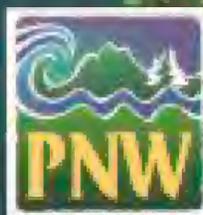
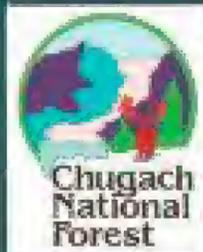


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Tables, one to a page, should be double-spaced throughout and be assigned consecutive Arabic numerals. Collect all figure legends on a separate page. Each illustration should be centered on a single page and be no smaller than final size and no larger than twice final size. The name of the author(s) and figure number, assigned consecutively using Arabic numerals, should be pencilled on the back of each figure.

Names for birds should follow the A.O.U. Checklist of North American Birds (7th ed., 1998) or another authoritative source for other regions. Subspecific identification should be cited only when pertinent to the material presented. Metric units should be used for all measurements. Use the 24-hour clock (e.g., 0830 H and 2030 H) and "continental" dating (e.g., 1 January 1999).

Refer to a recent issue of the journal for details in format. Explicit instructions and publication policy are outlined in "Information for contributors," *J. Raptor Res.*, Vol. 38(4), and are available from the editor. Submit manuscripts to J. Bednarz at the address listed above.

COVER: Northern Goshawk (*Accipiter gentilis*). Painting done in gouache by Michael Demain; for more information and images, visit www.michaeldemainwildlifeart.co.uk

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PREFACE

PROCEEDINGS OF THE INTERNATIONAL SYMPOSIUM ON THE ECOLOGY AND MANAGEMENT OF NORTHERN GOSHAWKS

CLINT W. BOAL¹

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For almost 20 years, the Northern Goshawk (*Accipiter gentilis*) has been the focus of considerable research effort, management and conservation planning, and litigation. This has been driven by conflict between conservation concerns and forest management practices. Due to increasing concern for the species, the symposium "The Biology and Management of Northern Goshawks," was held in conjunction with the Cooper Ornithological Society in 1993, with the goal of assembling the most current information available at that time.

Since that 1993 symposia, 10 years had passed during which a considerable amount of research had been conducted on goshawks, but a venue for sharing the information among researchers had not been made available. To provide an opportunity for researchers and managers to exchange information with which to assess the current state of knowledge on Northern Goshawks, a coordinating committee consisting of Steve DeStefano, Patricia Kennedy, Michael Goldstein, John Keane, and myself organized the "International Symposium on the Ecology and Management of Northern Goshawks." This symposium was held 4–5 September 2003, in conjunction with the 2003 Raptor Research Foundation Annual Meeting in Anchorage, Alaska. The symposium was well attended, with 32 papers presented. Topics included status reports; improvements in survey and monitoring methodology; information on population demography, food habits, habitat assessment, and winter ecology; and the use of genetic approaches to goshawk studies.

Given the obvious interest in goshawk ecology

and management, as indicated by attendance and number of papers presented at the symposium, there was a need to make this information more broadly available. We have attempted to do so with this issue of *The Journal of Raptor Research*, which includes peer-reviewed versions of some of the papers presented at the 2003 symposia. The lead paper is authored by a committee put together jointly by The Raptor Research Foundation and The Wildlife Society. This committee was charged with reviewing the status of Northern Goshawks in the western United States. This review provides a context for the rest of this issue in presenting an overview of the state of knowledge leading up to the symposium. Manuscripts following the lead paper are grouped topologically (i.e., Biology, Techniques, and Conservation).

All manuscripts in this issue went through the same peer-review process as required for regular issues of the *Journal*. For this issue, I served as a Coordinating Editor, with the symposia committee members serving as Associate Editors. I, the Associate Editors, and Jim Bednarz (Editor-in-Chief), would like to thank all of the individuals that served as peer-referees for the manuscripts in this issue. We would also like to acknowledge the U.S. Geological Survey Cooperative Research Units, the North American Falconer's Association, and the U.S. Forest Service Alaska Region and the Chugach National Forest, for providing support for publication of this issue of the *Journal*.

Finally, this issue of *The Journal of Raptor Research* is dedicated to the memory of Suzanne Joy, a friend and colleague to many of us working with goshawks. Please see the memoriam provided by Richard Reynolds on the following page.

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IN MEMORIAM
SUZANNE MERIDETH JOY
12 APRIL 1961–7 DECEMBER 2004

RICHARD T. REYNOLDS

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Suzanne Merideth Joy, microbiologist, photographer, animal ecologist, raptor biologist, tree climber extraordinaire, spatial analyst, and always a mentor, passed away on 7 December 2004 in Teramo, Italy. She was in Italy developing spatial models of the habitat of biting midge (*Ceratopogonidae*) vectors of bluetongue disease (*Reoviridae*) in cattle and sheep on behalf of the Italian government and the U.S. Department of Agriculture Animal and Plant Health Inspection Service (APHIS), her employer since 2003. Suzanne was born in Goose Bay, Labrador, but grew up in Virginia, Madrid (Spain), Minnesota, and Arizona. After graduating from Colorado State University with honors (Phi Beta Kappa, Phi Kappa Phi) and as the outstanding senior in Microbiology in 1983, she spent 2 yr with the Peace Corps in Kenya, East Africa. She was conversant in French, Swahili, and Kikuyu. Upon returning from Kenya, she worked as a radioimmunoassay technician for Hazleton Biotechnologies Company in Massachusetts and researched a pertussis vaccine for the Food and Drug Administration in Bethesda, Maryland.

In 1987, wanting to move from the confines of research labs to the natural habitats of birds and mammals, Suzanne returned to Colorado State University for a Master of Science (1990) degree in Fishery and Wildlife Biology. Her thesis topic was the feeding ecology and nest habitat of the Sharp-shinned Hawk (*Accipiter striatus*) in Colorado's Rocky Mountain forests. The experience and knowledge she gained while sampling for nesting *Accipiter*, collecting and identifying their food remains, and measuring the composition and structure of their forest nest sites was soon put to use in helping me establish in 1991 what would turn out to be an intensive and long-term study of the demography, genetics, and habitat of Northern Goshawks (*A. gentilis*) on the Kaibab Plateau, AZ. Before beginning a Ph.D. program at Colorado State University, Suzanne helped develop protocols for finding and trapping goshawks and managing budgets and large field crews through much of the Kaibab goshawk study. She loved being in the piney woods searching for and trapping goshawks, and making difficult tree climbs to goshawk nests to band their young. In 2002, Suzanne was awarded her Ph.D. by the Graduate Degree Program in Ecology at Colorado State University. Her dissertation, entitled "Northern Goshawk Habitat on the Kaibab National Forest in Arizona: Factors Affecting Nest Locations and Territory Quality," included a dynamic spatial simulation model that described the spatial dependence of goshawk nest locations on both territoriality and the availability of suitable nest sites. She identified the correlates of habitat quality by quantifying the relationship between the long-term reproductive performance of breeding goshawks and the composition and structure of habitats within their territories. Within a few months of completing her dissertation, Suzanne moved to APHIS, where she worked as a spatial analyst, and where once again she quickly became a star.

Suzanne Joy is survived by a son, Quinn, who shows his mother's love of nature, and husband, Vern Thomas, both of whom brought much additional joy to her life. Suzanne will be greatly missed by all those whose lives she touched. I was privileged to have known Suzanne as a student, employee, colleague, mentor, and above all, a friend.

The editors and authors of these proceedings dedicate the following contributions on the biology and conservation of the Northern Goshawk to Suzanne Joy's memory.

IN MEMORIAM
SUZANNE MERIDETH JOY
12 APRIL 1961–7 DECEMBER 2004



Suzanne Joy with captured Northern Goshawk in the Kaibab National Forest, Arizona.

TECHNICAL REVIEW OF THE STATUS OF NORTHERN GOSHAWKS IN THE WESTERN UNITED STATES¹

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ABSTRACT.—The U.S. Fish and Wildlife Service (FWS) was petitioned in 1997 to consider listing Northern Goshawks (*Accipiter gentilis atricapillus*) under the Endangered Species Act of 1973, west of the 100th meridian of the contiguous United States. In their 12-mo finding issued in June 1998, the FWS determined that listing this population as threatened or endangered was not warranted and based that decision on review of existing population and habitat information. Because the status of goshawks in the western U.S. continues to be contentious and the FWS finding has been challenged, the Raptor Research Foundation, Inc. and The Wildlife Society jointly formed a committee to review information regarding the status of the goshawk population in the contiguous U.S. west of the 100th meridian. The committee was requested to: (1) determine if there is evidence of a population trend in goshawks in the western U.S., excluding Alaska; (2) determine if there is evidence that goshawks nesting in the eastern and western U.S. represent distinctive, genetically unique populations; and (3) evaluate evidence for goshawk–habitat relations, including any association with large, mostly-unbroken tracts of old growth and mature forests. Based on existing information, the committee concluded: (1) existing data are not adequate to assess population trend in goshawks west of the 100th meridian; (2) existing analyses of phylogeography have not provided evidence of genetic differences among recognized (*atricapillus*, *laingi*) or putative (*apache*) subspecies, and the genetic distinctness of *atricapillus* goshawks in western and eastern North America is not known; and (3) at present, assessing the status of goshawks solely using distribution of late-successional forests is not appropriate, based on the current understanding of goshawk-habitat relations, although goshawks clearly use and often select late-successional forests for

¹ Summary of a report prepared by the Technical Committee on the Status of Northern Goshawks in the Western United States sponsored jointly by the Raptor Research Foundation, Inc. and The Wildlife Society. A copy of the complete report can be obtained from The Wildlife Society: (<http://www.wildlife.org>).

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nesting and foraging. We provide recommendations on information needs to assess status and population trend of goshawks in the western U.S.

KEY WORDS: *Northern Goshawk*; *Accipiter gentilis atricapillus*; *western U.S.*; *status*; *review*; *population trend*; *genetic structure*; *habitat relations*.

REVISIÓN TÉCNICA DEL ESTATUS DE *ACCIPITER GENTILIS ATRICAPILLUS* EN EL OESTE DE LOS ESTADOS UNIDOS

Resumen.—El Servicio de Pesca y Vida Silvestre de los Estados Unidos (FWS, por sus siglas en inglés) recibió en 1997 la petición de considerar a *Accipiter gentilis atricapillus* al oeste del meridiano 100 de los Estados Unidos (considerando sólo los estados contiguos) como un ave amenazada de acuerdo al acta de 1973. Luego de 12 meses, en junio de 1998 el FWS dictaminó que clasificar a esta población como amenazada o en peligro no era justificable, y basó dicha decisión en una revisión de la información poblacional y de hábitat existente. Debido a que el estatus de *A. g. atricapillus* en el oeste de los Estados Unidos es aún controversial y a que el hallazgo del FWS ha sido desafiado, la Raptor Research Foundation, Inc. y la Wildlife Society formaron un comité conjunto para revisar la información concerniente al estatus de la población de esta ave en los estados contiguos de los Estados Unidos al oeste del meridiano 100. Al comité se le solicitó que (1) determinara si existe evidencia de una tendencia de cambio en el tamaño poblacional de *A. g. atricapillus* en el oeste de E. U., excluyendo Alaska; (2) determinara si existe evidencia de que los individuos que nidifican en el este y el oeste de E. U. representan poblaciones distintivas, genéticamente únicas; y (3) evaluara la evidencia sobre las relaciones de *A. g. atricapillus* con el hábitat, incluyendo cualquier asociación con reductos grandes y no fragmentados de bosques maduros. Con base en la información existente, el comité concluyó que: (1) los datos disponibles son inadecuados para evaluar si existe una tendencia de cambio en el tamaño poblacional al oeste del meridiano 100; (2) los análisis de filogeografía existentes no han provisto evidencia que indique la existencia de diferencias entre las subespecies reconocidas (*atricapillus*, *laingi*) o putativas (*apache*), y no se conocen diferencias genéticas entre las poblaciones del oeste y el este de Norte América; y (3) en la actualidad, evaluar el estatus de *A. g. atricapillus* con base sólo en la distribución de bosques de estadios sucesionales tardíos no es adecuado de acuerdo al conocimiento actual de sus relaciones con el hábitat, aunque es claro que esta ave utiliza y a menudo selecciona bosques de sucesión avanzada para nidificar y forrajear. Ofrecemos recomendaciones en cuanto a la información necesaria para evaluar el estatus y las tendencias poblacionales de *A. g. atricapillus* en el oeste de Estados Unidos.

[Traducción del equipo editorial]

In 1997, the U.S. Fish and Wildlife Service (FWS) received a petition to list the Northern Goshawk (*Accipiter gentilis atricapillus*; hereafter referred to as goshawk) west of the 100th meridian of the contiguous United States under the Endangered Species Act of 1973. In its 90-d finding issued in September 1997 (United States Department of Interior [USDI] 1997), the FWS found that the petition “presented substantial information indicating that the listing of the Northern Goshawk as a threatened or endangered species in the contiguous United States west of the 100th meridian may be warranted” (USDI 1998). The FWS at that time initiated a status review (FWS 1998) for the goshawk, and in June 1998 issued its 12-mo petition finding (USDI 1998) and indicated that after “. . . reviewing all available scientific and commercial information, the Service finds that listing this popu-

lation as endangered or threatened is not warranted” (USDI 1998:35183).

The FWS used data from recent survey and monitoring that suggested goshawks had generally been located where intensive survey and monitoring efforts were implemented, and that goshawks remained widely distributed throughout their historical range. The FWS also reviewed existing habitat data and concluded that there was no evidence that habitat was currently limiting the goshawk population in the western U.S., and habitat was unlikely to limit this population in the foreseeable future. The petition for listing suggested that goshawks in the western U.S. were dependent upon large, unbroken tracts of late-successional forest, but the FWS concluded that there was little or no support for that assertion. Subsequent to release of the 12-mo finding by the FWS, several court chal-

lenges were submitted, both to the finding itself and to the process used to arrive at the finding.

Clearly, there is considerable concern for conservation of goshawk populations and their habitats in western North America. As some of the foremost professional societies concerned with conservation of wildlife in general, and raptors in particular, the Raptor Research Foundation, Inc. (RRF) and The Wildlife Society (TWS) formed a joint committee to review information regarding the status of the goshawk population in the western contiguous U.S. The purpose behind forming this committee was to provide an independent technical review of existing information related to goshawk status and to identify additional information necessary to assess population trend adequately. Specifically, the committee was requested to: (1) determine if there was evidence of a population trend in goshawks in the western U.S. west of the 100th meridian, excluding Alaska; (2) determine if there was evidence that goshawks nesting in the eastern and western U.S. represent genetically distinct populations; and (3) evaluate evidence for goshawk–habitat relations, including any association with large, mostly unbroken tracts of old-growth and mature forests. In addition, the committee was asked to evaluate existing information on population trend, genetic structure, and habitat relations and to identify types of information needed to assess the status of goshawks more conclusively in the western U.S., excluding Alaska. This manuscript summarizes the process used, information evaluated, and opinions of the Joint RRF-TWS Technical Committee on the status of Northern Goshawks in the western United States. A copy of the complete report can be obtained from TWS (<http://www.wildlife.org>).

METHODS

The scope of the committee's review and evaluation was restricted to pertinent technical information, comprised of peer-reviewed primary literature, theses, or unpublished technical information that the committee deemed credible and that related directly to the committee's charge. Information considered included that summarized in the FWS goshawk status review (USDI 1998) and related documents (e.g., FWS 1998), syntheses of the published literature (e.g., Squires and Reynolds 1997), and published and unpublished information not included in previous reviews and available to the committee through completion of its charge in 2003. Where possible, the committee reviewed primary literature and data, rather than relying solely on published or unpublished syntheses. Committee deliberations focused on three major areas: (1) population trends, (2) genetic

structure, and (3) goshawk–habitat associations. In addition, as a fourth area, the committee considered recent conservation efforts that focused on the possibility of using goshawk–habitat associations and habitat monitoring as a surrogate for population monitoring.

RESULTS

Population Trends. *Migration counts.* Migration counts have several major drawbacks as an index to the population size of goshawks in western North America. First, there is a nearly complete lack of knowledge of the geographic origin (e.g., breeding grounds) of goshawks observed at count locations. Second, migration routes for goshawks in western North America are poorly known (Squires and Reynolds 1997). Third, a primary limitation of migration counts is that changes in counts (FWS 1998) have an unknown relation to changes in the size of the target population (Kennedy 1998). Fourth, many migration counting stations, especially in western North America (FWS 1998), have small counts of migrating goshawks. Fifth, counting effort at some migration sites is variable through time and would need to be standardized if counts were to be used as an index to population size (Mueller et al. 1977, Bednarz et al. 1990, Bildstein 1998). Finally, continental counts included in the FWS status review (FWS 1998) are comprised primarily of counts of migrating goshawks from a single, more eastern site—Hawk Ridge near the western end of Lake Superior. For these reasons, migration counts at present are not a reliable index of goshawk population size in western North America.

Trend data. Breeding Bird Survey (BBS) data are inadequate to estimate population trends for goshawks across the western U.S., both because the number of routes on which goshawks were detected (<35) and the encounter rate of goshawks on these routes (mean detection rate <0.02 goshawks per route) were too low. Christmas Bird Count (CBC) data were also inadequate to estimate goshawk population trends at large scales because of low encounter rates. In addition, the CBC is conducted outside of the breeding season, thereby making the origin of observed birds uncertain. Thus, observed trends in CBC data cannot be related to the population of goshawks breeding in the western U.S.

Productivity. Existing data on goshawk reproduction in the western U.S. suggest that annual productivity (e.g., FWS 1998, Ingraldi 1998, Reynolds and Joy 1998) and nest success (Squires and Reyn-

olds 1997, FWS 1998, Ingraldi 1998, Reynolds and Joy 1998) are highly variable. Interpretation of studies of goshawk productivity is further confounded by small sample sizes (e.g., FWS 1998) and biases in estimates of breeding area occupancy and nest success. High annual variability in reproduction appears to be characteristic of all goshawk populations studied to date and is associated with annual variation in weather and prey (Kostrzewa and Kostrzewa 1990, Keane 1999, Doyle and Smith 2001). Finally, research on long-lived raptors suggests that some breeding areas consistently fledge more young than others, with the majority of young in the population being produced by a few females that occupy high-quality breeding areas (e.g., Newton 1989, 1991). Relations between and among productivity, habitat quality, population size, and trends in goshawks are not clear, and observed trends in productivity by themselves cannot be related to population status. As a result, it is difficult or impossible to discern any trends in goshawk reproductive success in the recent past over a wide geographic area. However, even if such temporal trends were discernable in the western U.S., such trends *per se* would not serve as an adequate foundation for concluding that similar trends would thereby exist in population size. Information on reproduction must be combined with survival and immigration–emigration data at appropriate scales to derive population growth rates (e.g., Maguire and Call 1993). To date, such information on goshawks in the western U.S. does not exist.

Distribution. Squires and Reynolds (1997) provided the most current delineation of known year-round and wintering ranges of goshawks in the western U.S. Contraction of historical breeding or wintering ranges could suggest a decline in population size (Kennedy 1997), but no historical or current evidence is available to suggest either a range contraction or expansion in the western U.S. Without reliable information on historical breeding and wintering ranges, knowledge of current ranges has limited utility to evaluate current population size or trends.

Encounter rates–detection surveys. Surveys for nesting goshawks in the western U.S. have been conducted in anticipation of proposed timber sales. While some land-management agencies adhere to established survey protocols (e.g., Kennedy and Stahlecker 1993, Joy et al. 1994), many have not, resulting in spatial and temporal variation in meth-

odology. Techniques that do not detect all goshawks present have not been validated by estimating density at multiple sites with known breeding densities (presumably all methods except complete searches of survey plots; even with complete searches, multiple years are probably necessary to detect all goshawk pairs present [DeStefano et al. 1994a, Reynolds and Joy 1998]). Thus, goshawk detection rates and estimated nest densities generally cannot be directly compared spatially, or even temporally at the same site.

Nest density and detection rates from surveys are also influenced by how study areas are defined and located (Smallwood 1998). The primary purpose of most goshawk surveys is not to estimate breeding densities or population parameters, but to locate nests for protection and to predict or mitigate the effects of proposed timber sales on goshawks. As a result, the locations of surveys for goshawks are generally not random with respect to potential goshawk habitat. Thus, the results from such surveys can appropriately be applied to the goshawk nests studied, but any inference beyond the sample is speculative. Comparing among studies is also inappropriate in some cases because of differences in survey techniques, interpretation, and reporting. Inconsistent definition and use of terms related to goshawk ecology (see the Appendix for proposed standard terminology) further confound comparisons among studies. These factors limit the utility of detection surveys as an index to goshawk densities and population trends in the western U.S. Existing data from detection surveys do not provide insight into goshawk population status beyond documenting occurrence of breeding birds at survey sites.

Demographic data. Demographic studies often focus on estimating λ (the annual rate of population growth) with Leslie-matrix projection models from estimates of age-specific fecundity and survival. However, even at the scale of local study areas, data necessary to estimate λ are generally inadequate for goshawks (e.g., DeStefano et al. 1994b, Reynolds and Joy 1998). While considerable information exists on fecundity, there are few estimates of adult survival, and data on juvenile survival are lacking (but see DeStefano et al. 1994b, Kennedy 1997, Ingraldi 1998, Reynolds and Joy 1998). With the possible exception of the ongoing long-term study on the Kaibab Plateau in Arizona (Reynolds and Joy 1998), studies have not been conducted for sufficient time periods with ad-

equate sample sizes to understand temporal variation in adult survival and fecundity. The proportion of adults attempting to breed has been estimated in only a few places (Reynolds and Joy 1998). Among-year movements, especially by adult female goshawks to different nesting areas, add complexity to estimating demographic parameters, because without radiotelemetry data, the fate of these birds will often be unknown (Flatten et al. 2001). Production of young (to fledging) has been estimated in a number of studies, but only in a few locations have these data been coupled with survival information. Finally, information regarding immigration and emigration of juvenile and adult goshawks is lacking. Thus, while demographic studies have significantly increased understanding of goshawk population dynamics, no studies to date have generated adequate empirical stage-specific estimates of survival and fecundity for estimating λ with matrix projection models at local scales, and demographic data are unavailable at larger scales, making it impractical to estimate λ for the western U.S. Recent alternative models for estimating λ (e.g., Pradel 1996), or models for assessing trends in adult survival, have not been applied to existing goshawk data, but they should be explored.

Direct estimation of trends in breeding population size on local study areas has been hampered by problems associated with searching large areas for nests, difficulty in detecting pairs that are present but not nesting, edge effects, limited methodology available to estimate density, and spatial and temporal variation in search effort and protocols. In addition, size and location of study areas can affect estimation of population size (Smallwood 1998) because study areas are seldom chosen randomly. Thus, similar to estimating population growth rate based on demographic rates, estimating population trends on the scale of local study areas has had limited success.

Trends in density. Breeding densities of goshawks vary considerably across their geographic range; densities in 10 published studies in North America ranged from 0.03–11.9 pairs or nests per 100 km². In the western U.S., excluding Alaska, densities in seven published studies ranged from 1.4–11.9 pairs or nests per 100 km² (Squires and Reynolds 1997, Reynolds and Joy 1998, FWS 1998, Bosakowski 1999). Goshawk density (number of breeding pairs/area) reported in unpublished work summarized by the FWS (1998) fell within the same

range. Comparison among existing estimates of breeding density are confounded by a number of factors, including variation among studies in definitions of densities, territories, pairs, “active” nests, and occupied nest areas (see Appendix). In addition, the small number of published studies of goshawk breeding density ($N = 7$), the limited duration of most studies (median = 2.0 yr; Squires and Reynolds 1997), and high temporal variability in reproduction preclude reliable assessment of temporal trends in breeding densities of goshawks across the western U.S. The logistical problems of determining density in goshawks and possible methodological bias in selecting nest search areas for some studies (Kennedy 1997, Squires and Reynolds 1997, Smallwood 1998, Trexel et al. 1999) may further confound analyses of breeding densities as an index to population size. Moreover, densities of the nonbreeding segment of goshawk populations (floaters) and their demographic role are entirely unknown (Hunt 1998). Theoretically, a population decline may occur without concurrent decline in nesting densities if floaters are available to fill vacant breeding territories. Declines in nesting density may only then become apparent after the floater population has been exhausted (Franklin 1992). Currently, existing data on nesting and breeding densities are not adequate to assess goshawk population trends across western North America.

Historical records. There have been no systematic efforts to synthesize existing historical goshawk records across North America, and only limited information is available for portions of their range (e.g., Grinnell and Miller 1944); therefore, historical data were not available to the FWS for assessing change in goshawk distribution in the western U.S. Use of historical records for assessing distributional change has limitations because natural history collections are not random or systematic samples from across the historical range of a species (Shaffer et al. 1998). The number of historical goshawk records represented in museum collections is also limited because of the relative rarity of goshawks, their secretive behavior, and predominant occurrence in remote locales. Because of these limitations, historical records are not available for assessing historical ranges and current changes in distribution for goshawks in all regions of North America. Data necessary to assess historical goshawk distribution across western North America have not been collected, and thus contrasts be-

tween historical and current ranges of goshawks in the western U.S. are only possible for limited areas.

Genetic Structure. *Observed morphological patterns.* Two subspecies of goshawks (*A. g. atricapillus*, *A. g. laingi*) were recognized in the western U.S. and southeast Alaska by the American Ornithologists' Union in 1957 (AOU 1957). *A. g. atricapillus* occurs across nearly all forested regions of the western U.S., Canada, the western Great Lakes region, and the northeastern U.S. *A. g. laingi* occurs from Vancouver Island, insular British Columbia, to the Alexander Archipelago of southeastern Alaska (Whaley and White 1994). A third, putative subspecies (e.g., Stresemann and Amadon 1979), *A. g. apache*, occurs in the mountains of southern Arizona, but was not recognized by the AOU (1957) and is currently not recognized by most taxonomists (Whaley and White 1994). Morphological differences between eastern and western *A. g. atricapillus* have not been demonstrated in the literature (see Whaley and White 1994). Ridgway (in Baird et al. 1875) speculatively divided eastern (*Astur atricapillus atricapillus*) and western (then termed *Astur atricapillus striatulus*) goshawks, but others, including Taverner (1940), have not made this distinction. Sample sizes have been small in the analyses of eastern *A. g. atricapillus*, or the analyses were confounded by migrants (Mueller et al. 1976). Since Whaley and White (1994), there have not been any in-depth analyses of *A. g. atricapillus* across the continent using larger sample sizes.

Genetic population structure. There are few publications on the phylogeography of DNA in North American goshawks. In an unpublished report, Gavin and May (1996) did not detect genetic differences among goshawks representing *A. g. atricapillus*, *A. g. laingi*, and *A. g. apache*. More recently, Sonsthagen et al. (2004) used eight microsatellite DNA loci and mitochondrial DNA control-region sequence data to assess population structure of goshawks breeding in Utah. Their pairwise comparisons using microsatellite markers found no differentiation among the sampled sites ($N = 49$ birds) from northern to southern Utah. Overall, they found low levels of population structuring.

During the 1990s, numerous goshawk tissue samples were collected from Arizona to Alaska, and many of these samples have been analyzed to evaluate genetic variation in North American goshawks. Preliminary data from markers assayed from goshawks nesting in Alaska (coastal and interior), British Columbia (coastal and interior),

and Utah suggest that genetic differences in populations will be found as analyses are completed.

Western goshawks as a discrete population. In the context of the Endangered Species Act, a discrete population of a vertebrate species is one that satisfies at least one of the following conditions: (1) it is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors or (2) it is delimited by international boundaries within which differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms exist that are significant in light of section 4(a)(1)(D) of the Act (USDI and United States Department of Commerce 1996). Goshawks that breed in the western and eastern U.S. are part of a continuous population that extends across Canada and into interior Alaska but that is segmented by international boundaries (Squires and Reynolds 1997). It was beyond the scope of our charge to assess differences in management of goshawks in the U.S. and Canada, and there is currently little evidence of biological differences between goshawks in the eastern and western U.S. Therefore, it is unclear whether goshawks breeding in the western and eastern U.S. should be viewed as discrete population segments under federal threatened and endangered species policy.

Habitat Relations. *Long-term forest-management patterns.* It is likely that past and current forest management on public and private lands in the western U.S. has resulted in existing landscapes that are quite different from historical landscapes and their natural range of variation. It was beyond the scope of our charge to project the condition and attributes of future forested landscapes in the western U.S. Clearly, though, forested landscapes that contain goshawk habitat will be necessary to support goshawk populations in the future. In 1998, the FWS (USDI 1998) concluded that current and projected land-management practices in the review area would not result in landscapes incapable of supporting goshawks. This conclusion was predicated on both an assessment of future landscape condition and goshawk response to that condition, both of which were speculative.

Status of prey populations. Across western North America, goshawks feed on a variety of prey species, including birds and mammals from small to moderately large in size. Passerines (primarily corvids and thrushes [Turdidae]), woodpeckers (Picidae), Galliformes (grouse, ptarmigan, quail),

tree (*Sciurus* spp.) and ground squirrels (*Spermophilus* spp.), and lagomorphs (including snowshoe hares [*Lepus americanus*] and cottontail rabbits [*Sylvilagus* spp.]) are the major prey species. Almost all information (but see Beier and Drennan 1997, Drennan and Beier 2003) regarding prey use of goshawks is derived from studies of nests during the breeding season, and it is based on observations of prey delivered to nests, prey remains collected at nests, or pellets and remains collected at nests or plucking perches. These data may primarily reflect prey selection by male goshawks, which provide most of the food during pre-incubation through fledging. Further, most studies report on the frequency of prey species pooled across years. Only a few North American studies have assessed annual variation in diet and related it to variation in demographic parameters, such as reproduction (e.g., Keane 1999, Maurer 2000, Doyle and Smith 2001). Diets during winter may differ from diets during the breeding season (e.g., Widén 1989) because of prey hibernation, goshawk migration, or changes in use of vegetation types by prey species or goshawks in different bioregions. Little information exists on winter diets for goshawks in western North America (Squires and Reynolds 1997).

In the western U.S., most diet studies report that prey associated with late-successional forests are important (Reynolds and Meslow 1984, Kennedy 1991, Reynolds et al. 1992, Keane 1999, Maurer 2000, Lewis 2001), although species associated with other forest age classes or vegetation associations are also used (e.g., Reynolds et al. 1992, Boal and Mannan 1994, Doyle and Smith 1994, Younk and Bechard 1994, Patla 1997, Watson et al. 1998). Although a large number of species are usually recorded in overall summaries of prey species, particular species or a smaller suite of prey species make a relatively greater contribution to total biomass and have been associated with temporal variation in reproduction. Further, these important prey species, or suites of prey species, vary among bioregions or major vegetation types (Reynolds et al. 1992, Watson et al. 1998, Keane 1999, Doyle and Smith 2001).

Although considerable information exists about diet of goshawks during the breeding season, the relations between goshawks and prey abundance, availability, and distribution in the landscape are difficult to study and will not be well understood in the near future, at least at the scale of the western U.S. Considerable additional information re-

garding the impacts of future forest conditions in the western U.S. on goshawk prey species is required before goshawk population responses to trends in prey abundance resulting from forest-management practices can be assessed.

Association of goshawks with habitat at multiple spatial scales. Goshawk-habitat relations have been investigated at a number of spatial and temporal scales. There is general agreement among biologists that goshawk breeding habitat can be discussed in terms of three nested spatial scales: a nest stand (and alternative nest stands; 10–12 ha), a post-fledging area (PFA; 120–240 ha), and a foraging area (1500–2100 ha; Reynolds et al. 1992). Considerable information exists regarding characteristics of nest trees, but comparatively fewer data exist on habitat use outside of the breeding season.

Breeding Season. *Nest tree.* Goshawks build and use nests in a variety of conifer and hardwood tree species. They often use trees that are among the larger or largest in the stand (e.g., Keane 1999). Common nest-tree species include ponderosa pine (*Pinus ponderosa*) in the southwestern U.S., Douglas-fir (*Pseudotsuga menziesii*) and other conifers in the Rocky Mountains, Sierra Nevada, Pacific Northwest, and Alaska, and aspens (*Populus* spp.) in portions of the Rockies and interior Alaska. Squires and Reynolds (1997:6) concluded that goshawks “tend to nest in a relatively narrow range of vegetation structural conditions,” suggesting that tree species used for nesting is secondary to structural characteristics of the tree and surrounding vegetation.

Nest stand. A nest stand is that area covered by a forested patch consisting of trees often characterized by similar size, species, and spacing, in which a goshawk nest is located. Studies of nests and nest stands have been widespread, covering much of the goshawk’s range in the western U.S. Stands where tree species such as ponderosa pine or lodgepole pine (*P. contorta*) predominate and stands of mixed conifer species are used for nesting. Aspen stands in mountain valleys and draws in the Great Basin of Nevada and Oregon are also used for nesting. Most studies of goshawk nest stands have focused on forest structure (e.g., Reynolds et al. 1982, Moore and Henny 1983, Hayward and Escano 1989, Daw et al. 1998) in the vicinity of the nest tree and indicate that large trees and well-developed canopies are important. The species of tree used for nesting or those that constitute the nest stand appear to be less critical. Goshawks

usually nest in stands of late-successional forest, where trees are often larger than those of other forested stands nearby (e.g., Reynolds et al. 1982). Habitat composition within these nesting stands may include single canopy or multi-story layer components. Forest management that fragments and reduces the extent and area of stands suitable for nesting in a breeding area may result in its less consistent use for nesting over time (e.g., Woodbridge and Detrich 1994, Desimone 1997).

Across the western U.S. and Alaska, many studies have documented goshawks selecting nest stands that are more mature or consist of late-successional forest compared with random assessments of nearby forest habitat, irrespective of scale of analysis (e.g., Moore and Henny 1983, Crocker-Bedford and Chaney 1988, Desimone 1997, Keane 1999). Some studies have suggested that high-canopy closure is one of the more uniform characteristics of goshawk nest stands (Hayward and Escano 1989, Keane 1999), and others have documented that a higher percent canopy closure was associated with a higher probability that goshawks would nest in a stand (Crocker-Bedford and Chaney 1988). Canopy closure in nest stands is variable across North America, and in some regions of the western U.S. and Alaska mean canopy closure near the nest might be rather low (ca. 50% in parts of Oregon and Washington [McGrath 1997] and southeastern Alaska [Iverson et al. 1996]). Differences in sampling methods probably account for some of this apparent inconsistency because measurement of canopy closure has not been conducted consistently among studies (Crocker-Bedford and Chaney 1988). However, even where canopy closure around a nest area is apparently low, it is still generally higher than the surrounding portions of the stand or other nearby stands. This suggests that high-canopy closure relative to the range of available canopy closure might be more important than absolute canopy closure, at least above some minimum threshold.

Why goshawks select stands with relatively larger trees and higher canopy cover is not known. Potential hypotheses include: (1) increased protection from predators, (2) increased food availability, (3) reduced exposure to cold temperatures and precipitation during the energetically stressful pre-laying period in late winter–early spring, (4) reduced exposure to high temperatures during the summer nestling period, (5) reduced competition with raptor species that nest in more open envi-

ronments (e.g., Red-tailed Hawk [*Buteo jamaicensis*]), or (6) increased mobility because of reduced understory vegetation in mature stands.

Use area–home range. How goshawks use habitats away from their nests during the nesting season is not well understood. Methods to evaluate goshawk–habitat associations at the home-range scale fall into a few different categories, including: (1) habitat evaluations based on circular areas centered on the nest that are often made using aerial photography or other remote sensing methods and Geographic Information Systems, (2) habitat-selection studies using radiotelemetry, (3) evaluating hunting habitat use with radiotelemetry and direct observation, and (4) evaluating patterns associated with habitat disturbance and logging versus frequency of nesting.

Most studies of habitat use based on a nest-centered evaluation have loosely linked the scale of measurement to a nest stand, PFA, or mean home-range size. In general, the preponderance of late-successional forest in the landscape decreases as the scale increases (i.e., as one moves from nest stand to PFA to foraging area; Iverson et al. 1996, Finn 2000, Daw and DeStefano 2001, Finn et al. 2002, McGrath et al. 2003).

Radiotelemetry studies to evaluate habitat use within the home range during the nesting season have found that goshawks selected for late-successional forests even beyond their nest stands (Widén 1989, Austin 1993, Bright-Smith and Mannan 1994, Hargis et al. 1994, Iverson et al. 1996, Beier and Drennan 1997). Goshawks used larger stands of late-successional forest than was available in southeastern Alaska (Iverson et al. 1996, Pendleton et al. 1998) and Sweden (Widén 1989); in Arizona, some goshawks selected for late-successional forest >200 m from openings (Bright-Smith and Mannan 1994). In California, goshawk locations had greater basal area, canopy cover, and more large trees than did random points (Austin 1993, Hargis et al. 1994). These results suggest a fine-scale selection for larger stands of mature forests within goshawk nesting-season home ranges.

Presumably, vegetative characteristics associated with foraging sites influence prey availability. For example, Beier and Drennan (1997) concluded that goshawks in Arizona did not select foraging sites based on prey abundance; rather, they selected sites based on vegetation structure. Goshawk foraging locations had a higher canopy closure, greater tree density, more large trees, and fewer

shrubs and saplings than random reference plots. There was also selection for dense stands with high canopy closure that were rare on their study area. Widén (1989) had previously reported that in Europe, hunting sites were associated with habitat structure and did not seem to be related to absolute prey abundance. A number of authors have noted that foraging sites typically are characterized by open space between the bottom of the canopy and the top of the shrub layer (e.g., Reynolds 1989, Widén 1989, Crocker-Bedford 1990, 1998, Beier and Drennan 1997) and have speculated that this space may increase prey vulnerability by providing a flight path for foraging goshawks.

Results of several studies suggest that goshawks are more likely to reoccupy breeding areas within landscapes that have larger proportions of late-successional forest, compared with landscapes that have smaller proportions of these forests (Ward et al. 1992, Woodbridge and Detrich 1994, Daw 1997, Patla 1997, Finn 2000, Finn et al. 2002). Widén (1997) concluded that intensive forest management was the prime factor in reductions in goshawk breeding density across nine study areas in Scandinavian boreal forests.

Assessing habitat use at the home-range–use area scale has several important limitations, including small sample sizes, variation in fecundity, and the small range of vegetation types in which these studies have been conducted. In addition, considerable variation likely exists among home range–use areas, with some use areas consistently producing young, and others only occasionally producing young (Newton 1989, Joy 2002, McClaren et al. 2002). Thus, habitat evaluations that are not related to productivity and population dynamics might have limited utility. Including use areas that rarely produce young in these evaluations might make it difficult to identify characteristics of use areas associated with high-quality habitat. Finally, habitat use at the home-range scale has been assessed in only a few vegetation types, limiting inference to scales below that of the western U.S. Clearly, additional information is necessary to better assess habitat use patterns at the scale of home range–use areas.

Non-nesting season. There are few studies of goshawk–habitat associations during the non-nesting season in North America. Iverson et al. (1996) examined year-round habitat selection by radio-tagged adult goshawks in southeastern Alaska within their seasonal use area and found no differences

in habitat selection between the nesting season and non-nesting season. Adult goshawks selected for larger size classes of late-successional coniferous forest compared with other habitat cover types. Beier (1997) and Drennan and Beier (2003) examined winter foraging habitat of adult goshawks in northern Arizona and found that goshawk locations were in areas with a slightly higher medium-size tree density and higher canopy cover than contrast plots. Females remained in the ponderosa pine vegetation type, and most males moved to pinyon–juniper (*Pinus-Juniperus*) woodlands. Some goshawks move to open or scrub habitats in the winter (Squires and Ruggiero 1995), while others seem to remain in forested areas, making it difficult to generalize across populations in terms of goshawk winter-habitat use.

Summary of goshawk habitat use. Goshawks have broad geographic and elevational distributions in North America and can be found in many different forest types and forest stand conditions (Squires and Reynolds 1997). Goshawks have relatively large home ranges, are able to move great distances—especially during times of low prey abundance, and use a wide variety of prey species across the range of landscapes in which they occur. Goshawks tend to nest in forest stands with specific structural characteristics, such as stands with large trees and moderate to high canopy closure that is high relative to the range of available canopy closure. Goshawks forage in a variety of habitats, ranging from early-successional forests, to mature forests, to open habitats adjacent to forested habitats. During the breeding season, late-successional forests appear to be used predominantly for foraging, although some of the prey taken by goshawks use young forests and open habitats.

Goshawk breeding habitat can be discussed in terms of three nested, spatial scales: a nest stand (and stands containing alternative nests), within a PFA, and within a foraging area. At the nest-stand scale, late-successional forest characteristics are often important determinants of where goshawks locate their nests. The preponderance of late-successional forest in the landscape decreases as the scale increases (e.g., as one moves from nest stand to PFA to foraging area), and existing data from telemetry and observational studies suggest that goshawks use late-successional forests within their home ranges for foraging, but use prey associated with both early- and late-successional forests, and in some cases, open habitats. Thus, goshawks ap-

pear to be associated with late-successional forests for nesting and foraging, but clearly also use, and use prey associated with, other cover types. Goshawk breeding habitat has been studied much more intensively than nonbreeding habitat. In some landscapes, goshawks appear to remain near breeding areas throughout the year, although there is considerable annual variation and variation between sexes in nonbreeding habitat use. In at least some landscapes, goshawks forage in late-successional forest habitats throughout the year. Conversely, some goshawks use landscapes during the nonbreeding season (e.g., pinyon–juniper and open sagebrush basins) that are quite different from landscapes used during the breeding season. In general, there appears to be a wider range of habitats used during the non-breeding season than during the breeding season.

Habitat as a Surrogate for Population Trends.

Context. The population status of goshawks and their association with late-successional forests in western North America has been debated for >10 yr. This debate has considerable bearing on the FWS decision that listing goshawks in the western U.S. under the Endangered Species Act was not warranted (USDI 1998). In 1990, Crocker-Bedford (1990) reported a relation between timber harvest and loss of goshawk territories on the Kaibab Plateau in Arizona and suggested that some forest-management practices might negatively affect goshawk populations. Considerable discussion of that conclusion and the evidence supporting it ensued. Kennedy (1997) later reviewed the status of goshawks and concluded that data were lacking to determine if populations of goshawks were increasing, decreasing, or stationary. She called for more in-depth demographic studies, including meta-analysis approaches, combining ongoing studies with marked goshawks. Smallwood (1998) and Crocker-Bedford (1998) both responded to Kennedy's review paper. Smallwood (1998) suggested that in lieu of appropriate sampling and agreement among scientists regarding additional variables that should be analyzed, evidence for a goshawk population decline should be based on availability and contiguity of habitat and migration counts. Crocker-Bedford (1998) hypothesized that distribution of foraging habitat across the landscape influenced goshawk home-range size, which in turn influenced breeding pair density and reproductive success. He suggested further development of models of goshawk–habitat relations,

inventory of current forest conditions, and assessment of population status based on habitat conditions at the landscape level.

In their status review (FWS 1998), the FWS attempted to assess population status from population data and also by using the distribution and extent of habitat, particularly older forest (specifically old-growth), as a surrogate for a direct measure of population trends. This effort represented the largest concerted attempt to date to document goshawk locations and habitat in North America. The FWS concluded that it was evident that “there [are] inadequate data available which could be used to determine the population trend for goshawks throughout the review area. Furthermore, our knowledge of the factors that affect the size of goshawk populations at local and regional levels, or in the entire area is incomplete. A clearer understanding of population size and factors affecting goshawk populations is needed. Much of what is known is currently applicable only to local populations and localized habitat conditions and effects, and should not be extrapolated to the larger range of the species” (FWS 1998). The FWS also noted that few studies have focused on goshawk population dynamics over a sufficient period of time to provide the kinds of demographic data needed for a status review. With this realization, FWS attempted to identify trends in habitat. The FWS concluded that they could not directly tie changes in goshawk populations to changes in habitat over time because of a lack of data and little confidence regarding how goshawk populations respond to changes in their habitat. The FWS decision that listing goshawks in the western U.S. under the Endangered Species Act was not warranted was based in large part on lack of evidence that habitat was currently limiting goshawks, and that habitat was unlikely to limit the goshawk population in the review area in the foreseeable future. Such an approach is clearly limited by how well the relations between goshawks and their habitat are understood, and how well existing vegetative conditions are known.

Existing goshawk–habitat models. Warren et al. (1990) developed a goshawk–habitat model based on a review of published and unpublished literature and expert opinion using the Delphi method. In their model, habitat suitability increased with increasing canopy cover, size of overstory trees, size of the nest stand, and decreasing slope. Suitability of foraging habitat was modeled in relation to prey

availability, forest type, and tree species composition. Reynolds et al. (1992) synthesized habitat associations for goshawks and 14 prey species and silvicultural prescriptions designed to produce suitable forest conditions for goshawks and their principal prey in the southwestern U.S. Such prescriptions were developed with the intent of (1) sustaining goshawk populations in the Southwest, (2) providing desired forest conditions for the goshawk and its prey, (3) using the natural, presettlement forest composition, structure, and landscape pattern of each forest type as a template for assembling, and assuring the sustainability of, goshawk and prey habitats in large landscapes, and (4) managing southwestern forests as an ecosystem (i.e., retaining all of the parts). For the goshawk, this is a conceptual model, but the recommendations that came from this model are being implemented on national forests throughout the Southwest while components of the model are being implemented throughout much of the western U.S. and in British Columbia, Canada. The model of Reynolds et al. (1992) has served as the primary model for goshawk management in the southwestern U.S. (Reynolds et al. 1996, Long and Smith 2000) and has been the subject of considerable debate and evaluation (e.g., Braun et al. 1996).

In Utah, Johansson et al. (1994) used elevation and vegetation models to predict potential goshawk nesting sites. They found elevation to be a better predictor of goshawk nest locations than vegetation, although elevation, vegetation, and vegetative characteristics of PFAs were the best predictors overall. In Idaho, Lillholm et al. (1994) applied a stand density index (SDI)—a measure of stand density that is based on mean tree size and density and is comparable among stands—to guide management practices intended to create forest conditions similar to those found in goshawk nest areas. Although this latter method was primarily intended to assist silviculturalists in managing forest stands, mean tree size and density of stands representing goshawk habitat (e.g., goshawk nest areas) can be used as models of desired future conditions. Similarly, Graham et al. (1994) pointed out that the way forests regenerate, develop, and die is highly variable in time and space, and recommended managing large tracts of forests as sustainable ecological units rather than managing smaller tracts as individual home ranges. DeStefano (1998) suggested that goshawk occurrence was related to characteristics associated with late-successional for-

est, but that goshawks are found in a wide variety of forest conditions. Crocker-Bedford (1998) hypothesized that distribution of foraging habitat across the landscape influences goshawk home-range size, which in turn influences breeding pair density and reproductive success. Landscapes that contain a higher concentration of foraging habitat with adequate prey abundance should support higher densities of breeding goshawks.

Joy (2002) developed spatial-simulation models to assess the relations between goshawk habitat composition and structure and the location of nests and use areas and the relations between the amount and arrangement of habitat components in high- and low-quality breeding areas. High- and low-quality breeding areas were distinguished based on long-term (10 yr) demographic data from 101 breeding areas in northern Arizona. Joy (2002) found that intraspecific territoriality plays a more significant role in nest location than availability of nest area habitat on the Kaibab Plateau. In addition to using habitat models to identify spatial and compositional differences between goshawk nests and random locations, Joy (2002) and Reich et al. (2004) used these models to predict nest locations likely to have high reproductive output.

McGrath et al. (2003) developed models relating habitat characteristics around goshawk nest sites at scales from 1–170 ha in eastern Oregon and Washington. At the 1-ha scale, structural stage (i.e., late-seral), topographic position (i.e., lower slopes and drainage bottoms), and stand-basal area (i.e., high basal area) were associated with goshawk nests, with high basal area being the most important. At larger scales (10–170 ha), later seral stages, high understory growth, and high canopy closure were associated with nests and these associations were prevalent up to 83 ha. They concluded that: (1) there is a core area around goshawk nests where the forest is generally mid- to late-successional stage (large trees with high canopy closure) and (2) this core is surrounded by diverse types of forest cover that are equally abundant (i.e., no one cover type dominates).

In summary, most existing models of goshawk-habitat relations are limited to vegetative structure used for nesting. Other habitat variables (such as microclimatic conditions at nest, foraging, or roost sites) and other aspects of life history (such as juvenile dispersal and territory establishment, non-breeding or failed breeding adults, and winter

ecology) have received relatively little attention compared to vegetative structure around nests, largely because of the difficulties in working with goshawks in the field.

Limitations on using current goshawk–habitat models for predicting population status. Currently, the relations between goshawks and their habitat in the western U.S. are not understood well enough to use trends in habitat as a surrogate for trends in goshawk populations. Fundamentally, this is because there are unknown functional relations among the amounts and distribution of goshawk habitat, the range of vegetation conditions that characterize goshawk habitat, and goshawk population densities and population dynamics. Therefore, it is not currently possible to predict how changes in habitat, or changes in specific types of vegetation such as old-growth forests, are related to changes in goshawk population densities or trends. The use of late-successional forests (specifically old-growth forest) as a surrogate for goshawk population status is limited because: (1) goshawks show a high degree of versatility in habitat use, and although late-successional forest is a commonly used habitat, other seral stages also are used; thus, reliance on distribution of late-successional forests alone for determining the status and distribution of goshawks in the western U.S. is not sufficient; (2) important prey species vary among bioregions and major vegetation types with late-successional forest associates (e.g., Douglas [*Tamiasciurus douglasii*] and red squirrels [*T. hudsonicus*]) important in some regions and early-seral species (e.g., snowshoe hares) relatively more important in other regions; (3) there is currently no consistent definition of old-growth forest as it pertains to goshawk habitat that can be applied across the entire western U.S. or at the scale of major vegetation types; (4) habitat may not be occupied if factors other than old-growth vegetative structure (e.g., weather, prey availability) are limiting goshawk populations; and (5) large-scale, regional vegetation mapping efforts (e.g., major portions of the western U.S.) are not sufficiently precise or accurate to assess current or future conditions. Multiple factors influence habitat use, especially on very large spatial or temporal scales, and relations between goshawks and habitats and goshawks and prey species, seem to be variable across vegetation types. Knowledge concerning the functional relation between the distribution and abundance of habitat and goshawk population densities and trends is required

in order to draw scientifically defensible inferences regarding how changes in habitat, or specific habitat types such as old-growth, relate to changes in goshawk populations. Currently this relation is unknown.

RECOMMENDATIONS

To assess goshawk population status in the western U.S. or any other portions of this bird's range in North America, several improvements in existing data-collection efforts and protocols are necessary. Additional data that do not currently exist will also need to be collected before adequate population status assessment can take place in the western U.S. Items we identified include:

- (1) *Compilation and accessibility of existing data.* We urge organization of existing data into a format that would make it readily accessible to management agencies and other interested parties. Development of standardized protocols for future monitoring and inventory data collection will benefit from an assessment of the existing information. In addition, development of procedures to systematically and regularly capture new information to maintain a current database is necessary.
- (2) *Sampling strategy.* Outside of intensive research studies, most existing goshawk distributional or occurrence records are based on *ad hoc* sampling generally associated with management activities. If goshawk population trends are to be assessed, sampling must represent the target population and yield defensible trend estimates. Monitoring approaches should be based on sample designs that address the definition of the target population, appropriate response variable, definition of a sampling frame and primary sample units, issues of probability of detection, and estimates of necessary sample sizes required to detect a specific change. Monitoring strategies should also be designed to assess both population trend and habitats, as defined through development of empirical goshawk–habitat relations models. Land managers and agency decision-makers should recognize that continued funding of uncoordinated, small-scale goshawk monitoring efforts will not yield useful results across a large land area. In addition, it may be fruitful to address population status at a scale smaller than that of the review area. Rather

than evaluating goshawk population status for the entire western U.S., consideration should be given to monitoring trends in goshawk populations and habitat at the ecoregion or biome scale (e.g., Sierra Nevada forests; coastal temperate forests and rainforests of Oregon, Washington, and southern coastal British Columbia; ponderosa pine forests of New Mexico, Arizona, and southern Colorado).

- (3) *Relation of populations and subspecies.* We recommend that variation in DNA be used to assess the phylogenetic relations among eastern and western North American *A. g. atricapillus*, and *atricapillus* to *A. g. laingi*, and to the putative *A. g. apache*.
- (4) *Addressing current limitations of existing data sources.* Potentially useful data are currently limited by a lack of knowledge about population affiliation (e.g., migration counts), small sample sizes (e.g., Breeding Bird Survey data), or inadequate sampling strategies. Consideration should be given to addressing these limitations where possible. For example, in the case of migration counts, population affiliation of goshawks counted at migration sites needs to be determined, perhaps through conservation genetic and stable isotope analyses (e.g., Meehan et al. 2001).
- (5) *Standardization of terminology and protocols associated with estimating breeding status and productivity.* We recommend that researchers and land managers cooperate in developing standardized protocols (including terminology and data-collection methods) based on peer-reviewed literature with the specific intention of performing pooled data analysis across the entire review area at a later date (e.g., Anderson et al. 1999). If a single set of protocols cannot be used for the entire western U.S., then standardized protocols should be used for large areas (e.g., biomes or ecological habitat types, but not political boundaries).
- (6) *Research priorities.* To assess demography and population trends adequately, goshawk-habitat relations and the effects of specific land-management practices on goshawks in the western U.S., coordinated studies of habitat use (possibly using radiotelemetry) are necessary. Studies of demography and habitat use also need to address the nonbreeding season, when factors regulating populations may be important. In addition, land managers need to continue to

work on remote-sensing applications so that broad-scale analysis of habitats such as late-successional forest and patch size can be evaluated. Finally, long-term experimental or quasi-experimental studies are necessary at the landscape scale to understand how forest management influences goshawks. These studies will be most beneficial when accomplished using an interdisciplinary approach in close collaboration with land managers. An integrated approach between research and management consisting of extensive population and habitat monitoring at the bioregional scale coupled with intensive, long-term demography studies in each of the major vegetation types will provide the data necessary to monitor goshawk populations and habitat and to generate a scientific understanding of goshawk ecology needed to improve management and conservation efforts.

Finally, we emphasize that in addition to assessing population trends and status in the western U.S., it is also important to better understand goshawk-habitat relations and the influence of various human activities, especially forest-management practices, on goshawks. Much of the controversy regarding goshawk conservation in the western U.S. and elsewhere has to do with concerns about forest management and how forest management affects goshawks. Thus, it is not sufficient to simply assess goshawk population trends in the western U.S.; it is also necessary to better understand the relations between goshawks and their habitat and how human activities affect that habitat. Considerable information regarding population ecology and goshawk-habitat relations currently exists, but additional information is necessary. Individual goshawks or goshawk pairs exhibit landscape-level use of space, and thus, occur naturally at relatively low densities. They are highly mobile, and as such, have proved difficult to study. Thus, a long-term investment of resources in a coordinated effort directed at large spatial scales will be required to assess goshawk population trends adequately and understand goshawk-habitat relations in the western U.S. and elsewhere.

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Appendix. Definitions of ecological terms as they apply to Northern Goshawks.

"Active" nest: The term "active" as applied to raptor nests was first defined by Postupalsky (1974) to describe a nest where ≥ 1 egg was laid. However, the term has been used in different ways since then, and is probably best avoided.

Breeding area: a nesting area used by goshawks in the present, past, or both.

Breeding area occupancy: goshawks are thought to defend use areas from conspecifics (territories) during the breeding season, and these territories are often used in subsequent years. However, because it is generally impractical to assess territory occupancy, occupancy of breeding areas has been assessed in field studies of goshawks. Breeding areas are occupied when goshawks are present, and what constitutes presence has been variable across studies, or is undefined. We suggest that breeding areas are occupied when any of the following occur: (1) nesting, (2) one or more goshawks are observed in association with a nest with evidence of recent use (e.g., fresh greenery or other evidence of recent nest construction), (3) goshawks respond aggressively to humans or respond to conspecific call broadcasts during the breeding season, or (4) pre-dispersal fledglings are located in the vicinity of a nest that has evidence of recently being used (e.g., fresh

whitewash, goshawk feathers, prey remains, or pellets). If none of these conditions exist, a breeding area cannot be assumed to be unoccupied without meeting additional criteria (e.g., no goshawk detection during systematic searching for nests or in response to conspecific call broadcasts). Consistent, specific criteria for categorizing a breeding area as unoccupied need to be developed.

Breeding density: the number of nests used by breeding goshawks per unit area; alternatively, the number of goshawk breeding areas through a specified time period per unit area.

Breeding population: a group of goshawks that interact in space and time and that breed or potentially breed and for which it is reasonable to discuss emergent population properties, such as rate of growth, productivity, etc. Goshawk populations are delimited by spatial boundaries based on where they breed, but these boundaries may not be relevant throughout an annual period (e.g., goshawks that annually migrate from breeding areas) or from one year to the next (e.g., goshawks that migrate from breeding areas in only some years).

Habitat: the collection of biotic and abiotic factors that produce occupancy by goshawks (*sensu* Hall et al. 1997).

Nest(ing) area: the immediate area surrounding (a) nest(s) used by breeding goshawks.

Nest(ing) attempt: a nest that has been used in any manner by goshawks during the breeding season. Goshawks can be observed at a nest, or there may be evidence of egg laying (e.g., eggs or egg fragments), nestlings, or fledglings. Other evidence is often used to infer that an egg has been laid or that a pair of goshawks is preparing to lay eggs, including observation of goshawks reconstructing an existing nest or building a new nest, observation of greenery added to existing nests, presence of recently molted goshawk feathers in or beneath a nest, etc. A nest attempt does not necessarily result in egg laying (i.e., nest failure can occur prior to egg laying).

Nest stand: the area covered by a forested patch consisting of trees that are often characterized by having a similar size, species, and spacing and in which a goshawk nest occurs.

Nest(ing) success: the proportion of nests in which eggs are laid that produce at least 1 fledgling.

Nest tree: the tree in which a goshawk nest is placed.

Occupied nest area: an area on which a pair of goshawks have established residency during the nesting season and includes ≥ 1 nest.

Post-fledging area: the area that is used by recently fledged goshawks before they become independent of adults (*sensu* Reynolds et al. 1992).

Successful nest: a nesting attempt that results in ≥ 1 young fledged.

Territory: an area defended by goshawks from conspecifics during the breeding season that generally contains the

nest, alternative nest(s), if any, nest stand(s), nesting area, post-fledging area, and at least some of the area used by adults for foraging.

Use area-home range: area traversed by a goshawk or pair of goshawks during the course of normal, daily activi-

ties. It is generally necessary to define specific time periods over which use areas or home ranges apply, as they can change in size and other attributes through time.



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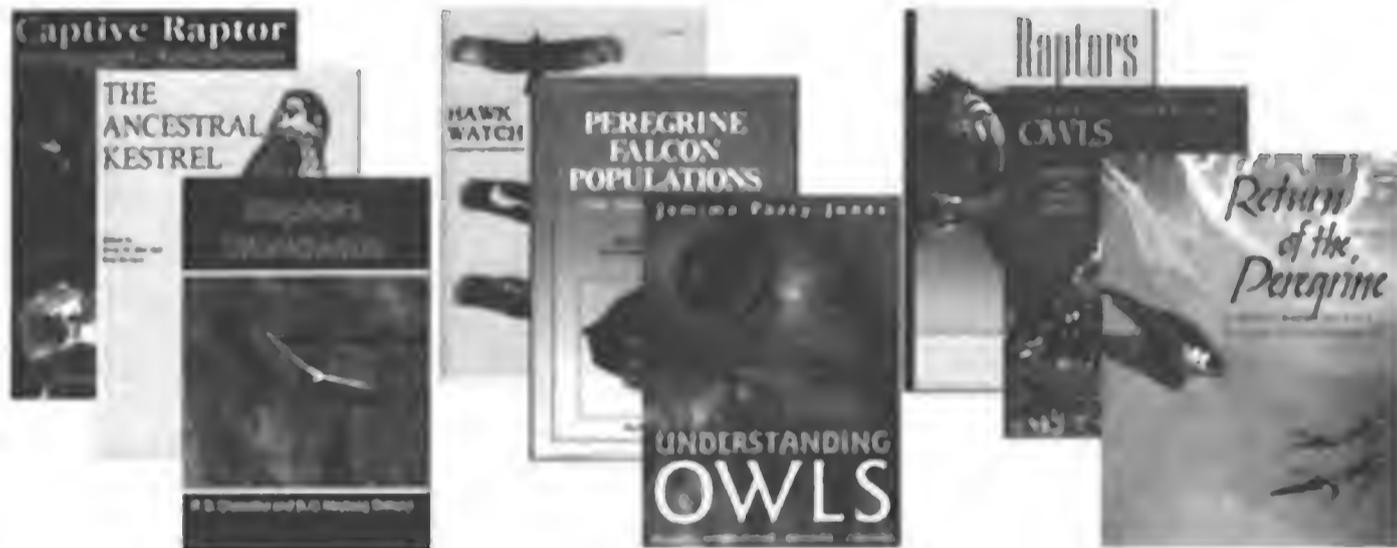
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IS FLEDGING SUCCESS A RELIABLE INDEX OF FITNESS IN NORTHERN GOSHAWKS?

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ABSTRACT.—Fledging success is often assumed to be a reliable index of reproductive success (i.e., fitness) in the ornithological literature. We examined the validity of this assumption in a large population of Northern Goshawks (*Accipiter gentilis*) on the Kaibab Plateau, Arizona, at both the population and individual levels. We used mark-recapture data from 558 fledglings produced at 494 nests over a 10-yr period to assess the hypothesis that the number of fledglings returning to breed from an annual fledgling cohort is positively correlated with the size of the cohort. Natal philopatry was low and recruitment was gradual: only 48 fledglings (8.6%) returned to breed between 2–8 yr of age ($\bar{x} = 3.5$ yr). We found no evidence that the breeding population produced more local recruits in years of high fledgling production than in years of low fledgling production. At the individual level, however, fledgling production for 290 breeding adults was related to their contributions to the future breeding population. Variation in fitness potential among territorial adults was high, as only 20% of the breeding population produced nearly 50% of the fledglings and 84% of the local recruits during the study. Our results indicate that measures of annual productivity for a large breeding population were not reflective of reproductive success, whereas measures of individual productivity were. We conclude that fledging success of individual goshawks is a reliable index of fitness, but that population productivity is a poor predictor of local recruitment.

KEY WORDS: *Northern Goshawk; Accipiter gentilis; fitness; individual heterogeneity; Kaibab Plateau; recruitment; reproductive success.*

¿CONSTITUYE EL ÉXITO DE EMPLUMAMIENTO UN ÍNDICE CONFIABLE DE ADECUACIÓN BIOLÓGICA EN *ACCIPITER GENTILIS*?

RESUMEN.—En la literatura ornitológica, a menudo se asume que el éxito de emplumamiento representa un índice confiable del éxito reproductivo (i.e., adecuación biológica). Examinamos la validez de este supuesto en una población de gran tamaño de *Accipiter gentilis* en Kaibab Plateau, Arizona, tanto a nivel de población como de individuo. Usamos datos de marcado y recaptura de 558 volantones provenientes de 494 nidos a lo largo de un período de 10 años para evaluar la hipótesis de que el número de volantones que regresan a reproducirse de una cohorte anual de volantones está positivamente correlacionado con el tamaño de la cohorte. La filopatría natal fue baja y el reclutamiento fue gradual: sólo 48 volantones (8.6%) regresaron a reproducirse con entre dos y ocho años de edad ($\bar{x} = 3.5$ años). No encontramos evidencia de que la población reproductiva produjo más reclutamientos locales en años de alta producción de volantones que en años de baja producción. A nivel individual, sin embargo, la producción de volantones correspondiente a 290 adultos reproductivos se relacionó con sus contribuciones a la futura población reproductiva. La variación en la adecuación biológica entre los territorios de los adultos fue alta, ya que sólo el 20% de la población reproductiva produjo cerca del 50% de los volantones y el 84% de los reclutamientos locales durante el estudio. Nuestros resultados indican que las medidas de productividad anual de una población reproductiva de gran tamaño no reflejaron el éxito reproductivo, mientras que las medidas de productividad individual sí lo hacen. Concluimos que el éxito de emplumamiento individual de *A. gentilis* representa un índice confiable de adecuación biológica, pero que la productividad a nivel poblacional predice de modo inadecuado el reclutamiento local.

[Traducción del equipo editorial]

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In birds, a commonly measured reproductive variable used to assess population performance over time is fledging success (the number of young that fledge per nest). A widely held assumption in avian studies is that fledging success is a reliable index of reproductive success (the number of offspring that survive to become breeding adults) and thus, fitness (Endler 1986, Weatherhead and Dufour 2000, Keedwell 2003). However, the spatial and temporal scales over which many populations are studied may not correspond well with the spatial extent of natal dispersal or the time periods over which recruitment occurs. These limitations, superimposed on a variety of stochastic factors, could easily disrupt the relationship between fledging success and fitness. Nevertheless, researchers often assume this relationship is positive, in part, due to the difficulties associated with estimating pre-breeding survival and emigration rates, even in long-term banding studies. Difficulties in attaining direct measures of reproductive success are therefore exemplified in long-lived, wide-ranging species that occur at low densities, have low natal philopatry, elude detection when not breeding, and initiate breeding at a delayed age (Weatherhead and Dufour 2000).

The Northern Goshawk (*Accipiter gentilis*) is a long-lived raptor that occupies mature temperate and boreal forests throughout the Holarctic (Squires and Reynolds 1997). The goshawk is a socially monogamous, territorial species that lays one clutch per year (Reynolds et al. 1994, Kennedy and Ward 2003). Although several studies have documented extensive temporal variation in fledging success in goshawk populations (e.g., McClaren et al. 2002, Reynolds and Joy in press), none have addressed the relationship between fledging success and local recruitment. The strength of this relationship is particularly relevant when the dynamics of a local population are more heavily reliant on external recruitment (i.e., immigration) than internal productivity, which may occur when natal philopatry is low and adult site fidelity is high (Stacey and Taper 1992, Martin et al. 2000). While mate and site fidelity in adult goshawks is high (75–95%; Detrich and Woodbridge 1994, Reynolds and Joy in press), the degree of natal philopatry is largely unknown due to low juvenile recapture probabilities, few recoveries of banded nestlings, and a general lack of information on the extent of natal dispersal (Kennedy and Ward 2003, but see Wiens 2004). However, molecular evidence has

shown that gene flow among subpopulations of goshawks over large geographic areas is high (Sonsthagen 2004, Bayard de Volo et al. 2005), indicating that juveniles may disperse over long distances because adults rarely disperse once they have settled on a breeding territory. Juvenile survival is one of the most difficult demographic parameters to estimate precisely in goshawks (Kennedy 1997, Wiens 2004), further emphasizing the need to assess the assumed relationship between fledging production and reproductive success.

In this paper we evaluate whether fledging success is a reliable predictor of reproductive success in goshawks. We examined this relationship at both the population and individual levels using a 13-yr mark-recapture (resight) data set obtained from a breeding population of goshawks exceeding 120 pairs on the Kaibab Plateau, Arizona. Our investigation was inspired by studies showing a positive relationship between fledging success and recruitment in bird species such as Red-winged Blackbirds (*Agelaius phoeniceus*), Eurasian Sparrowhawks (*Accipiter nisus*), Ural Owls (*Strix uralensis*), and Osprey (*Pandion haliaetus*; Weatherhead and Dufour 2000, Newton 1989a, Saurola 1989, Postupalsky 1989, respectively). At the population level, we assessed the hypothesis that the number of fledglings produced annually is positively correlated with the number of individuals from annual cohorts that were eventually recruited into the local breeding population. At the individual level, we anticipated that total fledgling production of color-marked male and female adult (≥ 2 yr old) goshawks would be positively related to the number of their descendants that were recruited into the local breeding population. In examining our hypotheses, we also report on local recruitment and ages at first breeding for goshawks on the Kaibab Plateau.

METHODS

Study Area and Field Procedures. The study area included all the coniferous forest above 2182 m elevation on the Kaibab Plateau of northern Arizona. This 1732 km² area included the northern portion of the Kaibab National Forest and the Grand Canyon National Park (North Rim). The Kaibab Plateau is a large (95 × 55 km), oval-shaped plateau that rises from a shrub-steppe plain at 1750 m elevation to the highest point at 2800 m and is dissected by moderately sloping valleys (Rasmussen 1941). Forests of the Kaibab Plateau are isolated from similar forests by variable distances (35–250 km) of pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodland, and sagebrush (*Artemisia* spp.) plains. See Reynolds et al. (1994) and Reynolds et al. (2005) for further detail on the study area, its management history, and protocols

used to locate, survey, and monitor goshawk breeding areas.

