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# POST-FLEDGING SURVIVAL OF NORTHERN GOSHAWKS: THE IMPORTANCE OF PREY ABUNDANCE, WEATHER, AND DISPERSAL

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*Abstract.* Effective wildlife conservation strategies require an understanding of how fluctuating environmental conditions affect sensitive life stages. As part of a long-term study, we examined post-fledging and post-independence survival of 89 radio-marked juvenile Northern Goshawks (*Accipiter gentilis*) produced from 48 nests in northern Arizona, USA, during 1998–2001. Information-theoretic methods were used to examine within- and among-year variation in survival relative to environmental (prey abundance, weather), territory (hatching date, brood size), and individual (gender, body mass) sources of variation. The results support age- and cohort-specific differences in survival that were best explained by behaviors occurring at distinct stages of juvenile development, annual changes in the density of primary bird and mammal prey species, and gender-related differences in body mass. Survival between fledging and independence increased linearly with age and varied among annual cohorts of radio-marked juveniles from 0.81 (95% CI = 0.60–0.93) to 1.00 (95% CI = 0.95–1.00) in association with annual differences in prey density; the slope coefficient for the additive effect of prey density on survival was 1.12 (95% CI = 0.06–2.19). Survival declined to 0.71 (95% CI = 0.60–0.93) shortly after juveniles initiated dispersal (weeks 8–12 post-fledging) and moved to more open habitats at lower elevations. Survival was not closely associated with weather or territory-level parameters. A comparison of the predictions of environmental-, territory-, and individual-based models of survival demonstrated that food availability was the primary factor limiting juvenile survival. This finding indicates that forest management prescriptions designed to support abundant prey populations while providing forest structural conditions that allow goshawks to access their prey within breeding areas should benefit juvenile survival.

*Key words:* Accipiter gentilis; *Arizona, USA; dispersal; distance sampling; juvenile survival; known-fate models; Northern Goshawk; prey abundance; radiotelemetry; weather.*

## INTRODUCTION

Understanding how sensitive life history stages respond to changing environmental conditions is a crucial step in developing conservation strategies for wildlife populations. In birds, survival over the first several months of life is perhaps the most sensitive life history component to environmental change, yet it is also one of the most difficult demographic parameters to reliably estimate. As a consequence, little is known about this life history stage and its contribution to population dynamics. Information on juvenile survival is needed to identify those life history parameters that most strongly affect rates of population change (Noon and Biles 1990). Such information can also improve estimates of reproductive success and help to identify important ecological factors that limit population size (Anders et al. 1997, Thomson et al. 1999). For example, high temporal variation in the number of new individuals entering the breeding segment of a population may result from temporal variation in juvenile survival (Franklin et al. 2000, Reed et al. 2003), which can arise from changes in the environment during sensitive stages of juvenile development (Monrós et al. 2002, Todd et al. 2003).

In birds of prey, it is generally believed that as many as half of the birds that fledge subsequently die in their first year, and that mortality peaks in the first several months after fledging (Newton 1979). During this time, fledglings are typically dependent on their parents for food and stay within the natal area until the initiation of juvenile dispersal (Kenward et al. 1993*a*). The period of transition from a dependent fledgling to an independent juvenile (the fledgling dependency period) is a critical stage for survival because feather growth is incomplete and flight skills are developing, leaving the young highly susceptible to predation, starvation, and exposure (Anders et al. 1997, Thompson et al. 1999, Naef-Daenzer et al. 2001). Indeed, raptor mor-

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tality during this time has often been linked to predation and starvation (Korpimäki and Lagerström 1988, Kenward et al. 1999, Dewey and Kennedy 2001). However, because juveniles are inexperienced foragers facing new hazards without parental protection, mortality is likely to increase during the period immediately following independence (the post-independence period).

The Northern Goshawk (*Accipiter gentilis*) is a large, forest-dwelling raptor that occupies mature boreal and temperate forests throughout the Holarctic (Squires and Reynolds 1997). Similar to controversies surrounding conservation of the Northern Spotted Owl (*Strix occidentalis caurina*) in the Pacific Northwest United States (Noon and McKelvey 1996), the goshawk's selection of nest sites in old and mature forests has resulted in conflicts with management activities such as tree harvests and fire suppression (Reynolds et al. 1992). Initial concern over the potential effects of forest management on goshawk viability led to the species being designated as ''sensitive'' by the U.S. Forest Service (Block et al. 1994). More recently, petitioners have sought to protect the goshawk and its habitat under the Endangered Species Act (Martin 1998). As a result, research has largely focused on developing models capable of assessing the effects of forest management alternatives on goshawk biology and habitat suitability (e.g., Finn et al. 2002, Joy 2002). However, to estimate the ultimate effects of forest management on goshawk populations, it is necessary to relate changes in life history traits and demography to management-induced changes in habitat. This objective requires partitioning the contributions of environmental factors (e.g., food, climate, forest structure) to variation in sensitive vital rates. Food availability, in particular, is often considered to be a primary factor limiting goshawk productivity (Doyle and Smith 1994, Ward and Kennedy 1996, Dewey and Kennedy 2001, Salafsky 2004), but few studies have attempted to discriminate the relative contributions of environmental-, territory- or individual-level factors to realized goshawk survival rates. This is important because spatial or temporal variation in goshawk survival may result from factors working at more than one ecological level.

In 1991, studies of goshawk demographics and habitat were established on the Kaibab Plateau of northern Arizona, USA (Reynolds et al. 1994, 2004). Capture–recapture studies have shown that goshawks on the Kaibab Plateau exhibit temporally invariant adult survival rates (75%) (Reynolds et al. 2004), high territory (95%) and mate (98%) fidelity (R. Reynolds, *unpublished manuscript*), and a delayed age at first breeding (Wiens 2004). However, despite the fact that >600 nestlings have been color-banded over a 13-year period, too few banded young have been relocated within the study population to reliably estimate juvenile survival. Efforts to estimate juvenile survival rates for this population are likely to suffer from the low probability of detecting juveniles that permanently disperse beyond the boundaries of the study site. Hence, failure to relocate juveniles could be due to either undetected mortality or emigration, and the extent of these is generally unknown in goshawks. In an attempt to circumvent these problems, we used radiotelemetry methods to investigate juvenile survival within the goshawk population on the Kaibab Plateau during 1998–2001. The overall goal was to identify critical periods of post-fledging survival and to determine what ecological factors are most strongly limiting to goshawk productivity at the level of juvenile survival. Our specific objectives were to (1) estimate age-, gender-, and cohort-specific survival probabilities of juvenile goshawks during the fledgling dependency and post-independence periods; (2) determine the relative importance of prey abundance, weather, brood size, hatching date, and body condition to survival; and (3) estimate the impact of fledging and the early stages of natal dispersal on juvenile survival rates. We will discuss further the multi-scale importance of juvenile survival and dispersal to goshawk demographics, and will relate our findings to current goshawk research and conservation efforts.

