FEATURE ARTICLES

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JUVENILE MOVEMENT AND NATAL DISPERSAL OF NORTHERN GOSHAWKS IN ARIZONA

J. DAVID WIENS[1,4], RICHARD T. REYNOLDS[2], AND BARRY R. NOON[3]
[1]*Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO 80523*
[2]*USDA Forest Service, Rocky Mountain Research Station, 2150 Centre Avenue, Building A, Suite 350, Fort Collins, CO 80526*
[3]*Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523*

Abstract. We investigated the departure, transient movement, and local settlement stages of natal dispersal in a population of Northern Goshawks (*Accipiter gentilis*) on the Kaibab Plateau of northern Arizona. The study included 614 color-banded juveniles produced at 555 nests during 1991–2003, 89 of which were radio-marked during 1998–2001. Radio-marked juveniles initiated dispersal between 71 and 103 days posthatching, and spent between 33 and 66 days in the natal territory after fledging. Our best-fitting proportional hazards models predicted the timing of dispersal as a function of annual differences in the density of primary bird and mammal prey species, weather conditions, and natal brood size. Once dispersal was initiated, most juveniles moved into the more open habitats that surrounded the study area and few eventually returned to breed; first-year fidelity to the local natal population was 28%, and only 69 (11%) color-banded juveniles had entered the territorial population by 2004. Median natal dispersal distance on the Kaibab Plateau was 15.0 km (range = 0.1–58.1 km), a distance equivalent to about four times the diameter of an average breeding territory (3.8 km). Local settlement behavior of Northern Goshawks appeared to be driven by a combination of intraspecific competition for a limited number of breeding opportunities and inbreeding avoidance. However, much of the natal dispersal process operated at broad spatial scales beyond our study population, indicating a potentially high level of demographic connectivity among naturally fragmented breeding populations in the American Southwest.

Key words: Accipiter gentilis*, Arizona, fidelity, gene flow, inbreeding avoidance, natal dispersal, Northern Goshawk.*

Movimiento Juvenil y Dispersión Natal de *Accipiter gentilis* en Arizona

Resumen. Investigamos la partida, el movimiento de paso y las etapas del asentamiento local de la dispersión natal en una población de *Accipiter gentilis* en la Meseta Kaibab del norte de Arizona. El estudio incluyó 614 juveniles marcados con anillos de color producidos en 555 nidos entre los años 1991 y 2003, 89 de los cuales fueron marcados con radios entre 1998 y 2001. Los juveniles marcados con radio iniciaron la dispersión entre 71 y 103 días luego de eclosionar, y pasaron entre 33 y 66 días en el territorio natal luego de emplumar. Nuestros modelos de riesgo proporcional con el mejor ajuste predijeron el momento de la dispersión como una función de las diferencias anuales en la densidad de las principales especies de presas, tanto aves como mamíferos, de las condiciones del tiempo y el tamaño de la nidada. Una vez iniciada la dispersión, la mayoría de los juveniles se mudaron a los ambientes más abiertos que rodearon al área de

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[4] Present address: Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331-3803. E-mail: david.wiens@oregonstate.edu

estudio y pocos eventualmente regresaron a criar. La fidelidad del primer año a la población local natal fue de 28% y sólo 69 (11%) juveniles marcados con anillos de colores entraron en la población territorial hasta 2004. La distancia mediana de dispersión natal en la Meseta Kaibab fue de 15.0 km (rango = 0.1–58.1 km), una distancia equivalente a aproximadamente cuatro veces el diámetro de un territorio de cría promedio (3.8 km). El comportamiento de asentamiento local de *A. gentilis* parece estar condicionado por una combinación entre competencia intraespecífica por un número limitado de oportunidades de cría y evitar el entrecruzamiento. Sin embargo, gran parte del proceso de dispersión natal ocurrió a escalas espaciales mayores que la de nuestra población de estudio, indicando un nivel potencialmente alto de conectividad demográfica entre las poblaciones de cría naturalmente fragmentadas en el sudoeste de los Estados Unidos de América del Norte.

INTRODUCTION

Natal dispersal, defined as movement between the natal area and the site of first breeding (Greenwood and Harvey 1982), is a complex process involving a series of individual decisions regarding when, where, how far, or even if to disperse. Such decisions can be cued by environmental (Byholm et al. 2003, Kennedy and Ward 2003), physiological (Verhulst et al. 1997, Dufty and Belthoff 2001), or social (McCarthy 1997, Pasinelli and Walters 2002, Serrano et al. 2003) conditions experienced during the departure, transient movement, or settlement stages of the dispersal process. Natal dispersal behavior can therefore vary extensively among individuals, populations, and landscapes. This highly variable dispersal behavior, coupled with a general lack of correspondence between the spatial and temporal scales at which many populations are studied and the scales at which dispersal often operates (Koenig et al. 1996, 2000), make it difficult to examine the mechanisms that shape the natal dispersal profile of a species. Consequently, natal dispersal is a poorly understood ecological process, particularly for wide-ranging, highly mobile birds occurring in low densities.

Dispersal ensures habitat connectivity in naturally fragmented landscapes. The direct consequences of this key life-history process are therefore of vital importance to the conservation and management of threatened species in light of human-induced habitat alteration and fragmentation (Simberloff 1988, Walters 2000). For example, large-scale conservation and management planning efforts have demonstrated the importance of accurate estimates of dispersal distances to evaluate alternative reserve designs for the Spotted Owl (*Strix occidentalis*, Murphy and Noon 1992, Noon and McKelvey 1992, Lamberson et al. 1994). Like Spotted Owls, Northern Goshawks (*Accipiter gentilis*) select nest sites within mature or old-growth coniferous forest (Squires and Reynolds 1997). The fragmentation and alteration of these forests through management activities such as timber harvest and fire suppression has led to considerable concern for the viability of goshawk populations (Kennedy 1997, Peck 2000). As a result, many national forests in the U.S. have adopted management plans to conserve and protect areas used by breeding goshawks (e.g., Reynolds et al. 1992). Adult goshawks exhibit high (75%–94%) site fidelity once they begin to breed (Detrich and Woodbridge 1994, Reynolds and Joy 2006), so high reported rates of gene flow over large geographic areas are likely being maintained by natal dispersal (Sonsthagen et al. 2004, Wiens et al. 2006). As goshawk conservation strategies become increasingly relevant to regional forest planning efforts, a better understanding of natal dispersal is needed.

The overall goal of this study was to document the onset and completion of natal dispersal in goshawks based on relocations of radio-marked and color-banded hawks. We considered the natal dispersal process as three interdependent stages: departure from the natal site (the *departure stage*), movement between the natal site and the site of first breeding (the *transient movement stage*), and eventual settlement on a breeding site (the *settlement stage*; Ims and Hjermann 2001). Our study of natal dispersal was part of a 14-year (1991–2004) demographic study of a population of goshawks inhabiting an island-like patch of coniferous forest on the Kaibab Plateau of northern Arizona (Reynolds et al. 1994, 2004, 2005). This broader study provided a context for examining natal dispersal parameters relative to environmental, demographic, and social