We defined a territory as a breeding area used, but not necessarily defended against conspecifics, by a single pair of goshawks during a breeding season (Reynolds et al. 2005). During 1991–2003, a high density of regularly-spaced goshawk breeding territories were identified on the Kaibab Plateau (Reich et al. 2004, Reynolds et al. 2005). Territories contained multiple alternate nests that were used one or more times over the years by goshawks. We visited all nests in early spring of each year to estimate occupancy and reproductive status of territorial pairs. If goshawks were not using a known nest, a three-stage territory survey protocol (Reynolds et al. 2005) was used to determine territory status. We classified a territory as “*active*” when eggs were laid, “*occupied*” when adult goshawks were observed on two or more occasions in the vicinity of a nest (or a single observation of an adult in combination with observations of molted feathers, feces, and fresh nest construction), and “*unknown*” if eggs were not laid and no evidence of goshawk occupancy was found (Reynolds et al. 2005). We determined nest fate (successful = fledged ≥ 1 young; failed = eggs laid but no fledglings produced), nest productivity (number of fledglings), and identity of adults during weekly visits to *active* territories. For our purposes here, we defined the number of young fledged as the number of nestlings present at the time of banding (ca. 1 wk prior to fledging). Nesting adults were captured, measured, sexed, and aged during the mid–late nestling period following methods described in Reynolds et al. (1994); nestlings were captured by climbing nest trees during the last week of the nestling period (mid–late June). Sex of nestlings was assigned on the basis of body mass, tarsometatarsal length, and toepad-length measurements (Wiens 2004). All captured hawks received a U.S. Geological Survey aluminum leg band and an anodized colored leg band with a unique alpha-numeric code (Aircraft Sign and Plate Co., Edmonton, Canada) readable to 80 m with 40–60 \times spotting scopes.

Age at First Breeding and Local Recruitment. We considered a goshawk to have been recruited locally if it was banded as a nestling on the study area and later observed breeding in the study population. Thus, hawks classified as “local recruits” had to have been recaptured or resighted at an active territory on the Kaibab Plateau. To attain an unbiased estimate of the age at first breeding, we included only banded (known-aged) hawks that we were confident had been detected on their first breeding attempt. This meant that banded recruits had to have been resighted on territories where the same-sex occupant during the prior year was known. Estimated ages at first breeding could have been biased high by breeding dispersal (i.e., undetected movement among territories between successive breeding attempts). However, this bias was likely to be small because <6% of adult goshawks moved to a different territory between successive breeding attempts (R. Reynolds unpubl. data). To attain a mean estimate of local recruitment, we subtracted the number of nestlings that were too young (based on the median age at first breeding) to have attained breeding territories by spring 2003 from the total number of nestlings banded during 1991–2003. Hence, local recruit-

ment was calculated as the total number of banded recruits detected during 1991–2003 divided by the total number of nestlings banded during 1991–2000.

Population Productivity. We were unable to capture and mark all nestlings produced in some years because several nests were not located until after fledging or, rarely, a nest tree was unsafe to climb. Thus, the number of young banded represented a portion (69% during 1991–2003) of the known number of young that actually fledged. For this reason, we defined “productivity” as the number of young banded. We assumed that banded young comprised a representative sample in terms of population productivity and local recruitment. Using the number of young banded annually, we assessed whether the size of each annual fledgling cohort was correlated with the number of local recruits originating from each cohort. We conducted analyses with sexes combined and then separately for males and females. Data were examined by sex for two reasons. First, patterns of post-fledging mortality have been found to differ for male and female goshawks on the Kaibab Plateau (Wiens 2004). Second, natal dispersal distances may differ between sexes (Greenwood and Harvey 1982, Byholm et al. 2003). One or both of these factors could result in sex-dependent local recruitment. For sex-specific analyses, the number of individuals of each sex that successfully recruited from a fledgling cohort was assessed relative to the total number of individuals of each sex that were banded as nestlings.

Individual Productivity. To examine the relationship between total fledgling production of individual adult goshawks and recruitment success of their offspring, we calculated the number of banded fledglings produced by each color-marked adult that bred during 1991–2000. As in the population-level analysis, excluding fledgling productivity during 2001–03 ensured that all fledglings in our analysis had at least three years to acquire a breeding territory and be detected. We then related the number of banded fledglings produced by each adult to the total number of their offspring that had successfully recruited to the local breeding population by 2003. We used fledgling production by adults during the study period rather than lifetime productivity because our interest was in the reliability of individual fledging success as a measure of an individual’s fitness potential, regardless of how often they bred or how long they had occupied a breeding territory. Nonetheless, lifetime fledgling production was captured for nearly all goshawks included in our analysis because of the duration of our study relative to the number of years goshawks successfully laid eggs (\bar{x} = 2.1 yr, min. = 1 yr, max. = 10 yr, 1991–2004; R. Reynolds unpubl. data). We assumed that adults captured or resighted at a nest were indeed the biological parents of the nestlings banded at that nest. In raptors, females are often alone before and during egg laying while their mates forage, which could result in extra-pair fertilizations by conspecific males (Reynolds and Linkhart 1990, Negro et al. 1996, Gavin et al. 1998). Although extra-pair fertilizations could confound the relationship between fledgling success and recruitment, genetic evidence demonstrated that extra-pair fertilizations are infrequent for goshawks on the Kaibab Plateau (Gavin et al. 1998).

Data Analysis. At the population level, we used Spear-

Table 1. Northern Goshawk survey effort, banding activity, and local recruitment (banded nestlings from annual cohorts that eventually returned to breed) on the Kaibab Plateau, Arizona, 1991–2003.

YEAR	TERRITORIES SURVEYED	USED NESTS (%) ^a	ADULTS BANDED	NESTLINGS BANDED	NESTLINGS RETURNED
1991	37	36 (97)	48	46	8
1992	64	59 (92)	43	32	2
1993	82	67 (82)	30	62	4
1994	88	21 (24)	13	18	2
1995	99	53 (54)	39	52	7
1996	105	46 (44)	18	41	1
1997	106	31 (29)	15	36	9
1998	109	58 (53)	37	84	9
1999	113	57 (50)	14	76	5
2000	120	66 (55)	33	111	1
2001	120	30 (25)	5	31	0
2002	121	21 (17)	5	16	0
2003	121	10 (8)	2	9	—

^a Percent of total territories under study that contained used nests (eggs laid).

man correlation coefficients (r_s) to characterize the strength of the relationship between the size of each annual fledgling cohort and the number of local recruits originating from each cohort. We estimated the expected number of fledglings recruited from each annual cohort by multiplying our overall estimate of local recruitment by cohort size. A chi-square analysis was then used to evaluate possible deviations from the expected number of fledglings recruited from each cohort. At the individual level, we used generalized linear models (PROC GENMOD; SAS Institute 1999) to investigate our prediction that total fledging production by individual adults would be positively related to the number of local recruits each produced. Specifically, we used Poisson regression in a log-linear model in which a count of recruits produced per adult was the response variable and the number of banded fledglings produced per adult was assessed as an explanatory variable. Chi-square tests or a Fisher's exact test were used to examine potential sex-related differences in the age at first breeding and local recruitment. All analyses were conducted using SAS (ver. 8.2). Results are reported as means \pm SE, with 95% confidence intervals (CI).

RESULTS

The number of territories surveyed increased from 37 in 1991 to 121 in 2003 (Table 1). All but two of the 121 territories contained nests with eggs or young in one or more years of the study. The exceptions were territories where goshawks occupied newly built or reconstructed old nests, but did not lay eggs. The percentage of territories under study that contained nests with eggs or young varied substantially among years, ranging from 8% in 2003 to 97% in 1991 (Table 1). This resulted in highly variable fledgling production among years,

ranging from only 9 fledglings in 2003 to 111 in 2000. Of the 13-yr total of 555 nests with eggs, 447 (80.5%) adult pairs fledged 897 young successfully (614 of which were banded), and 108 (19.5%) pairs lost their clutch during the incubation or nestling stages.

Age at First Breeding and Local Recruitment. In the 10 yr that we included for fledgling production (1991–2000), we banded 558 nestlings (278 females and 280 males) at 494 nests (Table 1). Forty-eight (8.6%) of these nestlings returned to breed on the study area—26 (9.4%) females and 22 (7.9%) males. Nestling return rates were similar between the sexes ($\chi^2 = 0.40$, $df = 1$, $P = 0.53$). Ages at first breeding could be determined with confidence for 28 of 48 fledglings that returned to breed (17 of 26 females and 11 of 22 males; Fig. 1). These hawks initiated breeding between 2–8 yr of age (3.5 ± 0.32 yr, 95% CI = 2.84–4.16, median = 3 yr). Only four hawks (all females) were older than 4 yr of age at first breeding. Differences between sexes in the age at first breeding were not supported (Fisher's Exact Test: $P = 0.49$). No hawks in first-year plumage were observed breeding at or occupying a nest during the 13-yr study. Two females banded as nestlings were later resighted in adult plumage occupying inactive breeding territories on the study area, and two locally banded nestlings were found breeding in forests beyond the Kaibab Plateau (Wiens 2004).

Population Productivity. We found no evidence

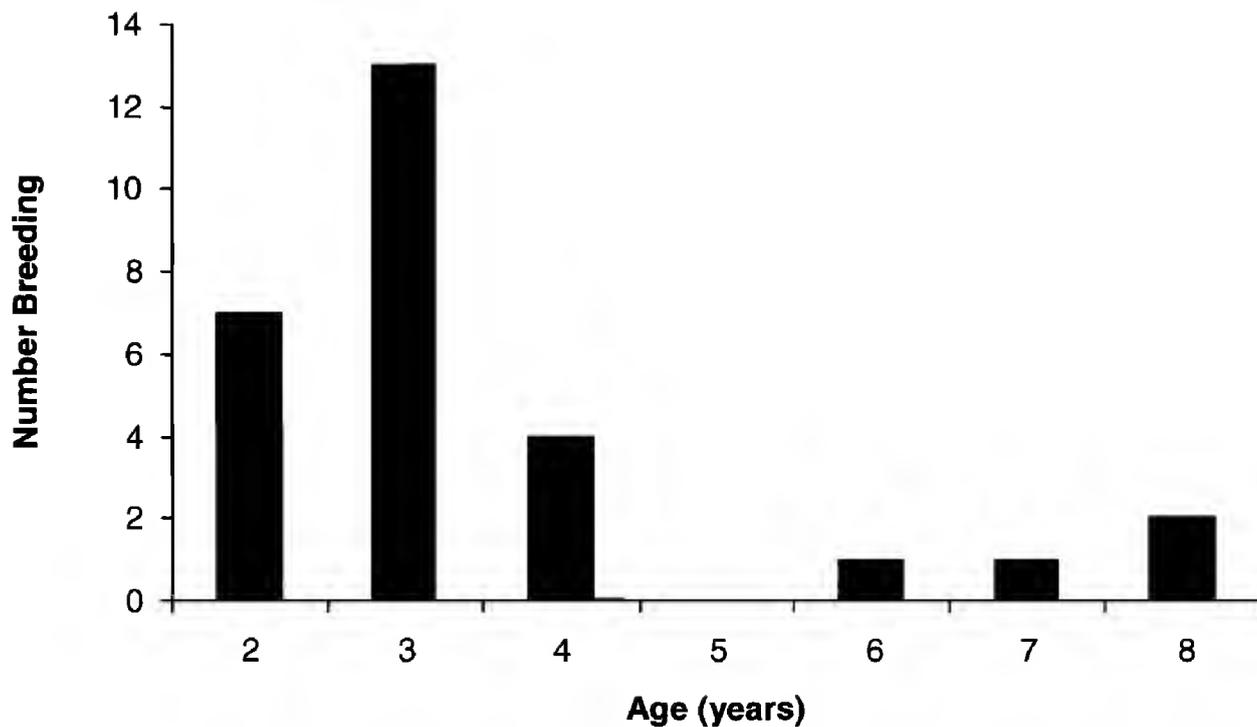


Figure 1. Distribution of ages at first breeding for 28 known-aged Northern Goshawks recaptured on their first breeding attempt on the Kaibab Plateau, Arizona, 1991–2003.

that the number of fledglings recruited from annual cohorts was correlated with cohort size ($r_s = 0.10$, $P = 0.79$, $N = 10$; Fig. 2). Likewise, there was no evidence of a correlation between annual estimates of fledging production and recruitment when sexes were analyzed separately (females: $r_s = 0.24$, $P = 0.50$; males: $r_s = 0.11$, $P = 0.76$). The number of local recruits produced was significantly higher than expected for the 1991 (8 observed, 3.9 expected; $\chi^2 = 4.13$, $df = 1$, $P = 0.04$) and 1997

(9 observed, 3.1 expected; $\chi^2 = 11.25$, $df = 1$, $P < 0.01$) fledgling cohorts, but much lower than expected for the 2000 fledgling cohort (1 observed, 9.5 expected; $\chi^2 = 7.65$, $df = 1$, $P < 0.01$). We found no other deviations in numbers of observed versus expected recruits in any other fledgling cohort. Thus, the 2000 fledgling cohort was the only one of the 10 cohorts in which significantly fewer fledglings returned to breed than expected. To ensure that including this year did not unduly bias

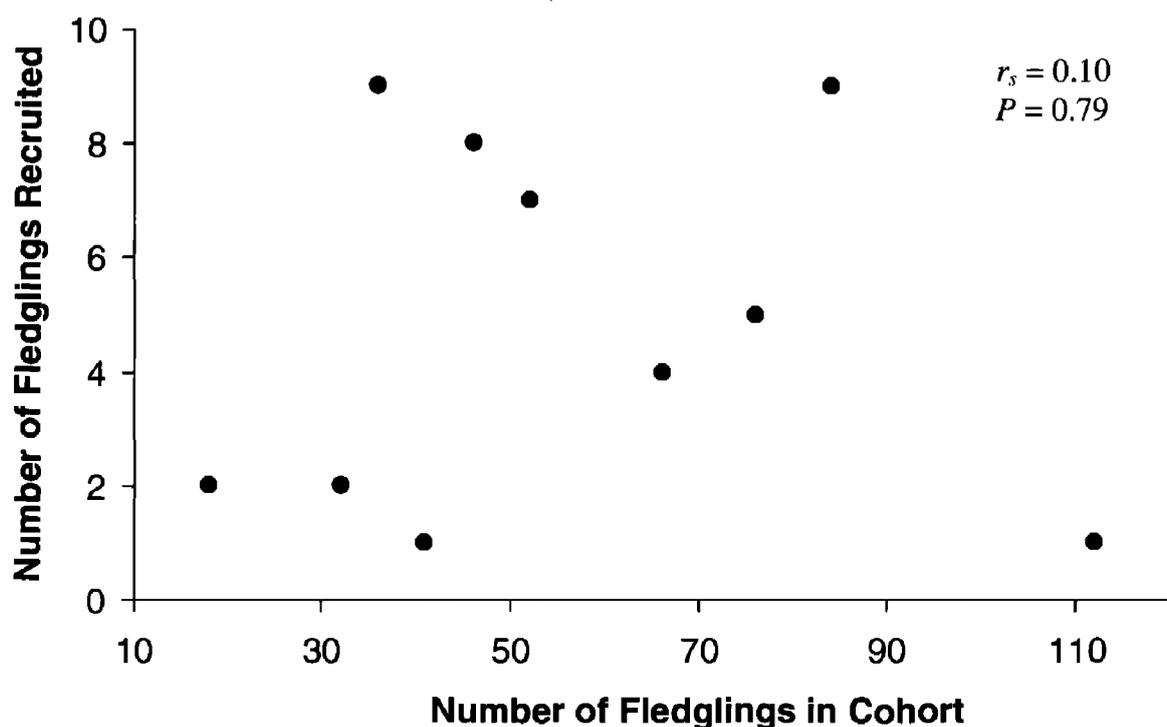


Figure 2. Number of locally produced Northern Goshawk fledglings recruited into the breeding population on the Kaibab Plateau, Arizona, relative to the number of young fledged within each annual cohort, 1991–2000. Each point represents one year.

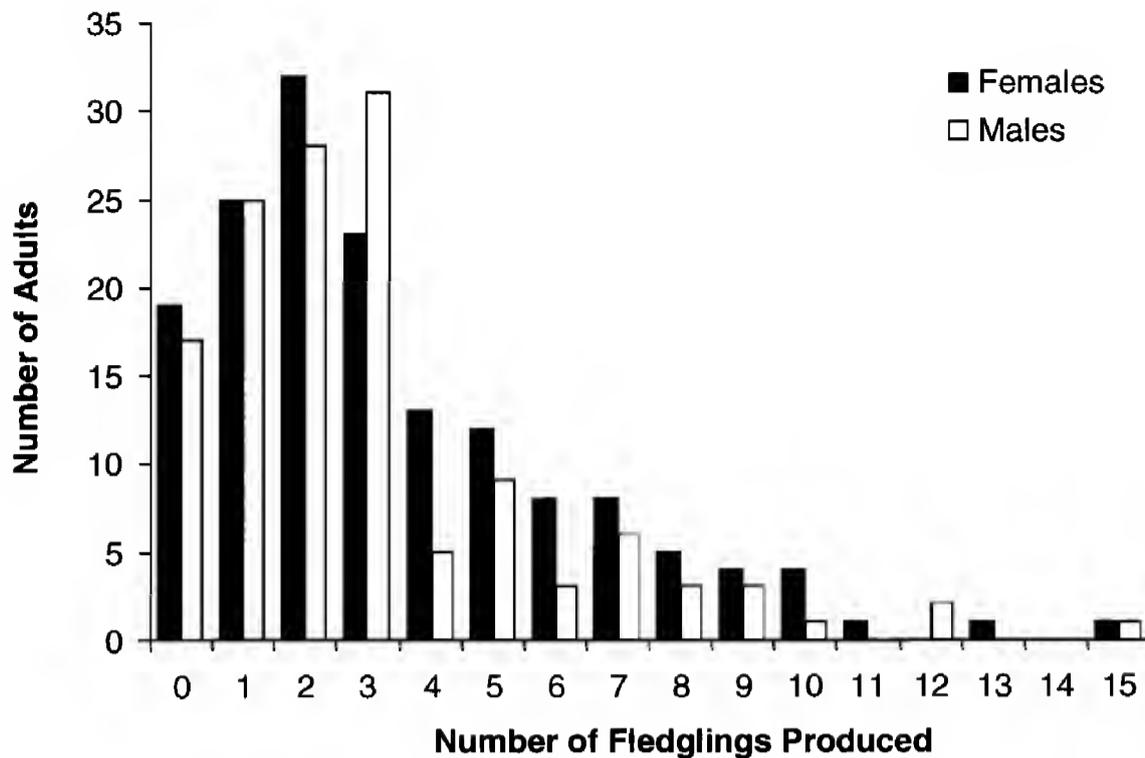


Figure 3. Fledgling production of 156 female and 134 male color-marked adult (≥ 2 -yr-old) Northern Goshawks breeding between 1991 and 2000 on the Kaibab Plateau, Arizona.

our results, we reanalyzed the data without this cohort. Although this improved the relationship slightly, the size of a fledgling cohort was still a poor predictor of the total number of goshawks that returned to breed from the cohort (sexes combined: $r_s = 0.46$, $P = 0.21$, $N = 9$; females: $r_s = 0.52$, $P = 0.15$; males: $r_s = 0.46$, $P = 0.21$).

Individual Productivity. Fledging success was calculated for 156 females and 134 males breeding during 1991–2000 (Table 1). During this period, females spent between 1–7 yr as breeders (2.18 ± 0.11 yr; 95% CI = 1.96–2.40) and fledged between 0 and 15 young (3.39 ± 0.23 young; 95% CI = 2.93–3.85). Similarly, males also spent between 1 and 7 years as breeders (1.96 ± 0.11 yr; 95% CI = 1.73–2.18) and fledged between 0 and 15 young (2.98 ± 0.23 young; 95% CI = 2.51–3.44). The distribution of fledgling production among breeders was highly skewed, with most individuals producing few or no fledglings and only a few individuals having extremely high success (Fig. 3). In total, 156 adult females produced 529 fledglings and 134 adult males produced 399 fledglings (the remaining 29 and 159 banded nestlings were parented by unknown adult females and males, respectively). Thirty-six adults (19 females and 17 males) laid eggs but failed to produce fledglings.

The recruitment success of an adult's offspring was significantly related to the total number of fledglings the adult produced (sexes combined: regression slope coefficient, $\hat{\beta} = 0.22 \pm 0.03$, Wald

$\chi^2 = 74.77$, $df = 1$, $P < 0.01$, $N = 290$; females: $\hat{\beta} = 0.22 \pm 0.04$, $\chi^2 = 38.2$, $df = 1$, $P < 0.01$, $N = 156$; males: $\hat{\beta} = 0.22 \pm 0.04$, $\chi^2 = 37.3$, $df = 1$, $P < 0.01$, $N = 134$; Fig. 4). We had two concerns regarding this result. First, we suspected that fledglings produced during the 2000 breeding season might not have had sufficient time to be recruited by 2003 (as was our concern in the population-level analysis). Second, there were 33 new unband-ed adults (17 females and 16 males) who first bred in the study population in 2000 (Table 1). Several of these individuals also bred in subsequent years, so our initial analysis may have not represented their contributions adequately to fledgling production. To address these concerns, we reanalyzed the data without individual productivity and recruitment data from the 2000 breeding season. Excluding the 2000 breeding season had little effect on the strength of the relationship (sexes combined: $\hat{\beta} = 0.28 \pm 0.03$, $\chi^2 = 71.0$, $df = 1$, $P < 0.01$, $N = 257$; females: $\hat{\beta} = 0.28 \pm 0.05$, $\chi^2 = 37.1$, $df = 1$, $P < 0.01$, $N = 139$; males: $\hat{\beta} = 0.28 \pm 0.05$, $\chi^2 = 36.5$, $df = 1$, $P < 0.01$, $N = 118$). Thus, fledging success of individual goshawks could be taken as a reasonable index of their contributions to the future breeding population.

Both sexes exhibited similar patterns of variance in fledgling production and in the number of recruits they produced (Figs. 3, 4). Moreover, fledging success and contributions of offspring to the future breeding population varied extensively

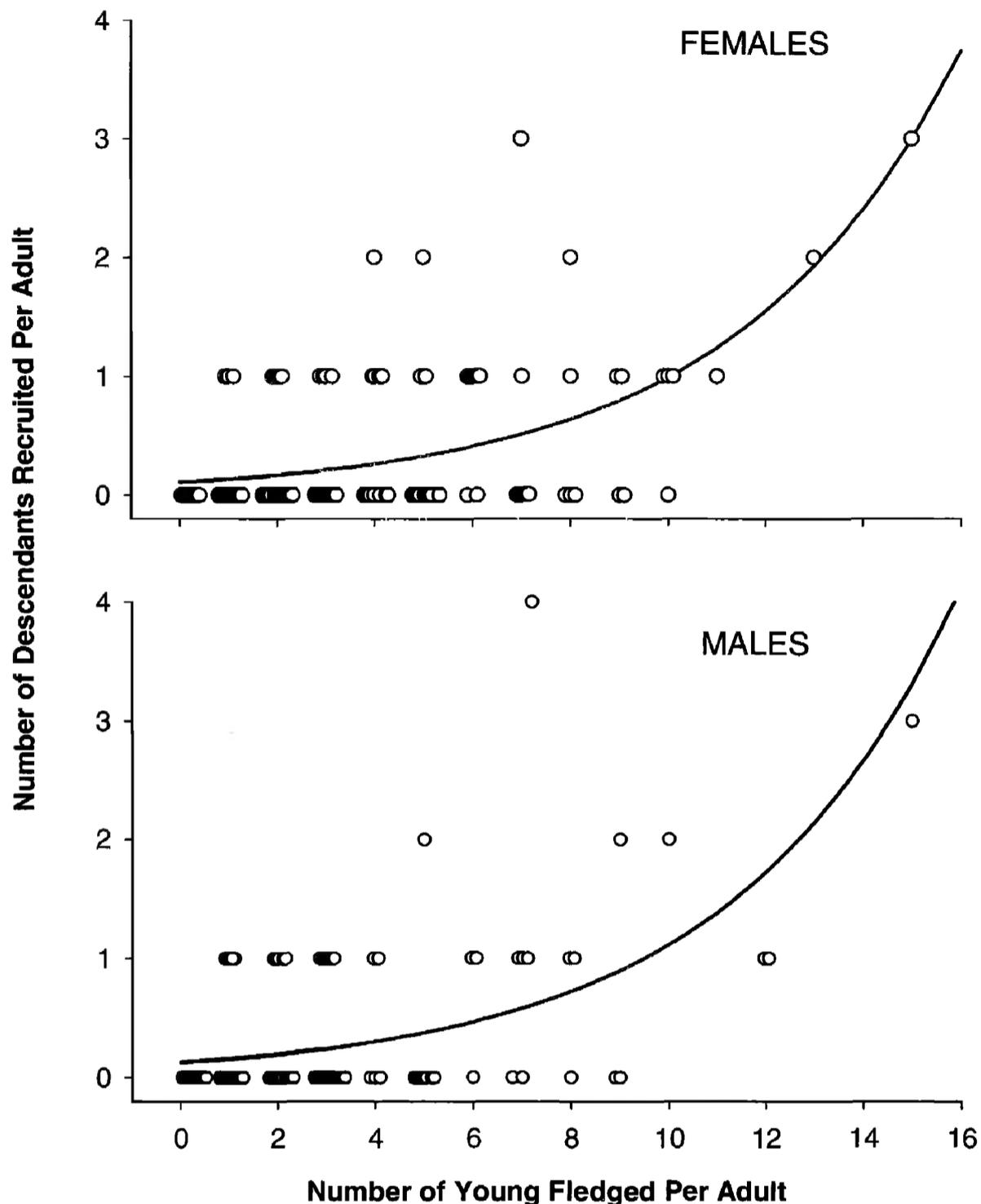


Figure 4. Number of descendants of individual female ($N = 156$) and male ($N = 134$) adult (≥ 2 -yr-old) Northern Goshawks that successfully recruited into the breeding population in relation to the number of fledglings each adult produced between 1991 and 2000 on the Kaibab Plateau, Arizona. Each point represents an individual adult. Trend lines determined by Poisson regression with a log-link function (females: $\hat{y} = \exp[-2.217 + 0.221x]$; males: $\hat{y} = \exp[-2.056 + 0.217x]$).

among territorial hawks; 20% of adults breeding during 1991–2000 contributed nearly 50% of the fledglings and 83% of the local recruits produced during this time (Fig. 5). Of 290 breeding goshawks, 73 (25.2%) produced at least one local recruit each, seven (2.4%) produced two recruits each, and three (1%) produced three recruits each. One male produced four local recruits, but no female produced more than three. In tracking lineages up to three generations, three females left one breeding descendant each who also produced young that were recruited, and two males left one

breeding descendant each who also produced young that were recruited.

DISCUSSION

When measured at the population level, our results failed to support the hypothesis that fledging success is a reliable index of local recruitment in goshawks. When measured on an individual basis, however, adult fledging success was significantly related to local recruitment, indicating that total fledgling production by individuals was a more reliable index of reproductive success than a mea-

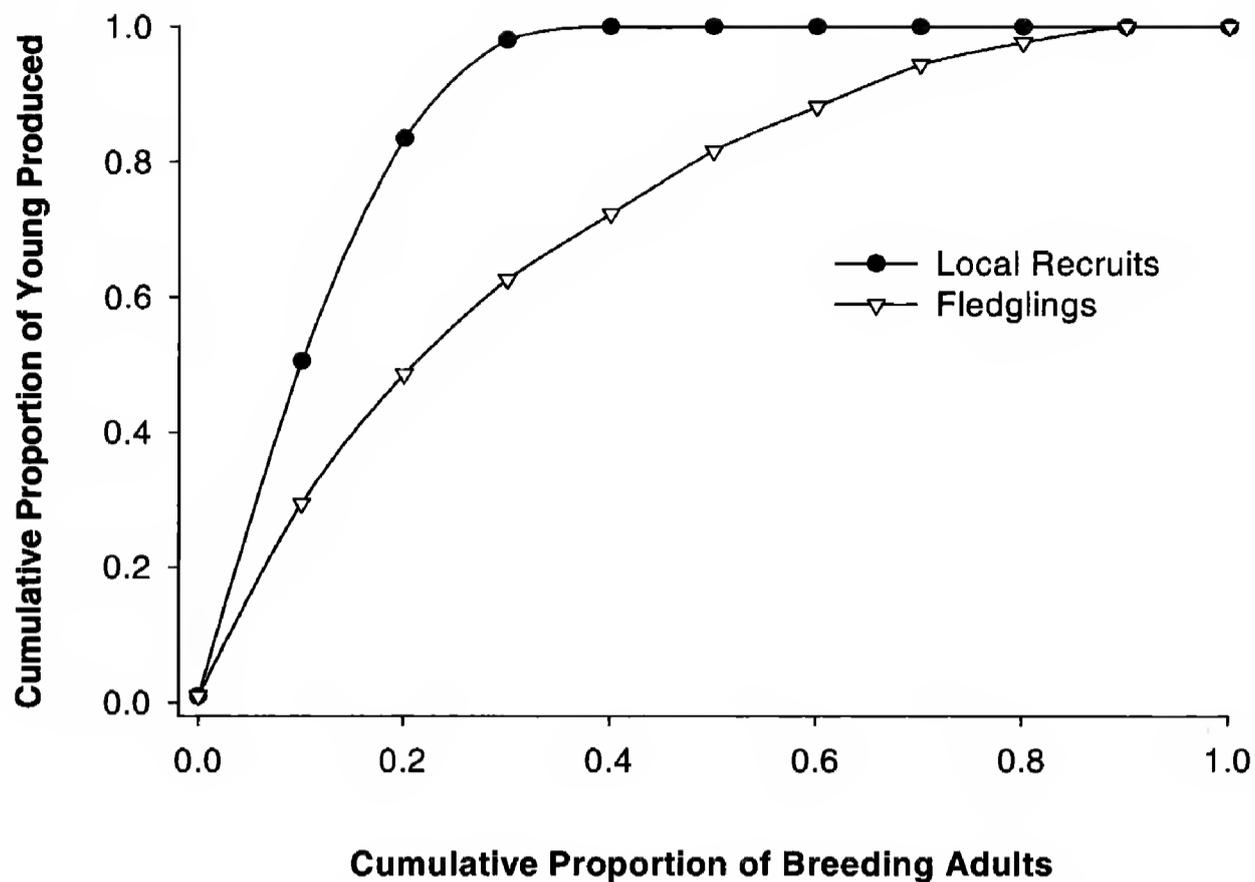


Figure 5. Individual variation in total fledgling production and reproductive success (number of offspring that were local recruits) among 290 color-marked adult (≥ 2 -yr-old) Northern Goshawks breeding between 1991 and 2000 on the Kaibab Plateau, Arizona. Whereas 254 (88%) adults successfully fledged young, only 73 (25%) made contributions to the future local breeding population.

sure of annual productivity. Another important finding was that reproductive success varied widely among breeding adults. Thus, the relationship between fledging success and recruitment appeared to be highly dependent upon the disproportionate contributions of fledglings and recruits made by a relatively small number of adults rather than overall population productivity. Our results further demonstrate that recruitment of goshawks on the Kaibab Plateau was a gradual process (as shown by a wide range among individuals in the age at first breeding) and that local recruitment was relatively low (8.6%). Given that 25% of adults fail to return to reclaim their territory each year (Reynolds et al. 2004), external recruitment (i.e., immigration) would need to be ca. 16% to maintain a stable breeding population.

Age at First Breeding and Local Recruitment. Goshawks are capable of breeding in their first year of life, and the proportion of breeders in first-year plumage has been reported to be as high as 35–40% (McGowan 1975, Reynolds and Wight 1978, Speiser and Bosakowski 1991, Younk and Bechard 1994). The proportion of young hawks in a breeding population may be reflective of density-dependent processes driven by the availability of nesting

territories, food, or mates (McGowan 1975, Newton 1989b, Ferrer et al. 2004). As breeder density and survival increases, fewer territories are available to prospective breeders, forcing socially subordinate younger hawks to wait, perhaps several years, to gain a breeding vacancy. Observations of individuals breeding in non-adult plumage may, therefore, reflect an important buffer mechanism compensating for an increased adult mortality rate (Ferrer et al. 2004). On the Kaibab Plateau, several demographic features such as a temporally stable adult survival rate (Reynolds et al. 2004), a high density of breeding territories (8.6/100 km²; Reynolds et al. 2005), and strong adult fidelity to territory and mate (R. Reynolds unpubl. data) suggest that young goshawks prospecting for breeding opportunities are faced with the alternatives of delaying breeding altogether or dispersing to recruit elsewhere (Wiens 2004). That some individuals remain (or return) as floaters in the vicinity of their natal population on the Kaibab Plateau has been confirmed by radiotelemetry (Wiens 2004) and a quick replacement of territorial hawks following mortality (Reynolds and Joy in press). Collectively, these features could explain the relatively advanced age of first-time breeders as well as the low

local recruitment level during our study. It is important to note, however, that these characteristics (territory density, adult fidelity, breeding age) appear to occur at higher levels on the Kaibab Plateau than reported for goshawks elsewhere.

Population Productivity. We found that the goshawk population on the Kaibab Plateau was no more successful in producing local recruits in years of high fledgling production than in years of low fledgling production. Thus, contrary to predictions, the size of an annual fledgling cohort was a poor predictor of local recruitment. In contrast, Weatherhead and Dufour (2000) found that local recruitment increased disproportionately with the size of Red-winged Blackbird fledgling cohorts, even though the overall return rate of banded nestlings in that study was small (2.4%) relative to our estimate for goshawks (8.6%). The strength of the relationship between population productivity and local recruitment, and our inability to detect such a relationship, may largely depend on the spatial extent of the study area relative to the extent of natal dispersal. For example, Red-winged Blackbirds disperse up to 40 km from natal territories (Moore and Dolbeer 1989), whereas young goshawks disperse up to 440 km from the Kaibab Plateau (Wiens 2004). The lack of a population-level relationship between fledging success and recruitment in our study may, therefore, simply reflect the difference between observing local recruitment within a relatively small subpopulation relative to general recruitment taking place over a regionally fragmented population that is connected by natal dispersal. Several lines of evidence indicate that most juveniles disperse long distances beyond the Kaibab Plateau in their first fall (Wiens 2004). Unfortunately, with the exception of two known cases of juvenile emigration, no information on the external recruitment success of locally-produced hawks exists for this study population.

Aside from a potentially inappropriate scale of investigation relative to the extent of the goshawk recruitment process, our data may have failed to support our hypothesis at the population level because of a lack of breeding opportunities during the later years of the study. During 2001–03, extreme drought conditions in northern AZ likely led to significant declines in goshawk prey populations (Salafsky 2004), and few adult pairs on the Kaibab Plateau attempted to breed. Under such poor breeding conditions, opportunities for inexperienced hawks attempting to breed for their first

time were reduced. For the most part, adult goshawks could only be captured or resighted when breeding, so newly recruiting hawks that acquired a breeding territory but did not lay eggs may have gone undetected during 2001–03. Poor breeding conditions during the later years of our study could also explain the lower than expected recruitment success of fledglings produced in the 2000 breeding season. However, removing the 2000 cohort from the analysis failed to substantially improve the relationship between population productivity and local recruitment. Our chi-square analysis showed that fledglings produced in 1991 and 1997 were twice as likely to be recruited as expected. With the exception of the 2000 fledgling cohort, we found no other significant deviations in the number of local recruits expected. We suggest that high juvenile survival, density-dependent effects, or changes in resource availability may have contributed to the disproportionately high recruitment success of fledglings produced during 1991 and 1997.

Individual Productivity. If fitness is defined as the contribution of an individual's genotype to subsequent generations proportional to that of other individuals (Lincoln et al. 1998), then our results clearly show a difference in fitness among goshawks on the Kaibab Plateau. Our results indicated that the likelihood of an adult contributing offspring to the future breeding population on the Kaibab Plateau increased disproportionately with the number of fledglings it produced. Therefore, goshawks appear to be similar to other monogamous raptor species in that reproductive success varies widely among individuals (Newton 1989b, Hakkarainen et al. 1997, Marti 1997). As would be expected for a monogamous raptor in a population showing high fidelity to territory and mate and equal survival rates of males and females, the sexes showed similar patterns of variance in reproductive success. Indeed, a few territorial pairs exhibited disproportionately high fitness levels in terms of the number of years they bred, total fledgling production, and the number of their offspring that survived to become breeding adults. Factors not explored in this study, such as breeding age, habitat quality, individual quality (as determined by genetic forces), or climate may contribute to individual heterogeneity in goshawk reproductive success.

On the Kaibab Plateau, the mean reproductive lifespan of adults (first breeding to disappearance) is 2 yr, but a few adults were found to breed for as

many as 10 yr (R. Reynolds unpubl. data). Adults who breed more often are likely to be more experienced, produce more fledglings, and show the highest fitness potential in terms of survival and reproduction (Cam et al. 1998). Newton and Rothery (2002), for example, demonstrated that almost all aspects of breeding performance in female Eurasian Sparrowhawks improved with age, but that the degree of improvement lessened with each successive year of life. In Denmark, Nielsen and Drachmann (2003) showed that fledgling production of European goshawks increased with female age from 1–7 yr, but declined thereafter. Similarly, Reynolds et al. (1994) reported a difference in fledging production between young-adult (second-year) and full-adult goshawks. These authors attributed changes in reproductive success to age-related trends in foraging efficiency, which could be buffered by pairing with more experienced mates.

Variation among individuals in fitness levels can have substantial effects on population growth, stability, and persistence (Bjørnstad and Hansen 1994, Conner and White 1999). Individual variation within raptor populations may be generated by temporal or spatial variations in resource availability and habitat quality (Hakkarainen et al. 1997, Franklin et al. 2000). Of particular interest is the relationship between individual fitness and habitat quality, as it is commonly supposed that birds prefer the habitat that will confer the greatest fitness (Fretwell and Lucas 1970). For goshawks, heterogeneity in fitness levels among territorial adults could be caused by spatial or temporal variations in food abundance, resource availability (as measured by qualitative differences in forest composition and structure among breeding areas), and individual hawk quality. However, recent efforts to detect spatial heterogeneity in goshawk reproductive parameters have had limited success. On the Kaibab Plateau, Joy (2002) ranked 101 goshawk territories as “high” or “low” quality based on differences in egg laying frequency and fledgling production. The length of time an adult female remained on a territory, breeder age, and the amount or spatial configuration of vegetative types within territories explained little of the variation (Joy 2002). Elsewhere, McClaren et al. (2002) found minimal spatial variation in the number of young fledged per nest among goshawk nest areas in three study sites in western North America. Given that these studies focused on territories (Joy 2002) and nest areas (McClaren et al. 2002) rather

than individual goshawks, we suggest that undetected turnovers between territory or nest occupants of different age, experience, or genetic quality could mask existing spatial patterns in reproduction. For the purposes of identifying the determinants of habitat quality for goshawks, we believe our finding of individual variation in reproductive success highlights the need to partition the effects of individual hawk quality from habitat quality. By controlling for individual hawk quality, researchers can more precisely estimate the effects of habitat versus non-habitat factors on components of goshawk fitness. Given the hypothesized role of forest composition and structure in generating individual variation in goshawk reproductive performance, long-term demographic research based on color-marked individuals can provide a powerful tool to guide goshawk conservation and management.

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PRODUCTIVITY AND MORTALITY OF NORTHERN GOSHAWKS IN MINNESOTA

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ABSTRACT.—Compared to other regions of North America, little information exists regarding Northern Goshawk (*Accipiter gentilis*) ecology and population dynamics in the western Great Lakes Region. We examined productivity and nesting habitat characteristics of goshawks in Minnesota from 1998–2001. Apparent nesting success varied annually from as low as 38% to as high as 83%. The Mayfield estimate of daily survival for nests was 0.992 ± 0.002 (SE). The mean fledgling number across years was 1.85 ± 0.14 for successful nests and 1.14 ± 0.17 for all nesting attempts. Twenty-one percent of all nesting attempts failed, primarily due to predation or suspected predation (52%) and inclement weather (35%). Overall, productivity of goshawks in Minnesota was at the lower end of the range reported in other studies across western North America, which is not atypical for peripheral populations. During the 3-yr study, we recorded mortalities of nine (four males and five females; eight radio-marked and one unmarked) adult goshawks—causes of mortality were avian (33%) and mammalian (22%) predation, human persecution (22%), and unknown causes (22%). Fifty-six percent of mortalities occurred during the breeding season, and 44% occurred during the winter. Based on radiotelemetry data, we estimated adult annual survival to be $74 \pm 7.8\%$, which is similar to survival estimated using mark-recapture analysis in three western North America studies.

KEY WORDS: *Northern Goshawk; Accipiter gentilis; breeding; Minnesota; mortality; productivity.*

PRODUCTIVIDAD Y MORTALIDAD DE *ACCIPITER GENTILIS* EN MINNESOTA

RESUMEN.—Existe poca información sobre la ecología y la dinámica poblacional de *Accipiter gentilis* en el oeste de la región de Grandes Lagos comparado con otras regiones de América del Norte. Examinamos la productividad y las características del ambiente de nidificación de *A. gentilis* en Minnesota desde 1998 hasta 2001. El éxito de nidificación aparente varió anualmente de modo drástico, desde 38% a 83%. El estimado de Mayfield de la supervivencia diaria de los nidos fue 0.992 ± 0.002 (EE). El número medio de volantones a lo largo de los años fue 1.85 ± 0.14 para los nidos exitosos y 1.14 ± 0.17 para todos los intentos de nidificación. El 21% de todos los intentos de nidificación fracasó, debido principalmente a la depredación o a la supuesta depredación (52%) y a las inclemencias del clima (35%). En total, la productividad de *A. gentilis* en Minnesota estuvo en el extremo inferior del rango reportado en otros estudios para el oeste de América del Norte, lo cual no es atípico para poblaciones periféricas. Durante los tres años de estudio, registramos la muerte de nueve adultos de *A. gentilis* (4 machos y 5 hembras; 8 marcados con transmisores y 1 sin marcar). Las causas de la mortalidad fueron depredación por aves (33%) y mamíferos (22%), persecución humana (22%) y causas desconocidas (22%). El 56% de las muertes ocurrieron durante la estación reproductiva y el 44% durante el invierno. Basados en datos de radio telemetría, estimamos que la supervivencia anual de los adultos fue del $74 \pm 7.8\%$, lo cual es similar a la supervivencia estimada usando análisis de captura-recaptura en tres estudios del oeste de América del Norte.

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The Northern Goshawk (*Accipiter gentilis*) is a large, forest-dwelling raptor generally associated with mature deciduous, coniferous, or mixed forests. Possible conflicts between timber harvest practices and goshawk habitat requirements have led to concern for the species' status (Kennedy 1997, United States Fish and Wildlife Service 1998). The goshawk has been proposed for listing several times under the U.S. Endangered Species Act and its status has been (and still is) the object of considerable litigation. In the western Great Lakes Region (WGLR) of North America, the goshawk is currently listed as a migratory non-game bird of management concern by the U.S. Fish and Wildlife Service (Region 3) and as a sensitive species by the U.S. Forest Service (Region 9). Few studies have examined goshawk productivity (Erdman et al. 1998) and mortality in the WGLR. Region-specific information on productivity and mortality factors is essential for development of sound management guidelines, but active management of the species in the WGLR has been hampered by the lack of data. In 1998, we initiated a broad-based ecological study of goshawks in Minnesota (Boal et al. 2001, Boal et al. 2003). Herein, we present the productivity and mortality data we collected on breeding goshawks in Minnesota, 1998–2000.

STUDY AREA

The study area encompassed most of northern Minnesota within the Laurentian Mixed-Forest Province (Minnesota Department of Natural Resources 2004; Fig. 1). Goshawks were distributed across the study area (Fig. 1), but a majority of goshawk nests were located on or near the Chippewa National Forest (47°23'N, 94°35'W). Study area elevation was ca. 200–400 m. Historical mean summer and winter temperatures were 18°C and –11°C, respectively, with maximum and minimum temperature records of 40°C and –46°C, respectively. Vegetation communities are described in Boal et al. (2003).

METHODS

Study Population. We did not systematically survey for breeding goshawks, so known breeding pairs in a single year were likely a relatively small proportion of all goshawks breeding in the study area (Daw et al. 1998). However, the goshawks monitored in this study were all known nesting goshawks in Minnesota during the study period of 1998–2000 (Boal et al. 2001, 2003). Nests in this study were from across the Laurentian Mixed-Forest Province of northern Minnesota and were likely representative of the Minnesota landscapes that goshawks use for nesting (Boal et al. 2001), but because our sample was not randomly selected, our inferences are limited to our sample.

Before this study, few goshawk nesting areas were known in Minnesota. We searched known goshawk nest

stands and areas where goshawks had been seen during previous breeding seasons. If a previous year's nest was not occupied, we conducted tree-by-tree searches of the stand, up to 500 m from the old nest (if the stand was sufficiently large for this search pattern). We also located new goshawk nest stands by searching likely areas or following up on reports of probable goshawk nests located serendipitously by personnel from cooperating agencies and the timber industry. We considered an area to be occupied if one goshawk was observed in or near a known nest stand, radio-tagged hawks were located in the area, or other evidence of activity was observed (e.g., recent construction of a nest). If an area was occupied by goshawks, we attempted to locate an occupied nest. An occupied nest was defined as a nest with eggs or young or the presence of an incubating goshawk.

Productivity. Once an occupied nest was located, we made periodic visits to monitor reproductive success. We considered goshawks to be nesting if a female was observed in an incubation position on the nest or during later stages of the nesting period when young were observed in the nest. We considered nestlings to have survived to fledge if they attained at least 80% of their first flight age (32 d old for goshawks; Boal 1994). We considered a nesting attempt as successful if at least one young fledged. We estimated both apparent nest success (e.g., the proportion of monitored nests known to have fledged young) and nest success using the Mayfield estimate based on exposure days (Bart and Robson 1982). Because confidence intervals can be more informative than tests of statistical significance (Johnson 1999), we assessed differences in productivity by examining overlap of 95% confidence intervals.

Nesting Failure. We attempted to determine cause of all nesting failures. In instances where dead adults or their remains were found at nests, we conducted in-field examinations of each carcass and location of death to attempt to identify the cause of death and, if depredated, the predator species. For example, claw marks ascending the nest tree and teeth marks on the carcass, feathers, and radio harness material of radio-tagged birds were indicative of mammalian predation (Einarsen 1956). In contrast, crimping plucks of feathers, stripped bones without tooth marks or evidence of mastication, single bill bite nips, and scrapes in bones indicated avian predators (Einarsen 1956).

Adult Mortality. There is little information on causes of adult mortality for raptors in general and goshawks in particular (Squires and Reynolds 1997). In addition to assessing causes of mortality of adult goshawks at nest sites, our sample of 32 radio-tagged goshawks (Boal et al. 2003) provided us with an opportunity to examine causes and timing of mortality among goshawks in Minnesota. We used telemetry to relocate all radio-tagged goshawks that died during the course of this study (Boal et al. 2001). We estimated the annual survival rate with the Kaplan-Meier survival model (Kaplan and Meier 1958) as modified by Pollock et al. (1989).

RESULTS

We located 13, 19, and 21 areas occupied by goshawks in 1998, 1999, and 2000, respectively. Two

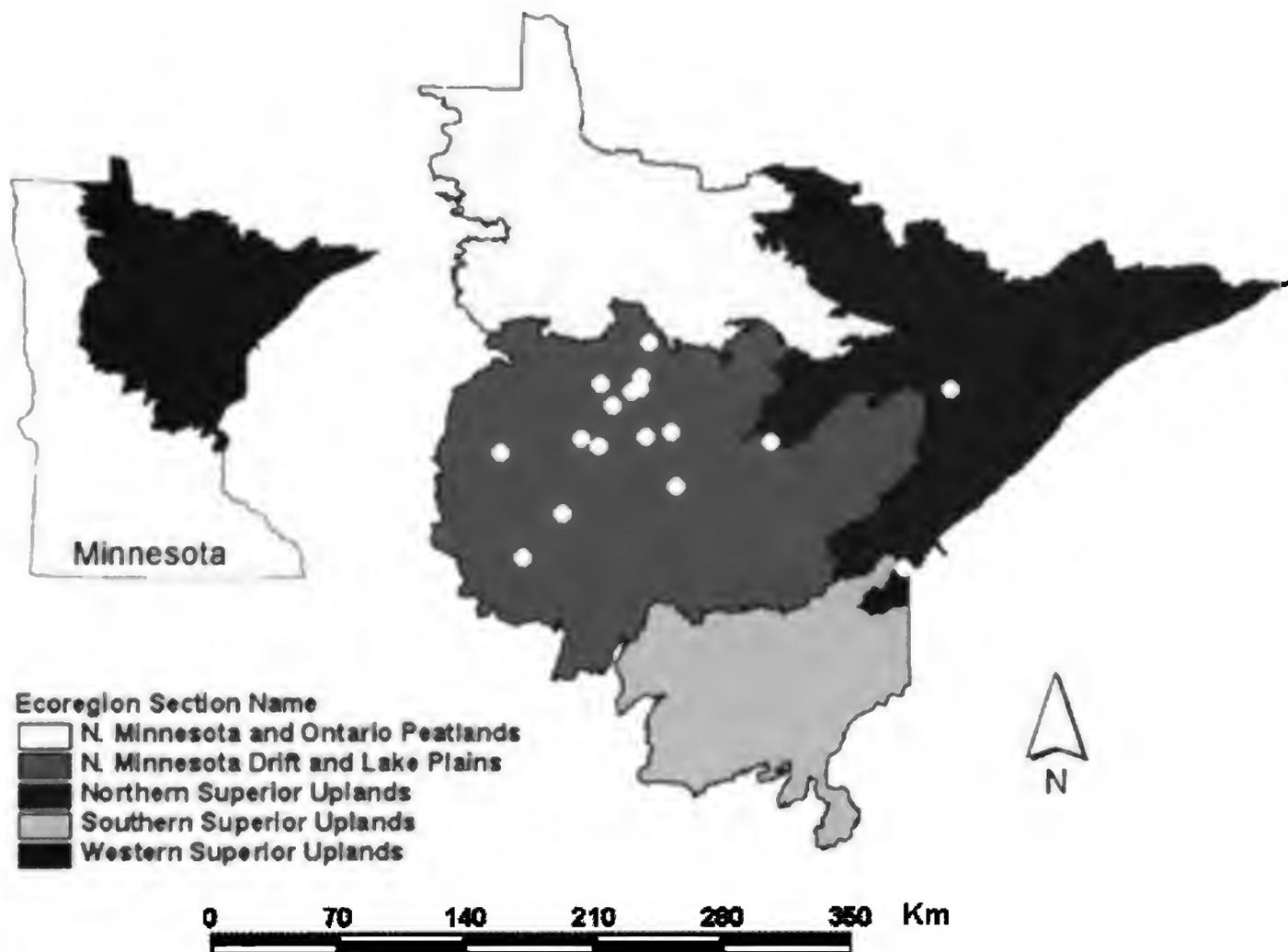


Figure 1. Study area and distribution of Northern Goshawk nests sites (open circles) included in this study, Minnesota 1998–2000. Ecoregions are based on Minnesota Department of Natural Resources (2004).

additional areas were located by cooperators in 1998, but were not reported to us until 1999. Although one of these nesting attempts was verified as successful, the two nests were not monitored to assess productivity. Thus, we only include the original 13 of 15 areas from 1998 for productivity assessment. Of the 15 breeding areas occupied in 1998, 11 (73%) were occupied in 1999. Of 23 known breeding areas occupied in 1998 and/or 1999, 13 (57%) were occupied in 2000. Although breeding did not occur in all occupied areas, 15 occupied areas were located in 1998, seven additional areas in 1999, and nine additional areas in 2000, for a total of 31 areas occupied by goshawks at least 1 yr during the 3-yr study period. We did not monitor productivity at one nest, and two others failed in 1998. Sixteen (84%) pairs of goshawks from 19 occupied areas nested in 1999, and 15 (71%) pairs from 21 occupied areas nested in 2000. We observed that some areas were occupied by non-breeding goshawks. For example, a widowed female, radio-tagged in 1998, was tracked in her breeding area, but did not breed in 1999. Likewise, in 2000 a widowed, non-breeding female

roamed more widely than she had while breeding in 1999, but still occupied her 1999 breeding area. A pair that had been radio-tagged and successfully nested in 1999 occupied their breeding area, but did not nest in 2000. In contrast, after her mate died during the winter, one widowed female moved 15 km to pair with a male in a previously unknown breeding area the following spring.

Productivity. We assessed success at 43 and productivity at 42 goshawk nests. Nesting success varied considerably among years, with a high of 83% in 1998 and a low of 37% in 1999. We observed that 67% of nesting attempts fledged young successfully in 2000 and the 3-yr mean for fledging success was $62 \pm 23.4\%$ (SE). Mayfield estimates for daily survival were 0.9998 ± 0.0006 (SE) in 1998, 0.985 ± 0.005 in 1999, and 0.993 ± 0.005 in 2000, with an overall daily survival rate of 0.992 ± 0.002 . Based on a 32-d incubation period (Squires and Reynolds 1997) and a 32-d period to 80% of first flight age (Boal 1994), Mayfield estimates of nest success were 99% in 1998, 39% in 1999, 65% in 2000, and 59% over the 3-yr study period.

Goshawk nests fledged a mean of 1.75 ± 1.05

young in 1998 ($N = 12$), 0.81 ± 1.17 young in 1999 ($N = 16$), and 0.93 ± 0.80 ($N = 15$) young in 2000. Fledglings per nesting attempt were not statistically different between 1998 and 1999 (\bar{x} difference = 0.938; 95% CI = 0.057–1.820), between 1998 and 2000 (\bar{x} difference = 0.817; 95% CI = 0.082–1.550), or between 1999 and 2000 (\bar{x} difference = -0.121 ; 95% CI = -0.861 – 0.619). In contrast, when examining only those nests that were successful, goshawks fledged a mean of 2.10 ± 0.74 young in 1998 ($N = 10$), 2.17 ± 0.75 young in 1999 ($N = 6$), and 1.40 ± 0.52 young in 2000 ($N = 10$). Fledgling numbers at successful nests were not statistically different between 1998 and 1999 (\bar{x} difference = -0.067 ; 95% CI = -0.890 – 0.757), but were higher in 1998 (\bar{x} difference = 0.700; 95% CI = 0.102–1.300) and 1999 (\bar{x} difference = 0.767; 95% CI = 0.895–1.440) than in 2000. Mean number of fledglings per nest for all years combined was 1.14 ± 1.07 for all nesting attempts and 1.85 ± 0.73 for successful nests only.

Nesting Failure. Of the 43 goshawk nests monitored, two failed in 1998, 10 failed in 1999, and five failed in 2000. Of these 17 failures, 23% were due to mammalian predation, 18% were due to avian predation, and we suspected another 12% were due to predation, but we were unable to determine whether the predator was avian or mammalian. Two of the mammalian predations resulted in mortalities of adult female goshawks (detailed below). Weather contributed to 35% of nesting failures, the majority of which occurred during the incubation stage of the nesting period in 1999 when the region experienced a 10–11 d period of almost constant rain. The cause of 12% of nesting failures was undetermined.

Adult Mortality. Nine goshawks, eight of which were radio-tagged, died during this study. Five (56%; four females and one male) of these nine mortalities occurred during the breeding seasons. One female and one male were preyed upon by Great Horned Owls (*Bubo virginianus*), two females were killed by mammals, and one female was consumed by a Red-tailed Hawk (*Buteo jamaicensis*). The remaining four (44%) mortalities (one female and three males) occurred during the winter months. The female that died during the winter had been shot. The mortality of one male appeared to also be due to human actions; only the radio that had been attached to the male was recovered and it had been obviously cut from the body of the goshawk. Furthermore, the radio

lacked any mastication or pecking marks typical of those on goshawks that were depredated. The causes of death could not be verified for the other two male goshawks.

We excluded the single, non-radio-marked female that was killed in 1999 from estimates of survival. The Kaplan-Meier estimate for annual survival based on 32 radio-tagged goshawks was $74 \pm 7.8\%$. Because our study was not originally designed to estimate adult survival, our survival estimate should be interpreted in the context of our sample of 32 radio-marked goshawks captured at breeding areas over the 3-yr study period. However, these data do provide some insight in the annual survival of goshawks in the study area.

DISCUSSION

Productivity. We observed annual variability in fledglings produced per nest attempt (range = 0.87–1.85) and per successful nest (range = 1.40–2.17) during the 3 yr of this study. Such variability is typical of temporal patterns in reproductive success in goshawks (e.g., DeStefano et al. 1994, Kennedy 1997, McClaren et al. 2002). McClaren et al. (2002) found high temporal variability in productivity among goshawk nests monitored 4–10 yr in three different populations in western North America. Within the WGLR, Erdman et al. (1998) reported fledgling numbers from Wisconsin goshawk nests over a 24-yr period, and found a mean of 1.7 fledglings per nesting attempt ($N = 184$) and 2.2 per successful nest ($N = 138$). However, Erdman et al. (1998) also indicated that fledging rates among nesting attempts decreased from the earlier years (1971–81) to later years (1982–92) of their study. We do not have historical data for this study area to evaluate temporal trends in productivity, but the fledging success over the 3-yr period of monitoring did not vary statistically. Productivity in the Upper Peninsula of Michigan was similar to ours, with a reported 1.1 and 1.7 fledglings per occupied ($N = 36$) and successful ($N = 24$) nests, respectively (Lapinski 2000). Fledgling rate among successful nests in our study and others conducted in the WGLR appear to be slightly lower than average, but well within the range reported in studies from the western United States (e.g., Kennedy 1997, Boal and Mannan 1994, Bull and Hohmann 1994, Reynolds et al. 1994).

Nesting Failure. The most common nest predator of goshawk nests in North America appears to be Great Horned Owls (Kennedy 2003), but wol-

verines (*Gulo gulo*; Doyle 1995) and fishers (*Martes pennanti*; Erdman et al. 1998) are known to prey upon goshawk nestlings, and raccoons (*Procyon lotor*) are also likely nest predators. Erdman et al. (1998) attributed predation by fishers as the primary cause of nesting failure among goshawks in Wisconsin, but did not provide details for the basis of their conclusion, nor did they report the actual number of nesting failures due to fishers. Mammal depredation (suspected to be fishers) of nests in our study was comparatively low (9%), but collective depredation (mammalian, avian, unknown) caused the failure of 21% of goshawk nests in Minnesota.

Weather can also influence productivity of goshawks. Cold weather and rain can reduce the number of goshawk pairs attempting to nest (Kostrzewa and Kostrzewa 1990) and can lead to egg and chick (Zachel 1985) mortality. In our study, inclement weather accounted for failure of 12% of all nesting attempts. These failures occurred primarily during the incubation stage in 1999 when our study area experienced a 10–11 d period of almost constant rainfall. We suspect that some male goshawks may have been unable to provision their mates adequately during this period, eventually leading females to either abandon their nests or temporarily leave their nests to forage, allowing the eggs to chill and die.

Adult Mortality. Mortality data for goshawks in the WGLR are based almost solely on females found killed at or near their nests (Erdman et al. 1998). Thus, there are no data available prior to our study on causes of goshawk mortality away from their nests or during the non-breeding season. Our estimate of annual survival ($74 \pm 7.8\%$) based on telemetry was quite similar to mark-recapture estimates in California (61–69%; DeStefano et al. 1994), New Mexico (60–96%; Kennedy 1997), and northern Arizona (69–87%; Reynolds and Joy 1998). All of these authors indicate imprecision in their studies due to a variety of reasons, and DeStefano et al. (1994) concluded accurate estimates of survival based on mark-resightings would require large numbers of marked birds, high resighting rates, and a minimum of 5 yr of data. This robust a data set has not been and is unlikely to be collected in the WGLR. In contrast, White and Garrott (1990) indicated survival estimates based on radiotelemetry requires smaller samples in general than mark-resighting estimates. Furthermore, backpack radio attachments appear to have no significant effect on survival of goshawks (Reynolds

et al. 2004). Our data supported White and Garrott's (1990) assertion; we were able to estimate survival rates with reasonable precision through marking considerably fewer birds than banding and resighting would require. However, we did not have a sufficient sample of radio-tagged birds to estimate temporal and gender differences in adult survival.

One male that died during the winter of 1999–2000 had been banded as a juvenile at Hawk Ridge, MN, during the fall migration of 1988 (D. Evans pers. comm.). This male and his mate had fledged two young successfully in 1999. To our knowledge this 11-yr male is the oldest known recorded breeding male goshawk reported for North America. Interestingly, the oldest reported female goshawk (12 yr old) in North America was also reported from Minnesota (Evans 1981).

The majority of information on causes of mortality among adult goshawks is anecdotal (Squires and Reynolds 1997). Goshawks succumb to several different diseases and parasites (Redig et al. 1980, Ward and Kennedy 1996, C. Boal unpubl. data). Accidents and injuries, such as flying into windows (C. Boal unpubl. data) or choking on prey (Bloxton et al. 2002), also result in mortality. The primary documented cause of mortality among free-ranging goshawks, however, appears to be predation (Squires and Kennedy in press).

Known predators of adult goshawks include Great Horned Owls (Rohner and Doyle 1992, Boal and Mannan 1994, Erdman et al. 1998), Golden Eagles (*Aquila chrysaetos*; Squires and Ruggiero 1996), Pine Martens (*Martes americana*; Paragi and Wholecheese 1994), and fishers (Erdman et al. 1998). Of five adult goshawks taken by predators in our study, two were killed by Great Horned Owls. In the WGLR, fishers may also be an important predator of goshawks; predation by fishers was identified as the cause of mortality for four adult female goshawks in Wisconsin (Erdman et al. 1998) and two of five goshawk deaths in our study. We believe the goshawk killed in our study by a Red-tailed Hawk may be an exceptional incident, but the two species have been observed engaged in physical agonistic encounters (Crannell and DeStefano 1992, C. Boal unpubl. data). In areas of sympatry (La Sorte et al. 2004), Red-tailed Hawk predation may be more common.

Most mortality data for goshawks is for the nesting season. We found that mortality occurred with equal frequency in the breeding and winter seasons, suggesting that survival outside of the breed-

ing season is an important aspect of goshawk population dynamics. Our data also suggested that, despite legal protection, persecution was still a factor affecting goshawk survival.

Results from Wisconsin (Erdman et al. 1998) and our study suggested predators were a major cause of goshawk mortality in the WGLR. However, the influence of predators on goshawk population demography and whether current predation rates are similar to historic rates or have increased as a consequence of human activities (e.g., timber harvest, reintroduction of fishers) in the WGLR, as suggested by Erdman et al. (1998), has yet to be assessed rigorously. The development and use of standardized field methods for evaluating causes of mortality of goshawks and publication of existing mortality data would be helpful in this regard. Without reliable survival data, rates of population growth or decline cannot be estimated accurately for the WGLR goshawk population.

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RELATIONSHIPS BETWEEN WINTER AND SPRING WEATHER AND NORTHERN GOSHAWK (*ACCIPITER GENTILIS*) REPRODUCTION IN NORTHERN NEVADA

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ABSTRACT.—Ecological factors, such as weather, play important roles in raptor population dynamics. We used logistic and Poisson regression analyses to investigate relationships between late winter, spring, and early summer temperatures and precipitation and Northern Goshawk (*Accipiter gentilis*) breeding, failure, and productivity in northern Nevada from 1992–2002. We also examined weather data for possible patterns that could explain reported trends in goshawk reproduction. Declines in occupancy of nesting territories by breeding goshawks were related to colder February and March temperatures and increased April precipitation. Warmer April temperatures and decreased precipitation in April–July favored reproductive success. Of all significant weather variables, only February and March temperatures had significant temporal trends. Although adverse weather is known to affect goshawk reproduction by decreasing nestling growth and survival, it is unlikely that direct weather effects were responsible for reported reproductive trends in our study area. Weather may have operated indirectly, influencing reproduction through changes in goshawk hunting behavior or food supply.

KEY WORDS: *Northern Goshawk; Accipiter gentilis; weather; breeding; population trends; Nevada.*

RELACIONES ENTRE EL CLIMA DE INVIERNO Y DE PRIMAVERA Y LA REPRODUCCIÓN DE *ACCIPITER GENTILIS* EN EL NORTE DE NEVADA

RESUMEN.—Factores ecológicos como el clima tienen un papel importante en la dinámica poblacional de las aves rapaces. Utilizamos análisis de regresión logística y de Poisson para investigar las relaciones entre las temperaturas y las precipitaciones de fines del invierno, de la primavera y del comienzo del verano, y los fracasos o éxitos reproductivos y la productividad de *Accipiter gentilis* en el norte de Nevada entre 1992 y 2002. También examinamos los datos de clima para encontrar posibles tendencias que puedan explicar las tendencias documentadas de la reproducción de estos halcones. La disminución en la ocupación de territorios de nidificación por halcones reproductivos se relacionó con las temperaturas más frías de febrero y marzo y el aumento de las precipitaciones en abril. Las temperaturas más cálidas de abril y la disminución de las precipitaciones en abril-julio favorecieron el éxito reproductivo. De todas las variables climáticas significativas, sólo las temperaturas de febrero y marzo presentaron tendencias temporales significativas. A pesar de que es sabido que las condiciones climáticas adversas afectan la reproducción de estos halcones al disminuir el crecimiento y la supervivencia de los polluelos, es poco probable que los efectos directos del clima fueran responsables de las tendencias reproductivas documentadas en nuestro sitio de estudio. Las condiciones climáticas pueden haber operado indirectamente, influenciando la reproducción a través de cambios en el comportamiento de caza de los halcones, o en la disponibilidad de alimento.

[Traducción del equipo editorial]

Weather can directly influence Northern Goshawk (*Accipiter gentilis*) population dynamics by affecting survival (Zachel 1985, Squires and Reynolds 1997, Bloxton 2002), movements (Marcström and Kenward 1981, Squires and Ruggiero 1995), and nestling development (Kostrzewa and Kostrze-

wa 1990). Temperature and precipitation may also indirectly affect prey populations (Van Horne et al. 1997, Bloxton 2002), foraging behavior (Zachel 1985), and other mortality factors (Newton 1979).

Studies addressing the relationships between weather and goshawk reproduction (Kostrzewa and Kostrzewa 1990, 1991, Patla 1997, Penteriani 1997, Ingraldi 1998, Bloxton 2002), generally agree that colder and wetter spring weather nega-

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tively affects goshawk reproduction; however, the association between winter weather and goshawk reproduction is not well studied. These studies have also only considered time periods <6 yr (Ingraldi 1998).

We previously reported declines in goshawk nesting territory occupancy and increases in breeding failure in northern Nevada from 1992–2002 (Bechard et al. in press). Determining the ecological factors responsible for these reproductive trends is difficult because any variable that showed a temporal trend from 1992–2002 will consequentially be correlated with reproduction. However, because of the known links between weather and goshawk reproduction and the abnormally low precipitation and drought conditions reported in the northern Great Basin from 1999–2002 (National Drought Mitigation Center 2003), we suspected that weather conditions affected goshawk reproduction in northern Nevada. Here, we address the associations between late winter, spring, and early summer temperature and precipitation and long-term trends in goshawk reproductive performance.

METHODS

Study Area. We conducted the study in the Independence and Bull Run Mountain ranges of Elko County, northern Nevada, during 1992–2002. The study area extended ca. 150 km north-to-south, 10–30 km east-to-west, and encompassed ca. 94 000 ha. The area is a mosaic of public lands administered by the United States Department of Agriculture Forest Service (Humboldt-Toiyabe National Forest) interspersed with private lands. Elevations range from ca. 1700–3000 m on the highest peaks. A mixture of land uses occurred in the study area, including cattle ranching, gold mining, and outdoor recreation (hunting, camping, and off-road vehicle use).

The sagebrush steppe was typified by big sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and rabbitbrush (*Chrysothamnus* spp.). Common native grasses included native bluebunch wheatgrass (*Pseudoroegneria spicata*) and Idaho fescue (*Festuca idahoensis*), and introduced cheatgrass (*Bromus tectorum*) and medusahead wildrye (*Taeniatherum caput-medusae*) also occur (Loope 1969; P. Jelinek, Humboldt-Toiyabe National Forest, pers. comm.). In the study area, goshawks nested exclusively in quaking aspen (*Populus tremuloides*), which occurred in naturally-fragmented stands where sufficient moisture was present. Subalpine fir (*Abies lasiocarpa*) replaces quaking aspen above elevations of 2500 m (Loope 1969).

