

THESIS

**POST-FLEDGING SURVIVAL AND NATAL DISPERSAL OF NORTHERN
GOSHAWKS IN ARIZONA**

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, CO

Fall 2004

COLORADO STATE UNIVERSITY

November 3, 2004

WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY JOHN DAVID WIENS ENTITLED POST-FLEDGING SURVIVAL AND NATAL DISPERSAL OF NORTHERN GOSHAWKS IN ARIZONA BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

POST-FLEDGING SURVIVAL AND NATAL DISPERSAL OF NORTHERN GOSHAWKS IN ARIZONA

Effective conservation and management plans for wildlife populations require knowledge of how fluctuating environmental conditions affect demographic rates. Due to their low densities and elusive behavior within the dense forest habitats they occupy, existing demographic information for the northern goshawk (*Accipiter gentilis*) is limited primarily to the non-juvenile age-class. However, juvenile survival and dispersal may make important contributions to northern goshawk population dynamics. As part of a long-term demographic study, I used information-theoretic methods to examine post-fledging survival and natal dispersal relative to environmental, spatial, and individual sources of variation within an isolated population of northern goshawks in Arizona. The study included 614 color-banded juveniles produced on 121 breeding territories during 1991 – 2004, 89 of which were radio-marked during 1998 – 2001. Survival during the first 12 weeks after fledging was 0.71 (95% CI = 0.53, 0.84). The best-fitting known fate models predicted survival as a function of time since fledging, annual changes in key bird and mammal prey populations on the study area, and gender-specific differences in pre-fledging body mass. Juveniles exhibited higher survival and initiated dispersal from natal territories at an earlier date, but not at a younger age, in years when food was more abundant. A low first-year fidelity rate of radio-marked juveniles to the study population

(28%), juvenile dispersal movements of up to 442 km, a low overall return rate of color-banded nestlings (11%), and a delayed age at first breeding ($\bar{x} \pm SE = 4.21 \pm 0.31$ years) suggested a high level of competition for breeding territories on the study area, forcing locally-produced juveniles to either wait several years to gain a breeding vacancy or emigrate. Color-banded nestlings that successfully recruited to the study population settled a median distance of 15.0 km from their natal nest (range = 0.1 to 58.1 km), a distance about four times the diameter of an average territory (3.8 km). In combination with data showing relatively short breeding dispersal distances of adults, my study provided evidence that movement and gene flow among naturally fragmented northern goshawk populations in the southwestern United States is achieved primarily through the survival and dispersal of juveniles. Of the sources of variation examined relative to juvenile survival and dispersal, food abundance was consistently found to be an important predictor, suggesting that conservation strategies for the northern goshawk should account for factors limiting key prey populations.

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ACKNOWLEDGEMENTS

I first extend my appreciation to my co-advisors, Dr. Barry Noon of the Department of Fishery and Wildlife Biology and Dr. Richard Reynolds of the Rocky Mountain Research Station. Richard was the first to encourage me to pursue this research, and has supported me throughout my degree as an employer, mentor, and friend. Barry provided me with the opportunity to formalize my work at Colorado State University, and I thank him for his encouragement, advice on data analysis and writing, and the large amount of time he contributed towards my academic development. I am also grateful to Dr. Gary White of the Department of Fishery and Wildlife Biology and Dr. Phil Chapman of the Department of Statistics for agreeing to serve on my graduate committee. Gary provided much assistance with analytical methods, and spent many hours discussing various stages of my research. Phil challenged and improved my knowledge of statistics, and was always willing to spend time discussing statistical details. I owe much to Barry, Richard, Gary, and Phil for providing me with these unique opportunities and taking an active part in my academic and personal development.

This study would not have been possible without the small army of field technicians (> 70) who collected data on the Kaibab Plateau. In particular, I thank John “Zig” Seyfried, Donna Laing, Cam Collins, Aaron Gillen, and Michelle Harmon for the difficult task of tracking radio-marked goshawks during dispersal. Susan Salafsky, Suzanne Joy, Shelly Bayard de Volo, Jeff Lambert, Carrie Erickson, and Zig provided

technical and field support throughout much of this study – I appreciate their hard work, enthusiasm, and friendship over the years.

John Klavitter of the U.S. Fish and Wildlife Service provided a basis for the radiotransmitter harness design I used, and Sherrie Roesner assisted with harness construction. Special thanks to Gene Cordero of Lake Mead Air for piloting flights over the Kaibab Plateau in search of radio-marked hawks, and Kai Olsen and Richard Madril of the North Kaibab Ranger District (NKRD) for donating their time as flight observers. Thanks also to Steve Rosenstock and Mary Ann McKenzie of the Arizona Game and Fish Department for their contributions to flight time. Many thanks to my fellow graduate students at the Noon Lab of Conservation and Landscape Ecology for their professional, academic, and moral support throughout my degree.

I express my deepest gratitude to my family and friends for their encouragement and support. I am especially grateful to my wife Susan Salafsky for her enduring love, friendship, and encouragement. This research benefited greatly from Susan's work on goshawk prey populations, and her sharp editing skills and many hours of discussion greatly improved the quality of the pages that follow.

This project was funded by Region 3 of the U. S. Forest Service, the Rocky Mountain Research Station, and a grant from the Heritage Program, Arizona Game and Fish Department. Housing and logistical support during the field component of this study were provided by the NKRD. This research was approved by the Animal Care and Use Committee at Colorado State University (Study No. 01-103A-01).

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PREFACE

This thesis has been written as two separate chapters to facilitate publication of manuscripts and to address two interdependent aspects of northern goshawk ecology: juvenile survival and dispersal. Chapter one focuses on prey abundance, weather, and post-fledging survival in a large northern goshawk population on the Kaibab Plateau in northern Arizona. Chapter two focuses on the onset and completion of natal dispersal within the isolated population of northern goshawks on the Kaibab Plateau. The format for each chapter is similar. Although the research methodology discussed in each chapter is topic-specific, some overlap in the introduction, description of the study area, field protocols, and analytical methods occurs between chapters.

INTRODUCTION TO THESIS

The Northern Goshawk

The northern goshawk (*Accipiter gentilis*) is the largest member of the forest dwelling hawk genus *Accipiter* that inhabits most boreal and temperate forests throughout North America. While goshawks occupy a wide range of forest types, they use a narrow range of forest structural conditions at nesting sites. Nesting sites are typically located in forest stands containing large, older trees and a relatively dense canopy with an open understory (Squires and Reynolds 1997). Escalating debate on the current status of goshawk populations fueled by several petitions to list the species under the Endangered Species Act has illuminated an apparent lack of empirical evidence required to support claims of a range-wide decline in abundance (Kennedy 1997, Andersen et al. 2004). The lack of information regarding the status of goshawk populations stems from the fact that too few demographic studies with adequate sample sizes have been conducted for sufficient time periods to fully understand the response of key vital rates to forest management. Demographic data on goshawks is costly and difficult to collect because they are long-lived, they naturally occur at low densities, they exhibit elusive behavior when not breeding, and they do not breed every year. These difficulties in combination with the vast implications of managing the wide range of forests occupied by the species has pronounced the need for long-term, properly designed demographic research.

Long-term Demographic Research

In 1991, a long-term study of goshawk demographics and habitat was established on the Kaibab Plateau in northern Arizona (Figs. 1.1, 2.1). To date, 121 goshawk territories comprised of more than 280 nests have been identified within this isolated expanse of coniferous forests, making this the largest known population of goshawks in North America. Capture-recapture studies including more than 290 breeding adults have been used to reliably estimate territory distribution and occupancy rates, adult survival, and adult fidelity to territory and mate. However, despite color-banding more than 600 nestlings over a 14-year period, too few young have been subsequently relocated to reliably estimate juvenile survival, and very little information exists regarding juvenile dispersal. Efforts to estimate these parameters likely suffer from the low probability of detecting juvenile goshawks that permanently disperse beyond the study area. Hence, failure to relocate juveniles could be due to either mortality or emigration, and the extent of either is generally unknown for goshawks.

Thesis Overview

In this thesis, I examined post-fledging survival and dispersal of juvenile goshawks during radiotelemetry and capture-recapture studies on the Kaibab Plateau. My goal was to provide empirical data regarding this important life stage that may be used in conjunction with data from the non-juvenile age-class to identify those life history parameters that are most sensitive to changes in forest structural conditions so that robust conservation and management strategies may be developed. My approach was to examine various aspects of juvenile survival and dispersal as a function of environmental,

spatial, and individual sources of variation. In chapter one, I focused on the effects of large inter-annual differences in local food and weather conditions on the post-fledging survival rates of radio-marked juvenile goshawks. In chapter two, I examined natal dispersal (movement between the birth site and site of first breeding) of goshawks relative to environmental and demographic conditions dispersing hawks experienced during the onset and completion of this fundamental population process. Throughout the thesis, I used information-theoretic methods (Burnham and Anderson 2002) which allowed me to assess the strength of evidence for competing survival- and dispersal-related hypotheses that were expressed as ecologically meaningful covariates.

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CHAPTER ONE

POST-FLEDGING SURVIVAL OF JUVENILE NORTHERN GOSHAWKS IN ARIZONA

ABSTRACT

Effective conservation strategies for wildlife populations require an understanding of how fluctuating environmental conditions affect demographic parameters. As part of a long-term study, I examined post-fledging survival of 89 radio-marked juvenile northern goshawks (*Accipiter gentilis*) produced from 48 nests located in mature forests in northern Arizona 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 key bird and mammal prey populations on the study area, and gender-related differences in pre-fledging body mass. Survival during the first seven-weeks post-fledging (the average length of the fledgling-dependency period) 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 response to annual differences in prey abundance; the slope coefficient for the additive effect of prey abundance on survival was 1.12 (95% CI = 0.06, 2.19). The best-fitting known fate

models including the first five weeks of juvenile dispersal predicted survival as a function of time since fledging, prey abundance, and body mass. Survival over the first 12 weeks post-fledging was 0.71 (95% CI = 0.53, 0.84). Juvenile survival was not associated with weather or territory-level parameters. A comparison of the predictions of individual, territory, and environmental-based models of survival demonstrated that variation in prey resources is a primary factor limiting goshawk productivity at the level of juvenile survival. This result suggests that conservation strategies to benefit goshawk populations should account for factors limiting prey populations. Sufficient prey resources facilitate successful juvenile survival, dispersal, and recruitment, which appear to be critical components of gene flow among naturally fragmented populations of goshawks in the southwestern United States.

Key words: *Accipiter gentilis; Arizona; radiotelemetry; survival; post-fledging; prey abundance; distance sampling; northern goshawk; known-fate models.*

INTRODUCTION

Understanding how various life history parameters respond to fluctuating environmental conditions is a crucial step in developing robust conservation strategies for wildlife populations. In birds, survival between fledging and breeding age 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.

Estimates of juvenile survival are needed to compute rates of population growth and identify those life history parameters that most strongly affect rates of population change (Noon and Biles 1990). Moreover, data regarding juvenile survival can improve estimates of reproductive success and identify important ecological factors that limit population size (Verner 1992, Anders et al. 1997, Thomson 1999, Keedwell 2003). For example, studies have shown that high temporal variation in the number of new individuals entering the breeding segment of a population is likely a result of highly variable juvenile survival rates (Franklin et al. 2000, Reed et al. 2003), and that much of the variation in juvenile survival can be explained by the environmental conditions experienced during the early stages of fledgling development (Anders 1999, Monrós et al. 2002, Reed et al. 2003, Todd et al. 2003).

In birds of prey, it is generally believed that more than half the birds that fledge die in their first year and that mortality often peaks in the first few months post-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 (Newton 1979, Bustamante 1993, Kenward et al. 1993a). The transition from a dependent fledgling to

an independent juvenile (the fledgling-dependency period) is a critical stage for survival since feather growth is incomplete and flight skills are developing, leaving young highly susceptible to predation, starvation, and exposure (Anders et al. 1997, Thompson et al. 1999, Naef-Daenzer 2001). Indeed, raptor mortality during the fledgling-dependency period has been closely linked to predation and starvation (Korppimäki and Lagerström 1988, Ward and Kennedy 1996, Dewey and Kennedy 2001, Kenward et al. 1999). However, because juveniles are inexperienced foragers, mortality rates are likely to increase during the period immediately following independence from adults (the post-independence period).

Although the influence of food availability on various raptor life history traits has been investigated (Korppimäki and Lagerström 1988, Doyle and Smith 1994, Kenward et al. 1993a., Ward and Kennedy 1996, Dewey and Kennedy 2001), few studies have attempted to discriminate the relative contributions of environmental factors from territory- or individual-level factors to realized survival rates of juveniles. This is important because spatial or temporal variation in survival may result from interactions among different factors working at more than one ecological level (e.g., population, territory, and individual levels). The ability to isolate the various factors affecting survival, and their relative contributions, depends on identifying biologically meaningful covariates and estimating their effects via an appropriate analytical model (Lebreton 1992, Skalski et al. 1993, Pollock 2002). Incorporating covariates into the survival modeling process can also yield a more parsimonious parameterization, increasing the precision of parameter estimates (Pollock 2002).

The northern goshawk (*Accipiter gentilis*) is a large forest raptor that occupies mature boreal and temperate forests throughout western North America (Squires and Reynolds 1997). Similar to controversies surrounding conservation of the northern spotted owl (*Strix occidentalis caurina*) in the Pacific Northwest (Noon and McKelvey 1996), the goshawk's selection of nest sites in old and mature forests (Reynolds et al. 1982, Speiser and Bosakowski 1987, Hayward and Escano 1989, Siders and Kennedy 1996) has resulted in conflicts with management activities such as timber harvest and fire suppression. Initial concern over the potential effects of forest management activities on goshawk viability led to the species being designated as "sensitive" by the U.S. Forest Service (Reynolds et al. 1992, Block et al. 1994). More recently, petitioners have sought to protect the goshawk and its habitat under the Endangered Species Act (Silver et al. 1991, Martin 1998). As a consequence, research has largely focused on developing models capable of assessing the effects of forest management alternatives on goshawk biology and habitat suitability (Finn et al. 2002, Joy 2002, McGrath et al. 2003). 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 habitat and non-habitat factors to variation in sensitive vital rates, such as juvenile survival.

In 1991, a long-term study of goshawk demographics and habitat was initiated on the Kaibab Plateau in northern Arizona (Reynolds et al. 1994, Reynolds and Joy *in press*). To date, 121 goshawk territories comprised of more than 280 nests have been identified, making this the largest known population of goshawks in North America.

Based on capture-recapture methods, this geographically isolated population has exhibited relatively high, temporally invariant adult survival rates (75%) (Reynolds et al. 2004), high territory (95%) and mate (98%) fidelity (Reynolds et al. *unpublished manuscript*), and a delayed age at first breeding (mean = 3.5 yrs.; Wiens and Reynolds *unpublished manuscript*). However, despite color-banding more than 600 nestlings over a 13 year period, too few have subsequently been detected as breeders within the population to reliably estimate pre-breeding survival rates. Efforts to estimate juvenile survival rates for this population likely 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 mortality or emigration, and the extent of either is generally unknown for goshawks.

Using radio telemetry methods, I estimated post-fledging survival within the large goshawk population on the Kaibab Plateau during 1998 – 2001. The primary goal was to identify critical periods of post-fledging survival and determine the relative importance of several ecological factors hypothesized to limit goshawk productivity at the level of juvenile survival. Specifically, my 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, body mass, and hatching date to post-fledging survival, and (3) estimate the impact of independence (i.e., the initiation of dispersal) on juvenile survival rates. I further discuss the importance of post-fledging survival and juvenile dispersal to goshawk demographics at local and regional scales, and relate my findings to current forest management and restoration efforts in the southwestern United States.

METHODS

Study Area

The study area on the Kaibab Plateau in northern Arizona is a 1,732 km² area comprising all of the coniferous forest above 2,182 m elevation (Fig. 1.1). This area includes the northern portions of the Kaibab National Forest (KNF) and the Grand Canyon National Park (GCNP). Between 1991 and 2004, 121 goshawk territories were located on the Kaibab Plateau, 104 of which were located on lands administered by the KNF. Post-fledging survival was studied on territories within the KNF (total area = 1,285 km²) and excluded territories within the GCNP. The Kaibab Plateau is a large, oval shaped landform that rises from a shrub-steppe plain at 1,750 m elevation to the highest point at 2,800 m, and is dissected by moderately sloping valleys (Rasmussen 1941). The Plateau is circumscribed by staircase cliff walls of the Grand Canyon of the Colorado River on its southern side, steep slopes on the east side, and gentle slopes on the north and west sides that gradually descend to sagebrush (*Artemisia* spp.) plains. Forested areas on the Kaibab Plateau include three principal forest types: pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodlands occur between 1,830 and 2,075 m, ponderosa pine (*Pinus ponderosa*) forests occur from 2,075 to 2,450 m, and mixed-conifer forests (*Picea engelmannii*, *Abies concolor*, *Pseudotsuga menziesii*, *P. ponderosa*, *Populus tremuloides*) occur from 2,450 to 2,650 m (Rasmussen 1941, White and Vankat 1993). Except for relatively small meadows, old burns, and recent 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. Mid to late summers are characterized by frequent (2 – 4 per week) thunderstorms with heavy rain showers.

Data Collection

Radio marking and tracking. – Goshawk nesting territories were monitored from 1998 – 2001 to determine location, occupancy, and reproductive status of territorial pairs. 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 approximately 32 to 35 days of age. Young goshawks were aged based on a photographic and behavioral guide (Boal 1994) and banded with a U.S. Fish and Wildlife Service aluminum leg band and a color leg band with a unique alpha-numeric code (Acraft Sign and Plate Co., Edmonton, CA). Due to the pronounced size dimorphism between sexes, young were easily sexed on the basis of body mass, tarsometatarsal length, and footpad length measurements (Reynolds et al. 1994).

Nestlings from randomly-selected nests were equipped with 17 g (including harness) backpack-style radiotransmitters (Wildlife Materials Inc. model # LPB 2380M), representing ~ 1.9 and 2.5% body mass at first flight for females and males, respectively. Backpack harnesses used four separate nylon straps with a “weak link” cotton attachment to allow the harness to fall off without entanglement ~ 1 yr after fitting (modified from Klavitter et al. 2003). Radiotransmitter packages were designed to lay flat and smooth to reduce aerodynamic drag that can increase metabolic rates during flight (Gessaman and Nagy 1988), and to reduce feather wear and skin irritation. Each radiotransmitter was

programmed with a mortality sensor and had a life expectancy of 500 days (Wildlife Materials Inc.).

Radio-marked individuals were monitored with model R4000 ATS (Advanced Telemetry Systems, Inc. Isanti, MN) receivers, using two-and three-element Yagi antennas. Status (location, alive, dead) and behavior was recorded within natal territories 4 – 5 times wk^{-1} by approaching on foot until the hawk was sighted or a change in signal strength was recorded. When a hawk's signal was lost, systematic searches were conducted throughout the study area using omnidirectional antennas mounted on trucks or by scanning for signals from fire lookout towers which provided high vantage points. Once hawks dispersed from their natal territories, survival checks from lookout towers were conducted 3 times wk^{-1} at night to ensure optimal signal detection from hawks roosting in trees (Kenward et al. 1999). In addition, fixed-wing aircraft were used to survey for missing hawks over the entire 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 E–W transect lines spaced 10 km apart within the established aerial survey area, and were conducted at monthly intervals from September through May during 1999 – 2002, and January and March in 1998. The probability of detecting radio-marked hawks during tracking flights was estimated as the proportion of 22 transmitters placed at random locations throughout the aerial survey area that were relocated by a naïve observer. Radiotransmitters used to estimate detection probability were randomly placed on the ground to mimic a dead hawk or a shed transmitter, or > 3 m high in the branches of trees to simulate perching hawks. Hawk carcasses and remains were examined to infer cause of death based on evidence found at recovery sites. All

mortalities were classified as predation, starvation (based on post-mortem differences in body mass), or unknown.