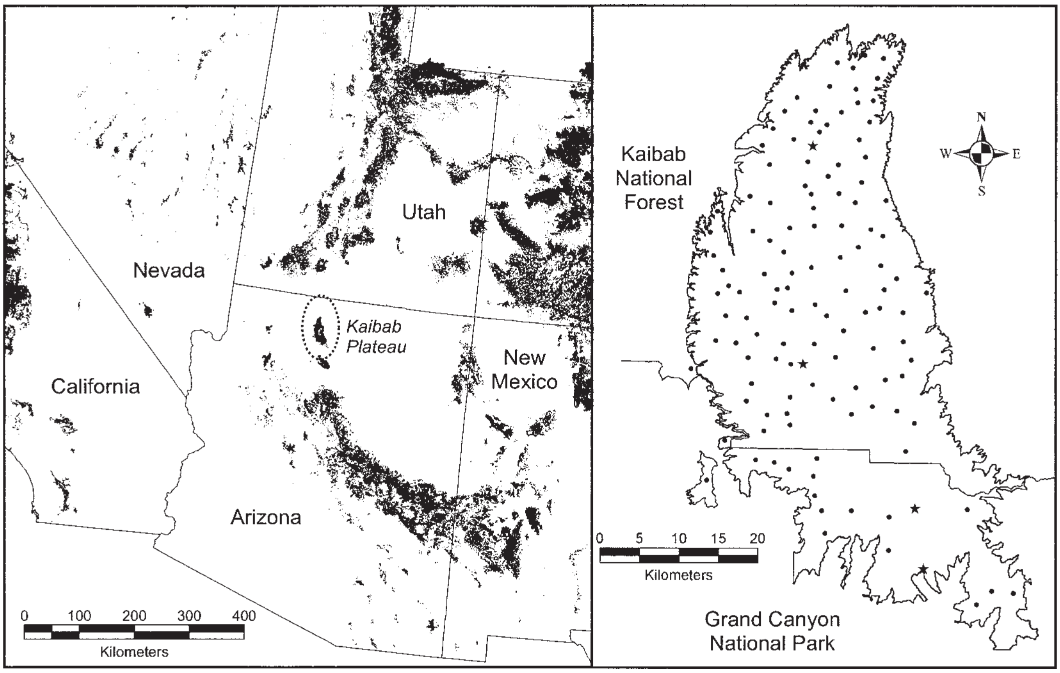

FIGURE 1. The regional distribution of Northern Goshawk breeding habitats (shaded areas) in the southwestern United States and the Kaibab Plateau study area showing the centers of 121 Northern Goshawk territories (dots), weather stations (stars), and the boundary between the Kaibab National Forest and Grand Canyon National Park. A 10 800 km^2 area in which radio-marked juveniles could be reliably detected during aerial surveys is indicated by a dashed ellipse.

conditions within the local natal population. Our specific objectives were to: (1) estimate the relative importance of factors hypothesized to affect the timing of natal dispersal, (2) describe juvenile movements and estimate first-year fidelity to the natal population, and (3) examine patterns of local settlement and natal dispersal distance for goshawks produced and recruited on the Kaibab Plateau.

METHODS

STUDY AREA AND POPULATION

The 1732 km^2 study area encompassed all of the coniferous forests on the Kaibab Plateau of northern Arizona (Fig. 1). The Kaibab Plateau is an oval-shaped limestone plateau that rises from a shrubsteppe plain (elevation 1750 m) to a maximum elevation of 2800 m (Rasmussen 1941), and includes the northern sections of the Kaibab National Forest and the Grand Canyon National Park. Forests on the study area are completely surrounded by unsuitable goshawk nesting habitat (Reynolds et al. 2005) and include three principal types: pinyon-juniper (*Pinus edulis–Juniperus* spp.) woodland occurs 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*, and *Populus tremuloides*) occur from 2450 to 2800 m (Rasmussen 1941, White and Vankat 1993). Annual precipitation on the Kaibab Plateau averages 67.5 cm (White and Vankat 1993). Mid to late summers are characterized by frequent (2–4 per week) thunderstorms with heavy rainfall.

In 1991, studies of goshawk demographics and habitat were established on the Kaibab Plateau (Reynolds et al. 2005). Protocols used to locate and monitor nesting goshawks are described in detail elsewhere (Reynolds et al. 1994, 2005). Goshawks on the Kaibab Plateau exhibit temporally invariant survival (75%; Reynolds et al. 2004) and strong site fidelity (94%; Reynolds and Joy 2006) once settled on a breeding territory. A "territory" was defined as an area used, but not necessarily defended against conspecifics, by a single pair of goshawks during a breeding season (Reynolds et al. 2005). Territories contained multiple alternate nests that were used (eggs laid) one or more times during the study by color-marked goshawks. The number of territories monitored increased from 37 in 1991 to 121 in 2004 (Appendix). By 2004, a high density of regularly spaced breeding areas had been identified on the Kaibab Plateau with a mean interterritory distance of 3.8 km (Reich et al. 2004, Reynolds et al. 2005).

BANDING DATA

From 1991 to 2004, capture-recapture studies of adult and nestling goshawks were conducted on the Kaibab Plateau. Nesting adults were captured near nests using dho-gaza traps (Reynolds et al. 1994); nestlings were captured by climbing nest trees during the last week of the nestling period (mid to late June). All captured goshawks were fitted with a U.S. Geological Survey leg band and an anodized colored leg band with a unique alphanumeric code. Colored leg bands could be read from 80 m using 40–60× spotting scopes so that hawks could be identified in subsequent years without recapture. For each nestling captured, we measured age (number of days posthatching) using a photographic and behavioral guide (Boal 1994), body mass (g), and gender (determined by body mass, tarsometatarsal length, and foot length, the span from the outer halix pad to the outer second toe pad). All known territories were searched annually to determine the location and reproductive status of territorial pairs and to detect previously banded hawks. A goshawk was considered to have been locally recruited if it had been banded as a nestling on the study area and was later observed breeding within the study population (Wiens and Reynolds 2005). Such cases were used to investigate patterns of local settlement and natal dispersal distance.

TELEMETRY DATA

In addition to observations of natal dispersal based on recaptures of color-banded nestlings, we radio-marked 89 nestlings (42 females, 47 males) at 48 nests during 1998–2001 to investigate the timing of dispersal and juvenile fidelity. Nests targeted for radio-marking young were randomly selected from a stratified sample of nests in the Kaibab National Forest containing one, two, or three young each. Nestlings were captured 2–6 days before fledging (32–35 days posthatching) and fitted with 17-g backpack-style radio-transmitters (model LPB 2380M, Wildlife Materials, Inc., Murphysboro, IL). Radio-transmitters were attached using four separate reinforced nylon straps with a "weak link" cotton attachment that allowed the harness to fall off without entanglement ~1 year after capture (modified from Klavitter et al. 2003). Radio-transmitters had a mean life expectancy of 500 days.

Radio-marked hawks were monitored with model R4000 ATS receivers (Advanced Telemetry Systems, Inc., Isanti, MN). Status of young goshawks (location, alive, dead) was recorded 4–5 times week^{-1} between fledging and dispersal. Once young goshawks venture beyond 2 km from the nest, they are generally not recorded within that radius on subsequent occasions (Kenward et al. 1993a, but see Kennedy and Ward 2003). We therefore defined dispersal as the first day a juvenile spent more than two consecutive days $\geq$2 km from its nest. After juveniles dispersed, ground crews attempted to record their locations daily but were often unsuccessful due to high movement rates or inaccessible terrain. Dispersal locations were estimated by quietly approaching on foot until the hawk was sighted, a change in signal strength was recorded, or a signal could be detected without an antenna (i.e., antenna cable or receiver only), indicating the hawk was within 10–20 m of the observer. Each hawk location was recorded using a Global Positioning System accurate to ±3 m. When a radio-transmitter signal was lost, searches were conducted throughout the study area using omnidirectional antennas mounted on trucks and from fire lookout towers in the study area. We also used fixed-wing aircraft to obtain locations of dispersing goshawks and to search for missing signals within 60–70 km of the study area boundary (aerial survey area = 10 800 km^2; Fig. 1). Tracking flights followed a series of transect lines spaced 10 km apart within the survey area, and were conducted regularly at bimonthly (September and October) and monthly (November–May) intervals during 1999–2002. The probability of detecting radio-marked hawks by aircraft was estimated as the proportion of 22 radio-transmitters

TABLE 1. Covariates used to model the timing of natal dispersal (1998–2001) and local natal dispersal distance (1991–2004) of Northern Goshawks on the Kaibab Plateau, Arizona.

Covariate	Level[a]	Response variable[b]	Description
Prey density	Cohort	*T*	Annual summation of red squirrel, Kaibab squirrel, Northern Flicker, and Steller's Jay density (ha^{-1}) on the Kaibab National Forest, 1998–2001.
Precipitation	Cohort	*T*	Cumulative precipitation (cm) during 1 July–30 September, 1998–2001, recorded daily at four weather stations on the study area and averaged among stations to obtain annual estimates.
Proportion of pairs breeding (POPB)	Cohort	*D*	Annual number of territories with used (eggs laid) nests divided by the total number of territories under study in the year of fledging.
Relative hatch date	Territory	*T*	Nest hatch date, estimated from nestling ages at the time of capture. Nest hatch dates were transformed to relative values with respect to median hatch dates, 1998–2001 (Appendix).
Brood size	Territory	*T*	Number of young fledged per nest, including the focal individual.
Body condition	Individual	*T, D*	Mass (g) of focal individual at time of capture (5–7 days prefledging).
Sex	Individual	*T, D*	Determined by body mass, tarsometatarsal length, and foot length.