## METHODS

### *Study area*

The study area on the Kaibab Plateau in northern Arizona is a 1732-km$^2$ area comprising all of the coniferous forest above 2195 m a.s.l. elevation. This area includes the northern portions of the Kaibab National Forest (KNF) and the Grand Canyon National Park (GCNP). Post-fledging survival was studied on a subset of territories within the KNF (total area 1285 km$^2$) and excluded territories within the GCNP. The Kaibab Plateau is a large, oval-shaped landform that rises from a shrubsteppe plain at 1750 m elevation to the highest point at 2800 m (Rasmussen 1941). Forested areas on the Kaibab Plateau include three principal forest types: pinyon–juniper (*Pinus edulis*–*Juniperus* spp.) woodlands occur between 1830 and 2075 m; ponderosa pine (*Pinus ponderosa*) forests occur from 2075 to 2450 m; and mixed-conifer forests (*Picea engelmanii*, *Abies concolor*, *Pseudostuga menziesii*, *P. ponderosa*, *Populus tremuloides*) occur from 2450 to 2650 m (Rasmussen 1941, White and Vankat 1993). Except for relatively small meadows, burns, and management areas, forests on the Kaibab form a continuous cover. Annual precipitation averages 67.5 cm, with winter snowpacks of 2.5–3.0 m (White and Vankat 1993).

### *Radio marking and tracking*

Goshawk breeding areas were monitored annually to determine location, occupancy, and reproductive status of territorial pairs (Reynolds et al. 1994). Active nests (eggs laid) were visited weekly to determine the number and age of nestlings. Nests targeted for radio-marking young were randomly selected from a stratified sample of nests containing one, two, or three young each. Nestling goshawks on the Kaibab Plateau first take flight at ~40 days of age (Boal 1994), so nest trees were climbed to measure, band, and radio-mark young at 32–35 days of age. Young goshawks were aged based on a photographic and behavioral guide (Boal 1994) and were banded with a U.S. Geological Survey aluminum leg band and a color leg band with a unique alpha-numeric code (Acraft Sign and Plate, Edmonton, California, USA). Young were sexed on the basis of body mass, tarsometatarsal length, and footpad length measurements (Wiens 2004). Nestlings from randomly selected nests were equipped with 17-g (including harness) backpack-style radiotransmitters (model # LPB 2380M, Wildlife Materials, Murphysboro, Illinois, USA) representing 1.9% and 2.5% average body mass at first flight for females and males, respectively. Backpack harnesses used four separate reinforced nylon straps with a ''weak link'' cotton attachment that allowed the harness to fall off without entanglement ~1 year after fitting (modified from Klavitter et al. 2003). Radiotransmitter packages were designed to lie flat and smooth to reduce feather wear, skin irritation, and aerodynamic drag that may increase metabolic rates during flight (Gessaman and Nagy 1988). Radiotransmitters were programmed with a mortality sensor (Wildlife Materials) and had a mean life expectancy of 500 days.

Radio-marked hawks were monitored with model R4000 ATS receivers (Advanced Telemetry Systems, Isanti, Minnesota, USA), using two- and three-element Yagi antennas. We recorded status (location, alive, dead) and behavior within natal territories 4–5 times per week by approaching on foot until the hawk was sighted or a change in signal strength was recorded. All mortalities were classified as predation, starvation (based on post mortem differences in body mass), or unknown, based on evidence found at recovery sites. Once radio-marked hawks initiated dispersal, systematic searches were conducted throughout the study area using omnidirectional antennas mounted on trucks, or from fire lookout towers, which provided high vantage points to scan for lost signals over large areas. In addition, fixed-wing aircraft were used to survey for missing signals over the study area (including GCNP) and within 60–70 km of the study area boundary (aerial survey area 10 800 km$^2$). Tracking flights typically followed a series of East–West transect lines spaced 10 km apart, and were conducted at monthly intervals from September through May during 1999–2002 and January and March in 1998. We estimated the probability of detecting radio-marked hawks from aircraft as the proportion of 22 radiotransmitters placed at random locations and heights (0–4 m) throughout the aerial survey area that were relocated by a naïve observer.

### *Developmental stages of young goshawks*

We defined *fledging* as the date on which young hawks were first observed out of the nest. Once juvenile goshawks venture beyond 1.5–2.0 km from the nest, they are rarely recorded within that radius on subsequent occasions and are assumed to be foraging independently (Kenward et al. 1993*a*, Kennedy and Ward 2003). We therefore defined *dispersal date* as the first day that a hawk spent more than two consecutive days ≥2 km from the nest. The *fledgling dependency period* was the length of time between the fledging and dispersal dates. If nests were not visited daily, we considered the dates of fledging and dispersal as the midpoint between two consecutive visits. When a hawk's radio signal was not detected within the vicinity of its nest, a search was initiated within a 2 km radius of the nest for three consecutive days. If a signal was not received or a hawk was located ≥2 km from the nest for more than two consecutive days, the hawk was determined to have initiated dispersal from its natal territory, marking the beginning of the *post-independence period*. This period coincided with the early stages of *natal dispersal*, defined as movement from the natal area to the site of first breeding (Greenwood and Harvey 1982).

### *Sources of variation and covariates to survival*

The ability to isolate the various factors affecting survival, and their relative contributions, largely depends on identifying biologically meaningful covariates and estimating their effects via an appropriate analytical model (Lebreton et al. 1992, Skalski et al. 1993, Pollock 2002). We selected six covariates to represent three ecological levels hypothesized to influence the survival of juvenile goshawks: two cohort-level covariates, two territory-level covariates, and two individual-level covariates. Cohort-level covariates (prey abundance, total precipitation) represented environmental effects and assumed the same level for each individual within an annual group of radio-marked hawks. Territory-level covariates (brood size, territory hatch date) represented potential spatial differences among natal areas and assumed the same value for each individual at a nest. Individual-level covariates (gender, body condition) were specific to individuals. We used body mass (g) at the time of capture (3–5 days prefledging) as an index of body condition. We assumed that age had a minimal effect on body mass measurements because nestlings were radio-marked within a narrow age range.