Developmental stages of young goshawks. – *Fledging* was defined as the date on which young hawks were first observed out of the nest (Ward and Kennedy 1996, Dewey and Kennedy 2001, Kennedy and Ward 2003). Once juvenile goshawks venture beyond 1.5 – 2.0 km from the nest, they are rarely recorded within that radius on subsequent occasions (Kenward et al. 1993a, Kennedy and Ward 2003). I therefore defined *dispersal date* as the first day a hawk spent more than two consecutive days ≥ 2 km from the nest, and the *fledgling-dependency period* as the number of days between the fledgling and dispersal dates. Once dispersal was initiated, young were assumed to no longer depend upon adults for food (Reynolds et al. 1992, Kennedy and Ward 2003). When a hawk's radio-signal was not detected within the immediate area surrounding the nest tree, a systematic search was initiated within a 2-km radius of the nest for three consecutive days. If a signal was not received, or if a hawk was located > 2 km from the nest for > 2 consecutive days, the hawk was determined to have initiated dispersal from the natal territory, marking the beginning of the *post-independence period*. This period coincides with the initiation of *natal dispersal*, defined as movement from the natal area to the site of first breeding (Greenwood and Harvey 1982). Thus, to distinguish the post-independence period from natal dispersal, I referred to the period following the fifth week post-independence as the *dispersal period*. Since nests were not visited on a daily basis, I considered the dates of fledging and dispersal as the middle of an interval between two consecutive visits.

Sources of Variation and Covariates to Survival

I selected six covariates to represent three ecological levels hypothesized to influence survival probabilities of juvenile goshawks (two cohort-level covariates, two territory covariates, and two individual covariates). Cohort-level covariates (prey abundance, total precipitation during the fledgling-dependency period) were representative of environmental effects and assumed the same level for each individual within an annual group of radio-marked juveniles. Territory-level covariates (brood size, territory hatch date) assumed the same value for each individual at a nest while individual-level covariates (gender, body mass) were specific to individuals. Body mass (g) at time of capture (3-5 days pre-fledging) was used as an index of body condition. I assumed that age had minimal effect on pre-fledging body mass measurements since I was able to radio-mark all young within a narrow age range.

Prey abundance. – Based on studies of goshawk diets on the Kaibab Plateau, the seven primary prey species in terms of diet frequency and biomass 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 on the KNF, abundance data were collected for these seven prey species during the goshawk breeding season (May – August) between 1994 and 2002 using two sampling methods: line-transect distance sampling (1999-2002), and counts of prey species detections per 100 minutes of observation (1994-2002) (*see* Salafsky 2004 for details). Species densities were estimated by ponderosa pine and mixed conifer forest

types using program DISTANCE (ver. 3.5; Buckland et al. 1993, Salafsky et al. *unpublished manuscript*). To investigate the importance of prey abundance to goshawk survival, I combined annual density estimates from 1999 – 2001 for the four prey species that were reliably estimated with program DISTANCE (red squirrel, Kaibab squirrel, northern flicker, and Steller’s jay). Insufficient sample sizes and inadequate sampling effort precluded using rabbits and golden-mantled ground squirrels in my analysis. However, the four species included represented a significant contribution to goshawk diet biomass when considered over the entire study area. To obtain prey densities and measures of precision in 1998 (prior to the initiation of distance sampling), a predicted density value was estimated for each prey species under a linear regression relating prey species counts (1994 – 2002) to concurrent prey density estimates (1999 – 2002; Salafsky 2004). Resulting R^2 values for each prey species ranged from 0.79 to 0.99, indicating a close relationship between density estimates and count data (Salafsky 2004).

Total precipitation. – In several raptor species, extreme precipitation events have affected survival by limiting foraging success, reducing prey availability, and causing direct mortality through exposure (Davis and Newton 1981, Kostrzewa and Kostrzewa 1990, Franklin et al. 2000). In northern Arizona, a seasonal shift in wind from a westerly direction to a more southerly direction in early July to mid-September creates atmospheric instability with surface heating of moist air from Mexico (National Climatic Data Center 2003 *public communication*; URL: www.ncdc.noaa.gov). This seasonal climate change is characterized by heavy precipitation, lightning, hail, and damaging winds. This Arizona “monsoon” thunderstorm season coincides with the fledgling-dependency period for goshawks on the Kaibab Plateau. I hypothesized that extreme

rainfall during the fledgling-dependency period may reduce juvenile survival directly through exposure or increased predation risk, or indirectly by limiting the adult's ability to provide sufficient food. To examine this hypothesis, I included the average total amount of precipitation (cm) during the fledgling-dependency period as an environmental covariate to survival. Daily precipitation records were accessed from three Remote Automated Weather Stations (RAWS) on the NKRK, and one U.S. Weather Service weather station in the GCNP (Fig. 1.1). The total amount of precipitation during the interval from earliest fledgling date to latest dispersal date was estimated separately for each cohort of radio-marked hawks, and averaged across the four weather stations by year. This covariate therefore measured the amount and duration of rainfall experienced by each fledgling cohort during fledgling development.

Territory hatching date. – In seasonal environments, egg hatch date may be an important determinant of fitness (Reed et al. 2003), territory quality (Korppimäki 1987), and survival (Krementz et al. 1989, Schmutz 1993, Verboven and Visser 1998). Moreover, nest hatch date is positively associated with the 1000 m gradient in elevation on the Kaibab Plateau ($r = 0.42$, $P < 0.001$; D. Wiens *unpublished data*). Based on these features, I hypothesized that juveniles who fledged earlier would experience higher survival rates since they may have higher quality parents and/or been raised on higher quality territories. To evaluate this hypothesis, I used egg hatch date as a territory-level covariate to survival. I defined “territory hatching date” as the average Julian date (1 – 365) on which radio-marked juveniles within a single brood hatched, backdated from the estimated age at the time of capture.

Data Analysis

Analytical approach. – I used an information-theoretic approach to assess time and covariate effects on post-fledging survival. The information-theoretic approach unifies parameter estimation and model-selection under an optimization framework, based on Kullback-Leibler information and likelihood theory (Burnham and Anderson 2002). Under this analytical framework, a series of *a priori* biological hypotheses are expressed as candidate statistical models that are subsequently ranked based on an objective model selection criterion (Lebreton et al. 1992, Burnham and Anderson 2002). *A priori* hypotheses were generated from previous research on post-fledging survival (Newton and Moss 1986, Korppimäki and Lagerström 1988, Kenward et al. 1993a., Ward and Kennedy 1996, Franklin et al. 2000, Dewey and Kennedy 2001, Monrós et al. 2002), current management strategies for the goshawk (Reynolds et al. 1992), and field observations. I used Akaike's Information Criterion, corrected for small sample sizes (AIC_c), to objectively rank candidate model sets and to select a best-approximating model(s) for inference (Burnham and Anderson 2002). Model comparisons were made with ΔAIC_c , which is the difference between the lowest AIC_c value and AIC_c from all other models. Normalized AIC_c weights (w_i) were used to evaluate the strength of evidence for each model, given the data and sampling design used. Candidate models were developed to represent the potential influences of time (among-and within-year variation), prey abundance, weather, brood size, gender, body mass, and hatching date on post-fledging survival. AIC_c weights and differences between AIC_c values were used to contrast models containing cohort-level effects (prey abundance, total precipitation) to see if environmental variables could explain hypothesized variation among annual

cohorts of radio-marked juveniles under a more parsimonious parameterization than a model including a generic “year” effect. The effects of prey abundance and total precipitation were balanced evenly among sets of candidate models, allowing direct comparison of their relative importance to post-fledging survival using cumulative AIC_c weights (i.e., sum of AIC_c model weights over models containing the covariate of interest; Burnham and Anderson 2002).

Modeling post-fledging survival. – I 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 models focus on the estimation of survival (S), defined as the probability of surviving an interval between sampling occasions. Known fate parameter estimation in program MARK is analogous to 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 likely valid once independence from adults is attained, yet may be compromised during the fledgling-dependency period in nests containing > 1 young.

When individual survival probabilities are not independent, the estimators of model parameters are unbiased but the theoretical variances are biased low due to extra-binomial variation or overdispersion of the data (McCullagh and Nelder 1989, Tsia et al. 1999). Overdispersion might be expected if broods behaved more as a unit rather than individuals, or if the fates of brood members were dependent. Overdispersion can typically be assessed under goodness-of-fit (GOF) tests of the general, fully parameterized time-specific model. However, there are no formal GOF tests available for

known fate modeling to directly estimate overdispersion, as the saturated model will fit the data perfectly and result in a deviance of zero (G. White *personal communication*). Instead, I tested for a significant violation of the assumption of independence by estimating overdispersion (\hat{c}) as χ^2/df , where χ^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 (= 9 possible outcomes). Expected values were calculated as:

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

where n = brood size, r = number of young surviving to independence, and p = the overall survival rate. Only broods where all young were radio-marked were used in the test for intrabrood dependency. Specifically, I tested the null hypothesis that survival probabilities of individuals within a brood size of > 1 young are independent. 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 for the presence of overdispersion in 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 an initial set of eight *a priori* hypotheses that considered both annual and weekly time variation in post-fledging survival (i.e., the effects of year, weekly categorical time (t), weekly continuous time (T), and their interactions; Table 1.1). Of particular interest was to examine if risk of mortality varied among post-fledging weekly age classes. Stage two introduced ecologically relevant covariates (or replaced time effects with covariates) to the most parsimonious model explaining time variation. An additional set of 18 covariate models considered additive single main effects and biologically meaningful additive

effects of multiple covariates. 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. Because juveniles were not monitored daily, survival models were based on weekly intervals.

Sex was included as an individual covariate accompanying each individual's encounter history (0 for females, 1 for males). Thus, individual covariates were scaled appropriately prior to the analysis in MARK to assure appropriate numerical optimization of parameter estimates (Franklin 2001). Slope parameters and their standard errors were subsequently rescaled for predictions based on the resulting equations. The precision of slope coefficient estimates (β_i) was evaluated using standard errors and the coefficient of variation (CV). I also used 95% confidence intervals of slope coefficients to supplement AIC_c evidence of an important effect, based on the degree to which intervals overlapped zero (Graybill and Iyer 1994). This approach was useful when there was only a small difference in AIC_c values between two competing models.

To estimate the impact of independence from adults on survival, I conducted a separate known fate analysis where the survival interval was extended to include the post-independence period. I assumed that young were both biologically and statistically

independent once dispersed since there were no observations of young with siblings or parents during this period. Thus, separating survival estimates obtained from the fledgling-dependency period from the post-independence period allowed a more detailed assessment of intrabrood dependency and covariate effects during these distinct stages of juvenile development. Modeling post-independence survival was achieved in two stages as in the post-fledging survival analysis. For stage one, the same set of eight time-related hypotheses previously considered were used in addition to two models representing the hypothesis that survival would follow a quadratic weekly time trend (with and without annual variation; Table 1.1). Total precipitation was expected to directly influence survival during the early stages of fledgling development and was not considered as a covariate in the post-independence survival analysis.

To quantify the amount of year-to-year variability in survival that could be explained by cohort-level covariates, I used an analysis of deviance (ANODEV). ANODEV is analogous to analysis of variance (ANOVA), but ANODEV partitions differences between the log-likelihoods of models rather than between the sums of squares of models (McCullagh and Nelder 1989, Skalski et al. 1993). ANODEV provided a means of evaluating cohort-level covariates by comparing explained to unexplained model deviance (White and Burnham 1999).

RESULTS

Eighty-nine nestlings were measured and radio-marked at 48 nests in 36 different territories during 1998 – 2001, representing 29% of the young produced and color-banded on the study area during this time (Table 1.2). Entire broods were radio-marked

at 37 of the 48 nests (10 broods of one young, 18 of two young, and 9 of three young). All 89 radio-marked nestlings successfully fledged, in addition to 12 non-radioed siblings that could not be captured. The exception was one non-radioed male nestling in the 2001 fledgling cohort that was 77% below average body mass and died in the nest prior to fledging. Juveniles that survived the fledgling-dependency period or did not prematurely shed their radiotransmitters dispersed between 30 July – 15 September (\bar{x} = 30 August) at 71 – 103 days post-hatching (\bar{x} = 86.54 days, SE = 0.79, n = 71; Chapter Two). The amount of time juveniles remained within their natal territories between fledging and dispersal ranged from 33 – 66 days (\bar{x} = 46.34 days, SE = 0.78).

From a total of 89 radio-marked juveniles, 41 (46%) were tracked until they were either recovered dead or they shed their radiotransmitter package by the following spring (40 weeks post-fledging; Table 1.2). Radio signals were lost for the remaining 48 (54%) juveniles due to dispersal beyond the aerial survey area (Chapter Two). Eleven juveniles prematurely shed their radiotransmitters during the fledgling-dependency and post-independence periods, and an additional six juveniles shed their radiotransmitters between weeks 13 – 40 post-fledging. A total of 24 hawks were recovered dead during the study (12 females and 12 males), with predation accounting for 46% of total mortality (Table 1.3).

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). In cases where the cause of death could be inferred, three juveniles died from predation or injuries attributed

to predation, three from starvation, and two from physical trauma. Great horned owls (*Bubo virginianus*) were identified as the main predators based on evidence such as molted owl feathers and feces found at recovery sites. Three mortalities occurred in broods of three young, five in broods of two young, and none in broods of one young. There was 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, hypotheses investigating intrabrood dependency in post-fledging survival were not well supported – models containing the effect of brood size accounted for < 16% of the AIC_c weight across the model set (Table 1.6). Post-fledging mortality was therefore considered as a random process, and individuals were used as independent units for parameter estimation (i.e., $\hat{c} = 1.0$).

Time effects. – The best-fitting survival model addressing time effects only, $\{S(\text{Year}+T)\}$, indicated that survival was year-dependent with an additive effect of continuous time (where T indexed weekly survival as a continuous covariate; slope coefficient $\hat{\beta}_T = 1.05$, 95% CI = 0.22, 1.87; Table 1.4). This model (Fig. 1.4) suggested that post-fledging survival probabilities differed among annual cohorts of radio-marked juveniles, and that survival followed an increasing trend over weekly intervals during the fledgling-dependency period. Derived survival estimates under this model ranged from 0.81 in 2001 to 1.00 in 2000 (Table 1.5). Model $\{S(T)\}$, without annual variation, was competitive (ΔAIC_c value = 1.22). However, model $\{S(\text{Year}+T)\}$ contained more than half of the AIC_c weight across the model set, and the effect of “year” received 70% of the AIC_c weight across the candidate set of models, indicating the presence of annual variation in post-fledging survival. All top three models also had a weekly continuous time-specific survival component (T), indicating the presence of weekly variation in

post-fledging survival. These models strongly supported the hypothesis of an increasing trend in survival probabilities over the length of the fledgling-dependency period, and together accounted for 97% of the AIC_c weight across the model set. Models with weekly categorical time-dependency (t) received poor support.

Covariate effects. – The effects of prey abundance, gender, and pre-fledging body mass occurred in the best-fitting model (Table 1.6). Replacing the effect of “year” with the cohort-level prey density covariate (Table 1.5; Figs. 1.2A, 1.3) resulted in a lower AIC_c model. Model $\{S(\text{Prey}+T)\}$ indicated a positive relationship between survival and prey density, with an additive effect of continuous time (Fig. 1.5). The form of model $\{S(\text{Prey}+T)\}$ was

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

where $\text{SE}(\hat{\beta}_0) = 1.12$, $\text{SE}(\hat{\beta}_{\text{prey}}) = 0.54$ (95% CI = 0.06, 2.19), and $\text{SE}(\hat{\beta}_T) = 0.42$ (95% CI = 0.22, 1.87). Derived survival estimates (\pm SE) over the duration of the fledging-dependency period under this model ranged from 0.79 ± 0.09 in 2001 to 0.97 ± 0.02 in 2000 when total prey density values were lowest and highest, respectively (Table 1.5). Replacing the effect of “year” with the cohort-level precipitation (“rain”) covariate (Fig. 1.2B) within model $\{S(\text{Year}+T)\}$ resulted in a model with poor support ($\Delta AIC_c = 5.39$; $\hat{\beta}_{\text{rain}} = -0.03$, 95% CI = $-0.05, 0.09$). Models containing the effect of prey abundance accounted for 62.8% of the AIC_c weight, while models containing the effect of precipitation accounted for only 13.1%. In contrast, the effect of “year” accounted for 20.5% of the AIC_c weight across the model set. ANODEV results indicated that 62.7%

of the annual variation in survival during the fledgling-dependency period was explained by prey abundance (Table 1.7).

Of the 26 time and covariate models considered, the overall best-fitting model (Table 1.6; $\Delta AIC_c = 0.00$) indicated that survival followed an increasing weekly time trend and was positively affected by annual differences in prey abundance and gender-specific differences in pre-fledging body mass. Confidence intervals for slope parameters demonstrated that the effects of continuous time ($\hat{\beta}_T = 1.00$; 95% CI = 0.18, 1.82), gender ($\hat{\beta}_{sex} = 2.25$; 95% CI = 0.15, 4.36), and body mass ($\hat{\beta}_{mass} = 0.01$; 95% CI = 0.00, 0.02) were reliably estimated. However, the confidence interval for the effect of prey abundance under this model marginally included zero ($\hat{\beta}_{prey} = 0.78$; 95% CI = -0.33, 1.88), reflecting the poor precision of the slope estimate for this effect ($CV[\hat{\beta}_{prey}] = 72.5\%$). The poor precision of the effect of prey in the top model was likely due to the fact that years of high prey abundance (e.g., 2000) also had a male dominated sample (17 males vs. 11 females), which may have confounded the effect of prey density with gender and body mass. Three closely competing models had ΔAIC_c values < 2.00 , yet estimates of S were only slightly different among these models. Gender and body mass effects received support 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.

Post-Independence Survival

By week 13 post-fledging, the effective sample size was reduced to fewer than 17 individuals due to movement beyond the detection range of aircraft. I therefore limited survival estimates to the first 12 weeks post-fledging, when sample sizes 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 juvenile independence, and an additional 10 (7 males, 3 females) occurred between weeks 13 and 40 post-fledging (Table 1.3).

Time effects. – The best survival model during the first 12-weeks post-fledging considering time effects only, $\{S(T+T^2)\}$, indicated that survival followed a quadratic trend over time ($\hat{\beta}_T = 1.12$; 95% CI = 0.45, 1.80, $\hat{\beta}_{T^2} = -0.09$; 95% CI = $-0.15, -0.04$). This model (Fig. 1.6) suggested that survival increased to near 1.0 over the duration of the fledgling-dependency period, yet declined shortly after juveniles attained independence from adults and initiated dispersal. This model estimated the probability of surviving the first 12-weeks post-fledging as 0.71 (SE = 0.08, 95% CI = 0.53, 0.84). One alternate time-only model, $\{S(\text{Year}+T+T^2)\}$, was competitive ($\Delta\text{AIC}_c = 1.09$; Table 1.8). This model indicated that survival probabilities differed in level, but not in slope, among annual cohorts of radio-marked juveniles. Survival estimates under this model ranged from 0.48 (SE = 0.18, 95% CI = 0.18 to 0.79) in 2001 to 0.87 (SE = 0.09, 95% CI = 0.60 to 0.97) in 2000. The top two models including a quadratic time effect accounted for 97% of the AIC_c weight, indicating the presence of weekly variation in survival in the form of a quadratic weekly time trend.

Covariate effects. – An addition of the effects of gender and body mass to model $\{S(T+T^2)\}$ resulted in a new minimum AIC_c model that contained 57.9% of the overall AIC_c weight (Table 1.9). This model included a gender-specific quadratic trend in survival (higher survival rates for males), but only when pre-fledging body mass appeared as an additive effect in the model. This model explained variation in survival over the first 12-weeks post-fledging as:

$$\hat{S} = \frac{1}{1 + \exp(-[-6.72 + 1.01T - 0.09T^2 + 2.39\text{sex} + 0.01\text{mass}])}$$

where $\text{SE}(\hat{\beta}_0) = 3.36$, $\text{SE}(\hat{\beta}_T) = 0.35$ (95% CI = 0.42, 1.78), $\text{SE}(\hat{\beta}_{T^2}) = 0.03$ (95% CI = -0.15, -0.04), $\text{SE}(\hat{\beta}_{\text{sex}}) = 0.81$ (95% CI = 0.79, 3.99), and $\text{SE}(\hat{\beta}_{\text{mass}}) = 0.01$ (95% CI = 0.00, 0.02). This model estimated survival of females at average body mass (852.98 g, SE = 14.28, $n = 42$) 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 g, SE = 7.55, $n = 47$) was estimated as 0.79 (SE = 0.09; 95% CI = 0.57, 0.92). This model suggested that incremental changes in pre-fledging body mass have a larger effect on female than male survival.

