54% of recruits were immigrants) was consistent with the high level of genetic diversity of goshawks on the Kaibab Plateau (Bayard de Volo et al. 2013). Dispersal of potential breeders appears to be more frequent over land than over water; the frequency of immigration to the Kaibab was considerably higher than the 3% immigration to a similar-sized goshawk population on the island of Gotland, 90 km from mainland Sweden across the Baltic Sea (Kenward et al. 1999). We were unable to document sex differences in dispersal distances by immigrants because their natal sites were unknown. Likewise, we were unable to determine absolute natal dispersal distances for nestlings banded in our study because the great majority emigrated from the Kaibab (Wiens et al. 2006). The lack of differences in sex-based recruitment of locally born goshawks (philopatry) and in natal dispersal distance (M = 16 km, F = 18 km) on the Kaibab was contrary to juvenile goshawks in Finland and Sweden where band recoveries of males showed they made longer dispersal movements than females (Haukioja and Haukioja 1970, Marcström and Kenward 1981, Byholm et al. 2003) but similar to goshawks in Finland (Byholm et al. 2003) where there were no sex-based differences in natal dispersal (M = 49 km, F = 64 km). Females in birds typically disperse farther than males, possibly as a consequence of females searching more widely for potential mates and territories, whereas males benefit by remaining near their natal site where they are more familiar with suitable habitat (Greenwood and Harvey 1982).

High territory fidelity, short movements of the few breeding dispersals (95% of 59 breeding dispersals were movements that were no farther than 4 territories distant; R. T. Reynolds, unpublished data), and the lack of reports of emigrant (from the Kaibab Plateau) breeding dispersals (possibility of discovering any emigrant breeding dispersals was indicated by reports of 2 emigrant natal dispersals from the Kaibab Plateau; Wiens et al. 2006) lead us to conclude that declines in apparent survival resulted from mortalities rather than emigration. Nonetheless, undetected emigration can affect survival estimates, especially near the end of capture–recapture occasions (Peñaloza et al. 2014). When emigration is random (all individuals have the same probability of being absent at any given time), mark–recapture survival estimates remain unbiased, whereas if conditioned on the current state of adults (i.e., Markovian), survival estimates can be biased (Peñaloza et al. 2014). Determining whether long-distance breeding dispersals off the Kaibab Plateau is Markovian or not will have to await future study using global positioning system tools such as Argos platform transmitter terminal (PTT) or Groupe Spécial Mobil (GSM) tags (Bridge et al. 2011, Limiñana et al. 2012).

Survival estimates of adult goshawks on the Kaibab Plateau were comparable to survival rates in other North American and European studies. Kaibab survival was consistently higher than in an 8-year study of 95 breeding goshawks in California (M = 0.52, F = 0.70; DeStefano et al. 1994). Kenward et al. (1999), using staggered entries of 318 radio-tagged goshawks on the Swedish island of Gotland, estimated adult survival rates of 0.79–0.83 for both sexes, slightly above maximum survival (0.78 at age 5) on the Kaibab. Krüger (2007), in a 30-year study of 74 female goshawks in Germany, estimated annual survival rates of 0.62–0.92 for ages 1–8 years old, which dropped sharply at age 9 with no female surviving beyond age 10. Although the range of survival in Krüger (2007) overlapped the Kaibab rates for ages for ages 2–10 years old, the maximum rate of 0.92 considerably exceeded the Kaibab maximum. Haukioja and Haukioja (1970) estimated mortality rates of goshawk from 552 band recoveries (assuming 60% band reporting rates) in Finland and Sweden, during periods when humans killed about 20% of goshawk populations per year. Converting mortality to survival rates (1 − mortality), both sexes survived at rates of 0.37 in the first year, 0.67 in the second year (1-yr-old), 0.81 in the third year, 0.83 in the fourth year, and 0.89 thereafter (Haukioja and Haukioja 1970). As in Krüger (2007), survival estimates for Finland goshawks ≥2 years old exceeded estimates from our study.

Although sex was not included as a covariate in the top CJS survival model, models including age and sex were competitive ($\Delta AIC_c < 1.0$). We think this is the consequence of breeding males on average not living as long as females as is evidenced by the set of CJS models not including age always showing male survival lower than female survival. The failure of the sex effect to manifest in the top CJS model was likely caused by a number of factors including 1) breeding males were generally younger than breeding females and, as a result, sex effects were embodied in the age effects when sex was not in the model, and 2) increased sampling variation resulting from the lower recapture probability of males (for every 10 F captured or resighted, about 7 M were captured or resighted) may have masked sex effects. Although our evidence of lower male survival was weak, we note that lower male survival in our study aligned with lower male survival in California (DeStefano et al. 1994), Gotland (Kenward et al. 1999), Finland (Haukioja and Haukioja 1970), and in the first 6 years (1991–1996) of our study (Reynolds and Joy 2006).

Rate of population change (λ) estimates from the Pradel models offered additional support for our CJS-based interpretation of lower adult male than adult female survival. Lambda estimates of 0.962 for females and 0.922 for males indicated yearly declines of 3.8% and 7.8% for females and males, respectively. We conjectured that lower male survival was the consequence of greater risk of injury associated with their food-provisioning role during breeding and pursuit of agile prey in vegetation-filled environments.