*Prey abundance*.—Survival of goshawks may be directly related to food availability (Ward and Kennedy 1996, Dewey and Kennedy 2001). We predicted that juveniles fledged in years of favorable food conditions would exhibit higher survival than those fledged in years of relatively poorer food conditions. Based on studies of goshawk diets on the Kaibab Plateau, the seven primary prey species in terms of diet biomass and frequency were: black-tailed jackrabbit (*Lepus californicus*), cottontail rabbit (*Sylvilagus* spp.), Kaibab squirrel (*Sciurus aberti kaibabensis*), golden-mantled ground squirrel (*Spermophilus lateralis*), red squirrel

(*Tamiasciurus hudsonicus*), Northern Flicker (*Colaptes auratus*), and Steller's Jay (*Cyanocitta stelleri*) (Boal and Mannan 1994, Reynolds et al. 1994, Salafsky 2004). In a concurrent study (see Salafsky 2004), abundance data were collected for these seven prey species during the goshawk breeding season (May–August) using two sampling methods: line-transect distance sampling (1999–2002) and counts of prey species detections (1994–2002). To estimate the importance of prey abundance to goshawk survival, we combined annual estimates of prey density during 1999–2001 for a subset of prey species (red squirrel, Kaibab squirrel, Northern Flicker, and Steller's Jay) that were reliably estimated using program DISTANCE (Buckland et al. 1993). Together, these four species contributed ~65% of the total diet biomass estimated from prey remains collected at 211 goshawk nests on the KNF during 1998–2001 (S. R. Salafsky, *unpublished data*). To obtain prey densities and measures of precision in 1998 (prior to the initiation of distance sampling), we estimated a predicted density value under a linear regression relating prey species counts to concurrent prey density estimates (Salafsky 2004).

*Total precipitation*.—In several raptor species, extreme precipitation has affected survival by limiting foraging success, reducing prey availability, and causing direct mortality due to exposure (Davis and Newton 1981, Kostrzewa and Kostrzewa 1990, Olsen and Olsen 1992, Franklin et al. 2000). In northern Arizona, the ''monsoon'' thunderstorm season (early July to mid-September) coincides with the goshawk fledgling dependency period. This seasonal shift in climate is characterized by extreme precipitation, lightning, hail, and damaging winds. We predicted that extreme rainfall during the fledgling dependency period would negatively affect juvenile survival directly (through exposure or increased vulnerability to predation) or indirectly (by limiting the adult's ability to provide sufficient food). We examined this prediction by evaluating the total amount of precipitation between fledging and independence as a cohort-level covariate to survival. Daily precipitation records from one U.S. Weather Service station and three Remote Automated Weather Stations on the study area were used to estimate total rainfall during the interval from earliest fledgling date to latest dispersal date for each cohort of radio-marked hawks. Precipitation totals were averaged across weather stations by year.

*Territory hatching date*.—In seasonal environments, egg hatch date may be an important determinant of fitness (Reed et al. 2003), territory quality (Korpimäki and Lagerström 1988), and survival (Krementz et al. 1989, Schmutz 1993, Verboven and Visser 1998). Given these features, we predicted that juveniles that fledged earlier would experience higher survival rates because they might have higher quality parents or might have developed on a higher quality territory. To examine this prediction, we assessed egg hatch date as a territory-level covariate to survival. We defined territory hatching date as the average Julian date (1–365; day 1 is 1 January) on which radio-marked juveniles within a single brood hatched, backdated from the estimated age at capture.

### *Data analysis*

We used an information-theoretic approach to assess the influences of time (among-and within-year variation) and ecological covariates on goshawk survival (Lebreton et al. 1992, Burnham and Anderson 2002). We developed multiple a priori hypotheses that were based upon previous studies of avian survival (Newton and Moss 1986, Korpimäki and Lagerström 1988, Kenward et al. 1993*a*, Ward and Kennedy 1996, Franklin et al. 2000, Newton and Rothery 2000, Monrós et al. 2002), current goshawk management strategies (Reynolds et al. 1992), and field observations. Each hypothesis was expressed as a candidate statistical model, and we used $\Delta\mathrm{AIC}_c$ (Burnham and Anderson 2002) to objectively rank sets of candidate models and to select a best-approximating model(s) for inference. Model comparisons were made with $\Delta\mathrm{AIC}_c$ (i.e., the difference between the lowest $\mathrm{AIC}_c$ value and $\mathrm{AIC}_c$ from all other models), and we used normalized $\mathrm{AIC}_c$ weights ($w_i$) to evaluate the strength of evidence for each model considered. Environmental variables were balanced evenly among sets of candidate models, allowing a direct comparison of their relative importance to goshawk survival using cumulative $\mathrm{AIC}_c$ weights (i.e., the sum of $\mathrm{AIC}_c$ model weights across models containing a covariate of interest; Burnham and Anderson 2002).

We used known-fate modeling in program MARK (White and Burnham 1999) to estimate post-fledging survival and to model time and covariate effects relative to survival. Known-fate parameter estimation in program MARK is based on the Kaplan-Meier product limit estimator (Kaplan and Meier 1958), allowing for staggered entry of individuals as they are added to the study (Pollock et al. 1989). Known-fate models assume that the fates of individuals are independent (White and Burnham 1999). This assumption is probably valid once juveniles disperse from the natal area, but may be compromised prior to dispersal in nests containing more than one young. When individual survival probabilities lack independence, the estimators of model parameters are unbiased, but the theoretical variances are biased low due to extra-binomial variation or overdispersion of the data (Tsia et al. 1999). Biologically, overdispersion might be expected if broods behaved more as a unit or if the fates of brood members were dependent. We tested for a significant violation of the assumption of independence by estimating overdispersion ($\hat{c}$) as $\chi^2/\mathrm{df}$, where $\chi^2$ was the summation of partial chi-square values ($[\text{observed} - \text{expected}]^2/[\text{expected}]$) calculated for each possible outcome of losses within brood sizes of 1, 2, or 3 young (nine possible outcomes). Expected values were calculated as follows:

TABLE 1. Number of juvenile Northern Goshawks under radio telemetry study in northern Arizona, USA, and their fates by week 40 after fledging, 1998–2001.

| Year | No. with transmitters (females, males) | Proportion with transmitters† | Recovered dead | Shed transmitter | Loss of signal |
|---|---|---|---|---|---|
| 1998 | 17 (10, 7) | 0.20 | 5 | 0 | 12 |
| 1999 | 22 (9, 13) | 0.29 | 5 | 1 | 16 |
| 2000 | 28 (11, 17) | 0.25 | 7 | 6 | 15 |
| 2001 | 22 (12, 10) | 0.71 | 7 | 10 | 5 |
| Total | 89 (42, 47) | 0.29 | 24 (27%) | 17 (19%) | 48 (54%) |

† Number of juveniles that carried transmitters divided by the total number of fledglings produced on the Kaibab Plateau, Arizona (Wiens 2004).

$$\binom{n}{r}p^r(1 - p)^{n-r}$$

where $n$ is brood size, $r$ is the number of young surviving to independence, and $p$ is the survival rate between fledging and independence. A rejection indicated that the fates of siblings were dependent (i.e., $\hat{c} > 1.0$), in which case a quasi-likelihood correction was used to adjust estimates of precision and model selection criterion (e.g., QAIC$_c$; Burnham and Anderson 2002).