The 12-week survival model incorporating the effect of prey density indicated a positive relationship ($\hat{\beta}_{\text{prey}} = 0.86$, 95% CI = 0.06, 1.66), yet this model was not selected as the overall best across the model set (Table 1.9). However, model $\{S(\text{Prey}+T+T^2)\}$ was more than three times as likely (AIC_c weight = 17.8%) than the base model including time effects only (AIC_c weight = 5.6%). ANODEV results indicated that 86.5% of the annual variation detected in survival over the first 12-weeks post-fledging was explained

by the prey density covariate (Table 1.10). As in the post-fledging analysis, the effects of hatching date and brood size received poor support.

Signal Detection and Censoring of Radio-Marked Hawks

Signal detection tests indicated that the probability of detecting a functioning radio (live or mortality signal type) within the aerial survey area was 0.91 (SE = 0.06, 95% CI = 0.79, 1.00). Simulation studies have shown that if relocation rates for live and dead animals are different, the estimator of survival will be biased, even when sample sizes are large (Tsai et al. 1999). However, I found no evidence that detection probability was related to signal type (Fisher's exact test: $P = 0.34$, $n = 22$), indicating that loss of a signal was not associated with disproportionate mortality.

Censoring is the removal of radio-marked animals from a sample when the transmitter signal can no longer be detected (White and Garrott 1990). Parameter estimation under the known fate framework in program MARK uses a modification to the risk set (Brunk et al. 1995), where animals are included in an interval only when they are actually relocated (G. White *personal communication*). Although uncertain relocation results in a loss of precision of the estimate, the estimator remains relatively unbiased under this modification (Brunk et al. 1995, Tsia et al. 1999). I recorded a substantial surge in the number of censored juveniles within the first several weeks following independence from adults (Fig. 1.7). This result would have been expected if juveniles dispersed beyond the aerial survey area or their radio ceased to function as a result of malfunction or mortality. It is unlikely that missing juveniles were simultaneously censored due to radio failure, and a near perfect detection probability indicated that the

high rate of censored individuals likely reflected the proportion of juveniles that initially dispersed beyond the study area (Chapter Two). Results indicated that the proportion of juveniles that were censored by week 12 post-fledging remained relatively constant among years ($\chi^2 = 28.88$, $df = 33$, $P = 0.67$), indicating that relocation rates were also consistent with respect to censoring. Several forays made by aircraft beyond the established aerial survey area failed to detect missing signals. Thus, the fate of juveniles that dispersed beyond this large detection region could not be determined, precluding an assessment of first-year survival.

DISCUSSION

Post-Fledging Survival of Juvenile Goshawks

Survival of juvenile goshawks during the fledgling-dependency period was consistently high among years, and most strongly related to the developmental stages of fledglings, annual changes in prey abundance, and gender-related differences in pre-fledging body condition. Contrary to predictions, I 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. Further, although juveniles without siblings tended to have higher survival rates than those with siblings, I was unable to detect intrabrood dependency in survival during the fledgling-dependency period. The data failed to support hatch date and brood size covariates, which represented potential differences in survival among territories. Rather, individual and environmental sources of variation received the strongest support. My

results showed that juvenile mortality was greatest following fledging and independence, likely due to increased risk of predation and starvation.

In New Mexico, Ward and Kennedy (1996) reported that post-fledging survival of a control group of goshawk fledglings in a supplemental feeding experiment was 93% in 1992 ($n = 15$) and 67% in 1993 ($n = 3$). In a similar experiment in Utah, Dewey and Kennedy (2001) reported 100% survival over the duration of the fledgling-dependency period in both 1996 ($n = 16$) and 1997 ($n = 10$). In East-central Arizona, Ingraldi (1999) reported survival rates of 90% for juvenile female goshawks during the first seven weeks post-fledging, 80% during the first twelve weeks post-fledging, and 43% for the first-year based on 16 female fledglings equipped with satellite transmitters. Although these estimates were based on small sample sizes, my results are consistent with these findings ($\bar{x} = 91\%$ and 71% for seven and twelve-weeks post-fledging, respectively). Together, these data illustrate that post-fledging survival in goshawks is highly variable among years, with mortality between fledging and dispersal ranging from 0 – 33%, and mortality during the early stages of natal dispersal from 7 – 50%.

Temporal variation in survival. – My results showed a consistent pattern of among-and within-year variation in post-fledging survival of goshawks. In all years except 2000, the risk of mortality decreased to nearly zero beyond the third week of the fledgling-dependency period, yet increased substantially in the fourth and fifth weeks following independence from adults. This finding demonstrates that the time since fledging and independence is strongly correlated to the risk of mortality. In general, juvenile movements within the natal area gradually expand as they gain flight skills (Kennedy and Ward 2003, Kenward et al. 1993a). Seven of the eight mortalities

observed prior to dispersal occurred within the first three to ten days after fledging when young were near the nest, feather growth was incomplete, and individuals could not fly quickly or for long distances. This pattern of age-dependent post-fledging survival has been documented in several 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 albobriata*; McFadzen and Marzluff 1996, Anders et al. 1997, Naef-Daenzer et al. 2001, Todd et al. 2003, Keedwell 2003, respectively). As survival increased beyond the third week post-fledging, juvenile goshawks had acquired reasonable flight skills, were typically located 100 – 300m from the nest, and were still attended by the adult female in most cases.

Predation risk increased as juveniles dispersed from their natal territories. At this stage, juveniles were foraging independently, were no longer attended by adults, and typically moved to open pinyon-juniper woodland and sagebrush plains at lower elevations surrounding the study area. Of the six juveniles recovered dead during this period, five were found within pinyon-juniper or sagebrush cover types. Movement to lower elevations during the early phases 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. (1993b) reported that juvenile European goshawks tended to gather in areas of high rabbit density following independence. In Arizona, black-tailed jackrabbit and cottontail rabbit abundance is typically higher in open or semi-open country (i.e., pinyon-juniper woodland and shrub-steppe) than in higher elevation mixed-conifer or ponderosa pine forests (Hoffmeister 1986). Alternatively, adults may force juveniles from natal sites into sub optimal

habitats. In either case, juveniles that disperse beyond ~ 40 km from their natal territories on the Kaibab Plateau will encounter an abrupt change from forest to shrub-steppe cover types. Movement through vegetation types that provide little cover and lower diversity and/or abundance of prey species could increase rates of predation or starvation (Squires and Reynolds 1997). There was convincing evidence of annual variation in post-fledging survival during the fledgling-dependency period. However, detecting annual variation in the early stages of the post-independence period was limited due to a reduction in sample sizes caused by the large number of hawks censored due to long-distance dispersal movements. The ultimate factors leading to annual variation in post-fledging survival are likely a consequence of annual differences in measured (e.g., prey abundance) and unmeasured (e.g., predator density) factors.

Factors Influencing Post-Fledging Survival

Prey abundance. – Reynolds et al. (1992) recommended managing forests in the southwest U.S. by providing habitat for the goshawk and 14 of its primary prey species. I detected changes in goshawk survival rates with respect to estimates of prey abundance on the study area, thereby lending support to this management strategy. The highest mortality during the fledgling-dependency period occurred in 2001 when prey abundance was lowest. In this year, starvation was the leading cause of mortality, particularly in males. In 2000, when prey densities were highest, no mortalities were observed prior to adult independence, and only two mortalities occurred during the first five weeks post-independence. In 1998 and 1999, when prey densities were at intermediate levels, predation was the leading cause of mortality and no mortalities were attributed to

starvation. Thus, prey abundance appeared to have strong direct and indirect influences on juvenile mortality, perhaps due to interactions with parental-care behavior (Dewey and Kennedy 2001). A reduced juvenile survival rate in 2001 from 2000 paralleled a reduction in the proportion of pairs breeding in the study population (Appendix) and a reduction in prey density on the KNF (Salafsky 2004). Thus, it appears that prey abundance not only limits goshawk productivity by affecting the reproductive efforts of adults, but at the level of juvenile survival as well. These findings demonstrate that even though adults may adjust production of offspring in response to prey availability, this does not result in constancy of juvenile survival rates.

Using supplemental-feeding experiments extending two years each, Ward and Kennedy (1996) and Dewey and Kennedy (2001) tested the hypothesis that food limits survival of juvenile goshawks. In both studies, food-supplemented juveniles had a significantly higher survival rate during the fledgling-dependency period than controls in one year, but not the other. The authors speculated that their treatment effect could have been obscured by unmeasured increases or decreases in natural prey availability between years (Ward and Kennedy 1996, Dewey and Kennedy 2001). Given the amount of annual variation in post-fledging survival explained by natural prey densities in my study, it is clear that variation in natural prey levels could confound the effects of experimentally manipulated food levels. By ranking competing models containing year, prey abundance, and weather covariates, a clear assessment of the relative explanatory power of these environmental effects was achieved. The fact that models accounting for prey abundance consistently ranked higher than those containing a “year” effect suggests that a high proportion of annual variability in post-fledging survival is attributable to

variation in local prey abundance. The ANODEV results were consistent with this finding. However, the relationship between post-fledging survival and prey abundance varied with juvenile age – low prey abundance apparently had its largest effect on survival in the first few weeks following fledging and independence from adults whereas survival between these critical periods of transition was consistently near 1 during all four years of the study. Without accounting for weekly variation in survival, this relationship may have been obscured.

Several prey species that contribute significantly to goshawk diets on the Kaibab Plateau were not included in the analysis (e.g., golden-mantled ground squirrel, black-tailed jackrabbit, and cottontail rabbit). However, count data indicate that golden-mantled ground squirrels experienced similar changes in abundance during the study period as those mammal species included in the analysis (Salafsky 2004). Therefore, I believe that inclusion of golden-mantled ground squirrels in the analysis would have strengthened the relationship between post-fledging survival and prey abundance. Jackrabbits and cottontails were seldom encountered on the study area and are likely to be more abundant at lower elevations. Since most juveniles moved to lower elevations during dispersal, rabbit densities probably have larger effects on survival during this time.

Total precipitation. – Contrary to predictions, the amount of rainfall experienced by fledglings during feather growth and flight development was not closely associated with their survival. This was unexpected because observations were made where juveniles had saturated natal plumage and impaired flight ability following a heavy rainstorm. Moreover, nestlings and fledglings have often disappeared following prolonged periods of rain in other years of the long-term demographic study (D. Wiens

personal observation). Substantial differences in precipitation measurements among weather stations indicated that late-summer monsoon thunderstorms were highly localized. Thus, some natal territories likely received heavier rain than others. By using total amount of precipitation as a cohort-level covariate rather than a territory-level covariate, differences in survival among territories may have been obscured. Measuring precipitation within territories directly could alleviate this concern by capturing spatial variation in rainfall caused by localized 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), while others have not (Newton and Moss 1986, McFadzen and Marzluff 1996). I found that female goshawks with below average pre-fledging body mass had higher mortality rates than males with below average pre-fledging body mass. As indicated by models containing additive effects of gender and body mass, the body mass-survival relationship differed in level between sexes. However, the data failed to support the singular effects of gender and body mass. Gender-related differences in pre-fledging body mass therefore appear to be important determinants of post-fledging survival in goshawks. Poor body condition during the later stages of the nestling period could lead to starvation immediately after fledging when feather growth and increased movement require higher energy expenditure. Increased metabolic rates during the initiation of dispersal could also exacerbate the effect of pre-fledging body mass, as indicated by the more pronounced effect of body mass on survival during the post-independence period. Although I observed slightly more female than male deaths by the end of the post-independence period, the sex ratio of deaths observed by the end of the study was equal. In contrast,

Kenward et al. (1999) reported female goshawks had higher survival rates than males during the first 9 months post-fledging.

Validity of Model Assumptions

The use of radio telemetry to estimate unbiased survival rates is based on several assumptions (*see* Tsia et al. 1999). The most critical assumption is that the radiotransmitter does not directly affect survival probabilities. On intact dead recoveries, I observed no obvious physical effects from wearing backpack radiotransmitters such as lost feathers or skin abrasions, and no obvious behavioral differences between radioed and non-radioed fledglings were observed. Of the 48 radio-marked juveniles remaining at risk by the end of the study, five (three females and two males) have been subsequently observed breeding as adults in the study population (Chapter Two). Low recapture rates for juveniles with radiotransmitters and with legbands only during 1998 – 2001 precluded a rigorous assessment of a radiotransmitter effect on survival. However, Reynolds et al. (2004) found that backpack-style transmitters (similar to those used in my study) had no detectable effect on apparent survival probabilities of adult goshawks.

Another important assumption in my survival analysis was that data censoring was not equivalent to death. Censoring does not bias survival estimates provided that it is independent of fate (Tsia et al. 1999). If this assumption was violated, and some hawks that died were classified as censored, resulting survival estimates would be biased high. That some hawks classified as “censored” actually died beyond the aerial survey area is likely. However, I restricted my estimates of survival during the post-independence period to goshawks that remained within the aerial survey area (where detection

probabilities were nearly perfect), thereby significantly reducing the likelihood of misclassifying deaths as “censored”. Although this restriction limited my inferences regarding mortality patterns to the aerial survey region, it reduced the bias associated with increased mortality as dispersal distance increases and detection probabilities decrease (Waser et al. 1994).

Juvenile Survival and Population Dynamics

Life history theory predicts that selection favors allocation of time and resources toward the life history stage at which survival or reproduction is least variable (Stearns 1992). In long-lived birds that mature late and lay few eggs, small changes in adult survival are generally found to have large effects on local 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. 2002). However, vital rates that account for a larger portion of the variance in population growth rates can have a greater impact on population dynamics than those with large elasticities (Sæther and Bakke 2000). Annual goshawk reproduction on the Kaibab Plateau was found to be highly variable among years (R. Reynolds *personal communication*; Appendix). The survival models I developed here indicate that post-fledging survival varies among annual fledgling cohorts, and that much of this variation can be attributed to variable prey populations. In contrast, estimates of adult survival on the Kaibab Plateau are constant over time and equal between sexes (Reynolds et al. 2004). This pattern of highly variable reproduction and juvenile survival coupled with temporally invariant adult survival has been found in several studies of long-lived raptors (Franklin

et al. 2000, Sæther and Bakke 2000, Blakesley et al. 2002, Seamans et al. 2002).

Although the relative contribution of adult and juvenile survival rates to population growth has not been estimated for the Kaibab Plateau goshawk population at this time, I suggest that juvenile survival plays a critical role in local population dynamics because of its considerable variation, sensitivity to environmental conditions, and its importance to recruitment and, hence, population regulation.

Juvenile survival, dispersal, and recruitment may also be critical to stable exchange rates among fragmented goshawk populations (Chapter Two). Although a metapopulation structure has not yet been demonstrated for goshawks, genetic evidence indicates that a functional population extends over a large geographic area (Sonsthagen et al. 2004). At a local scale, juveniles commonly dispersed beyond the “sky-island” forests of the Kaibab Plateau with few returning in subsequent years to gain breeding territories (Chapter Two). In contrast, breeding dispersal of adults occurs infrequently and over short distances (2 – 17 km; Reynolds et al. *unpublished manuscript*). Collectively, this evidence suggests that goshawk populations in the southwest are spatially-structured, and that gene flow among naturally fragmented populations is maintained by natal dispersal. Extensive external recruitment may be a general pattern in birds (Martin et al. 2000), and can be vital to the persistence and stability of small, isolated populations (Stacey and Taper 1992). High temporal variation in reproduction, juvenile survival, and recruitment may therefore have important implications to the regional stability of goshawk populations in the southwestern U.S., especially if sub-populations within the regional population have synchronous dynamics due to climate. In essence, the successful

survival and dispersal of juveniles may allow goshawks to occur at sites where local recruitment alone would not be sufficient for population persistence.

Management Implications

Telemetry data indicate that the greatest risk of post-fledging mortality occurs within the first two weeks after fledging. Management activities near nests should therefore be minimized during this period (late June to early September in Arizona), as disturbance may affect food provisioning rates or alert predators to the presence of nests. Moreover, using fledging success (the number of offspring that survive to fledging) as an index of true reproductive success (the number of offspring that survive to breed) fails to incorporate this important stage of juvenile mortality. Conducting fledging counts when young are still close to the nest one to two weeks after fledging may provide better estimates of goshawk productivity. Late fall and early winter months also appear to be critical to juvenile survival in goshawks. Pinyon-juniper woodland and shrub-steppe habitats clearly play an important role in juvenile survival and dispersal processes. Adequate food resources in such habitats may be essential for high survival, successful dispersal, and recruitment of juvenile goshawks. Future research is needed to address the importance of pinyon-juniper woodland and shrub-steppe habitats to goshawk population regulation processes and connectivity of breeding habitats.

Surmounting evidence suggests that changes in climate and prey populations drive temporal variation in goshawk reproduction (Keane 1999, Bloxton 2002, Salafsky 2004). My results indicate that prey abundance further limits goshawk productivity at the level of juvenile survival. To improve goshawk reproduction, juvenile survival,

dispersal, and recruitment, goshawk conservation strategies should entail a holistic management plan encompassing key goshawk prey species and their habitats. It is important to note, however, that prey densities appear to vary over small spatial and temporal scales, with mammals showing a higher level of variation than birds (Salafsky 2004). To effectively manage forests used by goshawks and their prey community, a research focus on the life history characteristics, habitat relationships, and factors limiting prey populations will ultimately be required.

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Table 1.1. Description of candidate models investigating annual (Year), weekly categorical (t), or weekly continuous (T) time effects on post-fledging survival (S) of juvenile northern goshawks in northern Arizona.

Biological Hypothesis	Model notation	Model Structure
1.) Survival is dependent on weekly categorical time	$S(t)$	$\beta_0 + \beta_1(t_1) + \beta_2(t_2) + \beta_3(t_3) + \beta_4(t_4) + \beta_5(t_5) + \beta_6(t_6)$
2.) Survival is constant over time	$S(\cdot)$	β_0
3.) Survival is dependent on year	$S(\text{Year})$	$\beta_0 + \beta_1(y_1) + \beta_2(y_2) + \beta_3(y_3)$
4.) Additive effects of year and weekly categorical time	$S(\text{Year}+t)$	$\beta_0 + \beta_1(y_1) + \beta_2(y_2) + \beta_3(y_3) + \beta_4(t_1) + \beta_5(t_2) + \beta_6(t_3) + \beta_7(t_4) + \beta_8(t_5) + \beta_9(t_6)$
5.) Linear increase/decrease in weekly survival over time (weekly continuous time)	$S(T)$	$\beta_0 + \beta_1(T)$
6.) Additive effects of year and weekly continuous time	$S(\text{Year}+T)$	$\beta_0 + \beta_1(y_1) + \beta_2(y_2) + \beta_3(y_3) + \beta_4(T)$
7.) Interactive effect of year and weekly continuous time	$S(\text{Year} \times T)$	$\beta_0 + \beta_1(y_1) + \beta_2(y_2) + \beta_3(y_3) + \beta_4(T) + \beta_5(y_1 \times T) + \beta_6(y_2 \times T) + \beta_7(y_3 \times T)$
8.) Interactive effect of year and weekly categorical time	$S(\text{Year} \times t)$	Fully parameterized time-specific model
9.) Quadratic time trend in survival (weekly continuous time)	$S(T+T^2)$	$\beta_0 + \beta_1(T) + \beta_2(T^2)$
10.) Year-specific, weekly quadratic time trend in survival	$S(\text{Year}+T+T^2)$	$\beta_0 + \beta_1(y_1) + \beta_2(y_2) + \beta_3(y_3) + \beta_4(T) + \beta_5(T^2)$

Notes: Hypotheses 1-8 address survival during the fledgling-dependency period (weeks 1-7 post-fledging), and hypotheses 9 and 10 address hypothesized changes in survival from fledging through the first five weeks after juveniles initiated dispersal (weeks 1-12 post-fledging).

Table 1.2. Annual numbers of juvenile northern goshawks under radio telemetry study in northern Arizona and their fates by week 40 post-fledging, 1998 – 2001.

	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%)

† The number of fledglings that carried radiotransmitters divided by the total number of fledglings banded on the Kaibab Plateau.

Table 1.3. Causes of death by developmental stage for radio-marked juvenile northern goshawks in northern Arizona during the first 40 weeks post-fledging, 1998 – 2001.

Developmental stage	Weeks after fledging	No. of hawks †	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%)
Post-independence	8 – 12	71	6 (4, 2)	4 (67%)	0 (0%)	2 (33%)
Dispersal ‡	13 – 40	48	10 (3, 7)	4 (40%)	2 (20%)	4 (40%)
Fledging through dispersal	1 – 40	89	24 (12, 12)	11 (46%)	5 (21%)	8 (33%)

† Accounts for mortalities and hawks that shed transmitters during the previous developmental stage.

