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DEMOGRAPHY OF NORTHERN GOSHAWKS IN NORTHERN ARIZONA, 1991–1996

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Abstract. We studied 282 nesting attempts on 107 territories of Northern Goshawks (*Accipiter gentilis*) on the Kaibab Plateau in northern Arizona from 1991–1996. Mark-recapture methods were used to estimate recruitment, turnover of adults on territories, fidelity to territories by adults, and apparent annual survival of breeding adults. Territories were regularly spaced at a mean nearest-neighbor distance of 3.9 km. Annual proportion of pairs breeding and recapture rates were high in 1991–1993, sharply declined in 1994, and partially recovered in 1995–1996. Average annual turnover of breeding goshawks was 42% for males and 25% for females. Breeding males stayed on their territories from one breeding year to the next in 97% of cases and females in 95% of cases. Of 64 capture-recapture models evaluated in program SURGE, the model with the lowest AIC {Phi_s, P_t} showed that, while survival differed between genders, it was constant for both genders over years. Probability of recapturing a goshawk varied with time (0.15 in 1994; 0.66 in 1992) but not with gender; recaptures were lowest in years when few of the territorial goshawks nested and highest when the majority of pairs nested.

Key Words: *Accipiter gentilis*, Arizona, capture-recapture, demography, Kaibab Plateau, nesting success, Northern Goshawk, reproduction, survival, territory fidelity, turnover.

DEMOGRAFÍA DE GAVILANES AZOR EN EL NORTE DE ARIZONA, 1991–1996

Resumen. Estudiamos 282 intentos de anidación en 107 territorios de Gavilanes Azor (*Accipiter gentilis*), en la meseta de Kaibab en el norte de Arizona, de 1991–1996. Métodos de Marqueo-recaptura fueron utilizados para estimar aislamiento y reemplazo de adultos en los territorios, fidelidad de los adultos al territorio, y sobrevivencia anual aparente de adultos reproductores. Los territorios fueron espaciados regularmente a una distancia vecino-cercano media de 3.9 km. La proporción anual de parejas reproductoras y las tasas de recaptura fueron altas en 1991-1993, declinaron agudamente en 1994, y se recuperaron parcialmente en 1995–1996. El promedio anual de reemplazo de gavilanes reproductores fue de 42% para machos y de 25% para hembras. Los machos reproductores permanecieron en sus territorios por un año reproductivo al otro en un 97% de los casos, y las hembras en el 95% de los casos. De 64 modelos captura-recaptura estudiados en el programa SURGE, el modelo con el más bajo AIC {Phi_s, P_t} mostró que, mientras la sobrevivencia difirió entre géneros, la sobrevivencia fue constante para ambos géneros a través de los años. La probabilidad de recapturar al gavilán varió con el tiempo (0.15 in 1994; 0.66 in 1992), pero no con el género; las recapturas fueron más bajas en los años en los cuales menos gavilanes territoriales anidaron, y más altas cuando la mayoría de las parejas anidó.

The effects of forest management on Northern Goshawk (*Accipiter gentilis atricapillus*) populations has been the focus of much research since the early 1970s (Boyce et al., *this volume*; Block et al. 1994). It has been hypothesized that harvesting older forests causes declines in goshawk populations by changing the structure of its habitat, the abundance and availability of its prey, and numbers of its predators and competitors. Collection of demographic data such as birth, death, emigration, and immigration rates is important for understanding how each of these is affected by forest management and for assessing goshawk population trends. Such understanding is also useful in developing conservations plans that guide resource management and conservation of species. We have conducted a long-term study of the ecology, diets, genetics, limiting factors (habitat, food, and predators), and vital rates of a goshawk population on the Kaibab Plateau in northern Arizona (Reynolds et al. 1994, Reynolds and Joy 1998, La Sorte et al. 2004, Reich et al. 2004, Reynolds et al. 2004). We report on the distribution and density of breeding pairs, inter-annual variations in proportion of pairs breeding and reproduction, fledgling sex ratio, territorial fidelity, and survival of adult goshawks on the Kaibab Plateau from 1991–1996. This paper is an update of an unpublished report to the Arizona Heritage Program (Reynolds and Joy 1998). It is our intent to present data, collected over the short-term, that will help assess the value of data from what has now become a long-term study of goshawk ecology and demographics.

STUDY AREA

The study area was all of the Kaibab Plateau above 2,182 m elevation (encompasses 1,732 km^2), including both the Kaibab National Forest and the Grand Canyon National Park-North Rim (GCNP). The Kaibab Plateau is an oval-shaped (95 × 55 km), limestone plateau that rises from a shrub-steppe plain at 1,750 m elevation to its highest point at 2,800 m, and is dissected by moderately sloping drainages (Rasmussen 1941). The plateau is bounded by escarpments of the Grand Canyon of the Colorado River on its south side, and by steep slopes on the east, and gentle slopes on the north and west sides, that descend to the plain. Pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodlands occur below the study area, and ponderosa pine (*Pinus ponderosa*), mixed conifer, and spruce-fir (*Picea* spp.-*Abies* spp.) forests predominant on the study area (Reynolds et al. 1994). Structure and composition of forests on the Kaibab Plateau are described in Rasmussen (1941) and White and Vankat (1993), and forest management history is described in Burnett (1991) and Reynolds et al. (1994). Several narrow meadows occur on top of the Kaibab Plateau containing grasses and herbaceous vegetation. Annual precipitation on the Kaibab Plateau averages 67.5 cm, with winter snow packs of 2.5–3.0 m (White and Vankat 1993). Winters are cold and summers are cool. A drought period typically occurs in May and June, followed by a mid- to late-summer monsoon season with frequent (2–4/wk) thunderstorms and heavy showers.