[a] Biological level at which each covariate was measured.

[b] T = timing of dispersal, expressed as the age (number of days postfledging) and date (1–365; day 1 = 1 January) at which radio-marked young initiated dispersal, 1998–2001; D = local natal dispersal distance, measured as the straight-line distance between the natal nest and nest site of first breeding for goshawks produced, color-banded, and recruited within the study population.

placed at random locations and heights (0–5 m) throughout the survey area that could be relocated by a naive observer. This test indicated that the probability of detecting a functioning radio-transmitter within the aerial survey area was 0.91 (95% CI: 0.79–1.00).

MODEL DEVELOPMENT

We developed statistical models to represent the potential influences of individual, social, and environmental conditions on local natal dispersal behavior of goshawks. These conditions were expressed as individual-, territory-, and cohort-level covariates and assessed relative to the onset and completion of natal dispersal in the study area. Our selection of covariates was guided by previous studies of natal dispersal (see below), existing knowledge of goshawk ecology on the Kaibab Plateau (Reynolds et al. 1994, 2005), and field observations.

Timing of dispersal. Variation in the timing of natal dispersal by raptors is often explained by individual characteristics such as gender and body condition (Kenward et al. 1993a), characteristics of the natal area such as hatching date and brood size (Strickland 1991, Ellsworth and Belthoff 1999, Forero et al. 2002, Byholm et al. 2003), or environmental conditions such as food availability (Bustamante 1994, Willey and van Riper 2000, Kennedy and Ward 2003). We selected six covariates to represent these effects in our assessment of the timing of natal dispersal in goshawks (Table 1). Of particular interest was our prediction that the abundance of several primary bird and mammal goshawk prey species on the Kaibab Plateau (Boal and Mannan 1994, Salafsky 2004) would be positively related to the timing of dispersal. We examined this prediction using annual density (ha^{-1}) estimates of Northern Flickers (*Colaptes auratus*), Steller's Jays (*Cyanocitta stelleri*), red squirrels (*Tamiasciurus hudsonicus*), and Kaibab squirrels (*Sciurus aberti kaibabensis*) obtained on the Kaibab National Forest during the goshawk breeding season (28 May–14

August, 1999–2001) using line-transect distance sampling methods (Salafsky 2004, Salafsky et al. 2005). Based on prey remains collected at 211 nest sites, these four species represented ~65% of total diet biomass for goshawks breeding in the Kaibab National Forest during 1998–2001 (S. Salafsky, Colorado State University, unpubl. data). We also anticipated that dispersal may have been delayed by prolonged periods of heavy rainfall that occurred during the later stages of the fledgling dependency period in 1998 and 1999. To examine our prediction, we acquired daily precipitation records from July to September (1998–2001) from four weather stations on the study area (Fig. 1).

Local natal dispersal distance. Natal dispersal distance in goshawks may be directly related to local resource conditions (Byholm et al. 2003, Kennedy and Ward 2003). On the Kaibab Plateau, annual differences in goshawk breeding density are highly correlated with food abundance (Salafsky 2004). We therefore considered the proportion of territorial pairs breeding in the year of fledging to be a good indicator of resource abundance for that year, and assessed this effect relative to local natal dispersal distance (the distance between the natal nest and the nest site of first breeding for locally recruited hawks). Inbreeding avoidance may also influence local natal dispersal distance (Greenwood 1980, Newton and Marquiss 1983, Wheelwright and Mauck 1998). To investigate the effect of inbreeding avoidance on local natal dispersal, we used the capture histories of adult goshawks to determine if local recruits settled farther from their natal area when their opposite-sex parent still occupied their natal territory in the year of recruitment. Finally, because natal dispersal distance may be influenced by gender (Greenwood 1980) or physiological differences among individuals (Paradis et al. 1998, Dufty and Belthoff 2001), we included gender and prefledging body mass as covariates in our assessment (Table 1).

STATISTICAL ANALYSES

Model selection. Candidate model sets for both the timing of dispersal and local natal dispersal distance included a fully specified general model with all main effects, reduced forms of the general model, and a base model without main effects. A base model without main effects was useful for assessing the relative explanatory power of models containing covariates of interest. Candidate model sets were constrained by *a priori* considerations (e.g., correlation among covariates) and by sample size: models containing more than $n/10$ parameters were excluded (Burnham and Anderson 2002). We ranked, compared, and evaluated candidate models using information-theoretic methods (e.g., AIC_c; Burnham and Anderson 2002). We also assessed the degree to which 95% confidence intervals (CI) of slope coefficients (β_i) overlapped zero to supplement AIC_c evidence of important effects. In cases where there was substantial uncertainty in model selection results, parameter estimates were averaged across models containing a covariate and standard errors were calculated from unconditional variances (Burnham and Anderson 2002). In such cases, the relative importance of each covariate (X) was assessed using cumulative Akaike weights ($w_+[X]$; Burnham and Anderson 2002). Variables with strong support have cumulative Akaike weights near 1. All analyses were performed using program SAS version 8.02 (SAS Institute 2000), and estimates are presented as means ± SE.

Timing of dispersal. We used proportional hazards regression (PROC PHREG; SAS Institute 2000) to evaluate covariates relative to the date (1–365; day 1 = 1 January) and age (number of days posthatching) that radio-marked juveniles initiated dispersal. The PHREG procedure performs failure-time analysis (Cox 1972), which is often used to analyze the effects of covariates on the time until an event, such as dispersal, occurs (Muenchow 1986, Bennetts et al. 2001, Kennedy and Ward 2003). Model fit to individual observations and assumptions of proportionality was evaluated using deviance and martingale residual plots (SAS Institute 2000).

Juvenile fidelity. Based on relocations of radio-marked juveniles, we used the Kaplan-Meier estimator (Kaplan and Meier 1958) to determine juvenile fidelity to the natal population during the first 11 months postfledging (Bennetts et al. 2001). We defined fidelity as the cumulative probability of detecting a radio-marked juvenile within the aerial survey area between fledging (time t = 0) and month 11 postfledging (time t = 11). A juvenile was considered to have dispersed beyond this area at time t if it was not detected during an aircraft survey. Hence, juveniles classified as "dispersed" included hawks that moved beyond the survey area and lived, hawks that moved beyond this area and died, and hawks present within this area but not detected as a result of radio-transmitter malfunction or other, unknown causes. The detection probability within our survey area was high (0.91), so we were confident that the majority of radio-marked hawks not detected by aircraft (i.e., censored) had dispersed beyond the Kaibab Plateau. Nonetheless, the number of juveniles censored during each time interval was multiplied by the signal detection rate to adjust for uncertain relocation. Hence, fidelity was estimated as: 1 − (the adjusted number of censored hawks at time t divided by the number of hawks available for detection at time t), and we approximated the variance using the delta method (Oehlert 1992). The number of juveniles available for detection at time t consisted of those hawks remaining in the sample after hawks that had died or shed their radio-transmitters in the previous time interval were removed.

Local natal dispersal distance. We measured local natal dispersal distance as the straight-line distance from the natal nest site to the nest site of first breeding for a goshawk that was produced, color-banded, and recruited within the local breeding population. As a simple measure of territory spacing between the natal and breeding sites, we calculated the "effective dispersal distance" (Shields 1983) as the median local natal dispersal distance divided by the mean interterritory distance among 121 territory centers (3.8 km; Reynolds et al. 2005). We used generalized linear models with an identity-link function (PROC GENMOD; SAS Institute 2000) to obtain maximum-likelihood estimates of local natal dispersal distance as a linear function of six covariates (Table 1). Distances were log-transformed to obtain a normal distribution of errors.