Dense willow (*Salix* spp.), thickets, and cottonwoods (*Populus* spp.) occurred in riparian areas at all elevations.

Field Methods. In April of 1991, 1992, and 1994–96, we used helicopters to initially locate and subsequently survey all historical goshawk nesting territories in the study area. We defined a nesting territory as the area containing one or more nests occupied by a single pair of goshawks in any breeding season (Postupalsky 1974,

Woodbridge and Detrich 1994, Reynolds and Joy 1998) We discontinued helicopter surveys after 1996.

Beginning in mid-May of each year from 1992–2002, we conducted ground surveys of all historically-occupied nesting territories (i.e., previously located by helicopter and used by goshawks) to determine occupancy by goshawk breeding pairs. We conducted ground surveys on foot and with all-terrain vehicles by returning to nesting territories and thoroughly searching stands and adjacent stands for the presence of breeding goshawks. Because territories in our study area were relatively small and nest structures obvious, we were able to search each territory completely and, therefore, assume a uniform probability of detection. We were unable to reach all nesting territories each year because roads throughout the study area were periodically snow-covered or washed-out, and private land was not always accessible.

Beginning in mid-June of each year, we revisited occupied nesting territories to determine productivity (Bechard et al., in press). We climbed all occupied nest trees and counted and banded nestlings when they were approximately 21–31 d old (age based on nestling plumage, Boal 1994). We considered a pair failed if there was no sign of goshawks (adults or nestlings) at or near an occupied nest when it was revisited in June.

Data Analyses. We determined nesting territory occupancy, productivity per breeding pair, breeding failure, and productivity per successful pair. Because we visited most nests only twice during the breeding season, there was as much as a 30-d interval between our nest visits. Therefore, we could not always determine the cause of a nest failure. There were no instances that clearly indicated the nesting attempt had failed due to depredation or any other factor unrelated to weather; therefore, we included all failures in our analysis.

We downloaded weather data for the study area from the Natural Resources Conservation Service/SNOTEL website (Jack's Creek Upper weather station; Natural Resources Conservation Service 2003). Because SNOTEL considered temperature data for 2002 unreliable, we did not include those data.

To analyze 11-yr trends in reproduction, we used logistic regression for binary outcomes (i.e., nesting territory occupancy and nesting failures) and Poisson regression for counted outcomes (i.e., productivity). To account for the fact that repeated measurements on a nesting territory over time might not be statistically independent (Allison 1999), we used Generalized Estimating Equations ("GEE;" PROC GENMOD; SAS Institute, Inc., Cary, NC U.S.A.), which allowed us to cluster our data by nesting territory (Stokes et al. 2000).

We modeled mean daily temperature (°C), cumulative monthly precipitation (cm; Fig. 1, 2), and year as continuous explanatory variables. We used only weather data from January–July, as we felt that they were most biologically relevant. We considered individual months and groups of months (i.e., January and February, February and March) in analyses, resulting in 27 possible explanatory variables per reproductive outcome (13 for mean daily temperature, 13 for cumulative monthly precipitation, and 1 for year). Due to low sample sizes ($N = 11$ yr), we did not consider more than one explanatory variable per model. Therefore, to avoid over specifying our

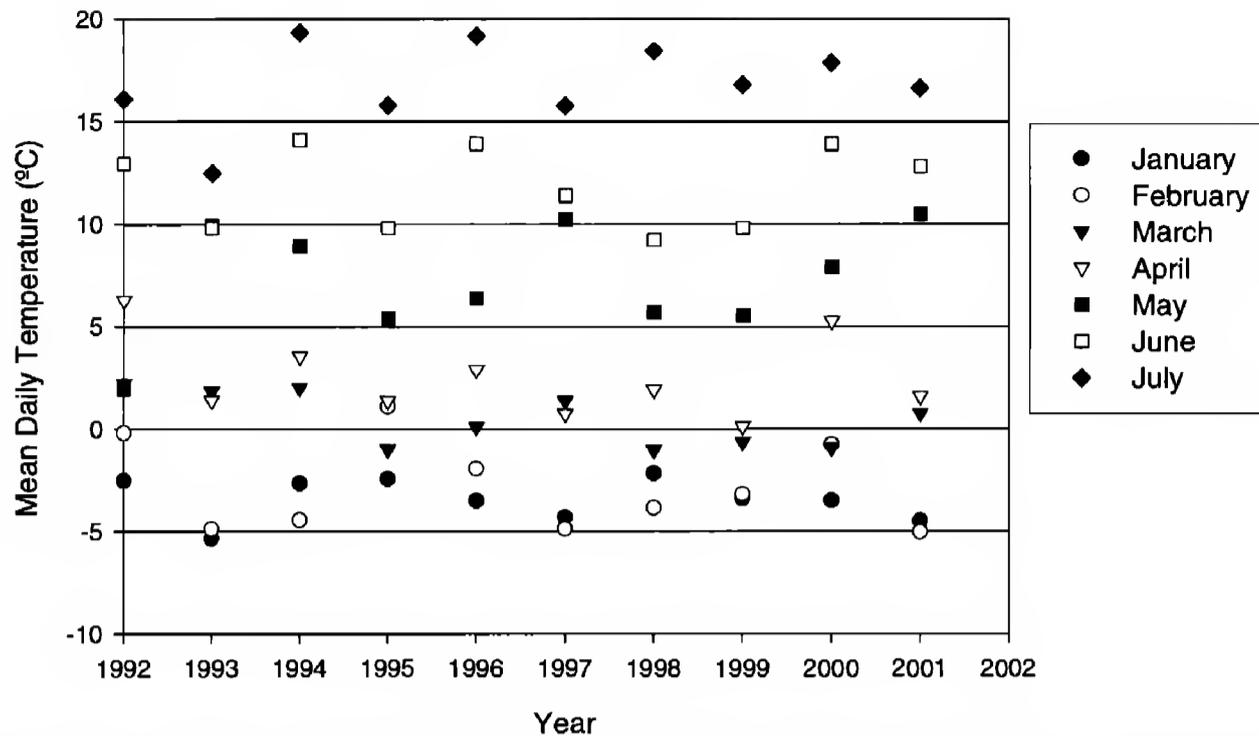


Figure 1. Mean daily temperature for January–July in the Independence and Bull Run mountains, Nevada for 1992–2002.

models, we ran separate univariate models for each explanatory weather variable and employed a pre-screening procedure to decide which models best explained the relationship between weather and goshawk reproduction.

During pre-screening, we only considered weather variables that appeared to be biologically relevant. For example, July weather would not be biologically related to occupancy in the same year because occupancy occurs before July. In addition, for each of the four reproductive outcomes, we ran several competing univariate models: each competing model used weather data from a single month or group of months as the explanatory variable. For example, 11 competing occupancy models used mean daily temperature as the explanatory variable, and an additional 11 occupancy models used cumulative monthly precipitation. For each reproductive outcome, we then selected the models with the single most statistically significant temperature and precipitation variables. Thus, for each reproductive outcome, we presented three separate univariate models: one for temperature, one for precipitation, and one for year. To avoid inflated Type I error rates, we assessed significance of all models using a step-down Bonferroni correction (Holm 1979). Although our statistical method has the potential to produce spurious results (Freedman 1983), the GEE has no other measure by which to assess multiple competing models.

We evaluated the results of logistic regression models by exponentiation of the model coefficient to obtain odds ratios, and we evaluated the results of Poisson regression by exponentiation of the model coefficient to obtain percent increase in the mean values of dependent variables. In the analyses, we only included nesting territories for which we knew the reproductive outcome.

To determine if any patterns existed in local weather variables, we used simple linear regression (JMP IN; SAS Institute, Inc., Cary, NC U.S.A.). For each weather variable that was significantly related to occupancy and fail-

ure (one temperature variable and one precipitation variable per each reproductive outcome), we regressed year against the temperature or precipitation variable.

RESULTS

We initially located 27 nesting territories in 1992, and found five, five, and four additional nesting territories in 1993, 1994, and 1996, respectively. We monitored a mean of 32.5 ± 4.7 ($\bar{x} \pm SD$) nesting territories annually (Table 1). Goshawks occupied an average of 20.3 ± 6.7 of these nesting territories each year. The odds of nesting territory occupancy by breeding pairs increased by 55.8% with each 1°C increase in combined February and March mean daily temperature (odds ratio = 1.558, $P = 0.018$; Table 2). The odds of occupancy of a nesting territory increased by 7.7% for every cm increase in cumulative April precipitation (odds ratio = 1.077, $P = 0.03$). We detected a significant cooling trend in combined February and March mean daily temperature in our study area ($r^2 = 0.41$, $P = 0.04$), but we found no trend in cumulative April precipitation ($r^2 < 0.0002$, $P = 0.97$).

Goshawk breeding pairs fledged a mean of 2.27 ± 0.76 young annually. Mean productivity per breeding pair increased 10.5% for every 1°C increase in the mean daily April temperature (Table 3; percent change in mean = 1.105, $P < 0.0001$). Mean productivity per breeding pair decreased by 1.9% for every 1 cm increase in combined April and May precipitation (percent change in mean = 0.981, $P < 0.0003$).

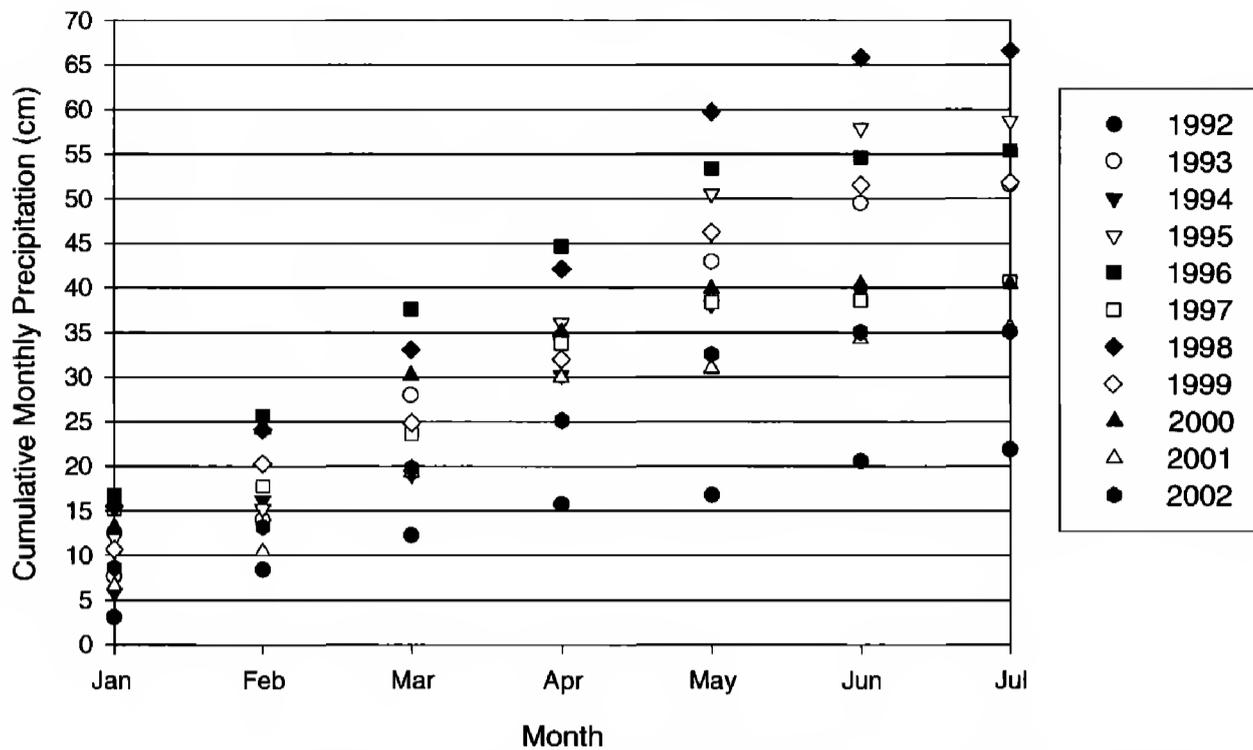


Figure 2. Monthly precipitation in the Independence and Bull Run Mountains, Nevada, for 1992–2002, expressed as cumulative monthly totals for January–July.

On average, 13.5% of breeding attempts failed. The odds of failure decreased by 40.5% with every 1°C increase in mean daily April temperature (Table 2; odds ratio = 0.595, $P < 0.0007$) and increased by 8.7% with each cumulative 1 cm increase in combined May and June cumulative precipitation (odds ratio = 1.087, $P < 0.006$). We found no trends in April ($r^2 = 0.094$, $P = 0.39$) or combined May and June ($r^2 = 0.007$, $P = 0.80$) temperatures.

Successful pairs produced a mean of 2.64 ± 0.57 young. For each 1°C increase in mean daily April temperature, we found a 6.4% increase in mean productivity per successful pair (Table 3; percent change in mean = 1.064, $P < 0.0001$). Mean productivity per successful pair decreased by 3.2% for each cumulative cm of combined June and July precipitation (percent change in mean = 0.978, $P = 0.042$).

DISCUSSION

Long-term trends in goshawk reproduction were significantly related to weather, with a stronger influence of temperature than of precipitation. Although late winter temperatures decreased in the study area from 1992–2002, our results suggested that warmer late winter temperatures favored goshawk breeding. Decreased productivity has been related to colder and wetter spring weather (Kostrzewa and Kostrzewa 1990, Patla 1997, Penteriani 1997, Bloxton 2002). Colder temperatures increase

energetic stresses and increase dietary demands on raptors and can result in non-laying (Newton 1979). Studies correlating winter temperatures with North American goshawk reproduction are lacking, but in European goshawks winter temperatures were not related to occupancy by breeding pairs (Kostrzewa and Kostrzewa 1991). However, the larger size of European goshawks may make them more robust to temperature and energetic demands early in the breeding season than the smaller North American subspecies (Kendleigh 1970).

Our finding of increased April precipitation favoring occupancy by breeding pairs was unusual, and we found no previous studies to support this result. Moreover, increased precipitation early in the breeding season is typically associated with reduced numbers of breeding pairs (Kostrzewa and Kostrzewa 1990, Ingraldi 1998, Bloxton 2002). Perhaps our finding of statistical significance does not necessarily relate to biological relevance, and the significant result is spurious.

The temporal trend in the failure of breeding attempts was strongly related to April temperature and cumulative May and June precipitation. Increased precipitation and decreased temperatures during the egg-laying and early nestling periods can increase egg and nestling mortality rates (Hoglund 1964, Zachel 1985) and affect nestling development (Kostrzewa and Kostrzewa 1990).

Table 1. Annual reproductive performance of Northern Goshawk nesting territories based on surveys conducted May–June 1992–2002 in the Independence and Bull Run Mountains, Nevada. All data previously reported in Bechard et al. (in press).

YEAR	No. NESTING TERRITORIES		OCCUPANCY (%)	No. BREEDING PAIRS ^a		FAILURE (%) ^c	TOTAL No. YOUNG ^d	No. YOUNG PER BREEDING PAIR	
	SURVEYED	NO. NESTING TERRITORIES OCCUPIED		BREEDING PAIRS ^a	SUCCESSFUL PAIRS ^b			YOUNG PER BREEDING PAIR	YOUNG PER SUCCESSFUL PAIR
1992	27	22	81.5	22	21	4.5	61	2.77 ± 0.92	2.90 ± 0.70
1993	32	25	78.1	24	22	12.5	50	2.08 ± 1.14	2.38 ± 0.86
1994	37	26	70.3	19	24	10.5	47	2.47 ± 1.22	2.76 ± 0.90
1995	37	27	73.0	25	20	28.0	46	1.84 ± 1.40	2.56 ± 0.92
1996	41	30	73.2	30	28	6.7	73	2.43 ± 0.94	2.61 ± 0.68
1997	24	20	83.3	19	19	5.3	39	2.05 ± 0.85	2.17 ± 0.71
1998	33	18	54.6	18	15	16.7	40	2.22 ± 1.17	2.67 ± 0.62
1999	33	17	51.5	17	12	29.4	26	1.53 ± 1.33	2.17 ± 1.03
2000	33	18	54.6	18	18	0.0	61	3.39 ± 0.78	3.39 ± 0.78
2001	30	13	43.3	13	10	23.1	25	1.92 ± 1.55	2.50 ± 1.27
2002	31	7	22.6	7	4	42.9	10	1.43 ± 1.40	2.50 ± 0.58
Total	358	223	—	212	193	—	478	—	—
Mean	32.5 ± 4.7	20.3 ± 6.7	62.4 ± 18.8%	19.3 ± 6.1	17.5 ± 6.8	13.5	43.5 ± 18.3	2.27 ± 0.76	2.64 ± 0.57

^a Reflects number of pairs for which productivity was determined.

^b Success defined as raising at least one young to ≥21 d post-hatching.

^c Percent of breeding pairs that were successful; includes pairs where productivity was not determined.

^d The number of young reaching ≥21 d post-hatching.

Table 2. Odds ratios, confidence intervals (CI), and significance of weather variables related to Northern Goshawk nesting territory occupancy in the Independence and Bull Run Mountains, Nevada, for 1992–2002.

MODEL TERM	ODDS RATIO	95% CI ^a	P-VALUE ^b
Occupancy by breeding pairs			
Year ^c	0.785	0.701–0.880	<0.0002
Mean daily combined February and March temperature	1.558	1.135–2.138	0.018
Cumulative April precipitation	1.077	1.014–1.143	0.03
Failure			
Year	1.157	1.021–1.312	0.044
Mean daily April temperature	0.595	0.455–0.780	<0.0007
Cumulative combined May and June precipitation	1.087	1.031–1.146	<0.006

^a Odds ratios are nonsignificant if confidence interval covers 1.0 (even odds).

^b Significance of terms assessed using a step-down Bonferroni adjustment (Holm 1979).

^c Data for year model terms taken from Bechard et al. (in press).

Despite evidence that weather can directly affect goshawk breeding, it is unlikely that direct weather effects are solely responsible for our reported trends in reproduction (Newton 1998). We found no significant temporal trends in weather related to nest failure, suggesting changes in that reproductive variable were due to other factors such as reduced hunting and food provisioning due to continued rainfall (Zachel 1985, Bloxton 2002). Also, depredation of goshawk nests can result in nest failures. Because our nest visits were several weeks apart, and we could not determine the exact cause of nest failure in all cases, we included all

failures in our analysis, possibly biasing our results. Nevertheless, we found no direct evidence indicating that other factors unrelated to weather, such as depredation by Great Horned Owls (*Bubo virginianus*), played a significant role in the breeding failures we observed.

The confounding influences of unmeasured, but plausible, factors that may have changed during the study period complicated the analysis. Obvious among these was a possible trend in prey populations. Goshawks respond numerically to changes in numbers of prey (McGowan 1975, Doyle and Smith 1994). In our study area, they relied heavily on

Table 3. Percent change in mean, confidence intervals (CI), and significance of weather variables related to Northern Goshawk productivity in the Independence and Bull Run Mountains, Nevada, for 1992–2002.

MODEL TERM	PERCENT CHANGE IN MEAN	95% CI ^a	P-VALUE ^b
Productivity per breeding pair			
Year ^c	0.985	0.963–1.008	0.20
Mean daily April temperature	1.105	1.070–1.140	<0.0001
Cumulative combined April and May precipitation	0.981	0.971–0.990	<0.0003
Productivity per successful pair			
Year	1.003	0.989–1.017	>0.90
Mean daily April temperature	1.064	1.040–1.089	<0.0001
Cumulative combined June and July precipitation	0.978	0.962–0.994	0.042

^a Percent changes in the means are nonsignificant if confidence interval covers 1.0 (even odds).

^b Significance of terms assessed using a step-down Bonferroni adjustment (Holm 1979).

^c Data for year model terms taken from Bechard et al. (in press).

Belding's ground squirrels (*Spermophilus beldingi*) for food (Younk and Bechard 1994, Younk 1996), but because we did not census ground squirrels, we could not determine what effect change in ground squirrel populations had on goshawk reproduction.

Further, interactions of weather and prey abundance may affect raptor reproduction (Gargett et al. 1995, Steenhof et al. 1997, Bloxton 2002). Weather has been shown to affect ground squirrel populations in other parts of the northern Great Basin (Van Horne et al. 1997). Bloxton (2002) attributed increased breeding failure and significantly lower productivity to reduced abundances of goshawk prey species following the wet and cold winter and spring of a La Niña weather event in western Washington. He noted that goshawks did not breed if weather had affected prey populations. Although the climate of the northern Great Basin differs markedly from western Washington, the interactive effects of weather and prey may not.

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PATTERNS OF TEMPORAL VARIATION IN GOSHAWK REPRODUCTION AND PREY RESOURCES

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ABSTRACT.—To investigate whether Northern Goshawk (*Accipiter gentilis*) reproduction is food-limited, we evaluated the reproductive output from 401 goshawk breeding opportunities on the Kaibab Plateau, Arizona during 1999–2002. Concurrently, we estimated densities of 10 goshawk prey species (seven birds, three mammals) using distance sampling. We then assessed the relationship between goshawk productivity (number of fledglings produced) and prey density within and among years by relating the contribution of individual prey species and total prey density to goshawk productivity. We also estimated the proportion of total diet and biomass for each species that contributed $\geq 3\%$ of all prey items. Total prey density was highly correlated with variation in goshawk productivity ($r^2 = 0.98$, $P = 0.012$). Red squirrel (*Tamiasciurus hudsonicus*) density explained more variation in goshawk productivity than any other species ($r^2 = 0.94$, $P = 0.031$), but density could not be estimated for every predominant prey species in goshawk diets. However, only red squirrels had a positive and significant relationship to goshawk productivity in terms of frequency ($r^2 = 0.97$, $P = 0.014$) and biomass ($r^2 = 0.95$, $P = 0.033$). Northern Flickers (*Colaptes auratus*) and cottontail rabbits (*Sylvilagus* spp.), which contributed the greatest frequency and biomass, respectively, to goshawk diets, showed no relationship with goshawk productivity. Even though goshawks on the Kaibab Plateau have a diverse diet and will readily switch to alternate prey species, goshawk productivity showed significant interannual variation. Our results suggest that the magnitude of goshawk productivity was determined by total prey density and annual variation was driven by differences in the densities of critical prey species.

KEY WORDS: Northern Goshawk; *Accipiter gentilis*; diet; distance sampling; predator-prey dynamics; prey density; productivity.

PATRONES DE VARIACIÓN TEMPORAL DE LAS PRESAS Y DE LA REPRODUCCIÓN DE *ACCIPITER GENTILIS*

RESUMEN.—Para investigar si la reproducción de *Accipiter gentilis* se encuentra limitada por la disponibilidad de alimento, evaluamos el rendimiento reproductivo de 401 oportunidades reproductivas de estos halcones en Kaibab Plateau, Arizona, entre 1999 y 2002. Al mismo tiempo, estimamos las densidades de 10 especies de presas para los halcones (siete aves, tres mamíferos) utilizando el método de conteo con distancias variables. Luego determinamos la relación entre la productividad de los halcones (número de volantones producidos) y la densidad de presas dentro y entre años, relacionando la contribución de cada especie de presa y la densidad total de presas con la productividad de los halcones. También estimamos la proporción de la dieta total para cada especie que contribuyó más del 3% de todas las presas en la dieta. La densidad total de las presas se correlacionó fuertemente con la variación en la productividad de los halcones ($r^2 = 0.98$, $P = 0.012$). La densidad de la ardilla *Tamiasciurus hudsonicus* explicó la mayor parte de la variación en la productividad de los halcones con relación a las otras especies ($r^2 = 0.94$, $P = 0.031$), pero no se pudo estimar la densidad de cada especie de presa predominante en la dieta de los halcones. Sin embargo, sólo la ardilla *T. hudsonicus* presentó una relación positiva y significativa con la productividad de los halcones en términos de frecuencia ($r^2 = 0.97$, $P = 0.014$) y biomasa ($r^2 = 0.95$, $P = 0.033$). Las aves del género *Colaptes* y los conejos, que contribuyeron la mayor frecuencia y biomasa de la dieta de los halcones, respectivamente, no se cor-

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relacionaron con la productividad de los halcones. A pesar de que los halcones en Kaibab Plateau tienen una dieta diversa y pueden cambiar fácilmente a especies de presas alternativas, su productividad mostró una variación interanual significativa. Nuestros resultados sugieren que la magnitud de la productividad de los halcones fue determinada por la densidad total de presas y que la variación anual fue producida por las diferencias en la densidad de especies de presas críticas.

[Traducción del equipo editorial]

To understand temporal variation in population size, it is necessary to focus on the factors that limit demographic processes, such as reproduction and survival. Ultimately, the availability of essential resources within a habitat regulates population growth. Resource availability, specifically food, is hypothesized to be an important limiting factor of many raptor populations (Newton 1979). Variations in food supply often result in extensive fluctuations in population demographic parameters (Gotelli 1998, Newton 1998), but the mechanisms of food-limitation are difficult to quantify, especially in complex systems. Consequently, most information on the influence of food resources on population dynamics comes from correlations between reproduction and food abundance (Martin 1987).

The magnitude of the effects of food-limitation on reproduction is poorly understood, especially for predators with broad diets, such as Northern Goshawks (*Accipiter gentilis*). Goshawks regularly consume a variety of prey including ground and tree squirrels, rabbits, medium to large passerines, woodpeckers, and gallinaceous birds (Squires and Reynolds 1997). The diversity of prey in their diets ultimately depends on the abundance and availability of the local bird and mammal fauna, which varies geographically. In Canada, although goshawks regularly consumed several prey species (≥ 5), goshawk reproduction showed a strong functional response to only one species—snowshoe hare (*Lepus americanus*; Doyle and Smith 2001). In contrast, 14 species of birds and mammals regularly contributed to goshawk diets in the southwestern United States (Reynolds et al. 1992). This diet diversity may stabilize their breeding rates. When prey populations vary asynchronously, the ability of goshawks to switch between alternative prey species may result in less annual variation in reproduction than in areas where goshawks rely primarily on cyclic populations of a single prey species (Newton 1979).

Our objectives were to: (1) determine if prey resources limit the reproductive rates of goshawks with relatively diverse diets and (2) describe how

changes in prey populations may influence goshawk productivity (number of fledglings produced). If food is a limiting factor of goshawk productivity, then variation in the number of fledglings produced should be associated with fluctuations in prey resources. However, if there is a difference in the contribution of individual prey species, then goshawk productivity should respond to fluctuations in the densities of individual prey species. Finally, if the densities of important prey species vary in synchrony, then goshawk productivity should exhibit greater temporal variation. To explore these relationships we studied goshawk productivity and prey resources on the Kaibab Plateau, Arizona during 1999–2002.

STUDY AREA

The Kaibab Plateau is a large (95 × 55 km) forested island, surrounded by shrub-steppe desert, in northern Arizona. Steep slopes and escarpments form the eastern, southern, and western edges of the Kaibab Plateau and create a distinct boundary between the shrub-steppe desert at 1750 m elevation above sea level and the plateau (maximum elevation 2800 m). The northern edge of the plateau gradually descends to sagebrush desert, forming an indistinct boundary between the two landforms.

The study area (1285 km²) on the Kaibab Plateau included forests above 2182 m elevation on the North Kaibab Ranger District of the Kaibab National Forest. Four forest types dominated the study area: Pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodlands occupied 106 km² at lower elevations, ponderosa pine (*Pinus ponderosa*) forests occupied 714 km² at mid-elevation zones, mixed conifer (*Abies concolor*, *Pinus ponderosa*, *Pseudotsuga menziesii*, *Picea engelmannii*) forests occupied 275 km² at the highest elevations, and quaking aspen (*Populus tremuloides*) forests occupied 112 km² interspersed among the other forest types (Joy 2002).

METHODS

Goshawk Productivity. We estimated annual goshawk productivity per territory in 1999–2002. A territory was defined as the area (approximately 11 km²) defended by a pair of goshawks during the breeding season (Reynolds et al. 2005). Because goshawks may use more than one nest within a territory among breeding years (Reynolds et al. 2005), all nest structures were visited annually in spring to determine the territory occupancy status. If an active nest (nest containing eggs or young) was not located within an existing territory, we conducted systematic surveys until we found an active nest or thoroughly

searched the entire territory, which required a minimum effort of 10 person-days (Reynolds et al. 2004). Each year, we also conducted surveys throughout the study area to locate territories not detected in previous years (Reynolds and Joy 2005). To determine nest status and fledgling production, all active nests were visited weekly throughout the breeding season. Goshawk offspring were counted in the nest 7–10 d prior to fledging or from the ground after fledging. Goshawk productivity was estimated annually as the mean number of fledglings produced per territory under study.

Prey Density. To obtain estimates of prey density, we conducted distance sampling (Buckland et al. 1993) along line transects from 1999–2002. Sixty 500-m transects were placed randomly throughout the study area within two strata defined by the forest types (mixed conifer, ponderosa pine) that occupied most of the study area. We established 30 transects per stratum and characterized each transect by its elevation, tree species composition, and tree density. Within a given year, we sampled each transect during three time periods that corresponded with specific goshawk reproductive stages: spring (28 May–24 June)—incubation/hatching stage, summer (25 June–22 July)—nestling stage, and late summer (23 July–14 August)—fledging stage. To reduce travel time between transects and to increase sampling efficiency, transects were grouped by location. Transects were sampled in groups of four per day, and the sampling order of groups was determined using a random number table. Daily sampling began 0.5 hr after sunrise and was completed within 3 hr. All transects were sampled by one observer (Salafsky) during the 4 yr of the study. Sampling was not conducted during inclement weather (rain, winds >20 kph) due to reduced probability of prey detection. Prey seen or heard during sampling were identified to species, and the perpendicular distance from the detected animal to the transect line was measured with a laser rangefinder (accurate to ± 1 m). Data were collected on 15 prey species common in goshawk diets on the Kaibab Plateau (S. Salafsky unpubl. data) and considered important components of goshawk diets in the southwestern United States (Reynolds et al. 1992).

Goshawk Diet. The species composition of goshawk diets was determined from prey remains (pelage, plumage, skeletal parts) that were collected from active goshawk nest sites during weekly visits throughout the breeding season. Prey remains were pooled by territory and date collected, identified to species, and paired to assess the minimum number of individuals consumed (Reynolds and Meslow 1984). The biomass contribution of individual prey was based on the published mass of each avian (Dunning 1993) and mammal (Hoffmeister 1986) species. All methods for quantifying raptor diets have inherent biases (Marti 1987). However, Kennedy (1991) reported that estimates of prey use were similar for prey remain, pellet, and direct observation methods of diet analysis for goshawks in New Mexico.

Data Analysis. We based goshawk productivity on the number of fledglings produced per territory under study. We classified territories based on ≥ 1 attempt to breed on the territory, the identity of the adult birds, and the average inter-territory distance (Reynolds et al. 2005). A high density of territories, a tendency of individuals to

retain the same territory for life, and a delayed age at first breeding (Wiens and Reynolds 2005) suggests that the breeding habitat on the Kaibab Plateau was saturated. This evidence combined with the observed patterns of territory occupancy for individual adults over a 14-yr period (S. Salafsky unpubl. data) indicated that goshawks occupied the territories, even when we found little evidence of birds present. By including all territories rather than only those that were confirmed “active” or “occupied,” we accounted for all potential breeding opportunities and the full range of variability in the reproductive quality of territories.

Variable distance sampling data were analyzed with program DISTANCE, Version 3.5 (Thomas et al. 1998). Reliable estimates of density from distance sampling depend on several critical assumptions: all individuals on the transect line were detected, all individuals were detected at their initial location, and all distances were measured accurately (Buckland et al. 1993). Data collection methods were designed to meet these assumptions. Because variable distance sampling uses a detection function that compensates for differences in detection probabilities among species, habitats, and distances from transects (Emlen 1971, Buckland et al. 1993), density estimates based on distance data are not confounded by factors affecting detectability and thus are representative of the true population size. Prey densities were estimated separately for mixed conifer and ponderosa pine to account for differences in detection probabilities among forest types. These estimates were then multiplied by the proportion of each forest type within the study area and added together to calculate prey densities for the entire study area. Annual density estimates were computed only for species with sufficient sample sizes. Total prey density was calculated as the sum of the individual prey densities for species with a sufficient number of detections. We stratified total prey density by sampling period within each year to estimate prey densities associated with goshawk breeding phenology.

We used the Tukey-Kramer adjustment for multiple comparisons of means to test for differences in goshawk productivity among years (PROC GLM, SAS Institute 1999). Z-statistics were used to test for differences in mean prey densities among years and sampling periods (Buckland et al. 1993). To control for Type I error, we only tested for differences in density between specific pairwise comparisons (e.g., years of highest and lowest density). To assess the relationship between goshawk productivity and prey density, we used linear regression (PROC REG, SAS Institute 1999), where annual goshawk productivity was the dependent variable, and estimates for individual prey species and summed over prey species were used as explanatory variables. Linear regression was also used to assess the relationship between goshawk productivity and prey species in the diet. In these regressions, annual goshawk productivity was the dependent variable and percent of total diet or biomass contribution for individual prey species were assessed as explanatory variables. We used an information-theoretic approach (Burnham and Anderson 2002) to identify the prey variables that explained the most annual variation in goshawk productivity per territory. *A priori* candidate models were developed to represent the potential effects of prey

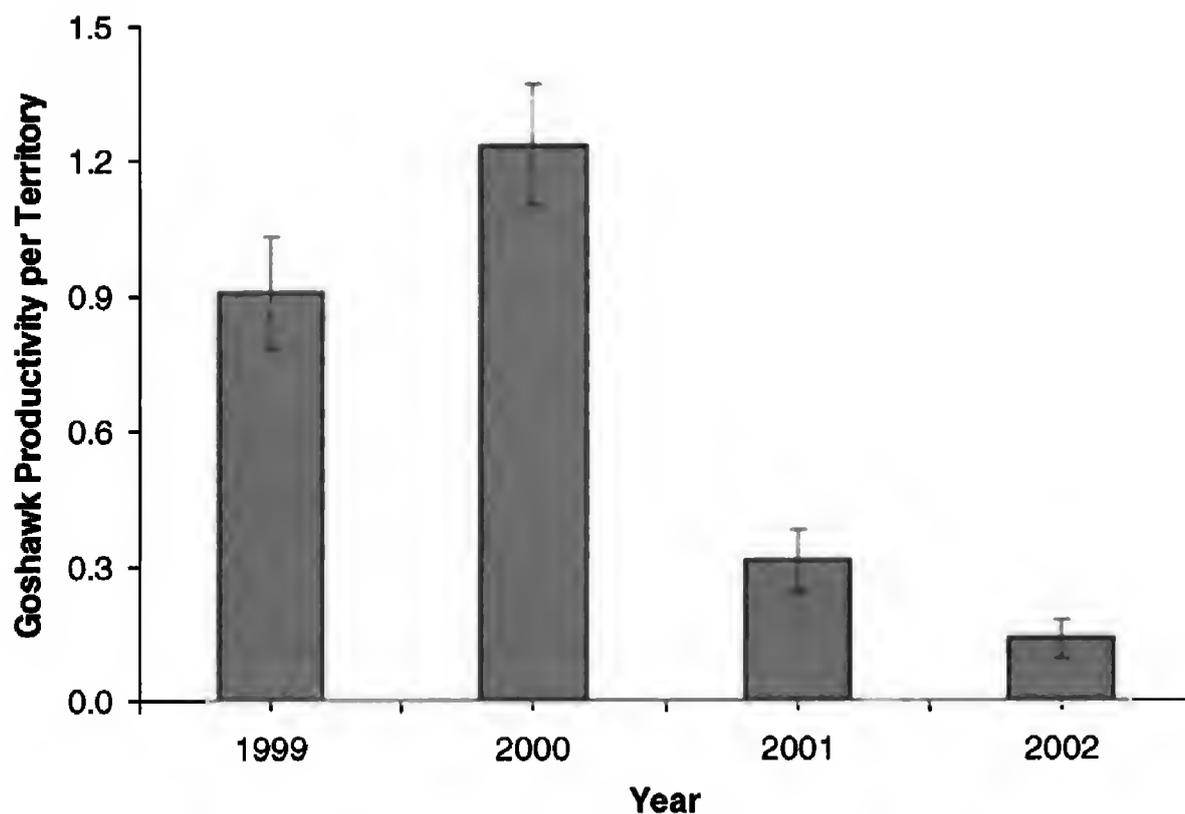


Figure 1. Mean number of Northern Goshawk fledglings produced per territory (\pm SE) on the Kaibab Plateau, Arizona, 1999–2002.

density on goshawk productivity. We hypothesized that goshawk productivity would be most strongly related to prey densities that contributed the most to goshawk reproduction. Competing models were ranked by their adequacy in explaining the variation in goshawk productivity using Akaike Information Criterion (PROC MIXED, SAS Institute 1999). To compare the relative importance of each prey species, we also used cumulative Akaike weights, which were calculated by summing the weights across all models that included the variable of interest (Burnham and Anderson 2002).

RESULTS

Variation in Goshawk Productivity. The number of goshawk territories used to estimate productivity was 97 in 1999, 98 in 2000, and 103 in 2001 and 2002 ($N = 401$). The proportion of territories with active nests was 54% in 1999, 58% in 2000, 28% in 2001, and 18% in 2002. Goshawk productivity ($\bar{x} \pm$ SE) varied among years ($F_{3,397} = 26.78$, $P < 0.001$) and ranged from 0.14 ± 0.04 fledglings produced per territory in 2002 to 1.23 ± 0.14 fledglings produced per territory in 2000 (Fig. 1). There was a significant decline ($F_{1,199} = 37.15$, $P < 0.001$) in goshawk productivity between 2000 and 2001 (Fig. 1).

Variation in Prey Density. Ten prey species had sufficient detections to estimate density: American Robin (*Turdus migratorius*), Clark's Nutcracker (*Nucifraga columbiana*), Downy Woodpecker (*Picoides pubescens*), golden-mantled ground squirrel (*Spermophilus lateralis*), Hairy Woodpecker (*Picoides vil-*

losus), Kaibab squirrel (*Sciurus aberti kaibabensis*), Northern Flicker (*Colaptes auratus*), red squirrel (*Tamiasciurus hudsonicus*), Steller's Jay (*Cyanocitta stelleri*), and Williamson's Sapsucker (*Sphyrapicus thyroideus*). We were unable to estimate densities for black-tailed jackrabbit (*Lepus californicus*), Blue Grouse (*Dendragapus obscurus*), chipmunk (*Eutamias* spp.), cottontail rabbit (*Sylvilagus* spp.), and rock squirrel (*Spermophilus variegatus*) due to low numbers of detections. Detection probability plots showed little evidence of heaping, measurement errors, and evasive movement prior to detection. Total prey density (\pm SE) varied annually and ranged from 2.22 ± 0.08 individuals ha^{-1} in 2001 to 3.96 ± 0.14 individuals ha^{-1} in 2000 ($z = 10.39$, $P < 0.001$). Density also varied significantly among years for most individual prey species (Table 1) including golden-mantled ground squirrel ($z = 2.18$, $P = 0.015$), Hairy Woodpecker ($z = -2.88$, $P = 0.002$), Kaibab squirrel ($z = 2.47$, $P = 0.007$), Northern Flicker ($z = 5.70$, $P < 0.001$), red squirrel ($z = 8.32$, $P < 0.001$), Steller's Jay ($z = 3.25$, $P < 0.001$), and Williamson's Sapsucker ($z = -2.78$, $P = 0.003$). Significant declines in prey densities were also observed between 2000 and 2001 for golden-mantled ground squirrel ($z = 2.18$, $P = 0.015$), Kaibab squirrel ($z = 2.47$, $P = 0.007$), Northern Flicker ($z = 2.62$, $P = 0.005$), and red squirrel ($z = 8.32$, $P < 0.001$), but only red squirrel

Table 1. Annual estimates of Northern Goshawk prey density ha^{-1} for American Robin (AMRO), Clark's Nutcracker (CLNU), Downy Woodpecker (DOWO), golden-mantled ground squirrel (GMSQ), Hairy Woodpecker (HAWO), Kaibab squirrel (KASQ), Northern Flicker (NOFL), red squirrel (RESQ), Steller's Jay (STJA), Williamson's Sapsucker (WISA), and all 10 prey species' densities combined (Total) on the Kaibab Plateau, Arizona, 1999–2002.

SPECIES	1999		2000		2001		2002	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
AMRO	0.23	0.05	0.22	0.07	0.27	0.06	0.25	0.06
CLNU	0.05	0.02	0.05	0.02	0.04	0.01	0.11	0.04
DOWO	0.20	0.05	0.11	0.03	0.20	0.06	0.11	0.03
GMSQ	0.28	0.30	0.64	0.18	0.22	0.06	0.32	0.10
HAWO	0.09	0.03	0.05	0.02	0.23	0.06	0.17	0.04
KASQ	0.11	0.04	0.26	0.07	0.07	0.03	0.08	0.02
NOFL	0.58	0.08	0.77	0.09	0.48	0.06	0.20	0.04
RESQ	1.16	0.17	1.38	0.15	0.12	0.04	0.23	0.05
STJA	0.41	0.07	0.12	0.05	0.30	0.07	0.33	0.05
WISA	0.18	0.04	0.36	0.08	0.28	0.06	0.45	0.09
Total	3.29	0.19	3.96	0.14	2.22	0.08	2.24	0.09

density decreased by an order of magnitude (Table 1).

Prey density also varied by sampling period (Fig. 2). However, there were too few observations to accurately estimate density by sampling period for most individual prey species, so we report only total prey density by sampling period. Total prey density in the spring sampling period was highest in 2000, followed by 1999, 2002, and 2001 (Fig. 2). However, the decrease in density was only statisti-

cally significant between 1999 and 2002 ($z = 1.74$, $P = 0.041$), and 2002 and 2001 ($z = 6.58$, $P = 0.005$). The only significant decrease in total prey density between the late-summer sampling period of one year and the spring sampling period of the next occurred between 2000 and 2001 ($z = 6.58$, $P < 0.001$; Fig. 2).

Goshawk Diets. Goshawks on the Kaibab Plateau captured and consumed a wide diversity of prey. A total of 710 individual prey items consisting of 30

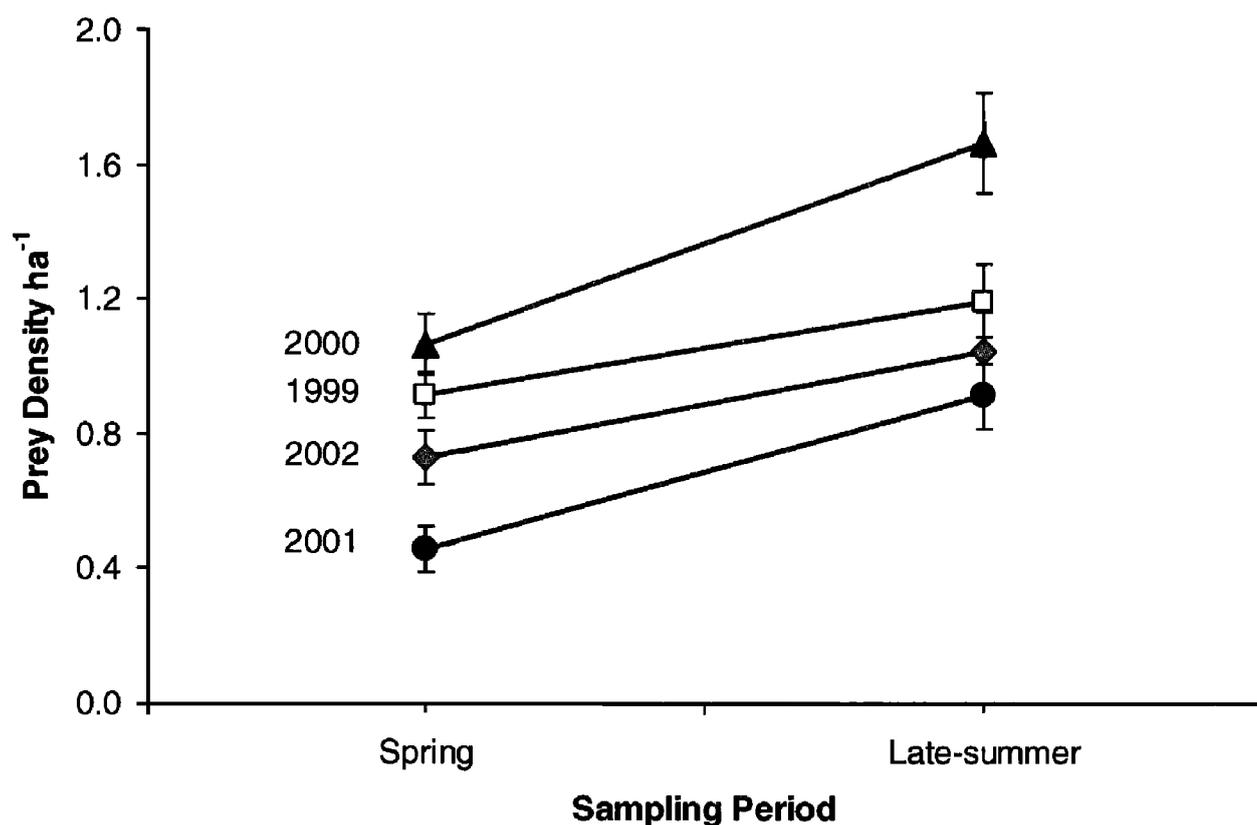


Figure 2. Total Northern Goshawk prey density estimates ha^{-1} (\pm SE) by sampling period on the Kaibab Plateau, Arizona, 1999–2002.

Table 2. Prey species each contributing $\geq 3\%$ of all items ($N = 710$) to Northern Goshawk diets in terms of percent frequency and biomass (kg), and their relationship to the number of fledglings produced per goshawk territory on the Kaibab Plateau, Arizona, during 1999–2002.

SPECIES	NO.	PERCENT FREQUENCY			PERCENT BIOMASS		
		R^2	P	R^2	P		
Black-tailed jackrabbit	23	3	-0.32	0.43	24	-0.36	0.40
Clark's Nutcracker	34	5	0.03	0.82	2	0.01	0.88
Cottontail rabbit	125	18	-0.13	0.64	42	-0.03	0.84
Kaibab squirrel	40	6	-0.05	0.78	13	0.02	0.87
Northern Flicker	141	20	0.87	0.07	8	0.87	0.07
Red squirrel	87	12	0.97	0.01	7	0.95	0.02
Steller's Jay	88	12	-0.09	0.70	4	0.04	0.81

species were collected from nest areas during 1999–2002. Seven species each contributed $\geq 3\%$ of all prey items collected in terms of percent frequency (Table 2). In descending order of percent of total diet, the most common prey items were Northern Flickers, cottontail rabbits, red squirrels, Steller's Jays, Kaibab squirrels, Clark's Nutcrackers, and black-tailed jackrabbits. The descending order of species biomass contribution to goshawk diets was: cottontail rabbits, black-tailed jackrabbits, Kaibab squirrels, Northern Flickers, red squirrels, Steller's Jays, and Clark's Nutcrackers (Table 2). The mean number of prey items per fledgling was 1.8 in 1999, 2.3 in 2000, 5.1 in 2001, and 7.6 in 2002. In contrast the mean biomass of prey items

per fledgling was 0.8 kg in 1999, 0.6 kg in 2000, 2.3 kg in 2001, and 2.8 kg in 2002.

Goshawk Productivity and Prey Resources. We found a strong positive relationship ($r^2 = 0.98$, $P = 0.012$) between total prey density and goshawk productivity from 1999–2002 (Fig. 3). Although annual goshawk productivity was highly correlated with prey density in the spring sampling period ($r^2 = 0.70$, $P = 0.163$), summer sampling period ($r^2 = 0.75$, $P = 0.131$), and late-summer sampling period ($r^2 = 0.79$, $P = 0.112$), annual prey density accounted for more of the variation in goshawk productivity. Based on regression models for each prey species, only red squirrel density had a significant and positive relationship to goshawk produc-

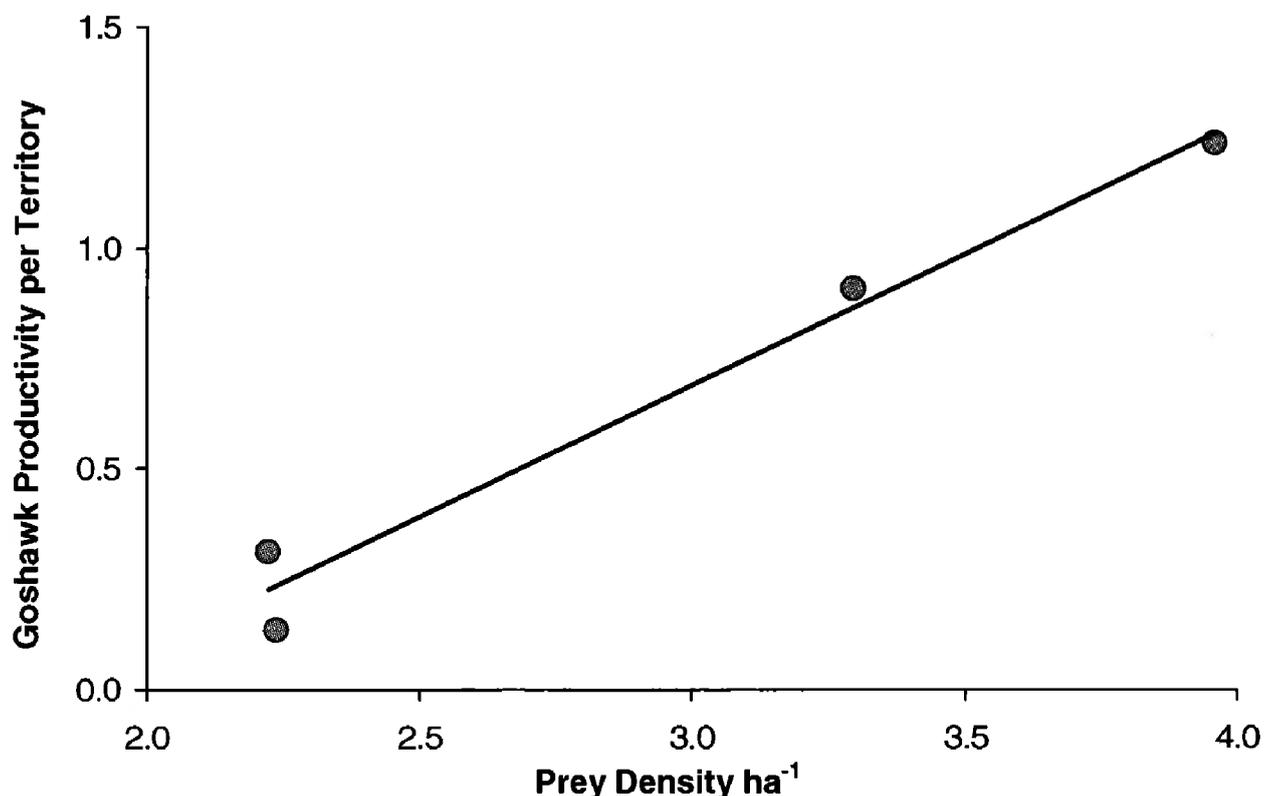


Figure 3. The relationship between total prey density ha^{-1} and the mean number of Northern Goshawk fledglings produced per territory on the Kaibab Plateau, Arizona, 1999–2002.

Table 3. Top 10 models for mean number of Northern Goshawk fledglings produced per territory on the Kaibab Plateau, Arizona, 1999–2002. Models are ranked based on Akaike's Information Criteria (AIC) and include model covariates, number of parameters (K), AIC differences (Δ AIC) and Akaike weights (w_i).

MODEL	AIC	K	Δ AIC	w_i
Total prey species	1134.80	3	0.00	0.70
Red squirrel	1137.70	3	2.90	0.16
Mammal prey species	1138.10	3	3.30	0.13
Northern Flicker	1144.20	3	9.40	0.01
Total prey in late-summer	1149.50	3	14.70	0.00
Hairy Woodpecker	1150.80	3	16.00	0.00
Total prey in summer	1152.20	3	17.40	0.00
Kaibab squirrel	1154.20	3	19.40	0.00
American Robin	1155.40	3	20.60	0.00
Total prey in spring	1156.90	3	22.10	0.00

tivity ($r^2 = 0.94$, $P = 0.031$). Red squirrel was also the only species that had a significant and positive relationship to goshawk productivity for percent of diet ($r^2 = 0.97$, $P = 0.014$) and biomass ($r^2 = 0.95$, $P = 0.024$; Table 2). The densities of mammal prey species ($r^2 = 0.94$, $P = 0.033$) explained more of the variation in goshawk productivity than avian prey species ($r^2 < 0.01$, $P = 0.949$).

Our model selection results showed that total prey density was clearly the top model (Table 3). This model, which included an annual summation of all prey species' densities, received $>70\%$ of the Akaike weight across the model set (Table 3) and was more than four times as likely as the next best model. The only single species models with some weight of evidence included those for red squirrel and Northern Flicker (Table 3). However, the red squirrel density covariate had a higher cumulative Akaike weight (99%) than Northern Flicker (71%). All other models based on individual prey species, avian density, and models of total prey density by sampling period had minimal support and failed to explain variation in goshawk productivity (Table 3). When we compared only the models with total prey density by sampling period in a separate analysis, total prey density summed over all sampling periods was selected as the best model (AIC = 811.10, K = 3, Δ AIC = 0.00, $w_i = 0.93$). All other models, including the model with the difference in prey density between late-summer and the successive spring (AIC = 873.00, K = 3, Δ AIC = 61.90, $w_i = 0.00$) and the lowest ranked model with late-summer prey density from the prior year (AIC = 883.60, K = 3, Δ AIC = 72.50, $w_i = 0.00$), were not supported by the data.

DISCUSSION

A short-term observational study cannot provide a strong basis for estimating the causal relationship between prey resources and annual goshawk productivity. Thus, our study only established a strong association between variation in prey resources within the study area and goshawk productivity. Because fluctuations in other limiting factors (e.g., climate) may have coincided with changes in prey resources, we cannot identify the factors ultimately responsible for variation in goshawk productivity. However, if the patterns we observed between prey resources and goshawk productivity were supported by experimental studies that established a relationship between food-supply and goshawk reproduction, then it would be reasonable to infer that prey resources may be an important limiting factor of goshawk reproduction on the Kaibab Plateau.

During 1999–2002 we observed high temporal correlations between goshawk productivity and annual prey density; changes in goshawk productivity paralleled changes in prey density. Total prey density, in addition to the proportion of active goshawk nests and mean number of fledglings produced, was high in 1999 and 2000 and low in 2001 and 2002. Therefore, it appears that goshawk reproduction on the Kaibab Plateau responded to inter-annual increases in prey density. Several other studies have also found close ties between measures of goshawk reproduction and the relative abundances of prey (Huhtala and Sulkava 1981, Doyle and Smith 1994, Keane 1999). Further, goshawk studies that experimentally manipulated food-supply found supplemental food may have in-

fluenced goshawk productivity by increasing nestling survival when background prey-levels were low (Ward and Kennedy 1996, Dewey and Kennedy 2001). Thus, we suggest that the number of goshawk fledglings produced may be influenced by fluctuations in prey density.

On an annual basis, the reproductive responses of goshawks depend on the abundance of prey during critical time periods. Low food resources may manifest through failure to lay eggs, smaller clutches, and reduced survival of young (Newton 1998). The abundance of prey may be an important determinant of the "decision" to breed. Goshawks initiate breeding before most prey species reproduce, so the density of prey during the incubation period is likely similar to prey levels prior to egg-laying. On the Kaibab Plateau, prey densities during the incubation stage were similar in 1999 and 2002, yet goshawk productivity was six times higher in 1999. In addition, although there was a significant increase in prey density during the incubation period between 2001 and 2002, goshawk productivity changed little between these years, suggesting that below a density of ca. 0.8 prey ha⁻¹, fewer fledglings are produced. However, prey density levels prior to egg-laying may alter the threshold effects of prey density on goshawk productivity through physiological constraints. Assuming our density estimates represented true population size, the difference in prey density between late-summer and the next spring should reflect prey density levels prior to egg-laying. The large decline we observed in prey density between August 2000 and May 2001 indicated that there was substantial overwinter mortality for prey species. The lower prey numbers prior to egg-laying may have affected the ability of females to accumulate sufficient reserves to produce eggs in 2001.

Our results suggest there is a difference in the contribution of individual prey species to goshawk reproduction. Red squirrel density and their percent frequency and biomass contribution to goshawk diet accounted for more variation in goshawk productivity than any other species. Although rabbits contributed the majority of biomass to goshawk diets (>66%), goshawk reproduction was lower in most years when rabbits contributed the greatest proportion of biomass to the diets. Further, in "poor" goshawk reproductive years (2001, 2002), the number of prey items and total biomass per fledgling was twice as high as in "good" reproductive years (1999, 2000). The difference in the

apparent influence of individual prey species is likely a result of encounter rates with goshawks. Goshawks are opportunists and will presumably attempt to capture whatever prey species are readily available. However, the limited distributions or different activity patterns of some prey species decreases the probability that diurnal goshawks will encounter them while foraging. Jackrabbits are less common in upper elevation forests, and although cottontails are widely distributed across the study area, they are crepuscular (Hoffmeister 1986). In contrast, red squirrels are among the heaviest of the diurnal prey species, with a wide distribution across the study area (Salafsky 2004). Red squirrels do not hibernate, which likely increases their importance to goshawks, particularly prior to egg-laying. However, the importance of other prey species may vary with the spatial distribution of goshawk territories relative to the spatial distribution of prey habitats. For example, goshawks with territories located primarily within lower elevation forests may rely more heavily upon jackrabbits.

In our study, goshawk productivity on the Kaibab Plateau was more closely associated with variation in mammal density than in avian density. Goshawks may consume more mammals than birds in some areas due to the availability and sizes of local prey species (Zachel 1985, Widén 1987, Doyle and Smith 1994). Similar to our study, Boal and Mannan (1994) and Reynolds et al. (1994) found that goshawks on the Kaibab Plateau consumed a higher proportion of mammalian prey. Other goshawk studies conducted in northern latitudes identified a strong link between goshawk reproductive rates and cyclical variation in hare abundance (McGowan 1975, Doyle and Smith 2001). Because annual variations in predator reproductive rates are greatest among species with limited diets that are dominated by cyclic prey (Newton 1979), goshawks on the Kaibab Plateau may be subject to more marked variations in productivity due to their reliance on prey species with fluctuating densities.

Goshawks have the ability to switch to alternate prey when the densities of essential prey species are reduced (Doyle and Smith 1994). However, if different prey species' populations decline simultaneously, then the opportunities for goshawks to switch to alternative prey species are limited. The densities of golden-mantled ground squirrels, Kaibab squirrels, Northern Flickers, and red squirrels declined significantly between 2000 and 2001. Further, these species contributed >39% of all prey

items to goshawk diets. Parallel fluctuations in annual densities of important prey species may result in potentially "poor" and "good" years of prey resources. Thus, it may be that the collective density of the entire prey community influences the magnitude of variation in goshawk productivity on the Kaibab Plateau.

In summary, our results indicate that prey density is an important limiting factor of goshawk productivity. Although the temporal correlations between goshawk productivity and prey resources were consistent over time, other factors may have varied with prey density and limited goshawk reproduction in our study. Synchronous declines in prey species' densities suggests that landscape-level factors acting at broad spatial scales, such as climate, may interact with prey abundance to limit goshawk productivity. Because unfavorable weather conditions may have a greater effect on goshawk productivity when prey resources are already low, it is important to study the relationship between goshawk productivity and prey density over long time periods and variable environmental conditions.

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A SKEWED SEX RATIO IN NORTHERN GOSHAWKS: IS IT A SIGN OF A STRESSED POPULATION?

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ABSTRACT.—I examined 6 yr (1993–98) of data on Northern Goshawk (*Accipiter gentilis*) reproductive performance in east-central Arizona. Forty-four breeding territories were monitored over the 6-yr period, yielding 109 nesting attempts and 141 fledglings produced from 76 successful broods. Among the 63 broods from which sex of nestlings could be determined by measurements, 29% fledged one young, 54% fledged two young, and 17% fledged three young. The mean sex ratio across years was 1.93 ± 0.70 ($\pm 95\%$ CI) males/females (annual range 1.1:1–3:1). When combining all fledglings of known sex (76 males and 43 females), a 1.77:1 male to female sex ratio was significantly different from 1:1 ($P = 0.002$). A male-biased fledgling sex ratio may be explained by one or more of the following hypotheses: (1) more males were produced due to nutritional stress resulting in minimization of investment in the larger sex (females) and (2) fewer females were produced because of differential mortality due to exposure to the elements during the nestling stage. I propose that environmental stress in the form of exposure to the elements during a critical life stage (e.g., rainfall during the nestling stage), combined with limited food availability, may be driving the skewed sex ratios observed in this local Northern Goshawk population.

KEY WORDS: *Northern Goshawk; Accipiter gentilis; nestling; sex ratio; sex allocation.*

¿ES EL COCIENTE DE SEXOS SESGADO DE *ACCIPITER GENTILIS* UNA SEÑAL DE UNA POBLACIÓN ESTRESADA?

Resumen.—En este estudio examiné datos sobre el desempeño reproductivo de *Accipiter gentilis* recolectados a lo largo de seis años (1993–98) en el centro-este de Arizona. Un total de 44 territorios de nidificación fueron monitoreados a través de los seis años, observando un total de 109 intentos de nidificación y 141 volantones producidos en 76 nidadas exitosas. De las 63 nidadas en las que el sexo de los pichones pudo ser determinado mediante mediciones, el 29% produjeron un volantón, el 54% dos volantones y el 17% tres volantones. El cociente de sexos promedio a través de los años fue de 1.93 ± 0.70 ($\pm 95\%$ IC) machos/hembras (rango anual 1.1:1–3:1). Al combinar todos los volantones de sexo conocido (76 machos y 43 hembras), el cociente de machos a hembras resultante de 1.77:1 fue significativamente diferente de 1:1 ($P = 0.002$). Un cociente de sexos sesgado hacia los machos en los volantones podría explicarse por las siguientes hipótesis: (1) se produjeron más machos como consecuencia de estrés nutricional que llevó a minimizar la inversión en el sexo de mayor tamaño (hembras) y/o (2) se produjeron menos hembras como resultado de una mortalidad diferencial debida a la exposición al ambiente durante la permanencia de los pichones en el nido. Propongo que el estrés ambiental causado por la exposición a las condiciones ambientales durante una etapa crítica de la vida (e.g., la lluvia durante la etapa de crianza en el nido), combinado con la disponibilidad limitada de alimento, podrían estar determinando el sesgo en el cociente de sexos observado en esta población local de *A. gentilis*.

[Traducción del equipo editorial]

Female Northern Goshawks (*Accipiter gentilis*) are approximately 20–30% heavier than males (Newton 1979, Palmer 1988, Squires and Reynolds 1997). Larger offspring require more food to at-

tain fledging age, and thus are more susceptible to food shortages (Clutton-Brock et al. 1985, Teather and Weatherhead 1988, Anderson et al. 1993). An underlying assumption of an adjustable sex ratio is that parents should bias the sex ratio of their offspring toward the sex whose production will most increase their own fitness (Trivers and Willard

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1973, Clark 1978, Charnov 1982, Clutton-Brock 1986). The sex ratio at fledging should be the inverse of the ratio of the cost of producing each sex (Fisher 1930). Consequently, under times of limited prey resources the sex ratio should be biased toward the "cheaper sex" (in Northern Goshawks: the male; Howe 1977, Cronmiller and Thompson 1981, Teather and Weatherhead 1988). In sexually-dimorphic species, differential survival between the sexes is most likely due to differing nutritional requirements, with higher mortality incurred by the larger sex (Torres and Drummond 1997, Sheldon et al. 1998). However, this may be offset in Northern Goshawks by the tendency of the female nestlings to seize prey items more readily than males (Lee 1980).

Sex allocation in sexually dimorphic raptors has provided mixed observations. Studies have shown prevalence toward male fledglings in Golden Eagles (*Aquila chrysaetos*; Edwards et al. 1988), Harris's Hawks (*Parabuteo unicinctus*; Bednarz and Hayden 1991), Montagu's Harriers (*Circus pygargus*; Leroux and Bretagnolle 1996), and Cooper's Hawks (*Accipiter cooperii*; Rosenfield et al. 1996). Other studies showed prevalence toward female fledglings in Northern Harriers (*Circus cyaneus*; Balfour and Cadbury 1979), Bald Eagles (*Haliaeetus leucocephalus*; Bortolotti 1986), and Peregrine Falcons (*Falco peregrinus*; Olsen and Cockburn 1991). However, most studies on raptors have revealed equal sex ratios in offspring (Newton 1979). In some previous work on Northern Goshawks, the sex ratio for fledglings has been shown not to differ from 1:1 (Newton 1979, Reynolds and Joy 1998).

A male-biased fledgling sex ratio may be explained by one or more of the following hypotheses: (1) more males were fledged due to nutritional stress resulting in minimization of investment in the larger sex (females) during the nestling stage (Trivers and Willard 1973, Torres and Drummond 1997) and (2) fewer females were produced because of differential mortality due to exposure to the elements during the nestling stage with larger young exhibiting a higher mortality rate (Newton 1979:136–137). Hypothesis 1 above may be a direct product of adaptive selection, whereas hypothesis 2 may simply be a nonadaptive by-product of differential mortality. The purpose of this paper is to discuss these potential explanations for the sex ratio exhibited by Northern Goshawk fledglings in east-central Arizona.

STUDY AREA

The Sitgreaves portion of the Apache-Sitgreaves National Forest is located on the Mogollon Plateau in east-central Arizona and encompasses approximately 330 300 ha. Elevation ranges from 1768–2417 m. To the south, the study area is bounded by the Mogollon Rim, a large escarpment extending east across central Arizona and into New Mexico. To the east, the study area is bounded by the Springerville Ranger District boundary on the Apache National Forest. A wide range of vegetation communities occurs within the study area (Brown 1994). The Mogollon Rim edge is dominated by deep drainages with mixed-conifer communities of Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and ponderosa pine (*Pinus ponderosa*), with pockets of aspen (*Populus tremuloides*), New Mexico locust (*Robinia neomexicana*), and Gambel oak (*Quercus gambelii*). Ridgetops are generally dominated by ponderosa pine forest. To the north, as elevation decreases, a ponderosa pine/juniper-pinyon ecotone transitions to a juniper-pinyon woodland dominated by alligator juniper (*Juniperus deppeana*), Utah juniper (*J. osteosperma*), and Rocky Mountain pinyon pine (*P. edulis*). As elevation decreases further, a plains grassland community develops, dominated by blue grama (*Bouteloua gracilis*), sand dropseed (*Sporobolus cryptandrus*), and fourwing saltbush (*Atriplex canescens*).

METHODS

I monitored demographic parameters of a Northern Goshawk population on the Apache-Sitgreaves National Forest from 1993–98 and specifically noted the sex of fledgling birds. I visited occupied nests periodically during the breeding season (ca. late April–early August) to monitor status and productivity. An occupied nest was one in which at least one egg was laid (usually inferred by observing a bird in incubation posture). I estimated the ages of nestlings using a photographic guide produced by Boal (1994). Birds were deemed to have survived to fledge when they were greater than 80% of fledgling age (31 d old; Steenhof 1987). When nestlings were between 30–40 d old, I banded them with U.S. Geological Survey aluminum leg bands and took the following standard morphological measurements: tarsus dorsal-ventral (smallest front to back measurement of the tarsus to nearest 0.1 mm), tarsus lateral (smallest side to side measurement of the tarsus to nearest 0.1 mm), hallux (tip of talon to the beginning of the fleshy pad of the hind toe to nearest 0.1 mm), bill depth (perpendicular to the bill from the top in front of the cere to the bottom of the bill to nearest 0.1 mm), culmen (top portion of the bill in front of the cere to the tip of the bill to nearest 0.1 mm), mass (taken to nearest 10 g). I used a *k*-means cluster analysis (SPSS 1997) to determine if morphological measurements could adequately identify sexes of nestlings. Only birds from broods in which all the measurements were collected were included in the analysis. In 1999, I collected blood samples from 22 nestlings and had them genetically analyzed for sex identification (Avian Biotech International, Tallahassee, FL U.S.A.) using a polymerase-chain reaction to amplify CHD (chromo-helicase-DNA binding) genes Z and W that are located on the avian sex chromosomes in birds. For detailed procedural information, see Griffiths et al. (1998), Fridolfsson

Table 1. Nestling sex-ratio and productivity of Northern Goshawks from territories monitored on the Apache-Sitgreaves National Forest, Arizona, (1993–98).