METHODS

FIELD METHODS

We defined territory as an area used by a single pair of goshawks during a nesting season. Territories typically contained multiple alternate nests used by the resident goshawks over years (Reynolds et al. 1994). The size of a goshawk territory (defended area) is unknown, but may be an area whose radius is half the distance between adjacent territories. An occupied territory was defined as a territory in which goshawks were observed on two or more occasions, or a single observation of an adult goshawk combined with the presence of molted feathers, feces, and new nest construction in a season. An active nest (and territory) was a nest in which eggs were laid, and failed nests were nests in which eggs or nestlings were lost (none fledged). A cohort of territories was a year's set of territories that contained active goshawk nests (in a few cases occupied by non-breeding goshawks). New territories found in a particular year were not included in that year's cohort of territories but were added to the next year's cohort (see below). A nest area was a 15–20 ha area surrounding a nest that included prey plucking sites, tree-roosts of the adult goshawks, and one or more alternate nests.

We began searches for goshawk nests (and territories) in the northwest of the Kaibab Plateau in 1991. We also visited historical (pre-1991) nest structures that were on record at the USDA Forest Service Kaibab National Forest that had been identified by forest managers prior to 1991 (see Crocker-Bedford 1990). In subsequent years (1992–1996), searches for nests and territories were expanded to the north, east, and south. At the end of the 1996 breeding season about 80% of the Plateau had been searched; only the extreme south-central portion of the Plateau had not been searched. Nest searches were conducted by systematically walking large areas (1,600–2,400 ha) while inspecting all trees for goshawk nests, and by broadcasting goshawk vocalizations from stations on transects in 2,400–4,800 ha areas using procedures and a broadcast-station distribution described by Kennedy and Stahlecker (1993) and Joy et al. (1994). Nest searches began each April and ended at the close of the post-fledging dependency period (mid-August).

We used a protocol consisting of three sequential components for annually determining the status of nests within territories. In initial visits, all goshawk nests discovered in this study, as well as all historical nests discovered prior to 1991, were visited within the first week post-egg laying (initial visits required one-person-day of effort per territory; historical nests not in known territories were visited independent of territory visits). If goshawks were not using a previously known nest within a territory, a foot search (effort of three–four person-days/territory) was conducted within an 800-m radius from the most recently used nest within a territory. If an active nest was not located in a foot search, a 1,500-m radius area, also centered on the last known active nest, was broadcast (effort of six–seven person-days/territory) with broadcast station distribution and at-station procedures as described in Joy et al. (1994). Once located, all active nests were visited weekly to determine the status of nesting attempts and to trap, band, or re-sight breeding adults. Nest trees were climbed once during the late nestling period to count and band nestlings. Nesting success in studies involving annual nest searches can be overestimated because nests failing early in a season are less likely to be detected than successful nests (Steenhof and Kochert 1982). To control for this, we determined the proportion of territories with breeding goshawks, the production of young, and nesting success only for nests in the previous year's cohort of territories;

that is, only for territories in which monitoring of goshawks and nests began early in a breeding season. However, some active nests were not found until later in the breeding season. We compared annual estimates of nest success in each cohort of territories to annual nest survival in each cohort estimated with the Mayfield (1961) method. This method estimates nest survival based on days of exposure regardless of when in a breeding season nests are found. We made weekly Mayfield visits to nests in 1992–1996. Beginning and ending dates of the incubation and nestling periods were estimated by back-dating from the estimated age of nestlings (see Boal 1994) or known egg laying, hatching, and fledging dates. From these, annual mean dates of egg laying, hatching, and fledging were determined. Days of exposure were calculated using a 32-d incubation period and a 35-d nestling period (Reynolds and Wight 1978). Standard errors of the Mayfield estimates of nest survival were calculated after Johnson (1979).

Nesting adults were trapped in nest areas with dho-gaza traps baited with a live Great Horned Owl (*Bubo virginianus*) during the nestling and early fledgling stages (Bloom 1987), or with falling-end Swedish goshawk traps (Kenward et al. 1983) baited with domestic pigeons (*Columba livia*) (Reynolds et al. 1994). The age (juvenile = 0 yr; adult 1 = 1 yr; adult 2 = 2 yr; adult 3 ≥3 yr) of goshawks was determined by plumage, and gender by behavior prior to capture and by morphometrics subsequent to capture (Reynolds et al. 1994). Fledglings were captured during the last 2 wk of the nestling period by climbing to nests. Adults and fledglings were weighed, measured, and fitted with USGS aluminum leg bands and colored leg bands with unique two-character alpha-numeric codes readable from up to 80 m with 20–40 power spotting scopes (Reynolds et al. 1994).

Locations of nest trees were recorded with global positioning system (GPS) (Trimble Navigation Ltd. 1992, Trimble Navigation Ltd. 1994) and mapped in ArcView (ESRI 1998) geographical information system (GIS). GPS coordinates for each nest tree were generated in the Universal Transverse Mercator (UTM) projection and verified using field plots, topographical knowledge, and site visits. Digital elevation models (DEMs) of 32 7.5-min USGS quadrangles were latticed together to produce a single DEM of the Kaibab Plateau.

Data Analysis

We used UTM coordinates of all nests and ArcView (ESRI 1998) to calculate distances between alternate nests within territories, nearest-neighbor distances among territories, and breeding-dispersal distances. Mean distance between alternate nests within territories was calculated as the mean of distances among all possible combinations of alternate nests within a territory (e.g., nest A-B, B-C, C-A). The nearest-neighbor distances among territories of adjacent pairs of goshawks were calculated as distances between centroids of territories, where territory centroids were the weighted geographic mean of coordinates between alternate nests in a territory (generated in ArcView; ESRI 1998). Means were weighted by the number of times a nest was used during the study period (a nest used in 2 yr was closer to the centroid than a nest used once). In territories in which only one nest was used, the single nest was the centroid for that territory. Nearest-neighbor distances between territory centroids were calculated without using reciprocal measures between nearest-neighbors (Diggle 1983).