RESULTS

TIMING OF DISPERSAL

All 89 radio-marked nestlings successfully fledged from 48 nests located in 36 distinct territories. Young goshawks fledged between 28 June and 12 August ($\bar{x}$ = 16 July) at 40.3 ± 0.4 days posthatching (range = 30–50 days). Excluding hawks that died (n = 8) or prematurely shed their radio-transmitters prior to dispersal (n = 10), juveniles spent an average of 46.3 ± 0.8 days in the natal territory (range = 33–66 days, n = 71). Annual means for the duration of this period varied from 43.7 ± 2.1 (95% CI: 38.9–48.4) days in 2001 to 49.1 ± 1.7 (95% CI: 45.5–52.8) days in 1998. Radio-marked juveniles initiated dispersal from their natal areas between 30 July and 15 September ($\bar{x}$ = 30 August) at 86.5 ± 0.8 days posthatching (range = 71–103 days).

Dispersal date. The date of dispersal varied among years, as indicated by a comparison between a base model without annual variation and a model incorporating a year effect (ΔAIC_c between models = 18.3; Table 2). Model-averaged parameter estimates and unconditional 95% confidence intervals indicated that dispersal date was positively influenced by prey abundance ($\hat{\beta}_{\text{prey}} = 0.60$; Wald 95% CI: 0.14–1.06), and negatively influenced by total precipitation during the July–September period of each year ($\hat{\beta}_{\text{precipitation}} = -0.11$; 95% CI: -0.16 to -0.06). Individual- and territory-level covariates received moderate to poor support with respect to dispersal date (Table 3).

Dispersal age. There was substantial uncertainty in model-selection results regarding the age of dispersal, and weak evidence of annual variation in this parameter (Table 2). Of the covariates considered, brood size received the strongest support (w_+[brood size] = 0.83), whereas total precipitation, hatch date, and sex covariates received moderate support (Table 3). Model-averaged parameter estimates and unconditional 95% confidence intervals showed that dispersal age was negatively influenced by brood size ($\hat{\beta}_{\text{brood size}} = -0.45$; 95% CI: -0.82 to -0.07; Fig. 2), and total precipitation ($\hat{\beta}_{\text{precipitation}} = -0.05$; 95% CI: -0.09 to -0.01). Large differences among years in prey density (Appendix) and differences among individuals in prefledging body mass had little influence on dispersal age. Observations of dispersal rates within the same brood may not be strictly statistically independent (Albercio et al. 1992, Massot et al. 1994). To see if intrabrood dependency unduly biased our results, we conducted a separate analysis using one randomly selected young per nest (Massot et al. 1994). This brood-randomization process was repeated over 60 iterations, result-

TABLE 2. Ranking of proportional hazards regression models used to explain variation in the timing of natal dispersal for Northern Goshawks on the Kaibab Plateau, Arizona, 1998–2001. Models are ranked from most plausible ($\Delta AIC_c = 0.00$) to least plausible. All models with $\Delta AIC_c \leq 2.50$ are listed, as well as the base model without covariates and the model containing a year effect for comparisons. See Table 1 for a description of covariates.

Covariates in model	Log likelihood	Number of parameters	ΔAIC_c	Akaike weight
Dispersal date				
Prey, Precipitation	−225.84	4	0.00	0.25
Prey, Precipitation, Sex	−224.98	5	0.60	0.19
Year	−225.48	5	1.59	0.11
Prey, Precipitation, Brood	−225.83	5	2.31	0.08
Prey, Precipitation, Sex, Body mass	−224.65	6	2.33	0.08
Year, Sex	−224.67	6	2.37	0.08
Base model (no covariates)	−239.06	1	19.89	0.00
Dispersal age				
Brood, Precipitation, Hatch date	−233.34	5	0.00	0.12
Brood, Precipitation	−234.52	4	0.04	0.12
Brood, Precipitation, Sex, Hatch date	−232.23	6	0.16	0.11
Brood, Precipitation, Sex	−233.55	5	0.41	0.10
Brood	−236.35	3	1.45	0.06
Brood, Hatch date	−235.44	4	1.86	0.05
Brood, Precipitation, Prey	−234.34	5	1.99	0.04
Brood, Sex	−235.58	4	2.14	0.04
Brood, Precipitation, Sex, Body mass	−233.31	6	2.32	0.04
Brood, Sex, Hatch date	−234.53	5	2.36	0.04
Base model (no covariates)	−239.38	2	5.32	0.01
Year	−237.47	5	8.25	0.00

TABLE 3. Likelihoods, parameter estimates, and unconditional 95% confidence intervals (CI) for covariates modeled relative to the timing of natal dispersal for Northern Goshawks on the Kaibab Plateau, Arizona, 1998–2001. See Table 1 for a description of covariates.

Covariate	Covariate likelihood[a]	Parameter estimate[b]	95% CI[c]
Dispersal date			
Precipitation	0.73	−0.11	−0.16 to −0.06
Prey density	0.67	0.60	0.14 to 1.06
Sex	0.51	0.26	−0.33 to 0.85
Year	0.28		
Brood size	0.20	0.05	−0.34 to 0.45
Body mass	0.16	<−0.01	−0.01 to 0.00
Dispersal age			
Brood size	0.83	−0.45	−0.83 to −0.07
Precipitation	0.55	−0.05	−0.09 to −0.01
Hatch date	0.50	0.04	−0.01 to 0.09
Sex	0.49	0.33	−0.26 to 0.91
Body mass	0.12	<−0.01	−0.01 to 0.00
Prey density	0.12	0.13	−0.37 to 0.63
Year	0.03		

[a] Calculated as the summation of Akaike weights across all models containing the covariate.

[b] Weighted average from all models containing the covariate (Burnham and Anderson 2002).

[c] Unconditional 95% confidence interval, calculated using unconditional variances to adjust for model selection uncertainty.

FIGURE 2. The effect of brood size on the probability of staying within the natal area (a 2 km radius surrounding the nest) between 70 and 105 days posthatching for Northern Goshawks on the Kaibab Plateau, Arizona, 1998–2001.

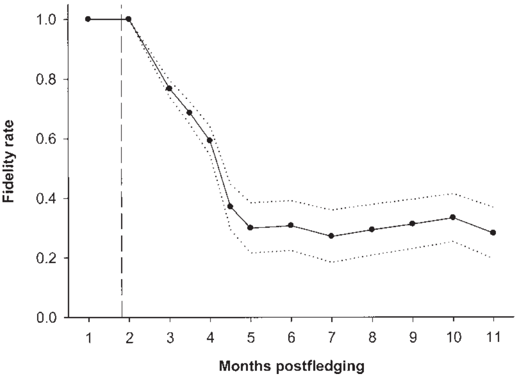

FIGURE 3. Kaplan-Meier estimates (± 95% CI) of Northern Goshawk fidelity to the natal population on the Kaibab Plateau, Arizona, over the first 11 months postfledging. Fidelity was estimated as the cumulative proportion of radio-marked juveniles detected within a 10 800 km^2 aerial survey area during 1999–2002. The dashed vertical line indicates the average age at which juveniles initiated dispersal. Increases in the function resulted from previously undetected juveniles returning to the survey area between successive time intervals.

ing in a distribution of log-likelihood values for each model considered. Median values were then used for AIC$_c$ model selection. A reduction in sample size (45 broods vs. 71 individuals) decreased the precision of parameter estimates and increased model selection uncertainty. Nonetheless, cumulative Akaike weights and model-averaged parameter estimates calculated under this approach were similar to those obtained using all individuals (w_+[brood size] = 0.71, $\hat{\beta}_{\text{brood size}} = -0.39$; 95% CI: −0.83 to 0.06).