Survival analyses were conducted in two stages. Stage one considered the following set of models that considered both annual and weekly time variation in post-fledging (models 1–8) and post-independence (models 1–10) survival:

1) survival is constant over time, $S(\cdot)$;
2) survival is dependent on weekly categorical time, $S(t)$;
3) survival is dependent on year, $S(\text{year})$;
4) additive effect of year and weekly categorical time, $S(\text{year} + t)$;
5) interactive effect of year and weekly categorical time, $S(\text{year} \times t)$;
6) linear time trend in weekly survival, $S(T)$;
7) year-specific linear time trend in weekly survival, $S(\text{year} + T)$;
8) interactive effect of year and a linear weekly time trend, $S(\text{year} \times T)$;
9) quadratic time trend in weekly survival, $S(T \times T)$;
10) year-specific quadratic time trend in weekly survival, $S(\text{year} + T \times T)$.

Models including a linear time trend in survival between fledging and independence (models 6 and 7) and a quadratic time trend in survival from fledging through the post-independence period (models 9, 10) represented our hypothesis that weekly survival would increase over the duration of the fledgling dependency period as fledglings gained flight skills, but would decline once juveniles initiated dispersal. To estimate the effect of dispersal on survival, we conducted a separate analysis in which the survival interval was extended beyond the mean length of the fledgling dependency period. We referred to this extended analysis as ‘‘post-independence survival.’’ Separating survival estimation between the fledgling dependency and post-independence periods facilitated a more detailed assessment of intrabrood dependency in survival.

Stage two of our analyses introduced ecologically relevant covariates to the most parsimonious model explaining time variation in survival. Relationships of estimated survival probabilities to covariates were modeled as a linear function under the logistic model

$$\hat{S}_i = \frac{1}{1 + \exp\{-[\hat{\beta}_0 + \hat{\beta}_1(X_i)]\}}$$

with the logit link function

$$\log_e\left(\frac{\hat{S}_i}{1 - \hat{S}_i}\right) = \hat{\beta}_0 + \hat{\beta}_1(X_i)$$

where $\hat{S}_i$ is the estimated survival rate for the $i$th individual, and $X_i$ is the covariate value for the $i$th individual. We evaluated the precision of slope coefficient estimates ($\hat{\beta}_i$) using standard errors and 95% confidence intervals, which were used to supplement AIC$_c$ evidence of an important effect based on the degree to which intervals overlapped zero (Franklin et al. 2000). To quantify the amount of year-to-year variability in survival that was explained by environmental covariates, we used an analysis of deviance (ANODEV), which provided a means of evaluating environmental covariates by comparing explained to unexplained model deviance (Skalski et al. 1993, White and Burnham 1999).

## RESULTS

We measured and radio-marked 89 nestlings at 48 nests during 1998–2001 (Table 1). Entire broods were radio-marked at 37 of 48 nests (10 broods of one young, 18 of two young, and 9 of three young). All 89 radio-marked nestlings successfully fledged. Juveniles that survived to independence ($n = 81$), excluding those ($n = 10$) that prematurely shed their radiotransmitters, dispersed between 71 and 103 days post-hatching (86.54 ± 0.79 d, mean ± SE; $n = 71$). The amount of time that juveniles remained within their natal areas between fledging and independence ranged from 33 to 66 days (46.34 ± 0.78 d). Post-fledging survival was therefore considered over seven weekly intervals. Of 89 radio-

TABLE 2. Causes of death by developmental stage for radio-marked juvenile Northern Goshawks in northern Arizona, 1998–2001.

| Developmental stage | Weeks after fledging | Hawks at risk† | Deaths (females, males) | Cause of death: Predation | Starvation | Unknown |
|---|---|---|---|---|---|---|
| Fledgling dependency | 1–7 | 89 | 8 (5, 3) | 3 (37.5%) | 3 (37.5%) | 2 (25%) |
| Postindependence | 8–12 | 71 | 6 (4, 2) | 4 (67%) | 0 (0%) | 2 (33%) |
| Dispersal‡ | 13–40 | 64 | 10 (3, 7) | 4 (40%) | 2 (20%) | 4 (40%) |
| Fledging through dispersal | 1–40 | 89 | 24 (12, 12) | 11 (46%) | 5 (21%) | 8 (33%) |

† Number of hawks remaining at risk once mortalities and hawks that shed their radiotransmitters during the preceding developmental stage were removed.

‡ Defined here as the period between the five-week post-independence period and spring of the following year.

marked juveniles, 41 (46%) were tracked until they were either recovered dead or they shed their radiotransmitter package by the following spring (week 40 post-fledging; Table 1). Radio signals were lost for the remaining 48 juveniles due to dispersal beyond the aerial survey area (Wiens 2004).

### *Post-fledging survival*

Eight mortalities (five females, three males) were recorded during the fledgling dependency period (two in 1998, two in 1999, and four in 2001). Based on evidence found at recovery sites, three juveniles died from predation or injuries attributable to predation by Great Horned Owls (*Bubo virginianus*), three from starvation, and two from unknown sources of physical trauma (Table 2). We found no evidence of overdispersion of the data due to lack of independence among brood mates ($\chi^2 = 3.97$, df = 8, $P = 0.86$). Moreover, models including the effect of brood size received poor support (see *Covariate effects*). We therefore considered post-fledging mortality to be a random process, and we used individuals as independent units for parameter estimation (i.e., $\hat{c} = 1.0$).

*Time effects*.—The best-fitting survival model addressing time effects during the fledgling dependency period, $\{S(\text{year} + T)\}$, indicated that survival was year-dependent with an additive effect of weekly continuous time. This model (Fig. 1) demonstrated that post-fledging survival differed among annual cohorts of radio-marked juveniles and that weekly survival followed an increasing linear time trend ($\hat{\beta}_T = 1.05$, 95% CI = 0.22–1.87). Derived survival estimates under this model ranged from 0.82 in 2001 to 1.00 in 2000 (Table 3). Model $\{S(\text{year} + T)\}$ contained more than half of the AIC$_c$ weight across the initial set of eight time-specific models, indicating the presence of annual variation in post-fledging survival. Models containing a continuous time-specific survival component ($T$) also received strong support, indicating the presence of weekly variation in post-fledging survival. Models with weekly categorical time dependency ($t$) or no time effects received poor support (Appendix).

*Covariate effects*.—When the effect of ''year'' was replaced with the cohort-level prey density covariate in the best time-specific model, a lower AIC$_c$ model was attained. Model $\{S(\text{prey} + T)\}$ indicated a positive relationship between survival and prey density, with an additive effect of weekly continuous time (Fig. 2). The form of this model was

$$\hat{S}_i = 1/\{1 + \exp[-(-0.30 + 1.12\text{prey} + 1.04T)]\}$$

where $\widehat{\text{SE}}(\hat{\beta}_0) = 1.12$, $\widehat{\text{SE}}(\hat{\beta}_{\text{prey}}) = 0.54$ (95% CI = 0.06–2.19), and $\widehat{\text{SE}}(\hat{\beta}_T) = 0.42$ (95% CI = 0.22–1.87). Derived survival estimates (mean ± SE) under this model ranged from 0.79 ± 0.09 in 2001 to 0.97 ± 0.02 in 2000, when total prey density was lowest and highest, respectively (Table 3). Replacing the effect of ''year'' with the total precipitation covariate in the best time-