Ripley's k-function (Ripley 1981, S-PLUS 1995) was used to model the distribution of 103 territory centroids (four territories in the southeastern portion of the GCNP where excluded due to incomplete nest searches there). This procedure counts centroids that fall within a designated distance of each centroid to provide a measure of dispersion, corrected for edge effects (Cressie 1991). Observed counts [L(t)] were plotted against the distances at which the counts were made and compared with 95% dispersion (confidence) envelopes estimated from 100 populations of 100 points simulated under complete spatial randomness (CSR process). Points below the envelopes reflect regular (simple sequential inhibition [SSI]) spacing; points within the envelopes reflect random spacing, and points above envelopes reflect aggregated spacing (Neyman-Scott). We modeled the k-function of centroids to 15 km to capture all possible inter-territory distances. The Cramer-von-Mises goodness-of-fit statistic (Cressie 1991) was used to test the null hypothesis that the data were from a CSR process at the $\alpha = 0.05$ level. Rejection of the null hypothesis required fitting the data to the alternative k-function of a regular (Pielou 1960, Strauss 1975) or aggregated (Neyman and Scott 1957) process and comparing the centroids' distribution against the appropriate simulation envelope. Alternate distributions were followed by a Cramer-von-Mises goodness-of-fit (Cressie 1991) test of suitability of the alternate process. All spatial analyses were performed using S-PLUS (1995) and the spatial library developed for S-PLUS by Reich and Davis (2002).

Territory fidelity was calculated from bird years, the number of successive years in which goshawks

TABLE 1. NUMBER OF NORTHERN GOSHAWK TERRITORIES UNDER STUDY AND THEIR ANNUAL STATUS (ACTIVE, OCCUPIED, UNKNOWN) ON THE KAIBAB PLATEAU, ARIZONA, 1991–1996.

	Year					
Territories	1991	1992	1993	1994	1995	1996
Total	37	64	82	88	100	107
Active	36	59	67	21	53	46
Occupied	1	2	6	13	20	23
Status unknown	0	3	9	54	27	38

were recaptured/re-sighted and, thus, were known to have stayed on the same territory or moved to a new territory (Newton and Wyllie 1996). Turnover is the replacement of a banded goshawk on a territory in a previous season by a new goshawk in a current season. A goshawk may be replaced on a territory due to its death or breeding dispersal. Turnover opportunities were cases where the identity of a male or female on a territory was known in successive years. The demographic portion of this study consisted of capturing, banding, and releasing nesting goshawks, followed by recapturing or re-sighting them in subsequent breeding seasons. Age, sex, and reproductive status of individuals were determined as described above. All nest trees were climbed within 14 d of fledging to band and count nestlings.

The number of young in nests at banding was our estimate of productivity. For nests found late in a breeding season (mostly in new territories), productivity was estimated by counting fledged young during the post-fledgling dependency period. Sex ratio was estimated by counts of male and female nestlings at banding. Nestlings were sexed on the basis of body mass and tarsus-metatarsus length. Only broods where the sex of all brood members was determined were used to estimate sex ratio. Capture-recapture histories of individual goshawks provided for parameter estimation and hypothesis testing in capture-recapture analysis of survival. Capture is defined as the capturing or re-sighting (i.e., reading a goshawk's alpha-numeric color band with telescopes) of individual goshawks. Estimates of annual survival rates were calculated using Cormack-Seber-Jolly open population models in program SURGE (Pollock et al. 1990, Franklin et al. 1996). Akaike's Information Criterion (AIC) was used to identify models that best fit the data (Akaike 1973, Anderson et al. 1985, Burnham et al. 1992, Franklin et al. 1996). Goodness-of-fit tests in program RELEASE were used to evaluate how well the data met the assumptions in the capture-recapture models (Pollock et al. 1985, Burnham et al. 1987).

RESULTS

NUMBER AND OCCUPANCY OF TERRITORIES

Numbers of territories in the study increased annually as searches for new territories were expanded (Table 1). By the end of the 1996 breeding season, about 95% of the national forest lands, and about 30% of the GCNP, had been searched for goshawk nests. A final total of 107 territories were located (Fig. 1), resulting in 478 territory-years of study. All but two of the 107 territories contained active nests in one or more breeding seasons. The two exceptions were territories occupied two or more years by goshawks that built new nests or

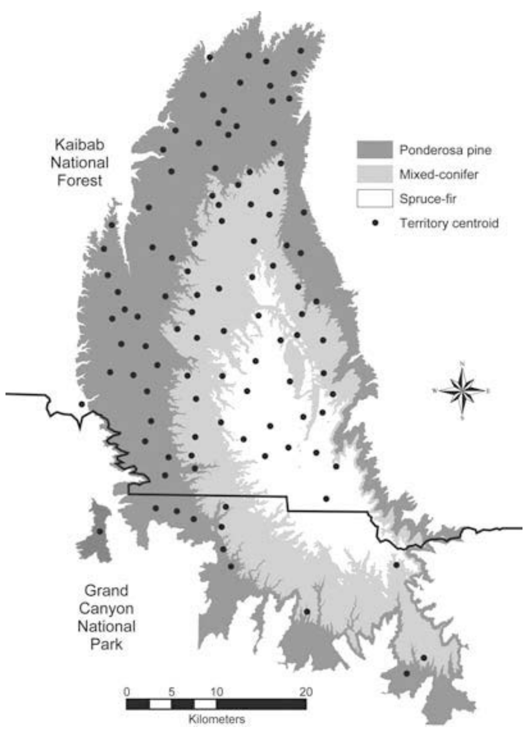

FIGURE 1. Locations of 107 Northern Goshawk territories on the Kaibab Plateau, Arizona, 1991–1996.

reconstructed old nests, but were not known to have laid eggs during the study.

From 1991 through 1993, the increase of territories with active nests was proportional to increases in territories under study (Table 1). However, in 1994 numbers of territories with active nests declined to 21, increased to 53 in 1995, and declined again to 46 in 1996. Annually, variable numbers of territories with unknown status reflected the difficulty of unambiguously determining the occupancy status (presence or absence) of goshawks on territories in years when they did not lay eggs. This ambiguity results from the difficulty of proving that goshawks are not present despite 8–12 person-days of searching for pairs in known territories.

Nesting Success and Productivity

The proportion of pairs breeding in the prior year's cohort of territories was highest in 1992 and 1993, declined in 1994, and partially recovered in 1995 and 1996 (Table 2). Annual percent of nests failing did not significantly differ among years (14–28%). Annual nesting success was similar for the cohort of territories and Mayfield estimates; the two estimates differed by no more than 4% in any year, and neither was consistently higher or lower than the other (Table 2).