YEAR	NO. NESTS MONITORED	NESTING OCCUPANCY RATE ^a	NO. SUCCESSFUL BROODS	NO. MALE FLEDGLINGS	NO. FEMALE FLEDGLINGS	NO. FLEDGLINGS		<i>P</i> ^d
						OF UNKNOWN SEX ^b	SEX RATIO ^c	
1993	30	0.69	17	10	9	11	1.1	0.819
1994	33	0.33	8	9	3	4	3	0.083
1995	39	0.66	14	17	10	0	1.7	0.178
1996	42	0.52	16	16	8	4	2	0.102
1997	42	0.31	6	7	3	0	2.3	0.206
1998	44	0.43	15	17	10	3	1.7	0.178
Total	230	$\bar{x} = 0.49$	76	76	43	22	1.7	0.003

^a The number of occupied nests (a nest where at least one egg was laid)/total number of nesting territories monitored.

^b Fledglings not measured, therefore gender indeterminate.

^c Male/female.

^d Significance of Chi-square test for difference from a 1:1 sex ratio.

and Ellegren (1999), and Avian Biotech International (2005). I calculated the sex ratio as the number of male per female fledglings. I used a chi-square analysis to test if the sex ratio was significantly different from 1:1 (Zar 1984). I used Spearman's correlation analysis to test for significance in relationships between demographic parameters (e.g., sex ratio versus the number of territories with an occupied nest per the number of territories monitored). All statistical tests were deemed significant at $P < 0.05$, and all means were expressed $\pm 95\%$ Confidence Interval (CI). I compiled monthly summaries of total precipitation from U.S. National Oceanic and Atmospheric Administration records collected at the Show Low, Arizona, municipal airport (elevation = 1950 m) located within the study area.

RESULTS

Breeding territories were monitored over the 6-yr period (range = 30–44 per yr), yielding 109 nesting attempts and 141 fledglings produced from 76 successful broods (Table 1). Among the 63

broods from which gender could be determined, 29% fledged one young, 54% fledged two young, and 17% fledged three young (Table 2). Two relatively homogenous groups of nestlings were discerned using a *k*-means cluster analysis, and their morphological measurements showed minimal overlap (Table 3). The two groups are easily recognized when the lateral tarsus and culmen length measurements are plotted (Fig. 1). I considered all members of the larger group as females. The measurements used above correctly classified to gender all 22 nestlings that were genetically analyzed in 1999. The mean sex ratio across years was 1.93 ± 0.70 ($\pm 95\%$ CI) males/female (range = 1.1:1–3:1). When combining all fledglings of known sex (76 males and 43 females), a 1.77:1 male to female sex ratio resulted that was significantly different from 1:1 ($\chi^2 = 9.15$, $df = 1$, $P = 0.002$).

Table 2. Observed brood size and sex ratio of Northern Goshawks fledged on the Apache-Sitgreaves National Forest, Arizona, (1993–98).

NESTING OUTCOME	BROOD SIZE		
	1	2	3
All males	13	13	2
All females	5	7	0
1 male and 1 female	—	14	—
2 males and 1 female	—	—	8
1 male and 2 females	—	—	1
Sex ratio (M/F)	13/5 = 2.6	40/28 = 1.43	23/10 = 2.3
<i>P</i> ^a	0.06	0.15	0.02

^a Significance of Chi-square test for difference from a 1:1 sex ratio.

Table 3. Summary statistics of Northern Goshawk morphological measurements taken on the Apache-Sitgreaves National Forest, Arizona (1993–98).

GROUP	MEASUREMENT ($\bar{x} \pm 2$ SE, RANGE) ^a		
	FLEDGLING GROUP 1 (PRESUMED MALE) N = 59	FLEDGLING GROUP 2 (PRESUMED FEMALE) N = 34	ADULT FEMALES N = 25
Culmen (mm)	19.05 \pm 0.27 16.2–21.7	21.36 \pm 0.34 18.5–23.4	24.53 \pm 0.34 23.0–26.3
Beak depth (mm)	14.63 \pm 0.18 13.3–16.1	16.63 \pm 0.21 15.1–17.8	17.93 \pm 0.18 17.2–18.7
Tarsus D/V ^b (mm)	7.04 \pm 0.13 6.0–8.1	8.38 \pm 0.19 7.4–9.3	10.48 \pm 0.36 8.7–12.0
Tarsus L ^c (mm)	5.36 \pm 0.07 4.8–6.0	6.50 \pm 0.13 5.9–7.4	7.48 \pm 0.15 6.9–8.5
Hallux (mm)	23.79 \pm 0.36 19.6–27.0	27.02 \pm 0.52 24.1–31.1	31.98 \pm 0.39 30.2–33.8
Mass (g)	702 \pm 14 565–810	894 \pm 36 620–1085	1026 \pm 39 845–1265

^a See text for detailed description of measurements.

^b D/V = the smallest front to back measurement of the tarsus (dorsal/ventral).

^c L = the smallest side to side measurement of the tarsus (lateral).

DISCUSSION

Hypothesis 1—Nutritional Stress Would Minimize the Investment in Larger Sex. Meyers (1978) predicted that during periods of lower than average resource abundance, offspring sex ratio in a population should shift toward the sex having the lower energy needs. In times of plentiful resources, adults should invest in the larger offspring, which benefit from greater size. I observed a negative relationship between the annual sex ratio and the

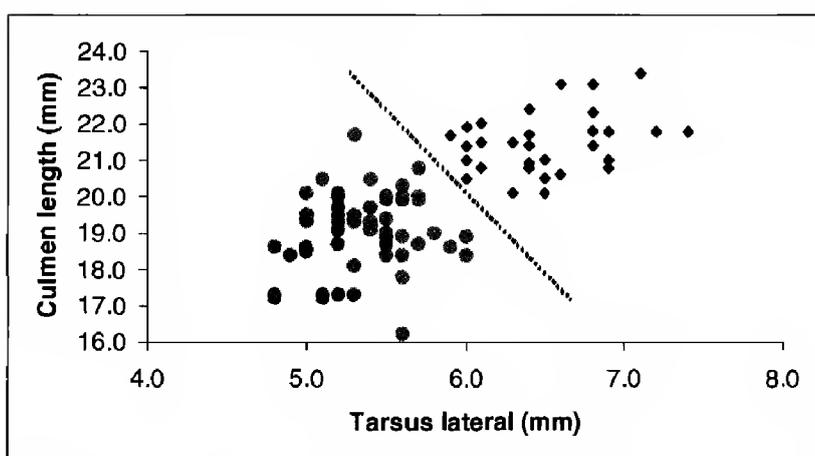


Figure 1. Plot of the culmen length and lateral tarsus measurements for Northern Goshawk nestlings measured on the Apache-Sitgreaves National Forest, AZ (1993–98). The two groups (circles presumed to be males and the diamonds females) were distinguished using a *k*-means cluster analysis of all morphological measurements collected.

nesting occupancy rate (Fig. 2A). A low nesting occupancy rate most likely reflects a lower than average abundance of some resource such as prey availability. Conversely, in years with a high nesting occupancy rate, which may have reflected an above average resource availability, the number of female offspring was greater (Fig. 2B). Yet, for this hypothesis to be an adaptive selection strategy, I would expect to find a sex ratio skewed toward females when the nesting occupancy was high. Instead when the nesting activity rate was high the sex ratio approached 1:1. This result may lend credence to the resource-shortage hypothesis being a nonadaptive by-product of differential mortality (Weatherhead and Teather 1991).

Hypothesis 2—Male Nestlings are Less Susceptible to Adverse Weather Conditions. Newton (1979) suggests that females would be more susceptible to mortality from exposure than smaller males. When being brooded, smaller nestlings may be more sheltered from environmental elements than larger siblings; or during episodes of rain, larger drenched female nestlings may hold more water and require more time to dry. Thus, larger female nestlings would remain cooler longer and be more susceptible to hypothermia. In years when more rainfall occurred during the nestling period (May and June), I observed more male fledglings

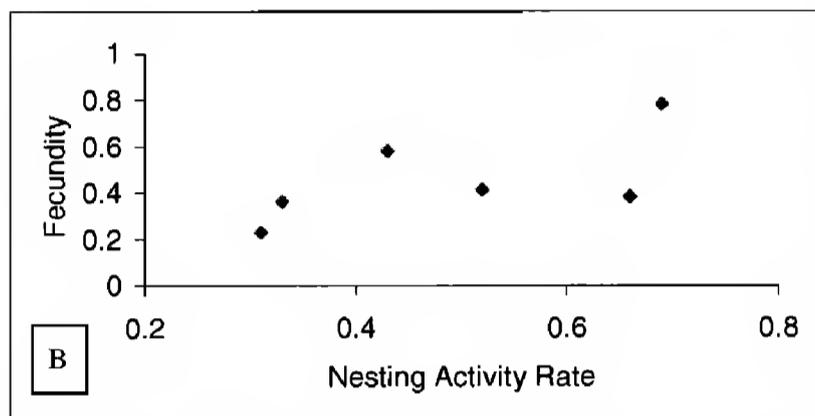
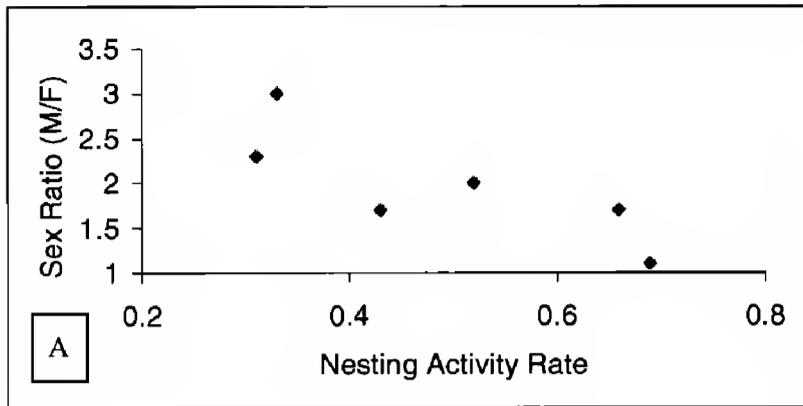


Figure 2. (A) Sex ratio of fledgling Northern Goshawks plotted against the annual nesting occupancy rate (number of occupied nests/total number of nests monitored) on the Apache-Sitgreaves National Forest, AZ, 1993–98 ($r = -0.84$, $P = 0.04$). (B) Fecundity rate (number of female fledglings produced/total number of breeding females) plotted against the nesting occupancy rate of Northern Goshawks on the Apache-Sitgreaves National Forest, AZ, 1993–98 ($r = 0.77$, $P = 0.07$).

produced (Fig. 3). This phenomenon of induced mortality due to exposure may also be compounded by nutritional stress (i.e., shortage of prey). Wet weather conditions have been shown to prevent adult raptors from hunting efficiently (Hiraldo et al. 1990, Kostrzewa and Kostrzewa 1990). Times of food shortage may force the nesting adult female to leave the nest in search of prey, thereby increasing the risk of exposure to the nestlings. For example, Boal et al. (2005) reported the failure of several nests in Minnesota after a 10-d period of constant rain.

CONCLUSION

I suggest that limited food availability combined with environmental stress in the form of exposure to the elements during a critical life stage (e.g., rainfall during the nestling stage) may be driving the skewed sex ratios observed in this local Northern Goshawk population. Of the two hypotheses

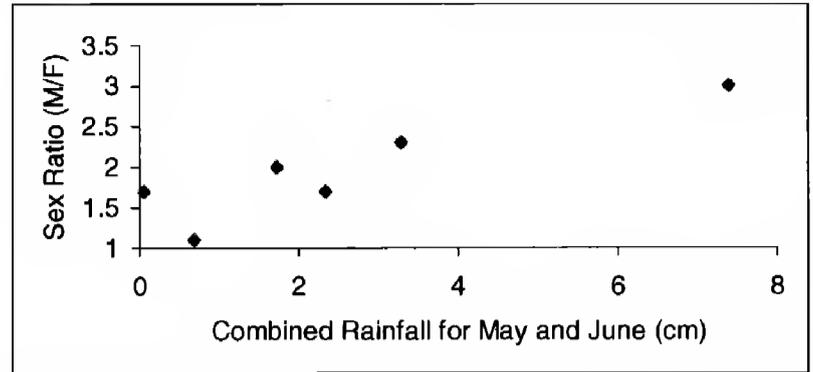


Figure 3. Relationship between the sex ratio of fledgling Northern Goshawks monitored from 1993–98 and rainfall ($r = 0.81$, $P = 0.05$) measured at the U.S. National Oceanic and Atmospheric Administration weather station located at the Show Low, Arizona, airport within the Apache-Sitgreaves National Forest, during the brood-rearing period (May and June).

presented, the available evidence supports that Northern Goshawks may exhibit selection toward the minimization of investment in the larger sex (i.e., support for the nutritional-stress hypothesis). But at this time the compounding phenomena of a potential increase in exposure time of nestlings because of the decrease in the adult female nest attentiveness due to a possible decrease in prey availability cannot be discarded. During the early nestling period, monitoring adult female nest attentiveness (i.e., her sheltering of the nestlings) and the amount of prey brought to the nestlings could help tease apart these two potential explanations that may be driving the skewed sex ratio (i.e., exposure or food shortage).

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NORTHERN GOSHAWK (*ACCIPITER GENTILIS LAINGI*) POST-FLEDGING AREAS ON VANCOUVER ISLAND, BRITISH COLUMBIA

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ABSTRACT.—The area used by immature birds from the time they fledge until independence is the post-fledging area (PFA). Published estimates of PFA size (170 ha) are only available from a Northern Goshawk (*Accipiter gentilis atricapillus*) population in New Mexico and applicability of this estimate to other regions and habitat types is unknown. Our objectives were to estimate PFA size and length of the post-fledging period for Northern Goshawk (*A. g. laingi*) nests on Vancouver Island, British Columbia. We estimated PFA size from 95% adaptive kernel estimates of telemetry locations from 12 fledglings at 12 nests between 29 June and 2 September 2001–02 ($N = 6$, 2001; $N = 6$, 2002). Because our adaptive kernel estimates are based on a small number of locations, we also estimated the precision of these home range estimates using a smoothed bootstrap approach. Almost all (93%) fledgling locations were within 200 m of nests during the early fledgling-dependency period, but less than half (42.4%) of these locations were within this distance during the late fledgling-dependency period. Northern Goshawks departed from PFAs 45.9 ± 1.3 d post-fledging. Mean PFA size was 59.2 ± 16.1 ha, and the bootstrapped variance around PFA estimates ranged from 12.7–1820.8 ha. Our estimate for the mean size of one PFA per nest area for *A. g. laingi* fledglings on Vancouver Island was much smaller than the mean size estimate reported for *A. g. atricapillus* in New Mexico. However, management plans should consider nest areas and PFAs to be one functional component of Northern Goshawk breeding habitat and should include multiple alternative nest trees, each with an associated PFA.

KEY WORDS: *Northern Goshawk; Accipiter gentilis laingi; activity centers; adaptive kernel; bootstrapping; fledging-dependency period; immature movements; natal dispersal.*

ÁREAS POST-EMPLUMAMIENTO DE *ACCIPITER GENTILIS LAINGI* EN VANCOUVER ISLAND, BRITISH COLUMBIA

RESUMEN.—El área utilizada por las aves inmaduras desde que abandonan el nido hasta que alcanzan la independencia de sus padres es el área post-emplumamiento (APE). El único estimado publicado del tamaño del APE de *Accipiter gentilis* (170 ha) corresponde a una población del estado de New Mexico (subespecie *atricapillus*), y la aplicabilidad de este estimado a otras regiones y tipos de hábitats es desconocida. Nuestros objetivos fueron estimar el tamaño del APE y la longitud del período post-emplumamiento para nidos de *A. g. laingi* ubicados en Vancouver Island, British Columbia. Estimamos el tamaño del APE a partir de estimados adaptativos de los kernels del 95% de ubicaciones obtenidas mediante telemetría para 12 volantones de 12 nidos, entre el 29 de junio y el 2 de septiembre de 2001–02 ($N = 6$, 2001; $N = 6$, 2002). Debido a que nuestros estimados de los kernels están basados en un número pequeño de ubicaciones, también estimamos la precisión de los estimados del rango de hogar empleando un método de bootstrap alisado. Casi todas las ubicaciones de los volantones (93%) estuvieron a menos de 200 m de los nidos durante el período temprano de emplumamiento-dependencia, pero menos de la mitad de las ubicaciones (42.4%) tuvieron lugar a menos de 200 m durante la fase tardía de este período. Los individuos abandonaron sus APE 45.9 ± 1.3 d después de abandonar el nido. El tamaño promedio del APE fue 59.2 ± 16.1 ha, y la varianza de los estimados obtenida mediante

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el método de bootstrap estuvo entre 12.7 y 1820.8 ha. Nuestro estimado del tamaño medio de un APE por área de nidificación para los volantones de *A. g. laingi* en Vancouver Island es mucho menor que el estimado medio documentado para *A. g. atricapillus* en New Mexico. Sin embargo, los planes de manejo deben considerar que las áreas de nidificación y las APE son un componente importante del hábitat de cría de *A. gentilis*, y deben incluir múltiples árboles que puedan servir como sitios alternativos para nidificar, cada uno con su APE asociada.

[Traducción del equipo editorial]

Suitable breeding habitat for avian species consists of adequate nest sites, roost sites, post-fledging areas (PFAs), and foraging areas. PFAs represent the habitat used by fledglings prior to independence and may be especially important for species with long post-fledging-parental-care periods, such as raptors. The survival of fledglings through the post-fledging period and their first year is likely influenced by PFA quality, which may be reflected by PFA size and habitat characteristics.

Several studies have reported areas around nests to be important for fledglings during the post-fledging period, before dispersal is initiated (Bald Eagles [*Haliaeetus leucocephalus*], Wood et al. 1998; Great Tits [*Parus major*], Naef-Daenzer et al. 2001; Scarlet Macaws [*Ara macao*], Myers and Vaughan 2004). However, the PFA concept (originally referred to as the post-fledging family area; Reynolds et al. 1992) and its integration with management prescriptions (Reynolds et al. 1992) have only been applied to Northern Goshawks (*Accipiter gentilis*), a species of concern in North America (Kennedy 1997, Crocker-Bedford 1998, DeStefano 1998) and Europe (Widén 1997). Kennedy et al. (1994) estimated the size of goshawk PFAs in New Mexico to be ca. 168 ha based on movement patterns of radio-tagged fledglings and adult female core-use areas. Currently, the British Columbia (BC) government recommends managing a 200-ha PFA around designated goshawk (*A. g. laingi*) nest areas (BC Ministry of Water, Land, and Air Protection, 2004). This recommendation was a modification of the southwestern U.S. guidelines (Reynolds et al. 1992) because local data were unavailable.

Our objective was to evaluate the applicability of PFA guidelines developed for goshawk populations in the southwestern U.S. to coastal BC, where habitat characteristics, harvest regimes, and goshawk subspecies differ. We provide the first PFA estimate for goshawks based on home-range estimates of fledglings prior to independence as well as precision estimates of PFAs, which are rarely provided in home-range analyses (Kernohan et al. 2001). Local knowledge of goshawk PFA size on Van-

ver Island is crucial for adequately managing the breeding habitat of *A. g. laingi* which is federally designated by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as Threatened in Canada (COSEWIC, in press) and is provincially Red-listed (BC Conservation Data Centre 2005).

METHODS

Study Area. Goshawk nest areas were located on Vancouver Island, BC (Fig. 1) in forests dominated by western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*), although western red cedar (*Thuja plicata*), amabilis fir (*Abies amabilis*), and red alder (*Alnus rubra*) were also abundant. Nest stands ranged in age from 45 to >250 yr. See McClaren et al. (2002, 2003) for more study area details.

Data Collection. Goshawk nests ($N = 17$) used in this study were located either through broadcast surveys of conspecific calls (McClaren et al. 2002, 2003), or incidentally by forest company personnel and the public, from 1994–2002. When nestlings were ca. 21 d, we climbed nest trees and lowered nestlings to the ground where they were weighed, measured, sexed, and aged by the senior author to maintain consistency in the data. Nestling gender was determined using tarsal width, recommendations provided by Kenward et al. (1993a). We aged nestlings from a photographic and behavioral key (Boal 1994) and from our estimated hatch dates. Nestlings were banded with U.S. Geological Survey bands and color-rivet bands (Acraft Sign and Nameplate Co. Ltd., Edmonton, AB Canada). With two exceptions, we fitted only the largest female nestling in each nest with a 9-g tarsal mount transmitter with a mortality switch (Advanced Technology Services, Isanti, MN U.S.A.). Males were fitted with transmitters when: (1) all nestlings were male ($N = 1$); and (2) the sole female nestling's transmitter battery died, and we fitted its male sibling with a new radiotransmitter. We chose the largest female to reduce potential variation in fledgling movements caused by gender differences (Byholm et al. 2003, J. Wiens unpubl. data) and to lessen possible impact of transmitter mass on survival probability. Radiotransmitters were attached to tarsi with a leather jesse (Ward and Kennedy 1996, Dewey and Kennedy 2001), so that fledglings could remove them after the 90 d transmitter battery expired. Trade name products are mentioned to provide complete descriptions of methods. The authors' institutions neither endorse these products nor intend to discriminate against products not mentioned.

Prior to collecting fledgling location data, we centered a 600×600 -m grid on nests with young with location

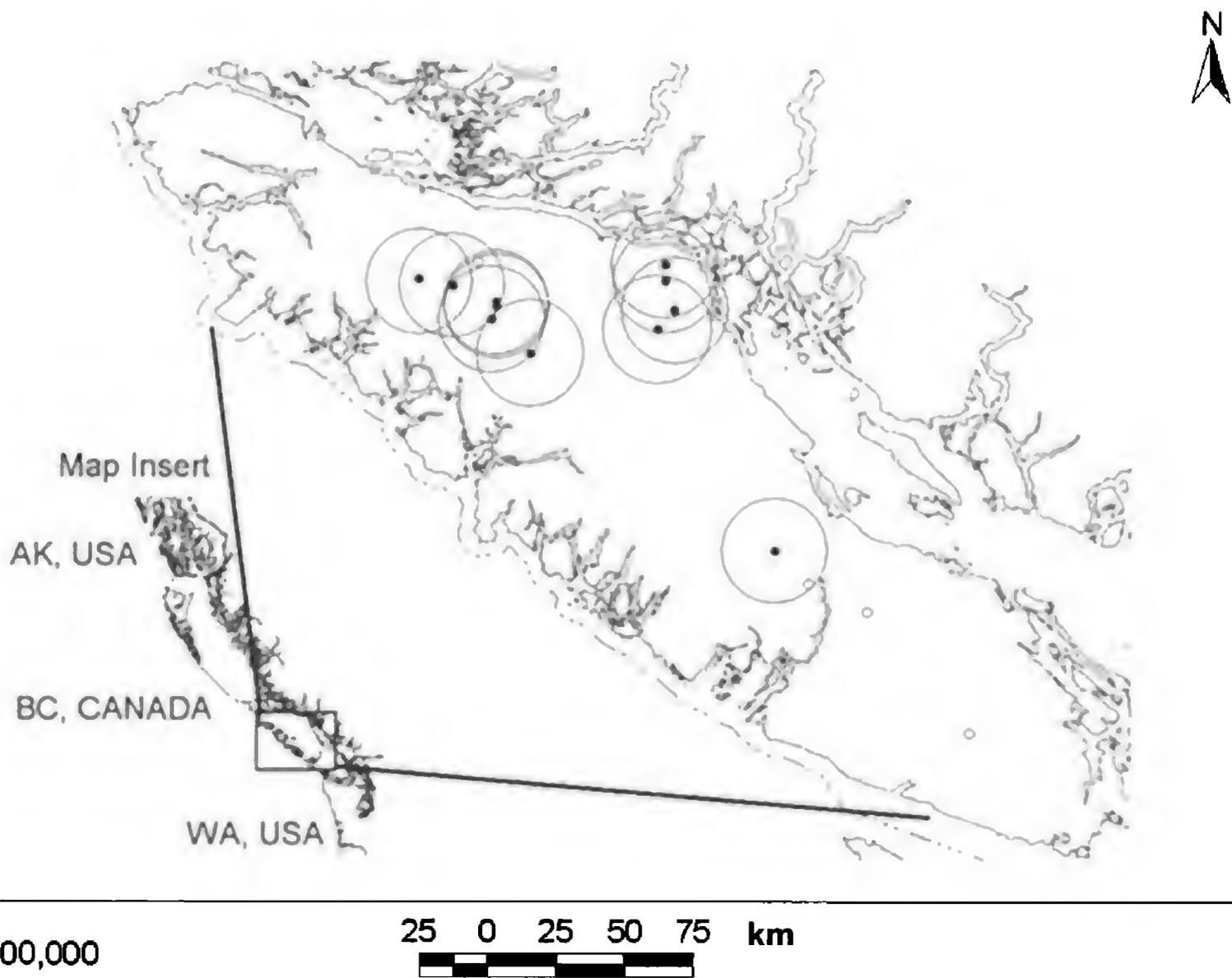


Figure 1. Northern Goshawk nest areas on Vancouver Island, British Columbia, where chicks were captured and radiotagged. Small open circles represent nests where there were insufficient radio locations ($N < 15$) to estimate post-fledgling area (PFA) size and small closed circles represent nests where there were sufficient radio locations to estimate PFA size. Larger circles around nests represent the 20 km ground search area for fledglings after they began to leave the natal area.

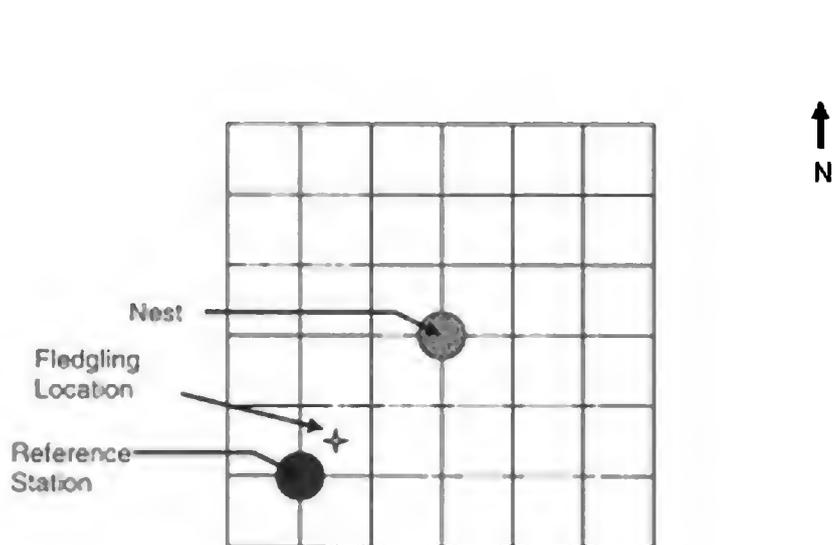


Figure 2. Reference station grid (600 m \times 600 m) at Northern Goshawk nests on Vancouver Island, British Columbia, used for geo-referencing radio-tagged fledgling locations from ground-based telemetry during the 2001–02 breeding seasons. Each grid cell represents 100 m \times 100 m.

reference stations at 100-m intervals (Fig. 2). After nestlings were radio-tagged, nests were visited weekly to monitor chick development, survivorship, and transmitter operation. Once tagged nestlings fledged, nest areas were visited every 1–3 d to collect fledgling location data. We rotated sampling equally among nest areas and sampling periods (<0800–1100 H, 1101–1400 H, 1401–1700 H, and >1700 H) to ensure all times of day were equally represented. Teams of two observers listened for radio signals prior to entering nest stands. Using a 3-element Yagi antenna (Telonics Inc., Mesa, AZ U.S.A.) and receiver (Models SRX-1000, SRX-400, Lotek Engineering Inc., ON, Canada), observers quietly approached fledglings on foot to obtain visual locations and to prevent influencing their movements. We verified the observed fledgling was radio-tagged by identifying color bands. At one nest site where the radio-tagged fledgling was predated 5 d prior to dispersal, we continued tracking the remaining two siblings through aural locations. We measured distance and direction of the fledgling to the closest reference grid station using a meter-marked rope and compass. When fledglings became more mobile and

moved outside the 600×600 -m grid, we either expanded the grid or used triangulation from roads to estimate fledgling locations. We estimated date of departure from natal areas as mid-way between the last visit when fledglings were verified <1.6 km from nests and when no radio signal was heard within this distance on two consecutive telemetry sessions (Kenward et al. 1993a, Kennedy and Ward 2003). Immediately after young departed from natal areas, we conducted intensive road searches for radio-tagged fledglings using a vehicle-mounted omnidirectional antenna (Telonics Inc., Mesa, AZ U.S.A.), and when a signal was detected, we used triangulation to obtain a location. Road searches were conducted within a 20-km^2 area surrounding each nest (Fig. 1). We also searched a 30-km area around nests using a single aerial telemetry flight.

Location Determination. We used the survey mapping extension of Road Engineering Software (Softree Technical Systems Inc. 1998) to calculate UTM coordinates for visual fledgling locations based on the known coordinates of the nest tree location, grid reference station locations, and measured offsets from grid reference stations to fledglings. Fledgling locations derived from triangulation and their associated error ellipses were estimated using Locate II, version 1.5 (Nams 2000), based on the number of bearings, angles between bearings, and the distance from bearing locations to radio-tagged birds.

Post-fledging Area Estimation. We used Home Ranger (version 1.5, Ursus Software, Revelstoke, BC Canada) to estimate PFA size and a smoothed bootstrap (Worton 1995) with 1000 replications to estimate variance of each PFA. Bootstrapping is a common technique for numerically estimating the precision of measurements for which sampling distributions and variances are unknown (Efron and Tibshirani 1991, Quinn and Keough 2002). Although PFAs are not equivalent to home ranges, we assumed the area used by fledglings prior to dispersal could be modeled using home-range estimation techniques. Ninety-five percent adaptive kernel estimates were used to estimate PFA size because kernel estimators were highest ranked in a recent review of the performance of home range estimators (Kernohan et al. 2001). Adaptive kernel estimates are non-parametric, indicate areas of concentrated use by fledglings (i.e., activity centers or core areas), and are more conservative than minimum convex polygon estimators because the home range boundaries are based on probability functions around bird locations rather than on linear connections between the outermost data points (Seaman et al. 1999, Kenward et al. 2001). We only included 95% of locations because we wanted to exclude exploratory or excursion behaviors that could artificially inflate PFA size (Walls and Kenward 1998, Kennedy and Ward 2003). We used the reference bandwidth (h_{ref}) smoothing parameter because it appeared to model most accurately the number of activity centers in our data. Triangulated locations with associated ellipsoid error polygons $>1\text{ km}^2$ were not included in PFA estimates ($N = 2$). We did not estimate PFA size for fledglings with <15 locations ($N = 3$). A minimum of 15 locations per fledgling appears small relative to the recommended minimum of 30 locations per individual for home-range estimation (Kernohan et al. 2001). However, the short post-fledging period limited

our ability to collect >30 locations per fledgling that were not temporally correlated. In addition, area-observation curves (Gese et al. 1990 in Kernohan et al. 2001) suggested our sample sizes adequately represented maximum distances moved from nests during the post-fledging period, prior to departure from natal areas.

Statistical Analyses. We considered fledgling location data collected from different nest sites within the same nest area in different years to be independent ($N = 2$). Mean and median hatching, fledging, and departure from natal area dates were estimated with Julian days. We used the correlation procedure in SAS (SAS Institute, Inc. 1997) to examine the relationship between fledging date and the number of days until dispersal was initiated. We used a Fisher's exact test (PROC FREQ; SAS Institute, Inc. 1997) to evaluate changes in the distance fledglings were from nests at three stages of maturity during the post-fledging period. Distances were calculated as the Euclidian distance from the nest tree to the fledgling location. We categorized the distance we observed fledglings (0–99 m, 100–199 m, 200–399 m, 400–799 m, >800 m) into three time intervals (1–3 wk, 4–5 wk, and 6–7 wk post-fledging). Distance categories were as fine scale as possible given the number of locations in each category required to run the analyses. We used Wilcoxon's rank-sum tests (PROC NPAR1WAY; SAS Institute, Inc. 1997) to compare hatching, fledging, dispersal dates, and PFA size between years. We used Wilcoxon's rank-sum tests for these pair wise comparisons because small sample sizes and non-normal data may invalidate the results provided by *t*-tests (Ott 1993). Results were considered statistically significant at $P < 0.10$. Means and standard errors are presented unless otherwise stated. Data from all radio-tagged fledglings were included in all analyses except PFA size estimates and comparisons in which we only included data from young with sufficient locations ($N = 12$).

RESULTS

Forty-two goshawk nestlings from 17 nests were banded and measured. Mean age of young at banding was 20.2 ± 0.8 d. Tarsus width for male ($N = 15$) and female ($N = 27$) chicks averaged 6.1 ± 0.1 mm and 7.3 ± 0.1 mm, respectively, and means were significantly different ($t_{38} = 2.0$, $P < 0.001$).

Breeding Phenology. Median hatch date was 29 May ($N = 17$), median fledge date was 7 July ($N = 17$), and median date of departure from PFAs was 25 August ($N = 15$). Goshawk nestlings spent a mean of 40.4 ± 0.3 d ($N = 17$) in their nests before fledging and 45.9 ± 1.3 d ($N = 15$) in PFAs before departing from natal areas. Goshawks hatched ($S = 65.0$, $P = 0.07$) and left PFAs ($S = 24.5$, $P = 0.003$) significantly earlier in 2002 than in 2001. In 2001, individuals that fledged later spent less time within PFAs than early fledged young (Fig. 3). Thus, hatching date ($r = -0.8$, P

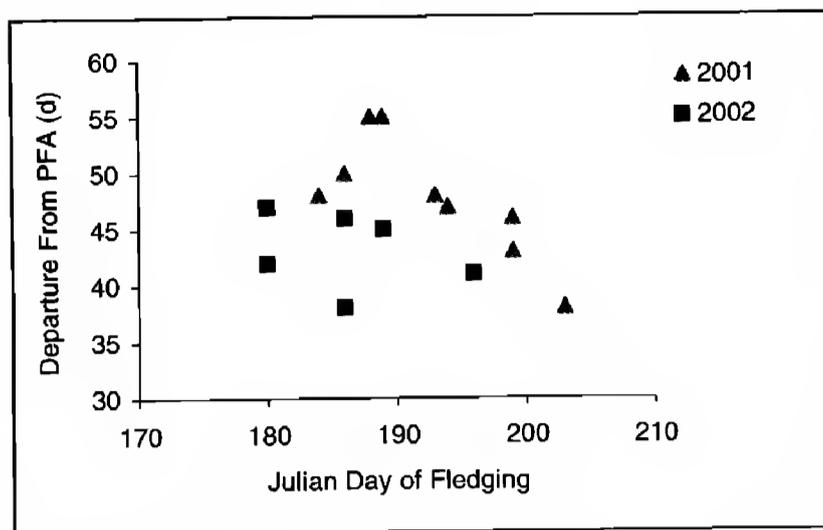


Figure 3. Relationship between fledging date and time spent within post-fledging areas (PFAs) before dispersal initiation for Northern Goshawk fledglings on Vancouver Island, British Columbia, in 2001 and 2002.

= 0.007) and fledging date ($r = -0.8$, $P = 0.01$; Fig. 3) were negatively correlated with the amount of time young spent in PFAs before initiating dispersal. In 2002, relationships between hatching date ($r = -0.3$, $P = 0.5$) and fledging date ($r = -0.3$, $P = 0.5$; Fig. 3) with the amount of time young spent within PFAs were weak because both early and late fledged young spent nearly equal time periods within PFAs. In both years, fledgling departure from PFAs occurred over a 2-wk period (2001: 10–25 August; 2002: 20 August–2 September).

Fledgling Location Data. We collected 236 radio-telemetry locations from 15 radio-tagged goshawk fledglings. Most of these were visual locations (93.2% $N = 220$). Triangulated locations (6.8%; $N = 16$) had a mean error ellipse of 0.029 ± 0.009 km², equivalent to a circle around each location with a mean radius of 96.1 m. Ninety-three percent of fledgling locations were within 200 m of nests ($\bar{x} = 107.8 \pm 8.9$ m, $N = 105$) during the first 3 wk post-fledging, but only 42.4% of locations were within this distance ($\bar{x} = 261 \pm 17.5$ m, $N = 131$) during the remaining 4 wk post-fledging (Fig. 4). As fledglings matured, we generally located them farther from nests (2001: $\chi^2 = 52.5$, $P < 0.001$; 2002: $\chi^2 = 32.4$, $P < 0.001$). However, we observed fledglings returning to nest trees throughout the post-fledging period, so fledglings did not continue to expand their PFA size indefinitely until they departed from natal areas. Maximum movements were observed in the 2 wk after fledglings completed feather growth and subsequent feather hardening, ca. 70–75 d of age (Fig. 4). We were

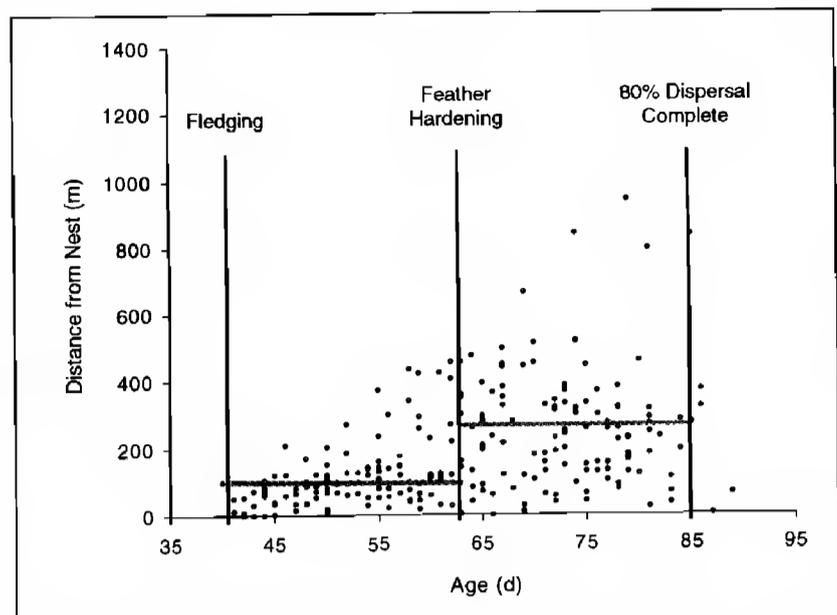


Figure 4. Distance of Northern Goshawk fledglings ($N = 15$) from nests during the post-fledging period on Vancouver Island, British Columbia, 29 June–2 September, 2001–02. Vertical lines represent median fledge date and estimated median feather-hardening date. Horizontal grey bars represent mean distances fledglings were observed from nests pre-feather hardening and post-feather hardening.

only able to relocate one fledgling 27 d after it left the PFA, and it was 82 km from its natal site.

We gathered 17.8 ± 0.6 (range = 15–22) locations per fledgling from the 12 fledglings for which we had sufficient locations ($N > 15$) to estimate PFA size (Table 1). We did not include locations from one male fledgling because he was sick and remained near the same perch tree until he was recovered dead 3 wk post-fledging. Overall, mean PFA size was 59.2 ± 16.1 ha ($N = 12$), and the range was 14.5–229.7 ha (Table 1). Variance around PFA estimates based on the bootstrap samples ranged from 12.7–1820.7 ha (Table 1). PFA size did not significantly differ ($S = 39.0$, $P = 1.0$) between 2001 (71.1 ± 32.3 ha) and 2002 (47.4 ± 6.8 ha), although small sample sizes may have reduced our power to detect annual differences.

The size and shape of PFAs varied among fledglings, and one fledgling used >1 activity centers. In 75% of PFAs, fledgling activity centers included nest trees. The three fledglings with PFAs that did not include nest trees had activity centers that were ca. 100 m, 150 m, and 300 m from nest trees.

Fledgling Fate. Brood reduction occurred at a minimum of seven nests prior to banding. At least three nestlings died post-banding, but pre-fledging. In 2001, 100% of radio-tagged fledglings survived through the post-fledging period (Table 2).

Table 1. Post-fledging area estimates for Northern Goshawk nests ($N = 12$) on Vancouver Island, British Columbia, 29 June–2 September 2001–02.

NEST AREA		PFA SIZE (ha)	BOOTSTRAP MIN., MAX.	PERCENT VISUAL LOCATIONS	N
NAME	YEAR				
Great Central Lake	2001	54.3	50.8, 173.8	69	17
Klaklakama No. 7	2001	229.7	182.7, 1820.8	53	20
Loon Lake	2001	34.7	26.4, 275.9	100	18
Paterson	2001	53.4	39.0, 446.3	95	21
Roberts Lake	2001	14.5	12.7, 101.0	95	23
Toad No. 2	2001	40.0	36.4, 107.6	100	20
Sutton	2002	26.7	24.5, 103.0	100	15
John Road	2002	77.8	36.2, 1120.0	100	17
Klaklakama No. 3	2002	46.6	32.0, 272.5	100	19
Toad No. 3	2002	47.9	23.4, 547.8	100	16
Surprise Lake	2002	40.9	34.0, 259.5	100	16
Pye Lake	2002	44.4	23.7, 372.1	100	17

However, in 2002, 37.5% ($N = 8$) of radio-tagged fledglings, and at least one untagged fledgling, died prior to leaving the natal area. We experienced one premature battery failure, and one fledgling removed its transmitter prior to initiating dispersal.

DISCUSSION

Post-fledging Period Behavior. Goshawk fledglings on Vancouver Island exhibited similar movement patterns during the post-fledging period to goshawks in Sweden (Kenward et al. 1993a) and New Mexico (Kennedy et al. 1994, Kennedy and Ward 2003). Within the first 3 wk post-fledging, fledglings remained within 200–300 m ($\bar{x} = 107.8 \pm 8.9$ m, $N = 105$) of nests, and they were often on the ground or in the lower canopy. Immediately after this period, fledglings experienced a behavioral transition in which they were frequently located farther from nests ($\bar{x} = 261 \pm 17.5$ m, $N = 131$); they were adept fliers and perched in the upper canopy, often in treetops. These changes in fledgling behavior correspond with completion of primary and retriex feather growth and subsequent feather hardening (Kenward et al. 1993a). Interestingly, goshawks did not continue to expand their PFA size indefinitely until departing from nest areas. Instead, the farthest distance we observed fledglings from nests during the post-fledging period peaked within 1–2 wk after they completed feather growth and approximately 10 d prior to departing PFAs. Kenward et al. (1993a) and Minguez et al. (2001) described a similar pat-

tern for goshawks in Sweden and for Bonelli's Eagles (*Hieraetus fasciatus*) in Spain, respectively. Such a pattern illustrates the importance of collecting fledgling locations uniformly throughout the post-fledging period when trying to characterize fledgling movement patterns.

In 2001, hatch and fledge dates were negatively correlated with the amount of time young spent within PFAs. Similar negative relationships between hatch date and age when dispersal was initiated were reported for goshawks in Sweden (Kenward et al. 1993b) and Finland (Byholm et al. 2003). However, in 2002 goshawks initiated breeding earlier on Vancouver Island than in 2001, and fledglings spent similar amounts of time within PFAs, regardless of their hatch and fledge dates. In several bird species, an early onset of breeding often indicates higher food availability within the nest area, which results in higher fledgling mass and survival (Dewey and Kennedy 2001, Naef-Daenzer et al. 2001, Aparicio and Bonal 2002). Because we did not manipulate any proximate factors that may have influenced the length of the post-fledging period, we can only speculate on what influenced the timing of fledgling departure from natal areas and length of post-fledging periods in our study. Food availability within home ranges, predator and competitor abundance, and weather are all possible influential factors (Kenward et al. 1993a, Dewey and Kennedy 2001, Byholm et al. 2003). We found no evidence that parental aggression caused fledglings to disperse on Vancouver Island, which supports

Table 2. Fate of radio-tagged Northern Goshawk fledglings 29 June–11 September 2001–02 during post-fledgling area (PFA) estimation on Vancouver Island, British Columbia.

FLEDGLING		DATE LAST OBS. (BIRD AGE IN d)	FATE
ID	YEAR TAGGED		
China	2001	27-Aug-01 (84)	Departed from PFA
Cous	2001	22-Aug-01 (88)	Departed from PFA
Great Central Lake	2001	27-Aug-01 (79)	Departed from PFA
Mesachie	2001	16-Aug-01 (89)	Departed from PFA
Klaklakama No. 7	2001	24-Aug-01 (94)	Departed from PFA
Loon Lake No. 3	2001	24-Aug-01 (88)	Departed from PFA
Paterson	2001	25-Aug-01 (82)	Departed from PFA
Roberts Lake	2001	25-Aug-01 (97)	Departed from PFA
Toad No. 2	2001	24-Aug-01 (90)	Departed from PFA
Claud Elliot	2002	29-Jul-02 (63)	Dead (unknown cause)
Toad No. 3	2002	05-Aug-02 (77)	Dead (predated)
John Road a ^a	2002	03-Aug-02 (75)	Battery failed
John Road b	2002	11-Sep-02 (114)	Mortality switch on
Loon Lake No. 3	2002	14-July-02 (41)	Dead (unknown cause)
Sutton	2002	10-Aug-02 (79)	Departed from PFA
Klaklakama No. 3	2002	19-Aug-02 (87)	Departed from PFA
Pye Lake	2002	21-Aug-02 (87)	Departed from PFA
Surprise Lake	2002	23-Aug-02 (83)	Departed from PFA

^a Two individuals were radiotagged at this nest because the first radiotransmitter battery died. We captured and radiotagged its sibling after a failed attempt to recapture the originally tagged individual.

experimental results provided by Kenward et al. (1993a).

Although the onset of fledgling dispersal varied by approximately 10 d between 2001 and 2002, fledglings departed natal areas abruptly between 80–96 d of age in both years. This seems to be a common pattern for goshawks (Kenward et al. 1993a, Dewey and Kennedy 2001) and for many other raptors (Spotted Owls [*Strix occidentalis*]: Willey and van Riper 2000; Bonelli's Eagles: Minguez et al. 2001). In contrast, Walls and Kenward (1998) reported a bimodal pattern of departure from natal areas for Common Buzzards (*Buteo buteo*) and Kennedy and Ward (2003) observed supplementally-fed goshawk fledglings returning to natal areas after they initiated dispersal. We were unable to evaluate movement patterns for radio-tagged goshawks during their first year of life because our transmitter batteries expired when young were ca. 110 d of age. However, we searched for fledglings within 30 km of nest areas after they initiated dispersal, and our inability to locate them suggested fledglings moved >30 km after departing PFAs. Initial departure distances were probably moderated by local food availability, whereby fledglings within food-rich areas moved shorter distances af-

ter leaving natal areas than fledglings from food-poor areas (Kenward et al. 1993b, Kennedy and Ward 2003).

Post-fledgling Area Size. Most fledglings included nest trees within their activity centers throughout the post-fledgling period. Similar patterns reported by Ward and Kennedy (1996: goshawks), Wood et al. (1998: Bald Eagles), and Belthoff and Ritchison (1989: Eastern Screech-Owls [*Otus asio*]) suggest that nest trees are important throughout the post-fledgling period for raptors. Some goshawk management guidelines recommend reduced disturbance levels around goshawk nests until young fledge (e.g., BC Ministry of Water, Land, and Air Protection 2004). However, the vulnerability of young during the early fledgling-dependency period (Wiens 2004) and their continued use of the nest site throughout the post-fledgling period, suggests there should be strict adherence to disturbance recommendations until young leave PFAs. Disturbance near nest areas during the post-fledgling period may interfere with adult prey deliveries to young and development of juvenile hunting and flight skills (Kenward et al. 1993a, Kennedy et al. 1994, Wood et al. 1998).

Our study reports the first published estimate of

goshawk PFAs based on home-range estimates derived almost entirely from visual locations, with no location error. Our estimated mean PFA size of 59.2 ha is smaller than that reported by Kennedy et al. (1994). Kennedy et al. (1994) based their PFA size estimate on adult female core use areas which were corroborated with fledgling location data, rather than calculating PFA size directly from fledgling locations. Also, reanalysis of fledgling location data from Kennedy et al.'s (1994) study indicated the non-visual observations of fledglings frequently had a 500-m radius error (Kennedy and Ward 2003). Similarly, fledgling distances provided by Kenward et al. (1993a) were likely inflated because their telemetry locations were accurate within only 100 m. Our PFA estimates may have been slightly inflated because they included one fledgling (Klaklakama No. 7) from which 47% of locations were collected using triangulation with an associated 104.4-m radius error (Table 1). However, our second largest PFA estimate was for a fledgling (John Road) for which 100% of locations were visual.

Additionally, post-fledgling movement patterns may be influenced by fledgling gender (Byholm et al. 2003, J. Wiens unpubl. data) and by landscape habitat characteristics surrounding nests. Our PFA estimates may be smaller than those reported by Kennedy et al. (1994) because all but one PFA estimate were for females that, in one northern Arizona study, were smaller than male PFAs (J. Wiens unpubl. data). PFA size on Vancouver Island may also be smaller than in New Mexico because the definitive forest edges of nest stands in coastal forest ecosystems may act as barriers to fledgling movements more than the less defined ecotones that occur between southwestern forest types (Siders and Kennedy 1996).

Because PFA size can only be estimated from location data, providing variance estimates for these and other types of home range data is extremely informative, but rarely done (Worton 1995, Kernohan et al. 2001). Our variance estimates of the PFA estimates include the 169 ± 129 ha PFA size reported by Kennedy et al. (1994) and the distances (100–1000 m) that Kenward et al. (1993a) observed fledglings from nests. Our PFA estimate was closer to the minimum bootstrapped estimate than the maximum bootstrapped estimate because a greater proportion of our location data were closer to nests. Few fledgling locations far from nests created more variability in the maximum boot-

strapped estimate, although maximum estimates provide important information (F. Hovey pers. comm.).

Home-range estimates also vary depending on the techniques used to collect location data and on the home-range estimation program used to calculate home range size (Lawson and Rodgers 1997, Seaman et al. 1999, Kenward et al. 2001). For example, Kennedy et al. (1994) used a harmonic mean estimator to calculate female core use areas, whereas we used an adaptive kernel estimate. Therefore, comparison of PFA size estimates among studies that use different data collection and size estimation techniques is difficult.

Management Implications. Most goshawk management guidelines in North America are based on Reynolds et al. (1992), which suggest managing for three hierarchical levels of goshawk home ranges: (1) nest area, (2) PFA, and (3) foraging area. However, Reynolds et al. (1992) also recommended managing for alternative nests within goshawk nest areas and they assumed that all alternative nests were within PFAs. Therefore, the biological functionality of a nest area independent of a PFA is questionable, and managing these habitat components in isolation may reduce the effectiveness of management plans. Recent studies comparing habitat characteristics around goshawk nests to random sites (areas assumed not to contain goshawk nests) at multiple spatial scales concluded that goshawk habitat could be discriminated from random sites by a larger proportion of large-diameter, late-seral, closed-canopy forests (Ethier 1999) at scales between 83 ha (McGrath et al. 2003) and 170 ha (Daw and DeStefano 2001). Additionally, Finn et al. (2002) reported occupied historic goshawk nests had a greater proportion of late-seral forest with high canopy closure, less stand initiation cover, and reduced landscape heterogeneity at 177 ha and 1886 ha scales, than at similar scales around unoccupied historic nests. These studies suggest goshawk PFAs may be characterized by unique habitat characteristics at spatial scales within the size range we have reported for PFAs as well as the size range reported by Kennedy et al. (1994).

Mean PFA size estimates on Vancouver Island were smaller than the 200-ha area currently recommended for managing the area around goshawk nests in coastal BC (BC Ministry of Water, Land, and Air Protection 2004). However, our results represent only one nest, and therefore, one PFA per nest area, within a given year. We moni-

tored fledglings from two different nest sites within two nest areas in 2001 and 2002, and there was minimal overlap between PFAs in different years. This suggests that each alternative nest site may have a unique PFA. Therefore, a more meaningful approach to managing goshawk breeding home ranges is to manage for areas that include multiple nests and associated PFAs. Our bootstrapping results suggest this PFA size is highly variable and likely depends upon methods used to estimate PFA size as well as environmental factors such as topography, habitat characteristics around nests, prey availability, and fledgling gender (Dewey and Kennedy 2001, Byholm et al. 2003, Kennedy and Ward 2003, J. Wiens, unpubl. data).

We developed a simplistic graphical depiction of how our information could be applied to develop management scenarios for *A. g. laingi* nest areas throughout coastal BC (Fig. 5). This figure is based on Vancouver Island data with a mean number of 3.0 ± 0.2 ($N = 34$ nest areas) alternative nests/nest area and a mean distance of 274 ± 37.2 m ($N = 65$) between alternative nest trees (E. McClaren unpubl. data). The total area to be managed would vary by nest area and depends on the juxtaposition of alternative nests and PFAs (Fig. 5). For example, Figures 5a and 5b depict areas that are 104.8 ha and 96.3 ha in size, respectively. In areas where the inter-alternate distance is larger (inter-alternate distances > 1.0 km are not uncommon; Dewey et al. 2003, Squires and Kennedy in press), the total management area would be larger. In the absence of fledgling radiotelemetry data and information on fledgling habitat selection patterns, multiple PFAs within one goshawk home range should be managed to create an area that maintains connectivity among alternative nests and to adjacent stands of similar habitat (i.e., reduce stand isolation) to minimize possible edge effects, facilitate food transfers from adults, and provide dispersal corridors.

Although our results suggested the area used by goshawk fledglings on Vancouver Island, and possibly elsewhere, was smaller than estimated in New Mexico (Kennedy et al. 1994), PFA habitat was not the only habitat necessary for goshawks to successfully reproduce. Prey availability in habitats outside of, but in proximity to, PFAs was also essential for adults to rear young (Reynolds et al. 1992, Kennedy and Ward 2003, Wiens 2004). For example, Bloxton (2002) reported radio-tagged adult goshawks in the Olympic Peninsula, WA, to concen-

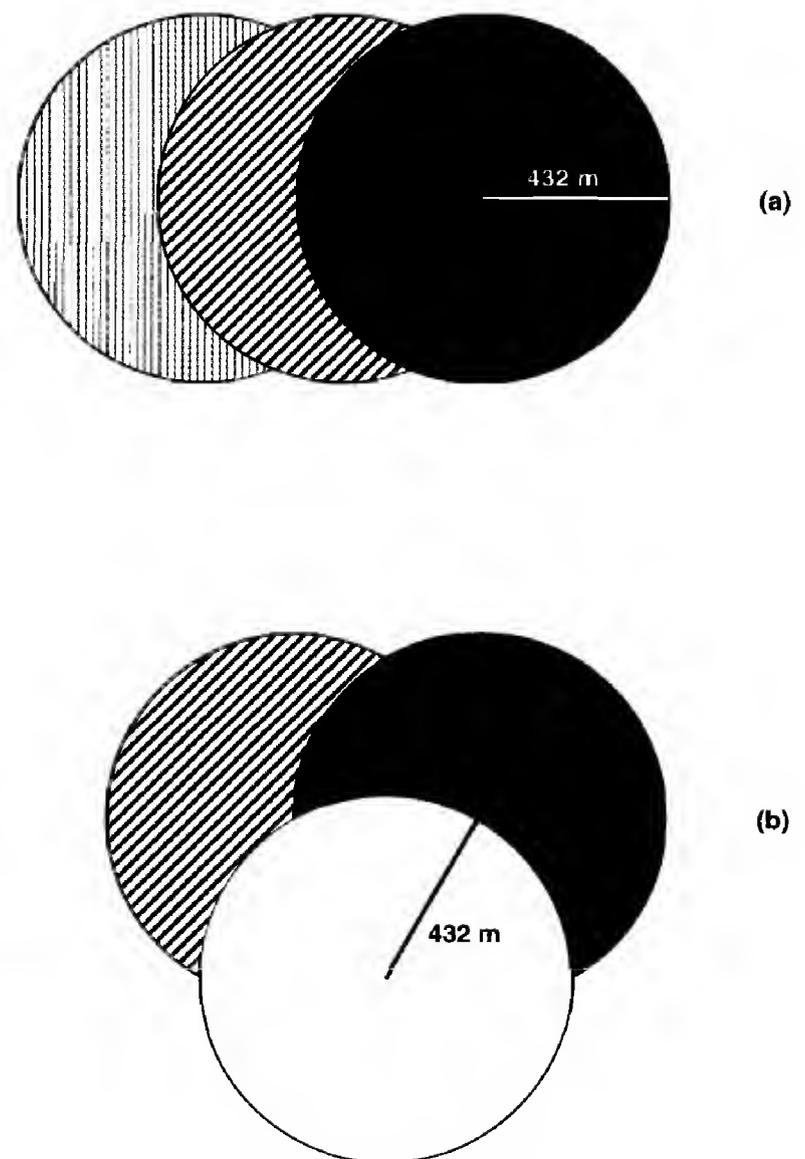


Figure 5. Conceptual representation of managing three alternative Northern Goshawk nests and their associated post-fledgling areas (PFAs). Two possible configurations, (a) all nests adjacent or (b) two adjacent and one below, are shown with 274 m as the mean distance between alternative nests and a mean PFA size of 59 ha on Vancouver Island, British Columbia. The diagram is drawn to scale.

trate their foraging efforts within 5 km of occupied nests during the breeding season. Current goshawk management guidelines in BC (BC Ministry of Water, Land and Air Protection 2004) do not include explicitly managing for goshawk foraging areas, and the effect of not managing goshawk foraging areas in landscapes actively managed for timber harvest is unknown.

Research Recommendations. In future PFA studies, we recommend increasing the minimum number of locations/fledgling to a minimum of 30 to improve the precision of PFA estimates (Kernohan et al. 2001). Goshawk post-fledgling periods are extremely short, and the timeframe for data collection is limited. Obtaining reasonable samples of locations will require collecting either daily locations

after young fledge or collecting multiple locations per sample day and relaxing guidelines around independence of locations. A sampling regime that spaces location data collection evenly throughout the duration of the study, enabling a reasonable amount of time for animals to relocate, may be more important than concerns about autocorrelation of data (Kernohan et al. 2001). Additionally, PFA size and habitat studies should be conducted across a diversity of ecosystems, so that management recommendations may be fine-tuned to reflect similarities and differences across broad geographic areas. This information may assist with designating suitable PFAs around nests when it is not feasible to collect radiotelemetry data.

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NORTHERN GOSHAWK DIET IN MINNESOTA: AN ANALYSIS USING VIDEO RECORDING SYSTEMS

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ABSTRACT.—We used video-recording systems to collect diet information at 13 Northern Goshawk (*Accipiter gentilis*) nests in Minnesota during the 2000, 2001, and 2002 breeding seasons. We collected 4871 hr of video footage, from which 652 prey deliveries were recorded. The majority of prey deliveries identified were mammals (62%), whereas birds (38%) composed a smaller proportion of diet. Mammals accounted for 61% of biomass delivered, and avian prey items accounted for 39% of prey biomass. Sciurids and leporids accounted for 70% of the identified prey. Red squirrel (*Tamiasciurus hudsonicus*), eastern chipmunk (*Tamias striatus*), and snowshoe hare (*Lepus americanus*) were the dominant mammals identified in the diet, while American Crow (*Corvus brachyrhynchos*) and Ruffed Grouse (*Bonasa umbellus*) were the dominant avian prey delivered to nests. On average, breeding goshawks delivered 2.12 prey items/d, and each delivery averaged 275 g for a total of 551 g delivered/d. However, daily ($P < 0.001$) and hourly ($P = 0.01$) delivery rates varied among nests. Delivery rates ($P = 0.01$) and biomass delivered ($P = 0.038$) increased with brood size. Diversity and equitability of prey used was similar among nests and was low throughout the study area, most likely due to the dominance of red squirrel in the diet.

KEY WORDS: *Northern Goshawk; Accipiter gentilis; diet; Minnesota; prey diversity; red squirrel; Tamiasciurus hudsonicus.*

DIETA DE *ACCIPITER GENTILIS* EN MINNESOTA: UN ANÁLISIS BASADO EN SISTEMAS DE GRABACIÓN EN VIDEO

RESUMEN.—Empleamos sistemas de grabación en video para recolectar información sobre la dieta de *Accipiter gentilis* en 13 nidos ubicados en Minnesota durante las temporadas reproductivas de 2000, 2001 y 2002. Obtuvimos 4871 hr de grabación, a partir de las cuales registramos 652 entregas de presas. La mayoría de las presas entregadas que identificamos fueron mamíferos (62%), mientras que las aves (38%) representaron una proporción menor de la dieta. Los mamíferos y las aves representaron el 61% y el 39% de la biomasa entregada, respectivamente. Los sciúridos y lepóridos representaron el 70% de las presas identificadas. Los mamíferos predominantes identificados en la dieta fueron *Tamiasciurus hudsonicus*, *Tamias striatus* y *Lepus americanus*, mientras que las aves llevadas a los nidos predominantemente fueron *Corvus brachyrhynchos* y *Bonasa umbellus*. En promedio, los individuos nidificantes entregaron 2.12 presas/d, y cada entrega tuvo un promedio de 275 g, para un total de 551 g entregados/d. Sin embargo, las tasas diarias ($P < 0.001$) y horarias ($P = 0.01$) de entrega de presas variaron entre nidos. Las tasas de entrega ($P = 0.01$) y la biomasa entregada ($P = 0.038$) incrementaron con el tamaño de la nidada. La diversidad y equitabilidad de las presas consumidas fueron similares entre nidos y bajas a través del área de estudio, probablemente debido a la dominancia de *T. hudsonicus* en la dieta.

[Traducción del equipo editorial]

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The Northern Goshawk (*Accipiter gentilis*) is a large, forest-dwelling raptor generally associated with mature deciduous, coniferous, or mixed forests (e.g., Bright-Smith and Mannan 1994, Siders and Kennedy 1996, Beier and Drennan 1997, Squires and Reynolds 1997). Goshawk research in North America has been conducted primarily in the western half of the continent (Boal et al. 2003). Consequently, there is little published literature describing ecology of the species in the Western Great Lakes Region (WGLR) of North America, where it is currently listed as a Migratory Non-game Bird of Management Concern by the U.S. Fish and Wildlife Service (Region 3) and as a sensitive species by the U.S. Forest Service (Region 9) due to loss of habitat (Reynolds et al. 1992).

Depending on region, season, and availability, goshawks capture a wide variety of prey and are considered prey generalists (Squires and Reynolds 1997, Squires and Kennedy 2005). Although breeding-season diet composition has been studied for many populations (e.g., Meng 1959, Grzybowski and Eaton 1976, Boal and Mannan 1994, Younk and Bechard 1994, Lewis 2001), site-specific studies of diet are necessary for developing management strategies for goshawk populations at regional and local levels (e.g., Reynolds et al. 1992). A number of records exist of prey items collected opportunistically at goshawk nests in the WGLR (Eng and Gullion 1962, Apfelbaum and Haney 1984, Martell and Dick 1996), but these reports are anecdotal and provide a prey list rather than a quantitative assessment of food habits (Roberson et al. 2003).

Methods used in goshawk food habits research have included indirect (i.e., identification of prey remains or contents of regurgitated pellets) and direct observations of prey deliveries to nests (Meng 1959, Grzybowski and Eaton 1976, Bosakowski and Smith 1992, Boal and Mannan 1994). Indirect methods of assessing raptor diet can lead to biased results (e.g., Bielefeldt et al. 1992), whereas direct methods should provide the least-biased results (Collopy 1983, Marti 1987, Boal and Mannan 1994). During the breeding seasons of 2000–02, we used videography as a modified method of direct observation of prey deliveries to examine diet of Northern Goshawks in northern Minnesota.

METHODS

Study Area. The study area was located in the Laurentian Mixed-Forest Province of north-central and north-

eastern Minnesota (46°50'N, 92°11'W) as described by Boal et al. (2001) and Roberson (2001; Fig. 1). The study area elevation ranged from ca. 200–400 m. Mean summer and winter temperatures were 18°C and –11°C, respectively, and maximum and minimum temperature records for the region were 40°C and –46°C, respectively (Daniel and Sullivan 1981). Annual precipitation averaged 60–70 cm. The study area was dominated by pine, mixed-hardwood, boreal, and second-growth forests with wetland community types interspersed among forest stands (Tester 1995).

Goshawk Nests. Nests included in this study were considered as sampling units and were selected from all known occupied nests in the study area (Boal et al. 2001). With the exception of one nest, where few data were collected during 2000, diet information was not collected at any nest for more than one breeding season. Nests were selected randomly within the constraints of accessibility and to include different land ownerships. Thus, our sample is not truly random and may not be representative of the goshawk population of our study area. However, to examine the applicability of our diet data to the goshawk population as a whole, we examined prey diversity and overlap among nests. High overlap and low diversity would suggest prey use was similar among goshawk pairs and that our data were representative of the population in general.

Video Recording. We used VHS (Model SL 800, Security Labs®, Noblesville, IN U.S.A.) and 8-mm video recording systems (Sony® Model M-350, Fuhrman Diversified, Inc., Seabrook, TX U.S.A.) with color or black-and-white cameras (Model CCM-660W, Clover Electronics®, Los Alamitos, CA U.S.A.). Cameras were installed on nest trees within 0.6 m of the nest or, for cameras with zoom lenses, on an adjacent tree up to 9 m from the nest. Video recorders were placed in weather-proof cases ca. 30 m from the base of each camera tree. Coaxial-video cables were used to convey power to and transmit images from the cameras. Recorders were programmed to record from 0530–2100 H (15.5 hr of footage) at the 48-hr (1.3 frames/sec) or the 72-hr (0.8 frames/sec) setting to optimize the amount of tape used per sampling session and battery life. We replaced tapes and batteries every 3–4 d.

Prey Identification. To identify prey delivered to nests, we reviewed video footage until a prey delivery occurred, then advanced frame by frame and freeze-framed to facilitate prey identification. We identified avian and mammalian prey by morphological features and developed a list of prey species delivered by goshawks to all nests (Table 1). Goshawks may cache prey and retrieve cached prey items (Boal and Mannan 1994), which could bias estimates of delivery rates and proportional use of species in the diets. We attempted to identify cached prey on basis of a successive, iterative process that included comparing prey items using flesh color, pelage or feather condition, and time of delivery from review of video footage, and then remove those items thought to be cached from analysis.