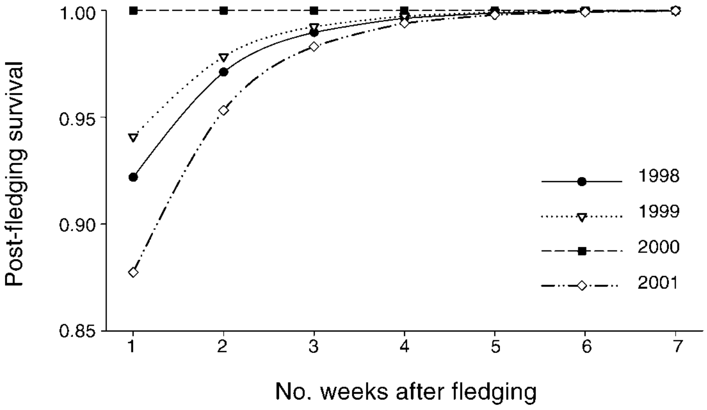

FIG. 1. Estimates of weekly survival during the fledgling dependency period (weeks 1–7 after fledging) under model $\{S(\text{year} + T)\}$ for radio-marked juvenile Northern Goshawks on the Kaibab National Forest in northern Arizona, USA, 1998–2001.

TABLE 3. Annual estimates of derived survival parameters for radio-marked juvenile Northern Goshawks during the fledgling dependency period (weeks 1–7 after fledging), and estimates of total prey density for four primary bird and mammal prey species on the Kaibab National Forest, Arizona, 1998–2001.

| | Post-fledging survival, $\hat{S}$ | | | Total prey density, $\hat{D}$ (no./ha) | | |
|---|---|---|---|---|---|---|
| Year | $\hat{S}$ | SE | 95% CI | $\hat{D}$ | SE | 95% CI |
| 1998 | 0.88 | 0.08 | 0.63–0.97 | 1.91 | 0.12 | 0.96–3.83 |
| 1999 | 0.91 | 0.06 | 0.70–0.98 | 2.27 | 0.10 | 2.08–2.47 |
| 2000 | 1.00 | 0.01 | 0.99–1.00 | 2.72 | 0.10 | 2.54–2.92 |
| 2001 | 0.82 | 0.08 | 0.60–0.93 | 0.97 | 0.05 | 0.88–1.07 |

*Notes:* Survival estimates were derived under the best fitting time-specific model, {$S$(year + $T$)}. Prey density estimates and measures of precision for 1998 were predicted under the regressed relationship between the number of species detections per 100 minutes of observation during 1998–2002 and line-transect density estimates from 1999–2002 (Salafsky 2004).

specific model resulted in a model with poor support ($\Delta$AIC$_c$ = 5.39; Appendix). Models containing the effect of prey density accounted for 62% of the AIC$_c$ weight across the model set, whereas models containing the effect of precipitation accounted for only 13%. In comparison, models including the effect of ''year'' accounted for 21% of the AIC$_c$ weight. ANODEV results indicated that 63% of the annual variation present in post-fledging survival was explained by the prey density covariate ($F_{1,6}$ = 3.4, $P$ = 0.21). Of the 24 time and covariate models considered, the overall best-fitting model ($\Delta$AIC$_c$ = 0.00; Table 4) indicated that survival followed an increasing weekly time trend that was positively influenced by annual differences in prey abundance ($\hat{\beta}_{\text{prey}}$ = 0.78, 95% CI = −0.33 to 1.88), and gender-specific differences in pre-fledging body mass ($\hat{\beta}_{\text{mass}}$ = 0.01, 95% CI = 0.00–0.02). Three closely competing models had $\Delta$AIC$_c$ values <2.00, but estimates of $S$ were only slightly different among these.

### *Post-independence survival*

By week 13 post-fledging, only 15 of 64 radio-marked juveniles remaining at risk could be detected during ground and aerial surveys. We therefore limited survival estimates to the first 12 weeks post-fledging, when sample sizes ($n$ = 19) were still sufficient to allow reasonable precision of parameter estimates. An additional six mortalities (four females, two males) occurred during the five-week period following independence, whereas 10 mortalities (seven males, three females) occurred between weeks 13 and 40 post-fledging. In total, 24 hawks were recovered dead during the study, with predation accounting for 46% of total mortality (Table 2).

*Time effects*.—The best-fitting survival model addressing time effects over the first 12 weeks after fledging, {$S$($T$ × $T$)}, indicated that weekly survival followed a quadratic time trend (Fig. 3). This model estimated survival over the first 12 weeks post-fledging as 0.71 (SE = 0.08, 95% CI = 0.53–0.84). Models including a quadratic time effect accounted for 97% of the AIC$_c$ weight across the initial set of 10 time-specific models, indicating strong support for weekly variation in survival. One alternate time-specific model, {$S$(year + $T$ ×$T$)}, was competitive ($\Delta$AIC$_c$ between the two best time-specific models = 1.08, Table 4). This model indicated that survival probabilities differed in level, but not in slope, among annual cohorts of radio-marked juveniles. Derived survival estimates under this model ranged from 0.48 (SE = 0.18, 95% CI = 0.18–0.79) in 2001 to 0.87 (SE = 0.09, 95% CI = 0.60–0.97) in 2000.

*Covariate effects*.—An addition of the effects of gender and body mass to model {$S$($T$ × $T$)} resulted in a new minimum AIC$_c$ model that contained 57% of the overall AIC$_c$ weight (Table 4, Appendix). This model included a gender-specific quadratic weekly time trend in survival (higher survival rates for males) with an additive effect of pre-fledging body mass. This model explained variation in survival over the first 12 weeks post-fledging as

$$\hat{S}_i = 1/\{1 + \exp[-(-6.72 + 1.01T - 0.09T \times T + 2.39\text{sex} + 0.01\text{mass})]\}.$$

Here $\widehat{\text{SE}}(\hat{\beta}_0)$ = 3.36, $\widehat{\text{SE}}(\hat{\beta}_T)$ = 0.35 (95% CI = 0.42–1.78), $\widehat{\text{SE}}(\hat{\beta}_{T\times T})$ = −0.03 (95% CI = −0.15 to −0.04), $\widehat{\text{SE}}(\hat{\beta}_{\text{sex}})$ = 0.81 (95% CI = 0.79–3.99), and $\widehat{\text{SE}}(\hat{\beta}_{\text{mass}})$ = 0.01 (95% CI = 0.00–0.02). This model estimated survival of females at average body mass (852.98 ± 14.28 g, mean ± SE; $n$ = 42) over the first 12 weeks post-fledging as 0.62 (SE = 0.13; 95% CI = 0.36–0.83), whereas survival for males at average body mass (689.68 ± 7.55 g; $n$ = 47) was 0.79 (SE = 0.09; 95% CI = 0.57–0.92). Incremental changes in pre-fledging body mass under this model had a larger effect on female than male survival. A model incorporating the effect of prey density indicated a positive relationship ($\hat{\beta}_{\text{prey}}$ = 0.86, 95% CI = 0.06–1.66), and was more than