In 1996, the first three cohorts of territories (1991–1993) had 6, 5, and 4 yr of data on territory status, respectively. The overall decline in the proportion of territories active from 1992–1994 is reflected in the declining numbers of years newly discovered territories in each of the first three territory cohorts were active in subsequent years. For the 36 new territories discovered in 1991, the largest proportion (31%) was active for five of the six (83% of years) subsequent study years, for the 27 new territories in the 1992 cohort, the largest proportion (41%) was active in three of the five (60% of years) years, and for the 18 new territories in the 1993 cohort, the largest proportion (50%) was active in two of the four (50% of years) years (Table 3).

Brood size on the Kaibab Plateau ranged from one to three nestlings (median = 2); 63 (28%) of a total 224 successful broods had one young, 112 (50%) had two young, and ten (22%) had three young. Mean number of fledglings produced per active and successful nests generally declined from the better breeding years in 1991–1993 to lows in 1994–1996 (Table 4), but nesting success remained relatively constant over years (Table 2).

Of 282 nesting attempts in which eggs were laid on the Kaibab Plateau, 46 (16%) were known to have failed. Of the 46 failures, 16 (35%) failed during incubation and 30 (65%) failed during the nestling stage. Of clutches that failed during incubation, four contained both fertile and infertile eggs, three contained only fertile eggs, and 12 contained only infertile eggs. Mean clutch size of failed nests was 1.6 eggs (SD = 0.63; range = 1–3 eggs). Nest failures in the nestling period typically occurred in the first two wks after hatching. Except in the 12 clutches with infertile eggs, we were unable to determine causes of nest failures. Eggs buried under fresh greenery in nests were recovered from 15 nests that fledged young; three of these nests contained buried fertile eggs (dead embryo), and 12 contained infertile eggs.

Nestling Sex Ratio and Recruitment

We determined the sex of each nestling in 125 broods. Combining years, there were 126 females

Table 2. Number of territories in cohort (know territories from previous years), number and percent of territories with active nests, number and percent with failed nests, and two estimates of nesting success (the Mayfield [1975] estimate of nest survival and our cohort method) of Northern Goshawks on the Kaibab Plateau, Arizona, 1991–1996.

	Year				
Territories	1992	1993	1994	1995	1996
Territories in cohort	37	64	82	88	100
Territories with active nests	32	49	18	44	40
% with active nests	87[a]	77[a]	22[b]	50[c]	40[bc]
Number with failed nests	6	7	5	11	9
% failed nests	19[a]	14[a]	28[a]	25[a]	23[a]
% successful	81	86	72	75	77
Mayfield estimate	0.79	0.83	0.75	0.76	0.73
se, Mayfield estimate	0.002	0.001	0.003	0.001	0.002

[a, b, c] Within rows, numbers followed by the same letter are not significantly different according to pairwise comparisons of multiple proportions ($\alpha = 0.05$) (Goodman 1964).

TABLE 3. NUMBER AND PROPORTION OF NEW NORTHERN GOSHAWK TERRITORIES DISCOVERED EACH SUCCESSIVE YEAR (1991–1996) THAT CONTAINED ACTIVE NESTS (EGGS LAID) IN N NUMBERS OF YEARS (NOT NECESSARILY CONSECUTIVE) ON THE KAIBAB PLATEAU, ARIZONA, 1991–1996.

Year	New territories found	Number of years with active nests 1	2	3	4	5	6
1991	36	0.06 (2)[a]	0.14 (5)	0.28 (10)	0.14 (5)	0.31 (11)	0.08 (3)
1992	27	0.04 (1)	0.33 (9)	0.41 (11)	0.15 (4)	0.07 (2)	
1993	18	0.28 (5)	0.50 (9)	0.11(2)	0.11 (2)		
1994	6	0.33 (2)	0.67 (4)				
1995	11	0.73 (8)	0.27 (3)				
1996	7	1.00 (7)					

Notes: Two territories were occupied by goshawks but never had active nests in the study (one occupied in 1991, one in 1995). Total number of territories under study in 1996 was 107.

[a] Number of territories with active nests in parentheses.

TABLE 4. NUMBER OF ACTIVE (EGGS LAID) AND SUCCESSFUL (FLEDGED AT LEAST ONE YOUNG) NESTS, AND MEAN NUMBER AND STANDARD DEVIATION (SD) OF FLEDGLINGS PER ACTIVE AND PER SUCCESSFUL NORTHERN GOSHAWK NEST ON THE KAIBAB PLATEAU, ARIZONA, 1991–1996.

	Year 1991	1992	1993	1994	1995	1996
Active nests[a]	36	59	64	21	49	44
Fledglings/active nest	2.0[c]	1.8[cd]	1.7[cd]	1.2[d]	1.3[d]	1.3[d]
SD	0.79	1.05	1.00	0.93	0.92	0.90
Successful nests[b]	34	49	54	15	39	33
Fledglings/successful nest	2.1[cd]	2.2[c]	2.0[ce]	1.7[ce]	1.6[e]	1.7[de]
SD	0.64	0.72	0.74	0.62	0.71	0.59

[a] Number of nests where exact number of fledglings was determined.

[b] Successful nests fledged ≥1 young.

[c, d, e] Within rows, means followed by the same letter are not significantly different according to the Tukey-Kramer multiple comparison procedure (α = 0.05).

(54.3%) to 106 males (45.7%), not significantly different from a 1:1 sex ratio (χ^2 = 1.72; df = 1; P = 0.212). Of the 256 nestlings banded as nestlings on the study area, only six (three males; three females) (2%) were subsequently recaptured as breeding adults on the study area. Males were 3–5 yr-old ($\bar{x}$ = 4.0 yrs-old) and females were 2–4 yr-old ($\bar{x}$ = 2.7 yr-old) at recruitment.