Age and Biomass Estimation. We assigned avian prey to age categories (e.g., adult, juvenile, or nestling) based on plumage (e.g., feathers and down) and amount of sheathing on flight feathers (Reynolds and Meslow

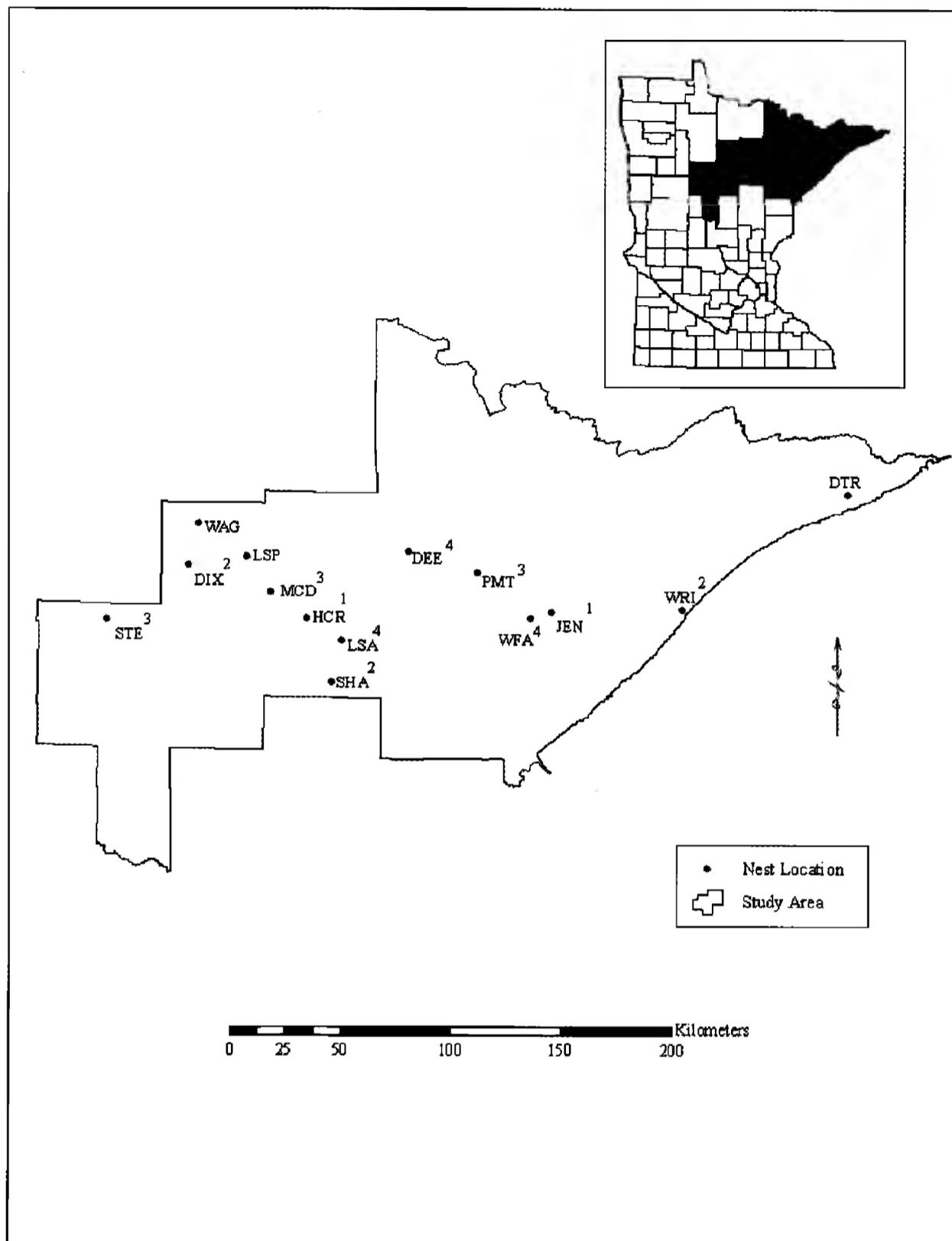


Figure 1. Study area and distribution of Northern Goshawk nests in Minnesota where food habits information was collected during the 2000–02 breeding seasons. The three-letter designations indicate individual nests. Breeding season diet information collected at the DTR breeding area was omitted from all analyses because of nest failure. Breeding areas with similar prey composition are indicated with the same superscripts. Superscripts indicate cluster number (see Fig. 2).

1984). We categorized mammalian prey as adults or juveniles based on size (Bielefeldt et al. 1992). Because of difficulty in estimating age of small mammals, we considered all mammals smaller than chipmunks to be adults. Biomass for partial prey items was calculated using the proportion of prey delivered to nests, and proportions were estimated qualitatively (e.g., 50% of adult size).

We estimated biomass for prey identified to family, genus, or species and used the mean mass of both sexes (Reynolds and Meslow 1984, Lewis 2001). Biomass esti-

mates were based on published information on mammalian and avian species occurring in the study area (Burt and Grossenheider 1980, Jones and Birney 1988, Dunning 1993, Dunn and Garrett 1997, Dunn 1999, Sibley 2000). We calculated mass for nestlings following Bielefeldt et al. (1992) using 100% of the adult mass for warbler-sized species, 65% of the adult mass for robin and jay-sized species, and 55% of the adult mass for large birds such as grouse. We calculated mass of juvenile red squirrel (*Tamiasciurus hudsonicus*), eastern chipmunk

Table 1. Number, percent occurrence, and biomass of mammalian and avian prey delivered to Northern Goshawk nests ($N = 13$) in Minnesota, 2000–02. Values represent pooled number of prey identified at nests during the 2000, 2001, and 2002 breeding seasons.

PREY CATEGORY	COMMON NAME	<i>N</i>	PERCENT	BIOMASS (g)	PERCENT
Mammals					
<i>Tamiasciurus hudsonicus</i>	red squirrel	202	31.0	38046	23.6
<i>Tamias striatus</i>	eastern chipmunk	95	14.6	8108	5.0
<i>Lepus americanus</i>	snowshoe hare	31	4.8	41027	25.5
<i>Sylvilagus floridanus</i>	eastern cottontail	7	1.1	7654	4.8
<i>Sciurus carolinensis</i>	eastern gray squirrel	3	0.5	1679	1.0
<i>Peromyscus</i> spp.		2	0.3	47	0.0
Family: Muridae		1	0.2	18	0.0
<i>Mustela frenata</i>	long-tailed weasel	1	0.2	210	0.1
Unknown mammal (MSC1) ^a		8	1.2	186	0.1
Unknown mammal (MSC2) ^a		9	1.4	1720	1.1
Birds					
<i>Corvus brachyrhynchos</i>	American Crow	37	5.7	14515	9.0
<i>Bonasa umbellus</i>	Ruffed Grouse	33	5.1	18448	11.5
<i>Aythya</i> spp.	diving duck	12	1.8	11360	7.1
<i>Cyanocitta cristata</i>	Blue Jay	8	1.2	664	0.4
<i>Fulica americana</i>	American Coot	6	0.9	3338	2.1
<i>Turdus migratorius</i>	American Robin	3	0.5	205	0.1
<i>Quiscalus quiscula</i>	Common Grackle	3	0.5	341	0.2
Family: Icteridae	blackbird	3	0.5	189	0.1
<i>Picoides</i> spp.	woodpecker	3	0.5	199	0.1
<i>Dryocopus pileatus</i>	Pileated Woodpecker	3	0.5	861	0.5
Unknown duckling		4	0.6	400	0.2
<i>Butorides virescens</i>	Green Heron	2	0.3	420	0.3
<i>Perisoreus canadensis</i>	Gray Jay	2	0.3	142	0.1
<i>Agelaius phoeniceus</i>	Red-winged Blackbird	2	0.3	105	0.1
<i>Strix varia</i>	Barred Owl	1	0.2	394	0.2
<i>Buteo platypterus</i>	Broad-winged Hawk	1	0.2	455	0.3
Genus: <i>Calidris</i>		1	0.2	73	0.0
<i>Bucephala clangula</i>	Common Goldeneye	1	0.2	900	0.6
<i>Accipiter cooperii</i>	Cooper's Hawk	1	0.2	439	0.3
<i>Gallus</i> spp.	domestic chicken ^b	1	0.2		
<i>Coccythraustes vespertinus</i>	Evening Grosbeak	1	0.2	59	0.0
<i>Pipilo erythrophthalmus</i>	Eastern Towhee	1	0.2	41	0.0
Genus: <i>Euphagus</i>		1	0.2	63	0.0
<i>Accipiter gentilis</i>	Northern Goshawk	1	0.2	820	0.5
<i>Picoides villosus</i>	Hairy Woodpecker	1	0.2	66	0.0
<i>Charadrius vociferus</i>	Killdeer	1	0.2	97	0.1
<i>Anas platyrhynchos</i>	Mallard	1	0.2	1082	0.7
<i>Sitta canadensis</i>	Red-breasted Nuthatch	1	0.2	10	0.0
<i>Seiurus aurocapillus</i>	Ovenbird	1	0.2	19	0.0
<i>Catharus fuscescens</i>	Veery	1	0.2	31	0.0
Unknown nestling		33	5.1	1190	0.7
Unknown bird (ASC1) ^a		18	2.8	173	0.1
Unknown bird (ASC2) ^a		23	3.5	1778	1.1
Unknown bird (ASC3) ^a		6	0.9	3459	2.1
Items not identified to class					
<i>Mammalia</i> or <i>Aves</i>		76	11.7		

^a MSC1 = mouse-sized prey item; MSC2 = red squirrel-sized prey item; ASC1 = warbler-sized prey item; ASC2 = robin-sized prey item; ASC3 = Ruffed Grouse-sized prey item.

^b Omitted from analysis.

(*Tamias striatus*), snowshoe hare (*Lepus americanus*), and eastern cottontail (*Sylvilagus floridanus*) using 95% of the adult mass; if ages could not be determined reliably, we assigned juvenile masses to these species.

To estimate biomass of unidentified prey, we pooled unidentified birds into three *a priori* size classes (SC) following Storer (1966) and Kennedy and Johnson (1986) that represented average mass of common species in our study area: SC1 = 10 g (e.g., warbler-sized), SC2 = 77 g (e.g., robin-sized), and SC3 = 576 g (e.g., Ruffed Grouse [*Bonasa umbellus*]-sized). Similarly, we pooled unidentified mammal prey into two *a priori* size classes: SC1 = 23 g (e.g., mouse-sized) and SC2 = 192 g (e.g., squirrel-sized).

Prey and Biomass Delivery Rates. We calculated delivery rates on the basis of number of prey delivered per day, number of prey delivered per nestling per day, and number of prey delivered per day at nests with one, two, and three nestlings. We calculated biomass estimates in the same manner. We calculated mean delivery rates over 5-d intervals from hatching to 5 d post-fledging (i.e., from 0–45 d).

Prey Diversity and Overlap. We calculated prey diversity for the study area using ungrouped prey categories (i.e., using each prey category identified to family, genus, or species separately). Because samples were smaller when examining individual nests, we generalized prey into similar species categories (Lewis 2001) to calculate prey diversity for individual nests. The generalized prey categories for among-nest diversity assessment were: (1) Scurids, (2) blackbirds and Corvids, (3) Leporids, (4) Ruffed Grouse, (5) diving ducks (*Aythya* spp.), (6) water and shore birds, (7) passerines, (8) Picidae, (9) Falconiforms, (10) miscellaneous mammals (e.g., long-tailed weasel [*Mustela frenata*]).

We calculated prey diversity using Williams (1964) and MacArthur's (1972) modified form of the Simpson's index (Simpson 1949) and diet equitability using Smith and Wilson's index of evenness (Smith and Wilson 1996). We used prey identified to family, genus, or species to estimate diet overlap among nests with the Simplified Morisita's Index of Overlap (Krebs 1999). Overlap measures are designed to measure the degree that two species share a set of common resources or utilize the same parts of the environment (Lawlor 1980). Overlap measures are scaled from zero to one, where zero overlap indicates dissimilarity in resource use, and one indicates complete overlap (Krebs 1999). We also assessed similarity in prey use among nests with cluster analysis using average linkage clustering (Romesburg 1984, Krebs 1999, McGarigal et al. 2000). As suggested by Romesburg (1984), we used the un-weighted pair-group method using arithmetic averages (UPGMA).

Statistical Analysis. We used analysis of variance (ANOVA) to examine relationships between delivery rate variables and brood size using log-transformed data (Zar 1999). Biomass of prey delivered per day per nest was transformed by taking the logarithm of biomass delivered per day and adding 1.0 (Zar 1999). Normality of experimental error was tested using the Shapiro-Wilk test procedure, and assumptions regarding homogenous variances were tested using Levene's test (Zar 1999). We examined differences in the number of mammals and

birds delivered among nests over 5-d intervals, because of missing data among sampled days, with a Kruskal-Wallis single-factor ANOVA (Zar 1999). Because observations within breeding areas were not independent, we examined differences in provisioning rates among breeding areas with multivariate repeated measures ANOVA. We used the General Linear Model (GLM) module of STATISTICA (Version 6.0, StatSoft, Inc., Tulsa, OK U.S.A.) for all statistical analyses except calculation of diet overlap and similarity, for which we used Ecological Methodology 6.1 (Exeter Software, Setauket, NY U.S.A.). An alpha level of $P = 0.05$ was used for all statistical tests, and we present means and standard errors.

RESULTS

Video Recording and Prey Identification. We installed video monitoring systems at three, five, and seven occupied goshawk nests during the 2000, 2001, and 2002 field seasons, respectively. We placed cameras at nests when nestlings were ca. 8 d old (± 1.18 ; range = 1–18 d). One of the 15 nests failed within 3 d of camera placement and was removed from analysis. Due to camera malfunctions, we were only able to collect 16 hr of footage at one of the nests in 2000. We placed a camera at the 2002 nest of the same pair, but pooled data from both years as one nest area for analysis. Thus, our sample of 4801 hr ($\bar{x} = 320 \pm 42$ hr/nest) of video footage is derived from 13 nesting pairs of goshawks.

We identified 59 (8.3%) of 711 prey deliveries as being retrievals of cached items. Of the 652 fresh prey deliveries, we identified 451 (69%) to the species level, 20 (3%) to genus, four to family (1%), and four (1%) as unidentifiable ducklings (Table 1). Eighty (12%) birds and 17 (3%) mammals were unidentifiable beyond class, and we were unable to identify 76 (12%) deliveries. The majority of prey deliveries identified to at least class ($N = 576$) were mammals (62%), whereas birds (38%) comprised a smaller proportion of diet.

When considering only those deliveries identified to family or finer resolution (i.e., to genus or species; $N = 476$), the dominant prey species were red squirrels (41.2%), eastern chipmunks (19.8%), American crows (7.7%), Ruffed Grouse (6.9%), and snowshoe hares (6.5%). No other individual species accounted for >5% of identified prey. As a group, Scurids and Leporids ($N = 338$) accounted for 70% of the identified prey. Among mammals, 51.8% were adults, 25.4% were juveniles, and we were unable to estimate age for 22.8%. Of the birds, 36.7% were adults, 9.6% were juveniles,

27.5% were nestlings, and we could not reliably estimate age for 26.2%.

Biomass. In context of the prey species and biomass proportion used by goshawks in our study, the delivery of one domestic chicken (*Gallus* spp.) was unusual and the mass would dramatically influence biomass estimates for avian prey. We therefore considered it an outlier and deleted it from biomass estimates.

We estimated the total biomass of all prey deliveries at nests as 161 kg. The mean mass for both avian and mammalian prey was 281 g (± 13.7 , 95% confidence interval = 254–308 g). Although average mass of avian prey ($\bar{x} = 292$ g; range = 10–1082 g) was similar to that for mammalian prey (275 g; range = 18–1361 g), avian prey accounted for only 39% of biomass delivered whereas mammals accounted for 61% of biomass delivered. Snowshoe hare (25%), red squirrel (24%), Ruffed Grouse (11%), American Crow (9%), diving ducks (7%), chipmunk (5%), and eastern cottontail (5%) accounted for 86% of biomass used by goshawks. No other species accounted for $\geq 5\%$ of biomass.

Delivery Rates. Breeding goshawks delivered 2.12 (± 0.14) prey per day (i.e., 0.14 deliveries/hr), each delivery had a mean mass of 275 g (± 20 g), for a total of 551 g (± 50 g) delivered per day. However, daily ($F_{13,253} = 3.44$, $P < 0.001$) and hourly ($F_{13,250} = 2.31$, $P = 0.01$) delivery rates varied among nests.

1.3 (± 0.1) prey items were delivered per nestling per day, but delivery rates increased with brood size ($F_{2,271} = 5.23$, $P = 0.01$). Daily prey delivery rates were 1.8 (± 0.1) at nests with one nestling, 2.3 (± 0.1) at nests with two nestlings, and 2.5 (± 0.2) at nests with three nestlings. Despite the increase in prey deliveries among nests with larger broods, there was an inverse relationship between brood size and the number of prey delivered per nestling per day ($r = -0.43$, $P < 0.05$). Each nestling in single broods received a mean of 1.8 (± 0.1) prey items per day, whereas each nestling in broods of two received only 1.2 (± 0.1) prey items per day, and each nestling in broods of three received only 0.9 (± 0.1) prey items per day.

322 g (± 32 g) of biomass were delivered per nestling. However, we observed a pattern of biomass delivered to broods of different sizes that was similar to that of number of prey delivered to broods of different sizes; biomass delivered per nestling per day ($F_{2,6} = 5.96$, $P = 0.038$) varied with

brood size. On average, daily biomass delivered was 509 g (± 84 g) to nests with one nestling, 555 g (± 42 g) to broods of two, and 756 g (± 107 g) to broods of three. Despite greater amounts of biomass being provided to larger broods, this resulted in nestlings in single broods receiving 509 g (± 84 g) of biomass per day, whereas nestlings in broods of two each received 278 g (± 3 g) of biomass per day and nestlings in broods of three each receiving 252 g (± 36 g) per day.

Dietary Overlap. The diversity and equitability of prey delivered to nests was low for the study area, as indicated by a reciprocal of the Simpson diversity index ($1/D$) of 4.28 and a Smith and Wilson evenness index (E_{var}) of 0.30. Similarly, diversity among nests was low, with a mean value of $1/D = 3.77$ (± 0.41 , range = 2.09–7.35). The mean value of E_{var} for all nests was 0.56 (± 0.04 , range = 0.36–0.80). Low prey diversity and evenness values may be attributable to goshawk diet being dominated by red squirrels and chipmunks in our study. Similarly, there was high dietary overlap (>0.8) among breeding pairs of goshawks in our study (Table 2), although one nesting area (LSP; Table 2) appeared to be measurably different from the rest. Cluster analysis indicated there were two groups of breeding goshawk diets that exhibited similar prey composition and proportion of use (Fig. 2) although, again, one nest (LSP; Fig. 2) appears to be an outlier. There was no apparent relationship between overlap measures and spatial distribution of nests across the study area (Fig. 1, 2).

DISCUSSION

Mammals were the dominant prey of breeding goshawks in Minnesota, with red squirrels and eastern chipmunks appearing to be the most important species in terms of both number delivered and biomass. These two species alone accounted for 62% of all prey identified to at least family and 51% of prey identified to at least class. Several studies have documented red squirrels as important prey for goshawks (Squires and Kennedy 2005) throughout their range. They may be especially important during the winter when other prey may be less available (Widén et al. 1987). Squirrels dominated goshawk diets in Sweden in terms of number (79%) and biomass (56%) during winters of both high and low squirrel abundance (Widén et al. 1987). Diet information for winter goshawks in the WGLR is not available, but the extensive use of red squirrels during the summer and the patterns of

Table 2. Dietary overlap values using the Simplified Morisita's Index of Overlap. Values range from 0 (no overlap) to 1 (complete overlap). The data presented were generated from prey frequency data collected at Northern Goshawk nests ($N = 13$) in Minnesota during the 2000, 2001, and 2002 breeding seasons. The three letter codes designate specific goshawk nests.

	DEE	DIX	HAC	JEN	LSP	LSA	MCD	PMT	SHA	STE	WAG	WFA	WRI
DEE	1	0.774	0.834	0.886	0.666	0.976	0.924	0.951	0.797	0.951	0.845	0.968	0.79
DIX		1	0.986	0.952	0.524	0.871	0.934	0.905	0.988	0.901	0.834	0.844	0.996
HAC			1	0.988	0.592	0.917	0.97	0.948	0.989	0.938	0.902	0.899	0.987
JEN				1	0.632	0.947	0.979	0.969	0.959	0.953	0.939	0.941	0.954
LSP					1	0.622	0.639	0.629	0.56	0.634	0.771	0.628	0.549
LSA						1	0.973	0.993	0.893	0.991	0.882	0.988	0.885
MCD							1	0.989	0.956	0.984	0.904	0.955	0.946
PMT								1	0.932	0.994	0.912	0.98	0.917
SHA									1	0.928	0.869	0.864	0.993
STE										1	0.889	0.964	0.917
WAG											1	0.893	0.845
WFA												1	0.857
WRI													1

squirrel use during winter in other areas (Widén et al. 1987) suggest this species may be of year-round importance to goshawks in the region. In terms of biomass, snowshoe hares also appear to be important for goshawks in our study area, accounting for 25% of the biomass delivered to nests. Rabbits and hares are also used extensively by goshawks throughout their range (Squires and Kennedy 2005).

Ruffed Grouse comprised 5% of prey deliveries and 11% of biomass delivered to goshawk nests during a 3-yr period of relatively low grouse abundance (Smithers 2003). There is anecdotal evidence that at least some goshawks in Minnesota may rely more heavily on Ruffed Grouse than other prey during some time periods (Eng and Gullion 1962, Apfelbaum and Haney 1984). Eng and Gullion (1962) focused on Ruffed Grouse mortality and did not assess proportional use of grouse in the diet of goshawks, and Apfelbaum and Haney (1984) reported on prey remains collected at a single nest in northern Minnesota. Because of the difficulties in accurately quantifying the extent of grouse predation by goshawks (Eng and Gullion 1962) and the biases associated with determining raptor diets based on prey remains (Smithers 2003), the results of these studies need to be interpreted cautiously. We suspect that the previous research on goshawk diet for our study area, all collected by indirect methods (Eng and Gullion 1962, Apfelbaum and Haney 1984, Martell and Dick 1996), may overestimate the proportion of birds, especially large birds such as grouse, and underestimate the proportion of mammals in goshawk diets.

Qualitative review of the data suggests the mean delivery rate of 0.14 deliveries/hr to nests in our study was less than that observed in Arizona (0.25 deliveries/hr; Boal and Mannan 1994), Nevada (0.31 deliveries/hr; Younk and Bechard 1994) and two areas of southeast Alaska (0.30 and 0.23 deliveries/hr; Lewis 2001). However, although mean biomass per delivery in our study (275 g) was less than that in Arizona (307 g/delivery) where Leporids and Sciurids were the dominant prey (Boal and Mannan 1994), it was greater than the two areas of Alaska (214 g and 173 g/delivery), where birds were the dominant prey (Lewis 2001).

Our study indicates that goshawks with larger broods provision with greater delivery rates and biomass. Biomass per nestling was similar between broods of two and three (16.3–18.0 g/hr), but only

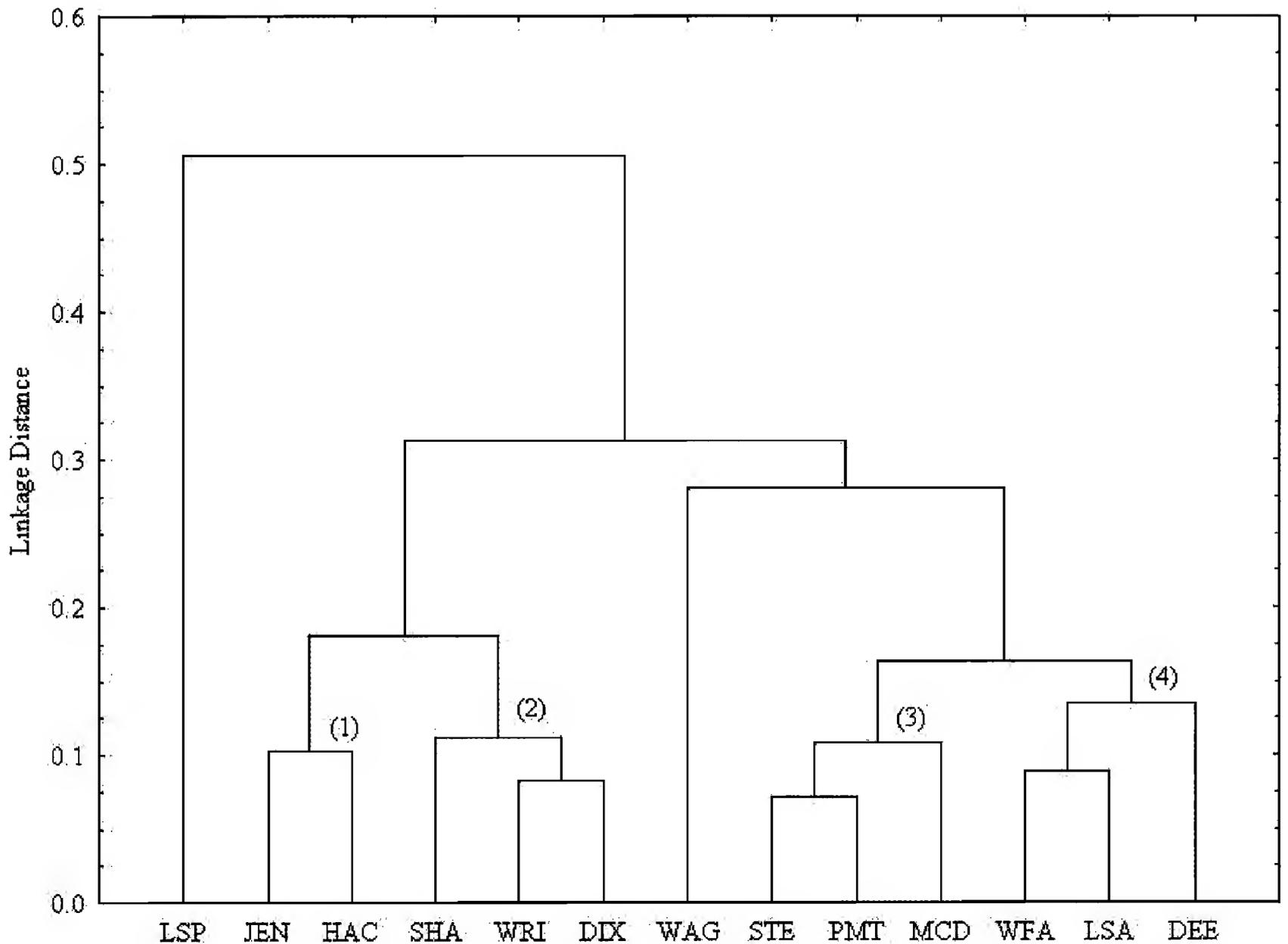


Figure 2. Cluster analysis dendrogram for food habits data collected at Northern Goshawk nests in Minnesota during the 2000, 2001, and 2002 breeding seasons. Parentheses indicate cluster number (see Fig. 1). The LSP and WAG breeding areas exhibited the least similarity of diet composition among breeding areas.

about half as much as that received by nestlings in broods of one (33.0 g/hr). This poses an interesting question regarding energetic aspects of goshawk productivity; what is the minimum biomass/hr necessary to fledge young successfully? The similarity between broods of two and broods of three suggests that, at least in our study area, and at nests with similar prey composition, a minimum of 16–18 g of biomass per hr may be required for successful nesting. However, a finer assessment of nestling energetics would likely require experimentation in a laboratory setting.

Given our prey use and delivery rate data, one can make a generalized prediction of the relative impact of a breeding pair of goshawks in our study area during the 45-d nestling period. With an expected delivery rate of 2.1 prey/d over a 45-d nestling period, ca. 94 prey deliveries can be expected.

Based on observed frequencies of prey use, this would translate to the average breeding goshawk pair capturing 29 red squirrels, 14 eastern chipmunks, six American Crows, five snowshoe hares, five Ruffed Grouse, two diving ducks, one cottontail, one Blue Jay, and 31 miscellaneous small birds and mammals. To put this level of predation in context, all of these prey captures would occur within a home range of 6376 ha for a goshawk pair in the study area (Boal et al. 2003).

Composition and richness of prey delivered to nests was similar across the study area, and estimates of prey diversity and equitability were generally low among nests. We suspect the high dietary overlap and similarity of prey use among breeding areas was most likely attributable to the dominance of red squirrels and chipmunks in goshawk diets. However, goshawk diets were dominated by red

squirrels and chipmunks, but snowshoe hare, Ruffed Grouse, and American Crow were also important in terms of biomass.

As pointed out by Reynolds et al. (1992), raptor populations are often limited by prey availability and their choice of foraging habitat is predicated on conditions in which prey are abundant and available. Thus, an understanding of goshawk prey species used and the relative importance of those prey species is an important step toward developing management plans for goshawks. By identifying key prey species, as we have done here, forest managers can develop a set of desirable conditions that fosters presence of those species while incorporating structural aspects of known goshawk foraging habitat (e.g., Boal et al. 2001). Those desirable forest conditions can be incorporated into goshawk management plans as one factor of foraging habitat (e.g., Reynolds et al. 1992) and facilitate conservation of the species.

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SAMPLING CONSIDERATIONS FOR DEMOGRAPHIC AND HABITAT STUDIES OF NORTHERN GOSHAWKS

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ABSTRACT.—We used mark-recapture methods to monitor Northern Goshawks (*Accipiter gentilis*) and their nests over 12 yr in an increasing sample of breeding territories (37 in 1991 to 121 in 2002) in northern Arizona. As many as 8 yr of repeated nest searching were required to identify the population of breeders, as individuals skipped egg-laying on territories for up to 7 consecutive yr. Extensive temporal (within territory) and spatial (among territory) variation in reproduction and a high annual frequency of movements among dispersed alternate nests in territories made finding and monitoring goshawks problematic. Low detectability of nonbreeding goshawks (combined with uncertainties stemming from variations in breeding and use of alternate nests) made it difficult to categorize territories unequivocally as “unoccupied” by goshawks in non-egg-laying years. Temporal and spatial variation in reproduction required large numbers of territories to attain reliable estimates of reproduction of goshawks; such estimates were achieved only when samples approached or exceeded 60–100 territories. Our within-territory goshawk searching protocol, designed to increase the low and variable detectability of goshawks, required extensive sampling efforts to detect among-alternate nests movements. In lieu of such efforts, samples of territories occupied by goshawks may “decay” over time and lead to false inferences of population declines. Low detectability, variations in breeding, and large samples require that demographic and habitat studies of goshawks employ intensive and repeated searches for goshawks in large study areas over at least 8 yr.

KEY WORDS: *Northern Goshawk; Accipiter gentilis; alternate nest; Arizona; bootstrap; detectability; monitoring; reproduction; sampling; territory occupancy.*

CONSIDERACIONES SOBRE EL MUESTREO EN ESTUDIOS DEMOGRÁFICOS Y DE HÁBITAT DE *ACCIPITER GENTILIS*

RESUMEN.—Usamos técnicas de captura-recaptura para evaluar las actividades de *Accipiter gentilis* y de sus nidos a lo largo de 12 años en una muestra creciente de territorios de nidificación (37 en 1991 a 121 en 2002) en el norte de Arizona. Para poder identificar la población reproductiva de *Accipiter gentilis*, requerimos hasta 8 años de búsqueda repetida de nidos, ya que esta especie evitó poner huevos en territorios por períodos de hasta 7 años consecutivos. La gran variación temporal (dentro de los territorios) y espacial (entre territorios) en la reproducción y una alta frecuencia anual de movimientos entre nidos alternos dispersos en los territorios dificultó encontrar y evaluar las actividades de *A. gentilis*. La baja detectabilidad de los individuos no-reproductivos de *A. gentilis* (combinado con incertidumbres provenientes de las variaciones en la reproducción y en el uso alternativo de nidos) hizo difícil categorizar los territorios de modo inequívoco como “desocupados” por *A. gentilis* en los años en que no pusieron huevos. Esta dificultad se manifestó por la presencia de nidos activos de los mismos individuos anillados de *A. gentilis* luego de más de un año sin presencia reproductiva en los territorios. La variación temporal y espacial en la reproducción requirió grandes números de territorios para alcanzar estimaciones confiables de reproducción en *A. gentilis*. Estas estimaciones fueron obtenidas sólo cuando las muestras alcanzaron o excedieron los 60–100 territorios. Nuestro protocolo de búsqueda de *A. gentilis* dentro de los territorios, diseñado para incrementar la detectabilidad baja y variable de *A. gentilis*, requirió esfuerzos de muestreo amplios para detectar movimientos entre nidos alternos. Sin estos esfuerzos, las muestras de los territorios ocupados por *A. gentilis* podrían “disminuir” a lo largo del tiempo y llevarnos a inferencias falsas sobre disminuciones poblacionales. La baja detectabilidad, las variaciones reproductivas y la necesidad de muestras de gran tamaño requieren que los estudios demográficos y de hábitat

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de *A. gentilis* empleen búsquedas intensivas y repetidas de esta especie en grandes áreas de estudio durante al menos ocho años.

[Traducción del equipo editorial]

The distribution, abundance, vital rates, and habitat occupancy of Northern Goshawks (*Accipiter gentilis*) are difficult to determine because of their elusive behavior in structurally-complex habitats, their low breeding densities, and annually variable breeding rates (DeStefano et al. 1994, Reynolds et al. 1994, Kennedy 1997, Reynolds and Joy in press). While locating and monitoring nests are common approaches in studies of avian demography and habitat, making valid inferences to a target population depends on reliable (unbiased and precise) estimates of the distribution and abundance of nests, demographic rates at nests, and habitat occupancy. In such studies, it is often too costly to detect all individuals and to sample all areas, making a census (complete count) impractical, especially in difficult-to-detect species. For such species, population parameters and habitat occupancy are often estimated using sampling methods. Making inferences about a species' distribution or habitat occupancy from samples requires inferences about the species' detection probability (probability that an individual is included in a sample when present). Biologists attempt to minimize influences of incomplete observations on estimates of a species' distribution, demographics, and habitats with sampling frameworks that increase the detection rates of the species (Peterson and Bayley 2004, McDonald 2004). The problem is to understand how detectability varies within and among individuals, both temporally (year-to-year) and spatially (among territories), and to develop sampling protocols and efforts that increase detection rates of all individuals.

We used mark-recapture methods from 1991–2002 to determine the distribution, abundance, vital rates, fidelity to mate and territory, natal and breeding dispersal, and habitat occupancy of goshawks breeding on territories that increased in number from 37 in 1991 to 121 in 2002 (Reynolds et al. 1994, Reich et al. 2004, Reynolds et al. 2004, Wiens 2004). Because these objectives required a census of breeding goshawks, we attempted to find all breeding goshawks in our study area. In this paper, we first describe the sampling protocols we used to initially locate and monitor breeding goshawks on the Kaibab Plateau. We then describe the

abundance and dispersion of breeding territories, the dispersion of alternate nests within territories, reproductive rates, and behaviors effecting goshawk detectability that resulted from 12 yr of implementing our protocols. Finally, we present bootstrap subsampling of our full samples of territories to estimate the number of breeding territories needed for precise estimates of the reproductive status and production of young by goshawks. Our purpose is to provide a framework for developing sampling protocols, sampling efforts, and sample sizes for demographic and habitat studies of goshawks in other populations.

STUDY AREA

The study area (1728 km²) was all of the Kaibab Plateau above 2182 m elevation above sea level, and contained ca. 122 400 ha of ponderosa pine (*Pinus ponderosa*) forests between 2075–2450 m elevation, ca. 51 600 ha of mixed-conifer forests between 2450–2650 m elevation, and ca. 30 600 ha of spruce (*Picea engelmannii*) fir (*Abies lasiocarpa*) forests between 2650–2800 m elevation (Rasmussen 1941, White and Vankat 1993). Pinyon (*Pinus edulis*) juniper (*Juniperus* spp.) woodlands occurred below the study area between 1830–2075 m elevation and shrub-steppe occurred below 1830 m. With the exception of several narrow (<1 km) meadows, several areas burned by wildfire, and numerous tree harvest areas, forests on the study area were contiguous (Reynolds et al. 1994, Joy et al. 2003). The southern one-third of the study area included the Grand Canyon National Park-North Rim (GCNP) and the northern two-thirds, the Kaibab National Forest (KNF). Forests on the Kaibab Plateau are isolated from other forests by varying distances of shrub-steppe; the nearest forest to the north, 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 (Reynolds et al. 2004).

METHODS

Field Procedures. We defined a breeding territory as an area exclusively occupied by a pair of goshawks during a breeding season. This definition implied that territories were defended by resident goshawks, and the dispersion of breeding pairs was constrained by territoriality. While uncertain if or how territories were defended by goshawks, we estimated their size on the Kaibab Plateau as the area whose radius was half the mean distance among neighboring pairs. Recapture of marked goshawks showed that territorial owners, as well as their replacements over time, had strong life-time fidelity to their territory (Reynolds and Joy in press, R. Reynolds unpubl. data), and territories on the Kaibab Plateau appeared to be spatially fixed over years.

We located goshawk territories using two protocols: systematic foot-searches for goshawks and their nests in areas <1600 ha and broadcasts of goshawk vocalizations from stations on transects (Kennedy and Stahlecker 1993, Joy et al. 1994) in areas >2400 ha. Both nest-searching procedures were used each breeding season (April–August). A new territory was identified when a used goshawk nest (or, in rare cases, an occupied-only nest area; see below) was discovered in an area not already in a known territory and when the new nest (or nest area) was used by unbanded goshawks. Once a territory was found, it was added to that year's cohort of territories and assessed in all subsequent years for goshawk occupancy. Because we were unable to search our study area completely in a single year, we extended our nest searching into previously unsearched areas each year; hence, the number of territories under study increased over years. In addition to expanded nest searches, we annually re-searched areas (using both foot and broadcast searches) suspected of having territorial goshawks based on goshawk nest spacing (Reynolds and Wight 1978, Reynolds et al. 1994).

Goshawk territories often contain one or more alternate nests that are used by the goshawks over several years (Squires and Reynolds 1997, Reynolds and Joy in press). To prevent misclassifying the reproductive status of goshawks that may have moved to an alternate nest, we used a within-territory nest-searching protocol consisting of three sequential steps (Reynolds et al. 2004). Each year, beginning 3 wk before egg laying, we conducted "initial visits" to all known alternate nests and historical nest structures (existing nests with unknown histories of use) to determine if goshawks were present. Searches for goshawks, their feces, molted feathers, and nests refurbished with green twigs (Reynolds and Wight 1982) were conducted within 100-m radii of each alternate and historical nest. Initial visits to nests were completed in all territories by 2 wk after egg-laying. If a used nest in a territory was not found in an initial visit, a "foot search" was conducted within a 500-m radius circle centered on the last-used nest or the centroid of the territory (determined subsequent to discovery of >1 alternate nests in a territory). Territory centroids were the geometric means of coordinates of alternate nests weighted by the number of yr each alternate nest was used during our study (Reynolds et al. 2004, Reynolds and Joy in press). A foot search involved systematically walking the 500-m radius circle looking for goshawks or signs of their presence (see above). Foot searches were conducted from egg laying to about 15–20 d after egg-hatching. In territories where used nests were not located in foot searches, a "broadcast search" was conducted in a 1600-m radius circle centered on either the last-used nest or the territory centroid. Broadcasting of goshawk vocalizations were conducted from stations on transects arranged as described by Joy et al. (1994). Broadcast searches were conducted from about 10 d after egg hatching to the end of the post-fledging dependency period (late August or early September). All nest trees were mapped to the nearest 3 m with a global positioning system.

Nests were "used" if goshawks laid eggs, and territories were "occupied-only" if eggs were not laid but evidence (goshawks observed, molted feathers, feces, reconstruct-

ed nest) of goshawk presence was found in association with a nest structure, or "unknown" if insufficient evidence of occupancy was found. All used nests were visited weekly to count numbers of nestlings and fledglings and to determine the approximate timing and causes of nest failure. Goshawk nestlings were banded in the 10 d before fledgling, and numbers of nestlings present at the time of banding was considered the number of young produced. Nesting adults were captured with dho-gaza nets placed in nest areas and baited with live Great Horned Owls (*Bubo virginianus*) during the nestling period (Reynolds et al. 1994). All goshawks received a U.S. Geological Survey leg band and a colored-aluminum leg band with a unique alpha-numeric code readable from 80 m with 40–60× telescopes (Reynolds et al. 1994). Annual field efforts of crews consisting of 15–23 persons were focused on finding new territories, finding nests within known territories, and capturing and recapturing (or resighting) goshawks on the study area.

Data Analysis. We used Dirichlet tessellation and Delauney triangulation (Cressie 1991) to estimate the distances between the centroids of first-order neighboring goshawk territories. To estimate the dispersion of alternate nests within territories, we measured the within-territory map distances between each alternate nest (inter-alternate nest distance) and the within-territory centroid to each alternate nest (centroid-to-alternate nest distance; excludes territories with only one nest). To test for differences in the spacing of goshawk territories in the KNF and the GCNP, we used a two-sample *t*-test. To characterize the strength of the relationship between the numbers of new territories found in a year and the proportion of territories used in a year, we used a Spearman's correlation coefficient (r_s). The annual proportion of territories with used nests was calculated as the proportion of those territories under study in the previous year (prior-year's cohort of territories) that had used nests in the current year (Reynolds and Joy in press). We did this because the number of territories under study increased annually, and we included only territories that were monitored from before egg-laying to minimize bias associated with missed failed nests. We defined nest success as the proportion of used nests in a prior year's cohort of territories that produced ≥ 1 fledgling. To examine annual differences between the proportion of territories with used nests and the mean number of young produced per used nest, we calculated 95% Confidence Intervals (CI) for these parameters and visually assessed the degree of CI overlap among estimates.

We used the bootstrap method (Efron and Tibshirani 1993) to estimate the number of goshawk territories that needed monitoring to attain precise estimates of the proportion of territories with used nests, nesting success, and number of young fledged per used nest. Our objective was to display variability in these parameters for different-sized samples given the full sample estimate. We conducted, with replacement, 1000 bootstrap iterations with sample sizes of 20, 40, 60, 80, 100, and 120 territories. We present the bootstrap results in box and whisker plots for only 2000 and 2002 because numbers of territories under study during those years were similar (120 and 121), and 2000 was a relatively good breeding year (55% of territories had used nests), while 2002 was a relatively

Table 1. Total territories, number of used nests (eggs laid), and number and percent of territories from previous year's cohort of territories with used nests on the Kaibab Plateau, Arizona, 1991–2002. Previous-year's territory cohorts were used because all territories in that cohort were monitored from before egg-laying in a current year, minimizing bias created by missing used nests due to early nest failure.

	YEAR											
	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
Total territories	37	64	82	88	99	105	106	109	113	120	120	121
Total used nests	36	59	67	21	53	46	31	58	57	66	30	21
Used nests in previous year's cohort		32	49	18	44	40	31	55	56	60	30	21
Percent used in cohort		86	77	22	50	40	30	52	51	53	25	17

poor breeding year (17% of territories had used nests). We plotted the medians of the estimates of the bootstrap subsampling for the proportions of territories with used nests and for nesting success. For mean young fledged per territory, we plotted the medians and coefficients of variation of the bootstrap estimates. We used a CV of 20% as a target criterion for identifying a level of sampling needed to attain adequate estimates of numbers of young per territory (see Pollock et al. 1990).

RESULTS

The Study Population. Numbers of goshawk territories under study increased from 37 in 1991 to 121 in 2002 as searches for new territories were annually extended into unsearched areas and as previously searched, but unoccupied areas, were searched again (Table 1). By 2002, about 95% of the KNF and 60% of the GCNP had been searched for nests. A total of 121 territories were discovered, and goshawks laid eggs in 1 or more years on all but six of these. Exceptions (two KNF, four GCNP territories) included territories occupied in ≥ 2 yr by goshawks that built new, or reconstructed old, nests but did not lay eggs during the study. Territory centroids were regularly spaced (Reich et al. 2004, Reynolds and Joy in press). The mean Delaunay triangle distance between 120 territory centroids (1 territory not included due to inadequate search for surrounding territories) was 3.8 km (SD = 1.3 km, min = 1.3 km, max = 8.1 km, $N = 302$ first-order neighbor distances; inter-centroid distances that crossed unsearched areas in the extreme southeast of the study area were not included; Fig. 1).

We estimated the total number of breeding territories on the study area by calculating an "exclusive" area for each pair of goshawks using one-half the mean distance between territory centroids (3.8

km) as the radius and dividing the study area (173 200 ha) by the exclusive area (1134 ha; Reynolds and Joy in press). This should result in an accurate estimate of the total number of territories because of the regular spacing of territories (known for 80% of our study area) and because forests on the study area were nearly contiguous (Reynolds and Joy in press). The study area was large enough for there to be approximately 150 territories, five territories more than our 1996 estimate (Reynolds and Joy in press). This increase reflected the discovery of 17 new territories between 1997 and 2002 and a subsequent 0.1 km reduction in the mean inter-centroid distance. Therefore, our sample of 121 known territories represented about 80% of the potential total number of goshawk territories in our study area.

Temporal and spatial variation in the frequency of egg-laying by goshawks on the study area was extensive. Temporal variation reflected periods of years with increasing or decreasing proportions of goshawks that laid eggs (Table 1, Fig. 2), and spatial variation reflected differences in the frequencies of egg-laying among territories (Table 2). In the 12 yr during which the 37 territories in the 1991 cohort were monitored, 13 territories (36%) had used nests in ≤ 6 yr and 23 (64%) had used nests in ≥ 7 yr (1 territory never had a used nest), and of the 27 new territories found in 1992, 17 (63%) had used nests in ≤ 5 yr and 10 (37%) had eggs in ≥ 6 of the 11 yr they were monitored (Table 2). Overall, 75% (86 of 115 territories that had used nests in ≥ 1 yr) of territories had used nests in ≥ 3 yr. Most (87%) territories in which egg laying was skipped in ≥ 1 yr had used nests or were occupied-only in subsequent years, often by the

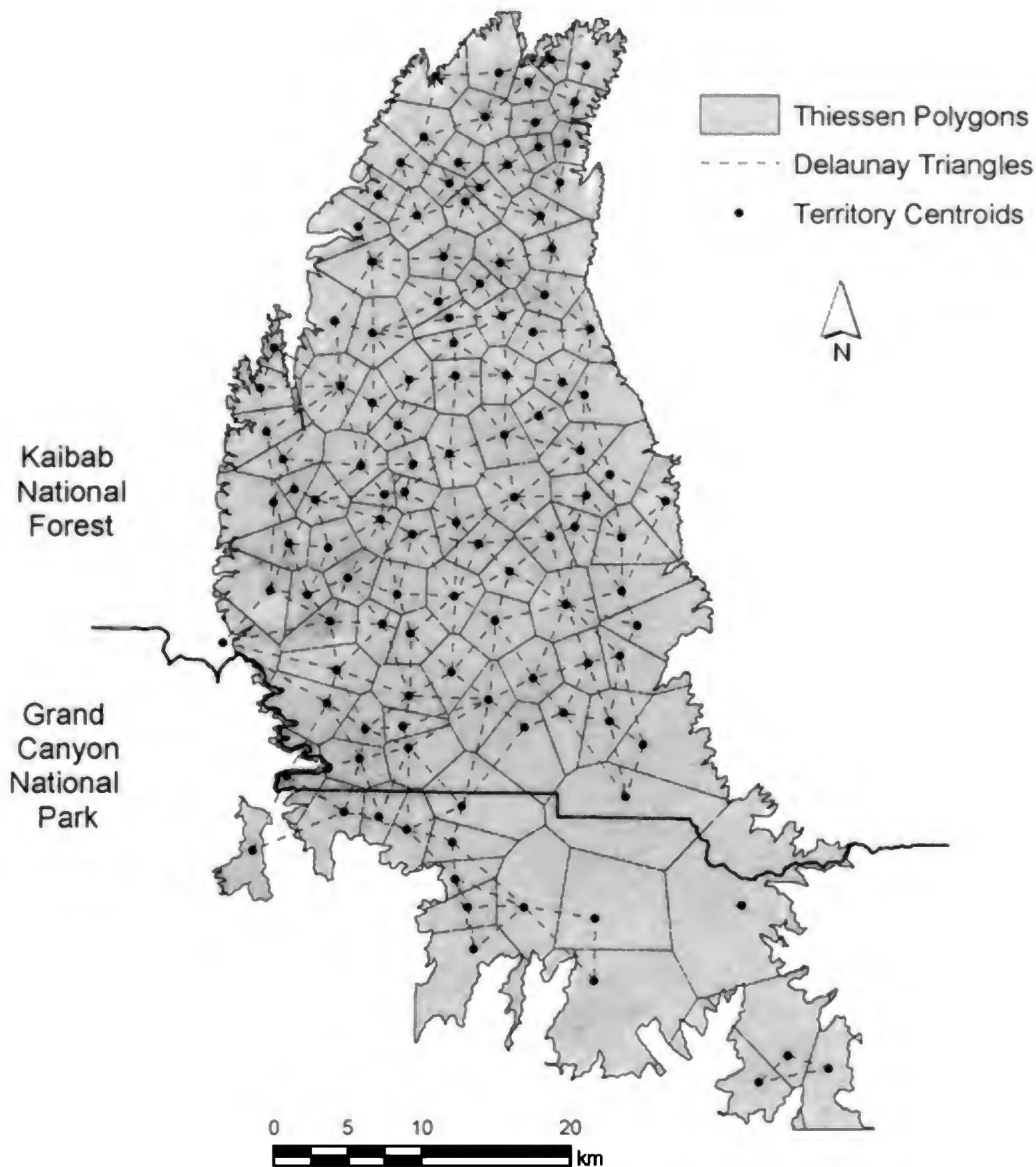


Figure 1. Thiessen polygons and Delaunay triangles used to calculate first-order nearest neighbor distances between Northern Goshawk territory centroids on the Kaibab Plateau, Arizona, 1991–2002 ($N = 120$, see text). Mean inter-centroid distance was 3.8 km (SD = 1.3 km, min = 1.3 km, max = 8.2 km, $N = 302$ triangle legs).

same banded goshawks that had previously laid eggs on the territory (R. Reynolds unpubl. data).

Of a combined total of 435 used nests in all 11 prior-year cohorts of territories, 341 (63%) were successful (Table 3). Of 94 nest failures, 59 (63%) failed during the incubation period, and 35 (37%) failed during the nestling period. There was minimal among-year variation in nesting success (Table 3, Fig. 2). In 459 broods (not limited to nests in

prior-year cohorts) with accurate counts of young, brood sizes ranged from 1–4 nestlings (median = 2; Table 2); 102 (22%) broods had one young, 219 (48%) had two young, 133 (29%) had three young, and five (1%) had four young. The mean annual number of fledglings produced per used nest was only moderately variable compared to the annual variation in the proportion of territories with used nests; the CV of the number of young produced

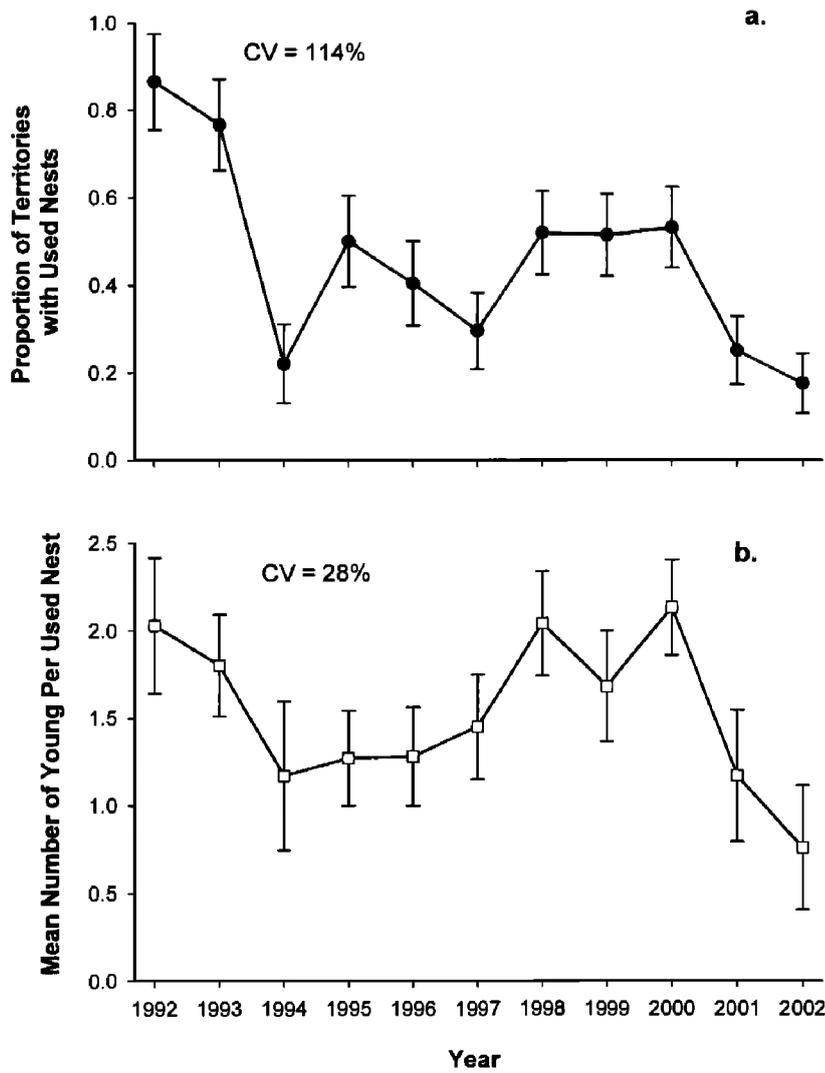


Figure 2. Annual variation in (a) the proportion of territories under study containing active (eggs laid) Northern Goshawk nests and (b) in the mean numbers of young produced per used nest in the previous year's cohort of goshawk nests (see text) on the Kaibab Plateau, Arizona, 1991–2002. Error bars represent $\pm 95\%$ CI.

per used nest was 28%, while the CV of the proportion of territories with used nests was 114% (Fig. 2). Likewise, the among-year variation in total young produced by the 1991 cohort of territories ($N = 37$) over 12 yr was also higher than the among-year variation of the means of young produced per used nest for the same territories and years. Total young produced ranged from 16 in 2002 to 65 in 1992 and had an among-year coefficient of variation (CV) of 68%, and mean number of young produced per used nest ranged from 0.6 in 2002 to 2.4 in 2000 and had a CV of 37%. Thus, both the annual proportion of territories with used nests and total young produced per year provide a more sensitive measure of the variable reproductive output of goshawks than the annual mean number of young produced per used nest.

Goshawk Behavior and Sources of Error. How well an estimate represents the true spatial distribution, density, or habitat occupancy of a species

Table 2. Number and percent of new Northern Goshawk territories discovered each year of the study and the numbers of years the new nests were used (eggs laid) in subsequent years on the Kaibab Plateau, Arizona, 1991–1996.

YEAR ^a	NEW TERRITORIES FOUND	NUMBER (%) OF YEARS WITH USED (EGGS LAID) NEST											
		1	2	3	4	5	6	7	8	9	10	11	12
1991	36 ^b	2 (6)	3 (8)	6 (17)	—	—	5 (14)	7 (19)	8 (22)	2 (6)	1 (3)	—	—
1992	27	—	5 (19)	4 (15)	6 (22)	2 (7)	4 (15)	1 (4)	1 (4)	—	—	—	—
1993	18	4 (22)	2 (11)	1 (6)	5 (28)	2 (11)	1 (6)	—	—	—	—	—	—
1994	6	1 (17)	—	—	—	2 (33)	—	—	—	—	—	—	—
1995	11	3 (28)	1 (9)	—	—	1 (9)	—	—	—	—	—	—	—
1996	6	1 (17)	2 (33)	3 (50)	—	—	—	—	—	—	—	—	—

^a 1997–2002 not displayed because too few years of monitoring were available.

^b One territory was occupied by goshawks who never laid eggs.

Table 3. Number of used (eggs laid) and successful (fledged ≥ 1 young) nests, mean and standard deviation (SD) of fledglings per used nest, and proportion of used nests within the prior year's cohort of Northern Goshawk territories that fledged young on the Kaibab Plateau, Arizona, 1991–2002.

	YEAR										
	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
Used nests	32	49	18	44	40	30	55	56	60	30	21
Fledglings/ used nest	2.0	1.8	1.1	1.3	1.3	1.5	2.0	1.7	2.1	1.2	0.8
SD	1.12	1.04	0.92	0.92	0.91	0.85	1.13	1.21	1.08	1.05	0.83
Successful nests	26	42	13	34	31	25	46	41	53	19	11
Percent nests successful	81	86	72	77	78	83	84	73	88	63	52

depends on the error associated with the estimate (Thompson et al. 1998). A potential source of sampling variation is an incomplete count of breeding goshawks. Counts are related to the actual size of the territorial goshawk population by the probability of detection, which may vary systematically. Because of their defensive behavior at nests, the detectability of breeding goshawks (still relatively low due to their elusiveness and complex habitats) is much higher than the detectability of non-nesting goshawks (including those whose nests failed). Low detectability of nonbreeders combined with the large annual variation in numbers of goshawks breeding can produce large sampling variation. To account for the low detectability of nonbreeders, we repeatedly searched areas suspected of containing goshawks. Eleven yr of repeated searching for nests showed that the KNF was nearly saturated with breeding territories (Fig. 1). We do not know if the GCNP was similarly saturated with territories because only ca. 60% of the GCNP was searched for goshawks. However, the mean distance between centroids of known territories in the GCNP was not significantly different from the mean distance between KNF centroids (KNF \bar{x} = 3722 m, SD = 1221 m, N = 271 triangle legs; GCNP \bar{x} = 4028 m, SD = 1477 m, N = 22 triangle legs; t = -1.1, df = 291, P = 0.27), suggesting that the density of goshawk territories in the GCNP was similar to territory density in the KNF. The success of finding new territories in a year was positively related to the proportion of territories with used nests in that year (r_s = 0.73, P = 0.011, N = 11); we found more new territories in good breeding years (1991–93, 1998–2000) than in poor breeding years (1994, 2002).

Another source of measurement error is misclassification of the breeding status of territorial goshawks. Detecting movements of goshawks among alternate nests required considerable sampling effort, the level of which depends on the number and distribution of alternates within territories and frequency of movement among the alternates. Because numbers of known alternates depends on years of monitoring, we only report the numbers of alternate nests in the 1991 and 1992 cohorts of territories. Mean number of alternates in these territories was 3.2 (SD = 1.5 nests, min = 1, max = 6, N = 36) and 2.9 (SD = 1.4 nests, min = 1, max = 6, N = 27), respectively. The frequency distribution of inter-alternate nest distances within all territories with ≥ 2 alternates (N = 91 territo-

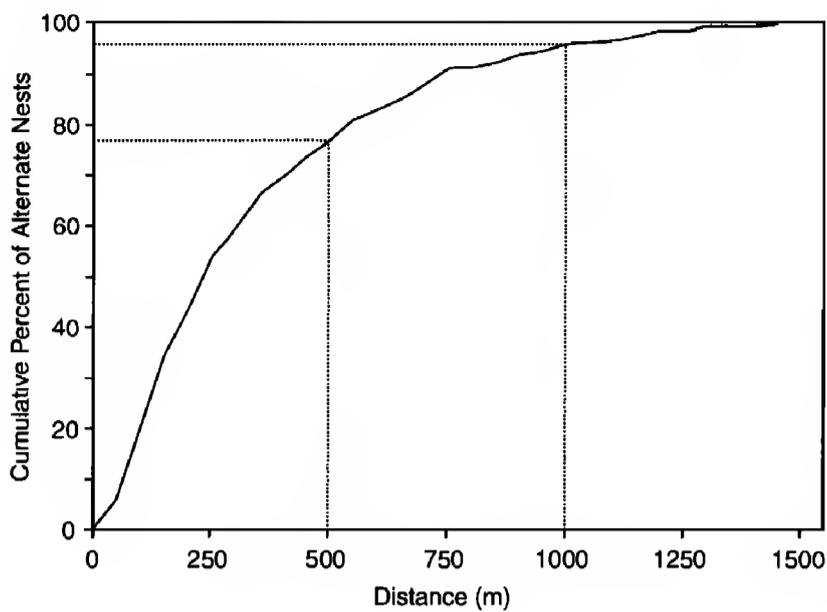


Figure 3. Cumulative percent of alternate nests within territories with increasing distance (m) between territory centroids to alternate nests on the Kaibab Plateau, Arizona. Maximum centroid-to-alternate nest distance was 1452 m.

ries) was right-skewed with a median of 402 m (\bar{x} = 612 m, SD = 569 m, min = 9 m, max = 2426 m, N = 308 alternate nests). When measured from territory centroids, the median centroid-to-alternate distance was 228 m (\bar{x} = 334 m, SD = 298 m, min = 6 m, max = 1452 m, N = 273 alternates in 91 territories), about half of the median inter-alternate nest distance. The cumulative proportion of alternates captured with distance from centroids showed that about 75% occurred within 0.5 km, and about 95% occurred within 1 km of centroids (Fig. 3). Thus, our territory-focused broadcast

searching protocol in areas of 1.6-km radius around centroids exceeded the maximum known centroid-to-alternate distance (1452 m). The frequency of movement of egg-laying goshawks to alternates was high; an annual mean of 64% of breeding goshawks moved to an alternate, and 42% of these movements were to new (unknown to us) alternates (Table 4).

Sample Size. Bootstrap subsampling showed that samples of ca. 60–80 territories in good breeding years and 80–100 territories in poor breeding years were needed for precise estimates of the full sample means of the proportion of territories with used nests and nesting success on the Kaibab Plateau (Fig. 4). Coefficient of Variation plots of the mean young per used nest in good breeding years showed that subsamples of ≥ 80 territories had bootstrap estimates entirely below a CV of 20%, although many of the estimates from subsamples of 60 territories were below 20% (Fig. 5). In poor breeding years, subsamples of 100 territories were insufficient to achieve a CV of less than 20%, reflecting the few (21) territories that were occupied in 2002. How temporal and spatial variation in reproduction on the Kaibab Plateau compares to other goshawk populations is unknown because other studies typically reported reproduction at only used or successful nests (e.g., Reynolds and Wight 1978, DeStefano et al. 1994, Doyle and Smith 1994, Younk and Bechard 1994); only Keane et al. (in press) and Reynolds and Joy (in press)

Table 4. Number (%) of breeding Northern Goshawks that stayed in the previous year's nest or moved to a new or previously-used alternate nest within their territory on the Kaibab Plateau, Arizona, 1991–2002.

YEAR	MOVEMENT			TOTAL PERCENT MOVING
	STAYED	TO NEW ALTERNATE	TO PRIOR ALTERNATE	
1992	14 (45)	17 (55)	—	55
1993	17 (35)	26 (53)	6 (12)	65
1994	7 (39)	7 (39)	4 (22)	61
1995	18 (43)	17 (40)	7 (17)	57
1996	9 (24)	16 (43)	12 (32)	76
1997	9 (30)	14 (47)	7 (23)	70
1998	19 (35)	27 (50)	8 (15)	65
1999	21 (38)	18 (32)	17 (30)	63
2000	18 (30)	20 (33)	22 (37)	70
2001	13 (43)	10 (33)	7 (23)	57
2002	7 (33)	8 (38)	6 (29)	67
Total	152 (36)	180 (42)	96 (22)	64

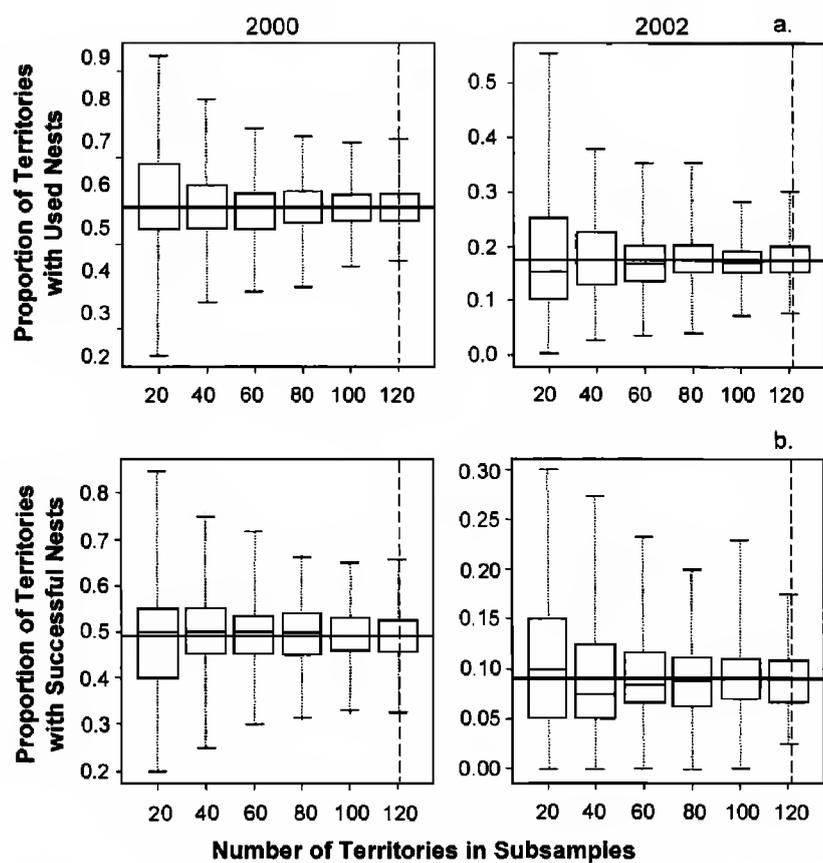


Figure 4. Box plots of bootstrap subsamples estimating the effects of sample size in good (2000) and poor (2002) breeding years on estimates of the proportion of Northern Goshawk territories with used nests (eggs laid) (a) and nesting success (b) on the Kaibab Plateau, Arizona, 1991–2002. Dotted vertical lines are numbers of territories (120 in 2000, 121 in 2002) used to estimate the true sample means (solid horizontal lines). Box plot whiskers extend to the maximum and minimum estimates, boxes represent the first and third quartiles of estimates, and the horizontal lines within boxes represent the medians of estimates.

reported the extent of temporal variation in the proportion of pairs breeding.

DISCUSSION

Goshawk populations are difficult to enumerate and monitor because of their elusive behavior, relatively low densities, and their structurally-complex forest habitats. Nonetheless, goshawk detectability increases during breeding (a 6-mo period) because of their aggressive nest defense. However, detectability of goshawks was highly variable among individuals because of extensive temporal (year-to-year) and spatial (among territory) variation in breeding. Within a year, nonbreeding territorial individuals have lower detectability than breeders, and among years, low-quality individuals (Wiens and Reynolds 2005) or individuals on low-quality territories have lower detectabilities than higher-quality individuals or those on higher-quality territories because they breed less often. Detectability

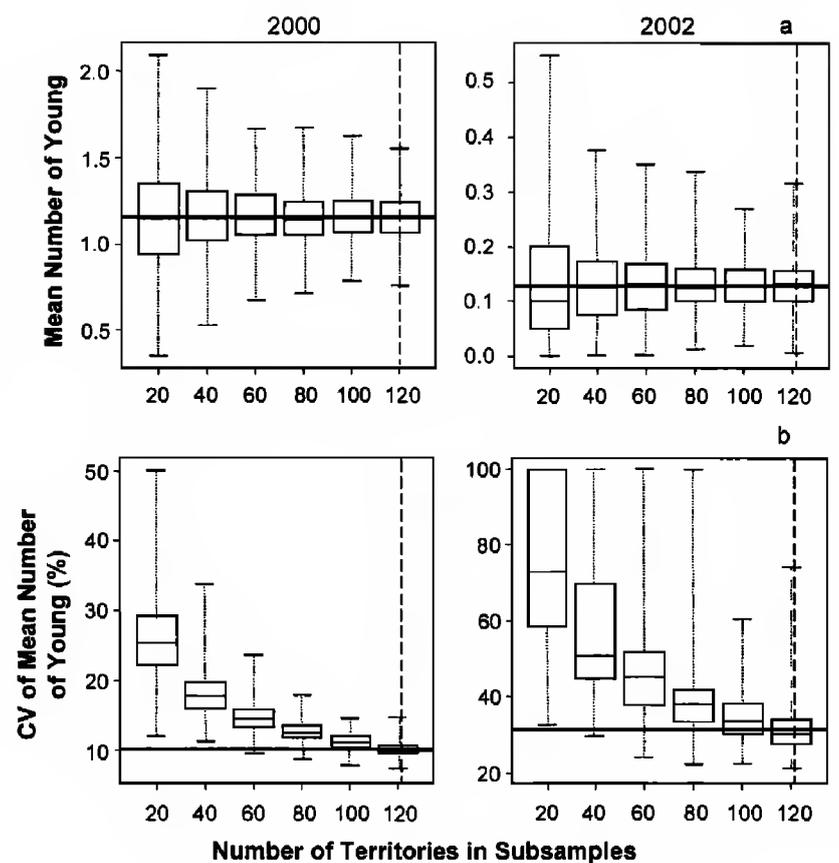


Figure 5. Box plots of bootstrap subsamples estimating the effects of sample size in good (2000) and poor (2002) breeding years on estimates of (a) the mean, and (b) the coefficient of variation (CV), of young produced per used (eggs laid) Northern Goshawk nest on the Kaibab Plateau, Arizona, 1991–2002. Dotted vertical lines are numbers of territories (120 in 2000, 121 in 2002) used to estimate the true sample means (solid horizontal lines). Box plot whiskers extend to the maximum and minimum estimates, boxes represent the first and third quartiles of estimates, and the horizontal lines within boxes represent the medians of estimates.

within and among individuals can also be variable from year-to-year because of the number and dispersion of alternate nests, and the frequency of movement among them. Finally, breeders whose nests fail have lower detectability than successful breeders. Therefore, determining the distribution, abundance, and habitat of a population of territorial goshawks and their annual breeding status requires sampling protocols and efforts that provide for the detection of both breeding and nonbreeding goshawks. Repeated nest searching of areas suspected of having breeding goshawks (“holes” based on territory spacing) eventually showed that our study area was saturated with breeding territories. Repeated searching was required because as many as 8 yr elapsed on some territories between egg-laying. Not surprisingly, our success in locating territories depended on the quality of the breeding year; more new territories

were found in years when larger proportions of goshawks laid eggs.