We found substantial variation in annual reproduction and our estimates of mean annual reproduction were on the low end of means reported for other goshawk populations in North America. We also found that fledging rate, a variable included to estimate effects of reproduction on survival, did not improve estimates of age-specific survival or population change, but that it did explain a proportion (60.5%) of the temporal variation in probability of detection in the CJS analyses and a small portion (17.6%) of the temporal deviance in survival in the Pradel analysis. Temporal effects were not unexpected given that we calculated fledgling rate as the annual mean number of fledglings produced by successful (fledgled ≥1 young) nests, thereby introducing into the models the observed variation in annual brood sizes and annual numbers of breeding pairs, which positively co-varied (Fig. 8). Thus, inclusion of fledgling rate introduced temporally variable detection

probabilities (only breeding hawks could be captured or resighted) but explained only a small portion of the temporal survival deviance in the Pradel analysis. The costs of reproduction may be more severe in variable and harsh environments (Barbraud and Weimerskirch 2005). However, instead of average fledgling rate as we used here, investigating variable environment costs to reproduction will require consecutive observations of individual breeding efforts and a modeling of the joint probabilities of individual capture histories to estimate state- and time-specific survival (Stoelting et al. 2015).

Population Status Overview

The sum of 20 years of goshawk demographic data indicated a Kaibab Plateau population with a stable breeding age structure but one that may be declining. Given that a species' life history is shaped by its environment (Roff 1992), it is expected that increased environmental variability causes increased stochasticity in vital rates. Because stochastic variability in adult vital rates reduces a population's growth rate (Tuljapurkar 1982, Sæther and Bakke 2000), high environment variability is expected to reduce the growth rate and abundance of the species. Annual fluctuations in prey populations on our study area (Salafsky et al. 2005, 2007), coupled with our modeling of precipitation effects, strongly suggests that environmental variation drives observed variation in goshawk productivity.

A regular distribution of territories in our study area suggested a saturated habitat, but there remained considerable uncertainties about the status (dead or alive) of territory owners during non-breeding years because of low detectability. Uncertainty was particularly problematic in the latter consecutive years of low breeding (i.e., 2003–2010). Non-breeding goshawks were observed and occasionally resighted (bands read) in occupied-only (no eggs laid) territories, but the status of most non-breeders was equivocal because their territories during these years typically contained little sign of goshawk presence (feces, molted feathers, refurbished nests, hawks observed). Despite uncertainties, there were indications that goshawks on many unknown-status territories continued to occupy them through non-breeding periods because banded territory owners were often resighted as breeders on their territories following up to 5 consecutive years of non-breeding, and we often observed state changes from non-breeding to breeding in the first of a series of good breeding years following poor years. We assumed that that these goshawks had been waiting on their territories for suitable breeding conditions.

We suspect that the overall 1992–2010 declining trend in the proportions of territories with breeders (Fig. 8) had much to do with the timing of our study. The first 3 years (1991–1993) coincided with exceptional breeding; egg-laying occurred on as many as 86% of territories monitored in a prior year and these years coincided with a multiple-year El Nino wet period and a high level of prey abundance that was not seen again in 10 follow-up years of transect prey counts on our study area (Salafsky et al. 2005, Lambert 2015). If the years following 1994 represented a norm in annual reproduction for this population, then clearly the declining trend was a consequence of the exceptional initial study years. Unfortunately, because our 20-year study did not include another equally long wet period, we cannot know whether the observed decline is real or part of a longer unobserved weather cycle.

Several demographic metrics of the population are indicative of a stable population: relatively high survival rates of breeders through 10 years of age with a few individuals surviving to 15 years old; a lack of recent demographic perturbations (recruitments, mortalities) propagating through the annual age structures (Caughley 1978); the 95% confidence intervals of λ values overlapping 1 indicating only weak evidence (stronger in M than in F) of a declining breeding population despite the fact that λ values for both sexes were <1; the complete absence of 1-year-old breeders combined with the 3.5- to 3.7-year-old mean ages at first breeding indicating low breeder mortality and low territory availability (McGowan 1975, Steenhof et al. 1983, Balbontin et al. 2003); a study area saturated with territories; a level of fledgling production at active ($\bar{x} = 1.6$, SE $= 0.04$) and successful nests ($\bar{x} = 1.9$, SE $= 0.03$) within the range reported in other North American goshawk populations (Kenward 2006, Squires and Kennedy 2006); and the high frequency of immigrant recruits to the breeding population. Frequent immigration, delayed ages of first breeding of many recruits, and recruitment of 2- and 3-year-old breeders in good breeding years attests to the presence of non-breeding floaters on the Kaibab Plateau. Indeed, both banded and unbanded 1-year-old floaters were occasionally observed on the study area.

The demographic characteristics of the Kaibab goshawk population seemed exemplar of a life-history response to a highly variable environment where mean adult lifespan exceeded the 3–5-year cycle of environmental variability. We were unable to determine whether potential breeders bet-hedged decisions to breed in poor prey years to survive and breed in future years, or they simply attempted to breed each year but were unable to acquire sufficient resources to produce a clutch. However, life-history strategies with relatively high reproductive rates (once eggs can be produced) coupled with long lifespans is an effective strategy in a highly variable environment (Sæther et al. 1996, Reid et al. 2004). Population growth in long-lived birds such as goshawks is known to be more sensitive to variation in adult survival rate than to variation in fecundity (Gaillard et al. 1998, 2000; Pfister 1998; Sæther and Bakke 2000; Krüger 2007).