‡ “Dispersal” was defined as the period between the five-week post-independence stage and spring of the following year.

Table 1.4. Ranking of juvenile northern goshawk survival models investigating time effects during the fledgling-dependency period (weeks 1 – 7 post-fledging) in northern Arizona, 1998 – 2001. See table 1.1 for a description of model notation.

Model †	K ‡	AIC_c §	ΔAIC_c	w_i	Deviance *
6.) $S(\text{Year}+T)$	5	71.789	0.00	0.533	61.674
5.) $S(T)$	2	73.012	1.22	0.289	68.989
7.) $S(\text{Year}\times T)$	8	74.349	2.56	0.148	58.070
4.) $S(\text{Year}+t)$	10	78.702	6.91	0.017	58.275
1.) $S(t)$	7	79.742	7.95	0.010	65.526
3.) $S(\text{Year})$	4	82.649	10.86	0.002	74.572
2.) $S(.)$	1	84.859	13.07	0.001	82.851
8.) $S(\text{Year}\times t) \bullet$	28	113.120	41.33	0.000	53.853

† Numbers correspond to hypotheses described in Table 1.1.

‡ Number of estimable parameters in model.

§ Akaike's information criterion corrected for small sample size.

|| Akaike's model weight.

* Difference in $-2\log(\text{Likelihood})$ of the current model and $-2\log(\text{Likelihood})$ of the saturated model.

• Fully parameterized time-specific model.

Table 1.5. Annual estimates of derived survival parameters (\hat{S}) for radio-marked juvenile northern goshawks over the duration of the fledgling-dependency period (weeks 1 – 7 post-fledging), and estimates of total prey density (\hat{D}) for four primary prey species sampled on the Kaibab National Forest in northern Arizona, 1998 – 2001. Survival estimates were derived under model $\{S(\text{Year}+T)\}$.

Year	Post-fledging survival				Total prey density ha ⁻¹			
	\hat{S}	SE	95% CI		\hat{D}	SE	95% CI	
			Lower	Upper			Lower	Upper
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: Prey density estimates and measures of precision for 1998 were predicted under the regressed relationship between the number of prey species detections per 100 minutes of observation during 1998 – 2002 and line-transect density estimates from 1999 – 2002 (Salafsky 2004).

Table 1.6. Ranking of models relating prey abundance (prey), total precipitation (rain), brood size (brood), gender, pre-fledging body mass (mass), and territory hatch date (hatch) to survival probabilities (S) of radio-marked juvenile northern goshawks over the first seven weeks post-fledging in northern Arizona, 1998 – 2001. Boldface denotes the two best fitting time-specific models.

Model	K †	AIC_c ‡	ΔAIC_c	w_i §	Deviance
$S(\text{Prey}+T+\text{sex}+\text{mass})$	5	69.418	0.00	0.208	59.303
$S(\text{Prey}+T)$	3	70.446	1.03	0.125	64.400
$S(\text{Rain}+T+\text{sex}+\text{mass})$	5	71.362	1.94	0.079	61.246
$S(\text{Prey}+T+\text{brood})$	4	71.606	2.19	0.070	63.530
$S(\text{Prey}+T+\text{mass})$	4	71.666	2.25	0.068	63.589
$S(\text{Year}+T)$	5	71.789	2.37	0.064	61.674
$S(\text{Prey}+T+\text{hatch})$	4	71.972	2.55	0.058	63.895
$S(\text{Prey}+T+\text{sex})$	4	72.069	2.65	0.055	63.992
$S(\text{Prey}+T+\text{brood}+\text{hatch})$	5	72.519	3.10	0.044	62.403
$S(\text{Year}+T+\text{mass})$	6	72.955	3.54	0.036	60.793
$S(\text{Year}+T+\text{brood})$	6	72.986	3.57	0.035	60.824
$S(T)$	2	73.012	3.59	0.035	68.989
$S(\text{Year}+T+\text{sex})$	6	73.459	4.04	0.028	61.297
$S(\text{Year}+T+\text{hatch})$	6	73.796	4.38	0.023	61.634
$S(\text{Year} \times T)$	8	74.349	4.93	0.018	58.070
$S(\text{Rain}+T)$	3	74.807	5.39	0.014	68.761
$S(\text{Rain}+T+\text{mass})$	4	75.434	6.02	0.010	67.357
$S(\text{Rain}+T+\text{hatch})$	4	75.468	6.05	0.010	67.392
$S(\text{Rain}+T+\text{sex})$	4	76.010	6.59	0.009	67.933
$S(\text{Rain}+T+\text{brood})$	4	76.798	7.38	0.005	68.721
$S(\text{Rain}+T+\text{brood}+\text{hatch})$	5	76.960	7.54	0.005	66.844
$S(\text{Year}+t)$	10	78.702	9.28	0.002	58.275
$S(t)$	7	79.742	10.32	0.001	65.526
$S(\text{Year})$	4	82.649	13.23	0.000	74.572
$S(\cdot)$	1	84.859	15.44	0.000	82.851
$S(\text{Year} \times t)$ *	28	113.120	43.70	0.000	53.853

† Number of estimable parameters in model.

‡ Akaike's information criterion corrected for small sample size.

§ Akaike's model weight.

|| Difference in $-2\log(\text{Likelihood})$ of the current model and $-2\log(\text{Likelihood})$ of the saturated model.

* Fully parameterized time-specific model.

Table 1.7. Analysis of deviance (ANODEV) results used to evaluate the amount (62.2%) of annual variation in juvenile northern goshawk survival during the fledgling-dependency period that was explained by annual estimates of prey density.

Source	df	Deviance	Mean deviance	<i>F</i>	<i>P</i>
Uncorrected total	5	68.989			
Grand mean	2	61.674			
Corrected total	3	7.315			
Total covariate	1	4.589	4.589	3.367	0.208
Error	2	2.726	1.363		

Notes: The prey density covariate describes 62.2% of the annual variation in survival during the fledgling-dependency period (i.e., “Total covariate” divided by “Corrected total”). Uncorrected total = deviance of model $\{S(T)\}$; Grand mean = deviance of model $\{S(\text{Year}+T)\}$; Corrected total = uncorrected total – grand mean; Total covariate = deviance of model $\{S(T)\}$ – deviance of model $\{S(\text{Prey}+T)\}$.

Table 1.8. Ranking of juvenile northern goshawk survival models investigating time effects over the first 12-weeks post-fledging in northern Arizona, 1998 – 2001. See table 1.1 for a description of model notation.

Model †	K ‡	AIC_c §	ΔAIC_c	w_i	Deviance *
9.) $S(T+T^2)$	3	127.514	0.00	0.614	121.477
10.) $S(\text{Year}+T+T^2)$	6	128.601	1.09	0.357	116.472
1.) $S(t)$	12	135.037	7.52	0.014	110.554
4.) $S(\text{Year}+t)$	15	136.762	9.25	0.006	106.015
2.) $S(.)$	1	137.553	10.04	0.004	135.547
3.) $S(\text{Year})$	4	139.147	11.63	0.002	131.086
5.) $S(T)$	2	139.407	11.89	0.002	135.388
7.) $S(\text{Year}+T)$	5	140.864	13.35	0.001	130.772
6.) $S(\text{Year}\times T)$	8	141.682	14.17	0.001	125.460
8.) $S(\text{Year}\times t) \bullet$	48	191.002	63.49	0.000	87.290

† Numbers correspond to hypotheses described in Table 1.1.

‡ Number of estimable parameters in model.

§ Akaike's information criterion corrected for small sample size.

|| Akaike's model weight.

* Difference in $-2\log(\text{Likelihood})$ of the current model and $-2\log(\text{Likelihood})$ of the saturated model.

• Fully parameterized time-specific model.

Table 1.9. Ranking of models relating prey abundance (prey), brood size (brood), gender, body mass (mass), and territory hatching date (hatch) to survival probabilities (S) of radio-marked juvenile northern goshawks over the first 12-weeks post-fledging in northern Arizona, 1998 – 2001. Boldface denotes the two best fitting time-specific models.

Model	K †	AIC_c ‡	ΔAIC_c	w_i §	Deviance
$S(T+T^2+\text{sex}+\text{mass})$	5	122.846	0.00	0.579	112.755
$S(\text{Prey}+T+T^2)$	4	125.209	2.36	0.178	117.148
$S(T+T^2+\text{sex})$	4	127.042	4.20	0.071	118.981
$S(T+T^2)$	3	127.514	4.67	0.056	121.477
$S(T+T^2+\text{hatch})$	4	128.292	5.45	0.038	120.231
$S(\text{Year}+T+T^2)$	6	128.601	5.75	0.033	116.472
$S(T+T^2+\text{mass})$	4	129.354	6.51	0.022	121.293
$S(T+T^2+\text{brood})$	4	129.524	6.68	0.021	121.463
$S(t)$	12	135.037	12.19	0.001	110.554
$S(\text{Year}+t)$	15	136.762	13.92	0.001	106.015
$S(.)$	1	137.553	14.71	0.000	135.547
$S(\text{Year})$	4	139.147	16.30	0.000	131.086
$S(T)$	2	139.407	16.56	0.000	135.388
$S(\text{Year}+T)$	5	140.864	18.02	0.000	130.772
$S(\text{Year} \times T)$	8	141.682	18.84	0.000	125.460
$S(\text{Year} \times t)$ *	48	191.002	68.16	0.000	87.290

† Number of estimable parameters in model.

‡ Akaike's information criterion corrected for small sample size.

§ Akaike's model weight.

|| Difference in $-2\log(\text{Likelihood})$ of the current model and $-2\log(\text{Likelihood})$ of the saturated model.

* Fully parameterized time-specific model.

Table 1.10. Analysis of deviance (ANODEV) results used to evaluate the amount (87.7%) of annual variation in juvenile northern goshawk survival over the first 12-weeks post-fledging explained by annual estimates of prey density.

Source	df	Deviance	Mean deviance	<i>F</i>	<i>P</i>
Uncorrected total	6	121.477			
Grand mean	3	116.472			
Corrected total	3	5.005			
Total covariate	1	4.329	4.329	12.819	0.069
Error	2	0.675	0.675		

Notes: The prey density covariate describes 85.71% of the annual variation in survival during the first 12-weeks post-fledging (i.e., “Total covariate” divided by “Corrected total”). Uncorrected total = deviance of model $\{S(T+T^2)\}$; Grand mean = deviance of model $\{S(\text{Year}+T+T^2)\}$; Corrected total = uncorrected total – grand mean; Total covariate = deviance of model $\{S(T+T^2)\}$ – deviance of model $\{S(\text{Prey}+T+T^2)\}$.

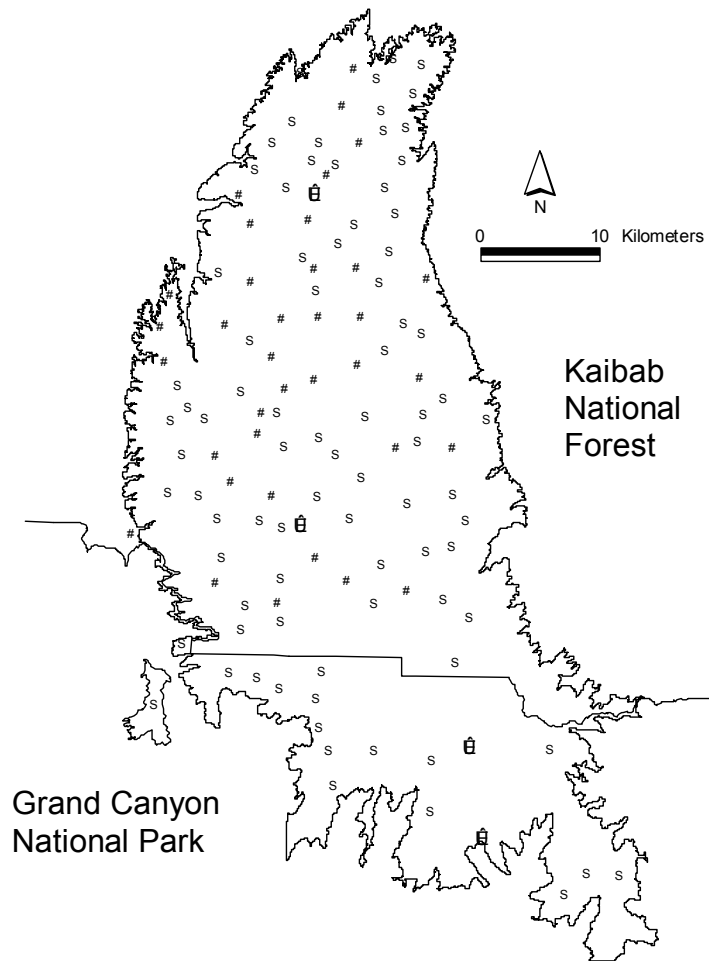


Figure 1.1. The Kaibab Plateau study area showing the location of 121 northern goshawk territories studied during 1991 – 2001 (circles and dots), the 36 territories where nestlings were radio-marked during 1998 – 2001 (dots), and weather stations (stars). Also shown is the boundary between the Kaibab National Forest and the Grand Canyon National Park.

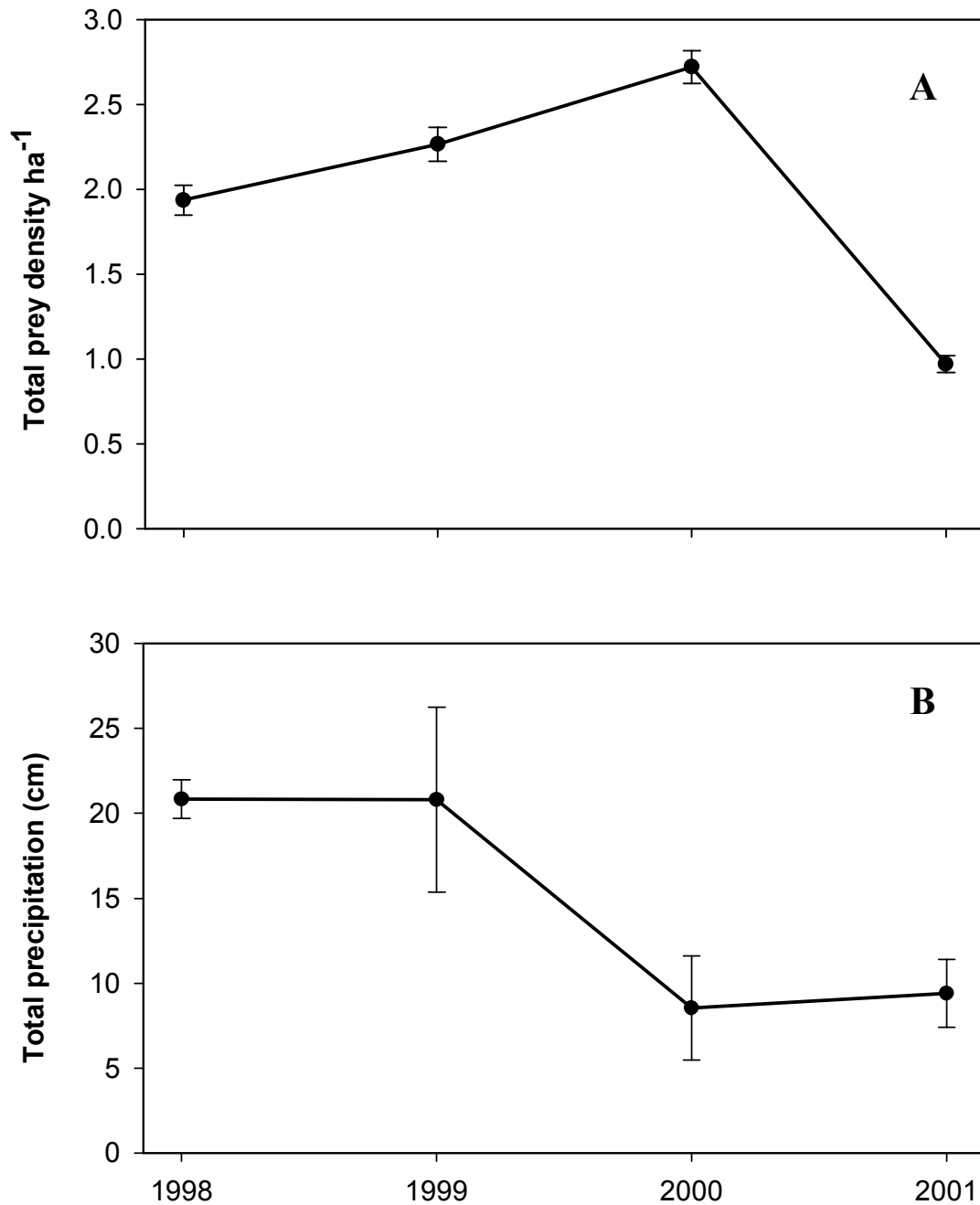


Figure 1.2. Change in (A) total prey density ha⁻¹ on the Kaibab National Forest in northern Arizona, and (B) average total precipitation (cm) measured over the duration of the fledgling-dependency period on the Kaibab National Forest and northern portion of Grand Canyon National Park, 1998 – 2001. Error bars represent ± 1 SE.

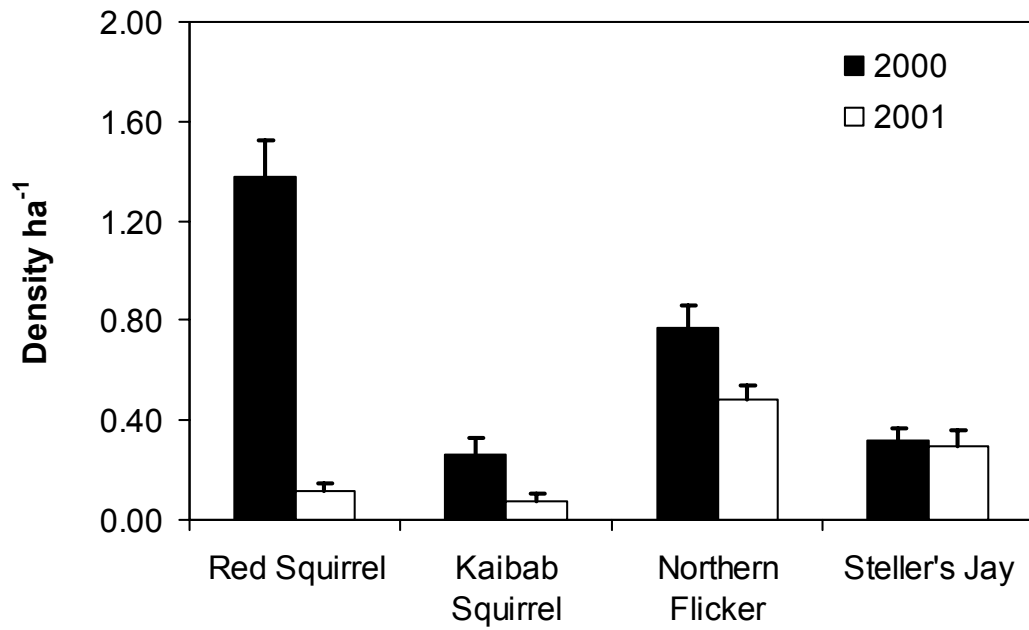


Figure 1.3. Density ha⁻¹ of each of the four prey species included in total prey density estimates for 2000 and 2001, when prey abundance was highest and lowest, respectively. Error bars represent ± 1 SE.