TERRITORY DISPERSION

Ripley's k-function (Fig. 2) showed that territory centroids were spaced regularly at distances of 1.4–2.5 km, distributed randomly at distances of 2.5–5.0 km, and appeared aggregated at distances >8.5 km. We rejected (Cramer-von-Misses; P <0.001) the null hypothesis of a CSR process in overall distribution. Because clustering evident at large (>8.0 km) inter-centroid distances was assumed to reflect the shape of the study area and not true territory aggregation, we tested only the alternative spatial distribution of centroids between distances of 0–2.5 km. This range of distances was correctly modeled using the SSI process (Cramer-von-Mises; P = 0.98; Fig. 3) indicating a regular distribution of centroids at these distances. The minimum distance between territory centers was 1.4 km. The mean nearest-neighbor spacing of the 103 territory centroids (excluding four territories in areas not fully searched) was 3.9 km (SD = 0.322 km). This is 0.9 km less than the mean distance between centroids for nests in 59 territories on the Kaibab Plateau in 1992 (Reynolds et al. 1994), and reflects the addition of 44 territories in an area only slightly larger than the area containing the 1992 sample of 59 territories (Reynolds et al. 1994).

We estimated the potential total number of nesting pairs of goshawks on the study area by calculating an exclusive circular area of the average pair of goshawks by using one-half (1.95 km) of the mean nearest-neighbor distances (3.9 km) as a radius and dividing the study area (173,200 ha) by that exclusive area (1,195 ha). We used the mean because the centroids were from a regularly distributed

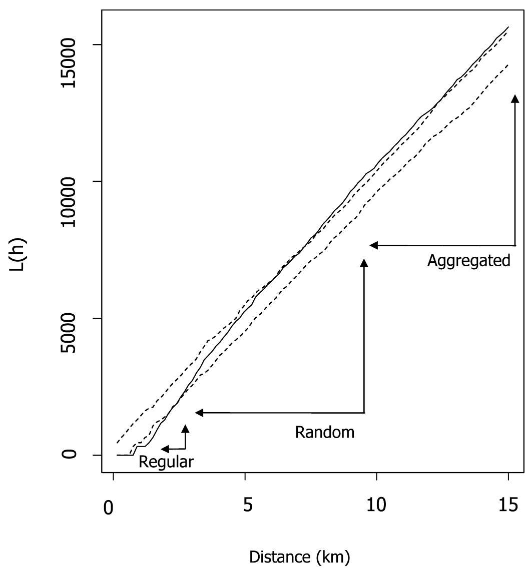

FIGURE 2. K-function showing the spatial distribution (solid line) of Northern Goshawk territory centroids on the Kaibab Plateau (1991–1996) within 0–15 km compared with the distribution of a hypothetical goshawk population modeled under complete spatial randomness (CSR). Regular spacing of centroids is indicated at inter-territory distances where the actual distribution falls below the confidence envelopes for CSR (dashed lines).

population (see above) suggesting that the mean distance was a good estimator of the dispersion of pairs. The extrapolation to the entire study area was reasonable because forests were nearly continuous throughout the study area (Fig. 1). Our estimate of the total breeding population on the study area was 145 pairs. Thus, the 107 territories identified in 1991–1996 comprised about 73% of the potential nesting population on the study area.

Spacing and Use of Alternate Nests

Territorial pairs of goshawks often nest in one or more alternate nests within their territories (Reynolds and Wight 1978, Detrich and Woodbridge 1994, Reynolds et al. 1994). On the Kaibab Plateau, Reynolds et al. (1994) showed that uniquely colored-marked goshawks moved up to 635 m to alternate nests. Of the 105 Kaibab territories in which eggs were laid in 1991–1996, 59 contained two or more alternate nests used during the study: 43 (41%) contained two alternate nests, 12 (12%) contained three alternate nests, and four (4%) contained four alternate nests. Of course, the longer a study, the greater the likelihood that more alternate nests will be used. The mean distance among alternate nests within territories was 489 m (SD = 541; min = 21 m; max = 3,410 m; median = 285 m; N = 103 alternate nests). The distribution of inter-alternate nest distances was strongly right skewed; 89% of alternate nests were within 900 m, and 95% within 1400 m, of one another (Fig. 4). On the Kaibab Plateau, the proportion of pairs that moved annually to alternate nests ranged between 55–76% ($\bar{x}$ = 63%; SD = 8.3%; Table 5). A mean of 27% (SD = 8.5%) of these annual movements were returns to alternate nests used earlier in the study.

Turnover on Territories

Annual turnover of adults on territories varied from 0–40% for males and from 0–50% for females (Table 6). For the sexes combined, the year with fewest turnovers was 1994—the year with the fewest breeding pairs and the fewest opportunities to detect turnovers had they occurred. The year of highest turnover for males was 1992, and for females, 1995. Male turnovers were relatively constant among years compared to female turnovers. Total turnover for males and females during the 6-yr study was 25% and 19%, respectively (Table 6).

Territory Fidelity

Tenure on territories by males and females ranged from 1–6 yr. Mean number of years breeding goshawks in the 1991 cohort (N = 36 active territories;

TABLE 5. PERCENT OF PAIRS OF NORTHERN GOSHAWKS THAT MOVED TO AN ALTERNATE NEST WITHIN THEIR TERRITORY EACH YEAR ON THE KAIBAB PLATEAU, ARIZONA, 1991–1996.

	Year					
Movement	1992	1993	1994	1995	1996	Total
Stayed	45 (14)[a]	35 (17)	39 (7)	43 (18)	24 (9)	37 (65)
To new alternate	55 (17)	53 (26)	39 (7)	40 (17)	43 (16)	47 (83)
To prior alternate		12 (6)	22 (4)	17 (7)	32 (12)	16 (29)
Percent of total moving	55 (17)	65 (32)	61 (11)	57 (24)	76 (28)	63 (112)

[a] Number of movements is in parentheses.