Threats to the viability of the Kaibab goshawk population remain, some immediate and others based on predictions of the effects of climate change on Southwestern forests. An immediate threat is continued loss of habitat to high-severity fire, a disturbance increasing in frequency and extent (Westerling et al. 2006, Littell et al. 2009, O'Conner et al. 2014). Future threats to forest productivity, biodiversity, and food webs include predictions of climate-induced changes in the frequency, duration, and depth of drought, especially in the Southwest. Deeper and longer droughts are expected to increase tree mortality, reduce forest growth and productivity, increase the frequency and size of forest-killing fires, and reduce prey availability (Albright et al. 2010, O'Conner et al. 2014, Allen et al. 2015, Jolly et al. 2015, McDowell et al. 2016). Given our findings, we expect increased variability in seasonal precipitation and forest productivity and increased habitat loss to high-severity fire to negatively affect food webs, goshawk reproduction, supplies of immigrants, and ultimately the viability of goshawk populations throughout the Southwest. Our expectations contrast with the modeled effects of climate warming that predicted breeding success of Finnish

goshawks to remain unchanged despite expected declines of 50% in the main prey (grouse) of goshawks (Lehikoinen et al. 2013). Breeding success of Finnish goshawks was predicted to remain unchanged because of compensating increases in the abundance of alternative and mainly migratory prey (e.g., thrushes, corvids, doves) as climate warming advances even in the face of primary prey declines (Byholm and Kekkonen 2008, Lehikoinen et al. 2013).

MANAGEMENT IMPLICATIONS

Our modeling of the effects of precipitation on forest primary productivity and small mammal and bird abundance suggest that goshawk reproduction on the Kaibab Plateau is strongly food-limited. Moreover, our earlier research showed that total prey abundance (summed over all prey species) accounted for more of the interannual variation in goshawk reproduction than abundances of any individual prey species or prey type (e.g., mammals vs. birds; Salafsky et al. 2005). The link between precipitation, total prey abundance, and goshawk reproduction underscores the importance of a diverse suite of prey species, and by extension, the importance of diverse prey habitats at the goshawk home range scale. Ponderosa pine and mixed-conifer forests are the predominant forest types on the Kaibab Plateau and goshawk prey in these forests include tree and ground squirrels, lagomorphs, phasianids, columbids, strigids, picids, corvids, and other passeriforms. Habitats of these different prey include groups or patches of mature and old trees with interlocking crowns, herbaceous and shrub vegetation, large snags, and logs. Most of these prey also depend to varying degrees on a fine-scale intermixture of these habitats for foraging and nest sites adjacency (Reynolds et al. 1992, 2006).

Historically frequent (<35 yr) low-severity fire in ponderosa pine and mixed-conifer forests maintained a fine-scale mosaic of these prey habitats (Cooper 1960, 1961; White 1985). However, a century of management activities, especially fire suppression and tree harvests, altered the vegetation composition and structure (horizontal and vertical) of these forests by permitting within-patch tree densities to increase and the spread of trees into herbaceous and shrub openings. Increased tree densities created continuous canopy fuels and favored the establishment of shade-tolerant, fire-sensitive trees at the expense of shade-intolerant, fire-resistant trees. Increased tree densities and associated shading lowered species diversity and productivity of herbaceous and shrub communities, and increased among-tree competition, diminishing tree vigor and productivity (Covington and Moore 1994, Moore et al. 2006, Larson and Churchill 2012). Furthermore, management focused on harvesting large trees resulted in forests dominated by young- to mid-age trees and a narrowing of vertical canopy profiles. Narrowed profiles and the establishment of young trees under residual canopies has reduced the sub-canopy foraging flight space for goshawks. We posit that these changes have led to fewer and less productive prey habitats, lowered prey abundance, and reduced goshawk reproduction. Our argument is supported by results showing higher odds of more frequent goshawk breeding in NKRD territories (where tree harvesting [including young tree thinning] counteracted the tree density increases associated with fire suppression) than in GCNP territories where trees were not harvested. In sum, our findings suggest that management of ponderosa pine and mixed-conifer forests that is focused on re-establishing the natural vegetation composition (i.e., shade-intolerant, fire-resistant trees), forest structure (moderately even-aged patches of mature and old trees), and spatial pattern (tree patches interspersed within herbaceous and shrub communities) would improve goshawk reproduction and population growth.

Re-establishing the natural vegetation composition and structure in these forested systems also would lower the risk of high-severity fire. Catastrophic fires have increasingly destroyed goshawk habitat on the Kaibab Plateau and elsewhere in the western United States. Likewise, re-establishing natural tree densities would lower among-tree competition and reduce tree shading, both of which should increase the vigor and productivity of overstory and understory vegetation. Improved tree vigor also would increase the resistance of these forests to insect and disease epidemics, and perhaps resilience to the deeper and longer droughts predicted with climate change (Fulé et al. 2002, Littell et al. 2009, O'Conner et al. 2014, Hessburg et al. 2016).