JUVENILE MOVEMENT AND FIDELITY

We obtained dispersal data on 48 of the 89 radio-marked juveniles. The remaining 41 juveniles either died before dispersal (n = 8), prematurely shed their radio-transmitter before dispersal (n = 10), or were immediately lost upon the initiation of dispersal due to long-distance movement, radio failure, or other unknown causes (n = 23). Maximum dispersal distances (straight-line distance between the natal nest and farthest postindependence location recorded for a radio-marked hawk) ranged from 2.7–79.1 km ($\bar{x}$ = 25.2 ± 1.2 km, median = 22.9 km), but was clearly constrained by the size of the aerial survey area (Fig. 1). As indicated by the fidelity function (Fig. 3), the cumulative probability of detecting a radio-marked juvenile within the aerial survey area by month 11 postfledging was 0.28 (95% CI: 0.19–0.37). By November (5 months postfledging), 72% of radio-marked juveniles had dispersed beyond the Kaibab Plateau with a large surge of movement beyond this area occurring three to five months postfledging. During winter months (December–February), radio-marked juveniles were predominantly relocated in pinyon-juniper woodland and shrub-steppe cover types at lower elevations. The slight increase in the fidelity function during months 8–10 postfledging resulted from previously undetected juveniles moving back into our survey area between monthly flight intervals. By their first spring (10 months postfledging), five radio-marked juveniles had settled into temporary home ranges at lower elevations and three others were relocated on the Kaibab Plateau. Four radio-marked hawks (two females, two males) eventually recruited to the study population by 2004. We also received information on five color-banded juveniles that were recovered dead in their first year 52–442 km beyond the study area boundary.

LOCAL SETTLEMENT AND NATAL DISPERSAL DISTANCE

We banded 614 nestling goshawks during 1991–2003 (Appendix). Of these, 69 (11%) were relocated as breeding adults within the study population, 39 (13%) females and 30 (10%) males. The annual percentage of goshawks

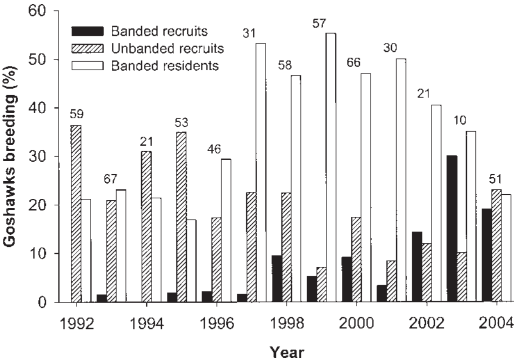

FIGURE 4. Percent of adult Northern Goshawks breeding during 1992–2004 on the Kaibab Plateau, Arizona, that were nestling recaptures (banded recruits), new adult captures (unbanded recruits), or previously banded adults (banded residents). Numbers above bars indicate the total number of pairs breeding (laid eggs) in each year.

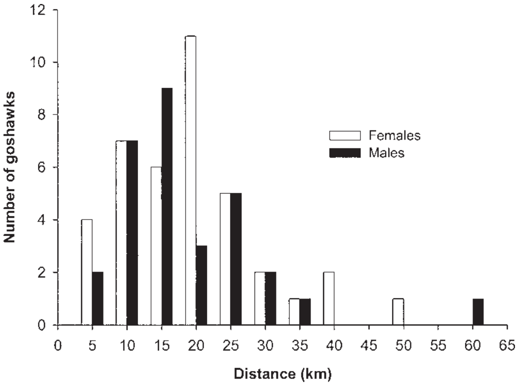

FIGURE 5. Distributions of local natal dispersal distances for male and female Northern Goshawks on the Kaibab Plateau, Arizona, 1991–2004. Local natal dispersal distance was the straight-line distance between the natal nest and the nest site of first breeding for goshawks (n = 69) that were produced, color-banded, and recruited on the Kaibab Plateau.

breeding that were nestling recaptures (banded recruits) increased over the years of our study (Fig. 4). The overall percentage of new recruits (nestling recaptures and new adult captures) accounted for 27% of goshawks breeding during the study period, with percentages ranging from 12% to 36%. By 2004 the ratio of banded to unbanded recruits was nearly equal (Fig. 4). Nestling return rates based on ages at first recapture (2, 3, 4, or $\geq$5 years) were 17%, 26%, 26%, and 31%, respectively. Assuming that banded recruits were detected on their first breeding attempt, mean age at first breeding was 4.2 ± 0.3 years for females (range = 2–9 years) and 3.9 ± 0.3 years for males (range = 2–11 years). Due to their elusive behavior, most adult goshawks could only be observed if they were breeding. As a result, the ages at first breeding may overestimate the age when goshawks first occupied a territory.

Local natal dispersal distance on the Kaibab Plateau ranged from 0.1–58.1 km ($\bar{x}$ = 16.7 ± 1.2 km, median = 15.0 km; Fig. 5). To examine the extent to which the size of our study area constrained the dispersal distances we could detect, we calculated the maximum distance between the natal nest of each observed dispersal event and every other nest that had been located in the study area by 2004. Possible maximum dispersal distances that we could detect within our study area ranged from 37.2–72.3 km ($\bar{x}$ = 52.6 ± 8.9 [SD] km, median = 51.1 km). Thus, we were generally able to detect local dispersal events at greater distances than the distances we actually observed. Estimates of effective dispersal distance indicated the site of first breeding was an average of four territories distant from the natal site (4.2 territories for females, 3.6 territories for males). Two females banded as nestlings were reported breeding in forests beyond the Kaibab Plateau, one on the south rim of the Grand Canyon (natal dispersal distance = 55 km; T. Bowden, Grand Canyon National Park, pers. comm.) and one in Utah (natal dispersal distance = 107 km; R. Rodriguez, U.S. Forest Service, pers. comm.). These two hawks were omitted from our analysis of local natal dispersal distance. The best-fitting model (ΔAIC_c = 0.00) was the base model (intercept only), evidence that our covariates were weak in predicting local natal dispersal distance. Univariate models containing the effects of sex, prefledging body mass, and brood size were somewhat competitive (ΔAIC_c < 2.00), but we did not consider these models to be informative since they failed to substantially improve upon a base model without covariates.

Inbreeding avoidance. Of 69 banded recruits, only 12 initiated breeding within two territories of their natal site. Only one hawk settled on its natal territory, where it constructed a new nest only 75 m from its natal nest. However, this female did not initiate breeding until 8 years of age, by which time both her parents had disappeared from the study. This was the single case in 605 breeding attempts over a 14-year period of a goshawk settling on its natal territory, and no cases of close inbreeding between parent-offspring or full siblings were documented. There were six cases in which full siblings nested during the same years, but siblings settled between one and seven territories apart (mean distance between siblings = 10.4 km). Inbreeding avoidance data (i.e., opposite-sex parent known) were available for 63 of 69 banded recruits. Only 12 recruits initiated breeding while their opposite-sex parent still occupied the original natal territory, but none of these settled within one territory of their natal site. Despite this evidence, the presence of an opposite-sex parent in the year of recruitment was a poor predictor of local natal dispersal distance ($\hat{\beta} = -0.04$; 95% CI: -0.29 to 0.19).

DISCUSSION

Three general findings characterized natal dispersal of goshawks on the Kaibab Plateau. First, annual differences in local environmental conditions (prey abundance, weather) and social conditions of the natal site (number of siblings) most strongly influenced when juveniles initiated dispersal. Second, most (72%) radio-marked juveniles dispersed >80 km beyond the natal population during their first year and few (11%) color-banded nestlings eventually returned to gain a local breeding territory. Third, local recruits initiated breeding at a delayed age and typically settled between three and five territories away from their natal site. In general, natal dispersal behavior of goshawks on the Kaibab Plateau appeared to be driven by a combination of local environmental conditions, intraspecific competition for a limited number of breeding opportunities, and inbreeding avoidance. As much of the natal dispersal process operated at broad spatial scales beyond our study area, we suspect that movement among naturally fragmented goshawk populations in the southwestern United States is common.

TIMING OF DISPERSAL

Early dispersers may settle significantly farther from their natal areas than late dispersers, suggesting that variation in the timing of dispersal may be important to exchange rates among fragmented raptor populations (Walls and Kenward 1998, Byholm et al. 2003). We were unable to assess the influence of the timing of dispersal on dispersal distance, but our results did indicate that the timing of dispersal was a function of local environmental conditions (food availability, weather) and social conditions of the natal area. Our estimates of the mean age at fledging, the mean amount of time fledglings spent in the natal area before dispersal, and the mean age at dispersal were similar to those reported for goshawks elsewhere (Kenward et al. 1993a, Kennedy and Ward 2003, Titus et al. 1994). Also similar to previous studies, there was little evidence of annual variation in the age of dispersal. In contrast to previous studies, however, we found substantial evidence for annual differences in the date of juvenile dispersal. Although the early dispersal date observed in 2000 coincided with the highest prey densities recorded during our study, large annual fluctuations in food availability appeared to have little influence on dispersal age. Thus, environmental and physiological changes associated with the onset of egg-laying in adults may dictate the time of year in which juveniles attain independence and disperse, whereas dispersal age may be more a function of social conditions or endogenous factors (Kenward et al. 1993a, Ellsworth and Belthoff 1999, Kennedy and Ward 2003).