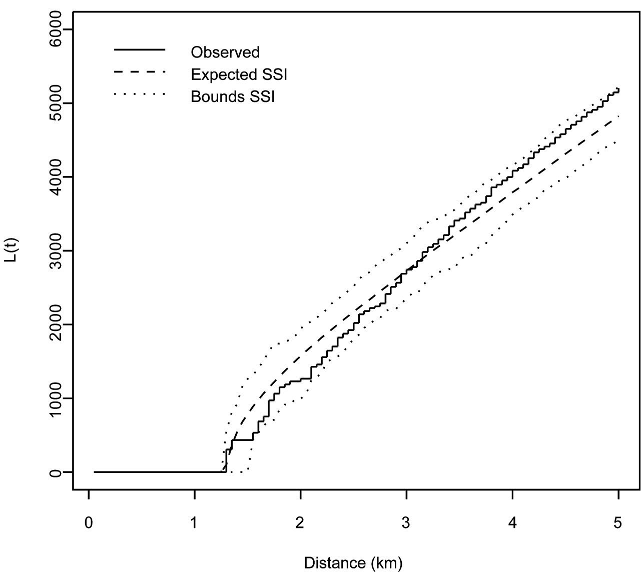

FIGURE 3. K-function showing the spatial distribution (solid line) of Northern Goshawk territory centroids on the Kaibab Plateau (1991–1996) at inter-centroid distances of 0–5 km compared with the distribution of a hypothetical Northern Goshawk population modeled with a simple sequential inhibition (SSI) process (dashed line). The model correctly captures the regular spacing of centroids between 2.5 km and 1.4 km. No territory centroids occurred within 0–1.4 km of other centroids in the actual population. Variegated lines represent 95% confidence limits around the SSI population.

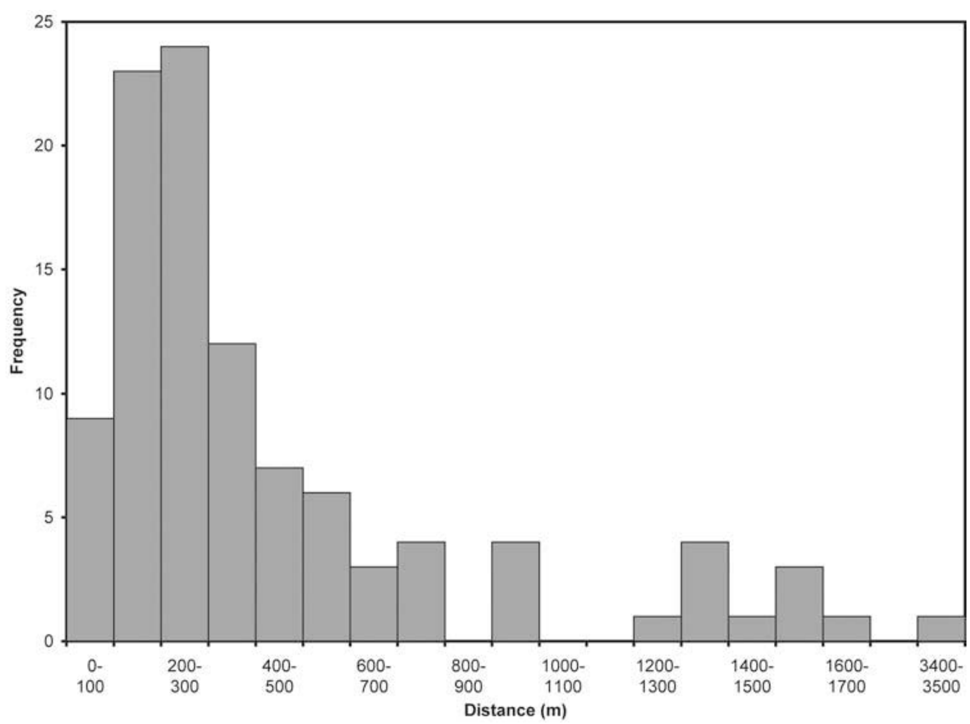

FIGURE 4. Frequency distribution of inter-alternate nest distances within Northern Goshawk territories on the Kaibab Plateau, Arizona, 1991–1996.

TABLE 6. ANNUAL TURNOVER OF MALE AND FEMALE NORTHERN GOSHAWKS IN TERRITORIES ON THE KAIBAB PLATEAU, ARIZONA, 1991–1996.

	1992		1993		1994		1995		1996		Total	
	M	F	M	F	M	F	M	F	M	F	M	F
Turnovers	4	3	3	2	0	0	1	3	1	2	9	19
Opportunities[a]	10	19	12	22	4	5	5	6	5	11	36	99
% turnover	40	16	25	9	0	0	20	50	20	18	25	19

[a] Opportunities = number of breeding seasons (subsequent to year when a breeding goshawk was first banded on a territory) in which either the original or new (= turnover) breeding goshawk was captured/re-sighted on the original territory.

6 yr of study) remained on their territories was 1.4 yr for males and 1.9 yr for females. For the newly discovered territories in the 1992 cohort (N = 27 territories; 5 yrs of study), males remained on territories a mean of 1.6 yr and females 1.8 yr. Too few years were available for meaningful fidelity estimates in later cohorts. Both male and female breeders showed high fidelity to their territories and there was no significant difference in gender fidelity rates (χ^2 = 0.22; df = 1; P = 0.71; Binomial Proportion test). Breeding males remained faithful to their territories in 97% of cases (55 of 57 bird yrs) and females in 94% of cases (92 of 97 bird yrs). In 154 opportunities (bird years) to detect breeding dispersal (change of territory), two males and five females did so; and none of these retained the same mate in the move.

SURVIVAL ESTIMATION

Sample size and goodness-of-fit

During the 6-yr study, we banded 449 goshawks, including 86 males and 87 females that were ≥3 yr old, eight males and 12 females that were 1or 2 yr old, and 256 nestlings. Because only six nestlings banded were recaptured on the study area in subsequent years, we were unable to estimate survival for the juvenile age class (<1 yr old). In addition, only eight male and 12 female 1- or 2 yr-old goshawks were captured, too few to estimate survival rates for these age classes. We therefore combined the 1- and 2-yr-old goshawks with the ≥3 yr old into a non-juvenile age class of goshawks ≥1 yr old. Total number of ≥1-yr-old goshawks included in the capture-recapture analysis was 193 (94 males; 99 females). The number of times these goshawks were captured (or re-sighted) and released (R_i) is displayed in an M-array (Table 7). Annual recapture/re-sighting rates ranged from a low of 15% (1994) to a high of 66% (1992) (model 1; see below). Goodness-of-fit tests in program RELEASE (Burnham et al. 1987) showed no differences in survival or recapture probabilities for males and females. Thus, there was no lack-of-fit to assumptions of Cormack-Seber-Jolly open population models.