Finally, this study established key considerations for designing goshawk population monitoring protocols. An objective of population monitoring is to obtain reliable estimates from samples to make inferences regarding the status of the target population. Because of their relatively low density and elusive behavior, monitoring goshawk populations is difficult and, as a result, have been largely restricted to determining the annual rates of nest-site occupancy and reproduction from relatively small samples of territories over short periods of time. However, the extensive interannual variations in egg-laying and low detectability of Kaibab Plateau goshawks when not reproductively active showed that monitoring goshawk occupancy and reproduction in small samples (territories and years) can be imprecise, if not biased, in regions characterized by highly variable environments like those under the influence of ENSO. The extensive variation in reproduction and periodic precipitation pulses that drives the variation indicates that rigorous inferences will require monitoring of at least 30–40 territories (see Reynolds et al. 2005) for at least 10–12 years (the equivalent of 3 or 4 ENSO cycles). This study's central finding for those interested in quantifying goshawk vital rates in variable environments is that such demography is necessarily a long-term endeavor.

SUMMARY

- The study area (1,728-km^2) included nearly continuous conifer forests on the Kaibab Plateau, Arizona, USA, a high-elevation plateau surrounded by a desert scrub plain. The area comprised the Kaibab National Forest, where fires were historically suppressed and trees were harvested under various prescriptions, and the Grand Canyon National Park North Rim, where fires were also suppressed but trees not harvested.
- Breeding northern goshawks were monitored in 125 territories spaced at an average center-to-center distance of 3.8 km. Territories contained a mean of 3.6 alternate nests (range = 1–10) that were spaced at a median distance of 306 m from territory centers. The

dispersion and use of alternates by banded goshawks showed that territories were spatially stable over years.

- The salient demographic feature of the goshawk population was extensive temporal and spatial variation in the number of territories fledging young. Egg-laying in 121 territories monitored ≥9 years occurred an average of only 40% (range = 8–87%) of years. Annual brood sizes and nest failure rates were positively and negatively related, respectively, with proportions of territories with breeding.
- Territories losing ≥64% of their forest canopies to the high-severity fires were never again occupied during our study, whereas territories losing ≤64% of forests to these fires had post-fire breeding rates only slightly less (35%) than the 40% average breeding rate for 121 territories monitored ≥9 years. Low-severity surface fire in active (with eggs) nest areas had no effects on nesting success.
- Models relating precipitation to goshawk reproduction supported the hypothesis that precipitation received up to 2 years prior to a current reproductive event was associated with annual variation in the number of young fledged Kaibab-wide, although evidence supporting a 2-year lag was weaker than a 1-year lag effect. The driver of the association was hypothesized to be precipitation-induced phenological responses of forest overstory and understory plants resulting in pulses of primary forest productivity that cascaded up through primary and secondary consumers to affect the frequency and extent of goshawk reproduction.
- There were significant departures from 1:1 brood sex ratios in 3 of the 20 years, with a male bias in 2 years and a female bias in 1 year. Although the pooled 20-year brood sex ratio was not significantly different from unity, it favored males (410 M, 366 F). The production of more males may have been an adaptive allocation of brood sex ratios by breeders to produce more of the rarer sex in the adult stage.
- Minimum age at both recruitment and first breeding was 2 years. The mean recruitment rate of locally born (*in situ*) and banded goshawks on the study area was 0.109. An estimated 46% of recruits (to the breeding population) were locally born and 54% were immigrants.
- Annual breeding age structures of both sexes were consistent with a population in a stable age distribution under a classic avian age-specific mortality pattern.
- Apparent age-specific survival among breeders initially increased with age from 0.74 at 2 years of age to 0.78 at 5 years of age, then declined to 0.34 at 15 years of age. Maximum observed age of both males and females was 15-years.
- Greater sampling variation may have masked a sex effect in the CJS models; males had a lower recapture probability because capturing and resighting them was more difficult.
- Rates of population change (M = 0.92, SE = 0.040; F = 0.96, SE = 0.041) from the top Pradel model provided only weak evidence (stronger in M) of a population decline (95% CI for both sexes overlapped 1). A lower male λ suggested that males had lower survival; females had a 13.4% chance of the population growing when projected for 20 years, whereas males had only a 1.0% chance.
- Highly variable annual breeding rates combined with low mean frequency of breeding, low male λ estimates, and loss of habitat to numerous large high-severity fires raised viability concerns for the Kaibab Plateau goshawk population. These concerns were somewhat countered by the stable breeding age structures, the relatively high annual survival of breeders, the 3.6-year mean age at first breeding, the absence of breeding by 1-year-old hawks, a study area saturated with territories, and estimates of frequent immigration.
- Model predictions of more frequent and deeper droughts due to climate change threatens forest productivity, prey abundance, goshawk reproduction, regional sources of immigrants, and ultimately the viability of this apex predator.
- Forest management creating a diversity of prey habitats in ponderosa pine and mixed-conifer forests is recommended. The desired habitat diversity includes all tree age classes with a focus on older trees in fine-scale mosaics composed of groups of trees, scattered individual trees, large snags and logs, and small openings with species-diverse and productive herbaceous-shrub communities.
- Increasing habitat diversity, forest productivity, and lowering the risk of catastrophic fire (loss of habitat) are the best management objectives for conserving biodiversity, food webs, and goshawk viability in ponderosa and mixed-conifer forests.