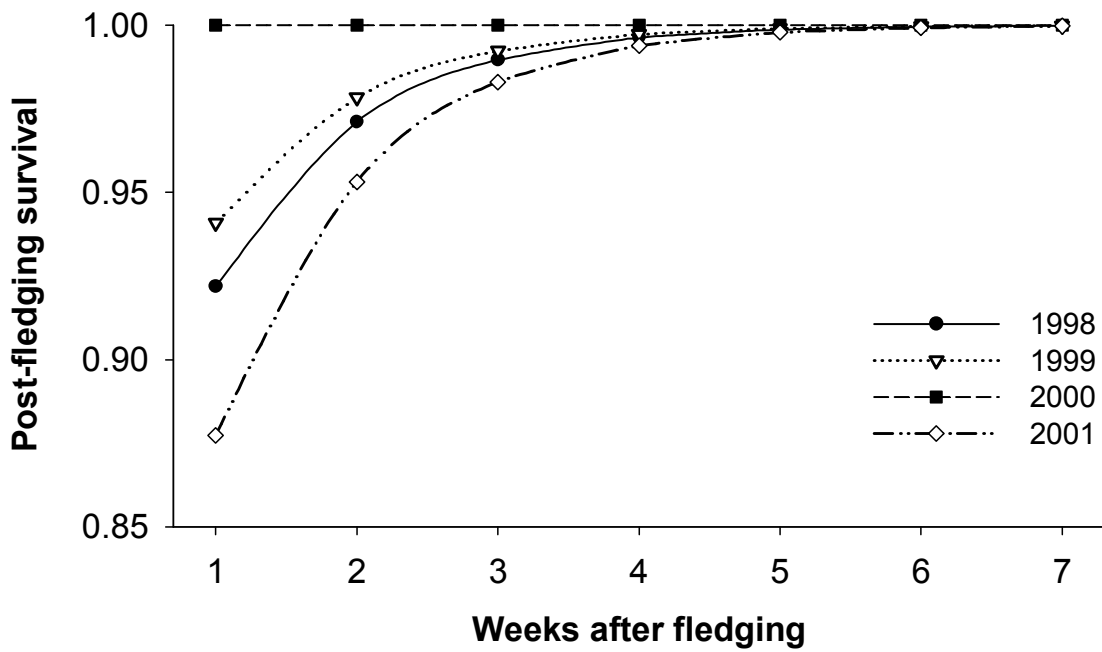


Figure 1.4. Estimates of weekly survival during the fledgling-dependency period (weeks 1 – 7 post-fledging) under model $\{S(\text{Year}+T)\}$ for radio-marked juvenile northern goshawks in northern Arizona, 1998 – 2001.

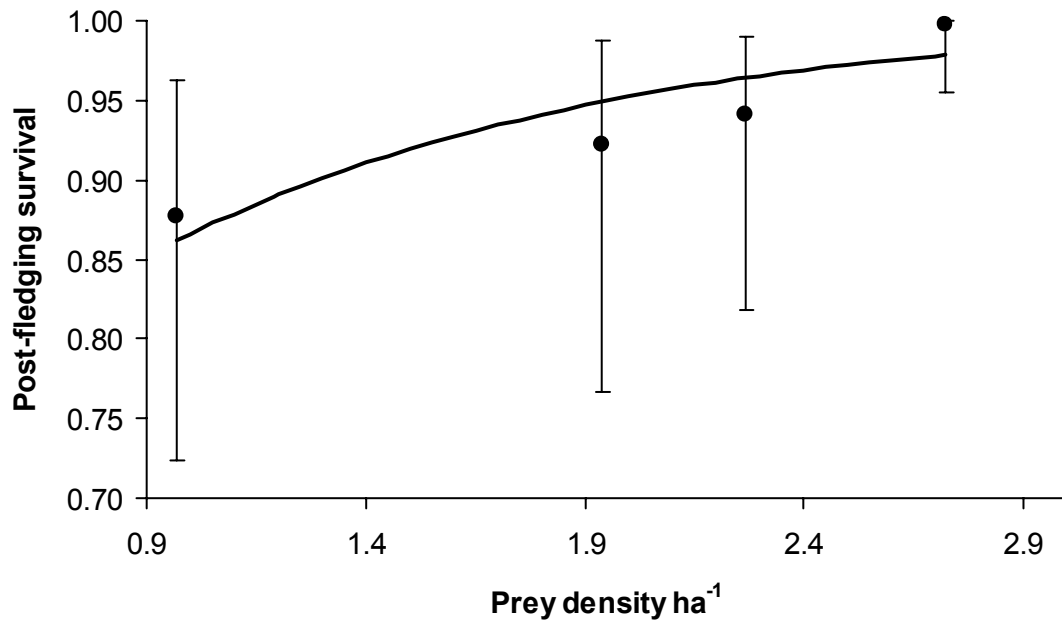


Figure 1.5. Relationship between post-fledging survival of juvenile northern goshawks and total prey density ha^{-1} on the Kaibab National Forest in northern Arizona, 1998 – 2001. Survival estimates (dots \pm 95% profile likelihood CI) are from the first weekly interval under model $\{S(\text{Year}+T)\}$. Line represents predicted values under model $\{S(\text{Prey}+T)\}$.

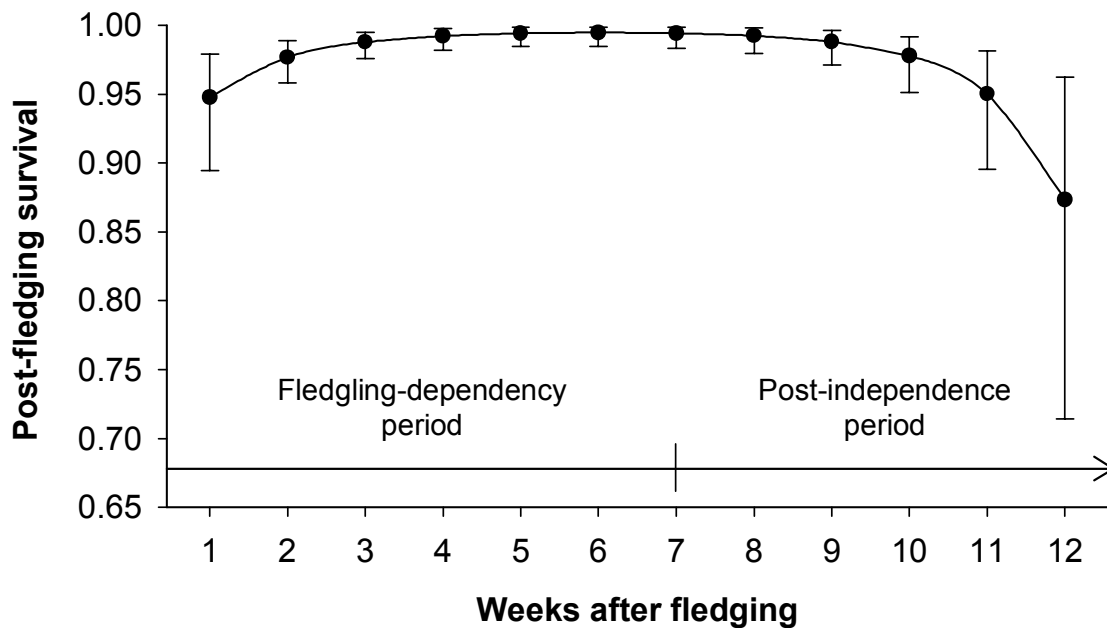


Figure 1.6. Estimates of weekly survival (\pm 95% profile likelihood CI) during the fledgling-dependency (weeks 1-7) and post-independence (weeks 8-12) periods under model $\{S(T+T^2)\}$ for radio-marked juvenile northern goshawks in northern Arizona, 1998 – 2001.

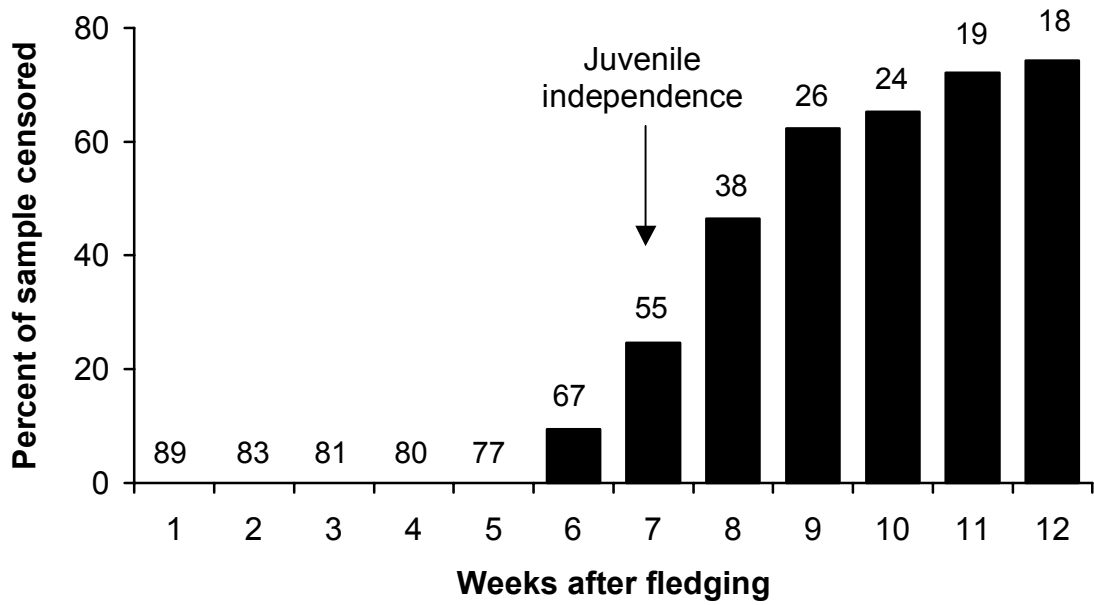


Figure 1.7. Percentage of radio-marked juvenile northern goshawks that were censored from post-fledging weekly intervals, 1998 – 2001. Numbers above bars indicate the number of juveniles remaining “at risk” once mortalities, hawks that prematurely shed transmitters, and censored hawks were removed.

CHAPTER TWO

NATAL DISPERSAL WITHIN AN ISOLATED POPULATION OF NORTHERN GOSHAWKS IN ARIZONA

ABSTRACT

As part of a long-term study, I examined the onset and completion of natal dispersal relative to local demographic and environmental conditions within an isolated population of northern goshawks (*Accipiter gentilis*) in northern Arizona during 1991 – 2004. The study included 614 banded (1991 – 2004) and 89 radio-marked (1998 – 2001) juveniles produced on 121 regularly-spaced breeding territories. Radio-marked juveniles dispersed from their natal territories during August and September between 71 and 103 days post-hatching ($\bar{x} \pm SE = 86.5 \pm 0.8$ days), and spent between 33 and 66 days in the natal territory after fledging ($\bar{x} \pm SE = 46.3 \pm 0.8$ days). The best-fitting proportional hazards regression models predicted the timing of dispersal as a function of annual changes in key bird and mammal prey populations on the study area, total amount of rainfall during fledgling development, and natal brood size. Both radiotelemetry and banding data were consistent in indicating overall low rates of juvenile fidelity to the natal population; the fidelity rate for radio-marked juveniles was 0.28 (95% CI = 0.20, 0.37), and 69 (11.2%) banded nestlings entered the local breeding population between two and eleven years of age. Median natal dispersal distance within the study population was 15.0 km (range = 0.1 to 58.1 km), a distance equivalent to about four times the

diameter of an average territory (3.8 km). A comparison of the predictions of individual, social, and environmental models of dispersal suggested that variation in local natal dispersal distance was best explained by a null model where dispersal distances are distributed evenly relative to these effects. The results of this study suggested that natal dispersal behavior of goshawks on the Kaibab Plateau is driven by a combination of local environmental conditions, intraspecific competition for a limited number of breeding territories, and inbreeding avoidance. A low juvenile fidelity rate coupled with juvenile dispersal distances ranging up to 442 km suggested that juvenile emigration to other, perhaps distant forests was common. This study suggests that external recruitment (i.e., immigration) can be expected to play a central role in goshawk population regulation processes in the southwestern United States.

Key words: *Accipiter gentilis; radiotelemetry; natal dispersal; prey abundance; northern goshawk; philopatry; recruitment; Arizona.*

INTRODUCTION

Natal dispersal, defined as movement away from the natal area to the site of first breeding (Greenwood and Harvey 1982), is a complex process where individuals exhibit a variety of 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 by individuals during the leaving, transient movement, or settlement stages of the dispersal process. Natal dispersal behavior can therefore vary extensively among individuals, populations, and landscapes. Moreover, because study areas are typically small in size relative to the extent of dispersal, the scale at which dispersal behavior is analyzed can strongly influence dispersal-related parameters (Koenig et al. 1996, 2000, LaHaye et al. 2001). Highly variable dispersal behavior within and among landscapes coupled with a general lack of correspondence between the spatial and temporal scales in which populations are studied and the scales at which dispersal often operates makes it difficult to examine the mechanisms that shape a given species' natal dispersal profile. As a consequence, natal dispersal is a poorly understood ecological process, particularly in wide-ranging species occurring at low densities.

Dispersal ensures the coupling of habitats in naturally fragmented landscapes. Thus, the direct consequences of this fundamental population process are 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*; Noon and McKelvey 1992, Murphy and Noon 1992, Lamberson et al. 1994, Forsman et al. 2002). Similar to the spotted owl, northern goshawks (*Accipiter gentilis*; hereafter referred to as goshawk) select nest sites within mature to old-growth forest structure (Squires and Reynolds 1997). The fragmentation and alteration of these forests due to 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 United States have adopted management plans to conserve and protect forests used by breeding goshawks (Reynolds et al. 1992). Adult goshawks exhibit high (75 – 95%) site and mate fidelity once they have secured a breeding territory (Detrich and Woodbridge 1994, Reynolds and Joy *in press*), suggesting that reportedly high rates of gene flow among disjunct populations is being maintained by natal dispersal (Sonsthagen et al. 2004). If juvenile movement among naturally fragmented populations is indeed common, then inter-population transition rates may be critical to the stability and persistence of local and regional populations. As goshawk conservation strategies become increasingly relevant to regional forest planning efforts (Greenwald 2004), a better understanding of natal dispersal, and how this process is affected by changing environmental conditions, is needed.

The overall goal of this study was to provide descriptive information regarding the onset and completion of natal dispersal in goshawks. I therefore considered the natal dispersal process as three interdependent stages: leaving the natal site (the leaving 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 Hjermmann 2001). Patterns of movement and behavior within these stages were assessed during radio-telemetry and capture-recapture studies of juvenile goshawks on the Kaibab Plateau in northern Arizona. My study of natal dispersal was part of a 14-year (1991 – 2004) demographic study of a population of goshawks inhabiting an isolated expanse of high-elevation coniferous forests (Reynolds et al. 1994, 2004), which allowed me to evaluate dispersal behavior relative to demographic, social, and environmental conditions within the natal population. My specific objectives were: (1) to identify the relative importance of factors hypothesized to affect the timing of dispersal, (2) describe post-independence movements made by juveniles and estimate juvenile fidelity to the natal population during the first year of life, (3) describe territory settlement patterns of locally-produced hawks during breeding recruitment, and (4) estimate the support for individual, social, environmental, and demographic models of dispersal in explaining variation in natal dispersal distances within a population of goshawks inhabiting a naturally fragmented landscape.

METHODS

Study Area and Population

The 1,732 km² study area on the Kaibab Plateau in northern Arizona included all of the coniferous forest above 2,182 m elevation (Fig. 2.1). This area comprised the northern portions of the Kaibab National Forest (KNF) and the Grand Canyon National Park (GCNP). The Kaibab Plateau is a large, oval-shaped landform that rises from a shrub-steppe plain at 1,750 m elevation to the highest point at 2,800 m (Rasmussen

1941). Forests of the Kaibab Plateau include three principal types: pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodland occur between 1,830 and 2,075 m, ponderosa pine (*Pinus ponderosa*) forests occur from 2,075 to 2,450 m, and mixed-conifer forests (*Picea engelmannii*, *Abies concolor*, *Pseudotsuga menziesii*, *P. ponderosa*, *Populus tremuloides*) occur from 2,450 to 2,650 m (Rasmussen 1941, White and Vankat 1993). Except for relatively small meadows, burns, and recent management areas, forests on the Kaibab Plateau form a continuous canopy cover. Forests on the Kaibab Plateau are isolated from similar forests by varying distances of shrub-steppe plains (Fig. 2.1). The nearest forest to the north is 97 km, to the east 250 km, to the west 80 km, and to the south 89 km, with the exception of a small area of ponderosa pine forest on the south rim of the Grand Canyon at 18 km. Annual precipitation on the Kaibab Plateau averages 67.5 cm, with winter snowpacks of 2.5 – 3.0 m (White and Vankat 1993). Mid to late summers are characterized by frequent (2 – 4 per week) thunderstorms with heavy rainfall.

In 1991, a long-term study of goshawk demographics and habitat was established on the Kaibab Plateau (Reynolds et al. 1994, 2004, Reich et al. 2004, Reynolds and Joy *in press*). Survey protocols used to locate nesting goshawks are described in detail elsewhere (Joy et al. 1994, Reynolds et al. *in review*). In general, goshawks on the Kaibab Plateau are territorial, socially monogamous, non-migratory, and exhibit temporally invariant survival (75%) and strong site fidelity (98%) once settled on a breeding territory (Reynolds et al. 2004). A “territory” was defined as an area used and defended by a single pair of goshawks during a breeding season (Reynolds et al. 1994). Territories were defined as “active” if egg were laid, “occupied” if eggs were not laid but evidence of goshawk occupancy (e.g., molted feathers, nest construction, hawk sightings)

was found in association with a nest structure, and “unknown” if eggs were not laid and no evidence of goshawk occupancy was found during a three-stage nest searching protocol described by Reynolds et al. (*in review*). The number of territories studied increased with annual searches from 37 in 1991 to 121 in 2004 (Table A1). By 2004, a high density of regularly-spaced breeding territories had been identified with a mean inter-territory distance of 3.8 km (Reich et al. 2004, Reynolds et al. *in review*).

Data Collection

Banding data. – From 1991 through 2004, capture-recapture studies of adult and nestling goshawks were conducted on the Kaibab Plateau. Individuals were classified as immature (0 – 1 yr), young-adult (1 – 3 yrs), or adult (> 3 yrs) based on plumage characteristics (Reynolds et al. 1994). Nesting adults were captured near nests using dho-gaza traps as described in Reynolds et al. (1994), and nestlings were captured by climbing nest trees during the last week of the nestling period (mid to late June). All captured goshawks were fit with a U.S. Fish and Wildlife Service leg band and an anodized colored leg band with a unique alpha-numeric code. Colored leg bands could be read from 80 m using 40 – 60× spotting scopes so that hawks could be visually identified in subsequent years without recapture. For each nestling captured, the following measurements were taken: body mass (g), gender (determined by body mass, tarsometatarsal length, and footpad length measurements; Reynolds et al. 1994), and age (number of days post-hatching), which was estimated using a photographic and behavioral guide (Boal 1994). All known breeding territories within the study area were monitored annually to determine reproductive status of 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 later observed breeding within the study population (Wiens and Reynolds *in review*). Such cases were used as a basis for examining patterns of local settlement and natal dispersal distance.

Radiotelemetry data. – In addition to observations of natal dispersal based on recaptures of color-banded nestlings, I radio-marked 89 juveniles (42 females, 47 males) at 48 nests on the KNF portion of the study area during 1998 – 2001 to examine the onset of dispersal and first-year movement patterns. Nests targeted for radio-marking young were randomly selected from a stratified sample of nests containing one, two, or three young each. Nestlings were captured 2 – 6 days before fledging (32 – 35 days post-hatching) and fit with 17-g backpack-style radiotransmitters (Wildlife Materials Inc. model # LPB 2380M) representing 1.9 and 2.5% of body mass at first flight for females and males, respectively (Chapter One). Radiotransmitters were attached to nestlings using four separate nylon straps with a “weak link” cotton attachment that allowed the harness to fall off without entanglement ~ 1 yr after the time of fitting (modified from Klavitter et al. 2003). Each radiotransmitter was programmed with a mortality sensor and had a life expectancy of ~ 500 days (Wildlife Materials Inc.).

Radio-marked individuals were monitored with model R4000 ATS (Advanced Telemetry Systems, Inc. Isanti, MN) receivers, using two- and three-element Yagi antennas. Individuals were monitored daily until fledging, defined as the first day a nestling was observed out of the nest. Once fledged, status (location, alive, dead) and behavior was recorded 4 – 5 times wk^{-1} until dispersal. Once juvenile goshawks venture beyond 1.5 – 2.0 km from the nest, they are rarely recorded within that radius on

subsequent occasions (Kenward et al. 1993a, Kennedy and Ward 2003). I therefore defined the date of dispersal as the first day a juvenile spent more than two consecutive days ≥ 2 km from its nest. Juveniles not detected within a 2-km radius of their nest for three consecutive days, or those located beyond this radius for more than two consecutive days, were considered to have initiated dispersal. For the most part, juveniles remained within 100 – 300 m of the nest before dispersal (D. Wiens *unpublished data*), making dispersal movements easy to identify. However, there were some cases where juveniles (particularly males) returned to the nest area several days after making wide-ranging “exploratory” movements > 2 km away from their natal area near the end of the fledgling-dependency period. In such cases, the age and date of dispersal was taken as the midpoint between the initial and final departure from the 2-km radius.