Model selection

Of 64 models examined, the five top models (those with the lowest AIC values) all had time effects, and two of the top five models had time and sex effects, associated with the recapture probabilities (Table 8). In these models, capture probabilities ranged from a high of 0.7 in 1992 to a low of 0.2 in 1994, and in models with sex effects (models 3 and 4) males had lower capture probabilities than females. Lower capture probabilities for males may have resulted from greater difficulties of capturing or resighting males than females, higher male mortality rates, or higher emigration rates. Time effects on recapture probabilities corresponded to the variable annual proportions of goshawk pairs laying eggs. This at least partially reflects the fact that only breeding goshawks could be captured or resighted. Survival varied with sex in all except one (model 4) of the five top models, and three models (models 2, 3, 5) had survival varying with time. The top model ({Phi_s, P_t}) had males and females surviving at different, but annually constant, rates—0.69 (SE = 0.062) for males and 0.87 (SE = 0.051) for females. The second best model ({Phi_{s+T}, P_t}) had a sex effect and a linear time trend increasing over years—from 0.54 (SE = 0.13) in 1992 to 0.94 (SE = 0.12) in 1996 for males, and from 0.83 (SE = 0.08) in 1992 to 0.99 (SE = 0.04) in 1996 for females (Figs. 5 a, b). The fourth model (Phi, P_{s+t}) had a no-sex effect survival estimate of 0.82 (SE = 0.048; both males and females). Likelihood ratio tests (LRT) for the top four nested models showed no significant difference in model fit (differences in deviance) among the four models, only two of which contained temporal survival effects. No strong evidence of a time effect on annual survival was found.

DISCUSSION

Mean annual numbers of fledglings produced per active nest on the Kaibab Plateau (range,

TABLE 7. CAPTURE-RECAPTURE DATA IN M-ARRAY FORMAT FOR FEMALE AND MALE NORTHERN GOSHAWKS INITIALLY CAPTURED AS ≥1-YR-OLD ADULTS ON THE KAIBAB PLATEAU, ARIZONA, 1991–1996.

			M_{ij} for j =					
Age class	i	R_i	2	3	4	5	6	r_i
Non-juvenile (>1yr) male	1	19	7	2	0	1	0	10
	2	19		8	1	1	1	11
	3	28			5	2	3	10
	4	14				4	0	4
	5	27					4	4
Non-juvenile (>1yr) female	1	28	18	11	3	0	0	21
	2	39		20	0	3	4	27
	3	37			5	4	5	14
	4	11				3	1	4
	5	30					9	9

Notes: R_i is the number of goshawks marked and released on the *i*th occasion in the study, M_{ij} the number of goshawks marked and released on occasion *i* which were recaptured (or re-sighted) on occasion *j*, and r_i the total number of goshawks marked and released on occasion *i* which were later recaptured (= Σm_{ij}).

TABLE 8. TOP FIVE OF 64 AIC RANKED CAPTURE-RECAPTURE MODELS FOR ESTIMATING SURVIVAL OF NORTHERN GOSHAWKS ON THE KAIBAB PLATEAU, ARIZONA, 1991–1996.

				LRT		
Model[a]	Deviance	K	AIC	χ^2	df	P
1. {Phi_s, P_t}	490.126	7	504.13			
2. {Phi_{s+T}, P_t}	488.192	8	504.19	1.93[b]	1	0.165
3. {Phi_{s+T}, P_{s+t}}	487.558	9	505.56	0.64[c]	1	0.424
4. {Phi, P_{s+t}}	491.695	7	505.69	4.14[d]	2	0.126
5. {Phi_{s+t}, P_t}	485.745	10	505.75	4.38[e]	3	0.126
16. {Phi, P_t}	497.349	6	509.32	7.22[f]	1	0.007

Note: Model 16 included for comparison to model 1, sex effects vs. no sex effects on survival.
[a] Models that best fit the data are indicated by lowest AIC values. K is the number of estimable parameters for each model. Subscripts associated with Phi (survival) and P (recapture probability) indicate these parameters have a linear time trend (T), a variable time effect (t), a sex effect (s), or some additive effect. Models of Phi and P without subscripts indicate no time or sex effects on survival or recapture rates.
[b] Comparison of model 2 vs. model 1.
[c] Comparison of model 3 vs. model 2.
[d] Comparison of model 4 vs. model 3.
[e] Comparison of model 5 vs. model 1.
[f] Comparison of model 16 vs. model 1.

1.2–2.0 young) were at the lower range of values reported in other North American goshawks (1.7 young/nests in Oregon [Reynolds and Wight 1978], 3.8 young in Utah [Lee 1981a], 2.5 young in Alaska [McGowan 1975], 2.0–2.8 young in Nevada [Younk and Bechard 1994a], 2.6 young in Montana [Clough 2000]), but were similar to production of young per active nest in Oregon (0.3–2.2 young [DeStefano et al. 1994a]). Mean number of young produced per successful nest on the Kaibab Plateau (1.6–2.2 young) was also at the lower end of the range reported elsewhere (3.9 young per successful nest in Canada [Doylele and Smith 1994]), 3.6 young in Utah [Lee 1981a], and 2.0–3.0 young in Alaska [McGowan 1975]). Mean annual nesting success on the Kaibab Plateau (77%; Mayfield method) was lower than some values reported for other goshawk populations (90% in Oregon [Reynolds and Wight 1978]), and 84–100% in Nevada [Younk and Bechard 1994a]), but higher than others (67% in Montana [Clough 2000]). To our knowledge there are no reports of unequal sex ratios of nestling goshawks in North America. However, in a sample of Cooper's Hawk (*Accipiter cooperii*) nestlings (N = 1,337) considerably larger than our sample of goshawks, (Rosenfield et al. 1996) reported a sex ratio significantly skewed in favor of males (54%) over females (46%). A significantly skewed sex ratio in favor of males has also been reported in Harris's Hawk (*Parabuteo unicinctus*) (Bednarz and Hayden 1991).

Goshawk survival varied by gender in four of the top five models, and male survival was lower than female survival in each of the four models. A similar gender effect in survival was also reported for goshawks in California (DeStefano et al. 1994b).