ACKNOWLEDGMENTS

This study was supported by the USDA Forest Service Southwestern Region, Rocky Mountain Research Station, Joint Fire Science Program, and Arizona Game and Fish Department. Housing and logistical support was provided by the North Kaibab Ranger District. We are indebted to many employees and volunteers who helped find nests, climb nest trees, trap and band goshawks, and count bird and mammal prey. The study would not have been possible without their hard work and dedication: 18 years, J. Seyfried; 15 years, S. Salafsky; 14 years, S. Joy; 12 years, A. Cofer, 11 years, D. Wiens; 10 years, M. Gavin, M. Snyder, C. Van Cleve; 7 years, D. Laing, W. Nimitz; 5 years, R. Hadwen, B. Reynolds; 4 years, S. Bedard, C. Boam, R. Brogel, J. Burns, W. Craven, D. Leslie, M. Mason, A. Meyer; 3 years, H. Danaceau, J. Feinstein, T. Gavin, A. Gillan, T. Hatfield, L. Horie, Z. Kaufman, J. Lawrence, M. Price, L. Tonino; 2 years, R. Albers, A. Alfonso, G. Baluss S. Baumeister, C. Boal, D. Bright-Smith, S. Chudacoff, P. Clark, S. Delgado, G. Dilworth, L. Dunn, H. Eichman, M. Estrella, M. Francis, T. Gamberg, M. Harmon, B. Heslin, B. Hunt, L. Hunt, K. McFall, G. Meigs, G. Merrill, K. Parmentier, M. Remsberg, D. Rubinoff, T. Weber; 1 year, L. Baltic, C. Bates, J. Benson, K. Boden, D. Bowen, R. Brunotte, D. Cavanaugh, C. Collins, T. Conway, J. Driscoll, J. Dudley, S. Dudley, A. Fellow, G. Frank, R. Gavin, C. Gigliotti, I. Gilmore, B. Griscomb, J. Hauck, E. Heinskill, D. Henstenberg, R. Jaffe, K. Kalin, T. Kelley, R. Klepac, J. Koloszar, M. MacGrath, N. Marymore, B. Messick, M. Miller, R. Miller, T. Moore, J. Moss, J. Nelson, K. Norman, J. Olsen, J. Plas, T. Reeves, T. Rice, B. Roberts, W. Rubenstein, J. Seig, L. Schultz, M. Sherman, L. Simpson, J. Slawson, J. Sneva, A. Sobotka, S. Spidle, D. Strait, A. Touliatos, J. Turner, M. Tyler, A. Vandenhoovel, N. VanVleet, E. Walton, N. Weprin, J. Whittier, L. Williams, E. Wilson, and D. Worthington. We thank Douglas (Sandy) Boyce, Patrik Byholm, and an anonymous reviewer for helpful comments on the manuscript. We also thank Yvonne Kullberg and Javier Mercado for proofing French and Spanish translations, and Suzy Stephens for her help with the graphics.

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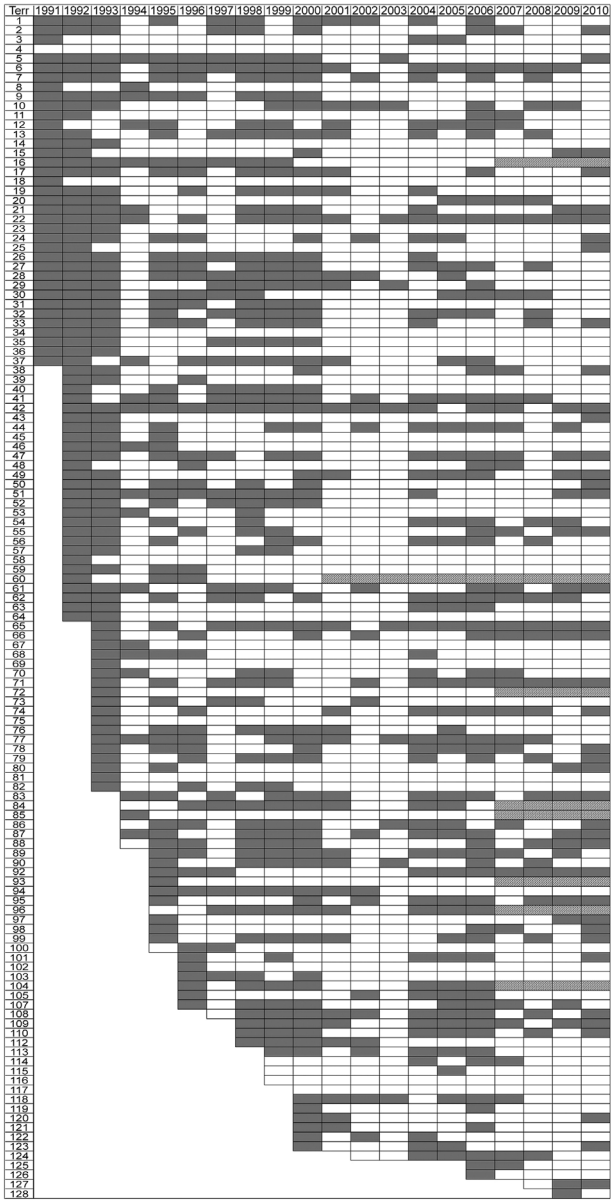
APPENDIX A: Temporal and spatial variation in breeding by goshawks on 125 territories on the Kaibab Plateau, Arizona, USA, 1991–2010. Dark cells indicate years with breeding (eggs laid) and open cells indicate years without breeding. Territory numbers 91, 106, and 111 do not exist because we combined them with an adjacent territory based on movements of banded goshawks among alternate nests subsequent to discovery of territories. Cross-hatched cells are territories where >64% of forest canopies within 1.9-km of the territory centroid were killed by high-severity fire; we never observed breeding on these territories in post-fire years.