Once juveniles dispersed, ground crews attempted to attain locations daily, but were often unsuccessful due to high movement rates, inaccessible terrain, or long-distance movement. Dispersal locations attained by ground 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 antennae (i.e., antennae cable or receiver only), indicating the hawk was within 10 – 20 m of the observer. For each estimated location, the UTM coordinates were recorded using a Global Positioning System (GPS) accurate to 3 m. When a radiotransmitter signal was lost, systematic searches were conducted throughout the study area using omnidirectional antennas mounted on trucks, or from fire lookout towers that provided high vantage points to scan for lost signals over large areas. Thus, high ground coverage of the study area was achieved by using a mixed strategy of scanning for lost signals from lookout towers and systematically searching areas

inadequately sampled from towers using trucks. In addition, fixed-wing aircraft were used to attain locations of dispersing hawks and to survey for missing radiotransmitter signals over the Kaibab Plateau and within 60 – 80 km of the study area boundary (aerial survey area = 10,800 km²; Fig. 2.1). Tracking flights followed a series of E-W transect lines spaced 10 km apart within the established aerial survey area, and were conducted regularly at monthly or bi-monthly intervals from September – May during 1999 – 2002, and January and March in 1998.

The probability of detecting radio-marked hawks within the aerial survey area was estimated as the proportion of 22 radiotransmitters placed at random locations throughout this area that were relocated by a naïve observer. Each radiotransmitter was randomly placed on the ground to mimic a dead hawk or a shed radiotransmitter, or > 3 m high in the branches of trees to simulate perching hawks. This test indicated that the probability of detecting a functioning radiotransmitter was 0.91 (SE = 0.06, 95% CI = 0.79, 1.00), regardless of signal pulse rate (Chapter One).

Dispersal-related Hypotheses and Covariates

Models were developed to represent the potential influences of individual, social, environmental, and demographic conditions relative to the leaving and settlement stages of natal dispersal. These conditions were expressed as individual-, territory-, and cohort-level covariates (Table 2.1, Appendix), and assessed relative to the timing (date and age) of dispersal and natal dispersal distances within the study population. My selection of ecologically-relevant covariates was guided by dispersal-related hypotheses receiving support in other studies of natal dispersal in raptors (Kenward et al. 1993a, 1993b,

Paradis et al. 1998, Forero et al. 2002, Forsman et al. 2002, Byholm et al. 2003, Kennedy and Ward 2003, Serrano et al. 2003), existing knowledge of goshawk ecology on the Kaibab Plateau (Reynolds and Joy 1994, Salafsky 2004, Wiens and Reynolds *in review*), and field observations.

Timing of dispersal. – Supplemental feeding experiments indicate that increased food availability at natal sites can advance the timing of dispersal and limit the extent of post-independence movements of juvenile goshawks (Kenward et al. 1993a, Kennedy and Ward 2003). I therefore predicted that the abundance of key bird and mammal prey species on the study area would be positively related to the date and age juveniles initiated dispersal. I examined this prediction using annual estimates of red squirrel (*Tamiasciurus hudsonicus*), Kaibab Squirrel (*Sciurus aberti kaibabensis*), Northern Flicker (*Colaptes auratus*), and Steller's Jay (*Cyanocitta stelleri*) density ha⁻¹ on the KNF acquired during the 1998 – 2001 goshawk breeding seasons (Appendix). I further hypothesized that the timing of dispersal could be negatively influenced by periods of heavy rainfall that are common to northern Arizona during the latter stages of goshawk fledgling development (late July – September). To examine the influence of severe weather on dispersal, I assessed the mean amount of precipitation (cm) recorded at four weather stations on the study area during July – September, 1998 – 2001, as a function of the Julian date and age of dispersal (Appendix). Alternatively, the timing of natal dispersal in goshawks may be associated with individual characteristics such as gender (Kenward et al. 1993a) and body condition, or characteristics of the natal territory such as brood size and hatching date (Byholm et al. 2003).

Dispersal distance. – Both observational and experimental evidence indicates that juvenile raptors disperse farther from areas with poor environmental conditions and remain on or close to natal areas when resource conditions are favorable (Paradis et al. 1998, Byholm et al. 2003, Kennedy and Ward 2003). In raptors, breeder density is a consistent indicator of environmental conditions such as area quality and resource abundance (Newton 1979). However, a high density of conspecifics has further been associated with increased competition for territory vacancies, which could result in increased dispersal distances of younger, socially subordinate individuals (Tonkyn and Plissner 1991). On the Kaibab Plateau, extensive inter-annual fluctuations in food abundance has been linked to annual variation in breeding density and fledgling production (Salafsky 2004), suggesting that the proportion of pairs that breed in a year is a good indicator of resource abundance for that year. If natal dispersal distances observed at a local scale are driven by breeding conditions or intraspecific competition for limited territory vacancies, then dispersal distance should be associated with ecological constraints such as the density of territorial conspecifics (Wheelwright and Mauck 1998) or number of dispersers in the year of fledging (Forero et al. 2002, Pasinelli and Walters 2002). Alternatively, subordinate individuals could respond to competitive pressures by delaying breeding and “floating” until a territory vacancy can be secured. In this sense, competition among dispersers and competition between dispersers and residents may have different effects on dispersal distances (McCarthy 1997). Assuming that juvenile goshawks monitor their environment at a local scale in making dispersal decisions (e.g., Kennedy and Ward 2003), I predicted that juveniles recruited in years of favorable breeding conditions (as measured by a relatively higher proportion of adult

pairs that breed) would settle closer to their natal territory than juveniles recruited during years of less favorable breeding conditions. If this pattern is a result of high competition for territories among dispersers, dispersal distance should be positively associated with population productivity in the year of fledging. To examine the predictions of resource abundance and/or intraspecific competition on dispersal behavior, I assessed breeding conditions in the year of recruitment, recruitment age, quality of the natal territory, and population productivity in the year of fledging relative to local natal dispersal distances (Table 2.1, Appendix).

Apart from environmental effects, individual variation in dispersal strategies could arise from gender-related differences in behavior (Greenwood 1980), social hierarchies at the natal site (Byholm et al. 2003), physiological differences (Dufty and Belthoff 2001), or inbreeding avoidance (Newton and Marquiss 1983, Negro et al. 1997, Forero et al. 2002, Pasinelli and Walters 2002, Serrano et al. 2003). For example, recovery distances of juvenile goshawks color-banded in Finland were most strongly related to hatching date and hatching rank within broods, with late-hatched, last-ranked hawks showing a lower probability of fidelity to their natal region than early-hatched, first-ranked conspecifics (Byholm et al. 2003). Given this finding, I expected fledglings without siblings to settle at closer distances to their natal areas than fledglings with siblings. Alternatively, inbreeding avoidance is often assumed to be a primary force driving natal dispersal distance (Greenwood 1980, Pusey 1987). The inbreeding avoidance hypothesis predicts that individuals disperse to reduce the probability of mating with close relatives through spatial segregation (Forero et al. 2002). If natal dispersal functions chiefly to reduce the likelihood of mating with parents, females whose

fathers occupied the natal territory in the year of recruitment would be expected to disperse farther than females whose fathers had disappeared from the study, and the same should hold true for males and their mothers (Wheelwright and Mauck 1998). To investigate this prediction, capture-recapture histories of male and female parents were used to assess if the opposite-sex parent of a successful disperser was still present on the original natal territory in the year of their offspring's recruitment.

Data Analysis

Model building and selection. – The set of models designed to investigate hypotheses regarding the timing of dispersal and natal dispersal distance included a fully-specified general model with all main effects, reduced forms of the general model that contained biologically-relevant combinations of covariates, and a base model without main effects. A base model without main effects was useful for assessing the relative explanatory power of models containing ecologically-relevant covariates. Candidate model sets were further constrained by *a priori* considerations (e.g., correlation among covariates) and by sample size – those models that contained more than $n/10$ parameters (including intercept and error terms) were excluded (Burnham and Anderson 2002).

Models specific to the timing of dispersal and dispersal distance were ranked, compared, and evaluated using information-theoretic procedures (Burnham and Anderson 2002). Akaike's information criterion, corrected for small sample size (AIC_c), was used to objectively rank sets of candidate models. Model comparisons were made with ΔAIC_c , the difference between the lowest AIC_c value and AIC_c from all other models; models with $\Delta AIC_c \leq 2$ have substantial support from the data (Burnham and Anderson

2002). Normalized AIC_c weights (w_i) were used to evaluate the strength of evidence for each model, given the data and sampling design used. In cases where there was substantial uncertainty in model selection results, parameter estimates were averaged across all models and standard errors were calculated using unconditional variances (Burnham and Anderson 2002:153-167). In such cases, I also estimated the relative importance of each covariate (X) using cumulative AIC_c weights ($w_+[X]$), calculated as the summation of AIC_c weights within a candidate set of models containing the covariate of interest (Burnham and Anderson 2002:167-169). Variables with good support have cumulative AIC_c weights near 1. All analyses were performed using program SAS (ver. 8.02; SAS Institute 2000), and all estimates are presented as means \pm SE.

Timing of dispersal. – Proportional hazards regression (PROC PHREG; SAS Institute, Inc. 2000) was used to model covariates relative to the age (number of days post-hatching) and Julian date (1 – 365) that radio-marked juveniles initiated dispersal. The PHREG procedure performs failure time analysis based on the Cox proportional hazards model (Cox 1972), which is commonly used to analyze the effects of covariates on the time until an event, such as dispersal, occurs (Muenchow 1986, Bennets et al. 2001, Kennedy and Ward 2003). I used six covariates to model the dates and ages when radio-marked juveniles initiated dispersal (Table 2.1). Prior to the analysis, I tested for collinearity between relative hatch date and dispersal date and detected a positive relationship ($r = 0.60$, $P < 0.001$, $n = 71$). Relative hatch date was therefore removed from the candidate set of models relative to dispersal date, yet this relationship was kept in mind. Model fit to individual observations and assumptions of proportionality were assessed using martingale and deviance residual plots (SAS Institute 2000).

Fidelity to the natal population. – I used the Kaplan-Meier estimator (Kaplan and Meier 1958) as a function of fidelity to the natal population during the first 11 months after fledging based on relocations of radio-marked hawks (Bennets et al. 2001). I defined the probability of fidelity during monthly time intervals (t) as the cumulative probability of detecting a radio-marked juvenile within the 10,800 km² aerial survey area from the time of fledging (time $t = 0$) through month 11 post-fledging (time $t = 11$; the following April-May period). A juvenile was assumed to have dispersed beyond this area at time t if it was not detected by aircraft. Thus, dispersed juveniles included hawks that moved beyond this area and lived, hawks that moved beyond this area and died, and hawks present within this area but not detected as a result of radiotransmitter malfunction or other unknown causes. Given the high probability of detecting a functioning radiotransmitter within the aerial survey area and the low likelihood of radio-failure within the first 300 days after attachment (Wildlife Materials, Inc.), I was confident that the majority of hawks not detected within the survey area had dispersed beyond the detection range of aircraft. The number of juveniles not detected (i.e., censored) during each time interval was multiplied by the estimated detection rate (0.91) to account for imperfect detection of radio-marked hawks. Fidelity was therefore estimated as: $1 -$ (the adjusted number of censored hawks at time t divided by the number of hawks available for detection at time t). I approximated the variance of this estimate using the delta method (Seber 1982). The numbers of juveniles available for detection at each time interval consisted of hawks remaining in the sample after individuals that died or shed their radiotransmitters in the previous time interval were subtracted. Since aircraft

surveys were not conducted regularly in 1998, juveniles radio-marked in that year were excluded from fidelity estimates.

Dispersal distance. – Variables measured relative to juvenile dispersal distances were: (1) natal dispersal distance, the straight-line distance from the natal nest to the nest of first breeding, (2) maximum dispersal distance, the straight-line distance from the natal nest to the farthest location recorded for a radio-marked juvenile, and (3) final dispersal distance, the straight-line distance from the natal nest to the final location recorded for a radio-marked juvenile. Estimates of natal dispersal distance were based on nestlings produced, banded, and recruited within the study population during 1991 – 2004, while estimates of maximum and final dispersal distance were based on relocations of radio-marked juveniles tracked during the transient movement stage of dispersal, 1998 – 2001. Dispersal distances based on radio-marked hawks excluded those juveniles who lost their radiotransmitters or died before initiating dispersal. I also estimated the “effective dispersal distance” (Shields 1983) of banded juveniles as the median natal dispersal distance divided by the mean inter-territory distance among 121 territory centers on the study area (3.8 km; Reynolds et al. *in review*). Effective dispersal distance provided a simple means of evaluating the number of territories or pairs between the natal site and the site of first breeding. I used generalized linear models (PROC GENMOD; SAS Institute 2000) to obtain maximum-likelihood estimates of natal dispersal distance as a linear function of six covariates (Table 2.1). Dispersal distances were log transformed to obtain a normal distribution of errors, applying an identity link function. Settling behavior was investigated by examining the previous year’s occupancy status of territories on which locally-produced hawks first settled to breed.

RESULTS

Timing of Dispersal

All 89 radio-marked nestlings successfully fledged from 48 nests in 36 different territories during 1998 – 2001. Young goshawks fledged between 28 June – 12 August (\bar{x} = 16 July) at 40.37 ± 0.43 days post-hatching (range = 30 – 50 days). Excluding hawks that died ($n = 8$) or prematurely shed their radiotransmitter ($n = 10$) prior to dispersal, juveniles spent an average of 46.34 ± 0.78 days in the natal territory (range = 33 – 66 days, $n = 71$). Annual means for the duration of this period varied from 43.67 ± 2.05 (95% CI = 38.93, 48.41) days in 2001 to 49.13 ± 1.70 (95% CI = 45.50, 52.77) days in 1998. The number of days spent in the natal area between fledging and dispersal did not differ between sexes ($\hat{\beta}_{\text{sex}} = 0.02$; 95% CL = -0.46, 0.50) or among brood sizes ($\hat{\beta}_{\text{brood size}} = -0.20$; 95% CL = -0.55, 0.16). Juveniles dispersed from their natal areas between 30 July – 15 September (\bar{x} = 30 August) at 86.54 ± 0.79 days of age (range = 71 – 103 days post-hatching). Adults were rarely observed with their young or near nests in the days prior to dispersal, suggesting that adults stopped associating with their young rather than aggressively displacing juveniles from natal territories.

Dispersal date. – The data supported annual differences in the Julian date of dispersal, as indicated by a comparison between the base model and a model incorporating a “year” effect (ΔAIC_c between models = 18.3; Table 2.2). The best-fitting proportional hazards regression model relative to the date of dispersal indicated that juveniles initiated dispersal earlier in the year when total prey abundance was high and precipitation was low (Table 2.2). Such conditions were experienced during the 2000 breeding season (Table A1), when juveniles dispersed an average of 10 days earlier in the

year as compared to 1998, 1999, or 2001. Model-averaged parameter estimates and unconditional 95% confidence intervals indicated that the Julian date of dispersal was positively influenced by prey abundance ($\hat{\beta}_{\text{prey}} = 0.60$; Wald 95% CL = 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% CL = $-0.16, -0.06$; Table 2.3). Brood size and body mass covariates received poor support with respect to dispersal date (Table 2.3).

Dispersal age. – There was substantial uncertainty in model selection results regarding the age of dispersal, and little evidence of annual variation in this parameter (Table 2.2). Of the factors examined relative to dispersal age, brood size received the greatest support ($w_+[\text{brood size}] = 0.83$), whereas total precipitation, relative hatch date, and sex effects received similar support (Table 2.3). Model-averaged parameter estimates and unconditional 95% confidence intervals indicated that dispersal age was negatively influenced by brood size ($\hat{\beta}_{\text{brood size}} = -0.45$; 95% CL = $-0.82, -0.07$; Fig. 2.2) and total precipitation ($\hat{\beta}_{\text{precipitation}} = -0.05$; 95% CL = $-0.09, -0.01$). Changes in total prey density ha^{-1} among years and individual differences in pre-fledging body mass appeared to have little influence on the age at which radio-marked juveniles initiated dispersal.

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 in the age of dispersal unduly biased the results, a separate analysis was conducted using one randomly selected young per brood (without replacement) following a method suggested by Massot et al. (1994). This brood randomization process was repeated over 60 iterations, resulting 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. However, cumulative AIC_c weights calculated under this approach revealed that brood size was most strongly related to dispersal age (w_+ [brood size] = 0.71, $\hat{\beta}_{\text{brood size}} = -0.39$; 95% CL = $-0.83, 0.06$).

Fidelity to the Natal Population

Of the 89 juveniles that were radio-marked in 1998 – 2001, I obtained dispersal data on 48. The remaining 41 juveniles either died ($n = 8$), shed their radiotransmitter prior to dispersal ($n = 10$), or were lost immediately following dispersal due to movement beyond the aerial survey area, radio-failure, or other unknown causes ($n = 23$). Maximum dispersal distances for radio-marked juveniles ranged from 2.7 – 79.1 km, and final dispersal distances ranged from 1.3 – 75.5 km (Fig. 2.4, Table 2.4). The mean age of juveniles at maximum dispersal distance locations was 175.4 ± 11.6 days post-hatching, and the mean age of juveniles at final dispersal distance locations was 218.5 ± 17.6 days post-hatching.

As indicated by the fidelity function (Fig. 2.3), the cumulative probability of detecting a radio-marked juvenile from aircraft within the aerial survey area by month 11 post-fledging was 0.28 ± 0.04 (95% CI = 0.19, 0.37). By November (5 months post-fledging), 70% of radio-marked juveniles had presumably dispersed beyond the aerial survey area, with a large pulse of dispersal beyond this area occurring during September and November (3 – 5 months post-fledging). Nearly all juveniles detected within the aerial survey area during fall and winter months were located in pinyon-juniper woodland

and shrub-steppe habitats at lower elevations. Increases in the fidelity function during months 8, 9, and 10 post-fledging indicated that some juveniles moved back into the detection area between survey flight intervals. By the following spring (10 months post-fledging) five juveniles had settled into temporary home ranges at lower elevations beyond the study area boundary while three others were relocated on breeding territories on the study area (D. Wiens *unpublished data*). By 2004, four radio-marked juveniles (two females and two males) had entered the local territorial population (without their radiotransmitters). One radio-marked female bred at two years of age in a nearby forest.

Local Settlement and Natal Dispersal Distance

During 1991 – 2003, 897 fledglings were produced on the study area, of which 614 (68.5%) were captured and banded. The remaining 283 fledglings could not be captured because their nests were not detected until after fledging or their nest trees were unsafe to climb. Of the 614 nestlings banded (302 females and 312 males), 69 (11.2%) were relocated as breeding adults within the study population by 2004; 39 (12.9%) females and 30 (9.6%) males. Nestling return rates based on ages at first recapture (2, 3, 4, or ≥ 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 4.21 ± 0.31 years for females (range = 2 – 9 years) and 3.93 ± 0.32 years for males (range = 2 – 11 years). Due to their elusive behavior, however, most adult goshawks could only be captured or resighted if they were breeding. As a result, the age of banded recruits when first detected as breeders may overestimate the age when hawks first occupied a territory. In examining the occupancy status of territories in the year prior to

settlement, 15 (22%) banded recruits settled on territories that were active the previous year, 11 (16%) settled on territories that were occupied, 38 (55%) settled on territories with unknown occupancy status (see *Methods*), and 5 (7%) settled on territories added to the study in the year of recruitment. Thus, 66% of juveniles produced and recruited to the local breeding population settled on territories where no breeding attempt had been made the previous year.

Natal dispersal distance within the study population ranged from 0.1 – 58.1 km (Fig. 2.4, Table 2.4). Estimates of effective dispersal distance indicated that the site of first breeding was typically four territories away from the natal site (Table 2.4); only 12 hawks (17.4%) settled within the first two territories adjacent to their natal site. Two females banded as nestlings on the study area successfully bred in nearby forests: one on the south rim of the GCNP (natal dispersal distance = 54.8 km; T. Bowden *personnel communication*), and one on the Dixie National Forest (natal dispersal distance = 106.9 km; R. Rodriguez *personnel communication*).