The age at which juveniles dispersed in our study was highly variable among individuals, with some dispersing up to 30 days later than others. Gender-related differences, social conditions of the natal area, and severity of rainfall near the onset of dispersal were factors that best explained this wide range of dispersal behavior. Kenward et al. (1993b) also reported that male goshawks dispersed at a younger age than females, but that juvenile males stayed in the natal area longer when there were few other young in the brood. We did not rank siblings within broods by their dominance level, but intrabrood social patterns appeared to influence the onset of dispersal in a similar way to that reported for other raptors (Strickland 1991, Ferrer 1993, Ellsworth and Belthoff 1999). Weather conditions also affected the onset of dispersal. Daily precipitation records confirmed that rainfall lasted for several days longer and was substantially heavier in 1998 and 1999 relative to 2000 and 2001 (Appendix).

Heavy rainfall near the time of independence may have suppressed prey availability or the capacity for juveniles to initiate long-distance dispersal movements.

TRANSIENT MOVEMENT AND LOCAL SETTLEMENT

Juvenile goshawks on the Kaibab Plateau moved rapidly away from their natal territories during August–September of each year, and most moved beyond their natal population shortly thereafter. However, dispersal behavior was highly variable among individuals—most hawks moved beyond the Kaibab Plateau into the surrounding low-desert landscapes immediately after leaving their natal territory whereas others made this transition more gradually. The relatively small number of color-banded nestlings that were later found breeding within the study population provides further evidence that many juveniles disperse beyond the Kaibab Plateau and do not return. Thus, both radiotelemetry and capture-recapture data were consistent in indicating that only a small fraction of locally produced juveniles remain within the vicinity of their natal population to eventually gain a local breeding territory.

As juvenile goshawks disperse from their natal areas on the Kaibab Plateau, they are quickly faced with the decision of whether to remain in the vicinity of their natal population and wait (perhaps for several years) for a territory vacancy to arise, or to disperse into the surrounding landscape of deep canyons and shrubsteppe plains and attempt to recruit elsewhere. Our radio-tracking results showed that a large fraction of juveniles chose to emigrate, at least temporarily. The banding data also showed that only a small fraction of goshawks either returned or remained close to their natal population when prospecting for a breeding site. Thus, similar to other raptors (Walls and Kenward 1998, Bennetts and Kitchens 2000), a fraction of goshawks appeared to base their territory settlement decisions on knowledge of their local environment. Evidence that some goshawks began exploring their natal neighborhood at an early age was provided by a small number of radio-marked juveniles that remained within 5–10 km of their natal site for several weeks following independence. In contrast, several radio-marked juveniles returned to the vicinity of their natal population after their first winter. Goshawks reach sexual maturity in their first year (Squires and Reynolds 1997), so return to the natal population at this time could be used by immature hawks to assess territory vacancies and pair-formation possibilities. This pattern of juvenile goshawks making long-distance movements following independence and subsequently returning to the vicinity of their natal area has been noted elsewhere (Ingraldi 1998), and may be a common territory-prospecting strategy employed by raptors inhabiting fragmented landscapes (Ferrer 1993).

Although a high proportion of breeding goshawks in immature plumage has been reported elsewhere (Reynolds and Wight 1978, Henney et al. 1985, Speiser and Bosakowski 1991), no hawks in immature plumage have been observed breeding on the Kaibab Plateau (Wiens and Reynolds 2005). A delayed age at first breeding can indicate competition for limited nesting space, food, or mates (Newton 1979). The predicted effects of intraspecific competition on population structure include: (1) a high density of territories, (2) a large number of nonterritorial floaters, (3) a rapid replacement of territorial hawks following mortality, and (4) replacement by older individuals. Although the size of the nonterritorial "floater" population on the Kaibab Plateau is unknown, the remaining conditions predicted to arise from competition are consistent with features reported for our study population (Reynolds et al. 1994, Reich et al. 2004, Wiens and Reynolds 2005, Reynolds and Joy 2006). Despite this evidence, our hypothesis that competition drives local settlement behavior was not supported. However, a high level of individual variation in breeding success (Wiens and Reynolds 2005), spatial differences in habitat quality (Joy 2002), or inbreeding avoidance may have produced considerable spatial heterogeneity in the form of competitive pressure among breeding territories. We did not account for this form of heterogeneity in our assessment, so the influences of competition on settlement behavior may have been obscured.

NATAL DISPERSAL DISTANCE

Due to a lack of information on the external recruitment success for goshawks produced on the Kaibab Plateau, the range of natal dispersal distances we report here was explicitly constrained to a local (population) scale. Our study area is large, contains nearly contiguous forests surrounded by unsuitable goshawk breeding habitat, and 121 (81%) of an estimated 150 possible breeding territories (based on territory spacing and habitat availability; Reynolds et al. 2005) were monitored by 2004. Thus, breeding goshawks and their young had a high probability of being detected on the study area. However, color-banded young that emigrated beyond the Kaibab Plateau had very little chance of being detected, and aerial surveys for radio-marked juveniles were logistically constrained to a 10 800 km^2 area encompassing the study site. As most radio-marked juveniles dispersed beyond this area, we conclude that there was a systematic short-distance bias in the natal dispersal distance distribution when considered over a broad geographic scale.

Our radio-tracking results showed a wide range of dispersal movements for juvenile goshawks, reflecting great mobility and variation in dispersal behavior among individuals. A wide range of juvenile goshawk dispersal distances was also recorded in Alaska (15.9–151.1 km; Titus et al. 1994) and in central Arizona (38.6–186.7 km; Ingraldi 1998). The long-distance dispersal capabilities of juvenile goshawks considered with the highly fragmented nature of suitable breeding habitat in northern Arizona and southern Utah indicates that the true distribution of natal dispersal distances for our study population is multimodal. Two cases of juvenile emigration and five band recoveries of dead juveniles ranging from 52 to 442 km beyond the study area also provide evidence that natal dispersal distances commonly extend beyond the Kaibab Plateau to other, perhaps distant, forests. Elsewhere (Wiens et al. 2006), we found that mortality increased by >13% as radio-marked juveniles dispersed into the open landscapes that surround our study area, indicating the hazards involved in long-distance dispersal. Nevertheless, young goshawks readily dispersed beyond the forests of the Kaibab Plateau into the surrounding matrix of pinyon-juniper woodland and shrubsteppe cover types. Such habitats clearly play an important role in juvenile survival, dispersal, and recruitment processes for goshawks inhabiting the fragmented landscapes of the southwestern U.S.

We found no support for sex- or age-related differences in natal dispersal distances that have been reported in other raptors (Newton and Marquiss 1983, Marti 1999, Forero et al. 2002, Forsman et al. 2002), including juvenile goshawks in Finland (Byholm et al. 2003). It is therefore possible that such effects act more heavily on broad-scale, interpatch dispersal patterns of goshawks than on local recruitment. On the Kaibab Plateau, local recruits typically initiated breeding 3–5 territories away from their natal area. However, the regular size and spacing of goshawk territories on the study area (Reich et al. 2004, Reynolds et al. 2005) and the rate at which adult goshawks fail to return to reclaim their territories each year (25%, or 1 – the adult survival rate of 75%; Reynolds et al. 2004) indicated that several territories adjacent to the natal site would be expected to have same-sex vacancies the year following fledging. Despite the fact that local natal dispersal was not associated with the presence of an opposite-sex parent in the year of recruitment, no cases of close inbreeding were documented. This evidence, and the spatial aggregation exhibited by local recruits, demonstrates that natal dispersal resulted in inbreeding avoidance. This conclusion is also supported by molecular evidence from goshawks on the Kaibab Plateau, which showed an absence of inbreeding and a population genetic structure consistent with that produced by a high rate of gene flow (Bayard de Volo et al. 2005).