APPENDIX B: Model selection results from Pradel (1996) seniority models for 5 combinations (., s, *t*, s + *t*, and s × *t*) of sex (s) and time (*t*) for models of apparent survival (φ), detection probability (p), and seniority (γ) for breeding male and female goshawks on the Kaibab Plateau, Arizona, USA, 1991–2010. We examined the effect of fledging rate (fledge rate) in 3 models (2 with apparent survival; 1 with seniority). Models are ranked by minimum corrected Akaike's Information Criterion (AIC_c) values (Burnham and Anderson 2002) and AIC_c weights (w_i) across 128 models. Also reported are changes (ΔAIC_c) in AIC_c from the top model, the weight (w_i) of model *i*, the number of parameters (*K*) in the model, and the model's likelihood (L).

Model	AIC_c	ΔAIC_c	w_i	*K*	−2log(L)
{φ(s + fledge rate) p(s + *t*) γ(*t*)}	4,761.00	0.00	0.553	42	4,673.311
{φ(s) p(s + *t*) γ(*t*)}	4,763.30	2.30	0.175	41	4,677.787
{φ(s) p(s + *t*) γ(s + *t*)}	4,765.08	4.08	0.072	42	4,677.388
{φ(s) p(*t*) γ(*t*)}	4,765.79	4.79	0.050	40	4,682.450
{φ(.) p(s + *t*) γ(s + *t*)}	4,766.09	5.09	0.043	41	4,680.574
{φ(fledge rate) p(s + *t*) γ(*t*)}	4,766.27	5.27	0.040	41	4,680.760
{φ(s) p(*t*) γ(s + *t*)}	4,766.30	5.30	0.039	41	4,680.788
{φ(.) p(s + *t*) γ(*t*)}	4,768.41	7.41	0.014	40	4,685.063
{φ(.) p(*t*) γ(s + *t*)}	4,769.33	8.33	0.009	40	4,685.982
{φ(.) p(*t*) γ(*t*)}	4,770.72	9.72	0.004	39	4,689.544
{φ(s + *t*) p(s + *t*) γ(*t*)}	4,775.51	14.51	0.000	58	4,652.403
{φ(s + *t*) p(s + *t*) γ(s + *t*)}	4,777.04	16.04	0.000	59	4,651.679
{φ(s + *t*) p(*t*) γ(*t*)}	4,777.63	16.63	0.000	57	4,656.768
{φ(s + *t*) p(*t*) γ(s + *t*)}	4,777.86	16.86	0.000	58	4,654.757
{φ(s) p(s + *t*) γ(.)}	4,778.48	17.48	0.000	24	4,729.274
{φ(*t*) p(s + *t*) γ(s + *t*)}	4,779.21	18.21	0.000	58	4,656.103
{φ(s) p(s + *t*) γ(fledge rate)}	4,780.25	19.25	0.000	25	4,728.941
{φ(s) p(s + *t*) γ(s)}	4,780.41	19.41	0.000	25	4,729.110
{φ(.) p(s + *t*) γ(s)}	4,780.52	19.52	0.000	24	4,731.318
{φ(*t*) p(s + *t*) γ(*t*)}	4,781.36	20.36	0.000	57	4,660.505
{φ(.) p(s + *t*) γ(s × *t*)}	4,781.45	20.45	0.000	53	4,669.540
{φ(*t*) p(*t*) γ(s + *t*)}	4,781.86	20.86	0.000	57	4,661.003
{φ(s + *t*) p(s + *t*) γ(.)}	4,782.69	21.69	0.000	41	4,697.179
{φ(*t*) p(*t*) γ(*t*)}	4,782.86	21.86	0.000	56	4,664.246
{φ(.) p(s + *t*) γ(.)}	4,783.08	22.08	0.000	23	4,735.969