Factors affecting natal dispersal distance. – The best supported model of natal dispersal distance ($\Delta AIC_c = 0.00$, Table 2.5) was the base model (intercept only), evidence that *a priori* models containing ecologically relevant covariates were weak in predicting dispersal distance within the study population. Although natal dispersal distances for females tended to be slightly farther than males (Table 2.4), the effect of “sex” only received 14% of the AIC_c weight across the model set, indicating weak evidence of gender-dependent dispersal distance at a local scale ($\hat{\beta}_{\text{sex}} = -0.04$; Wald 95% CL = $-0.17, 0.08$). Models containing the singular effects of gender, body mass and brood size were somewhat competitive ($\Delta AIC_c < 2.00$, Table 2.5). However, I did not

consider these models to be informative since they failed to improve upon a base model containing no explanatory variables. Thus, it appeared that natal dispersal distances were distributed evenly throughout the study area relative to the ecological effects examined.

Inbreeding avoidance. – One female settled on her natal territory, constructing a new nest structure only 75 m from her natal nest. However, this female did not initiate breeding until eight years of age, at which point both her parents had disappeared from the study population. This was the single case in 605 breeding attempts over a 14-yr period where a goshawk settled on its natal territory, and no cases of close inbreeding between parent-offspring or full siblings were documented. There were six cases in which siblings from the same brood (four sets of sibling pairs and two sets of triplets) returned to breed in the same years, yet full siblings settled on territories spaced between one and seven territories apart (mean settlement distance between siblings = 10.4 km). Inbreeding avoidance data (i.e., opposite-sex parent known) were available for 63 of 69 banded recruits, precluding the inclusion of this effect in the dispersal distance model selection procedure due to a difference in sample size. There were 12 cases (19%) where dispersers settled to breed while their opposite-sex parent continued to occupy the original natal territory. Examination of these cases revealed that the presence of an opposite-sex parent in the year of recruitment was a poor predictor of dispersal distance ($\hat{\beta}_{\text{parent present}} = -0.04$; 95% CL = $-0.29, 0.19$). However, no hawk settled to breed within one territory adjacent of the natal site when an opposite-sex parent was still present, whereas four hawks settled to breed on the first territory adjacent to the natal site when the opposite-sex parent had disappeared or been replaced.

DISCUSSION

Four general patterns characterized natal dispersal of goshawks on the Kaibab Plateau: (1) inter-annual fluctuations in local environmental conditions (prey abundance, amount of rainfall) and social conditions at the natal site (number of siblings) most strongly influenced when individuals initiated dispersal, (2) most (72%) radio-marked juveniles dispersed beyond the Kaibab Plateau within their first year and few (11%) color-banded nestlings eventually returned to gain breeding territories within their natal population, (3) color-banded nestlings that successfully recruited to the local breeding population required at least two years to become territorial and tended to settle on territories between three and five territories distant from their natal site, and (4) variation in natal dispersal distances within the study population was best explained by a null model where dispersal distances were distributed evenly relative to individual, social, and environmental sources of variation. The results of this study suggest that natal dispersal behavior of goshawks on the Kaibab Plateau is driven by a combination of local environmental conditions, intraspecific competition for a limited number of breeding opportunities, and inbreeding avoidance.

Timing of Dispersal

Early dispersers are often found to 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 disjunct raptor populations (Walls and Kenward 1995, Byholm et al. 2003). Although I was unable to assess the influence of the timing of dispersal on natal dispersal distance, I found that the timing of dispersal was primarily a

function of local environmental conditions (food availability, weather) and social conditions of the natal area. My estimates of the mean age at fledging (40 days post-hatching), the mean amount of time fledglings spent in the natal area before dispersal (46 days), and the mean age at dispersal (87 days post-hatching) are similar to estimates reported for goshawks elsewhere (Kenward et al. 1993a, Kennedy and Ward 2003, Titus et al. 1994). Also similar to previous findings, there was little evidence of annual variation in the age of dispersal and a tendency for males to disperse at a slightly younger age than females. In contrast to these studies, I found substantial evidence of annual variation in the time of year juveniles initiated dispersal. The early dispersal date in 2000 coincided with the highest prey densities documented on the study area over a seven-year period (1994 – 2000; S. Salafsky *unpublished data*). However, annual changes in prey populations appeared to have little effect on dispersal age. The disparity between dispersal age and date was likely due to adults initiating the breeding process earlier in the year when food conditions were favorable, resulting in an earlier date of juvenile dispersal. This conclusion is supported by a strong negative correlation between annual estimates of median egg hatching dates and prey density ha^{-1} over a seven year period ($r_s = -0.82$, $P = 0.02$; R. Reynolds *unpublished data*). This conclusion is also in line with Kennedy and Ward (2003), who found that extra food supplied at goshawk nests in New Mexico did not influence the age of independence. Thus, physiological changes associated with the onset of nesting in the parents may dictate the time of year in which juveniles attain independence and disperse, whereas the age of dispersal may depend on fledgling growth and maturation rate (e.g., completion of feather growth), which provides

the capacity to initiate self feeding and increase foraging success (Kenward et al. 1993a, Kennedy and Ward 2003).

The age at which young dispersed in my study was highly variable among individuals, with some dispersing up to 30 days later than others. Social conditions at the natal site, the amount of precipitation near the time of dispersal, and gender were factors that best explained this wide range of dispersal behavior. Likewise, Kenward et al (1993b) reported that male goshawks dispersed earlier than females. In contrast, however, that study found that juvenile males stayed in the natal area longer when there were few other young in the brood. These findings suggests that intrabrood social patterns add to a juvenile goshawk's decision of how long to remain in the natal area, a pattern observed in several other bird species as well (Strickland 1991, Forero 1992, Ellsworth and Belthoff 1999). The support for the effect of total rainfall recorded during fledgling development (July – September) relative to the timing of dispersal showed that weather conditions can delay the onset of dispersal. Examination of daily precipitation records obtained from weather stations on the study area revealed that rainfall lasted for several days longer and was twice as heavy near the time of dispersal (late August to early September) in 1998 and 1999 relative to 2000 and 2001. The most likely explanation for the importance of this effect was that juveniles chose to remain within their natal areas during prolonged periods of severe weather, perhaps because heavy rainfall suppresses long-distance movement or reduces prey availability during the critical transition from dependent fledgling to independent juvenile.

Dispersal and Settlement Strategies of Juvenile Goshawks

A general finding in my study was that juvenile goshawks not only moved rapidly away from their natal territories during August – September of each year, but most moved well beyond the Kaibab Plateau shortly thereafter. However, as illustrated by the wide range of dispersal distances of radio-marked hawks during this stage, dispersal behavior among individuals was highly variable – some hawks moved away from the Kaibab Plateau immediately after leaving their natal territories while a small number gradually moved out of forested habitats into sagebrush plains at lower elevations. Further evidence that many juveniles dispersed beyond the Kaibab Plateau and did not return was provided by the relatively small number of color-banded nestlings that were later found breeding within the study population. Thus, both radiotelemetry and capture-recapture data were consistent in indicating that only a small fraction of locally-produced juveniles remained within the vicinity of their natal population to eventually gain local breeding territories.

Juvenile goshawks dispersing from their natal territories on the Kaibab Plateau are faced with the decisions of remaining on or near the natal population and waiting, perhaps several years, for a territory vacancy to arise or dispersing into the unfamiliar matrix of deep canyons and shrub-steppe desert that surround the study area to recruit elsewhere. Thus, the fragmented “sky island” nature of forests in northern Arizona and southern Utah appears to have created a dichotomy of spatial scales on which the natal dispersal process operates. Results based on radio-marked juveniles demonstrated that long-distance (> 80 km) dispersal movements were common and that fidelity to the natal population during the first year of life was low, suggesting that most juveniles choose to

emigrate, at least temporarily. In contrast, banding data illustrated that hawks produced and recruited within the local breeding population tended to settle between three and four territories distant from their natal site, suggesting that some individuals based their dispersal decisions on knowledge of their environment at a local scale. This pattern was also evident in a small number of radio-marked hawks during the early stages of dispersal, indicating that some juveniles began to explore their natal neighborhood at a relatively early age. However, since most radio-marked juveniles dispersed well beyond the study area immediately after leaving their natal territories, it is unlikely that this was a prevalent strategy used in prospecting for breeding sites or mates. Rather, there was some evidence that juveniles returned to the natal population in their first spring, when pair formation and courtship takes place on the study area. Goshawks are capable of breeding by the end of their first year, so return to the natal population could be used by immature hawks to assess territory vacancies and pair formation possibilities. This pattern of juvenile goshawks making long-distance movements shortly after leaving their natal territories and subsequently returning to the vicinity of their natal area after their first winter has been noted elsewhere (Ingraldi 1998), and may be a prevalent strategy used in prospecting for breeding opportunities in many other raptor species (Ferrer 1993).

Competition and settling behavior. – Long-distance dispersal movements, low nestling return rates, a delayed age at first breeding, a stable adult survival rate, and strong adult site fidelity are features consistent with the premise that the limited number of breeding territories within the isolated study area has resulted in a high level of competition for breeding opportunities. Life-history theory predicts that individuals not breeding when first reaching sexual maturity suffer a fitness loss in comparison with

individuals that begin breeding as early as possible (Wittenberger 1979, Sibly and Calow 1986). On the Kaibab Plateau, Wiens and Reynolds (*in review*) demonstrated that the age at first breeding for locally-produced goshawks averages between three and four years. Although several other studies have reported goshawks breeding in immature plumage (Reynolds and Wight 1978, Henney et al. 1985, Speiser and Bosakowski 1991), no territorial hawks in immature plumage have been observed in 605 nesting attempts over a 14 yr period on the Kaibab Plateau. A delayed age at first breeding is likely to arise from competition for territory vacancies, resulting from limited nesting space, food, or mates (Newton 1979). The predictions from this process include: (1) a high density of territories, (2) a large number of non-territorial floaters, (3) a rapid replacement of territorial hawks following mortality, and (4) replacement via older individuals. Although no information exists on the size of the non-territorial floater pool for this population, these other conditions appear to occur at higher levels on the Kaibab Plateau than reported elsewhere (Reich et al. 2004, Reynolds et al. 2004, Reynolds et al. *in review*, Wiens and Reynolds *in review*), suggesting that competition may act to regulate natal dispersal behavior and recruitment rates within this population.

Despite the fact that intraspecific competition for breeding vacancies appears to be high on the study area, the hypotheses that competition drives natal dispersal distance was not supported; dispersal distance was not related to the number of young produced in the year of fledging or the proportion of pairs breeding in the year of recruitment. The density and regular spacing of breeding territories on the Kaibab Plateau suggests that territories are roughly similar in size and occur in all available forest habitats. Combined with the previous finding that 25% of adult males and females fail to return to reclaim

their territory each year (Reynolds et al. 2004), this suggests that several territories within the first two rings of territories immediately adjacent to the natal site would be expected to have same-sex vacancies in the first year following fledging (i.e., the number of territory vacancies increases with the square of the distance dispersed; Waser 1985, Tonkyn and Plissner 1991). However, individual variation in breeding lifespan (Wiens and Reynolds *in review*) and potential differences among territories in habitat “quality” (Joy 2002) suggests that heterogeneity in competitive pressures among territories also exists on the Kaibab Plateau. Without accounting for this potential source of heterogeneity in the cohort-level covariates I used as indicators of competition, existing variation in dispersal behavior due to competition may have been obscured. Individual-based models (e.g., McCarthy 1997) where territories surrounding the natal site are assigned unique values of quality or competition (e.g., occupancy rate, number of young produced year⁻¹) may have provided better insight to the influence of competition on dispersal behavior.

Natal Dispersal Distance

The study area on the Kaibab Plateau is relatively large (hawks can disperse up to 60 km and still be within the study area boundary), contains nearly contiguous breeding habitat within a geographically isolated landform, and more than 85% of the total number of possible territories (150) have been located with most breeding hawks uniquely color-banded (Reynolds et al. *in review*). Thus, breeding goshawks and their young have a high probability of being detected and identified within the study area. This suggests that the negatively skewed distribution of local natal dispersal distances was not a result of

short-distance bias. However, color-banded hawks that permanently emigrate and settle in distant forests have very little chance of being detected, and tracking long-distance movements of radio-marked juveniles from aircraft was neither feasible nor financially efficient. As a consequence, there was likely a systematic short-distance bias in the dispersal distance distributions for both banded and radio-marked hawks when considered over a broad geographic scale. Because much of the natal dispersal process appeared to be operating on spatial scales beyond the limited scope of the study area, short-distance bias could have obscured gender-and/or age-related differences in natal dispersal that have been found in other raptor species (Newton 1983, Marti 1999, Forero et al. 2002, Forsman et al. 2002) and band recovery distances for juvenile goshawks in Finland (Byholm et al. 2003). Unfortunately, the low number of live or dead hawks detected beyond the study site precluded a quantitative assessment of the magnitude of short-distance bias (e.g., Koenig et al. 2000, Thomson et al. 2003). Inferences regarding natal dispersal behavior of goshawks are therefore highly dependent on the scale of investigation.

At a local scale, successful dispersers systematically distanced themselves between three and five territories away from their natal territory despite the fact that vacancies were likely to occur at shorter distances. A lack of support for the predictions of individual, social, environmental, and demographic models of dispersal suggested that dispersal distances were distributed evenly throughout the study area relative to these effects. Although the distances juveniles dispersed within the study area were not associated with the presence of the opposite-sex parent, no dispersers with parents known to still be on the natal territory in the year of recruitment settled within two territories of

their natal sites, while four hawks whose parents had disappeared from the study settled within one territory of the natal site. This evidence, coupled with the fact that no cases of close inbreeding were documented over a 14-yr period, clearly demonstrated that natal dispersal resulted in inbreeding avoidance. Genetic evidence from this population is consistent with this finding (S. Bayard de Volo *personnel communication*).

Beyond the local scale, I found a wide range of dispersal distances for both radio-marked (1.7 – 79.1 km) and color-banded (0.1 – 106.9 km) juveniles, reflecting the great mobility and variation among individuals in dispersal behavior. Wide ranging dispersal distances for juvenile goshawks has also been noted in Alaska (15.9 – 151.1 km; Titus et al. 1994) and in central Arizona (38.6 – 186.7 km; Ingraldi 1998). It is important to note, however, that these studies measured dispersal distances during the transient movement stage and do not reflect genetic dispersal between birth and breeding sites. The degree of isolation of breeding habitat on the Kaibab Plateau coupled with the dichotomous nature of dispersal decisions individuals are faced with suggests that the true distribution of natal dispersal distances for this goshawk population is bimodal. Two cases of successful emigration to surrounding forests and five juvenile band recoveries from beyond the study area (3 females and 2 males recovered at distances 52 – 442 km from their natal sites) provide further evidence that natal dispersal distances commonly extend beyond the Kaibab Plateau to other, perhaps distant, forests. Mortality rates increase as juveniles initiate dispersal, suggesting that there is considerable risk involved with long-distance movements through habitats that provide little cover for dispersers (Chapter One). Nonetheless, juvenile goshawks appeared to readily disperse from the familiar, contiguous forests on the Kaibab Plateau into the unfamiliar surrounding matrix of deep

canyons and open desert landscapes. Moreover, some juveniles remained within the xeric landscape surrounding the study area for several months during winter, demonstrating the hawk's capability of sustaining itself in environments not usually associated with this species. Clearly, much of this critical life history stage was carried out over long time periods at a broad geographic scale.

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 move to a different territory between successive breeding attempts (Reynolds et al. *in review*). The strong fidelity behavior exhibited by adults combined with the common long-distance movements made by radio-marked juveniles, an overall low return rate of hawks banded as nestlings, emigration of locally produced young to alternate forests, recoveries of dead juveniles from well beyond the study area boundary, and a high rate of gene flow among disjunct goshawk populations (Sonsthagen 2004) suggests that interpopulation movements are common. Movements of individuals into and out of subdivided populations can act to stabilize local population growth rates and decrease extinction probability (the "rescue effect"; Johnst and Brandl 1997, Bowne and Bowers 2004). If the stability of the regional goshawk population in the southwestern United States is maintained by inter-patch movements of juveniles, a reduction in transition rates among isolated breeding areas can lead to a situation where mortality exceeds that of productivity, resulting in a decline in persistence (Stacey et al. 1997). It is clear that external recruitment (i.e., immigration) can be expected to play a key role in regulating goshawk populations inhabiting a fragmented landscape.

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Table 2.1. Covariates used to model the timing of dispersal and natal dispersal distances of juvenile northern goshawks in Arizona.

Covariate	Level †	Response variable ‡	Description
Prey abundance	Cohort	T	Annual summation of red squirrel, Kaibab squirrel, northern flicker, and Steller's jay density ha^{-1} on the KNF, 1998 – 2001 (Salafsky 2004).
Total precipitation	Cohort	T	Cumulative precipitation (cm) during June – September, 1998 – 2001. Recorded daily at four weather stations on the Kaibab Plateau and averaged among stations to obtain annual estimates.
Proportion of pairs breeding (POPB)	Cohort	D	Number of active (eggs laid) territories on the study area divided by the number of territories under study in the first year of breeding, 1991 – 2000.
Population productivity	Cohort	D	Total number of young produced on the study area in year of fledging given 150 possible territories, 1991 – 2000.
Relative hatch date	Territory	T	Nest hatch date, backdated using the fledging age at time of capture (Boal 1994). Nest hatch dates were transformed to relative values with respect to annual median hatch dates, 1998 – 2001.
Brood size	Territory	T, D	Number of fledglings in the natal nest, including the focal individual.
Natal territory quality	Territory	D	Number of years the natal territory was active (eggs laid) divided by the total number of years the territory was monitored.
Body mass	Individual	T, D	Mass (g) of focal individual at time of capture (5 – 7 days pre-fledging).
Age at recruitment	Individual	D	Age (years) at first breeding for locally produced and recruited hawks.

† Biological level that each covariate was measured.

‡ T = Timing of dispersal, measured by the age (days) and Julian date (day 1 = 1 January) dispersal was initiated by radio-marked hawks, 1998 – 2001;

D = Natal dispersal distance, the straight-line distance between the natal nest and nest of first breeding for color-banded hawks, 1991 – 2004.

Table 2.2. Ranking of proportional hazards regression models used to examine variation in the timing of dispersal of radio-marked juvenile northern goshawks in northern Arizona, 1998 – 2001. Models are ranked from most plausible ($\Delta AIC_c = 0.00$) to least plausible; K is the number of estimable parameters; w_i is the Akaike weight. All models with $\Delta AIC_c \leq 2.50$ are listed, as well as the base model without covariates and a model containing a “year” effect for comparisons. See Table 2.1 for a description of covariates.

Covariates in model	Log likelihood	K	ΔAIC_c	w_i
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 2.3. Likelihoods, parameter estimates, and standard errors (SE) for covariates used to examine the timing of dispersal of radio-marked juvenile northern goshawks in northern Arizona, 1998 – 2001. Covariate likelihoods are Akaike weights summed across all models containing the covariate, and are indicative of variable importance. Parameter estimates are weighted averages from all candidate models using renormalized model Akaike weights. Standard errors were calculated from all candidate models using unconditional variances (Burnham and Anderson 2002). See Table 2.1 for a description of covariates.

Response variable	Covariate	Covariate likelihood	Parameter estimate	SE
Dispersal date	Precipitation	0.73	-0.109	0.025*
	Prey abundance	0.67	0.599	0.233*
	Sex	0.51	0.260	0.302
	Year	0.28	–	–
	Brood size	0.20	0.052	0.201
	Body mass	0.16	-0.001	0.002
Dispersal age	Brood size	0.83	-0.449	0.192*
	Precipitation	0.55	-0.048	0.023*
	Hatch date	0.50	0.038	0.025
	Sex	0.49	0.327	0.297
	Body mass	0.12	-0.001	0.002
	Prey abundance	0.12	0.132	0.254
	Year	0.03	–	–

* Unconditional 95% confidence interval does not include zero.

Table 2.4. Natal, maximum, final, and effective dispersal distances (km) for color-banded and radio-marked juvenile northern goshawks in northern Arizona. Natal dispersal distance was estimated from individuals produced, color-banded, and recruited to the local breeding population (1991 – 2004), and do not include two cases of emigration. Maximum and final dispersal distances were estimated from radio-marked individuals tracked during the transient movement stage of dispersal (1991 – 2001).