Nest searching did not cease with the discovery of a territory. Annually, between 50–75% of egg-laying goshawks moved to alternate nests within their territories, and in some years, more than half of these moves were to alternates unknown to us, some of which were more than 1.4 km apart. Such movements have long been recognized as making the monitoring of breeding goshawks difficult (Woodbridge and Detrich 1994, Reynolds et al. 1994, Kennedy 1997). In attempts to locate goshawks that may have changed nests, Kennedy (1997) and Woodbridge and Detrich (1994) searched 0.7–1.0 km and 1.6 km around the previously-used nest in a territory, respectively. If the distribution of alternates within territories on the Kaibab Plateau is representative of the distribution of alternates elsewhere, then these radii would contain 95 and 100% of alternate nests, respectively, but only if the nest last used was close to the center of the territory. However, the farther the last-used nest was from the center of a territory, the higher the probability of missing alternates with these radii. This suggests that in the early years of a monitoring study, longer search radii should be used, at least until centroids of territories can be estimated.

In studies of goshawk demography (e.g., Reynolds and Wight 1978, DeStefano et al. 1994, Reynolds et al. 1994, Kennedy 1997, Reynolds and Joy in press) and habitat (e.g., Bosakowski et al. 1999, Daw and DeStefano 2001, Finn et al. 2002, Joy 2002, McGrath et al. 2003, La Sorte et al. 2004), valid inferences to the target population depend on an adequate temporal and spatial sampling. Our study showed that, because breeding is temporally and spatially variable and the detectability of nonbreeders is low, accurate estimates of the number and location of nests and territories depends on constancy in annual sampling efforts and numbers of years over which surveys are conducted. Insufficient sampling for territories results in underestimates of breeding densities and habitat occupancy, and insufficient searches for nests within territories results in underestimates of annual proportions of pairs breeding and production of young. Because of large variation in the frequency of breeding, high rates of movement among nests, and low detectability of nonbreeders, it is particularly difficult to demonstrate unequivocally that territories are unoccupied in a year in which a used

nest is not found. These factors, especially when combined with insufficient sampling, may result in an apparent decrease in territory occupancy and, ultimately, a population decline. The difficulty of confirming that a territory is actually unoccupied is the basis for our assigning territories with insufficient evidence of occupancy as “unknown.” That territories continue to be occupied during non-breeding years was demonstrated by the fact that in many cases, the same color-marked goshawks were found to nest on the same territory before and after up to a 7 yr break in egg-laying (R. Reynolds unpubl. data). Because of this, we suggest that “territory occupancy rate” (proportion of known territories occupied), a commonly used reproductive parameter for goshawks (Crocker-Bedford 1990, Kennedy 1997), may be a biased estimator of the number of breeders in a population. Finally, the frequency of movements among alternate nests suggests that the scale of measurement for determining the breeding status and reproduction of goshawks should be at the territory level and not at the nest area.

An objective of population monitoring is to obtain reliable estimates from samples to infer changes in a target population. Our bootstrapping results showed that large samples of territorial goshawks (often larger than attained in many goshawk studies) were needed for precise estimates of the proportion of territorial goshawks breeding and their nesting success and reproduction. Large samples are needed because of the extensive annual variation in the proportion of territories with reproductive goshawks. Whether equally large samples of territories or pairs of goshawks are needed for reliable estimates of these parameters in other populations will likely depend on whether these populations are as temporally and spatially variable in reproduction as the Kaibab Plateau population. DeStefano et al. (1994) in Oregon, Doyle and Smith (1994) in northwestern Canada, Woodbridge and Detrich (1994) in northern California, Kennedy (1997) in New Mexico, and Keane et al. (in press) in central California, all reported moderate to extensive temporal variation in goshawk reproduction. Both the proportion of territories with egg-laying goshawks and total young produced on the Kaibab Plateau were more variable among years than mean numbers of young produced per used nest per year, the most commonly reported goshawk reproductive parameter (Kennedy 1997 and references therein). Because the proportions

of goshawks breeding and total young produced in a year more accurately portrayed the extent of annual variation in reproduction of the Kaibab goshawk population, both are likely to better describe a population's response to fluctuations in resources (e.g., food abundance; Salafsky 2004, Salafsky et al. 2005) and habitat quality than numbers of young produced per used nest.

CONCLUSION

Stratification of a study area, protocols for detecting species, and sampling efforts in studies are based on subjective and previous information (Morrison et al. 2001). Our nearly complete census of breeding goshawks on the Kaibab Plateau provides information on the distribution, density, variation in reproduction, and breeding behavior of territorial goshawks in one population. Our intent in presenting these data was to provide a framework for developing sampling protocols and identifying sampling efforts that may be needed to reliably estimate the distribution, density, vital rates, and habitats of breeding goshawks in other populations. Extensive temporal and spatial variation in reproduction on the Kaibab Plateau required as many as 8 yr of repeated nest searching to identify a population of breeders and annual searches of areas of 1.4-km radius around territory centers for reliable estimates of the reproductive status of territorial pairs. Further, as many as 60–80 goshawk territories were needed for precise estimates of the annual production of young by a population. The specific sampling protocols and efforts used in our study, and the samples of territories identified in this paper, demonstrate that demography and habitat studies of goshawks may have to employ intensive and repeated searches for goshawks in large study areas over at least 8 yr.

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POPULATION GENETICS AND GENOTYPING FOR MARK-RECAPTURE STUDIES OF NORTHERN GOSHAWKS (*ACCIPITER GENTILIS*) ON THE KAIBAB PLATEAU, ARIZONA

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ABSTRACT.—Advances in molecular techniques have facilitated use of genetic data in demographic wildlife studies. An important first step in genetic mark-recapture is selecting markers that uniquely “mark” and reliably “recapture” individuals. Markers should be tested on reliable DNA from known individuals (blood) before being used on non-invasively sampled DNA (hair, scat, or molted feathers). To evaluate whether Northern Goshawks (*Accipiter gentilis*) can be uniquely identified by genotyping, 113 known (banded, sexed) goshawks from the Kaibab Plateau, Arizona, were genotyped using DNA from blood and five microsatellite markers and a sex-linked gene. We used mean relatedness to test whether adults in the population were related and probability of identity ($P_{(ID)}$ = probability that two random individuals from the population have the same genotype) to test the ability of multi-locus genotyping for uniquely identifying goshawks. We used genetic data to assess inbreeding and demographic data to estimate the effective population size. Sixty-nine adult goshawks were sexed correctly and genotyped. Expected heterozygosity was high ($H_E = 0.81$), and relatedness among adults was low ($r = -0.017$). All individuals sampled (69 adults, 44 nestlings) had unique five-locus genotypes, the overall probability of identity was low ($P_{(ID) \text{ unbiased}} = 7.03 \times 10^{-7}$), and the observed $P_{(ID)}$ was <0.0001 . Thus, Kaibab goshawks were uniquely “marked” by genotyping. Despite a small effective population size ($N_e = 37$ individuals), goshawks on the Kaibab Plateau functioned as a large breeding population with no inbreeding ($F_{IS} = -0.001$). We hypothesized that genetic diversity is maintained by gene flow via immigration of individuals from distant forests.

KEY WORDS: *Northern Goshawk; Accipiter gentilis; capture-recapture, genetic tagging, individual identification; molecular sexing, probability of identity.*

GENÉTICA POBLACIONAL Y GENOTIPIFICACIÓN PARA ESTUDIOS DE MARCADO-RECAPTURA DE *ACCIPITER GENTILIS* EN KAIBAB PLATEAU, ARIZONA

RESUMEN.—Los avances en las técnicas moleculares han facilitado el uso de información genética en estudios demográficos de fauna silvestre. Un primer paso importante en estudios genéticos de marcado

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y recaptura es seleccionar marcadores que “marquen” inequívocamente y que permitan “recapturar” confiablemente a los individuos. Los marcadores deben ser probados en ADN confiable de individuos conocidos (sangre) antes de ser usados en muestreos no invasivos de ADN (pelo, excremento, o plumas mudadas). Para evaluar si los individuos de la especie (*Accipiter gentilis*) pueden ser identificados por genotipificación, estudiamos 113 gavilanes conocidos (sexados y anillados) de la meseta Kaibab, Arizona, usando ADN de la sangre y cinco marcadores microsatélites y un gen ligado al sexo. Usamos el parentesco promedio para probar si los adultos en la población estaban relacionados y la probabilidad de identidad ($P_{(ID)}$) = la probabilidad que dos individuos al azar de la población tengan el mismo genotipo) para probar la habilidad de la genotipificación mediante múltiples loci para identificar individualmente a los gavilanes. Utilizamos datos genéticos para determinar el grado de endogamia e información demográfica para estimar el tamaño efectivo de la población. Sesenta y nueve gavilanes adultos fueron correctamente sexados y genotipificados. La heterocigocidad esperada fue alta ($H_E = 0.81$) y el parentesco entre adultos fue bajo ($r = -0.017$). Todos los individuos analizados (69 adultos, 44 polluelos) tuvieron genotipos únicos con cinco loci, la probabilidad de identidad total fue baja ($P_{(ID) \text{ unbiased}} = 7.03 \times 10^{-7}$), y la $P_{(ID)}$ observada fue <0.0001 . Así, los gavilanes de Kaibab fueron “marcados” singularmente por genotipificación. A pesar de un tamaño efectivo de la población pequeño ($N_e = 37$ individuos), los gavilanes en el Kaibab Plateau funcionaron como una población reproductiva grande y sin endogamia ($F_{IS} = -0.001$). Nuestra hipótesis es que la diversidad genética es mantenida por flujo genético a través de la inmigración de individuos de los bosques lejanos.

[Traducción de Mauricio Cotera]

Northern Goshawks (*Accipiter gentilis*) are highly secretive and are most easily detected during the breeding season when they aggressively defend their nests and young. While their defensive behavior at nests facilitates capture-recapture studies of breeding individuals, population monitoring is difficult because individuals often forgo breeding, or their nests fail early in a breeding season. Even in years of high productivity, mark-recapture studies can be prohibitively expensive because population sampling requires large field crews and multiple nest visits to many breeding territories to capture and recapture breeding goshawks (Reynolds et al. 2005).

Because of recent improvements in molecular techniques (Haig 1998, Parker et al. 1998), genetic capture-recapture may be a viable alternative to traditional capture-recapture methods for goshawks. Collecting molted feathers requires fewer nest visits than traditional capture-recapture methods. Breeding goshawks begin an annual molt during spring (Squires and Reynolds 1997) and because they spend much of the breeding season near their nests, they drop many of their molts within their nest areas, including years when nesting attempts fail. Thus, goshawk feathers are readily collected from nest areas and may provide an efficient means to non-invasively sample their populations.

Several factors influence the success of genetic capture-recapture studies. An appropriate number of highly variable genetic markers for identifying individuals are required, and potential biases must

be identified. “Shadow effects” (lack of discrimination of individuals because of low variability or sampling too few markers) can negatively bias estimates of population abundance and positively bias estimates of survival (Mills et al. 2000). On the other hand, when more markers than necessary are used, population abundance may be overestimated and survival underestimated if genotyping errors add unique “genotypes,” and thus individuals, to population samples (Lukacs and Burnham 2005). Both biases will inflate variance and lower precision of parameter estimates (Lukacs and Burnham 2005).

Microsatellites are currently a preferred molecular marker for identifying individuals because they are easily interpreted (i.e., heterozygous genotypes are easily distinguished from homozygous genotypes), highly variable, bi-parentally inherited, and generally appear to be selectively neutral. Further, a large body of literature exists on microsatellite evolution (Jarne and Lagoda 1996, Goldstein and Pollock 1997, Estoup et al. 2002), which has facilitated the development of much statistical theory and analytical software (Hedrick 2005). However, microsatellites are expensive and time consuming to develop for each newly-studied species. Occasionally primers used to amplify microsatellite markers in one species can be used in related species (Ellegren 1992, Primmer et al. 1996, Galbusera et al. 2000, Martinez-Cruz et al. 2002).

Prior to starting a non-invasive genetic study, establishing intrapopulation genetic structure (i.e.,

levels of inbreeding and relatedness) and the frequency of null alleles (alleles that fail to amplify) is necessary for providing baselines against which feather samples can be compared (Mills et al. 2000). Likewise, it is important to establish statistical power of multi-locus genotyping for identifying individuals with an independent population sample. We present results from a pilot study where we assessed the feasibility of implementing a non-invasive genetic capture-recapture study on a population of Northern Goshawks on the Kaibab Plateau, Arizona. Before assessing the utility of molted feathers as a viable source of DNA, we established a dependable genotyping marker set using DNA derived from blood (Taberlet and Luikart 1999).

Our objectives were to: (1) screen species-specific and cross-specific (among species) microsatellite markers, (2) test a sex-linked gene in goshawks known to distinguish males and females in other raptors (Kahn et al. 1998), (3) assess the power of multi-locus genotyping to uniquely identify individuals using probability of identity analysis (P_{ID} ; probability that two individuals drawn at random from the same population share the same multi-locus genotype), and (4) estimate average relatedness, inbreeding, and effective population size for the goshawk population on the Kaibab Plateau.

METHODS

Field Collection. The goshawk study population is located on the Kaibab Plateau in northern Arizona, an area that includes the North Kaibab Ranger District of the Kaibab National Forest and the North Rim of the Grand Canyon National Park (for descriptions of the study area see Reich et al. 2004, Reynolds and Joy 2005). It is a forested plateau surrounded by shrub-steppe habitat—the nearest forests being 97 km to the north, 250 km to the east, 80 km to the west, and 89 km to the south—except for a small patch of forest 18 km south on the south rim of the Grand Canyon. Sampled nests were well distributed across the study area. We captured 69 adult, breeding goshawks (1991–93, 2000–02) and 44 of their nestlings (Reynolds et al. 1994). We sexed adult goshawks using morphometrics (mass, tarsus length) and behavior. Blood was sampled from the brachial vein with 22-gauge needles and non-heparinized capillary tubes (volume \leq 0.10 ml). Blood was transferred into STE (Sodium Chloride-Tris-EDTA) buffer-filled storage tubes kept cool in insulated containers with frozen cold-packs until crews returned to the field station, where samples were subsequently frozen (-20°C). At the close of the field season, blood was transferred to and stored at -80°C at Colorado State University, Fort Collins, CO.

Laboratory Methods. We extracted DNA using QIAamp mini blood kits (Qiagen, Inc., Valencia, CA U.S.A.) following the manufacturer's protocol. To find microsatellites, we screened published and unpublished

primer sets that included microsatellites originally isolated from Northern Goshawks (Topinka and May 2004), European goshawks (*Accipiter gentilis gentilis*), Golden Eagles (*Aquila chrysaetos*), and Red Kites (*Milvus milvus*, Peck 2000). We also tested primers that amplify an intron within the avian CHD (chromo-helicase-DNA binding), which was used to determine gender in Red-tailed Hawks (*Buteo jamaicensis*) and Great Horned Owls (*Bubo virginianus*; Kahn et al. 1998). The CHD gene is located on the Z and W sex chromosomes. We expected males to be homozygous (ZZ genotype) and females to be heterozygous (ZW genotype).

We used PCR (Polymerase-Chain-Reaction) to amplify microsatellites in 25 μl reactions using 0.5 μl (AGE 1a) or 1.0 μl (all other markers) of template DNA, 2.5 μl 10 \times buffer containing 15 mM Mg_2Cl_3 (Promega Corp. Madison, WI U.S.A.; for markers AGE 1a, AGE 2 and AGE 4 an additional 3 mM Mg_2Cl_3 was added), 20 mM dNTPs, 25 pM each primer, 1U Taq polymerase, and one drop mineral oil to prevent evaporation. Negative controls (reactions that include all reagents except template DNA) were included in every set of reactions, and we used "cold start" PCR where tubes (in racks) were kept on ice to prevent premature non-specific priming. We used MJR PTC-100 thermocyclers programmed for the following protocol: denature at 94°C for 4 min, 31 cycles of denature at 94°C for 40 sec, annealing at 58°C for 40 sec, and chain extension at 72°C for 40 sec, with a final extension at 72°C for 5 min.

We used PCR to amplify the CHD sex-linked gene in 25 μl reactions using 1.0 μl template DNA and the same reaction buffer described above. The PCR protocol included an initial 5 min at 95°C denature, 11 cycles of denature at 94°C for 30 sec, annealing at 52°C for 35 sec, and chain extension at 72°C for 2.0 min, 31 cycles of denature at 92°C for 30 sec, annealing at 56°C for 35 sec, and chain extension at 72°C for 2.0 min, with a final extension at 72°C for 7 min.

We used gel electrophoresis to separate alleles. For microsatellites, we used 8% polyacrylamide (Long Ranger, Cambrex Corp., Rockland, MA U.S.A.) denaturing gels (55 cm long) that were run at 45 watts for 4–5 hr, depending on allele size. For the CHD sex-linked gene, we used single-strand-conformation-polymorphism (SSCP) methods (Hiss et al. 1994) and electrophoresed alleles on non-denaturing gels at 5 watts for 15 hr.

For microsatellites, we established allele standards using representative samples from our first gel and then standardized all other gels using those same samples. Gels were scored visually, and allele standards were run on both sides of a gel to account for gel ambiguities that cause slight variations in migration distances. Further, a subset of individuals ($N = 23$) was genotyped a second time to validate scores for microsatellite markers. For the CHD marker, we ran all known females together ($N = 40$) and all known males ($N = 29$) together to familiarize ourselves with allele morphology. Although not sequenced, the fragments were ca. 240–260 base pairs, and Z and W alleles were similar in size, but were differentiated by the SSCP analysis (Hiss et al. 1994).

Population Genetic Analysis. Population substructure, inbreeding, and genetic drift can reduce heterozygosity in populations. However, low yield and degraded DNA

sampled from sources such as molted feathers can artificially reduce population heterozygosity if allelic dropout (ADO; one of two alleles in a heterozygous individual fails to amplify) at one or more markers occurs. It is, therefore, important to use high yield sources of DNA (typically blood) from a known reference population to determine frequency of ADO (or null alleles) and true levels of heterozygosity (Taberlet et al. 1999).

We used CERVUS 2.0 (Marshall et al. 1998) to estimate observed (H_O) and expected (H_E) population heterozygosity and null allele frequencies. CERVUS provides estimates of null allele frequencies with an iterative algorithm based on differences between observed and expected homozygote frequencies. We used GENEPOP 3.4 (Raymond and Rousset 1995) to test for departures from Hardy-Weinberg equilibrium (random mating) and GDA 1.0 (Lewis and Zaykin 2001) to test for linkage-disequilibrium (genotypes at one marker are independent from genotypes at other markers) and to estimate F_{IS} , an indicator of population substructure and inbreeding. For a review of F -statistics and microsatellite genetic markers, see Balloux and Lugon-Moulin (2002).

To test our assumption that our sample of adult goshawks was not comprised of closely-related individuals, we used IDENTIX 1.1 (Belkhir et al. 2002) to estimate mean pairwise relatedness. We used Queller and Goodnight's (1989) estimator option, and tested the null hypothesis of no relatedness by comparing our estimate to a distribution of coefficients derived through conventional Monte Carlo resampling procedures (1000 permutations).

Probability of Identity. The uniqueness of an individual's genotype depends on the number and polymorphism (heterozygous) of the markers. Multi-locus genotypes based on few highly-variable markers can be as powerful as those based on many less variable markers (Waits et al. 2001). Mills et al. (2000) suggested for studies of genetic demography that profiles should be based on multi-locus genotypes capable of discriminating individuals with 99% certainty. Estimating probability of identity ($P_{(ID)}$) is one way to establish this certainty when it is expressed as $1 - P_{(ID)}$. $P_{(ID)}$ is similar to the match probability used in human forensics (Evet and Weir 1998, Avise 2004, Hedrick 2005), but is less susceptible to violations of linkage-disequilibrium and Hardy-Weinberg equilibrium, both of which can be prevalent in small, isolated, or substructured populations (Waits et al. 2001).

$P_{(ID)}$ analysis includes two steps. First, two theoretical $P_{(ID)}$'s, one for unrelated individuals ($P_{(ID)unbiased}$) and one for siblings ($P_{(ID)sibs}$), are estimated (for equations see Waits et al. 2001). Both estimators use population allele frequency data, and $P_{(ID)unbiased}$ is corrected for bias in small samples. The two estimators provide lower and upper confidence bounds on the number of markers needed to discriminate individuals accurately. If the study population is composed of many related individuals, then resolving those individuals requires more markers. Step two involves calculating an observed $P_{(ID)obs}$ based on actual multi-locus genotypes from a known population sample and is simply the proportion of all possible pairs of individuals with identical multi-locus genotypes (Waits et al. 2001).

To estimate both theoretical $P_{(ID)}$'s and to quantify

$P_{(ID)obs}$ (the proportion of individuals that share genotypes), we used PROB-ID5 (Waits et al. 2001). We used multi-locus genotypes derived from 69 adult goshawks, which we assume to be unrelated (see below), and 44 of their nestlings (sibling groups of 2–4 nestlings). We first analyzed the adults and then added the offspring/sibling groups. We used all five microsatellite markers and the CHD sex-linked gene and added markers sequentially starting with those having the highest number of alleles.

Effective Population Size. To evaluate whether immigration and gene flow influenced genetic structure of the Kaibab population we estimated its effective size (N_e). Effective population size is the idealized number of individuals in a population measured either demographically, in terms how many individuals actually contribute to breeding (i.e., variance in productivity), or genetically, using F -statistics and measures of inbreeding where the assumption of non-overlapping generations exists (Barton and Whitlock 1997, Hedrick 2005). Goshawks sampled on the Kaibab Plateau during the study period likely represent at least three overlapping generations; thus, we relied on reproductive data to estimate N_e .

Effective population size is generally smaller than the censused population (N). Counts of breeding pairs of goshawks can be used to index N_e , but not all goshawk pairs on the Kaibab produced an equal number of offspring during the study (Wiens and Reynolds 2005). We therefore estimated annual N_e 's (equation 6.8a in Hedrick 2005) as:

$$N_e = \frac{N\bar{k} - 1}{\bar{k} - 1 + \frac{V_k}{\bar{k}}}$$

where \bar{k} is mean productivity measured as the number of young fledged per used nest, eggs laid, subsequent young fledged, or the nest failed (1991–2003; Reynolds et al. 2005), V_k is the variance in annual mean productivity, and N is the annual count of breeding pairs for the year. We then calculated a 13-yr harmonic mean of annual N_e 's (equation 6.12b in Hedrick 2005) for our final size estimate.

RESULTS

Genetic Markers. Of nine cross-specific and sub-specific markers tested, two did not resolve alleles successfully, six amplified successfully but lacked variability, and one both amplified and was polymorphic (AGE 1a, Table 1). All four microsatellites originally isolated from Northern Goshawks amplified and were polymorphic (Table 1). The CHD sex-linked gene amplified and SSCP genotypes were consistent within the sexes (females, $N = 40$; males $N = 29$), making it useful for distinguishing between male and female goshawks. We validated our amplification and scoring of microsatellite markers after all individuals were genotyped and scored the first time. We genotyped the 23 individuals used as standards a second time using DNA that was archived and remained untouched in our

Table 1. Statistics for microsatellites tested on blood-derived DNA sampled from female ($N = 40$) and male ($N = 29$) Northern Goshawks (*Accipiter gentilis*), Kaibab Plateau, AZ (1991–1993, 2000–2002).

MARKER	SPECIES	ALLELES	NA ^a	H _O	H _E	H-W ^b	
						P (SE)	F _{IS} (95% CI) ^c
AGE 1	<i>A. g. atricapillus</i>	15	0.0425	0.77	0.84	0.21 (0.020)	0.0825
AGE 2	<i>A. g. atricapillus</i>	11	0.0006	0.83	0.83	0.08 (0.009)	0.005
AGE 6 ^d	<i>A. g. atricapillus</i>	11	0.3805	0.38	0.85	0.00 (0.000)	0.556
AGE 4	<i>A. g. atricapillus</i>	10	-0.0062	0.86	0.85	0.06 (0.005)	-0.007
AGE 1a	<i>A. g. gentilis</i>	5	-0.0506	0.77	0.70	0.09 (0.005)	-0.100
All markers		52		0.72 ^e	0.81	See text	0.115 (-0.039, 0.346) -0.001 ^f (-0.070, 0.063)

^a Frequency of null alleles estimated with CERVUS 2.0.

^b Departures from Hardy-Weinberg expectations. Exact *P*-values and SE derived using Markov-Chain methods (1000 dememorizations, 200 batches and 1000 iterations) in GENEPOP 3.4.

^c 95% Confidence Interval (CI) calculated using bootstrapping over markers (10 000 replicates) in GDA 1.0.

^d Suspected sex-linked marker.

^e Simple average.

^f AGE 6 omitted.

freezers from the time of original DNA extraction. We found only a single scoring error out of 230 opportunities (23 samples genotyped twice for five markers). This was a recording error; the sample had actually genotyped correctly.

In comparisons of expected (H_E) and observed (H_O) heterozygosity at each marker, four of the five microsatellites were similar. However, one marker (AGE 6) significantly departed from Hardy-Weinberg expectations ($P < 0.01$) due to a deficiency of heterozygote genotypes (Table 1). Based on our data, we suspected this marker was sex-linked, as we found strong linkage-disequilibrium between AGE 6 and the sex-linked CHD marker ($P < 0.001$, Fisher's method, 3200 runs) indicating that the two markers segregate together. It appeared that the marker was located on the Z sex-chromosome because all females (ZW) had only a single allele (homozygous), while most males (ZZ) were heterozygous. We hypothesize that alleles on the female's W-chromosome are non-amplifiable (null) because of mutations in the priming sequences flanking the marker (Scribner and Pearce 2000) or because the marker on the Z-chromosome simply has no homologous region on the W-chromosome. We found no evidence for linkage-disequilibrium between the other four microsatellite markers (Table 1) when AGE 6 and CHD were excluded from the analysis. We found no evidence of null alleles, which is important for future assessments of genotyping error when using feathers as a source of DNA.

Population Genetics. F_{IS} measures departures of observed and expected heterozygosity under assumptions of random mating and indicates either inbreeding ($F_{IS} > \text{zero}$) or inbreeding avoidance ($F_{IS} < \text{zero}$). Thus, highly structured or isolated populations that experience genetic drift generally exhibit positive F_{IS} values. Alternatively, large populations or those experiencing high gene flow generally exhibit nonsignificant or negative F_{IS} values.

We found no evidence of inbreeding or inbreeding avoidance ($F_{IS} = -0.001$; 95% CI = -0.070 – 0.063 ; AGE 6 excluded; Table 1), suggesting that Kaibab goshawks mate randomly. Lack of inbreeding could result from large population size, gene flow by immigrants, or both. However, our demographically derived estimate of effective population size ($N_e = 37$ individuals; range = 10–86) indicated that the population was demographically small, thus making gene flow a more likely source of genetic variability. This is consistent with our estimate

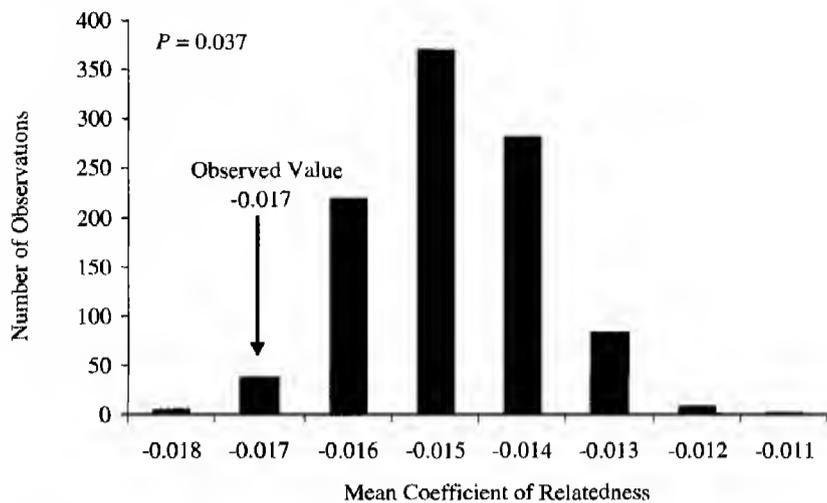


Figure 1. Observed mean relatedness relative to 1000 randomized populations assumed to lack relatedness. The observed mean falls below that which is expected at random, occurring with a probability of 3.7%, indicating that Northern Goshawks (*Accipiter gentilis*) on the Kaibab Plateau, Arizona, are less related than expected at random.

of relatedness among adults goshawks, where mean relatedness ($r_{xy} = -0.017$) was less than expected by random (Fig. 1).

Probability of Identity. Certainty of individual identification is equal to $1 - P_{(ID)}$, and therefore the goal in estimating probability of identity is to obtain small values of $P_{(ID)}$. Waits et al. (2001) suggested a value ≤ 0.0001 for forensic investigations where estimates of demographic parameters are needed. This threshold is interpreted as a 1:10 000 chance that two individuals sampled from the same population will have the same multi-locus genotype.

We found that all 69 unrelated adults had unique multi-locus genotypes with the inclusion of the first three markers ($P_{(ID)obs} < 0.0001$), and likewise the estimated $P_{(ID)}$ met the 0.0001 threshold ($P_{(ID)unbiased} = 1.13 \times 10^{-4}$; Fig. 2a). With five markers, the same sample had a $P_{(ID)unbiased} = 7.03 \times 10^{-7}$. However, based on demographic data, we know that siblings and parent-offspring nested simultaneously in the Kaibab population (R. Reynolds unpubl. data). To model this effect we added 44 nestlings-siblings to the sample. While the two theoretical $P_{(ID)}$'s did not change, all five markers were required to differentiate individuals ($P_{(ID)obs} < 0.0001$, Fig. 2b).

In both cases (adult only and adults with offspring-sibling groups), our sample of markers was insufficiently large to bring the $P_{(ID)sibs}$ to the 0.0001 threshold. Thus, we were not able to estimate an upper number of markers needed for this

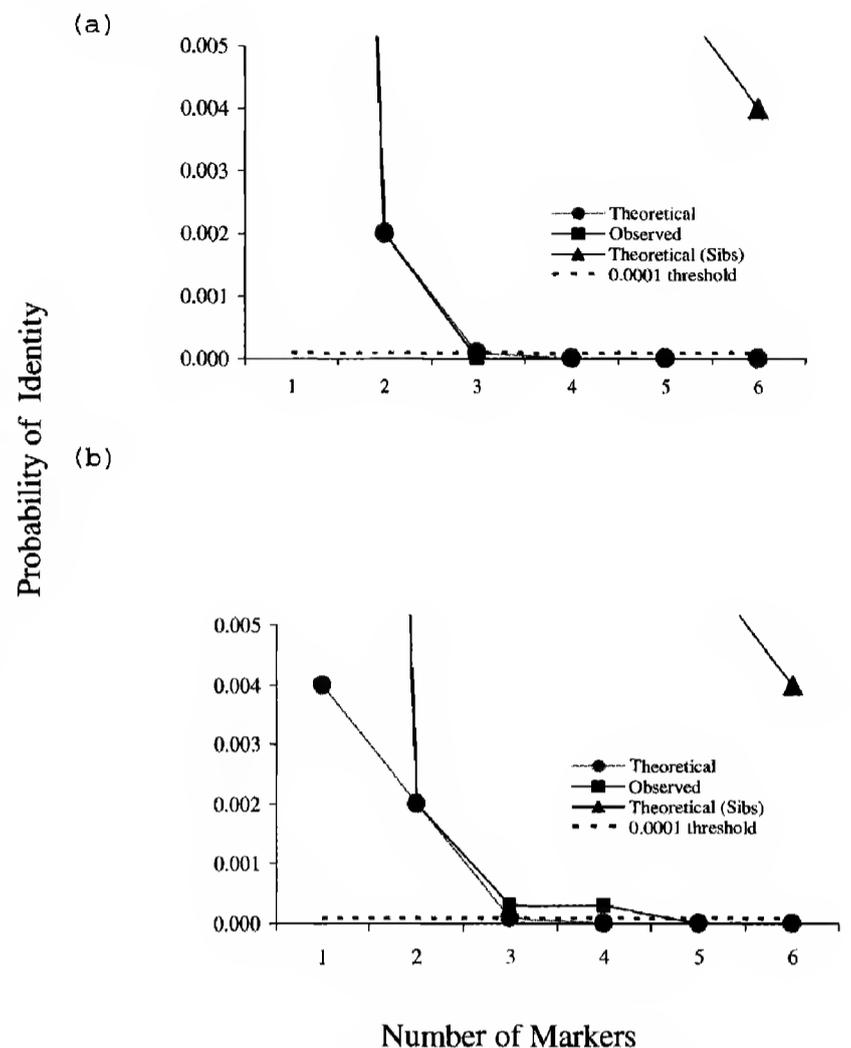


Figure 2. Relationship between theoretical, observed, and sib probability of identity ($P_{(ID)}$) for Northern Goshawks (*Accipiter gentilis*) on the Kaibab Plateau, Arizona. The first five markers are microsatellites and the sixth is the CHD sex-linked gene. Observed data closely tracked that of the theoretical estimator; however, while (a) all 69 unrelated adult goshawks were resolved after the first three markers (observed $P_{(ID)} < 0.0001$), (b) it took an additional two markers to resolve sibling and parent-offspring goshawks when 44 nestlings were added to the sample. In both cases, the theoretical $P_{(ID)}$ met our 0.0001 threshold (a 1:10 000 chance that two individuals sampled from the same population have identical multi-locus genotypes). However, we did not analyze enough markers to bring the sibling $P_{(ID)}$ to the threshold level.

resolution. Nonetheless, with five markers $P_{(ID)sibs} = 6.17 \times 10^{-3}$, which translates into a six in a 1000 chance of drawing two identical genotypes. Because we sampled many parent-offspring pairs that we could nevertheless distinguish, we are confident the five combined markers provide unique genetic marks.

DISCUSSION

Our intent in this study was to develop a set of genetic markers that uniquely identified individual goshawks. We desired to establish this marker set using high-yield DNA (blood) sampled from a

known reference population. While most microsatellites tested did not amplify or were monomorphic (most *A. g. gentilis* markers), we did find a set of highly variable markers that consistently amplified DNA from blood. Elsewhere (S. Bayard de Volo unpubl. data), we found that the same genetic markers consistently and reliably amplified DNA from molted feathers. We note that because AGE 6 is probably on the Z sex chromosome, its utility for estimating within population relatedness and levels of inbreeding is limited to samples from males. However, differences in allele frequencies between populations will still be useful for larger-scale studies comparing populations. In a study of goshawks in Utah, Sonsthagen (2002) used a different set of microsatellite markers than ours. Of eight markers, only one of theirs exhibited the same number of alleles (11 alleles, $H_O = 0.73$, $H_E = 0.74$) as AGE 6 did in our study. This alternative marker (BV 20; Gautschi et al. 2000) would be useful if it exhibited similar levels of heterozygosity and allelic diversity in the Kaibab population. Replacing AGE 6 with a less variable marker would result in having to add more markers to the entire genetic profile, which would introduce more opportunities for genotyping error. We are currently testing BV 20 to see if it is an effective replacement for AGE 6.

With the five microsatellite markers tested (Table 1), all 113 goshawks sampled had unique multilocus genotypes resulting in a $P_{(ID)obs} < 0.0001$ (Fig. 2b) and a $P_{(ID)unbiased} = 7.03 \times 10^{-7}$. This was a powerful result considering that our sample included many parent-offspring and sibling pairs from the same nest. Likewise, the five microsatellites showed a high level of expected heterozygosity ($H_E = 0.81$). Others have shown that marker sets composed of five markers that result in $H_E \geq 0.80$ will have a theoretical $P_{(ID)} \leq 0.0001$ (Waits et al. 2001). In Paetkau's (2003) retrospective analysis of 21 non-invasive genetic studies in bears (*Ursus americanus*, *U. arctos*), the number of markers used was determined by whether the first five most-variable microsatellite markers together had $H_E > 0.80$. He found that for some black bear populations H_E was >0.80 for five markers; however, for others, and for all grizzly bear populations, that H_E was <0.80 , requiring the marker set to be increased to six or seven loci in order to discriminate among individuals.

We note that our estimates of $P_{(ID)}$ are specific to the Kaibab goshawk population; we cannot pre-

dict with complete certainty that these same markers will uniquely mark goshawks from other populations. Power of discrimination depends on population-specific levels of genetic variability (heterozygosity); goshawk populations that are less variable because of geographic isolation or habitat fragmentation may require more markers to uniquely genotype individuals (Paetkau and Strobeck 1994). However, goshawks are highly vagile, and we suspect gene flow is high among populations. These goshawk populations will probably exhibit similar heterozygosity, and the marker set tested here should prove useful for other studies.

The Kaibab goshawk population exhibits high genetic variability (Table 1), despite its geographic isolation and small effective population size (based on demographic data; 13-yr $\bar{x} = 37$ individuals). Several explanations may account for this. First, it is possible that the markers used in this study are under selective sweeps with genes that are affected by balancing selection for heterozygous genotypes. Such selection has been found for the genes of the MHC (major histocompatibility complex) in mammals (Awise 2004), in which heterozygous individuals experience a fitness advantage. However, we suggest it is unlikely that all four nonsex-linked markers would be under the same selective pressures, given that they exhibit independent segregation (no evidence of linkage disequilibrium; see Black et al. 2001).

A second and more likely explanation is that actual N_e for this goshawk population is much larger because geographically distant populations in the region are connected by migration and gene flow. While adult goshawks are mostly sedentary on breeding territories (Detrich and Woodbridge 1994, Squires and Ruggiero 1995, Reynolds and Joy 2005), band recoveries of first-year goshawks from the Kaibab Plateau indicate dispersal distances of up to 440 km (Wiens 2004). In addition, telemetry data show that juvenile goshawks disperse from the Kaibab Plateau in their first year, with the majority moving beyond the 80 km detection distance (Wiens 2004). Further, Wiens (2004) showed that only 11% of 614 banded nestlings returned to be recruited into the Kaibab breeding population, indicating high first-year mortality or low natal-site fidelity. Evidence for the latter is indicated by the lack of population genetic structure for goshawks in Utah (Sonsthagen et al. 2004). To better assess actual effective population size for goshawks in western North America, we are expanding our

studies to include populations in the western portion of the species range. Data from these studies should allow a more comprehensive evaluation of the genetic structure and effective population size for goshawks in the West.

CONCLUSIONS

Genetic marking of Northern Goshawks on the Kaibab Plateau is both feasible and reliable. Likewise, non-invasive genetic sampling will provide an alternative method for demographic and genetic data collection, as we have found that molted feathers are as reliable a source of DNA as blood (S. Bayard de Volo unpubl. data). Because goshawks show high territory fidelity (e.g., Detrich and Woodbridge 1994, Reynolds and Joy 2005), they are particularly well suited for non-invasive genetic sampling. We recommend that monitoring programs implement rigorous field collection of molted feathers. As with any demographic study, valid inferences to the population depend on appropriate spatial and temporal sampling from that population. Researchers and managers interested in implementing non-invasive genetic mark-recapture to study goshawks should contact the corresponding author or refer to Bayard de Volo (2005).

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Appendix. Source, repeat qualities and accession numbers or primer sequences for microsatellites found to be useful for genotyping Northern Goshawks (*Accipiter gentilis*) on the Kaibab Plateau, Arizona.

MARKER	REPEAT MOTIF ^a	ALLELE SIZE IN BASE PAIRS	ACCESSION NO. OR PRIMER SEQUENCES 5' TO 3'	AUTHOR
AGE 1	(gggaa) ₈ ..(gaga) ₉ ..(gagaa) ₃	216	AY312451	
AGE 2	(gagaa) ₁₀ (ga) ₄	170	AY312452	Topinka and May 2004
AGE 6	(gagaa) ₄ ..(gagaa) ₂ ..(gagaa) ₅	259	AY312456	
AGE 4	(gagaa) ₁₉	275	AY312454	
AGE 1a	(ggat) ₅	208 ^b	f acaactgggctgtgctttgc r cttcccgggtggctgaggctt	Peck 2000

^a Sequenced by authors.

^b Mean allele size in European goshawk (*A. g. gentilis*).

WHEN ARE GOSHAWKS NOT THERE? IS A SINGLE VISIT ENOUGH TO INFER ABSENCE AT OCCUPIED NEST AREAS?

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ABSTRACT.—We tested the efficacy of three methods (historical nest search, broadcast search, and tree transect search) for detecting presence of the Northern Goshawk (*Accipiter gentilis*) at occupied nest areas during the 1994 breeding season using only a single visit to a previously known nest area. We used detection rates in a probability model to determine how many visits are required to have confidence in reporting absence of goshawks. The purpose of this study is to understand if the three methods for detecting goshawks are robust enough for managers to rely on them for making land management decisions that may impact goshawk nest areas. Blind tests were conducted throughout the western United States. Results were similar among methods with goshawk presence going undetected at 36–42% of the occupied nest areas after a single visit. These results indicate that a single visit to a nest area is inadequate to provide reliable information on nest area occupation. Our probability of detection model showed that if each detection method is repeated three (historical or tree transect) or four (broadcast) times, goshawk absence can be inferred with a high level of confidence. Conclusions regarding nest area occupation using a single visit sampling method should be made with utmost caution. Classifying a nest area as vacant, when in fact goshawks are present, is a serious concern and leads to spurious conclusions. Land managers making habitat-altering decisions should not rely on a single visit to nest areas to establish the absence of goshawks. Possibilities for improving the detection of nesting goshawks include multiple independent visits using the same method, using a sequence of techniques in combination to yield an improved cumulative probability of detection, or developing a new method yielding a higher probability of detection. The historical nest search obtained the best results, followed by the tree transect and broadcast search.

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KEY WORDS: *Northern Goshawk*; *Accipiter gentilis*; *detection rates*; *forest management*; *nest area*; *occupancy*; *repeated sampling*

¿CUÁNDO ESTÁ AUSENTE ACCIPITER GENTILIS? ¿ES SUFICIENTE UNA SOLA VISITA PARA INFERIR AUSENCIA EN ÁREAS DE NIDIFICACIÓN OCUPADAS?

RESUMEN.—Probamos la eficiencia de tres métodos (búsqueda de nidos histórica, búsqueda por medio reproducción de grabaciones, búsqueda a lo largo de transectos de árboles) para detectar la presencia del halcón *Accipiter gentilis* en áreas de nidificación activas durante la época reproductiva de 1994, utilizando una sola visita a un área de nidificación previamente conocida. Utilizamos las tasas de detección en un modelo de probabilidad para determinar cuántas visitas se requieren para tener certeza al reportar una ausencia de esta especie de halcón. El propósito de este estudio es entender si los tres métodos para detectar a esta especie son suficientemente robustos para confiar en ellos al tomar decisiones de manejo de tierras que pueden afectar áreas de nidificación. Realizamos pruebas ciegas a través del oeste de los Estados Unidos. Los resultados fueron similares entre los métodos; la presencia de los halcones no fue detectada en el 36–42% de las áreas de nidificación activas luego de una sola visita. Estos resultados indican que una sola visita a un área de nidificación no es adecuada para obtener información confiable sobre la actividad de nidificación en el área. Nuestro modelo de probabilidad de detección mostró que si cada método es repetido tres (histórico o transecto de árboles) o cuatro (reproducción de grabaciones) veces, la ausencia de halcones puede ser inferida con un alto grado de confianza. Las conclusiones con respecto a la actividad de las áreas de nidificación utilizando el método de muestreo de una sola visita deben tomarse con gran precaución. La clasificación de un sitio de nidificación como vacío, cuando de hecho los halcones están presentes, es una preocupación seria y puede llevar a conclusiones falsas. Las personas encargadas de manejar las tierras y tomar decisiones con relación a la alteración de los hábitats no deberían confiar en una sola visita a los sitios de nidificación para determinar la ausencia de estos halcones. Algunas de las posibilidades para mejorar la detección de halcones que se encuentran nidificando incluyen realizar visitas múltiples e independientes utilizando la misma metodología, utilizar conjuntamente una secuencia de técnicas para producir mejores probabilidades de detección acumulativas o desarrollar un método nuevo que pueda proveer de una probabilidad de detección mayor. La metodología de búsqueda de nidos histórica obtuvo los mejores resultados, seguida por la de los transectos de árboles y la búsqueda por medio de reproducción de grabaciones.

[Traducción del equipo editorial]

The U.S. Department of Interior Fish and Wildlife Service (FWS) reviewed the status of the Northern Goshawk (*Accipiter gentilis atricapillus*) for Federal protection (i.e., listed as threatened or endangered under provisions of the Endangered Species Act) three times since 1991. In each case the FWS ruled that listing was unwarranted. Population trend is one of five factors used by the FWS for determining whether to list a species as threatened or endangered. The majority of nesting goshawks in the western United States are located on lands managed by the U.S. Department of Agriculture Forest Service (FS). Since the FS is required by the National Forest Management Act (NFMA) to maintain species population viability, monitoring the occupancy of goshawk nest areas is necessary to evaluate population trends.

Lacking a formal national goshawk monitoring program, the FS management approach to protecting goshawks in the southwestern United States

is to locate goshawk nest trees and post-fledging family areas (Kennedy et al. 1994) prior to habitat alterations and then to apply goshawk management recommendations (varying from region to region) to conserve the nest area, manage the post-fledging family area, and manage the foraging area (Reynolds et al. 1992). After implementation of habitat management prescriptions, follow-up management practices should include monitoring the effect of habitat changes on species; however, this is rarely done. The untested assumption is that the management program will work as designed.

Finding and monitoring nesting goshawks is a critical component of successful adaptive land management practices if goshawks are to persist in managed landscapes. Goshawks exhibit strong fidelity to nest areas (Reynolds and Joy in press), but have fluctuating population numbers and nesting success year to year. Goshawks also frequently change nest locations within a nest area or between

nest areas within a territory. Because a proportion of the local population of goshawks moves to alternate nest areas on an annual basis, sampling only the historical nest areas over time without finding the alternate nest areas will result in fewer and fewer occupied nest areas (i.e., the unwarranted appearance of a declining population).

Counting, sampling, and detecting birds are important concerns of avian researchers (Bart and Earnst 2002, Farnsworth et al. 2002, Rosenstock et al. 2002, Thompson 2002). Developing techniques to find goshawks efficiently has been an ongoing process (Kimmel and Yahner 1990, Kennedy and Stahlecker 1993, Joy et al. 1994, Watson et al. 1999, Penteriani 1999, Roberson et al. in press). Biologists have yet to develop an accurate, cost-effective method that will detect goshawks throughout the nesting period. This is because the species is secretive, difficult to find and study, and their behavior changes during the breeding season. Kennedy and Stahlecker (1993) tested a technique for broadcasting goshawk vocalizations from calling stations positioned on parallel transects that were placed tangential to the occupied nest. Their tests were conducted in the southwestern U.S. during the nestling to fledging stage. They found that the probability of detecting a goshawk, when within 100 m of a nest, averaged 70% throughout the season using multiple visits. The median detection distance was 141 m. On control transects, without broadcasting, detection rates dropped to between 30% (courtship) and 60% (fledgling).

In Washington, Watson et al. (1999) tested Kennedy and Stahlecker's (1993) broadcast method using three stations (400 m, 250 m, and 100 m) on a single transect that passed tangential to the nest at 100 m at its closest point. They found five visits at 100 m from the nest, eight visits at 250 m from the nest, and 10 visits at 400 m attained a 90% or higher detection rate. In another study using the broadcast technique from courtship to fledgling dependency, only 52% of goshawks were detected (McClaren et al. 2003); but, detections were lower during courtship (40%) and highest during fledgling dependency (75%). Kennedy and Stahlecker (1993), Watson et al. (1999), and McClaren et al. (2003) are examples of experienced goshawk biologists evaluating goshawk survey techniques. Their prior experience with goshawks and knowledge of nest locations may have positively influenced experimental results (i.e., their detection

rates probably represent maximum rates under test conditions).

A problem with past goshawk inventory and monitoring efforts has been a reliance on methodologies whose bias, probability of detection, and magnitude of detection error were unknown. There has always been uncertainty associated with misclassifying a goshawk territory as unoccupied when it may be occupied (i.e., error of omission). In 1994, the FS identified the need to test the efficacy of techniques for finding goshawks. This was driven by the FS desire to implement specific habitat altering management actions designed to protect goshawk nest areas, post-fledging family areas, and the surrounding foraging area from harm (Reynolds et al. 1992), or to allow for flexible management options if goshawks were not present. Three commonly used detection methods available at that time were identified as needing testing (historical nest tree search, broadcast search, and tree search within potential nest areas). No investigators had compared the potential errors associated with the three typical inventory techniques.

Our objectives were to: (1) document the error associated with each of these three detection techniques and (2) use the error rates to estimate the number of nest area visits needed to infer absence of goshawks with different levels of confidence. We conducted a blind test of these methods for detecting breeding goshawks to reveal the magnitude of error associated with each technique. The reason we conducted blind tests was to control the variability introduced in previous tests conducted by experienced goshawk biologists that had prior knowledge of the nest area and its status (Kennedy and Stahlecker 1993, Joy et al. 1994); possibly influencing their results. We then input our results into a probability model to conceptually explore various combinations of detection rates, errors associated with these detection rates, and predict the number of sampling visits needed to have confidence in the information collected.

METHODS

We tested the efficacy of revisiting historical nest trees, broadcasting goshawk vocalizations in nest areas, and scanning all trees along transects established throughout nest areas within an 800 m diameter area centered on occupied (nest with eggs/young) nest areas. The size of our sampling unit was 1/35 the estimated size of the territory (2400 ha) (Reynolds et al. 1992) and was selected to account for alternate nest locations within a single nest area. Field tests were conducted from June to early mid-July 1994 during nestling and fledgling dependency pe-

riods (Squires and Reynolds 1997). Experienced field biologists determined that each nest area tested had nesting goshawks present prior to the test. During the testing period, occupancy was determined by observing goshawks incubating eggs, adults brooding young, or observing young at the nest. The same criteria were used at all study areas. Personnel naive to the presence and location of occupied nests were used to test the three methods. Only one method was tested, and only one visit was made, at each occupied nest area. The three methods were randomly assigned to active nest areas. To simulate normal field conditions, experience was allowed to vary among field members; no effort was made to randomize field crew experience among the three detection methods. Results from each state were pooled to improve sample size.

Study Areas. Tests were conducted in Arizona, California, New Mexico, and Wyoming. In Arizona ($N = 44$), tests were conducted in the Apache/Sitgreaves, Coconino and Kaibab National Forests. Forests in Arizona were dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), and Douglas-fir (*Pseudotsuga menziesii*). In California ($N = 10$), tests were conducted in the Klamath National Forest, where at higher elevations, forests were dominated by red fir (*Abies magnifica*), white fir, ponderosa pine, lodgepole pine (*Pinus contorta*), Douglas-fir, and incense cedar (*Calocedrus decurrens*), and lower elevation forests by ponderosa pine and white fir (Kuchler 1977). In New Mexico ($N = 11$) tests were conducted in the Santa Fe National Forest where forests contained ponderosa pine, Douglas-fir, white fir, and quaking aspen (*Populus tremuloides*) and at higher elevations subalpine fir (*Abies lasiocarpa*) and Englemann spruce (*Picea engelmannii*). In Wyoming ($N = 12$), tests were conducted in the Medicine Bow National Forest where lower elevation forests contained lodge pole pine with scattered quaking aspen, and higher elevation forests contained subalpine fir and Englemann spruce (Alexander et al. 1986, Marston and Clarendon 1988).

Historical Nest Search. The most common goshawk search technique used prior to 1990 was to visit historical nest areas and relocate previously used nest trees to determine occupancy. Typically, little effort was spent in a broader search of a nest area if goshawks were not found. To simulate this method, biologists were given 1:24 000 scale maps marked with the approximate locations of nest trees within a nesting area where goshawks had previously nested. Biologists were instructed to relocate the nest trees and determine if goshawks were present and nesting. The strength of this method relies on goshawk fidelity to nest areas (Reynolds et al. 1994) and that field personnel often detect goshawk presence by observing the defensive behavior of goshawks near their nests. Other clues to goshawk nest area occupancy with this method included observing fecal material, prey remains, or molted goshawk feathers in the vicinity of nests. When these clues were found, the area was searched further to find the occupied nest.

Broadcast Surveys. This goshawk detection technique was developed in the early 1990s and involved broadcasting taped goshawk calls (alarm and juvenile food begging) to elicit a response. Field crews followed the procedure of Kennedy and Stahlecker (1993), as modified

by Joy et al. (1994). Recorded calls of goshawks were broadcast from stations located at 300-m intervals, on parallel transects, in an 800 m radius area. A search was initiated to locate visually the nest once a goshawk responded. The broadcast method is a means of systematically searching the landscape for goshawks. This method is also useful for locating nesting pairs that move to alternate areas within their territory. A problem with the technique is that goshawks do not always respond to the broadcast call when they are present, may respond with a silent approach, or may respond to broadcast calls when they are far away from their nest areas and, thus, confound results. Additional confounding factors include seasonal effects and misidentification of calls such as Steller's Jay (*Cyanocitta stelleri*) mimicking goshawks (Kennedy and Stahlecker 1993).

Tree Transect. The tree transect technique is a systematic visual search of a forested area centered on the occupied nest. This method involved field crews walking along parallel transects spaced 50 m apart while examining individual trees along either side of and directly along the transect path for goshawk nests in tree crowns (Squires and Reynolds 1997). At 50 m, the probability of eliciting goshawk defensive behavior was assumed to be high because they could presumably hear or see the field crew. Crews also looked for prey plucking posts, fecal material or stains, and scattered prey remains that would provide evidence of a potential occupied nest nearby.

The Model. To address our second objective, we input the estimates of detection obtained from each search method above into a probability model (McArdle 1990). This allowed an estimation of the sample size needed to have confidence that goshawks were absent. In other words, how many revisits to the nest area are necessary to conclude goshawks are absent? Guynn et al. (1985) and Reed (1996) used probability models to retrospectively estimate confidence in detecting a species. Kery (2002) applied their model prospectively to infer how many visits were needed to be statistically confident that the species being sampled was absent.

McArdle's (1990) probability model includes: (1) the number of sampling visits (N) to an area, (2) the species probability of detection (ρ) during any visit, (3) and confidence (α) levels acceptable to the investigator (usually 95%, and therefore $\alpha = 0.05$). Assuming all visits to goshawk nest areas are similar and independent, the probability of not detecting nesting goshawks after N visits (Kery 2002) is:

$$\text{Probability} \\ (\text{N unsuccessful visits}) = \alpha = (1 - \rho)^N \quad (1)$$

We can solve for N and get:

$$\log(\alpha) = N \times \log(1 - \rho) \quad (2)$$

$$N = \log(\alpha) / \log(1 - \rho) \quad (3)$$

The minimum number of visits, N_{min} , needed to conclude that a 800-m radius circle containing a previously used nest area is unoccupied within a 95% confidence interval ($\alpha = 0.05$) can be estimated by substituting the probability of detection values (historical = 0.64, broadcast = 0.58, transect = 0.62; see Results for details) into Equation 4.

$$N_{min} = \log(0.05) / \log(1 - \rho) \quad (4)$$

RESULTS

The results were similar for each method tested; between 58–64% of the occupied nest areas were found (historical nest search [16/25], tree transect [16/26], broadcast surveys [15/26]). Conversely, between 36–42% of the occupied goshawk nest areas were missed. The broadcast result for a single visit is identical to what Kennedy and Stahlecker (1993) reported. We did not test for temporal differences in the methods due to limited sample sizes. Despite the poor performance of each method for detecting goshawks using a single visit to a nest area, each method may be repeated several times to increase the probability of detection (Kennedy and Stahlecker 1993, Watson et al. 1999, McClaren et al. 2003). Using the detection results, we estimated the number of visits (N_{min}) needed to infer goshawk absence at nest areas at the 95% confidence level ($\alpha = 0.05$) as 2.9 for the historical nest search, 3.1 for the tree transect, and 3.5 for the broadcast survey. These detection results are only relevant to active nest areas.

Increasing the confidence level while maintaining a consistent detection rate quickly increases the number of visits needed to infer goshawk absence at nest areas and renders the sampling effort unrealistic (Table 1). For example, if we set the confidence level to 0.95, and want to limit the number of visits to two, then the probability of detection required for a method to be effective would have to be nearly 80%. Given this scenario, the goal for developing new or improved detection techniques should be to achieve a probability of detection level of at least 80%. If the confidence level is increased to 0.99 ($\alpha = 0.01$) to further reduce the misclassification error while retaining the detection probability at 80%, then the number of required

visits to nest areas is three and is still a feasible management option (i.e., not cost prohibitive). McKelvey and Pearson (2001) examined a series of simulations for measuring small mammal populations with different detection probabilities and their results revealed the same general pattern as ours in that low detection probabilities require a large number of sampling sessions to attain confidence in the findings.

DISCUSSION

Our results were from occupied nest areas only. Although we controlled as much variation as possible, there were many sources of variation we did not control. We did not test for false positive detections at unoccupied sites (Kennedy and Stahlecker 1993), which are needed for a broader description of detection probabilities. Detection frequencies of goshawks at nest areas may vary for any number of reasons, but perhaps most important are changes in goshawk behavior as breeding season progresses (Squires and Reynolds 1997). Breeding goshawks become more defensive at nest areas later in the nesting season and generally are easier to detect (Squires and Reynolds 1997). Young goshawks also are easier to detect later in the breeding season as they grow and become more active (McClaren et al. 2003). Because detection methods may be temporally sensitive, managers must interpret the results cautiously (McClaren et al. 2003, Roberson et al. in press).

As the breeding season progresses from March through July, goshawk nest failures continue for a host of reasons. A difficult sampling problem is to account for these nest failures. Sampling after reproductive failure occurs may lead to misclassification of nest areas as inactive. In addition, nesting areas are occupied by adults that do not breed ev-

Table 1. Theoretical number of visits to Northern Goshawk nest areas to infer goshawk absence using different detection probabilities (ρ) and confidence levels (α).

α	PROBABILITY OF DETECTION								
	60	65	70	75	80	85	90	95	
0.25	1.51	1.32	1.15	1.00	0.86	0.73	0.62	0.46	
0.20	1.76	1.53	1.34	1.16	1.00	0.85	0.70	0.54	
0.15	2.07	1.81	1.58	1.37	1.18	1.00	0.82	0.63	
0.10	2.51	2.19	1.91	1.66	1.43	1.21	1.00	0.77	
0.05	3.26	2.85	2.49	2.16	1.86	1.58	1.30	1.00	
0.01	5.03	4.39	3.83	3.32	2.86	2.43	2.00	1.54	

ery year and thus, detection probabilities at individual nest areas are likely to vary temporally (Boal et al. 2005, R. Reynolds pers. comm.). We did not test the ability to detect nonbreeding pairs occupying nest areas; we tested only the breeding portion of the population (i.e., actively nesting in pairs). This has important ramifications for understanding the population's status (Kennedy 1997) and for managers making decisions based on results for years when few pairs are breeding. The ability to detect nonbreeding goshawks and breeding goshawks that have failed are likely to be different. Improved probabilities of detection may be possible by regulating the timing of when different methods are used.

Another source of variation that affects detection probabilities is the timing of egg-laying by females within and between populations: variation in the timing of egg-laying introduces inherent error to detection rate estimates. Thus, there will likely be differential success in detecting goshawks because the detection method used will not be perfectly sequenced to the breeding phenology of all pairs within or between populations. We recommend that managers determine the breeding phenology of their target population before implementing goshawk surveys (see Dewey et al. 2003).

Variation also exists in the experience of field crews and therefore, accuracy and reliability of survey data. In addition, goshawks may move to alternate nesting areas within a territory; this constant shifting among alternate nests may result in a perceived decay in the number of occupied nests and a fallacious conclusion of population decline if only the historical nest areas are visited (R. Reynolds pers. comm.). Given that multiple factors influence detection probabilities, the implication for monitoring populations at regional scales is that detection protocols should consider these sources of variation so that data sets from different locations and times are comparable for later use in analyzing large-scale population trends.

None of the goshawk detection methods tested in this study, when applied once, were adequate to conclude goshawks were absent at nest areas. The usefulness of new detection methods is dependent on understanding the associated detection probabilities and error rates for different spatial and temporal scales. Future approaches might include combining several different methods in a temporal sequence that improves the cumulative probability of detection throughout the breeding season

(Dewey et al. 2003). Highly accurate methods appropriate early in the breeding season (e.g., listening stations; Dewey et al. 2003) may be ineffective late in the breeding period. However, by combining methods and taking advantage of their strengths, improved results may be obtained, but this remains to be tested. Another approach is to test the detection probability of successive applications of the historical and tree-transect methods (i.e., multiple visits) and determine if the results match the outcome reported for the broadcast method (70%; Kennedy and Stahlacker 1993). The predictions in this paper related to cumulative detection probabilities from multiple applications of one technique should be tested. If these predictions are supported empirically, then managers could design a monitoring program that relies on multiple applications of a single technique (e.g., tree transects).

Detection success may be optimized by using listening stations prior to egg-laying (March and April; Penteriani 1999, Dewey et al. 2003), tree searches on parallel transects during incubation and the nestling stage (May–June), and broadcast calling (wail and food begging) during the post-fledging dependency period (Kennedy and Stahlacker 1993, McClaren et al. 2003). Although broadcast surveys are frequently used during the nestling stage, recent tests of this approach by Roberson et al. (in press) in Minnesota suggest broadcast surveys may not be an effective tool during this stage. Roberson et al. (in press) report high detection rates with broadcast surveys during courtship (70%) and fledgling-dependency phases (68%). Detection rates were lowest during the nestling phase (28%), when there appeared to be higher variation in likelihood of detecting individuals.

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QUANTIFYING NORTHERN GOSHAWK DIETS USING REMOTE CAMERAS AND OBSERVATIONS FROM BLINDS

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ABSTRACT.—Raptor diet is most commonly measured indirectly, by analyzing castings and prey remains, or directly, by observing prey deliveries from blinds. Indirect methods are not only time consuming, but there is evidence to suggest these methods may overestimate certain prey taxa within raptor diet. Remote video surveillance systems have been developed to aid in monitoring and data collection, but their use in field situations can be challenging and is often untested. To investigate diet and prey delivery rates of Northern Goshawks (*Accipiter gentilis*), we operated 10 remote camera systems at occupied nests during the breeding seasons of 1999 and 2000 in east-central Arizona. We collected 2458 hr of useable video and successfully identified 627 (93%) prey items at least to Class (Aves, Mammalia, or Reptilia). Of prey items identified to genus, we identified 344 (81%) mammals, 62 (15%) birds, and 16 (4%) reptiles. During camera operation, we also conducted observations from blinds at a subset of five nests to compare the relative efficiency and precision of both methods. Limited observations from blinds yielded fewer prey deliveries, and therefore, lower delivery rates (0.16 items/hr) than simultaneous video footage (0.28 items/hr). Observations from blinds resulted in fewer prey identified to the genus and species levels, when compared to data collected by remote cameras. Cameras provided a detailed and close view of nests, allowed for simultaneous recording at multiple nests, decreased observer bias and fatigue, and provided a permanent archive of data.

KEY WORDS: *Northern Goshawk; Accipiter gentilis; prey-delivery rate; diet; remote camera; video surveillance.*

CUANTIFICACIÓN DE LA DIETA DE *ACCIPITER GENTILIS* UTILIZANDO CÁMARAS DE VIDEO CON SISTEMA REMOTO DE VIGILANCIA Y OBSERVACIONES DESDE UN ESCONDITE

RESUMEN.—Comúnmente la dieta de las aves rapaces es medida indirectamente por medio de análisis de egagrópilas y restos de presas, o directamente por medio de observaciones de entregas de presa desde un escondite de observación. Los métodos indirectos no sólo toman mucho más tiempo sino que también existe evidencia que sugiere que estos métodos pueden sobre-estimar la importancia de ciertos taxa de presa en la dieta de las rapaces. Se han desarrollado sistemas remotos de vigilancia con cámaras de video para ayudar con la observación y la recolección de datos, pero su uso en situaciones de campo puede ser difícil y en muchos casos no es un método probado. Para investigar la dieta y las tasas de entrega de presa de *Accipiter gentilis*, utilizamos 10 sistemas de cámaras remotas en nidos activos durante las épocas reproductivas de 1999 y 2000 en el centro oriente de Arizona. Recolectamos 2,458 horas de video útil y logramos identificar 627 (93%) restos de presa hasta Clase (Aves, Mammalia o Reptilia). Entre los restos de presa identificados a nivel de género, identificamos 344 (81%) mamíferos, 62 (15%) aves y 16 (4%) reptiles. Durante la operación de las cámaras también hicimos observaciones desde escondites de un subgrupo de cinco nidos para comparar la eficiencia relativa y precisión de los dos métodos. Las observaciones limitadas desde escondites rindieron menos entregas de presa y por lo tanto rindieron tasas de entrega más bajas que la documentada simultáneamente con cámaras. Los datos obtenidos mediante observaciones desde escondites indicaron una habilidad reducida de este método

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para identificar presas a nivel de género y especie al ser comparados con los datos colectados de los videos de las cámaras remotas. Las cámaras produjeron una vista detallada y cercana de los nidos, permitieron la grabación simultánea de varios nidos, redujeron el sesgo y la fatiga del observador y produjeron un archivo permanente de datos.

[Traducción del Equipo Editorial]

Information on diet is important in understanding aspects of avian ecology such as diet overlap among species, predation, and prey selection (Rosenberg and Cooper 1990, Redpath et al. 2001). Diet assessment in raptors is usually done indirectly, by recovering pellets and prey remains, or directly, by observing prey deliveries from blinds; however, accurate estimates of raptor diet can vary depending on the technique employed (Marti 1987).

Indirect diet assessment can provide quantitative and qualitative information because raptors often leave behind undigested remnants of bones, feathers, and keratinous material as pellets, or as prey remains (Reynolds and Meslow 1984, MacLaren et al. 1988, Steenhof and Kochert 1988, Boal and Mannan 1994). However, prey remains and pellets may bias the representation of certain prey items (e.g., bird feathers are more easily detected than small bones); therefore, avian prey may be over-represented in raptor diet (Simmons et al. 1991, Bielefeldt et al. 1992). Marti (1987) suggested that pellet analysis is accurate only for raptor species that swallow their prey whole. Loss of prey remains to scavengers, investigator disturbance in the nesting area, and miscounting of remnant and incomplete remains may also bias or limit results.

Direct observation of raptors is a more accurate method for investigating diet in species that do not swallow their prey whole. Observations can be made from a blind within the nesting area; however, observations near nests can disturb hawks, are labor intensive and require dawn to dusk observations to obtain complete samples. In addition, direct observation requires positioning of the blind so that a view inside the nest bowl is possible (Collopy 1983).

A more recent technology for studying diet involves remote cameras at raptor nests (Ouchley et al. 1994, Booms and Fuller 2003, Lewis 2004a). Advantages of video surveillance for measuring diet include a reduction in observer bias and fatigue, minimal impact on an animal's behavior, detailed information on diet composition, and an archival record of footage (Kristan et al. 1996, Stewart et al. 1997, Delaney et al. 1999).

Lewis et al. (2004b) compared three methods for assessing raptor diet: video recording, pellet analysis, and prey remain analysis. They found that quantifying prey using either prey remains or pellet analysis did not provide as complete a description of diet when compared to remote cameras. They did not, however, compare observations from blinds to remote cameras. In this paper, we describe a camera system, monitoring, and data collection using remote video technology, and discuss advantages and disadvantages. In addition, we conducted limited observations from blinds at five nests and simultaneously collected data with remote cameras to compare the two methods.

STUDY AREA

We conducted this study on the Sitgreaves portion of the Apache-Sitgreaves National Forest in east-central Arizona. The Sitgreaves portion encompasses ca. 350 800 ha (elevation = 1768–2417 m) and is located atop the Mogollon Rim on the southern edge of the Colorado Plateau. The Mogollon Rim is a large glacial escarpment that extends east across central Arizona into New Mexico. The Mogollon Rim edge has deep drainages with mixed-conifer communities of Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), trembling aspen (*Populus tremuloides*), ponderosa pine (*Pinus ponderosa*), New Mexican locust (*Robinia neomexicana*), and Gambel oak (*Quercus gambelii*; Brown 1994). Ridgetops are dominated by ponderosa pine forest.