{φ(s) p(*t*) γ(.)}	4,783.43	22.43	0.000	23	4,736.322
{φ(s) p(s + *t*) γ(s × *t*)}	4,783.72	22.72	0.000	55	4,667.346
{φ(s) p(*t*) γ(s)}	4,784.24	23.24	0.000	24	4,735.040
{φ(s + *t*) p(s + *t*) γ(s)}	4,784.57	23.57	0.000	42	4,696.880
{φ(*t*) p(s + *t*) γ(s)}	4,785.69	24.69	0.000	41	4,700.172
{φ(.) p(s × *t*) γ(s + *t*)}	4,785.91	24.91	0.000	57	4,665.055
{φ(.) p(*t*) γ(s)}	4,786.93	25.93	0.000	23	4,739.819
{φ(s + *t*) p(*t*) γ(.)}	4,787.42	26.42	0.000	40	4,704.075
{φ(s + *t*) p(*t*) γ(s)}	4,788.10	27.10	0.000	41	4,702.585
{φ(.) p(*t*) γ(.)}	4,788.27	27.27	0.000	22	4,743.261
{φ(*t*) p(s + *t*) γ(.)}	4,788.52	27.52	0.000	40	4,705.176
{φ(g) p(s × *t*) γ(*t*)}	4,790.79	29.79	0.000	60	4,663.178
{φ(*t*) p(*t*) γ(s)}	4,791.51	30.51	0.000	40	4,708.169
{φ(*t*) p(*t*) γ(.)}	4,792.91	31.91	0.000	39	4,711.734
{φ(g) p(s × *t*) γ(s + *t*)}	4,793.06	32.06	0.000	61	4,663.177
{φ(.) p(s × *t*) γ(*t*)}	4,795.89	34.89	0.000	59	4,670.526
{φ(s) p(*t*) γ(s × *t*)}	4,797.90	36.90	0.000	59	4,672.538
{φ(.) p(*t*) γ(s × *t*)}	4,799.76	38.76	0.000	58	4,676.653
{φ(s + *t*) p(s × *t*) γ(*t*)}	4,803.91	42.91	0.000	77	4,637.186
{φ(s) p(s × *t*) γ(.)}	4,805.73	44.73	0.000	43	4,715.860
{φ(s + *t*) p(s × *t*) γ(s + *t*)}	4,806.17	45.17	0.000	78	4,637.104
{φ(s × *t*) p(s + *t*) γ(*t*)}	4,806.63	45.63	0.000	76	4,642.243
{φ(*t*) p(s × *t*) γ(s + *t*)}	4,807.01	46.01	0.000	77	4,640.286
{φ(.) p(s × *t*) γ(s)}	4,807.02	46.02	0.000	43	4,717.149
{φ(s) p(s × *t*) γ(s)}	4,807.89	46.89	0.000	44	4,715.837
{φ(s × *t*) p(*t*) γ(*t*)}	4,808.66	47.66	0.000	75	4,646.614
{φ(s × *t*) p(s + *t*) γ(s + *t*)}	4,808.75	47.74	0.000	77	4,642.020
{φ(s × *t*) p(*t*) γ(s + *t*)}	4,809.48	48.48	0.000	76	4,645.093
{φ(s + *t*) p(s + *t*) γ(s × *t*)}	4,809.94	48.94	0.000	77	4,643.214
{φ(.) p(s × *t*) γ(.)}	4,809.97	48.97	0.000	42	4,722.279
{φ(*t*) p(s × *t*) γ(*t*)}	4,810.84	49.84	0.000	76	4,646.459
{φ(s × *t*) p(s + *t*) γ(.)}	4,810.89	49.89	0.000	58	4,687.780
{φ(s + *t*) p(s × *t*) γ(.)}	4,811.31	50.31	0.000	60	4,683.695
{φ(s × *t*) p(s + *t*) γ(s)}	4,812.98	51.98	0.000	59	4,687.619
{φ(*t*) p(*t*) γ(s × *t*)}	4,813.28	52.28	0.000	75	4,651.231
{φ(*t*) p(s × *t*) γ(s)}	4,813.53	52.53	0.000	60	4,685.909
{φ(s + *t*) p(s × *t*) γ(s)}	4,813.57	52.57	0.000	61	4,683.690
{φ(s + *t*) p(*t*) γ(s × *t*)}	4,814.68	53.68	0.000	76	4,650.296
{φ(*t*) p(s + *t*) γ(s × *t*)}	4,815.97	54.97	0.000	76	4,651.587