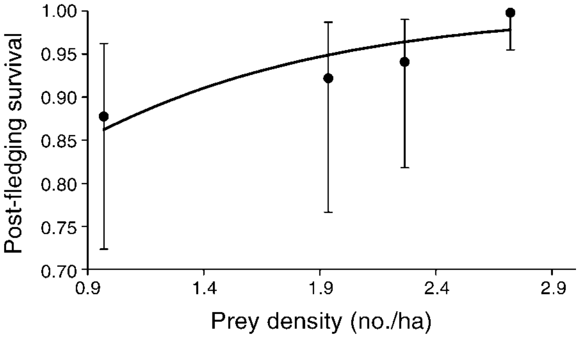

FIG. 2. Relationship between post-fledging survival of juvenile Northern Goshawks and total prey density on the Kaibab National Forest in northern Arizona, 1998–2001. Survival estimates (±95% profile likelihood CI) are from the first weekly time interval under model {S(year + $T$)}. The line represents the predicted values under model {S(prey + $T$)}.

TABLE 4. Ranking of juvenile Northern Goshawk survival models investigating time and covariate effects during the post-fledging and post-independence periods in northern Arizona, 1998–2001.

| Model | $K$ | $\text{AIC}_\text{c}$ | $\Delta\text{AIC}_\text{c}$ | $w_i$ | Deviance |
|---|---|---|---|---|---|
| Post-fledging survival | | | | | |
| $S$(prey + $T$ + sex + mass) | 5 | 69.49 | 0.00 | 0.22 | 59.30 |
| $S$(prey + $T$) | 3 | 70.45 | 1.03 | 0.13 | 64.40 |
| $S$(rain + $T$ + sex + mass) | 5 | 71.36 | 1.94 | 0.08 | 61.25 |
| $S$(prey + $T$ + brood) | 4 | 71.61 | 2.19 | 0.07 | 63.53 |
| $S$(prey + $T$ + mass) | 4 | 71.67 | 2.25 | 0.07 | 63.59 |
| **$S$(year + $T$)** | 5 | 71.79 | 2.37 | 0.07 | 61.67 |
| $S$(prey + $T$ + hatch) | 4 | 71.97 | 2.55 | 0.06 | 63.89 |
| $S$(prey + $T$ + sex) | 4 | 72.07 | 2.65 | 0.06 | 63.99 |
| Post-independence survival | | | | | |
| $S$($T \times T$ + sex + mass) | 5 | 122.85 | 0.00 | 0.57 | 112.76 |
| $S$(prey + $T \times T$) | 4 | 125.21 | 2.36 | 0.17 | 117.15 |
| $S$($T \times T$ + sex) | 4 | 127.04 | 4.20 | 0.07 | 118.98 |
| **$S$($T \times T$)** | 3 | 127.51 | 4.67 | 0.05 | 121.48 |
| $S$($T \times T$ + hatch) | 4 | 128.29 | 5.45 | 0.04 | 120.23 |
| $S$(year + $T \times T$) | 6 | 128.60 | 5.75 | 0.03 | 116.47 |
| $S$(rain + $T \times T$) | 4 | 129.29 | 6.45 | 0.02 | 121.23 |
| $S$($T \times T$ + mass) | 4 | 129.35 | 6.51 | 0.02 | 121.29 |

*Notes:* The top eight selected models are shown for each period. Boldface denotes the best-fitting time-specific models. Models are ranked by ascending $\Delta\text{AIC}_\text{c}$; $w_i$ is the model weight, and $K$ is the number of estimable parameters. Deviance is the difference in $-2[\log_e(\text{Likelihood})]$ of the current model and $-2[\log_e(\text{Likelihood})]$ of the saturated model. Factors in models include year, sex, a linear weekly time trend ($T$), a quadratic weekly time trend ($T \times T$), prey abundance (prey), total precipitation (rain), natal brood size (brood), pre-fledging body mass (mass), and territory hatch date (hatch). The postfledging period is weeks 1–7 after fledging; the post-independence period is weeks 1–12 after fledging.

three times as likely as the best time-specific model (Table 4). ANODEV results indicated that 87% of the annual variation present in survival was explained by prey density ($F_{1,6} = 12.8$, $P = 0.06$). A model including the effect of total precipitation received poor support ($\Delta\text{AIC}_\text{c} = 6.45$).

### *Signal detection, data censoring, and model assumptions*

Our signal detection test showed that the probability of detecting a functioning radiotransmitter within the aerial survey area was 0.91 (SE = 0.06, 95% CI = 0.79–1.00), regardless of signal type (Fisher's exact test; $P = 0.34$, $n = 22$). Known-fate parameter estimation in program MARK uses a modification to the risk set (Brunk et al. 1995), in which animals are included in an interval only when they are relocated (G. C. White, *personal communication*). Although uncertain relocation (i.e., data censoring) results in a loss of precision of the estimate, this estimator remains relatively unbiased as long as data censoring is independent of fate (Brunk et al. 1995, Tsia et al. 1999). We recorded a substantial surge in the number of censored juveniles during the first several weeks following independence. This result would have been expected if juveniles had dispersed beyond the aerial survey area or if their radio had ceased to function as a result of malfunction or mortality. A sudden surge in radio failure within the first 100 days following activation was unlikely, and a high detection probability by aircraft indicated that the majority of data censoring was due to long-distance movement rather than undetected mortality. However, predation events leading to the destruction of radiotransmitters could have produced a slight positive bias in estimates of post-independence survival. Another critical assumption was that the radiotransmitters did not affect survival, but low recapture rates of juveniles with and without radiotransmitters precluded a rigorous test of this. However, Reynolds et al. (2004) reported that backpack transmitters (similar to those used here) had no detectable effect on the survival of adult goshawks. We also did not observe any adverse physical effects (such as lost feathers or skin abrasions) from

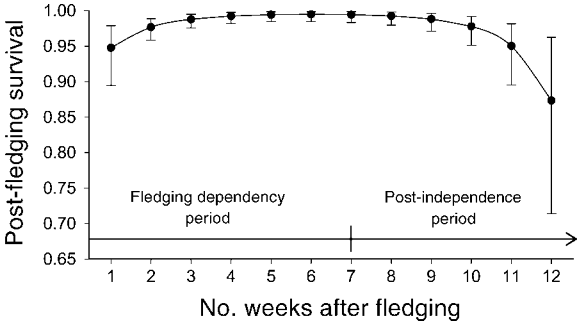

FIG. 3. Estimates of weekly survival (±95% profile likelihood CI) during the fledgling dependency (weeks 1–7) and post-independence (weeks 8–12) periods under model {$S(T \times T)$} for radio-marked juvenile Northern Goshawks in northern Arizona, 1998–2001.

wearing radiotransmitters on intact dead recoveries or live recaptures. Of the 48 radio-marked juveniles whose fates remained uncertain, five were subsequently resighted as adults (without their transmitters) by 2004.