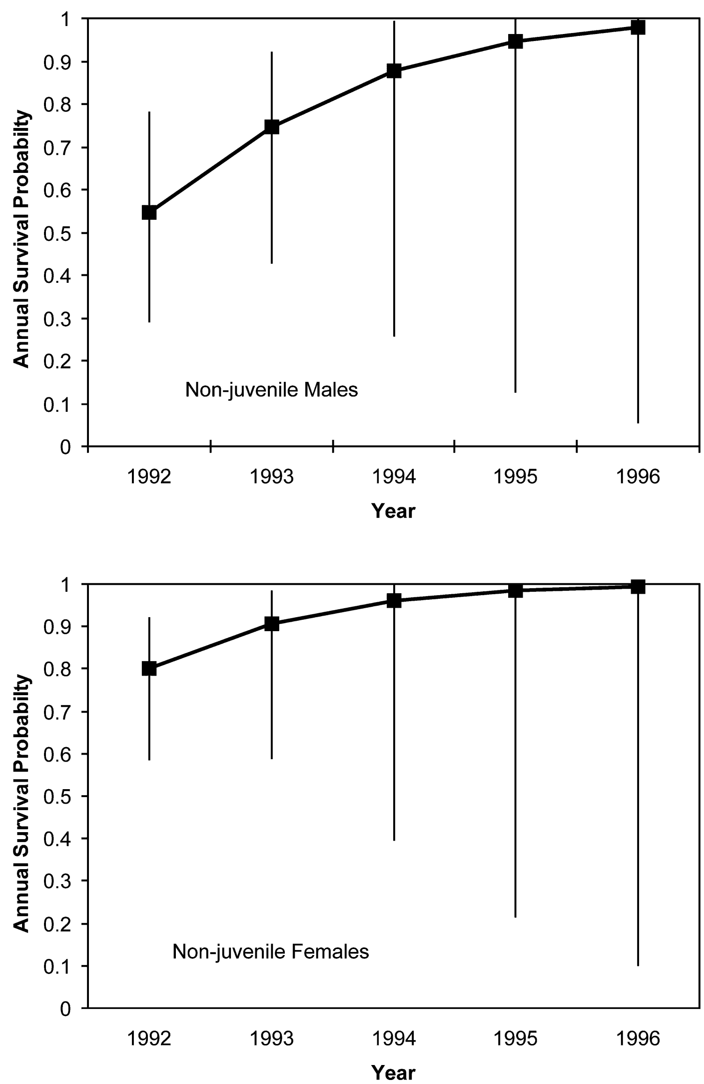

FIGURE 5. Estimates of annual survival for non-juvenile (≥1 yr old) male (a) and female (b) Northern Goshawks under the second-best model (Phis+T, Pt) on the Kaibab Plateau, Arizona, 1991–1996.

While the number of goshawks born, banded, and subsequently recruited as breeders on the Kaibab Plateau was small, ages of Kaibab goshawks at first breeding were greater for males than females. Delayed breeding in males relative to females on the Kaibab Plateau parallels the rarer reports of juvenile males nesting compared to more common reports of juvenile females nesting (McGowan 1975, Reynolds and Wight 1978, Younk and Bechard 1994a). A more advanced age of males at first breeding might result from greater difficulties for males to gain breeding territories. However, the lower apparent survival of males on the Kaibab Plateau argues that there ought to have been more male vacancies on territories, allowing males to be recruited at younger ages. More years of capture-recapture study of survival, and additional known-aged recruits, are needed to confirm gender effects on survival and recruitment.

The precision of capture-recapture estimates of survival are sensitive to recapture probabilities (Pollock et al. 1990). While our survival estimates of breeding goshawks were based on capture-recapture histories of 193 individuals and 6 yr of study, capture probabilities of these goshawks were quite low in some years (1994 and 1996). A large part of the annual variation in capture probabilities stemmed directly from the difficulties of capturing non-breeders and the large annual variations in the proportions of goshawks breeding. However, some variation in capture probabilities was surely the result of mortality, emigration, or both. While the relative contribution of mortality and emigration to the variable recapture rates was unknown, we argue that emigration of adults from the Kaibab Plateau was likely to have been rare because of a near lifetime fidelity of both genders to their breeding territories (Reynolds, unpubl. data), the lack of detected medium- or long-distance breeding dispersals within our study area (maximum distance of seven known breeding dispersals was 8.6 km, or less than the width of three territories), and that the isolation of our study area would have required emigrants to travel long distances in shrub-steppe habitat to find other suitable forests (Reynolds et al. 2004). Thus, emigration was probably rare, making it likely that mortality was a more important contributor to variation in recapture rates.

Since 1998, the lower survival estimate of male relative to female Kaibab Plateau goshawks has been of concern. However, an analysis of seven additional years (1997–2003) of capture-recapture of breeders on the Kaibab Plateau, showed that survival was the same for both males and females (no sex effects on survival) (Reynolds et al. 2004). Also, in the 2004 analysis, the survival estimates of 14 adult males that had received tail-mounted radio transmitters in 1991 and 1992 was nearly two-thirds lower than survival of males without tail-mounts (0.29 vs. 0.75) (Reynolds et al. 2004). Thus, the lower survival of males vs. females in 1991–1996 likely reflected the reduced survival of these 14 males with tail-mounts. The 14 males also comprised a relatively large proportion of the males included in that 1998 survival analysis.

Goshawk territories on the Kaibab Plateau appeared to be spatially and temporally fixed. Territories were occupied by known (banded) goshawks, most of which remained on the same territories their entire reproductive lives, and, when these goshawks did not return in the spring, they were replaced by new (unbanded or locally-banded hawks) goshawks typically within 1–3 yr. Furthermore, replacement goshawks continued to use the same nests and nest areas as the preceding goshawks. Regular spacing of territories at short nearest-neighbor distances (compare to Reynolds and Wight 1978, but see Woodbridge and Detrich 1994), the nearly complete filling of searched forests with territories, the low recruitment rates of locally produced goshawks and their relatively advanced age when first recruited as breeders, suggest the habitat on the Kaibab Plateau is saturated with territories and that the population of breeders is somewhat stable over years. Low recruitment and advanced age of goshawks at first breeding suggest that territories were occupied and young goshawks had to wait 2–5 yr before territories became available.

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