Natal dispersal accounts for nearly all of the dispersal in the life of goshawks on the Kaibab Plateau, as fewer than 6% of adult hawks moved relatively short distances (2–17 km) to a different territory between successive breeding attempts (RTR, unpubl. data). This strong site fidelity of adults considered with the propensity for juveniles to disperse long distances and a population genetic structure consistent with a high rate of gene flow (Bayard de Volo et al. 2005) provides evidence that movement among fragmented breeding populations in the Southwest is primarily achieved via natal dispersal. Movements of individuals into and out of subdivided populations can act to stabilize local and regional population growth rates and decrease extinction probability (Johnst and Brandl 1997, Bowne and Bowers 2004). If naturally fragmented goshawk populations in the southwestern U.S. function as a metapopulation maintained by interpatch movements of juveniles, a reduction in juvenile movement among subpopulations could lead to a situation in which local mortality exceeds that of productivity and immigration, leading to a decline in population viability (Stacey and Taper 1992). Our study provides evidence that the nonforested habitats (e.g., shrubsteppe and pinyon-juniper woodland) used during dispersal between disjunct mountain forests may play an important role in maintaining demographic connectivity among fragmented goshawk populations in the American Southwest.

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LITERATURE CITED

ALBERICO, J. A. R., J. M. REED, AND L. W. ORING. 1992. Non-random philopatry of sibling Spotted Sandpipers *Actitis macularia*. Ornis Scandinavica 23:504–508.

BAYARD DE VOLO, S., R. T. REYNOLDS, J. R. TOPINKA, B. MAY, AND M. F. ANTOLIN. 2005. Population genetics and genotyping for mark-recapture studies of Northern Goshawks (*Accipiter gentilis*) on the Kaibab Plateau, Arizona. Journal of Raptor Research 39:286–295.

BENNETTS, R. E., AND W. M. KITCHENS. 2000. Factors influencing movement probabilities of a nomadic food specialist: proximate foraging benefits or ultimate gains from exploration? Oikos 91:459–467.

BENNETTS, R. E., J. D. NICHOLS, J. D. LEBRETON, R. PRADEL, J. E. HINES, AND W. M. KITCHENS. 2001. Methods for estimating dispersal probabilities and related parameters using marked animals, p. 3–17. *In* J. Colbert, E. Danchin, A. A. Dhondt, and J. D. Nichols [EDS.], Dispersal. Oxford University Press, Oxford, UK.

BOAL, C. W. 1994. A photographic and behavioral guide to aging nestling Northern Goshawks. Studies in Avian Biology 16:32–40.

BOAL, C. W., AND R. W. MANNAN. 1994. Northern Goshawk diets in ponderosa pine forests on the Kaibab Plateau. Studies in Avian Biology 16: 97–102.

BOWNE, D. R., AND M. A. BOWERS. 2004. Interpatch movements in spatially structured populations: a literature review. Landscape Ecology 19:1–20.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.

BUSTAMANTE, J. 1994. Family break-up in Red Kites *Milvus migrans* and *M. milvus*: is time of independence an offspring decision? Ibis 136: 176–184.

BYHOLM, P., P. SAUROLA, H. LINDEN, AND M. WIKMAN. 2003. Causes of dispersal in Northern Goshawks (*Accipiter gentilis*) in Finland. Auk 120:706–716.

COX, D. R. 1972. Regression models and life tables. Journal of the Royal Statistical Society B 34: 187–220.

DETRICH, P. J., AND B. WOODBRIDGE. 1994. Territory fidelity, mate fidelity, and movements of color-marked Northern Goshawks in the southern cascades of California. Studies in Avian Biology 16:130–132.

DUFTY, A. M., JR., AND J. R. BELTHOFF. 2001. Proximate mechanisms of natal dispersal: the role of body condition and hormones, p. 217–229. *In* J. Colbert, E. Danchin, A. A. Dhondt, and J. D. Nichols [EDS.], Dispersal. Oxford University Press, Oxford, UK.

ELLSWORTH, E. A., AND J. R. BELTHOFF. 1999. Effects of social status on the dispersal behavior of juvenile Western Screech-Owls. Animal Behaviour 57:883–892.

FERRER, M. 1993. Juvenile dispersal behavior and natal philopatry in a long-lived raptor, the Spanish Imperial Eagle *Aquila adalberti*. Ibis 135:132–138.

FORERO, M. G., J. A. DONÁZAR, AND F. HIRALDO. 2002. Causes and consequences of natal dispersal in a population of Black Kites. Ecology 83: 858–872.

FORSMAN, E. D., R. G. ANTHONY, J. A. REID, P. J. LOSCHL, S. G. SOVERN, M. TAYLOR, B. L. BISWELL, A. ELLINGSON, E. C. MESLOW, G. S. MILLER, K. A. SWINDLE, J. A. THRAILKILL, F. F. WAGNER, AND D. E. SEAMAN. 2002. Natal and breeding dispersal of Northern Spotted Owls. Wildlife Monographs 149.

GREENWOOD, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. Animal Behavior 28:1140–1162.

GREENWOOD, P. J., AND P. H. HARVEY. 1982. The natal and breeding dispersal in birds. Annual Review in Ecology and Systematics 13:1–21.

HENNY, C. J., R. A. OLSEN, AND T. L. FLEMING. 1985. Breeding chronology, molt, and measurements of *Accipiter* hawks in northeastern Oregon. Journal of Field Ornithology 56:97–112.

IMS, R. A., AND D. Ø. HJERMANN. 2001. Condition-dependent dispersal, p. 203–216. *In* J. Colbert, E. Danchin, A. A. Dhondt, and J. D. Nichols [EDS.], Dispersal. Oxford University Press, Oxford, UK.

INGRALDI, M. F. 1998. Population biology of Northern Goshawks. Arizona Game and Fish Department Technical Report NGTR 133.

JOHNST, K., AND R. BRANDL. 1997. The effect of dispersal on local population dynamics. Ecological Modeling 104:87–101.

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

KAPLAN, E. L., AND P. MEIER. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistics Association 53: 457–481.

KENNEDY, P. L. 1997. The Northern Goshawk (*Accipiter gentilis atricapillus*): is there evidence of a population decline? Journal of Raptor Research 31:95–106.

KENNEDY, P. L., AND J. M. WARD. 2003. Effects of experimental food supplementation on movements of juvenile Northern Goshawks (*Accipiter gentilis atricapillus*). Oecologia 134:284–291.

KENWARD, R. E., V. MARCSTRÖM, AND M. KARLBOM. 1993a. Post-nestling behavior in goshawks, *Accipiter gentilis*: I. The causes of dispersal. Animal Behavior 46:365–370.

KENWARD, R. E., V. MARCSTRÖM, AND M. KARLBOM. 1993b. Post-nestling behavior in goshawks, *Accipiter gentilis*: II. Sex differences in sociality and nest-switching. Animal Behavior 46: 371–378.

KLAVITTER, J. L., J. M. MARZLUFF, AND M. S. VEKASY. 2003. Abundance and demography of the Hawaiian Hawk: is delisting warranted? Journal of Wildlife Management 67:165–176.

KOENIG, W. D., P. N. HOOGE, M. T. STANBACK, AND J. HAYDOCK. 2000. Natal dispersal in the cooperatively breeding Acorn Woodpecker. Condor 102:492–502.

KOENIG, W. D., D. VAN VUREN, AND P. N. HOOGE. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Ecology & Evolution 11:514–517.

LAMBERSON, R. H., B. R. NOON, C. VOSS, AND K. S. MCKELVEY. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. Conservation Biology 8:185–195.

MARTI, C. D. 1999. Natal and breeding dispersal in Barn Owls. Journal of Raptor Research 33: 181–189.

MASSOT, M., J. COLBERT, A. CHAMBON, AND Y. MICHALAKIS. 1994. Vertebrate natal dispersal: the problem of non-independence of siblings. Oikos 70:172–176.

MCCARTHY, M. A. 1997. Competition and dispersal from multiple nests. Ecology 78:873–883.

MUENCHOW, G. 1986. Ecological use of failure time analysis. Ecology 67:246–250.