(*Continued*)

(*Continued*)

Model	AIC_c	ΔAIC_c	w_i	K	−2log(L)
{φ(s × *t*) *p*(*t*) γ(.)}	4,817.23	56.23	0.000	58	4,694.118
{φ(s × *t*) *p*(*t*) γ(s)}	4,818.24	57.24	0.000	59	4,692.884
{φ(*t*) *p*(s × *t*) γ(.)}	4,818.59	57.59	0.000	59	4,693.226
{φ(.) *p*(s × *t*) γ(s × *t*)}	4,821.42	60.42	0.000	77	4,654.696
{φ(s) *p*(s × *t*) γ(s × *t*)}	4,822.10	61.10	0.000	78	4,653.036
{φ(s × *t*) *p*(s × *t*) γ(*t*)}	4,833.16	72.16	0.000	94	4,625.897
{φ(s × *t*) *p*(s × *t*) γ(s + *t*)}	4,835.56	74.56	0.000	95	4,625.863
{φ(*t*) *p*(s × *t*) γ(s × *t*)}	4,836.07	75.07	0.000	94	4,628.807
{φ(s + *t*) *p*(s × *t*) γ(s × *t*)}	4,836.57	75.57	0.000	95	4,626.871
{φ(s × *t*) *p*(*t*) γ(s × *t*)}	4,839.14	78.14	0.000	94	4,631.875
{φ(s × *t*) *p*(s + *t*) γ(s × *t*)}	4,839.30	78.30	0.000	95	4,629.605
{φ(s × *t*) *p*(s × *t*) γ(.)}	4,840.00	79.00	0.000	77	4,673.274
{φ(s × *t*) *p*(s × *t*) γ(s)}	4,842.33	81.33	0.000	78	4,673.265
{φ(s × *t*) *p*(s × *t*) γ(s × *t*)}	4,867.09	106.09	0.000	112	4,615.244
{φ(s + *t*) *p*(s) γ(*t*)}	4,926.41	165.41	0.000	41	4,840.898
{φ(s + *t*) *p*(s) γ(s + *t*)}	4,927.64	166.64	0.000	42	4,839.946
{φ(s + *t*) *p*(.) γ(*t*)}	4,928.89	167.89	0.000	40	4,845.547
{φ(s + *t*) *p*(.) γ(s + *t*)}	4,928.96	167.96	0.000	41	4,843.447
{φ(*t*) *p*(s) γ(s + *t*)}	4,929.87	168.87	0.000	41	4,844.358
{φ(*t*) *p*(s) γ(*t*)}	4,931.07	170.07	0.000	40	4,847.730
{φ(*t*) *p*(.) γ(s + *t*)}	4,933.57	172.57	0.000	40	4,850.223
{φ(*t*) *p*(.) γ(*t*)}	4,934.16	173.16	0.000	39	4,852.979
{φ(g) *p*(g) γ(*t*)}	4,946.53	185.53	0.000	23	4,899.421
{φ(g) *p*(g) γ(s + *t*)}	4,947.87	186.87	0.000	24	4,898.665
{φ(g) *p*(.) γ(*t*)}	4,948.67	187.67	0.000	22	4,903.660
{φ(g) *p*(.) γ(s + *t*)}	4,948.88	187.88	0.000	23	4,901.770
{φ(.) *p*(s) γ(s + *t*)}	4,949.43	188.43	0.000	23	4,902.322
{φ(.) *p*(s) γ(*t*)}	4,951.09	190.09	0.000	22	4,906.080
{φ(.) *p*(.) γ(s + *t*)}	4,952.76	191.76	0.000	22	4,907.748
{φ(.) *p*(.) γ(*t*)}	4,953.83	192.83	0.000	21	4,910.908
{φ(s × *t*) *p*(s) γ(*t*)}	4,957.27	196.27	0.000	59	4,831.906
{φ(s × *t*) *p*(.) γ(*t*)}	4,958.90	197.90	0.000	58	4,835.794
{φ(s × *t*) *p*(s) γ(s + *t*)}	4,959.30	198.30	0.000	60	4,831.683
{φ(s × *t*) *p*(.) γ(s + *t*)}	4,960.33	199.33	0.000	59	4,834.973
{φ(s + *t*) *p*(s) γ(s × *t*)}	4,961.64	200.64	0.000	60	4,834.025
{φ(*t*) *p*(s) γ(s × *t*)}	4,961.76	200.76	0.000	59	4,836.402
{φ(s + *t*) *p*(.) γ(s × *t*)}	4,963.05	202.05	0.000	59	4,837.687
{φ(*t*) *p*(.) γ(s × *t*)}	4,964.65	203.65	0.000	58	4,841.541
{φ(s) *p*(s) γ(s × *t*)}	4,979.43	218.43	0.000	42	4,891.736
{φ(s + *t*) *p*(s) γ(.)}	4,980.06	219.06	0.000	23	4,932.949
{φ(s) *p*(.) γ(s × *t*)}	4,980.07	219.07	0.000	41	4,894.559
{φ(.) *p*(s) γ(s × *t*)}	4,980.32	219.32	0.000	41	4,894.806
{φ(s + *t*) *p*(s) γ(s)}	4,981.62	220.62	0.000	24	4,932.415
{φ(.) *p*(.) γ(s × *t*)}	4,982.73	221.73	0.000	40	4,899.382
{φ(*t*) *p*(s) γ(s)}	4,982.83	221.83	0.000	23	4,935.721
{φ(s + *t*) *p*(.) γ(.)}	4,984.11	223.11	0.000	22	4,939.102
{φ(s + *t*) *p*(.) γ(s)}	4,984.42	223.42	0.000	23	4,937.315
{φ(*t*) *p*(s) γ(.)}	4,985.02	224.02	0.000	22	4,940.007
{φ(*t*) *p*(.) γ(s)}	4,988.31	227.31	0.000	22	4,943.297
{φ(*t*) *p*(.) γ(.)}	4,989.75	228.75	0.000	21	4,946.824
{φ(s × *t*) *p*(.) γ(s × *t*)}	4,990.09	229.09	0.000	77	4,823.365
{φ(s × *t*) *p*(s) γ(s × *t*)}	4,990.35	229.35	0.000	78	4,821.285
{φ(s × *t*) *p*(s) γ(.)}	5,010.73	249.73	0.000	41	4,925.214
{φ(s × *t*) *p*(s) γ(s)}	5,012.56	251.56	0.000	42	4,924.869
{φ(s × *t*) *p*(.) γ(.)}	5,013.84	252.84	0.000	40	4,930.492
{φ(s × *t*) *p*(.) γ(s)}	5,014.65	253.65	0.000	41	4,929.134
{φ(s) *p*(s) γ(.)}	5,040.31	279.31	0.000	5	5,030.247
{φ(s) *p*(s) γ(s)}	5,042.00	281.00	0.000	6	5,029.916
{φ(.) *p*(s) γ(s)}	5,042.37	281.37	0.000	5	5,032.316
{φ(s) *p*(.) γ(.)}	5,043.88	282.88	0.000	4	5,035.845
{φ(s) *p*(.) γ(s)}	5,044.34	283.34	0.000	5	5,034.283
{φ(.) *p*(s) γ(.)}	5,044.47	283.46	0.000	4	5,036.426
{φ(.) *p*(.) γ(s)}	5,047.40	286.40	0.000	4	5,039.359
{φ(.) *p*(.) γ(.)}	5,048.70	287.70	0.000	3	5,042.673