## DISCUSSION

Post-fledging survival of juvenile goshawks was consistently high among years and was most strongly related to fledgling age, annual changes in prey abundance, and gender-related differences in pre-fledging body condition. Contrary to predictions, we found no evidence that fledgling survival was negatively affected by periods of heavy precipitation, or that early-hatched juveniles experienced different mortality risks than those hatched later in the year. Our data failed to support differences in post-fledging survival among goshawk breeding areas, as shown by a lack of support for territory-level covariates. Rather, measures of environmental and individual heterogeneity received the strongest support. Our results clearly show that the risk of post-fledging mortality of goshawks on the Kaibab Plateau was greatest following fledging and independence, probably due to an increased vulnerability to predation and/or starvation during these critical periods of transition. Low prey abundance appeared to exacerbate this vulnerability.

In New Mexico, USA, Ward and Kennedy (1996) reported that post-fledging survival of a control group of goshawks in a supplemental-feeding experiment was 93% (*n* = 15). In a similar experiment in Utah, USA, Dewey and Kennedy (2001) reported 100% survival between fledging and independence (*n* = 16). In east-central Arizona, Ingraldi (1998) reported survival of ~90% for juvenile female goshawks during the first seven weeks post-fledging and ~80% during the first 12 weeks, based on fledglings equipped with satellite transmitters (*n* = 14). Our estimates are consistent with previous findings from the southwestern United States ($\bar{x}$ = 91% and 71% for seven and 12 weeks post-fledging, respectively). Together, these studies show that survival of juvenile goshawks is highly variable, with mortality between fledging and independence ranging from 0% to 33%, and mortality during the early stages of natal dispersal from 7% to 50%.

### *Temporal variation in survival*

Our results showed a consistent pattern of within- and among-year variation in post-fledging survival of goshawks. In all four years of the study, mortality risk decreased to nearly zero beyond the third week post-fledging, yet increased substantially once juveniles dispersed from their natal areas. In general, fledgling movements within the natal area gradually expand as the birds gain flight skills (Kenward et al. 1993*a*, Kennedy and Ward 2003). Seven of the eight mortalities observed prior to dispersal occurred within the first 3–10 days after fledging, when young stayed close to the nest, feather growth was incomplete, and individuals were incapable of extended flights. Survival increased as fledglings gained flight skills, began to traverse areas within 100–300 m of the nest, and, for the most part, were still regularly attended by the adult female. This pattern of age-dependent post-fledging survival has been documented in many bird species including Prairie Falcons (*Falco mexicanus*), Wood Thrushes (*Hylocichla mustelina*), Great and Coal Tits (*Parus major*, *P. ater*), Burrowing Owls (*Athene cunicularia*), and Black-fronted Terns (*Sterna albostriata*) (respectively, McFadzen and Marzluff 1996, Anders et al. 1997, Naef-Daenzer et al. 2001, Todd et al. 2003, Keedwell 2003).

Mortality risk increased as juveniles dispersed from their natal areas. At this stage, juveniles were no longer attended by adults, began foraging independently, and typically moved to more open habitats at lower elevations. Of the six juveniles recovered dead during the post-independence period, five were found within pinyon–juniper or sagebrush cover types. Movement to lower elevations during the early stages of dispersal may coincide with the availability of important prey species that are not available in goshawk breeding habitat this time of year (mid-September to October). For example, Kenward et al. (1993*b*) reported that juvenile goshawks tended to gather in areas of high rabbit density following independence. In Arizona, rabbit abundance is higher in open or semi-open country than in higher elevation mixed-conifer or ponderosa pine forests (Hoffmeister 1986). Alternatively, territorial adults may force juveniles from optimal breeding habitats. In either case, juveniles dispersing beyond their natal population on the Kaibab Plateau will encounter an abrupt change from forest to nonforest cover types. Because dispersing juveniles must quickly adapt to markedly different foraging habitats that provide little cover, rates of starvation and predation are likely to increase. We also found substantial evidence for annual differences in juvenile survival. Annual variation in juvenile survival is likely to be a consequence of annual differences in measured (e.g., prey abundance) and unmeasured (e.g., predator density) factors.

### *Factors influencing juvenile survival*

*Prey abundance*.—Perhaps due to extreme drought conditions in Arizona, there was a dramatic decline between 2000 and 2001 in the density of four primary goshawk prey species on the KNF (Wiens 2004). This decline was largest in red squirrels and Kaibab squirrels, species that contributed a disproportionate amount of biomass to goshawk diets on the study area (Salafsky 2004). Fledgling mortality increased by 12% between these years, and whereas no mortalities occurred prior to independence in 2000, four (three due to starvation) occurred in 2001. When the survival interval was extended to include the early stages of natal dispersal, the difference between these years was even more dramatic: juveniles that fledged during a four-year peak in prey density had a 39% higher chance of surviving the first 12 weeks post-fledging than those fledged during a four-year low. In 1998 and 1999, when prey densities were at intermediate levels, predation was more pronounced and no mortalities prior to independence were attributed to starvation. Thus, prey abundance appeared to have strong direct and indirect influences on post-fledging survival, perhaps due to interactions with parental-care behavior, predation, or disease (Dewey and Kennedy 2001). A decline in juvenile survival rates between 2000 and 2001 also paralleled a decline in the proportion of 120 territorial adult pairs that successfully laid eggs on the Kaibab Plateau (from 0.53 to 0.25; R. Reynolds, *unpublished data*). Prey abundance apparently limited goshawk productivity not only by affecting the reproductive efforts of adults, but also by limiting juvenile survival. These findings demonstrate that although adults are able to adjust their reproductive efforts in response to food availability, this does not result in constancy of juvenile survival rates.

Using supplemental-feeding experiments, Ward and Kennedy (1996) and Dewey and Kennedy (2001) tested the hypothesis that food limits the survival of young goshawks. In each two-year experiment, food-supplemented fledglings had significantly higher survival prior to independence than did controls in one year, but not in the other. The authors attributed the lack of a consistent treatment effect to unmeasured changes in natural food availability. In our study, large differences among years in prey density, coupled with observations of starvation when prey density was lowest, showed that large fluctuations in prey abundance could override the effects of experimentally manipulated food levels. By ranking competing models containing year, prey abundance, and weather covariates, we achieved a clear assessment of the relative explanatory power of these environmental effects. The fact that models accounting for prey density consistently ranked higher than those containing year or weather effects showed that a large amount of annual variation in juvenile survival was attributable to changes in food availability. ANODEV results were consistent with this finding. Moreover, the relationship between juvenile survival and prey abundance was age-specific: prey abundance most strongly affected survival immediately after fledging and independence, whereas survival between these distinct stages of transition was consistently high among years.