MURPHY, D. D., AND B. R. NOON. 1992. Integrating scientific methods with habitat conservation planning: reserve design for Northern Spotted Owls. Ecological Applications 2:3–17.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD.

NEWTON, I., AND M. MARQUISS. 1983. Dispersal of Sparrowhawks between birthplace and breeding place. Journal of Animal Ecology 52:463–477.

NOON, B. R., AND K. S. MCKELVEY. 1992. Stability properties of the Spotted Owl metapopulation in southern California, p. 187–206. *In* J. Verner, K. S. McKelvey, B. R. Noon, R. J. Guitiérrez, G. I. Gould Jr., and T. W. Beck [TECH. COORDS.], The California Spotted Owl: a technical assessment of its current status. USDA Forest Service General Technical Report PSW-GTR-133.

OEHLERT, G. W. 1992. A note on the delta method. American Statistician 46:27–29.

PARADIS, E., S. R. BAILLIE, W. J. SUTHERLAND, AND R. D. GREGORY. 1998. Patterns of natal and breeding dispersal in birds. Journal of Animal Ecology 67:518–536.

PASINELLI, G., AND J. R. WALTERS. 2002. Social and environmental factors affect natal dispersal and philopatry of male Red-cockaded Woodpeckers. Ecology 83:2229–2239.

PECK, J. 2000. Seeing the forest through the eyes of a hawk: an evaluation of recent efforts to protect Northern Goshawk populations in southwestern forests. Natural Resources Journal 40: 125–155.

RASMUSSEN, D. I. 1941. Biotic communities of the Kaibab Plateau, Arizona. Ecological Monographs 11:230–273.

REICH, R. M., S. M. JOY, AND R. T. REYNOLDS. 2004. Predicting the location of Northern Goshawk nests: modeling the spatial dependency between nest locations and forest structure. Ecological Modeling 176:109–133.

REYNOLDS, R. T., R. T. GRAHAM, M. H. REISER, R. L. BASSETT, P. L. KENNEDY, D. A. BOYCE JR., G. GOODWIN, R. SMITH, AND E. L. FISHER. 1992. Management recommendations for the Northern Goshawk in the southwestern United States. USDA Forest Service General Technical Report TM-217.

REYNOLDS, R. T., AND S. M. JOY. 2006. Demography of Northern Goshawks in northern Arizona, 1991–1996. Studies in Avian Biology 31, in press.

REYNOLDS, R. T., S. M. JOY, AND D. G. LESLIE. 1994. Nest productivity, fidelity, and spacing of Northern Goshawks in northern Arizona. Studies in Avian Biology 16:106–113.

REYNOLDS, R. T., G. C. WHITE, S. M. JOY, AND R. W. MANNAN. 2004. Effects of radiotransmitters on Northern Goshawks: do tailmounts lower survival of breeding males? Journal of Wildlife Management 68:25–32.

REYNOLDS, R. T., J. D. WIENS, S. M. JOY, AND S. R. SALAFSKY. 2005. Sampling considerations for demographic and habitat studies of Northern

Goshawks. Journal of Raptor Research 39: 274–285.

REYNOLDS, R. T., AND H. M. WIGHT. 1978. Distribution, density, and productivity of *Accipiter* hawks breeding in Oregon. Wilson Bulletin 90:182–196.

SALAFSKY, S. R. 2004. Covariation between prey abundance and Northern Goshawk fecundity on the Kaibab Plateau, Arizona. M.Sc. thesis, Colorado State University, Fort Collins, CO.

SALAFSKY, S. R., R. T. REYNOLDS, AND B. R. NOON. 2005. Patterns of temporal variation in goshawk reproduction and prey resources. Journal of Raptor Research 39:237–246.

SAS INSTITUTE. 2000. SAS/STAT Software. Version 8.02. SAS Institute, Inc., Cary, NC.

SERRANO, D., J. L. TELLA, J. A. DONÁZAR, AND M. POMAROL. 2003. Social and individual features affecting natal dispersal in the colonial Lesser Kestrel. Ecology 84:3044–3054.

SHIELDS, W. M. 1983. Optimal inbreeding and the evolution of philopatry, p. 132–159. *In* I. R. Swingland and P. J. Greenwood [EDS.], The ecology of animal movement. Clarendon Press, Oxford, UK.

SIMBERLOFF, D. 1988. The contribution of population and community biology to conservation science. Annual Review of Ecology and Systematics 19:473–511.

SONSTHAGEN, S. A., S. L. TALBOT, AND C. M. WHITE. 2004. Gene flow and genetic characterization of Northern Goshawks breeding in Utah. Condor 106:826–836.

SPEISER, R., AND T. BOSAKOWSKI. 1991. Nesting phenology, site fidelity, and defense behavior of Northern Goshawks in New York and New Jersey. Journal of Raptor Research 25:132–135.

SQUIRES, J. G., AND R. T. REYNOLDS. 1997. Northern Goshawk (*Accipiter gentilis*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No 298. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

STACEY, P. B., AND M. TAPER. 1992. Environmental variation and the persistence of small populations. Ecological Applications 2:18–29.

STRICKLAND, D. 1991. Juvenile dispersal in Gray Jays: dominant brood members expels siblings from the natal territory. Canadian Journal of Zoology 69:2935–2945.

TITUS, K., C. J. FLATTEN, AND R. E. LOWELL. 1994. Northern Goshawk ecology and habitat relationships on the Tongass National Forest. Final Annual Project Report, Alaska Department of Fish and Game, Douglas, AK.

VERHULST, S., C. M. PERRINS, AND R. RIDDINGTON. 1997. Natal dispersal of Great Tits in a patchy environment. Ecology 78:864–872.

WALLS, S. S., AND R. E. KENWARD. 1998. Movements of radio-tagged Buzzards *Buteo buteo* in early life. Ibis 140:561–568.

WALTERS, J. R. 2000. Dispersal behavior: an ornithological frontier. Condor 102:479–481.

WHEELWRIGHT, N. T., AND R. A. MAUCK. 1998. Philopatry, natal dispersal, and inbreeding avoidance in an island population of Savannah Sparrows. Ecology 79:755–767.

WHITE, M. A., AND J. L. VANKAT. 1993. Middle and high elevation coniferous forest communities of the North Rim region of the Grand Canyon National Park, Arizona, USA. Vegetation 109: 161–174.

WIENS, J. D., B. R. NOON, AND R. T. REYNOLDS. 2006. Post-fledging survival of Northern Goshawks: the importance of prey abundance, weather, and dispersal. Ecological Applications 16:406–418.

WIENS, J. D., AND R. T. REYNOLDS. 2005. Is fledging success a reliable index of fitness in Northern Goshawks? Journal of Raptor Research 39: 210–221.

WILLEY, D. W., AND C. VAN RIPER III. 2000. First-year movements by juvenile Mexican Spotted Owls in the Canyonlands of Utah. Journal of Raptor Research 34:1–7.

APPENDIX. Northern Goshawk monitoring effort, breeding proportions, and banding activity on the Kaibab Plateau, Arizona, 1991–2004. Means ± SE are shown for the prey density and precipitation covariates used in modeling the timing of natal dispersal, 1998–2001. See Table 1 for covariate definitions.

Year	Territories monitored	Proportion of pairs breeding[a]	Nestlings banded	Median hatch date[b]	Prey density (ha^{-1})	Precipitation (cm)
1991	37	0.97	46			
1992	64	0.87	32			
1993	82	0.77	62			
1994	88	0.22	18			
1995	99	0.50	52			
1996	105	0.40	41			
1997	106	0.30	36			
1998	109	0.51	84	160	1.9 ± 0.1	20.9 ± 1.2
1999	113	0.51	76	159	2.3 ± 0.1	22.9 ± 6.0
2000	120	0.53	111	152	2.7 ± 0.1	9.3 ± 3.3
2001	120	0.25	31	161	1.0 ± 0.1	11.4 ± 2.8
2002	121	0.18	16			
2003	121	0.08	9			
2004	121	0.41				

[a] Calculated from the previous year's cohort of territories under study (except 1991; Reynolds et al. 2005).

[b] Annual median hatch date calculated from individual nestling ages at time of capture; day 153 = 1 June.