METHODS

We chose video monitoring as the primary method to quantify the diet of breeding Northern Goshawks (*Accipiter gentilis*) in east-central Arizona (Rogers et al. in press). During the breeding seasons of 1999 and 2000, we randomly selected 10 nests (four in 1999 and six in 2000) from a pool of known territories ($N = 48$). During June 1999 and 2000, we mounted EOD-1000 Electro-optics™ remote cameras (Electro-Optics, St. Louis, MO U.S.A.) when nestlings were between 4–7 d old (nestlings were shaded during camera installation). Cameras ran from 22 June–18 July 1999 and 6 June–31 July 2000. We needed a minimum of three people for camera placement with a mean setup time of 110 min per nest (range = 80–132 min). Nest trees were ponderosa pine or Douglas-fir, and nest heights were ca. 20 m above ground.

Cameras were 3.5 × 12 cm and equipped with 3.6 mm lenses. Each camera had 380 lines of resolution and a one-lux digital color system. During installation, the ground crew viewed the nest using a Broksonic D.C. TV/VCR combination (Broksonic Corporation of America,

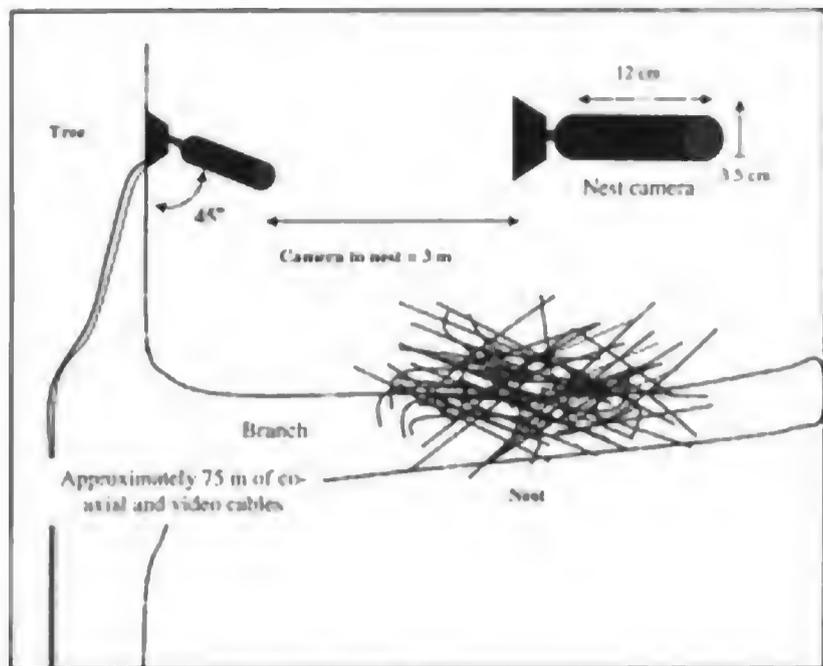


Figure 1. Schematic of camera system for monitoring Northern Goshawk nests in east-central Arizona in 1999 and 2000.

New York, NY U.S.A.) while a person in the nest tree positioned the camera. Once positioned, we secured the camera to the trunk of the tree or an overhanging branch. The goal in camera placement was a field of view that contained the entire nest structure and focused on the nest bowl. This was achieved by positioning cameras about 3 m away from nests at about a 45° angle to the nest structure (Fig. 1). Cameras were connected to 75 m of durable telephone-power cord and coaxial video cable (copper coated RG-59) tacked along the trunk of the tree. Camera cords were attached to a Panasonic™ AG-1070 DC (Panasonic, Secaucus, NJ U.S.A.) or Sony™ SVT-DL224 (Sony, Park Ridge, NJ U.S.A.) time-lapse VHS recorder, which were placed at least 50 m from the nest tree. Both time-lapse VCR models were industrial grade, 12-volt DC models with time-lapse programming capability. VCRs were housed in military ammunition cans (20 mm) and powered by one 12-volt, 64 amp-hr sealed Optima™ (Optima, Denver, CO U.S.A.) rechargeable lead acid battery (22 kg each). Batteries were kept dry under a plastic bin. Ammunition cans were locked, and all ground equipment was secured to a tree. Finally, we covered equipment with forest litter for shade and camouflage. Cost for one complete system was about \$1470 US (Table 1).

We programmed VCRs to record 5 frames/sec, which provided up to 24 hr of footage per videotape. We recorded activity at each nest in a 2-d sequence (12 hr/d), and cameras recorded 6 of 7 d of the week. We recorded from 0450–1650 H on day one and 0800–2000 H on day two. During 1999, all batteries and tapes were changed at night to reduce disturbance to hawks. In 2000, battery and tape changes occasionally occurred before nightfall, but only if ground equipment was located out of sight of nests. No more than 5 min were spent within nest stands changing batteries and tapes every other night or day. We continued to record video at nests until fledgling Northern Goshawks did not receive prey deliveries for 2 consecutive days.

Table 1. Cost of video surveillance equipment used for a diet study of Northern Goshawks in Arizona during breeding seasons 1999 and 2000. Prices based on 1999 retail costs associated with assembly of one system.

COMPONENT	APPROXIMATE COST (\$ US)
VHS time-lapse recorder ^a	675
Remote video camera	250
DC television monitor	190
Rechargeable battery	180
2-amp battery charger ^b	85
Coaxial and power cables and connectors	80
50 caliber ammunition can/locks and cables	50
Total	1470

^a Cost of Panasonic and Sony VHS recorder were averaged (Panasonic = \$810.00/Sony = \$520.00).

^b TV/VCR combo used for multiple units.

We viewed video footage on a 19 in Toshiba™ television (Toshiba, Irvine, CA U.S.A.) with a JVC™ SuperVHS VCR (JVC, Wayne, NJ U.S.A.). Prey items were identified to Class (Mammalia, Aves, or Reptilia), genus and species when possible, or classified as unknown. Prey items identified to class only were characterized as small, medium, or large based on *a priori* size class categories from Cockrum and Petryszyn (1992) and Dunning (1993).

To compare methods, we observed goshawks (2000 breeding season) at a subset of five nests from blinds constructed 25–40 m from nests. We erected blinds on ground prior to sunrise before each observation period. Blinds were constructed of camouflage heavy-duty canvas with screen windows in all directions, which allowed for observation of hawks within the immediate nesting area. We used 8 × 32 binoculars and a 20 × 60 spotting scope to count and identify prey items delivered to nests. Items were identified to Class (Mammalia, Aves, or Reptilia) and to genus and species when possible. We initiated blind observations when nestlings were between 8–12 d old and continued observing prey deliveries until young fledged. We conducted observations in 3–4 hr blocks each day starting at sunrise, and blinds were disassembled upon completion of each observation period. We allowed a 20-min acclimation period for adults and young before beginning observation. Observations from blinds were done in conjunction with video monitoring to compare accuracy of the two methods. In addition, observations from blinds and video reviewing were done by one person (Rogers) to minimize bias.

RESULTS

Camera Results. Adult Northern Goshawks actively defended the nest while we placed cameras in nest trees. However, adult females returned to the nest within 10–20 min after we vacated terri-

tories, as documented from video. In addition, we had no nest abandonment due to camera presence, and eight of 10 nests were successful (i.e., fledged ≥ 1 young). One nesting attempt failed due to adult female mortality (Bloxtton et al. 2002), and one was depredated by a Great Horned Owl (*Bubo virginianus*). Adults did not flush during nighttime battery and tape changes. Adults flushed infrequently during daytime changes because we were out of sight of the nest tree.

We collected 2458 hr of usable video footage, and about 500 hr were spent viewing tapes to identify and quantify prey items. Approximately 50 hr were spent changing batteries and tapes, excluding travel time. We documented 676 prey deliveries from camera footage. Of these, we identified 627 (93%) prey items to Class (Aves, Mammalia, or Reptilia) and observed a mean delivery rate of 0.28 (SE = 0.02) prey items/hr. We were able to identify, at least to genus, 422 (62%) of all prey items. Of items identified to at least genus, 344 (81%) were mammals, 62 (15%) were birds, and 16 (4%) were lizards.

Direct Observations. Because blinds were constructed before sunrise, adults infrequently flushed from nests. However, during disassembly and exiting nest territories, adults actively defended nests. When adults did flush from nests prior to an observation period, they returned to the nest within about 10 min. We observed goshawks for a total of 43 hr at five nests. We viewed seven prey deliveries, all of which were identifiable to Class. Mean prey delivery rate observed from blinds was 0.16 (SE = 0.06) items/hr.

Camera Versus Direct Observation. Camera footage yielded a higher total number of prey items delivered; therefore, our estimated prey delivery rate derived from video footage was higher than that derived from direct observation. An important result was that the camera footage revealed 12 deliveries during our observation period in which we visually documented only seven deliveries. Accuracy of prey identification to class was 100% using both methods, but we were able to document 58% of all prey to genus and/or species from the video footage compared to 0% from direct observations.

DISCUSSION

Use of remote camera systems is becoming a popular technique in wildlife studies, especially as equipment costs decrease. For example, the video surveillance equipment used in Lewis et al.

(2004a) was over \$2000 US and did not include batteries and chargers. Our equipment was similar to Lewis's, but the cost was \$1470 US, which included batteries and chargers.

Cameras have been used to monitor diet, predation events, and various behaviors of many species of wildlife (e.g., Wisniewski 1983, Sykes et al. 1995, Hughes and Shorrock 1998, King et al. 2001). Responses to camera installation may vary by species and individuals, timing of camera placement during the nesting season, and length of time needed for camera installation. Several workers reported no sign of nest abandonment due to cameras (Estes and Mannan 2003, Booms and Fuller 2003, Lewis et al. 2004a). However, Cain (1985) reported nest abandonment by Bald Eagles (*Haliaeetus leucocephalus*) due to camera installation. During our study, goshawks were distressed when cameras were installed, but did not seem to be affected by camera presence. In videos, adult and juvenile goshawks occasionally could be seen looking up at cameras, and there were several occasions when hawks perched directly below or on cameras. Goshawks were also distressed during our observations from blinds, especially during our exit from territories, which suggested that direct observations were more stressful to the nesting hawks than use of cameras.

Remote cameras can facilitate sampling for extended periods of time with a reduction in observer bias (Delaney et al. 1999). In contrast, observations from blinds are often done by more than one person, which increases the risk of observer bias (Boal and Mannan 1994). Video monitoring can also increase daily coverage because unmanned units can operate continuously. For example, we were able to collect nearly 2500 hr of observations in 2 yr with 10 cameras, whereas Boal (1993) and Boal and Mannan (1994) collected 1500 hr of observation from blinds, which required three field assistants per year for 3 yr. Observer fatigue could also bias the results based on direct observation, and the cost of labor would be high.

Using remote cameras, we were able to record prey deliveries at the nest for up to 1 mo after Northern Goshawk young fledged (Rogers et al. in press). In contrast, observations from blinds and pellet and prey remains collection are often discontinued shortly after young fledge (MacLaren et al. 1988, Seguin et al. 1998). Although prey delivered to nests during branching and fledgling stages often occurred out of camera range, allowing



Figure 2. Images of Northern Goshawk nests taken from video footage in east-central Arizona: (a) Female goshawk feeding 5-d-old young. (b) Golden-mantled ground squirrel and plucked Stellar's Jay in the nest with 25–30 d old goshawk young.

cameras to operate longer provided additional qualitative information on post-fledgling diet. Additional advantages of cameras include decreased frequencies of observer entrances and exits within territories. We spent no more than 5 min in nest stands every other day and usually did not flush adults from nests. We strongly recommend changing batteries and tapes at night, or alternatively locating ground equipment 50 m or more from nest trees.

Most importantly, using remote cameras greatly increased our ability to identify genus and species of prey delivered to nests. With cameras, we were able to see shape and color of most prey items (Fig. 2). Mammals were easiest to identify to genus and species due to their size and distinctive pelage, as well as the ability to see feet and tails. Small birds were the most difficult to identify, but the ability to see feathers, and hence make an identification, distinctly increased if the adults plucked avian prey in the nest.

Our data indicated that observations from blinds resulted in underestimates of prey numbers and delivery rates, but this needs further investigation. Prey items were missed in two ways during observations from blinds. First, on some occasions we failed to notice small prey items brought by the female because we were focusing on identifying an item brought previously by the male. Second, we missed some prey items that were delivered to nests after dark or prior to daybreak. We did not use these items in calculating prey delivery rates, but included them in total prey deliveries. Without the ability to play back the videotape, we would not have noticed these prey items.

A final advantage of video monitoring was the ability to record infrequent behavioral events. For example, during the 1999 nesting season, we documented an attempted predation by a Red-tailed Hawk (*Buteo jamaicensis*), and in 2000, we recorded a bobcat (*Lynx rufus*) scavenging prey from a nest that had already fledged young.

There are some limitations and constraints to using camera systems. We experienced technical difficulties including rodent and ungulate damage to cords, battery failure, loose connections, and water damage. In addition, when cameras' angles were $>45^\circ$ to the nest, the view was often obstructed by the adult female's back. To alleviate this problem, we searched for alternative branches or nearby trees that allowed for a 45° angle to the nest bowl. We recommend placing cameras opposite the di-

rection of the adult flight pathway to the nest. Therefore, observing adult movement patterns near nests before camera placement is recommended. Video monitoring involves a relatively high initial cost. Also, as of 2000, no audio capability was available within a waterproof system. Thus, collecting data on vocalizations during prey deliveries was not possible. One additional disadvantage of video technology is the additional time required to transcribe video data. Even though tapes were fast forwarded during non-prey delivery times, it took ca. 1 hr of viewing to transcribe data for every 5 hr of video footage collected. We suggest viewing collected tapes daily to minimize backlog and to allow researchers to become aware of system problems before data collection is complete.

In conclusion, we think remote cameras allowed us to collect more accurate diet data than if we would have solely used blind observations. Camera-monitoring systems are efficient, relatively noninvasive tools for quantifying diet and behavior of raptors.

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TEMPORAL PATTERNS OF NORTHERN GOSHAWK NEST AREA OCCUPANCY AND HABITAT: A RETROSPECTIVE ANALYSIS

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ABSTRACT.—We studied occupancy and habitat associations of Northern Goshawks (*Accipiter gentilis*) at nest areas in south-central Oregon in 1992–94. We surveyed 51 pre-1992 nest areas (i.e., historical breeding areas first discovered during 1973–91) for goshawks and used aerial-photograph interpretation to document forest cover conditions and changes over time between areas that were occupied by goshawks and those where we did not detect goshawks (no-response sites). We also surveyed for new nests during 1992–94. Of 38 occupied nests first found in 1992–94 (i.e., post-1992 nest areas), 86% (33/38) were in mid-aged (mean stand DBH 23–53 cm, <15 trees/ha >53 cm DBH) or late (≥ 15 trees/ha >53 cm DBH; mean stand DBH >53 cm) closed (>50% canopy closure) structural-stage forest. Occupancy of historical (pre-1992) nest areas by goshawks was 29% (15/51). Of 46 pre-1992 nest areas that we examined for habitat change, 15 were occupied by goshawks in 1994 and had more mid-aged closed and late closed forest in 12-, 24-, 52-, 120-, and 170-ha circular areas centered on nest locations than did 31 no-response areas. There was no difference in the amount of late closed and mid-aged closed forest in pre-1992 nest areas compared with occupied pre-1992 nest areas. A logistic regression model for all occupied nest areas confirmed that late closed and mid-aged closed forest variables were important indicators of forest conditions that supported breeding pairs. Goshawks were more likely to persist in the historical nest areas that had about 50% of mature and older closed-canopy forest within the 52-ha scale. We recommend retaining existing late closed, late open, and mid closed structure within 52-ha scale of the nest site. Moreover, late closed and mid closed structure combined should not fall below 50% within the 52-ha scale and should exceed 40% within the 170-ha scale surrounding the nest site. To optimize conditions for breeding goshawks, we recommend retaining large trees (>53 cm DBH) to help preserve stand integrity, maintain closed canopies, and provide connectivity to alternative nest sites within nest areas.

KEY WORDS: *Northern Goshawk; Accipiter gentilis; habitat; historical nest areas; landscape change; Oregon.*

PATRONES TEMPORALES DE OCUPACIÓN DE ÁREAS DE NIDIFICACIÓN Y HÁBITAT DE *ACCIPITER GENTILIS*: UN ANÁLISIS RETROSPECTIVO

RESUMEN.—Estudiamos la ocupación y las asociaciones de hábitat de *Accipiter gentilis* en áreas de nidificación del centro-sur de Oregon entre 1992 y 1994. También censamos 15 áreas de cría históricas descubiertas entre 1973 y 1991 (i.e., nidificación pre-1992), y usamos fotografías aéreas para documentar las condiciones de cobertura de bosque y cambios en el tiempo entre áreas que estaban ocupadas por esta especie y áreas en las que no la detectamos (sitios sin respuesta). También realizamos censos para buscar nidos nuevos entre 1992 y 1994. De 38 nidos activos encontrados por primera vez entre 1992 y 1994 (i.e. nidificación post-1992), el 86% (33/38) se encontró en bosques de sucesión media (promedio de DAP 23–53 cm, <15 árboles/ha >53 cm DAP) o bosques cerrados antiguos (≥ 15 árboles/ha >53 cm DAP; promedio de DAP >53 cm; >50% de cobertura del dosel). La ocupación de las áreas de nidificación históricas (pre-1992) por parte de *A. gentilis* fue del 29% (15/51). De 46 sitios de cría pre-1992 para los cuales evaluamos los cambios en el hábitat, 15 estuvieron ocupados en 1994 y presentaron mayor cantidad de bosques cerrados de edad media y bosques antiguos en áreas circulares de 12, 24, 52, 120 y 170 ha centradas en sitios en donde se ubicaban nidos, que 31 sitios sin respuesta. No existió

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diferencia en la cantidad de bosques cerrados de edad media y bosques antiguos entre áreas de nidificación pre-1992 en comparación con las áreas ocupadas pre-1992. Un modelo de regresión logística que incluyó todas las áreas de nidificación ocupadas confirmó que las variables de los bosques cerrados de edad media y sucesión tardía fueron indicadores importantes de las condiciones del bosque propicias para las parejas reproductivas. Las aves presentaron mayor probabilidad de persistir en las áreas de nidificación histórica que presentaban aproximadamente el 50% de bosques maduros antiguos de dosel cerrado a la escala de 52 ha. Recomendamos mantener la estructura de bosques antiguos cerrados y abiertos y bosques de edad media cerrados en las 52 ha circundantes a los sitios de nidificación. Además, la estructura combinada de bosques cerrados antiguos y de edad media no debe caer por debajo del 50% a la escala de 52 ha y no debe exceder el 40% en la escala de las 170 ha circundantes a los sitios de nidificación. Para optimizar las condiciones para la nidificación de *A. gentilis*, recomendamos mantener árboles grandes (>53 cm DAP) para ayudar a preservar la integridad de los bosques, mantener doseles cerrados y proveer conectividad entre sitios de nidificación alternativos ubicados en las mismas áreas de cría.

[Traducción del equipo editorial]

The ability of breeding pairs of Northern Goshawks (*Accipiter gentilis*; hereafter, goshawks) to persist in intensively managed and selectively harvested forests over time is largely unknown. Evidence suggests tree harvest impacts nest site selection (Crocker-Bedford 1990, Penteriani and Faivre 2001), use (Woodbridge and Detrich 1994), and ultimately nesting persistence (Crocker-Bedford 1995). Penteriani and Faivre (2001) examined logging disturbance and habitat change over a limited time (6–11 yr) in a European shelterwood harvest regime, but the effects of habitat alteration in western North American forests are not fully understood. Mature forest, consisting of large trees (diameter at breast height [DBH] >50 cm) and closed canopy cover (>50%), was demonstrated to be preferred by breeding goshawks for nest sites in western North America (e.g., Hayward and Escano 1989, Bull and Hohmann 1994, Squires and Ruggiero 1996, Daw and DeStefano 2001, McGrath et al. 2003).

There has been concern and debate that goshawk populations in western North America may be declining in response to habitat alteration and loss of these forests (Kennedy 1997, DeStefano 1998, Smallwood 1998, Crocker-Bedford 1998). Using aerial photographic records of timber harvest areas (Reutebuch and Gall 1990) on the Fremont National Forest and adjacent private forest lands dating from 1969–92, we evaluated temporal changes to forest structure around goshawk nests during 1992–94. Our objectives were to: (1) determine if a random sample of historical goshawk nest areas (i.e., nests first found in 1973–91) were occupied in 1994, (2) document post-1992 forest conditions and quantify change in forest cover on his-

torical nest areas, and (3) compare 1994 forest cover between historical nest areas that were occupied by goshawks between 1992 and 1994 to those historical nest areas where presence of goshawks was not detected.

STUDY AREA

Research took place on the Fremont National Forest (FNF) and the Klamath Tree Farm of the Weyerhaeuser Company in south-central Oregon, encompassing >5000 km². Elevations ranged from 1200–2200 m. Ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), and lodgepole pine (*P. contorta*) were the dominant commercial tree species. Generally, large expanses of lodgepole pine interspersed with small stands of pure ponderosa pine on higher ground dominated the northern half of the study area; dry mixed-conifer stands (white fir, incense cedar [*Libocedrus decurrens*], ponderosa pine, and sugar pine [*P. lambertiana*]) dominated the southern half of the study area. Douglas-fir (*Pseudotsuga menziesii*) was rarely encountered or absent, and most adjacent private lands had extensive ponderosa pine plantations. Natural forest openings consisted of xeric rocky flats, which contained sagebrush (*Artemisia* spp.) and bitterbrush (*Purshia tridentata*) near ponderosa pine and mixed-conifer stands, and moist meadows, which were typically associated with lodgepole pine and had a vegetative cover of sedges (*Carex* spp.), sagebrush, and willow (*Salix* spp.) next to perennial streams or springs. The landscape was a mosaic of forest cover types, containing two large burned areas from the 1950s and 1992, natural openings, and human-created openings. Dominant silvicultural practices on Forest Service lands were partial harvest, selective removal, and shelterwood treatments in mixed-conifer and ponderosa pine. All forest management terms used in this paper follow Helms (1998). Regeneration (clearcut) harvest was more typical in lodgepole pine habitat, although observational data and Forest Service records (Fremont National Forest Supervisor's Office, Lakeview, OR U.S.A.) documented that regeneration harvest occurred in mixed conifer and mature ponderosa pine types. Private land management was dominated by mostly early seral and some mid-seral plantations of *P. ponderosa*

in large clearcuts or past overstory removal with few scattered large seed trees. Forest Service management, regulated timber harvest and aggressive fire suppression dates back >50 yr; selective railroad logging took place around 1920 (Hopkins 1979, Laudenslayer et al. 1989). Regional historical accounts state that ponderosa pine stands were typically composed of large trees with a mean DBH of 40–70 cm and basal area (BA) ranging from 13 to 23 m²/ha (Munger 1917), stands rarely encountered in managed forests during our study.

METHODS

We defined *nest site* as the tree containing the occupied nest or the mapped location of the historically occupied nests and ≤ 1 ha around the location. A *nest area* for this study was the area that we surveyed out to 1000 m (about 300 ha), centered on a nest site. We defined post-1992 nest areas as occupied (breeding) nest areas first discovered during our study, which was conducted during 1992–94. Historical nest areas were defined as pre-1992 nest areas if they were first discovered occupied 1973–91 by Forest Service or Weyerhaeuser personnel, or other researchers. Occupied nest areas were areas we surveyed during 1992–94, where at least one adult goshawk was present or actively nesting. For purposes of habitat-change comparisons in 1994, occupied nest areas were a subset of the historical pre-1992 nest areas that were found occupied in 1994. No-response areas were a subset of pre-1992 nest areas surveyed in 1994 that had no detections.

Goshawk Nest Area Occupancy Surveys. We compiled a list of historical goshawk nest area locations from original data collected by Reynolds (1975, 1978), U.S. Forest Service (unpublished data, Fremont National Forest, Lakeview, OR U.S.A.), and Weyerhaeuser Company (unpublished data, Klamath Tree Farm, Klamath Falls, OR U.S.A.) and evaluated each dataset based on quality of documentation (e.g., written reports, legal and area descriptions, mapped locations), observer reliability (e.g., biologist or experienced observer), and number of years the nest area was documented as occupied. Nest records were included if there was adequate documentation of a goshawk attending a nest structure, incubating, or if fledglings or nestlings were present at the nest site. Locations meeting the above criteria were mapped, and forest cover type was validated by aerial photograph or field examination before surveys commenced. We stratified sites into one of three forest cover types: dry mixed-conifer, ponderosa pine (<20% other tree species), and lodgepole pine (<20% other tree species).

We broadcast conspecific vocalizations to elicit responses from nesting goshawks or fledglings from late May to early August 1992–94 (Kennedy and Stahlecker 1993, Joy et al. 1994). Surveys were centered on the last known occupied historical nest location, with at least 35–40 calling stations per survey area (see below), spaced 320 m apart and staggered on adjacent and parallel transect belts. To ensure coverage of potential nest areas, we examined the literature for estimates of inter-nest distances between alternative nest sites (273 m in the Klamath NF, California [Woodbridge and Detrich 1994]; 266 m [Reynolds et al. 1994], and 489 m [Reynolds and Joy 1998] in Arizona; and 432 m in Utah [Dewey et al. 2003]), sizes

of post-fledging family areas (PFA; ca. 168 ha, Kennedy et al. 1994), and the effective auditory range of the megaphone (≥ 150 m; Joy et al. 1994; S. Desimone unpubl. data). Based on this information, we established our survey area size as a circle with an approximate 1000-m radius centered around the nest location (ca. 40 stations). This resulted in a search area of about 300 ha, nearly twice the area of mean PFA size reported by Kennedy et al. (1994). If a response was detected, we immediately searched the vicinity for an occupied nest. For those surveyed areas where there were no detections during the nestling period (first survey), we resurveyed the area at least once in July–August during the fledgling period using the same stations so that each “no-response” area was visited and surveyed at least twice in a season. We also conducted systematic and opportunistic searches (Destefano et al. 1994a, Daw et al. 1998) for new goshawk nests (i.e., post-1992) during May–August 1992–94. When surveying a known occupied nest area from the previous survey season (i.e., 1992 or 1993), we used multiple observers to conduct a silent search at the last known occupied site to minimize disturbance. If there were no detections, we extended the search pattern by radiating out from the nest tree while using a combination of intermittent taped broadcast calls near the nest and regularly spaced calling stations. These areas had the same level of survey effort as the systematic searches: about 300 ha around the last known occupied nest.

Vegetation Sampling. We used 1:12 000 and 1:15 800 scale aerial photographs to describe and classify historical (1969–91) forest vegetation conditions and post-1992 conditions, obtained from the U.S. Forest Service and Weyerhaeuser Company for years 1969, 1972, 1976, 1978, 1980, 1983, 1988, and 1992 (the most recent available) for reference stands. Harvest inventory data from the Fremont National Forest were used to update 1988 and 1992 photos to 1994 conditions.

We used a 3× Dietzgen stereoscope to delineate cover in an 11% random sample (25 of 227) of reference stand polygons representing the range of forest conditions and habitats on the 1992 photographs. The variable-plot vegetation sampling method (Bell and Dilworth 1988) was used to verify the condition of these reference polygons on the ground. We sampled 7–11 plots ($\bar{x} = 8.1$ plots/reference polygon, SD = 1.8), 160 m apart, on a transect located through the longest axis of the habitat polygon or in parallel transects if the polygon was >300 m wide. Plots were measured for basal area (BA) using a 20-factor (ft²/acre, later converted to m²/ha) wedge prism at plot center to sort trees into diameter classes. We recorded DBH for all count trees by combining plots within a stand to determine trees/ha (TPH) and BA for each forest structure class. The stem count per sample point multiplied by the BA factor equaled the total BA occupied by tree stems on a per ha basis (Bell and Dilworth 1988). We followed the U.S. Forest Service Region 6 Vegetation Structural Stage (VSS) guidelines for general forest cover type descriptions in eastern Oregon (U.S. Department of Agriculture 1994).

We used two non-forest categories (open wet [moist meadows] and open dry [xeric flats]) and four forest structure categories (late, mid-age, early, very-early), combined with two canopy closure classes ($\leq 50\%$ or

Table 1. Forest structure classification for aerial photograph interpretation on the Fremont National Forest and adjacent private lands in Oregon U.S.A., based on mean tree diameter at breast height (DBH), mean canopy closure, and trees per ha (TPH) ≥ 53 cm DBH (USDA 1994). Very early stage was forest regeneration or clearcut.

FOREST STRUCTURE	DBH (cm)	CANOPY CLOSURE (%)	TPH ≥ 53 cm
Late closed	>53	>50	≥ 15
Late open	>53	≤ 50	≥ 15
Mid-aged closed	23–53	>50	<15
Mid-aged open	23–53	≤ 50	<15
Early closed	12–23	>50	none
Early open	12–23	≤ 50	none
Very early	≤ 12	<50	none

>50%), to identify and delineate vegetative cover on aerial photographs. Stands were then typed into forest vegetative cover classes based on total BA of trees per diameter class and TPH > 53 cm (Table 1). We defined canopy closure as the amount of sky obscured by tree foliage and branches as measured by a Lemmon spherical densitometer (Vales and Bunnell 1985). Canopy measurements were taken 5 m from plot center in four cardinal directions, averaged, and mean percent canopy closure was calculated from all plots for the polygon.

Following reference plot validation, all remaining habitat on photographs within a 170-ha circle around nest locations was delineated into vegetative cover polygons based on the validated reference plots and assigned vegetation structure categories. When 1994 photographs were not available, the 1994 Fremont National Forest Harvest Inventory (U.S. Forest Service, Fremont NF, Lakeview, OR U.S.A.) was used to update the habitat condition. A 19% ($N = 102$) random sample of polygons ($N = 546$), stratified by general forest cover type, was ground-verified using the same variable-plot sampling method outlined for reference stands. We assessed stand-typing accuracy by constructing an error matrix to determine the accuracy of our photograph interpretation (Desimone 1997).

To delineate historical forest conditions, we used U.S. Forest Service and Weyerhaeuser Company aerial photographs (1:12 000, 1:15 800, and 1:24 000 scales) that

represented stand conditions present in the year of the last known occupied nest. We extrapolated our reference set results to type stands into vegetative structure classes on the remaining historical photographs. All completed polygons were transferred to 1:24 000 scale U.S. Geological Survey (USGS) quadrangle maps using a zoom transfer scope (Bausch and Lomb Corporation, Rochester, NY U.S.A.) and digitized into a Geographic Information System, where area was calculated for each habitat polygon.

Annual Variation in Occupancy. We estimated annual variation in occupancy by resident pairs of western North American goshawks by examining data from five other study areas (Table 2). We then compared the mean annual occupancy rates of goshawks from these five study areas to our findings for post-1992 nest areas and pre-1992 (historical) nest areas assessed in 1994. Annual occupancy was defined as the mean (SE) annual percent of occupied areas. We assumed (1) territory occupancy was determined using similar survey techniques with equal effort (Joy et al. 1994, Reynolds et al. 1994, Woodbridge and Detrich 1994, Kennedy 1997) and (2) little or no major stand disturbance or habitat alteration occurred within territories since discovery (S. Dewey, P. Kennedy, R. Reynolds, and B. Woodbridge pers. comm.). An occupied territory was defined by all researchers as ≥ 1 adult goshawk present in or near the nest on ≥ 2 separate occasions during the breeding season and in-

Table 2. Mean occupancy rates of Northern Goshawk nest areas (NA) among six concurrent studies in the western U.S., including occupied nest areas found on the Fremont National Forest (NF) and adjacent private lands 1992–94, Oregon, U.S.A. (this study). Occupancy is defined as a territory used regularly by at least one adult goshawk during the breeding season. The first year a nest was discovered is not included in the calculations.

STUDY AREA	SOURCE	NA	MEAN	SE	YEARS ^a
Kaibab NF, AZ	R.T. Reynolds pers. comm.	32	0.72	0.05	4–5
New Mexico	Kennedy 1997	22	0.74	0.07	4–11
Klamath NF, CA	Woodbridge and Detrich 1994	26	0.74	0.01	5–9
Utah	Kennedy 1997	26	0.75	0.06	4–7
Malheur NF, OR	S.K. Daw pers. comm.	33	0.66	0.02	2–4
Fremont NF, OR	This study	20	0.79	0.04	2

^a Number of years of occupancy data for known nests in the study area.

cluded pairs attempting to nest (Reynolds et al. 1994, Woodbridge and Detrich 1994, Kennedy 1997).

Habitat Change Analysis. Using nest tree locations as nest area centers, we established five different radius categories of 12, 24, 52, 120, and 170 ha. These areas had biological or managerial significance: 12 ha was recommended as a minimum nest area size for goshawks (Reynolds 1983, Reynolds et al. 1992); 24 ha was the size of goshawk habitat areas designated on the Fremont NF to protect nesting stands (U.S. Department of Agriculture [USDA] 1989); 52 ha was about the mean size of the aggregate of alternative nest areas associated with the primary nest area of goshawks nesting in the Klamath NF in northern CA (Woodbridge and Detrich 1994); 120 ha was the area of old-growth habitat allocated for management of Pileated Woodpeckers (*Dryocopus pileatus*) on the Fremont NF (USDA 1989); and 170 ha was the size of the goshawk PFA (Reynolds et al. 1992, Kennedy et al. 1994).

We conducted comparisons at both "disk" (12, 24, 52, 120, and 170 ha) and "ring" (the area between the 12–24, 24–52, 52–120, and 120–170 ha disks) scales. Disks represent cumulative effects as scale increases, since smaller disks are included within the larger disks. Rings were tested individually so that influence of inner disks was removed (Ramsey et al. 1994, McGrath et al. 2003).

We examined how forest structure around historical nest sites changed over time by calculating the % change for each vegetation cover (forest and non-forest) variable (equation 1):

$$\%Change = [(Area_{1994} - Area_{HISTORIC}) / Area_{HISTORIC}] \times 100 \quad (1)$$

where $Area_{1994}$ is the area of a cover category for 1994, and $Area_{HISTORIC}$ is the area of the same cover category in the year the site was last known to be occupied. This calculation was made for each of the paired sites for all scales of disks and rings. We used Wilcoxon signed-rank test for paired comparisons to test for changes in forest cover between pre-1992 and post-1992 conditions and Kruskal-Wallis one-way analysis of variance by ranks followed by multiple comparison tests for least significant difference (LSD) to test for differences in forest cover among pre-1992, pre-1992 occupied, and pre-1992 no-response nest areas (Conover 1980; JMP Statistical Software version 3.1, SAS Institute, Cary, North Carolina, U.S.A.).

Logistic Regression Model. We wanted to know the likelihood of predicting the suitability of historical nest areas by considering the amount of area of each vegetation structure category (forest and non-forest) around occupied and no-response sites. Thus, we constructed a logistic regression model (Hosmer and Lemeshow 1989, Ramsey et al. 1994) using the binary response variable of occupied ($Y = 1$) or no-response ($Y = 0$) by goshawks in a historical nest area in 1994. The importance of a particular habitat variable was determined by a stepwise analysis (PROC LOGISTIC; SAS Institute, Inc., 1992). The alpha for entry level (p_E) of the variable to be considered for the model was 0.15 because we wanted to detect possible trends in the event of a nonsignificant P -value. Models were run for each of the five disks and four rings. The full model included all explanatory habitat variables (equation 2):

$$\begin{aligned} \text{logit } P(Y) = & B_0 + B_1 \times \text{VeryEarly} \\ & + B_2 \times \text{EarlyClosed} \\ & + B_3 \times \text{EarlyOpen} \\ & + B_4 \times \text{MidClosed} \\ & + B_5 \times \text{MidOpen} \\ & + B_6 \times \text{LateClosed} \\ & + B_7 \times \text{LateOpen} \\ & + B_8 \times \text{OpenWet} \\ & + B_9 \times \text{OpenDry} \quad (2) \end{aligned}$$

where B_0 is constant, and B_1 through B_9 are the coefficients. The model was run in *logit P(1)* mode (stepwise descending) to calculate odds ratios for significant variable(s) associated with a nest area being occupied (i.e., $Y = 1$). Interaction terms were evaluated in the final model.

RESULTS

Nest Area Surveys. During 1992–94, we found 38 occupied goshawk nest areas (15 pre-1992 and 23 post-1992) that composed our sample of nests for vegetation analysis. Of the 51 pre-1992 nest areas we reexamined, 10 had evidence of nesting and five more had goshawks present, for a total of 15 historical occupied nest areas. Twelve of the 15 occupied nest areas were contained wholly on Forest Service ownership, two were on Weyerhaeuser land, and one was mixed ownership. Of 36 no-response areas, 23 were on Forest Service, 11 on Weyerhaeuser, and two were mixed ownership. We removed five nests from the historical sample for our vegetation analysis because of inadequate photographic records. Therefore, of the remaining 46 pre-1992 nest areas surveyed to protocol, 15 were occupied, and 31 were no-response areas. Number of nestlings per nest was similar for pre-1992 areas occupied in 1994 and post-1992 nests (1.5 ± 1.2 [$N = 10$] and 1.4 ± 1.0 [$N = 18$] young/nest, respectively).

Annual Variation in Territory Occupancy. Of 38 occupied nest areas, we were able to consistently survey 20 for at least two seasons from 1992–94; these had a mean annual occupancy rate of 79% (SE = 4; Table 2). This was similar to the mean annual occupancy rates from five other concurrent studies in the western U.S. (73%, SE = 2, for Arizona, California, New Mexico, Utah, and Oregon; Table 2). Occupancy of all historical (pre-1992) nest areas surveyed in 1994 was 29% (15/51), which was significantly different from the occupan-

cy rate for post-1992 areas ($\chi^2 = 12.4$, 1 df, $P = 0.0004$) and substantially lower than reported in the literature (Table 2).

For post-1992 nest areas, mean inter-alternative nest distance was 245 m (SE = 48, $N = 23$; no data for private lands). This was comparable to the inter-alternative nest distances reported in the literature (Reynolds et al. 1994, Woodbridge and Detrich 1994, Dewey et al. 2003).

Habitat Typing. Overall typing accuracy based on ground verification of reference polygons was 80%. Mid-age and late categories were 80–90% for reference polygons (Desimone 1997); we thought this was an acceptable rate to proceed with the analysis (Lillesand and Kiefer 1994). Our highest classification accuracies were for dry open and wet open non-forest categories (100% each) from reference polygons, followed by late open and late closed forest structure (90% each), mid-aged open (84%), and mid-aged closed forest (80%). Early open and early closed forest structure was least accurately classified (67% and 69%, respectively).

Forest Cover Distribution. For post-1992 nest areas, 25 of 42 (60%) occupied nest trees were within late closed forest structure, and 11 of 42 (26%) were in mid-aged closed structure. Distribution of post-1992 and pre-1992 nest sites was similar among the three forest cover types: 56% versus 47% in mixed conifer, 24% versus 28% in lodgepole pine, and 20% versus 25% in ponderosa pine, respectively.

Habitat Change Analysis. Mean percent change of the seven forest-structure categories (Table 1) for pre-1992 nest areas over time occurred in all scales (i.e., five disks and four rings) (see Desimone 1997: Tables 11 and 12 for details). For disks, the largest increases were in the amounts for very-early (642%, SE = 93%) and early open (238%, SE = 17%) categories. The largest decreases over time were in the late open (−54%, SE = 3%), late closed (−49%, SE = 1%), and mid closed (−30%, SE = 3%) categories. The magnitude of the percent change decreased with increasing scale; for example, increase in very-early cover went from 742% to 640% to 435% at 12-, 52-, and 170-ha disk scales, respectively, while decreases in late open cover went from −58% to −56% to −47% for 12-, 52- and 170-ha scales, respectively. Similar results were noted for rings, although at lower magnitudes.

In Figure 1, we presented late closed, early open, and very-early structural stages because they rep-

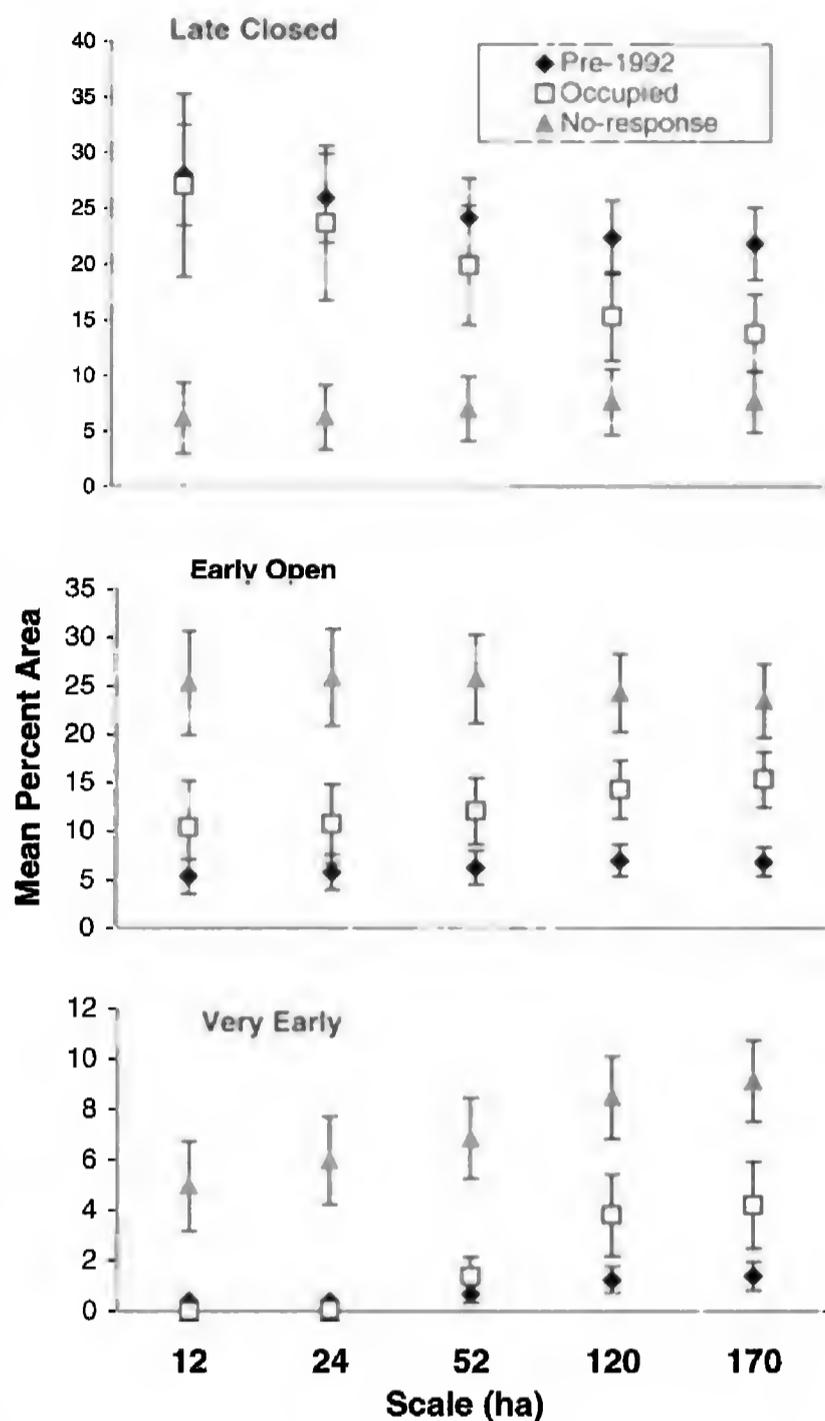


Figure 1. Mean (SE) area of late closed, early open, and very early structural stages among 5 circular analysis scales surrounding 46 historical (pre-1992; first discovered during 1973–91) goshawk nest sites in south-central Oregon, U.S.A.; 15 were occupied by goshawks and 31 had no evidence of occupancy in 1994. See text and Table 1 for further description of forest structure categories.

resented most confidence in correctly classifying habitat types, and therefore most confidence in detecting a decrease in area of highest suitable habitat (late closed) and an increase in area of known non-nesting habitat (early open and very early). For the 12-, 24- and 52-ha scales, mean percent late closed forest at all occupied nest areas in 1994 remained nearly the same as at pre-1992 areas (i.e., no significant difference). However, mean percent late closed forest at no-response areas was about

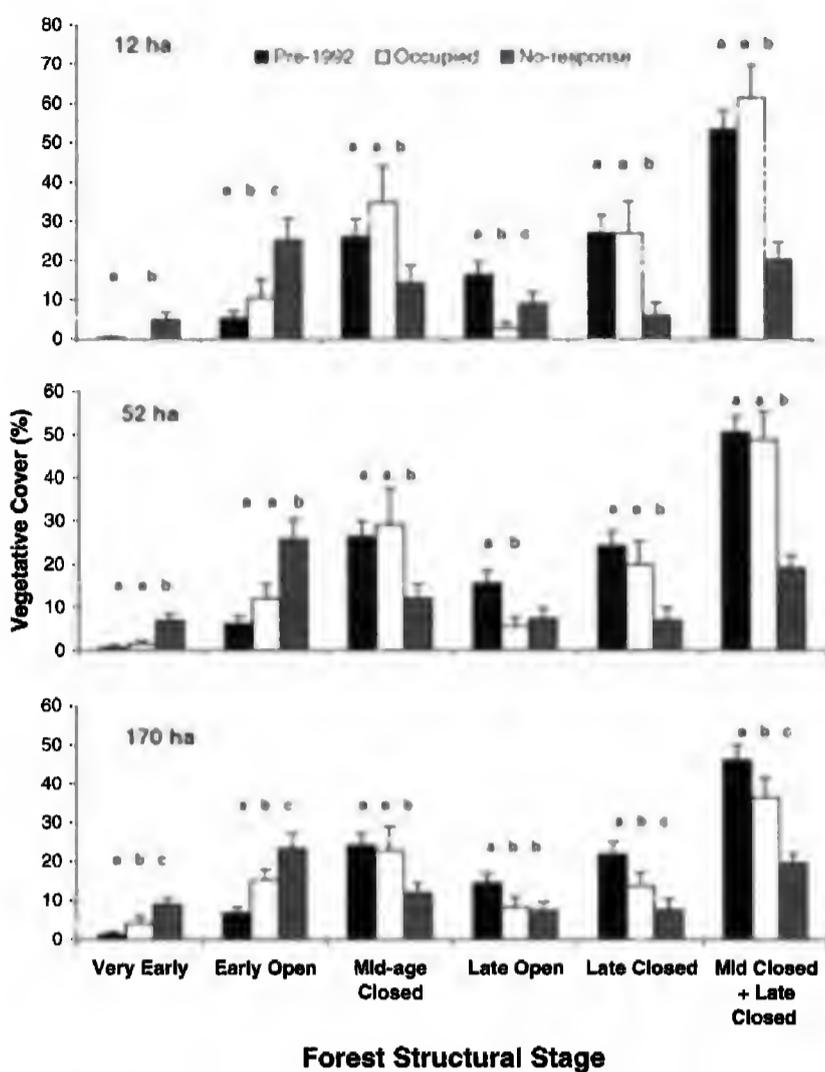


Figure 2. Mean (SE) distribution of forest structural stage categories (plus a combination of mid-aged and late closed canopy forest) at 12-, 52-, and 170-ha scales surrounding 46 historical (pre-1992—first discovered during 1973–91) goshawk nest sites in south-central Oregon, U.S.A.; 15 were occupied by goshawks and 31 had no evidence of occupancy in 1994. We omitted the 52- and 120-ha data because results were similar. See text and Table 1 for further description of forest structure categories. Difference in grouped means assessed by Kruskal-Wallis test ($\alpha = 0.05$). Within each group, Fisher's test of least significant difference for multiple comparisons was used; pairs within each forest structure stage not significantly different share common letters.

one-fourth to one-fifth the amount of late closed at pre-1992 and occupied pre-1992 areas (Fig. 1). With increasing scale, the mean proportion of early open structure at no-response nest areas was 4–5 times greater than pre-1992 nest areas, and over twice that of occupied pre-1992 areas (Fig. 1). The mean proportion of very early stage increased with increasing scale and was 4–6 times greater at 12-, 24- and 52-ha scales for no-response areas than pre-1992 and occupied pre-1992 areas (Fig. 1). For 120- and 170-ha scales, mean proportion of very early was about half that in occupied compared to

no-response areas; pre-1992 areas had about 1/8th that of no-response areas.

No-response areas ($N = 31$) showed significant changes in the general distribution of forest structure compared to all pre-1992 areas and also differed significantly from occupied pre-1992 areas for 12-, 52- and 170-ha disk scales (Kruskal-Wallis test, all $P < 0.0454$; Fig. 2). Histograms for 24- and 120-ha scales were not presented, as patterns in results were similar but intermediate in values between their adjacent scales. Mean proportion of area was significantly different for late closed forest, mid-aged closed forest, early open forest, and very early among pre-1992, occupied pre-1992, and no-response areas (LSD for pairs of means, $P < 0.05$). The greatest single change in a category was in the mean amount of late closed forest in pre-1992 ($\bar{x} = 22$ –27% among all disk scales) and no-response areas ($\bar{x} = 6$ –8%, all disks; Kruskal-Wallis, $P < 0.0003$).

At the 52-ha scale, the mean percent area of late closed forest (20%) for occupied pre-1992 areas remained similar to historical pre-1992 areas (24%; Fig. 2). Less than half of the mean area of mid-aged closed forest that once existed in pre-1992 areas (25%) occurred in no-response areas (12%). This corresponded with an increase in mean percent mid-aged open forest in no-response (24%) compared to the occupied pre-1992 areas (15%). In no-response areas, mean percent area of early open canopy forest was >4 times the historical mean (pre-1992) amount, and more than twice that of occupied pre-1992 areas (LSD test of means, $P < 0.05$). Very early mean percent area was significantly greater in no-response than occupied pre-1992 areas (LSD test of means, $P < 0.05$; Fig. 2). We point out comparisons at the 52-ha scale because it represents, in theory, the aggregate of alternative nest sites for a nesting area, and the persistence of goshawk use or occupancy appears to be correlated with higher amounts of mature forest at about this scale (Woodbridge and Detrich 1994).

Logistic Regression Model of Forest Structure Association. For post-1992 occupied nest areas, both late and mid-aged closed variables were associated with the 52-ha disk model (drop in Deviance $\chi^2 = 9.5$; 1 df; $P < 0.01$) and the 24–52 ha ring model (drop in Deviance $\chi^2 = 20.7$; 1 df; $P < 0.01$), as described by the reduced model (Equation 3):

Table 3. Results of stepwise logistic regression analysis for occupied ($Y = 1$) goshawk nest areas ($N = 15$), Fremont National Forest and adjacent private lands, Oregon, U.S.A., 1994. Stepwise entry level was at $\alpha = 0.15$. Scales emanate from territory centers; ring size is the area between two concentric disk areas. Parameter estimates are natural log (ln) of odds ratios. The interaction term (late closed \times mid-aged closed) was not significant ($P = 0.23$).

DISK SIZE ^a (ha)	VARIABLE	PARAMETER ESTIMATE	SE	WALD χ^2	P-VALUE	ODDS RATIO ESTIMATE	95% CONFIDENCE INTERVAL OF ODDS RATIO
12	Intercept	-83.9333	24.4576	11.7771	0.0006	—	—
	Late closed	0.4771	0.1650	8.3594	0.0038	1.611	0.1537-0.8005 (1.166-2.227)
	Mid-aged closed	0.3344	0.1157	8.3554	0.0038	1.397	0.1076-0.5612 (1.114-1.753)
24	Intercept	-46.5816	13.664	11.6205	0.0007	—	—
	Late closed	0.2660	0.0947	7.8850	0.005	1.305	0.0804-0.4516 (1.084-1.571)
	Mid-aged closed	0.1729	0.0616	7.8829	0.005	1.189	0.0522-0.2936 (1.054-1.341)
52	Intercept	-21.9700	6.3879	11.8290	0.0006	—	—
	Late closed	0.1131	0.0401	7.9426	0.0048	1.120	0.0345-0.1917 (1.035-1.211)
	Mid-aged closed	0.0818	0.0307	7.1046	0.0077	1.085	0.0216-0.1420 (1.022-1.155)
RING SIZE ^b (ha)							
12-24	Intercept	-85.3932	25.1893	11.4925	0.0007	—	—
	Late closed	0.5126	0.1798	8.1303	0.0044	1.670	0.2109-0.9366 (1.235-2.551)
	Mid-aged closed	0.3175	0.1215	6.8264	0.009	1.374	0.0984-0.5913 (1.103-1.806)
24-52	Intercept	-33.9116	10.7673	9.9193	0.0016	—	—
	Late closed	0.1754	0.0691	6.4489	0.0111	1.192	0.0533-0.3301 (1.055-1.391)
	Mid-aged closed	0.1423	0.0579	6.0437	0.0140	1.153	0.0376-0.2719 (1.038-1.313)

^a Forest structure classes were not significantly associated with the 120- and 170-ha disk scales.

^b Forest structure classes were not significantly associated with the 52-120 and 120-170 ring scales.

$$\text{logit}(I) = B_0 + B_1 (\text{late closed}) + B_2 (\text{mid-aged closed}) \quad (3)$$

There was a strong association between nest area occupancy and both late closed and mid-aged closed forest at the 12, 24, and 52 ha scales (Table 3). At the 12-ha nest area scale, the odds that a site was occupied increased by 61% (odds ratio 1.61) for each unit (1 ha) increase of late closed forest habitat, while holding the mid-aged closed forest variable constant. For each unit increase of mid-aged closed forest habitat, the odds that a site was occupied increased by 37% (odds ratio 1.37), while holding the late closed forest variable constant.

The reduced model was also significant for the 12-24 and 24-52 ha rings. The stepwise descending model procedure did not yield a significant model for any variables associated with occupied sites for 120 or 170 ha disks, or for 52-120 and 120-170 ha rings. The interaction term (*late closed* \times *mid-aged closed*) of the reduced model for disks was not significant ($\chi^2 = 43.1$; 1 df; $P = 0.23$).

DISCUSSION

Not all goshawk territories may be occupied in all years (Detrich and Woodbridge 1994, Reynolds et al. 1994), and even in the absence of human-caused habitat alteration, some territories can be

expected to be lost due to natural (e.g., stand senescence, disease, fire) changes in the forest over time (Graham et al. 1994). Mean annual occupancy of goshawk nesting areas in six studies across the western U.S. (concurrent with this study) were consistently in the 65–80% range over 2–11 yr of study. An occupancy rate of 29% (15/51) of the historical nest areas on our study area in 1994 is low by comparison. The low occupancy rate may be due in part to attrition of some suitable nest areas due to natural disturbance over time; one fire partially burned two nest areas in our study. It is also possible that our goshawk surveys did not extend out far enough to include some of the alternative nests used. Recent data from Arizona suggests that about 67% of goshawks move to alternative nest locations every year and that a 1000 m broadcast calling radius accounted for about 95% of the alternative nest attempts (R. Reynolds unpubl. data). If these findings are applied to our study, we likely missed about 5% of all alternative nests in our study.

Like many raptors, individual goshawk pairs may not breed every year, and determining trends in territory occupancy using 2 yr survey data is tentative (DeStefano et al. 1994a). Pairs not nesting in a given year, but still occupying the nest area, are difficult to find when surveys are conducted after courtship (Dewey et al. 2003). However, we searched large areas (>300 ha) multiple times around each historical nest location during a period when local weather conditions were not particularly inclement for the region and when goshawk productivity was relatively high: 74% (17/23) of nests on the Fremont NF and 91% (20/22) of nests on the nearby Malheur National Forest successfully fledged young in 1994 (S. Rickabaugh, S. Danver, and S. Daw unpubl. data). Other studies in eastern Oregon and Washington reported similar high occupancy and nest success levels for 1994 (McGrath et al. 2003; S. Finn unpubl. data). In addition, Kostrzewa and Kostrzewa (1990) reported that weather did not affect the density of territorial goshawk pairs over an 8-yr period in Europe, but was an influential limiting factor to breeding success. Thus, we concluded that the low occupancy rates of the historical nest areas were not attributed to low detectability, although we could not completely rule this out as a possibility.

The difference in forest structure between post-1992 occupied and no-response nest areas was compelling. Late structural stage forest, especially with canopy cover >50%, was much more preva-

lent around occupied than no-response nest areas. Conversely, very early and early structural stage forest was much more prevalent in no-response than occupied nest areas. Our results indicated that late forest structure declined by 20–50%, and very early and early forest structure increased by >400% around no-response nests. These trends were detectable at all scales, but were strongest at the smaller scales (12 and 52 ha) and decreased with increasing scale. Although we do not have detailed history of stand management for all cases, the observed difference in habitat is attributed to levels of timber harvest, which we verified by photographic evidence and field examination. The loss of large trees (>53 cm DBH) and a reduction in canopy cover to <50% appeared to influence nest area occupancy. Penteriani and Faivre (2001) and Penteriani et al. (2002) found that nest sites (ca. 0.8 ha) around the nest tree altered by more than 30%, either by selective tree harvest (shelterwood) or windthrow, caused goshawk pairs to change locations to new nest stands. The general conclusions reached by Penteriani and Faivre (2001) and Penteriani et al. (2002) on habitat disturbance were consistent with our results: goshawks were absent from nest areas where there was $\geq 30\%$ mean decrease in late and mid closed forest (12-ha scale) compared to the pre-1992 condition. Our data showed that this pattern was consistent at larger (12–52 ha) scales as well.

Our results suggested that nest area habitat alteration (loss of nesting habitat) was the most likely reason for the low occupancy rates of historical nest areas in 1994. The habitat alteration was likely the result of timber harvest (documented by aerial photographs), which reduced the proportion of late and mid-aged forest with high canopy closure and increased the proportion of very early and early open forest conditions within 52 ha (scale of logistic model significance) of goshawk nests.

Management practices for nesting habitat protection on the Fremont NF were limited during 1973–91, ranging from no protection (unrestricted harvest) of nest areas to 12-ha no-harvest buffers around nests during the breeding season (Reynolds 1983, USDA 1993). In 1983, the Fremont National Forest Plan established several 24-ha goshawk habitat management areas. However, conditions on most of these management areas ranged from early successional forests (unsuitable to marginal for nesting habitat) to mid-aged forest with only small patches of late-successional forest. Some

goshawk management areas were reassigned or relocated in subsequent years to achieve timber harvest objectives (K. Palermo and W. Watkins, Fremont NF, pers. comm., S. Desimone unpubl. data).

The photographic record revealed that little or no long-term habitat protection was implemented for the 31 no-response areas as of 1994. All were historical sites that had some portions within 52 ha of the nest site harvested during or after the historical nesting season. In contrast, most goshawk territories in the western U.S. study areas we reviewed (Table 2) had little or no habitat loss from timber harvest practices since discovery by the researchers and had yearly monitoring programs that documented relatively high occupancy rates (B. Woodbridge, P. Kennedy, R. Reynolds, and S. Dewey pers. comm.). This further supported our conclusion that timber harvest was a determining factor leading to significantly lower occupancy rates in the no-response nest areas compared to the occupied areas.

Nest area fidelity (as indexed by occupancy rates) is likely to be higher in good quality habitats as compared to poor quality habitats. This may be advantageous because there is an increased likelihood of nesting success where they may have been successful before (Newton 1979, Newton and Wyllie 1992, Rosenfield and Bielefeldt 1996). Our results suggest nest areas with >50% proportion of older and larger structural classes may be higher quality nest areas than areas dominated by younger seral stages (Woodbridge and Detrich 1994, Finn et al. 2002). Detrich and Woodbridge (1994) and Reynolds et al. (1994) reported that 70–75% of banded goshawks occupied the same nest area in successive years, which was similar to findings for Cooper's Hawks (*A. cooperii*; Rosenfield and Bielefeldt 1996) and Eurasian Sparrowhawks (*A. nisus*; Newton and Wyllie 1992). Although anecdotal, in 1992–94 we found an occupied nest in each of two nest areas that were both within 100 m of their respective historical nest site in nest areas that received special protection as old growth management areas in the early 1980s (Fremont NF unpubl. data); these sites were first found 20 yr earlier by Reynolds (1975).

In Arizona, Reynolds and Joy (1998) reported that over a 6-yr period, 92% of breeding male and 79% of breeding female goshawks had fidelity to their territories and mates. However, in extreme conditions such as food stress (Newton 1979) or in disturbed habitats (Woodbridge et al. 1988, Bosa-

kowski et al. 1993, Woodbridge and Detrich 1994, Crocker-Bedford 1995), there is evidence to suggest that species with strong site fidelity might behave differently. Bosakowski et al. (1993) reported five of six Cooper's Hawk nest sites were abandoned and not reused in the year following clearing of adjacent forests and human encroachment within a range of 40–500 m of the nest site. Hargis et al. (1994) postulated that monitoring site fidelity of breeding goshawks might provide a valuable indicator of the quality of the surrounding home range. If specific habitats needed for foraging and development of fledglings are subjected to habitat alteration outside nest areas (defined as >12 ha in Hargis et al. [1994]), hawk pairs might vacate even though individual nest sites (i.e., ≤ 12 ha) are being protected (Woodbridge et al. 1988, Bosakowski et al. 1993, Hargis et al. 1994, Woodbridge and Detrich 1994, Crocker-Bedford 1998).

To infer that goshawk populations have declined on our study area is beyond the scope of this study. It is possible that goshawks not found in our historical no-response nest areas in 1994 had relocated to more suitable areas elsewhere. However, in these no-response nest areas, forest structural conditions were significantly altered from past timber harvest, suggesting that habitat quality had been substantially reduced, which precluded goshawks from occupying those nest areas (i.e., out to the 300-ha surveyed area in our study) through time.

Our results indicated that pre-1992 nest areas still occupied by goshawks in 1994 had >50% of their mean area in mid closed + late closed forest within the 52-ha scale (Fig. 2), and most resembled their historical photograph conditions. Moreover, late forest (i.e., late closed and late open) structure was most predominant in occupied nesting areas at the 12-ha scale for all forest cover types examined, supporting studies in Oregon (Moore and Henny 1983, Bull and Hohmann 1994, Daw and DeStefano 2001), northern California (Woodbridge and Detrich 1994), and elsewhere (Reynolds et al. 1982, 1994, Crocker-Bedford and Chaney 1988, Hayward and Escano 1989, Siders and Kennedy 1996, Squires and Ruggiero 1996). In 1994, only 2–8% of the forested area in the Fremont NF was composed of ponderosa pine or pine-associated, late structured, old forest (Henjum et al. 1994). Because of the decline of areas of contiguous large and old trees (>50 cm DBH or >150 yr of age; Henjum et al. 1994), late-successional and old ponderosa pine forest has become an in-

creasingly threatened forest ecosystem in North America (Noss et al. 1995).

Implications of Vegetative Cover Loss. A mosaic of vegetative cover best describes goshawk nest areas (i.e., 170 ha) on the Fremont and private lands we examined. For a goshawk population to persist in this mosaic, sufficient breeding habitat must exist to promote positive net reproduction (Rosenzweig 1985, Urban and Shugart 1986). Although recent analyses of goshawk demography in the U.S. reported no evidence of population trends (Destefano et al. 1994b, Kennedy 1997), forest management activities such as intensive harvest and road building, as well as human development in the last 50–100 yr have changed the forest mosaic proportions to a far greater degree than natural disturbance regimes. In recent decades, for example, older forest has been harvested at a more rapid rate than it can develop (USDA 1993, Henjum et al. 1994, DellaSalla et al. 1995). The accelerated pace of habitat change has greatly increased the proportion of early successional forest and resulted in a skewed distribution favoring younger age classes compared to what was present historically in our study area (Henjum et al. 1994, 1996, Noss et al. 1995, Weyerhaeuser Corporate Photographic Archives unpubl. data). The net effect is that suitable nesting and foraging habitat for goshawks is reduced (McCarthy et al. 1989, DellaSalla et al. 1995, Henjum et al. 1996), and positive net reproduction of goshawks and other species that use older forests is potentially affected.

Our results lend evidence to the hypothesis that long-term occupancy of nest areas is correlated with larger proportions of mature forest (Woodbridge and Detrich 1994) and indicates that substantial amounts of late and mid-aged closed forest were important to the continued use of historical nest areas by goshawks. Significant differences in the amounts of mid-age closed and late closed forest between historical (pre-1992) and occupied (post-1992) nest areas were not apparent in 1994 at the 52-ha scale (Fig. 1, 2), suggesting that relatively intact forest structure resembling historical conditions contributes to its persistent use by goshawks. However, there was a slight significant difference at the 170-ha scale for late closed and mid closed + late closed habitat. We could not predict the response of goshawks to limited alterations of habitat (e.g., thinning, light selection harvest). However, tree harvest prescriptions that create large areas with sparse cover are potentially detri-

mental to nest area occupancy in our study area, especially if the percent of open canopy forest (i.e., very early, early open, mid open, late open) is >34% (mean) of the 52-ha scale or >44% (mean) of the 170-ha scale (Fig. 2).

Management Implications. Our results showed that the presence of late and mid-aged closed forest (combined, 60% and 48% within the 12-ha and 52-ha scale, respectively) were important to the continued use of historical nest areas by goshawks. We recommend a no-harvest zone within the 12-ha around nest sites and discourage further cutting of large trees within the 52 ha. These recommendations would help to preserve stand integrity, maintain closed canopies, promote connectivity to alternative nest stands, and maximize conditions for breeding goshawk pairs to persist. Retaining existing mid-aged closed and late closed forest structure to levels of >50% at the 52-ha scale and >40% within the 170-ha scale, as well as managing to promote this structure in the future, would also likely benefit goshawks. Based on our results, we also recommend that about 10–20% of the surrounding forest structure outside the nest site be in very early or early open categories with the lesser amounts in the smaller scales (12 and 24 ha; Fig. 1). Management within the 170-ha scale should be limited to light thinning or carefully prescribed burning of overstocked stands outside of the breeding season (October–February) to promote mature, uneven-aged stand development. This could also improve foraging opportunities for goshawks by removing some of the dense understory of shade tolerant conifers.

Finally, logistic regression analyses suggest that habitat alteration that reduces the proportion of mature closed-canopy forest, and which is subsequently replaced by early successional forest, reduces the probability of an area as a potential nesting habitat for breeding goshawks, supporting McCarthy et al. (1989). More severe alterations (clearcuts and moderately high alteration, partial removal of stands resulting in <50% canopy closure) increase the likelihood of goshawks not re-occupying areas due to deterioration in the quality of potential nest-areas.

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MONITORING RESULTS OF NORTHERN GOSHAWK NESTING AREAS IN THE GREATER YELLOWSTONE ECOSYSTEM: IS DECLINE IN OCCUPANCY RELATED TO HABITAT CHANGE?

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ABSTRACT.—I monitored a subset of Northern Goshawk (*Accipiter gentilis*) nesting areas on the Targhee portion of the Caribou-Targhee National Forest in eastern Idaho and western Wyoming from 1998–2002 (recent period) to provide occupancy and productivity data for U.S. Forest Service monitoring requirements. A total of 16 randomly-selected nesting areas, half in undisturbed and half in timber-sale project areas, were surveyed each year. Occupancy in 1998–2002 averaged 34%, which was significantly lower than the 61% measured at these nesting areas from 1992–95 (baseline period) using similar survey methods and effort. Productivity of successful nests was similar between the two periods. I used the dawn vocalization survey method in 2001–02, in addition to standard broadcast survey methods, to determine if low occupancy reflected a poor detection rate of pairs that occupied sites, but failed to reproduce. Detection rate of goshawks during the courtship period in these 2 yr averaged less than 50%, indicating that number of pairs reoccupying known nesting areas surveyed was low. I found no relation between weather factors and lower occupancy. Occupancy at nesting areas located in past timber-harvest areas in the recent period was significantly lower compared to those in less disturbed habitat (22% occupancy versus 45%, respectively) suggesting that occupancy may be influenced by the long-term effects of timber-management practices. Whether the observed decline during the recent period reflects spatial shifts of nesting pairs, short-term demographic responses to variation in weather or prey, or longer-term responses to changes in forest structure and age resulting from timber-management activities, cannot be determined using the current monitoring program. Long-term monitoring of study areas in the western United States, based on statistically valid study designs and adequate sample size, is needed to understand if the apparent decline in goshawk occupancy reported here and in other recent studies has serious implications for conservation of this species.

KEY WORDS: *Northern Goshawk; Accipiter gentilis; nest-site occupancy; raptor monitoring; survey techniques; forest management.*

RESULTADOS DEL MONITOREO DE ÁREAS DE NIDIFICACIÓN DE *ACCIPITER GENTILIS* EN EL AMPLIO ECOSISTEMA DE YELLOWSTONE: ¿ESTA RELACIONADA LA DISMINUCIÓN EN LA OCUPACIÓN CON EL CAMBIO DEL HÁBITAT?