	<i>n</i>	\bar{x}	SE	Median	Min. – Max.	Effective dispersal distance
Females						
Natal	39	17.0	1.6	15.8	0.1 – 46.0	4.2
Maximum	23	27.2	3.6	24.4	2.7 – 75.5	
Final	23	22.4	3.8	22.0	1.7 – 75.5	
Males						
Natal	30	16.4	2.0	13.7	2.9 – 58.1	3.6
Maximum	25	23.3	3.5	19.0	5.9 – 79.1	
Final	25	19.4	3.4	14.6	1.3 – 61.6	
Sexes combined						
Natal	69	16.7	1.2	15.0	0.1 – 58.1	3.9
Maximum	48	25.2	2.5	22.9	2.7 – 79.1	
Final	48	20.8	2.5	16.1	1.3 – 75.5	

Notes: Natal dispersal distance = straight-line distance from the natal nest to the nest site of first breeding for locally-recruited hawks. Maximum dispersal distance = straight-line distance from the natal nest to the farthest location recorded for a radio-marked individual. Final dispersal distance = straight-line distance from the natal nest to the final location where a radio-marked individual lost its radiotransmitter, died, or disappeared. Effective dispersal distance was the median natal dispersal distance divided by the mean interterritory distance (3.8 km; *n* = 121).

Table 2.5. Ranking of generalized linear models used to examine variation in natal dispersal distances for locally recruited color-banded northern goshawks in northern Arizona, 1991 – 2004. Models are ranked from most plausible ($\Delta\text{AIC}_c = 0.00$) to least plausible; K is the number of estimable parameters; w_i is the Akaike weight. See Table 2.1 for a description of covariates.

Covariates in model	Log likelihood	K	ΔAIC_c	w_i
Base model (intercept only)	-6.61	2	0.00	0.25
Sex	-6.39	3	1.76	0.10
Body mass	-6.43	3	1.83	0.10
Brood size	-6.43	3	1.84	0.10
Age at recruitment	-6.60	3	2.17	0.09
Natal territory quality	-6.60	3	2.18	0.08
Population productivity	-6.61	3	2.19	0.08
POPB [†]	-6.61	3	2.19	0.08
Sex, Body mass	-6.38	4	4.00	0.03
Brood size, Natal territory quality	-6.41	4	4.05	0.03
Population productivity, POPB	-6.60	4	4.44	0.03
Sex, Brood size, Natal territory quality	-6.16	5	5.89	0.01
General model (includes all main effects)	-6.09	9	15.88	0.00
Year captured	-4.66	12	21.60	0.00

[†] Proportion of pairs breeding in year of recruitment.

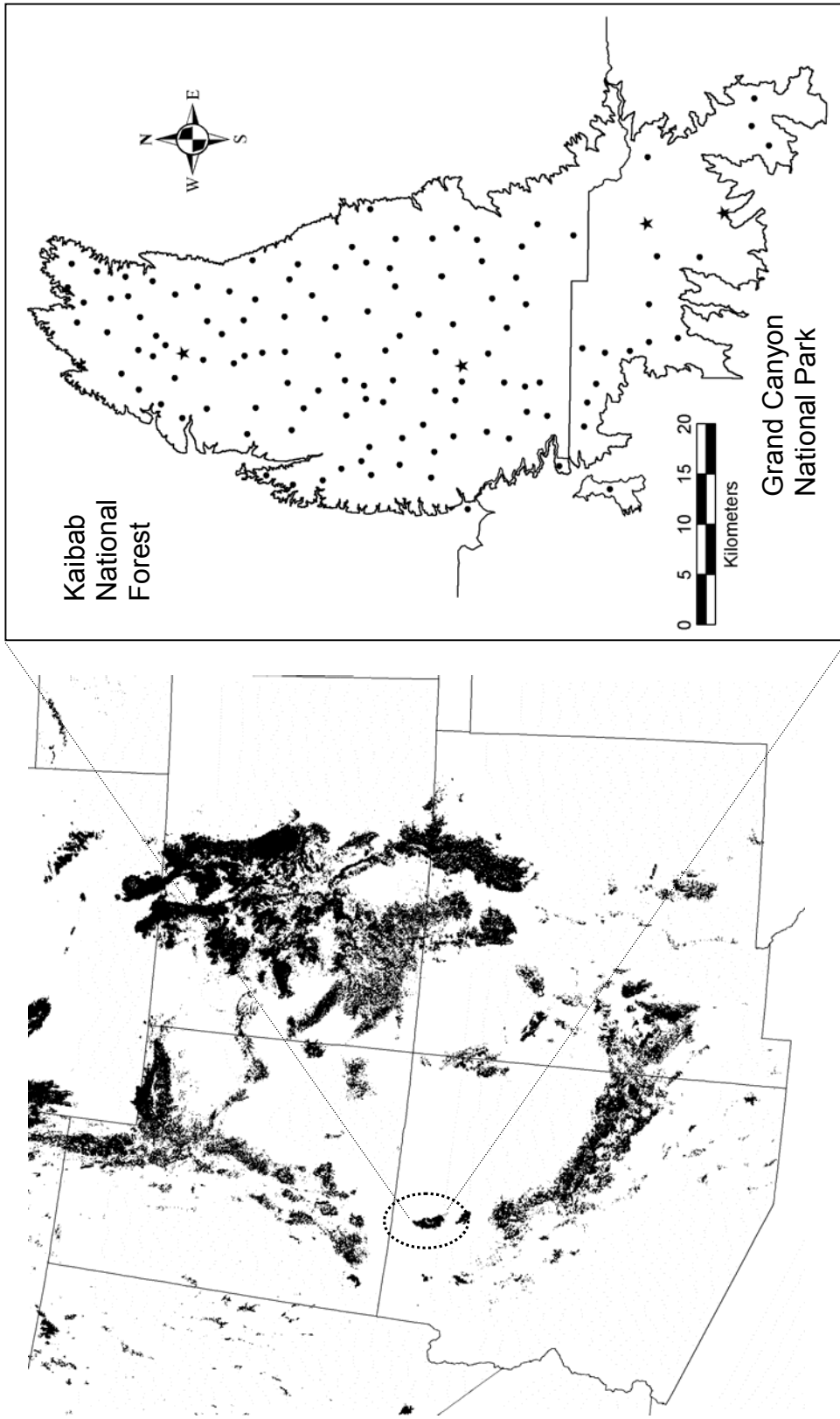


Figure 2.1. The regional distribution of forested areas in the Southwestern United States that support northern goshawks and the Kaibab Plateau study area showing the locations of 121 northern goshawk territories (dots), weather stations (stars), and the boundary between the Kaibab National Forest and the Grand Canyon National Park. The dashed ellipse illustrates the 10,800 km² aerial survey area in northern Arizona where signals from radio-marked juveniles could be reliably detected by aircraft.

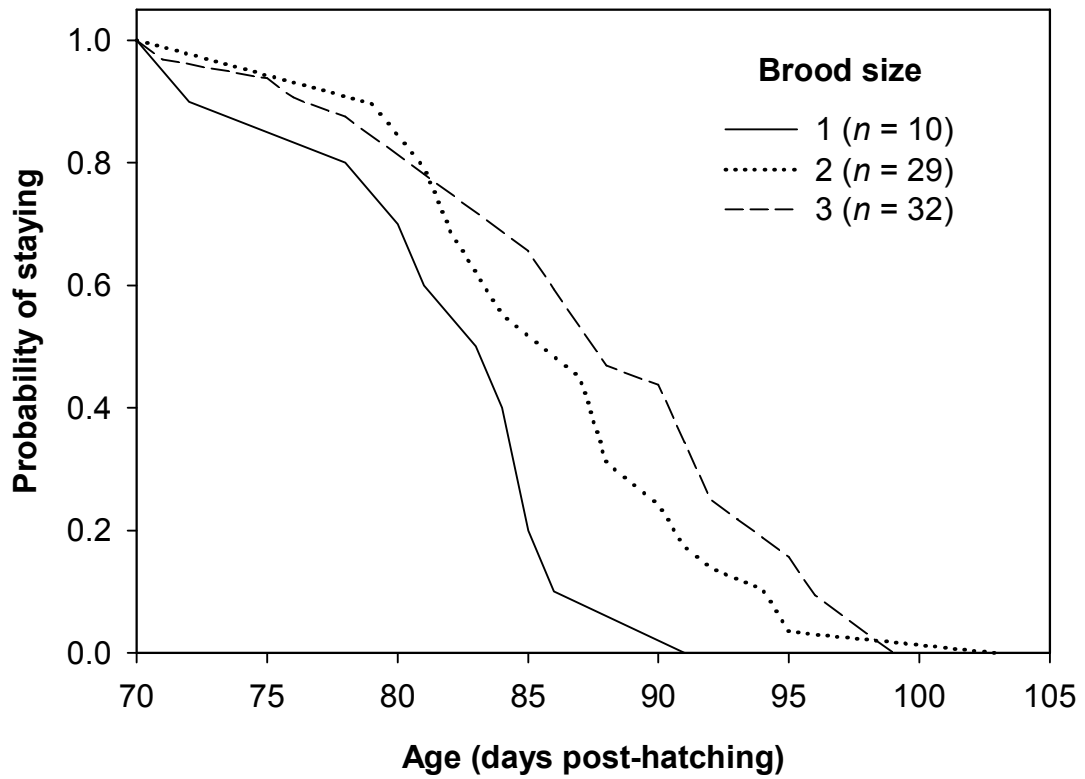


Figure 2.2. The probability of staying within the natal territory between 70 and 105 days post-hatching for individual juvenile northern goshawks within different brood sizes in northern Arizona, 1998 – 2001.

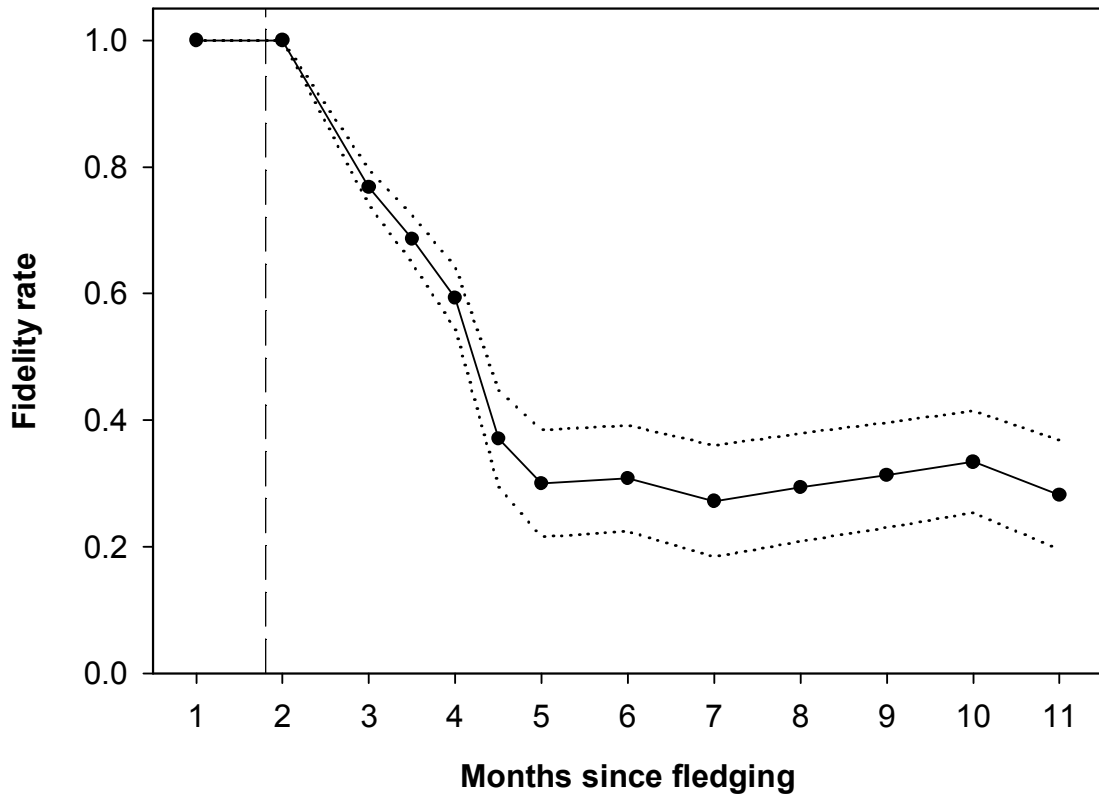


Figure 2.3. Kaplan-Meier estimates (\pm 95% CI) of northern goshawk fidelity to the natal population in northern Arizona during the first 11 months post-fledging, 1999 – 2001. Fidelity was estimated as the cumulative probability of detecting radio-marked juveniles from aircraft at monthly or bi-monthly intervals within a 10,800 km² aerial survey area that included the Kaibab Plateau. The dashed vertical line indicates the average age at which juveniles initiated dispersal from natal territories (= 87 days post-hatching). Increases in the function resulted from juveniles moving back into the aerial survey area or juveniles present within this area but not detected during previous survey intervals.

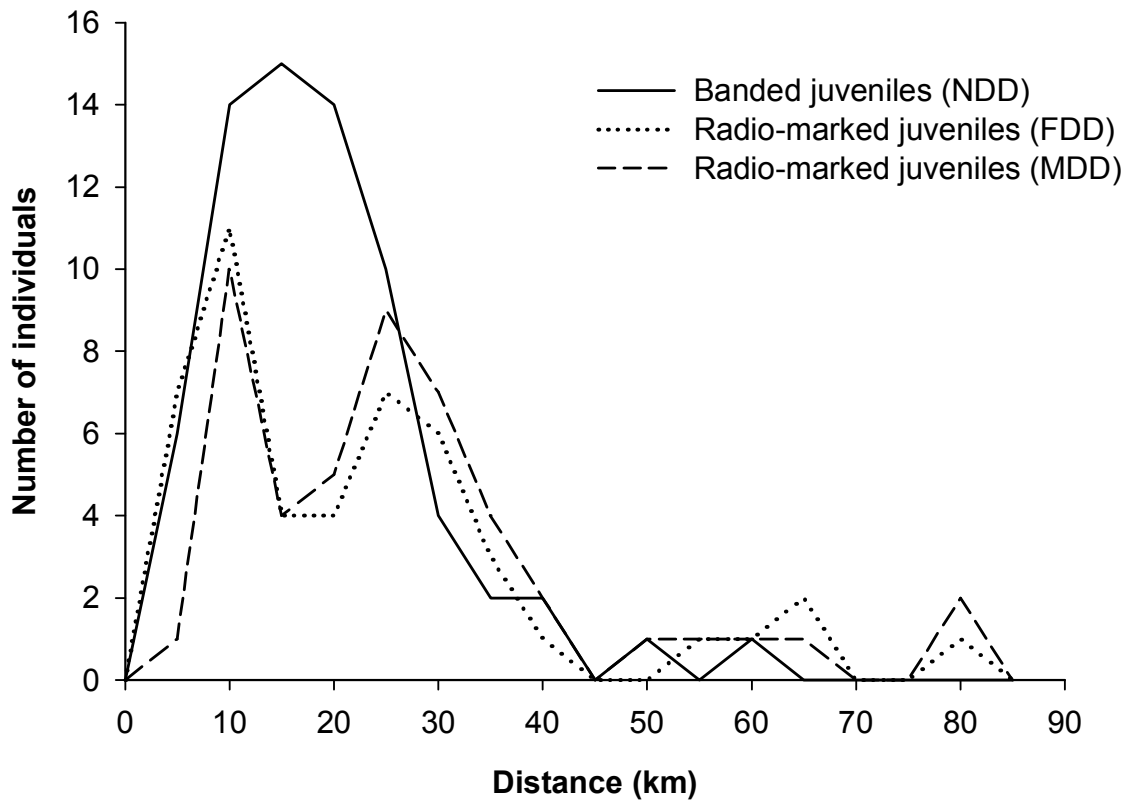


Figure 2.4. Distribution of dispersal distances for 69 color-banded and 89 radio-marked juvenile northern goshawks in northern Arizona, 1991 – 2004. Natal dispersal distance (NDD) was the straight-line distance between the natal nest and the nest site of first breeding for juveniles born and recruited on the Kaibab Plateau. Final (FDD) and maximum (MDD) dispersal distances were the straight-line distances between the natal nest and the final and farthest locations where radio-marked hawks were relocated, respectively.

APPENDIX

Estimation of environmental and demographic covariates

Prey abundance. – Bird and mammal prey species densities during 1998 – 2001 were obtained from Salafsky (2004). Density ha^{-1} was estimated during the goshawk breeding season for northern flicker (*Colaptes auratus*), Steller's jay (*Cyanocitta stelleri*), Kaibab squirrel (*Sciurus aberti kaibabensis*), and red squirrel (*Tamiasciurus hudsonicus*) prey species on the KNF using two sampling methods: line-transect distance sampling (1999 – 2001), and counts of prey species detections (1998; Salafsky 2004). Density was estimated by species using program DISTANCE (ver. 3.5; Buckland et al. 1993). A summation of annual density estimates from each individual prey species was used to obtain an estimate of total prey density ha^{-1} . These four prey species represented a significant proportion of goshawk diets on the Kaibab Plateau (Boal and Mannan 1994, Reynolds et al. 1994). To obtain prey densities and measures of precision for 1998 (prior to the initiation of distance sampling), predicted density values were generated under a linear regression relating prey species counts during 1994 – 2002 (the number of individual prey species detected during 100 minutes of observation) to line-transect density estimates from 1999 – 2002 (Salafsky 2004).

Total precipitation. – Daily precipitation records from July – September, 1998 – 2001, were obtained from three Remote Automated Weather Stations (RAWS) on the KNF, and one U.S. Weather Service weather station on the GCNP (Fig 2.1). Monthly precipitation totals were averaged for the four weather stations within the three-month period to obtain annual estimates of the total amount of precipitation on the study area.

Proportion of pairs breeding. – Estimated as the annual number of northern goshawk pairs breeding (laid eggs) divided by the number of pairs or territories under study during the previous year. Only territories studied during the previous year (i.e., the prior year's cohort of territories) were used to account for annual increases in the number of territories under study (Reynolds et al. *in review*).

Relative hatch date. – Hatching dates were calculated for each nestling banded on the study area, 1993 – 2003, by backdating from the estimated age at capture (estimated using a behavioral and photographic guide; Boal 1994). Nestling hatch dates were expressed as Julian dates and averaged for nests containing > 1 nestling. Nest hatch dates were transformed to relative values with respect to the annual median hatch date of the study population.

Population productivity. – Expressed as the predicted number of young fledged in each year, given 150 possible pairs or territories on the study area. Reynolds et al. (*in review*) estimated the possible number of breeding territories on the Kaibab Plateau by calculating exclusive circular areas for each pair of goshawks based on a radius equal to one-half the mean distance between territory centers (1.9 km) and dividing the study area (173200 ha) by the resulting exclusive area (1134 ha). This produced an estimate of 150 possible pairs or territories. I then calculated the expected total number of young that fledged on the study area during each year (\hat{F}_t) as:

$$\hat{F}_t = \left(\frac{N_t^{(A)}}{N_t^{(T)}} \right) N_t^{(E)} \times \text{observed mean number of young fledged per nest in year } t$$

where $N_t^{(A)}$ is the observed number of active territories observed in the previous years cohort of monitored territories (Reynolds et al. *in review*), $N_t^{(T)}$ is the number of territories under study in year t , and $N_t^{(E)}$ is the estimated number of possible pairs or territories within the study area (= 150). This procedure was likely to produce a reliable index of the number of fledglings produced each year since territories are regularly spaced, similar in size, and are likely to occupy all available breeding habitat on the Kaibab Plateau (Reich et al. 2004, Reynolds et al. 1994).

Table A1. Number of territories under study annually and values of environmental covariates used in modeling the timing of dispersal and natal dispersal distance of juvenile northern goshawks in northern Arizona. Environmental covariates are defined in Table 2.1. Estimates \pm SE are shown for total prey density ha^{-1} and total precipitation covariates.

Year	Number of territories monitored	Proportion of pairs breeding	Population productivity (expected number of young fledged) [†]	Median hatch date [‡]	Prey density ha^{-1}	Total precipitation (cm)
1991	37	0.97	292			
1992	64	0.87	152			
1993	82	0.77	161	155		
1994	88	0.22	36	162		
1995	99	0.50	85	163		
1996	105	0.40	73	161		
1997	106	0.30	64	166		
1998	109	0.51	154	160	1.94 ± 0.09	20.91 ± 1.15
1999	113	0.51	125	159	2.28 ± 0.10	22.92 ± 5.95
2000	120	0.53	160	152	2.72 ± 0.10	9.32 ± 3.28
2001	120	0.25	44	161	1.07 ± 0.04	11.36 ± 2.81
2002	121	0.18	20	163		
2003	121	0.08	11	162		
2004	121	0.41				

[†] Assumes 150 possible territories on study area.

[‡] Day 153 = June 1.