Three prey species that contribute significantly to goshawk diets on the Kaibab Plateau could not be included in our analysis: golden-mantled ground squirrels, black-tailed jackrabbits, and cottontail rabbits. Nevertheless, ancillary data showed that golden-mantled ground squirrels experienced changes in abundance similar to those of the mammals that we did include (S. R. Salafsky, *unpublished data*). Rabbit species were seldom encountered on the study area and are likely to be more abundant at lower elevations. Goshawk territories near the edge of the study area, therefore, may have a higher proportion of rabbits in their diet than interior territories at higher elevations, suggesting that some level of spatial variation may be inherent to goshawk diets on the Kaibab Plateau. How this potential spatial variation in goshawk diet might have affected juvenile survival was unknown. Dispersing juveniles relocated at lower elevations were often visually observed preying upon rabbits, so rabbit densities may have larger effects on survival during this time.

*Total precipitation*.—Contrary to predictions, extreme rainfall during the fledgling dependency period was not closely associated with post-fledging or post-independence survival. This was unexpected, because prolonged periods of heavy rainfall have resulted in increased mortality of late-term nestlings on the Kaibab Plateau (D. Wiens, *personal observation*), and total precipitation measurements varied notably among years of our study (Wiens 2004). Differences in precipitation measurements among weather stations indicated that late-summer monsoon thunderstorms were highly localized, affecting different portions of the study area with varying intensity. Hence, some natal areas probably received heavier rainfall than others. Because we assessed the total amount of precipitation as a cohort-level covariate rather than as a territory-level covariate, differences in survival among territories due to rainfall may have been obscured. Measuring precipitation within natal territories could alleviate this concern by capturing existing spatial variation in rainfall resulting from isolated thunderstorm activity.

*Body condition and gender*.—In raptors, some studies have found nestling mass to be positively associated with juvenile survival (Todd et al. 2003), whereas others have not (Newton and Moss 1986, McFadzen and Marzluff 1996). We found that female goshawks with below-average body mass prior to fledging had higher mortality rates than males with below-average body mass. Gender and body mass covariates were supported only when they appeared in a model jointly as additive effects, indicating that the relationship between body mass and post-fledging survival was gender specific. Poor body condition during the later stages of the nestling period could lead to starvation near fledging, when feather growth and increased movement require higher energy expenditure. Increased physical demands during the initiation of dispersal also may accentuate the importance of pre-fledging body condition, as indicated by a more pronounced effect of body mass on survival following independence. Although we observed slightly more female than male deaths over the first 12 weeks post-fledging, the mortality sex ratio was equal by the end of the study. In contrast, Kenward et al. (1999) reported that juvenile female goshawks had higher survival rates than males during the first year of life.

### *Juvenile survival and population dynamics*

In long-lived birds that mature late and lay few eggs, small changes in adult survival are generally found to have large effects on population growth rate, whereas fecundity and juvenile survival have lower elasticities and make smaller contributions (Noon and Biles 1990, Sæther and Bakke 2000, Blakesley et al. 2001). However, vital rates that account for a larger portion of the variance in population growth rate, such as fecundity and juvenile survival, can have larger effects on population dynamics than those with large elasticities (Franklin et al. 2000, Sæther and Bakke 2000). Like juvenile survival, goshawk reproduction on the Kaibab Plateau varies greatly among years and closely tracks changes in prey abundance (Salafsky 2004). In contrast, adult survival is relatively constant over time (Reynolds et al. 2004), apparently less sensitive to fluctuations in prey abundance. This pattern of high temporal variation in reproduction and juvenile survival, combined with temporally invariant adult survival, is often documented in studies of long-lived raptors (Franklin et al. 2000, Sæther and Bakke 2000, Blakesley et al. 2001). For our study population, we suspect that reproduction and juvenile survival may significantly affect population dynamics because of their sensitivity to environmental conditions and potential role in maintaining a nonterritorial population, which can act to stabilize the size of a territorial population (Franklin 1992, Kenward et al. 2000). Although the role of a nonterritorial goshawk population in maintaining long-term population stability is unknown, it ultimately must be sustained by local reproduction or immigration.

Juvenile survival and dispersal may also be critical to the regional stability of goshawk populations when considered in a metapopulation context. For example, genetic evidence indicates that a functional population extends over a large geographic area in the southwestern United States (Sonsthagen et al. 2004; S. Bayard de Volo, *unpublished data*). In northern Arizona, juveniles disperse over a wide range of distances (59–442 km) during their first year of life, with few returning to eventually gain local breeding territories (Wiens 2004). In contrast, breeding dispersal of adults occurs infrequently and over shorter distances (2–17 km; R. Reynolds, *unpublished data*). Thus, fragmented goshawk populations may be heavily reliant upon the interpopulation movements made by juveniles in order to maintain a high rate of gene flow and immigration (Sonsthagen et al. 2004, Wiens 2004). Widespread external recruitment may be a common pattern in birds (Martin et al. 2000), and can be vital to the persistence and stability of small, isolated populations (Stacey and Taper 1992). We suspect that juvenile survival and dispersal may make larger contributions to the regional stability of goshawk populations than what is generally considered in localized studies of goshawk demographics.

### *Management implications*

Reynolds et al. (1992) recommended managing forests in the southwestern United States by providing suitable conditions for the goshawk and 14 of its primary prey species. We detected changes in goshawk survival rates with respect to the abundance of four of these species, thereby supporting the underlying logic of this management strategy. Goshawks are closely tied to their food resources, so forest management prescriptions designed to support abundant prey populations while providing forest structural conditions that allow goshawks to access their prey within breeding areas should benefit goshawk reproduction and fledgling survival. However, prey densities appear to vary greatly over small spatial and temporal scales, with mammals showing a higher level of variation than birds (Salafsky 2004). How this variation of the goshawk's prey community is linked to management activities that alter forest composition and structure is poorly understood, and will ultimately require a research focus on the life history traits and habitat relationships of key prey populations.

We found that mortality increased as juveniles dispersed into the pinyon–juniper woodland and shrub-steppe cover types that surround our study area, suggesting that these habitats may play a critical role in juvenile survival and dispersal processes for goshawks inhabiting the fragmented landscapes of the Southwest. Use of these habitat types by goshawks has also been reported in adults during the nonbreeding season (e.g., Underwood 2003). Such findings provide indicators that management activities in mature coniferous forest, pinyon–juniper woodland, and sagebrush ecosystems can collectively affect resources relevant to goshawk survival. Management applications in pinyon–juniper woodlands such as prescribed fire, chaining, and mechanical treatments, and the use of biological agents and herbicides to remove sagebrush for reseeding with nonnative grasses for livestock forage have significantly altered these ecosystems throughout North America. Because food resources within these habitats may facilitate successful juvenile survival and dispersal, we recommend that future goshawk research and conservation efforts consider the effects that these land use practices have on the abundance and distribution of pinyon–juniper woodland and sagebrush prey communities.

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## APPENDIX

A table showing the ranking of the full set of juvenile Northern Goshawk survival models considered (*Ecological Archives* A016-018-A1).