RESUMEN.—Evalué un conjunto de áreas de nidificación de *Accipiter gentilis* en la porción Targhee del Bosque Nacional de Caribou-Targhee en el este de Idaho y oeste de Wyoming desde 1998 hasta 2002 (período actual) para proveer datos de ocupación y productividad para los requerimientos de evaluación del Servicio Forestal. Un total de 16 áreas de nidificación seleccionadas al azar fueron evaluadas cada año (la mitad en áreas no perturbadas y la mitad en áreas de proyectos de venta de madera). La ocupación promedio durante el período actual fue de un 34%, lo cual fue significativamente menor que el 61% medido en áreas de nidificación desde 1992 hasta 1995 (período de línea de base) usando métodos y esfuerzos de muestreo similares. La productividad de los nidos exitosos fue similar entre los dos períodos. Realicé muestreos de vocalizaciones durante el amanecer en 2001 y 2002, además de otros métodos estándar de reproducción de grabaciones, para determinar si la baja ocupación reflejaba una tasa de detección baja de las parejas que ocupaban los sitios pero que no se reproducían. La tasa de detección de *A. gentilis* durante el período de cortejo en estos dos años fue en promedio menos del 50%, indicando que el número de parejas que ocuparon nuevamente las áreas conocidas de nidificación fue bajo. No encontré una relación entre los factores climáticos y una baja ocupación de individuos. La ocupación durante el período actual en las áreas de nidificación en las que se cosechó madera en el pasado fue significativamente menor comparada con la de ambientes menos perturbados (22% de

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presencia comparado con 45%, respectivamente), sugiriendo que la ocupación podría estar asociada con los efectos de largo plazo de las prácticas de manejo forestal. Usando el plan actual de evaluación, no es posible determinar si la disminución observada durante el período actual refleja desplazamientos espaciales de parejas nidificantes, respuestas demográficas de corto plazo a la variación en el clima o las presas, o respuestas de largo plazo a los cambios en la estructura del bosque y en las clases de edad resultantes de las actividades de manejo forestal. Es necesaria una evaluación a largo plazo de las áreas de estudio en el oeste de los Estados Unidos, basada en estudios con diseños estadísticamente válidos y tamaños de muestreo adecuados, para entender si la disminución aparente en la ocupación de *A. gentilis* presentada aquí y en otros estudios recientes tiene implicancias serias para la conservación de esta especie.

[Traducción del Equipo Editorial]

Concern over potential effects of forest management on Northern Goshawk (*Accipiter gentilis*) populations nesting in western North America has stimulated research on this species since the early 1970s (Squires and Reynolds 1997). The U.S. Forest Service (USFS) controls a large proportion of forested lands in the western United States, and how forest habitat is managed on these lands has been a primary focus of past goshawk research (Reynolds 1983, Crocker-Bedford 1990, Reynolds et al. 1992). The goshawk is classified as a Sensitive Species and a Management Indicator Species for forested habitats on the Caribou-Targhee National Forest (CTNF) where this study was conducted (USDA 1997a). The USFS is required to monitor goshawk population trend and its relationship to habitat change for designated Management Indicator Species by federal regulations resulting from implementation of the National Forest Management Act of 1982.

Little information existed on goshawk nesting ecology or habitat on the CTNF prior to the 1990s. From 1989–95, I conducted surveys and collected data on demographic and habitat parameters at four historic and 27 occupied nesting areas located in a variety of habitats and management areas across the forest (Patla 1997). In 1997, the CTNF adopted a revised Land Management Plan (LMP) that required monitoring a minimum of 15 randomly-selected nesting areas for adult occupancy each year as an indicator of population trend (USDA 1997b). I conducted these surveys annually for occupancy and productivity from 1998–2002. To provide some insight on potential associations between timber harvest and resultant habitat change on goshawk demographics, I selected 16 nesting areas each year: half located within past timber-sale project areas and half from relatively undisturbed areas.

The objectives of this study were: (1) to compare

demographic data collected from 1998–2002 (recent period) to comparable data collected during a baseline-study period from 1989–95, as an indication of population trend of known nesting areas, (2) to compare demographic data collected at nesting areas in relatively undisturbed habitat to those in timber-harvest management areas to examine if goshawk occupancy patterns changed related to timber-harvest activities, (3) to provide information on survey methods and results including a description of a dawn-vocalization survey, and (4) to discuss implications of this study and the need to improve monitoring efforts in study areas in the Intermountain West.

STUDY AREA

The Targhee portion of the CTNF contains ca. 728 000 ha in eastern Idaho and western Wyoming and comprises the western portion of the Greater Yellowstone Ecosystem (GYE) as described by Clark and Zaunbrecher (1987; Fig. 1). Most of the CTNF falls within the Middle Rocky Mountain physiographic province except for a small portion, which is included in the Northern Rocky Mountain Province (Steele et al. 1983). Elevations range from 1585–3470 m. The climate is characterized by long, cold winters with heavy snowfall and mild, dry summers. Mean temperatures are -8° and 18° C for January and July, respectively, and total annual precipitation ranges between 61 and 102 cm (Patla 1997).

Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) and lodgepole pine (*Pinus contorta*) are the most common conifer species within the montane zone, between 1800–2500 m (Habeck 1994), and are the primary commercial tree species harvested on the forest. The dominant cover type at 31 goshawk nesting areas within a radius of 2428 ha centered at known nest trees was Douglas-fir ($N = 14$), mixed conifer ($N = 9$), and lodgepole pine ($N = 8$; Patla 1997). I found the majority of goshawk nests ($N = 49$) in mature Douglas-fir (78%) and lodgepole pine (8%) trees. Mean age of Douglas-fir and lodgepole pine trees used for nesting was 143 yr and 96 yr, respectively.

The CTNF initiated a commercial timber sale program in the early 1960s, and an estimated 1935 million board feet (MBF) of mature timber was harvested from 1963–2001 (Fig. 2; M. Jenkins, CTNF Silviculturist, unpubl. data). The mean annual harvest was 62.0 MBF (1963–92)

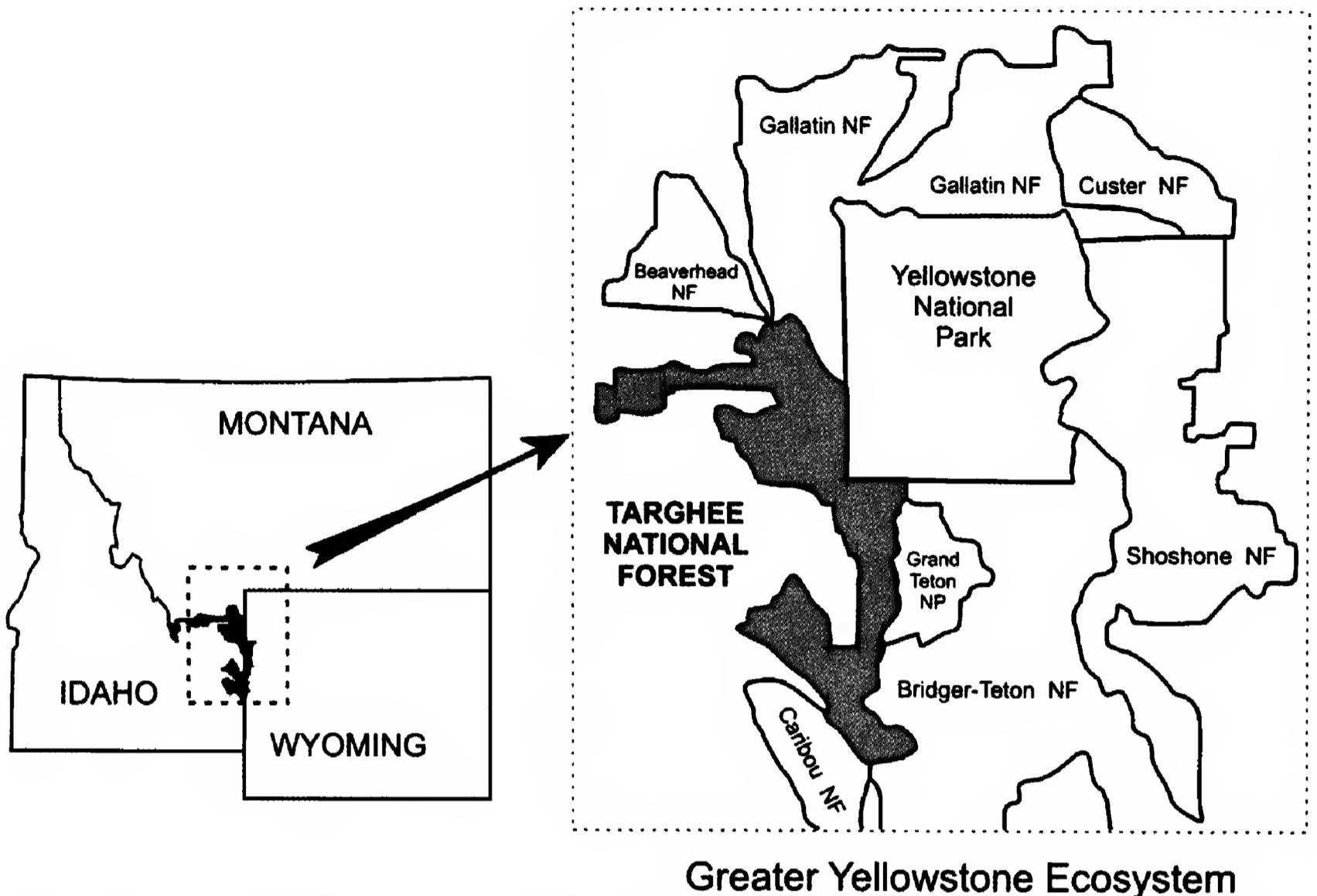


Figure 1. Location of the study area of the Caribou-Targhee National Forest in the Greater Yellowstone Ecosystem in relation to adjacent national forests and parks.

but dropped to 8.2 MBF in recent years (1993–2001). Harvest methods included clear-cutting of lodgepole pine and seed tree or shelterwood cuts of Douglas-fir (Patla 1997). No large-scale timber harvesting projects occurred in the vicinity of known goshawk nesting areas during the current study period.

The revised 1997 CTNF Land Management Plan manages goshawk nesting habitat by specifying the level, type, and timing of management activities that can be conducted at different spatial areas surrounding historical and current nesting areas (USDA 1997b). Prior to the late 1990s, a few occupied goshawk nests found in timber sale units were protected by creation of small buffers (a few trees up to 4 ha; Patla 1997). The majority of harvesting occurred on the CTNF prior to the implementation of goshawk monitoring protocols.

METHODS

Sampling Unit and Scheme. The sampling unit monitored in during the recent period, 1998–2002, was the *nesting area* which included all known nests used by a pair of goshawks and the surrounding area of 1.6 km radius measured from a centroid based on known nest locations (Woodbridge and Detrich 1994, Siders and Kennedy 1996). The size of the defined nesting area (2428 ha) was based on known nearest-neighbor distance data and

territory spacing measured in this study area and others in the western United States and should be sufficient to distinguish between nesting pairs (Reynolds et. al. 1994, Woodbridge and Detrich 1994, Patla 1997).

I monitored 16 nesting areas each year, randomly selected from a master list of 34, that had been occupied by a pair of goshawks at least once since 1989. I excluded from the selection process a few nesting areas in difficult to access locations, and also some historical nesting areas occupied prior to 1989 in which harvesting had subsequently eliminated known nest stands, and where I had found no evidence of goshawk use during the baseline study (1989–95). Prior to selecting monitoring sites, I classified the 34 nesting areas into one of two categories: (1) undisturbed sites located outside of the boundaries of timber-management project areas ($N = 15$) with little or no harvesting within the defined nesting area, or (2) timber-harvest sites ($N = 19$). Eight nesting areas from each category were monitored each year 1998–2002.

I included in the timber-harvest category all goshawk nesting areas with nest sites that fell within the boundaries of past timber sale projects. Thus, timber-harvest sites included a range of disturbance conditions. I did not quantify differences between undisturbed and timber-harvest sites as a detailed vegetation analysis of nesting areas was beyond the scope of the current study.

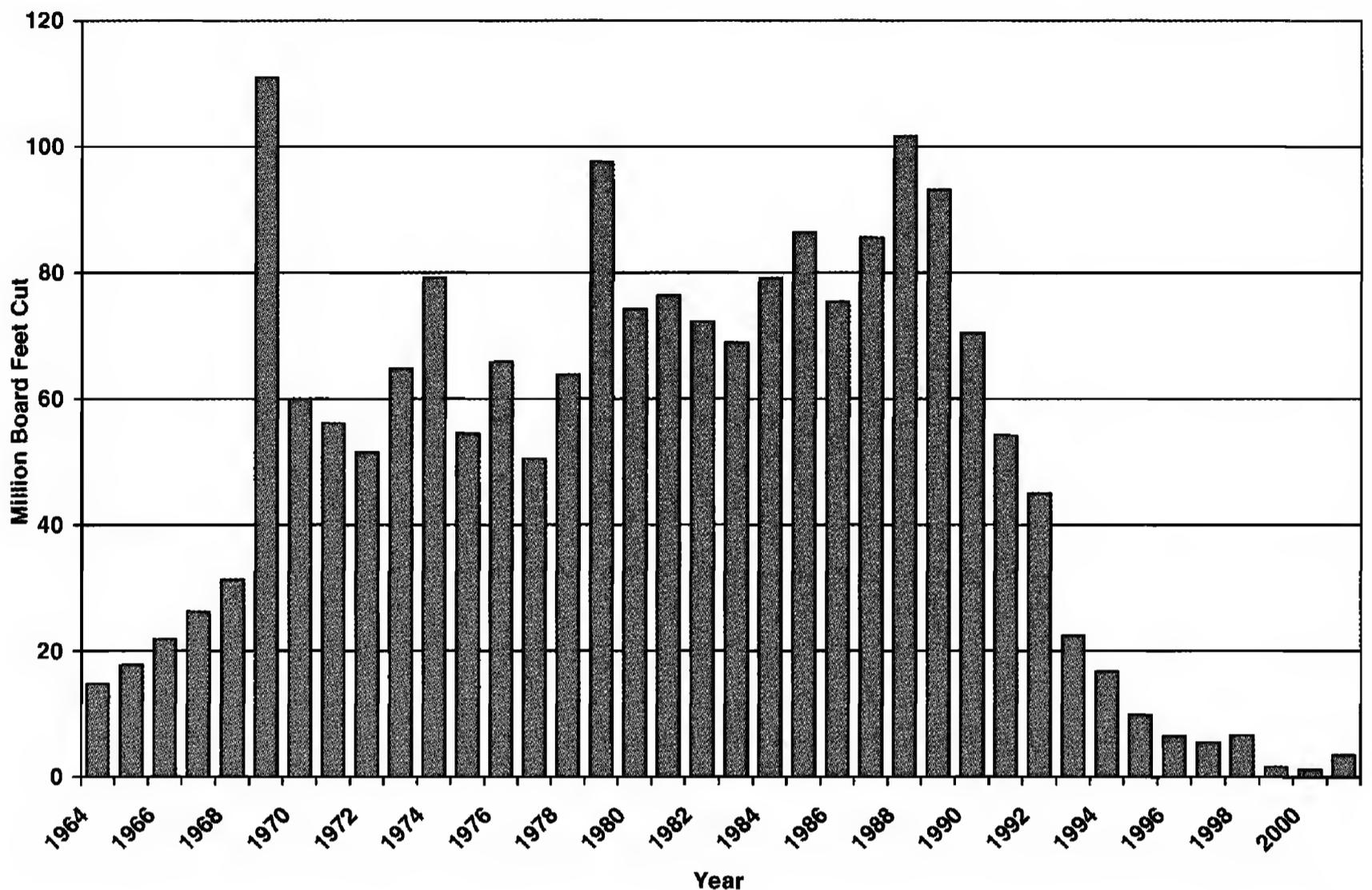


Figure 2. Timber harvest activity on the Targhee section of the Caribou-Targhee National Forest showing volume cut in million board feet per year, 1964–2002. Northern Goshawk monitoring was initiated in 1989.

Based on previous analysis of ten nesting areas found in timber-sale project areas and subsequently harvested between 1985–92, harvesting resulted in a reduction in mature forest cover within the defined nesting area (Patla 1997). Prior to harvest, mature forest habitat averaged 80% (range = 63–95%) within the nesting area compared to 61% (range = 51–80%) post-harvest. Reduction of forest habitat was greatest in the center of the nesting area (see Patla 1997).

To compare monitoring results from the recent period to the baseline period, I first removed data for baseline sites not surveyed at the same spatial scale using the broadcast survey method (see Patla 1997 for description of baseline survey methods). I then made a random selection of 16 sites from those years, 1992–95, for which I had a sample pool greater than 16 that met sampling criteria. I did not include results from 1990–91 due to inadequate number of nesting areas and from 1996–97 because I did not monitor nesting goshawks during these years.

Monitoring Terms. I considered a nesting area occupied if: (1) a pair was observed vocalizing, copulating, or nest building in the vicinity of known nests, or a single adult was heard vocalizing in the vicinity of a known nest tree during the pre-nesting period on more than one day (mid-March–early May), (2) a single adult or pair defended a nest site during the incubation/nestling period, or evidence of nest building or egg laying was confirmed

(late April–early June), or (3) young of the year were found during the nestling (June–mid-July) or fledgling periods (July–mid-August; Postupalsky 1973, Steenhof 1987, Woodbridge and Detrich 1994). I classified a nesting area as not occupied if a single adult was heard making a few calls on only one day during the courtship period, or if an adult was seen on a single occasion later in the season, and no additional signs of goshawk presence were detected within the 1.6-km radius survey area. I classified a pair as having laid eggs and attempted to nest when an adult was found incubating or young were observed in the nest (Postupalsky 1973). Nests were classified as successful if at least one fledgling or fully-feathered nestling (ca. 5-wk post hatching) was observed. Each year that a nesting area was monitored was considered a territory year for calculating occupancy rates (Woodbridge and Detrich 1994).

Survey Methods. I based timing of surveys in the recent period on nesting chronology calculated from 37 successful nest attempts, 1989–94 (Patla 1997). I used similar survey methods during both time periods. The mean onset of incubation was 5 May (range = 20 April–20 May), mean hatching date was 6 June (range = 22 May–June 21), and the mean fledge date was 15 July (range = 1 July–3 August).

All known nest trees and stands were checked visually in April or May for goshawk activity (e.g., fecal deposits, molted feathers, conifer sprigs on nests). If pairs were

not detected, standardized broadcast calling surveys (Kennedy and Stahlecker 1993, Joy et al. 1994) were conducted in forest habitat within a 0.8-km radius of the last used nest during the nestling period (early June–mid-July). Survey effort was expanded in the fledgling period (mid-July–end of August), if no detections were obtained on earlier surveys, to cover a 1.6-km radius area based on a centroid of known nests. Transect lines were 260 m apart, and calling stations ranged from 150–300 m, depending upon terrain and density of forest cover. Surveys were not conducted on days when wind or rain interfered with the ability to transmit calls or hear detections. Occupied nests were monitored every 2 wk to determine number of young and approximate fledging date.

In 2001 and 2002, in addition to broadcast surveys during the nestling and fledgling periods, I surveyed all selected nesting areas using the dawn vocalization survey method to increase the likelihood of detecting pairs that abandoned the nesting effort early in the season, prior to egg laying or incubation (Penteriani 1999, Dewey et al. 2003). Observation points were selected within 100–200 m from the last nest tree occupied, or centered between clusters of alternate nest trees located within a few hundred meters of each other. At nesting areas with nests located >200 m apart, either two observers stationed within 100–200 m of known nests were used, or a single observer completed surveys on different days. Observation periods lasted for a minimum of 2 hr starting 30–45 min prior to sunrise and ending 1.5–2 hr after sunrise. If no goshawk activity was detected during the initial survey, follow-up surveys were conducted 1–3 wk later, if possible.

Statistical Analysis. To compare demographic results between the baseline and recent monitoring periods, and undisturbed and timber harvest nesting areas in the recent monitoring period, I treated the 16 nesting areas selected each year as independent samples.

For most statistical analyses, I applied a multi-response permutation process (MRPP) that is analogous to one-way analysis of variance (or *t*-test), using *Blossom* software (Cade and Richards 2001). MRPP statistical procedures have no distribution assumptions and work well for ecological data with small sample sizes that lack normal distribution even after data transformations (Cade and Richards 2001). I used the chi-square contingency test to compare number of occupied nesting areas in undisturbed and timber sale areas in the recent period. Significance level for all tests was $P = 0.05$.

Analysis of Weather Parameters. Weather factors have been shown to influence occupancy of goshawk nests (Kostrzewa and Kostrzewa 1991, Patla 1997). To analyze potential effects of drought, I compared total annual precipitation between the baseline and recent periods including the year prior to each defined time segment based on precipitation measured at Driggs, ID (Climate Station No. 2676, Teton County, elevation 1866 m) near the center of the study area (Idaho State Climate Services 2002). I also compared snow water equivalents (SWE) in March between the baseline and recent periods (Pine Creek Pass, Climate Snow Station No. 6720, Teton County, elevation 2049 m) (Idaho State Climate Services 2002). SWE is computed from snow density to determine percent water content in the snow pack.

RESULTS

Survey Effort. Eighty territory-year checks were completed (16 nesting areas monitored/yr) during the current monitoring period. Thirty of the 34 nesting areas (88%) on the master list were monitored at least once. Sampling frequency ranged from 0–5 yr ($\bar{x} = 2.4$ yr) for individual nesting areas.

Observers visited nesting areas on average 5.7 ± 0.87 (SD) times per breeding season. At nesting areas where no occupied nests or young were detected, observer effort averaged 64 ± 18 (SD) calling stations, and 15.9 ± 7.9 hr/territory in suitable habitat. Similar effort was expended during 1992–95 with calling stations played within a 1.6-km radius at similar intervals using the same protocol.

Occupancy and Productivity. The mean occupancy rate in the recent period was 34% and was significantly lower compared to the baseline period (61%; MRPP: $P = 0.031$; Table 1). Occupancy rate was highest in 1992 and then declined in subsequent years (Table 1, Fig. 3).

In the current monitoring period, 20% of nesting areas had successful nests and produced a total of 35 young (Table 1). Nest success and total number of young produced was significantly higher (MRPP: $P = 0.003$ and $P = 0.004$) during 1992–95 (Table 1). However, mean number of young per nesting pair and per successful nest was nearly identical between the two study periods (Table 1).

Weather Analysis. I found no significant difference in two weather factors analyzed that might have influenced comparative occupancy rates. Mean annual precipitation was similar between the 1992–95 period (30.9 ± 3.5 cm) and recent period (1996–2002; 36.6 ± 7.1 cm; MRPP, $P = 0.109$). March SWE was also similar: 32% in 1992–95 compared to 33% in 1996–2002 period (MRPP, $P = 0.928$).

Undisturbed Versus Timber-harvest Nesting Areas. In the recent period (1998–2002), a significantly greater number of undisturbed nesting areas ($18/40 = 45 \pm 14\%$) compared to timber-harvest nesting areas ($9/40 = 22.5 \pm 10\%$) were occupied (χ^2 , $P = 0.033$; Table 2). Pairs in undisturbed nesting areas produced a greater number of young per yr (Table 2, MRPP: $P = 0.027$). The mean number of young produced per nesting pair and per successful territory was similar (Table 2).

Mean occupancy rates during the 1996–2002 monitoring period at both undisturbed (45.0%)

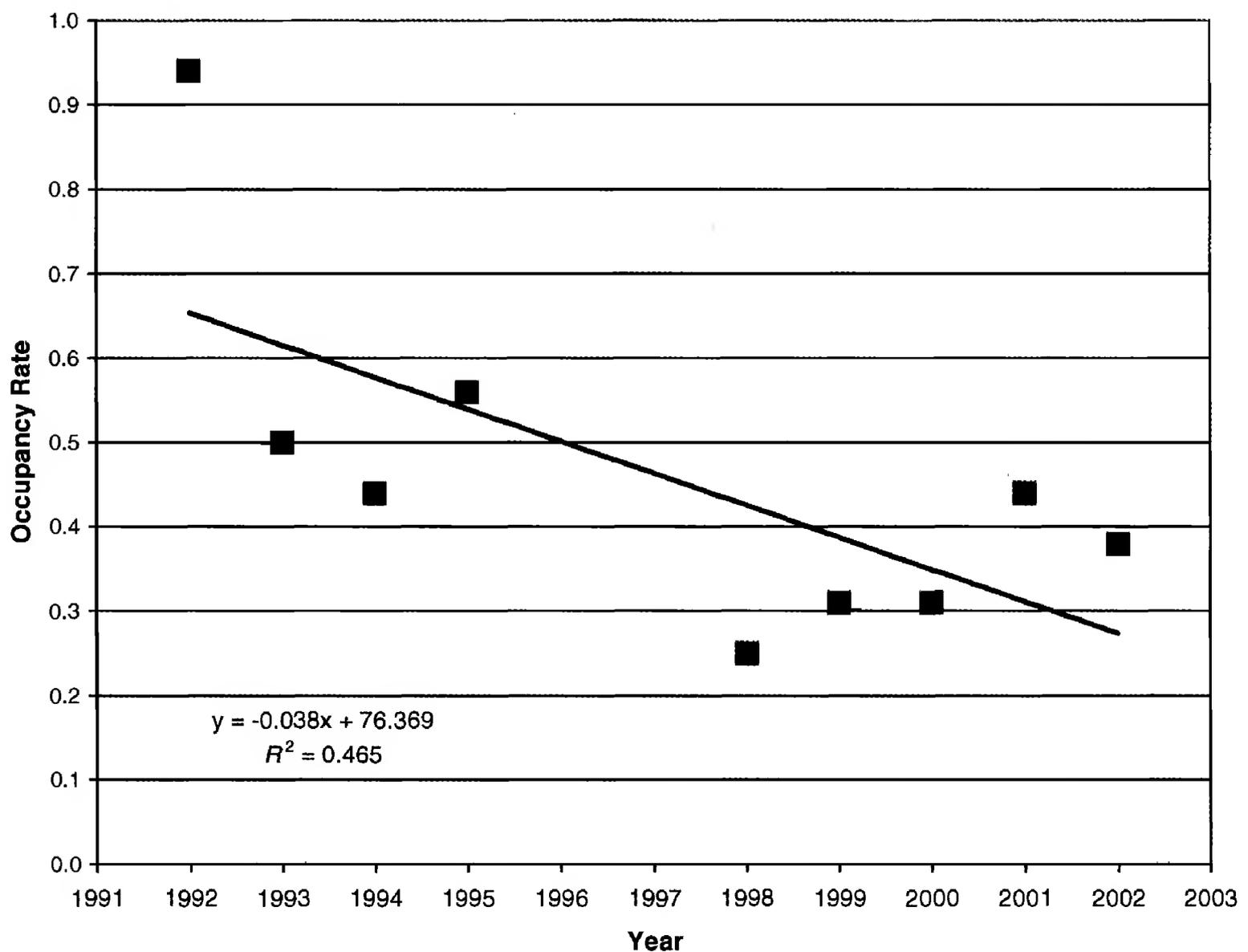


Figure 3. Regression analysis of occupancy rate 1992–2002 of Northern Goshawk nesting areas on the Caribou-Targhee National Forest. Data not available for years 1996 and 1997.

and timber-harvest nesting areas (22.5%) were lower compared to the 61% mean occupancy rate measured 1992–95 (Table 1). The observed decline in the recent period was over twice as high in timber-harvest nesting areas (63%) compared to undisturbed nesting areas (26%).

Use and Spacing of Alternate Nest Trees. Of 18 nest attempts documented from 1996–2002, only three (17%) occurred in previously identified nest trees. Eighty percent ($N = 12$) of new alternate nest trees found were located within 800 m of the last nest tree used. Mean distance between alternate nest trees used within a nesting area was 572 ± 352 m, (range = 77–1381 m, $N = 15$). I found no relationship in the distance between nest trees used and the span of years since goshawks had been documented nesting in a particular area (Pearson correlation, $r = 0.009$, $P = 0.975$). Nest trees tended to be clustered within the defined nesting areas.

Goshawk Detections and the Dawn Survey Meth-

od. The majority of initial detections confirming occupancy of nesting areas (63%, 17/27) occurred during the courtship period compared to 26% in the nestling ($N = 7$) and 11% in the fledgling periods ($N = 3$). Most detections in the courtship period (71%) were obtained using the dawn vocalization survey method in 2001–02, which resulted in detections of pairs or single adults at 15 sites (Table 3).

Number of dawn surveys completed averaged 3.0 per nesting area in 2001 (range = 1–5) and 1.9 (range = 1–3) in 2002. During these two years, 92% of all nesting areas confirmed occupied resulted from use of dawn surveys with only one false negative at a site where an occupied nest was found later in the fledgling period 655 m from the last used nest tree. At three sites, detections were documented only on one day, with no other goshawk activity being observed during the remainder of the nesting season. I did not classify these nesting areas as occupied (Table 3) given the brevity of the

Table 2. Comparison of monitoring data from randomly-selected Northern Goshawk nesting areas in undisturbed and past timber-harvest areas, Caribou-Targhee National Forest (1998–2002).

YEAR	OCCUPIED NESTING AREA	NESTING PAIRS	SUCCESSFUL PAIRS	TOTAL NUMBER OF YOUNG	YOUNG PER OCCUPIED NEST AREA	YOUNG PER NESTING PAIR	YOUNG PER SUCCESSFUL NEST AREA
Undisturbed (<i>N</i> = 8/yr)							
1998	3	3	3	7	2.33	2.33	2.33
1999	2	0	0	0	0.00	0.00	0.00
2000	4	3	3	7	1.75	2.33	2.33
2001	5	3	3	8	1.60	2.67	2.67
2002	4	2	2	4	1.00	2.00	2.00
Mean	3.6	2.6	2.2	5.2	1.34	1.87	1.87
(SD)	(1.1)	(0.5)	(1.3)	(3.3)	(0.9)	(1.1)	(1.1)
Timber-harvest (<i>N</i> = 8/yr)							
1998	1	1	1	3	3.00	3.00	3.00
1999	3	3	1	2	0.67	0.67	2.00
2000	1	1	1	2	2.00	2.00	2.00
2001	2	1	1	1	0.50	1.00	1.00
2002	2	1	1	1	0.50	1.00	1.00
Mean	1.8	1.4	1.0	1.8	1.33	1.53	1.80
(SD)	(0.8)	(0.9)	(0.0)	(0.8)	(1.10)	(1.00)	(0.80)

vocalizations and lack of other evidence confirming occupancy. Without use of the dawn survey method, 43% of nesting areas in 2001 (*N* = 3) and 33% in 2002 (*N* = 2) would not have been classified as occupied. However, even with use of courtship surveys, occupancy of nesting areas during these two years fell below the 61% average from 1992–95 (Table 1). Occupancy in 2001, the highest occupancy year during 1996–2002, was the same (44%) as 1994, the lowest occupancy year from 1992–95. Even if goshawk pairs or individuals were detected during the courtship period, follow-up broadcast calling surveys were required at many sites later in the season to locate an occupied nest tree and determine number of young.

DISCUSSION

Monitoring Effort and Study Design. Monitoring Northern Goshawk nesting populations is challenging given the secretive nature of the species, its use of widely-spaced alternate nests, spatial and temporal variability in numbers of nesting pairs, and density of the mature forest habitat used for nesting (Woodbridge and Detrich 1994, Kennedy 1997, Squires and Reynolds 1997). Comparison of occupancy among studies is also difficult as occupancy estimates appear to be positively correlated with amount of effort expended to determine nesting area status (Kennedy 1997). Multiple visits to nesting areas over the course of a season and broadcast-calling surveys at least up to 1.6-km ra-

Table 3. Results of dawn vocalization surveys during March and April at Northern Goshawk nesting areas (*N* = 16/yr) on the Caribou-Targhee National Forest (2001–02).

YEAR	TOTAL NO. SURVEYS	EARLIEST DETECTION DATE	LATEST DETECTION DATE	NO. DETECTIONS ^a (OCCUPANCY)	NO. DETECTIONS SINGLE BIRD ^b	ERROR RATE ^c
2001	48	31 Mar	2 May	7 (0.44)	1	0.00
2002	30	26 Mar	20 April	5 (0.31)	2	0.06
Total	78	26 Mar	2 May	12 (0.38)	3	0.03

^a Number of territories classified as occupied where a pair was detected or a single adult was heard or seen on more than 1 day

^b Number of territories where detections consisted only of a few “kek” calls heard briefly one day.

^c Error rate defined as the proportion of territories misclassified as unoccupied and later confirmed as occupied.

dius around nest sites are required to monitor previously identified nesting areas effectively (Reynolds et al. 1994, Woodbridge and Detrich 1994, Finn et al. 2002).

The amount of survey effort expended per nesting area (mean number of visits per site and area surveyed) for the current goshawk monitoring period matches or exceeds that reported in other long-term goshawk studies (Kennedy 1997, Boyce et al. 2005, Reynolds et al. 2005). The total number of nesting areas monitored per year was relatively low, however, and included only a subset of known areas scattered throughout the CTNF.

The goshawk-monitoring plan for the CTNF is based on the assumption that goshawks exhibit territorial behavior and that "a stable population should revolve around some average occupancy rate" of known nesting areas (USDA 1997b). The plan assumes that the occupancy measured at a subset of known nesting areas can be used as an index of population stability or decrease for the species. The plan states: "A sustained downward trend of adult occupancy for at least four years may indicate a need for action" (USDA 1997b). There are no specific requirements that monitoring protocols developed for land management plans follow statistically rigorous study design criteria. The approach to monitoring on a forest level tends to be pragmatic and based on limited funding availability. Whether the study design used on the CTNF is adequate as an index for local population trend requires further statistical evaluation. For this analysis, I assumed that occupancy results apply to the target population of known nesting areas monitored and may not reflect forest-wide population trends.

Decline in Occupancy. Results of this study indicate that occupancy of known goshawk nesting areas on the CTNF was significantly higher in the early 1990s compared to later in the decade with no rebound evident through the 2002 nesting season (Fig. 3). Results are consistent with those reported from other goshawk study areas suggesting that there may have been a decline in some goshawk populations across the Intermountain West during the late 1990s (Fairhurst and Bechard 2005, Reynolds et al. 2005).

Results from dawn vocalization surveys on the CTNF indicated that the lower occupancy measured in the recent period likely did not result from failure to detect pairs that occupied sites but did not reproduce (Woodbridge and Hargis 2005).

However, it is possible, given the study design and low sample number that spatial shifts by pairs outside of areas surveyed may have confounded results. Studies of marked goshawks have shown that shifts between nesting areas by individual breeding adults occur to some extent and that some ephemeral territories are occupied only occasionally (Woodbridge and Detrich 1994, Reynolds and Joy 1998, Reynolds et al. 2005). If a proportion of pairs at study sites on the CTNF shifted each year between sites, or used certain sites only occasionally, occupancy results could be misleading.

Weather conditions can influence goshawk occupancy, but I did not find a significant difference between the recent and baseline periods in relation to total annual precipitation and snow water equivalents. The latter factor was negatively related to occupancy in the baseline study period (Patla 1997). There may be other local or regional weather/climatic trends not analyzed in this study that were influencing occupancy rates during the study period.

The amount and structure of forest habitat surrounding nest sites has been related to occupancy of historical goshawk nest sites in the western United States (Crocker-Bedford 1990, Woodbridge and Detrich 1994, Desimone 1997, Finn et al. 2002, McGrath et al. 2003). During the baseline study period, I also found an association between the proportion of mature forest habitat and occupancy rate of nesting areas on the CTNF. High occupancy nest clusters in timber harvest areas, defined as those with $\geq 50\%$ occupancy rate ($N = 16$, \bar{x} occupancy = 81%), contained a significantly greater proportion of mature forest cover and less young forest/seedling cover within a 240 ha area surrounding known nests compared to low occupancy nest clusters ($N = 6$, occupancy = 37%; Patla 1997).

In the recent study period, occupancy of nesting areas on the CTNF in timber-harvest areas showed a greater proportional decline than those in less disturbed habitat, but vegetation differences between these categories were not quantified. There appears to be an association between reduction in mature forest habitat within nesting areas on the CTNF as a result of harvesting and decline in occupancy. This hypothesis requires further investigation of vegetation conditions at nest areas in relation to goshawk occupancy patterns.

In contrast to occupancy data, I found no difference in productivity of nesting goshawk pairs be-

tween the baseline and recent periods or between timber harvest and undisturbed sites in the recent period. Pairs that nested successfully produced similar number of young supporting the suggestion by McClaren et al. (2002) that number of young fledged may not be useful for assessing spatial variability in goshawk nest habitat quality.

Whether the decline in occupancy measured at known nesting areas on the CTNF reflects a response to decline in quality of primary habitat, a shorter-term response to variation in weather and prey, or sampling error due to shifting of pairs outside of surveyed sites cannot be determined using the current monitoring study plan employed by the U.S. Forest Service. However, data from the CTNF reflects a pattern documented at other locations in the western U.S. that indicated a peak in the number of occupied goshawk nest sites in 1992 and a subsequent decline. It remains unknown if goshawk populations exhibit periodic cyclical highs in the western U.S. similar to those documented farther north (Doyle and Smith 2001) or if trend data indicates the onset of a more serious, longer-term decline related to habitat or climatic change. Because many goshawk studies and monitoring projects were initiated during or after the early 1990s, baseline data prior to 1992 are lacking from most areas. How to interpret recent trends since 1992 remains challenging.

Results of the current study emphasize the need to develop more comprehensive, well-funded, and statistically valid monitoring plans for goshawks that can track population trend, reproductive success, and habitat relationships in a timely and meaningful way. However, declines at known nesting areas measured since 1992 suggest that a conservative approach for managing remaining mature/old growth forests would be most prudent until our knowledge and understanding concerning the relationship between goshawk demographic parameters and loss of mature forest habitat increases (DeStefano 1998).

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EFFECTS OF TIMBER HARVESTING NEAR NEST SITES ON THE REPRODUCTIVE SUCCESS OF NORTHERN GOSHAWKS (*ACCIPITER GENTILIS*)

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ABSTRACT.—We assessed the effects of timber harvesting near nest sites on the reproductive success of the Northern Goshawk (*Accipiter gentilis*). Harvest trials were implemented at 27 of 79 known nest areas, and the median post-treatment monitoring period was 3 yr (range = 1–7). We used a mean nest area size of 24 ha, based on the average number and spacing of nests within nest areas, to assess the impact of harvesting. Harvesting trials consisted of clearcutting, with the amount of nest area harvested ranging from 5–95%. From 1996–2002, we found no significant difference in nest area reoccupation frequencies or fledging rates of goshawks between treatment areas and control areas ($P > 0.10$). Even treatment areas with >50% of the nest-area stand removed ($N = 7$) did not exhibit reduced reoccupation or fledging rates. These results are preliminary, pending longer post-treatment monitoring to address high annual variation and a potential lag effect that may be exhibited by the goshawks. If these results are consistent over a longer period, they may support de-emphasis of management and research effort at the nest-area scale and greater emphasis at the territory and landscape scales to examine correlations between timber harvesting and territory abandonment and population declines reported in other studies.

KEY WORDS: *Northern Goshawk; Accipiter gentilis; timber harvesting; nest area; reproductive success; adaptive management; British Columbia.*

EFFECTO DE LA COSECHA DE MADERA CERCA DE LOS SITIOS DE NIDIFICACIÓN SOBRE EL ÉXITO REPRODUCTIVO DE *ACCIPITER GENTILIS*

RESUMEN.—Determinamos el efecto de la cosecha de madera realizada cerca de los nidos sobre el éxito reproductivo de *Accipiter gentilis*. Los tratamientos de cosecha fueron implementados en 27 de 79 áreas de nidificación conocidas, y la mediana del periodo de observación post-tratamiento fue de 3 años (rango = 1–7). Para determinar el impacto de la cosecha de madera, utilizamos un área de nidificación promedio de 24 ha basándonos en el número y espaciado promedio de nidos dentro de las áreas de nidificación. Los tratamientos de cosecha consistieron en tala rasa y variaron entre un 5% y un 95% de área cosechada del área de nidificación. Entre 1996 y 2002, no encontramos diferencias significativas en las frecuencias de reocupación de sitios de nidificación o en las tasas de emplumamiento de los halcones entre las áreas de los tratamientos y las áreas control ($P > 0.10$). Incluso los tratamientos en que se removió >50% del bosque del área de nidificación ($N = 7$) no exhibieron tasas reducidas de re-ocupación o de emplumamiento. Estos resultados son preliminares hasta que se obtengan resultados de un monitoreo post-tratamiento más largo para dar cuenta de la alta variabilidad anual y posibles efectos retardados que puedan estar exhibiendo los halcones. Si estos resultados son constantes a lo largo de un periodo de tiempo mayor, éstos pueden apoyar una disminución del énfasis de los esfuerzos de manejo e investigación a la escala de sitio de nidificación y un aumento del énfasis a las escalas de territorio y de paisaje para examinar las correlaciones entre la cosecha de madera y el abandono de los territorios y disminuciones poblacionales que se han descrito en otros estudios.

The Northern Goshawk (*Accipiter gentilis*) is widely recognized as a species sensitive to timber har-

vest (Squires and Reynolds 1997). In 1995, British Columbia established the Forest Practices Code, which strengthened management requirements for non-timber resources and included a variety of coarse- and fine-filter management strategies for

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wildlife under the Identified Wildlife Management Strategy (IWMS; BC Ministry of Environment and BC Ministry of Forests 1999). The Northern Goshawk was identified as a focal species in the IWMS, and habitat-management guidelines were developed that included protection of nest areas, maintenance of a high proportion of mature and old forest in the post-fledging area, and for the threatened *A. g. laingi*, broad seral stage targets for the foraging area (BC Ministry of Environment and BC Ministry of Forests 1999). However, conflicting policy limited the number of goshawk territories that IWMS guidelines were applied to. For forest managers, the question became whether alternative management strategies that were less conservative than the IWMS guidelines could still maintain goshawk nest-area habitat requirements and reproductive success. We have attempted to answer that question within an adaptive management framework by monitoring the response of goshawk reproductive success to timber-harvesting trials at nest areas.

Few previous studies have monitored the response of goshawks to timber harvest near occupied nest areas within an experimental framework. Crocker-Bedford (1990) measured the effects of timber harvest on goshawk reproduction by examining the success of 16–200 ha reserves in maintaining goshawk occupation in nest areas surrounded by large partial-cut units (1000–5000 ha). Only 25% of 12 treatment territories were reoccupied at least once over a 3-yr period, compared to 79% of 19 control areas that were reoccupied (Crocker-Bedford 1990). Woodbridge and Detrich (1994) observed a correlation between nest area (nest stand cluster) size and occupancy, with occupancy frequencies at stand clusters <20 ha, 40–60 ha, and >60 ha of <50%, 75–80%, and nearly 100%, respectively. In that study, timber harvesting was one factor that affected nest-stand cluster size, but it was not explicitly isolated from other factors potentially affecting stand patterns and sizes. Patla (1997) found that occupancy was higher at nest areas prior to timber harvesting (79%) than after (47%), and that post-harvest areas with >50% occupancy had higher percent mature forest cover than nest areas with <50% occupancy. Penteriani and Faivre (2001) found that goshawk reproductive productivity did not differ between shelterwood harvested and untreated nest stands.

Our study differs from previous work that evaluated the effects of timber management on gos-

hawk nest area reoccupancy and productivity for several reasons: (1) we monitored a larger sample of territories than previously studied (27 treatment areas and 52 controls); (2) our study was replicated in two forest types with ca. equal sample sizes in each area; (3) we examined a range of treatment levels (amount of nest area removed by clearcutting), and were able to control those levels experimentally; and (4) we compared responses pre- and post-treatment, as well as post-treatment responses to controls. Here we summarize the results of this ongoing study from 1996–2002.

STUDY AREA AND METHODS

We replicated this study in two different forest types in west-central British Columbia, Canada, with approximately equal numbers of nest areas in each. The first study area was within the Interior Cedar Hemlock (ICH) and Coastal Western Hemlock (CWH) biogeoclimatic zones (Banner et al. 1993) in the Kispiox Forest District (55°25'N, 127°45'W). This area (ICH/CWH) is along the eastern side of the Coast Mountain Range and consists of mountain ranges bisected by broad glaciated valleys with an elevation range of 200–2500 m. The climate is transitional between cool, wet coastal conditions and drier interior conditions with greater seasonal temperature variation. The mean annual precipitation varies from 600–1200 mm (Banner et al. 1993), with rain occurring on half the days during the goshawk breeding seasons we monitored. Forests within the ICH and CWH are predominantly old growth (>200 yr), coniferous stands dominated by western hemlock (*Tsuga heterophylla*), and included subalpine fir (*Abies lasiocarpa*), western redcedar (*Thuja plicata*), and Roche spruce (*Picea sitchensis* × *glauca*). Zonal ecosystems consist of hemlock forests with moderate-high canopy closure, sparse shrub and herb layers, and a thick feathermoss carpet.

The second study area is 200 km to the southeast in the Sub-Boreal Spruce (SBS) biogeoclimatic zone (Banner et al. 1993) in the Lakes and Morice Forest Districts (N54°25'N, 126°00'W). It occurs on the interior Nechako Plateau, with elevations of 500–1000 m. The climate in the SBS is primarily continental and is characterized by greater seasonal temperature extremes than in the coast mountain range, with cold, snowy winters and relatively warm, moist, short summers. Annual precipitation is 440–650 mm (Banner et al. 1993), with rain occurring on less than 20% of the days during the breeding seasons we monitored. Forests in the SBS have been subject to frequent fires (mean fire interval <150 yr), and zonal sites are frequently dominated by mature seral stands of lodgepole pine (*Pinus contorta*) with subalpine fir, hybrid white spruce (*Picea glauca* × *engelmannii*), and trembling aspen (*Populus tremuloides*). The shrub and forb layers are usually sparse, though variable, and are generally more developed than in the ICH.

In both study areas, ca. 55% of the forested land base is mature forest, 25% is young forest, and 20% is in a shrub/herb stage. Forestry roads and clearcuts are present in all portions of both study areas, and the latter

account for the majority of area in the shrub/herb stage. Minimum goshawk densities of ca. four pairs per 100 km² are similar between the ICH and SBS based on inventory work in core portions of each study area (T. Mahon and F. Doyle unpubl. data). Potential avian competitors for nest sites and habitat occur at low densities and included Red-tailed Hawks (*Buteo jamaicensis*), which are found in open areas, Barred Owls (*Strix varia*), mostly in the ICH, Great Gray Owls (*Strix nebulosa*), mostly in the SBS, and Great Horned Owls (*Bubo virginianus*), which occur within riparian and mixed forest habitats at lower elevations throughout the region.

Nest Area Size and Habitat Characteristics. The estimated size of goshawk nest areas in the literature ranges from 8 ha (Reynolds 1983) to 50 ha (McCarthy et al. 1989). We calculated a theoretical "typical" nest-area size in our study based on the mean number of nest sites and the mean spacing distance among nest sites for 21 nest areas located early in the study and applied a 200 m buffer around the nests. The 200 m buffer was based on observed distance of nest sites from forest edges, concentrated sign (plucking perches, "white wash" [fecal deposits], and roosts), juvenile movements during the early post-fledging period, and nest defense behaviors displayed by adult birds, which are recognized as key features that determine the boundaries of goshawk nest areas (Reynolds et al. 1992, Squires and Reynolds 1997). Using our observed mean of three nests per nest area, mean spacing of 188 m between nest trees, and a 200 m buffer resulted in a nest-area size of 24 ha.

To test the appropriateness of this theoretical nest area size, we overlaid a 24-ha circle on each of the 79 known nest areas in 2002 to assess how many nest sites were encompassed within the 24-ha circular area. On the basis that only 4% of the nest sites fell outside of the 24-ha circles, we accepted that this size was the appropriate size to use.

Nest area stands in the ICH/CWH were dominated by western hemlock and typically had larger diameter and taller trees than in the SBS, which were dominated by lodgepole pine, but otherwise habitat characteristics were similar between study areas. Most nest areas were in mature (>100 yr) or old growth (>240 yr) stands with relatively closed primary canopies (45–65%) and open sub-canopy flyways, on mesic sites. We observed no evidence of nest area selection with respect to slope or aspect in either study area, except for avoidance of very steep slopes (>45%). In most cases, nest areas were located in contiguous mature forest matrix, and in all cases suitable alternative nest area stands were available within 800 m of the original nest area. Forest composition, stand age, stand height, and canopy closure did not differ between treatment and control nest areas within each study area ($P > 0.10$).

Experimental Design. We employed an adaptive management framework in this study to integrate our research into operational timber harvesting and to maximize the utility of research outcomes to forest managers. This approach involved four key steps: (1) defining an area of scientific uncertainty; (2) developing and implementing management trials as real world experiments to test that uncertainty; (3) evaluating the outcomes of the trials; and (4) adjusting management guidelines on the

basis of the knowledge gained (Morrison et al. 1998). The key uncertainty we investigated was how much goshawk nest area habitat can be removed via clearcutting before nest area reoccupation and productivity are impacted.

Design of harvesting trials included operational factors identified by forest licensees, as well as experimental factors associated with our study. In this context, these trials were not tightly controlled experiments because we could not completely control aspects of the timber harvesting relating to pattern and overall size. However, the resultant harvesting trials do provide a range of scenarios with respect to our primary treatment variable (amount of nest area harvested). Timber harvesting consisted of clearcuts with patch retention. Patch retention areas did not have any harvesting within them and were generally located to provide a mature forest buffer (25–200 m) around known goshawk nest trees. Other mature forest patches were occasionally retained in goshawk nest areas, including 20–60 m wide riparian buffers and 0.1–4.0 ha upland "wildlife tree patches." Within the clearcut areas, all merchantable trees were removed and in-block retention, if any, was limited to sporadic deciduous trees, scattered advanced regeneration, and occasional snags that were topped at 2 m. Timber harvesting was conducted outside of the breeding season to minimize the confounding effect of logging disturbance (Toyne 1997).

We quantified two response variables related to reproductive success. Our primary variable was the rate of nest area reoccupation into the incubation period, which represents the evaluation of nest areas by goshawks and their commitment to use them. Importantly, we present reoccupation rates, opposed to occupation rates. This was necessary because we found new nest areas each year and added them to the study. Therefore, the sample of nest areas used to calculate reoccupation rates in year \times is the sample of nest areas that were known at the end of year $\times - 1$.

We tested for overall differences in reoccupation rates between treatments and controls using a chi-square analysis and pooled data from study areas and years. To assess the effect of treatment level (amount of nest area harvested), we also summarized the reoccupation rates separately for treatment areas that had >50% of the nest area stand removed and which we had monitored for at least 2 yr post-treatment.

We also examined nest productivity—the number of fledglings produced per nesting attempt—as a response variable. Nest productivity must be interpreted with caution, because once a commitment is made to nest in an area, overall fledging rates are more likely dependent on breeding season food supply than nest area habitat (Doyle 2000). An exception to this would be if timber harvesting led to higher nestling depredation rates. To address this issue, we evaluated the cause of nestling mortalities whenever possible. Similar to reoccupation rates, mean annual fledging rates were summarized excluding new nest areas found for that year. We tested for overall differences in fledging rates between treatments and controls using a t -test, again pooling data from study areas and years.

Nest-area Monitoring. We used a combination of telemetry and nest area searches at areas without tagged birds

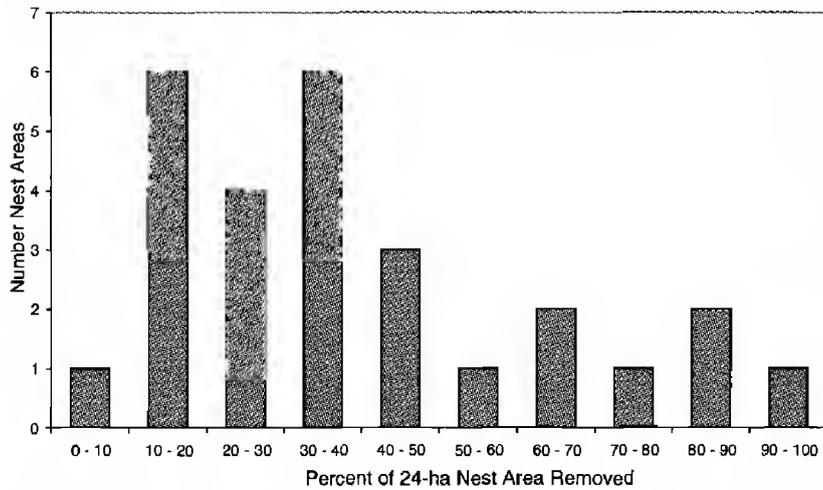


Figure 1. Distribution of treatment levels (amount of nest area clearcut) for harvesting trials at 27 Northern Goshawk nest areas in west-central British Columbia 1996–2002.

to monitor annual reoccupation and fledging rates at treatment and control nest areas. Initially, we attempted to radio-tag an individual at every treatment area and at a subsample of the control areas. However, as the study progressed, we determined that nest-area searches were sufficient to document reoccupation. Due to the extra time and cost associated with radio-tagging, and the potential negative impacts of radio-tagging to goshawks (Reynolds et al. 2004), we reduced our annual sample of nest areas with tagged birds to ca. 10% and only tagged birds at treatment areas. Adult goshawks were captured and tagged during the nestling period and early post-fledging period using box traps baited with Rock Pigeons (*Columba livia*; Kenward and Marcstrom 1983) or mist nets around a tethered pigeon or owl decoy. Tail-mounted radios were used instead of backpacks, so that we did not have to recapture the birds to remove the tags. Tagged birds were monitored the following breeding season using ground-based telemetry tracking to determine their breeding status and location.

For nest areas without tagged birds, we conducted in-

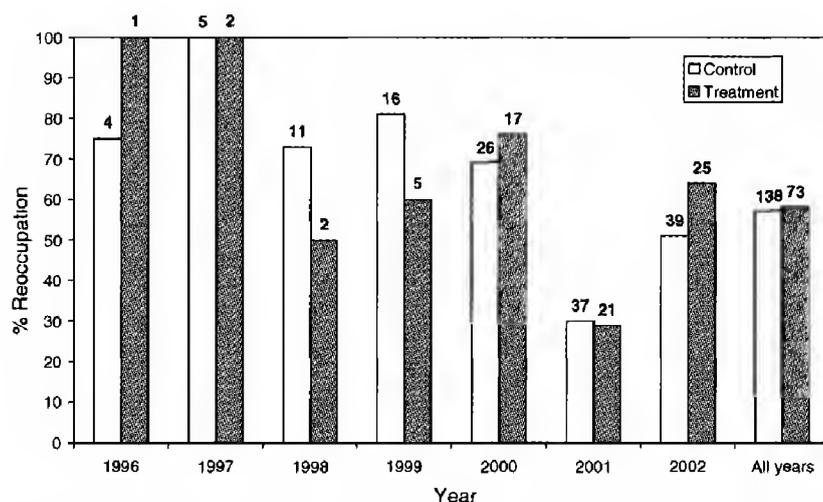


Figure 2. Annual reoccupation rates at Northern Goshawk nest areas at treatment sites, where timber harvest occurred, and control areas in west-central British Columbia, 1996–2002. Values above the bars equal number of nest areas available for reoccupation.

tensive ground searches within ca. 1 km of the original nest area to ascertain the occupancy of each nest area. This involved surveying all known nests within a nest area, and if none of the known nests were occupied, intensively searching for new nests and other signs of use such as presence of goshawks, “white-wash,” and plucking perches. If no occupied nest was found using visual searches, we conducted systematic call playback surveys (Kennedy and Stahlecker 1993) using a 300 × 300 m grid to elicit responses from goshawks in the vicinity. Nest area searching was conducted during the courtship, incubation, and post-fledging periods. All occupied nests were monitored biweekly to determine their success and fledging rates.

RESULTS

Of the 79 nest areas located in the two study areas, harvesting trials were implemented at 27 areas (13 ICH/CWH, 14 SBS). The treatment levels (amount of nest area clearcut) ranged from 5–95% (Fig. 1). The median time since timber harvest at treatment nest areas was 3 yr (range = 1–7).

We found no difference in reoccupation rates of nest areas between treatment and control areas ($\chi^2 = 0.021$, $P = 0.89$). We combined data from the two study areas for analysis because they showed a similar pattern of response with reoccupation rates for treatments and controls of 54% and 53% in the ICH/CWH, and 61% and 63% in the SBS. The total reoccupation rates from 1996–2002 were 58% at treatment areas ($N = 73$ potential breeding attempts) and 57% at controls ($N = 138$; Fig. 2). We found consistent patterns of reoccupation rates between treatment and controls across years, with greater variation among years than between treatments and controls.

Seven nest areas had >50% of the nest area stand removed. Goshawks returned and bred successfully at all seven of these nest areas in at least one year post-treatment. For the years 2000–02 combined (the post-treatment period for these seven treatments), the reoccupation rates were 62% at treatment areas compared to 50% at controls.

The mean number of chicks fledged per nesting attempt did not differ between treatments (1.63 ± 1.05 [SD], $N = 44$) and controls (1.31 ± 1.13 , $N = 73$; $t = 0.306$, $P = 0.77$). The mean nest productivity by study area was 1.54 ± 0.70 ($N = 22$) for treatments and 1.29 ± 1.03 ($N = 35$) for controls in the ICH/CWH and 1.67 ± 1.16 ($N = 22$) for treatments and 1.43 ± 1.06 ($N = 38$) for controls in the SBS.

DISCUSSION

All nest areas we monitored for ≥ 2 yr showed evidence of multiyear use and strong nest-area fi-

delity. Further, occupancy has been maintained at several nest areas where at least one of the original occupants has died or disappeared. This is consistent with other studies that have observed high fidelity even after the nest area is modified (Reynolds 1983, Woodbridge and Detrich 1994, Patla 1997). The implication of this behavior is that fidelity to nest areas may override response to reduced suitability and result in a lag effect before goshawks relocate to more suitable habitat.

Another major implication of the nest-area fidelity exhibited by goshawks relates to forest management. Effectively, nest-area fidelity is so strong in our study areas that nest areas can be considered spatially-fixed resources for forest management purposes. Once a nest area is located and protected, forest managers can proceed with harvesting in other parts of the territory, as estimated by territory spacing data, with low risk of impacting another nest area. Where goshawk nest area protection is a management objective, this provides forest licensees with a strong incentive to locate and to maintain nest areas because it reduces potential constraints within the remainder of the territory. Failing to adequately protect a nest area may result in the goshawks relocating to another stand scheduled for timber harvesting, which was the case with two of three relocations we observed in 2003. Management strategies to maintain alternate nesting habitat, post-fledging area habitat, and suitable foraging habitat would still be desirable at the territory scale, but those strategies are typically more flexible, at least in a spatial context, than protection measures for the nest area.

In addition to nest-area fidelity, inaccuracy in our estimate of nest-area size or variability in sizes could also affect the interpretation of our results. For example, if our estimates were too large, and included area outside of the true nest area, then the actual treatment impact would be less than reported. We estimated the "typical" nest-area size in our study areas based on mean number of nest sites, spacing between nest sites, evidence of occupation, and defensive behavior around nest sites. These characteristics were variable among nest areas, which probably corresponded to different nest-area sizes. We considered estimating the size of each nest area individually, but decided that would be even more problematic and biased than our systematic approach. Because of the uncertainty associated with nest-area size and its relationship to estimated treatment level, we did not focus our

analysis on treatment level beyond two classes: all treatment areas and nest areas where >50% of the stand have been clearcut.

Despite nest-area fidelity by goshawks and potential lag effects, our study supports the findings of other research (Penteriani and Faivre 2001) that indicated goshawks tolerated modification of nest area stands, or relocated to new stands, without decreased reproductive output (assuming that alternative nest area habitat was available and distributed within the landscape appropriate to goshawk territory spacing). In Italy and France, Penteriani and Faivre (2001) reported a similar response by goshawks to shelterwood harvesting. They found that breeding frequency and the number of young produced per breeding pair did not differ between logged and unlogged stands. They also reported that where timber harvesting exceeded 30% of the nest stand, goshawks often relocated to the neighboring mature stands, but that overall reproductive success was not affected.

Several independent studies in Fennoscandia have shown that goshawk populations declined by 50–60% from the 1950–80s (Widén 1997). Widén (1997) examined several factors most often associated with declining raptor populations, including pesticides, persecution, prey populations, and nesting and foraging habitat loss associated with forest development. Of these factors, only decreases in the amount and patch size of mature forest at the foraging habitat scale showed a clear correlation with the decline in goshawk populations.

North American studies that suggested decreased nesting productivity in response to timber harvesting (Crocker-Bedford 1990, Patla 1997) were limited by their study design or by issues regarding scale of analysis relative to scale of harvesting. In Idaho, Patla (1997) compared reproductive success pre- and post-treatment, but not post-treatment areas to controls. Pre- and post-treatment comparisons in the absence of controls depend on the assumption that other factors affecting reproductive success are similar over the entire monitoring period, or at least have a minor effect relative to the treatment effect being studied. However, the reproductive success of goshawks is known to vary considerably from year to year depending on prey abundances (Doyle and Smith 1994) and weather (Younk and Bechard 1994).

Crocker-Bedford (1990) examined 16–200 ha nest area reserves surrounded by large partial cuts in Arizona and found much lower occupancy in

the logged territories than at controls. However, the timber harvesting being evaluated was carried out over 1000–5000 ha units, which would have influenced both nesting and foraging area suitability. Crocker-Bedford (1995) later reanalyzed reoccupation rates and nestling production with respect to amount of harvesting that had occurred at the home-range scale of 2290 ha and found an inverse correlation between the reproductive success variables and harvesting.

To address high annual variation and a potential lag effect in responses by the goshawks, we will continue this study through 2005. If our longer-term results are consistent with Penteriani and Faivre (2001) and continue to show no decreased reproductive success by goshawks at nest areas modified by timber harvesting, it would support Widén's (1997) theory that habitat changes at the foraging area scale are the primary factor affecting goshawk populations. Notwithstanding the need for additional manipulative studies at the nest-area scale, we recommend that research on goshawks needs to shift from descriptive nest-area scale studies, which are numerous, to territory and landscape scale studies, which are few. Specifically, research should attempt to examine habitat requirements at the territory and landscape scale that can be incorporated into forest management strategies, such as seral-stage and patch-size distributions.

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A REVIEW OF THE STATUS AND DISTRIBUTION OF NORTHERN GOSHAWKS IN NEW ENGLAND

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ABSTRACT.—The Northern Goshawk (*Accipiter gentilis*) is a resident breeder throughout much of the forested landscape of New England and a winter resident in most of New England, except possibly for extreme northern portions. Historically, goshawk numbers and distribution presumably declined as agriculture and logging grew to dominate the region in the 19th century when large parts of New England were cleared upwards of 75% of the forest cover. Goshawks likely responded to reforestation during the middle and latter decades of the 20th century. However, most biologists agree that although goshawk numbers may be stable or perhaps increasing slightly today, their true status and distribution in this six-state region is largely unknown. Goshawks in New England nest in mature regrown coniferous, deciduous, and mixed forest. From a landscape perspective, conservation, maintenance, and enhancement of mature forest, as well as early successional-stage cover, are both necessary for this species in New England. Restoration and management of these cover types would benefit not only goshawks and their prey, but also a significant portion of the region's biodiversity. Because of the extensive and intensive relationships humans have had with the New England landscape over the past three centuries, the region would make a valuable subject area for long-term monitoring and research on a wide-ranging top-level predator such as the goshawk.

KEY WORDS: *Northern Goshawk; Accipiter gentilis; Connecticut; distribution; Maine; Massachusetts; New Hampshire; New England; northeastern U.S.; Rhode Island; Vermont; status.*

UNA REVISIÓN SOBRE EL ESTADO Y LA DISTRIBUCIÓN DE *ACCIPITER GENTILIS* EN NUEVA INGLATERRA

RESUMEN.—*Accipiter gentilis* es un ave residente que nidifica a lo largo de la mayor parte de los bosques de la región de Nueva Inglaterra, y un residente invernal en casi toda Nueva Inglaterra con excepción posiblemente de las porciones más extremas del norte. Históricamente, los números y la distribución de *A. gentilis* presumiblemente disminuyeron a medida que la agricultura y la tala aumentaron hasta dominar la región durante el siglo XIX, cuando grandes partes de Nueva Inglaterra fueron deforestadas, transformándose más del 75% de la cobertura del bosque. Luego *A. gentilis* probablemente respondió a la reforestación a partir de mediados del siglo XX. Sin embargo, la mayoría de los biólogos coinciden con que, aunque los números de *A. gentilis* pueden permanecer estables o tal vez haber incrementando levemente en la actualidad, su verdadero estatus y distribución son básicamente desconocidos en esta región que comprende seis estados. *A. gentilis* nidifica en Nueva Inglaterra en bosques regenerados maduros de coníferas, en bosques deciduos y en bosques mixtos. Desde una perspectiva del paisaje, la conservación, mantenimiento y mejoramiento del bosque maduro y de las etapas sucesionales tempranas, son una preocupación en Nueva Inglaterra. La restauración y el manejo de estos tipos de cobertura beneficiarían no sólo a *A. gentilis* y a sus presas, sino también a una porción significativa de la biodiversidad de la región. Debido a las relaciones extensas e intensas que los humanos han tenido con el paisaje de Nueva Inglaterra a lo largo de los últimos tres siglos, la región sería un área piloto interesante y valiosa para el monitoreo y la investigación a largo plazo de un depredador tope con un área de acción amplia como *A. gentilis*.

[Traducción del equipo editorial]

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Much attention has focused on the Northern Goshawk (*Accipiter gentilis*) in the western United States west of the 100th meridian (Kennedy 1997, Crocker-Bedford 1998, DeStefano 1998, Andersen et al. 2003). However, the species is holarctic in distribution and is found in boreal and northern temperate forests in the northern hemisphere of North America and Eurasia (Squires and Reynolds 1997). In the northeastern U.S., the goshawk is found regularly throughout this region, including in all six New England states and as far south as Maryland and West Virginia (Squires and Reynolds 1997).

Much of the interest and concern for goshawks in the western U.S. is related to forest management practices, in particular the cutting of large trees and conversion of the forested landscape from late to early-seral-stage forest (DeStefano 1998). However, in the eastern U.S., woody vegetation and re-growth forest has increased to such an extent that biologists are now concerned with the lack of early-seral-stage habitats, such as grasslands and shrublands, and the loss of some forest types such as aspen (*Populus* spp.) and the species they supported (Askins 2001, Thompson and DeGraaf 2001).

The northeastern U.S., and New England in particular, have a long history of human occupation and land-use change, even before European settlement (Cronin 1983). In the 18th and 19th centuries, clearing for agriculture and timber altered the entire region (DeGraaf and Yamasaki 2001). Much of New England is reforested today, and it is unknown but unlikely that these second- or multiple-growth forests are similar—and certainly are not identical—to the original forests of 300–350 yr ago (Cogbill et al. 2002).

The primary question in the eastern U.S., one that has implications for goshawk management in the western U.S., is what is the status and distribution of Northern Goshawks in the greatly transformed landscapes of the Northeast? The objectives of this paper are to examine that question by reviewing recent accounts and expert opinion on the status of Northern Goshawks, describe the distribution of goshawks in the New England states in light of historical changes and current conditions, and attempt to assess the status of the species in this region. I then make suggestions for potential long-term, multi-state research over large landscapes in New England.

STUDY AREA

I restricted my review of the status and distribution of Northern Goshawks in the Northeast to New England. The six New England states (Connecticut, Rhode Island, Massachusetts, Vermont, New Hampshire, and Maine) cover ca. 163 200 km² and form an identifiable political and regional entity. This review could have also included New York, Pennsylvania, Maryland, New Jersey, and other states to the south, but New England forms a convenient and manageable region for addressing questions of status and distribution. More importantly, there are more extensive long-term records and documentation of land-use change for New England than any other region of the country (Cogbill et al. 2002, Foster 2002), in addition to well-studied, species-habitat relationships (DeGraaf and Yamasaki 2001). Nonetheless, many other parts of the Northeast share similar land-use histories with New England, and at least some of the insights and speculation provided here regarding the status and distribution of Northern Goshawks in New England will be similar for other northeastern states.

New England is diverse in vegetation, topography, climate, and other ecological factors, but in general is dominated by deciduous, mixed deciduous-coniferous, and coniferous forest as one moves from south to north (DeGraaf and Yamasaki 2001). Summers are warm and humid; winters are usually cold and snowy. Precipitation in the form of rain and snow is highly variable and based on many factors, such as latitude, elevation, and proximity to the coast, but generally ranges from 90–140 cm annually. Numerous lakes, ponds, rivers, and wetlands cover the region. Major mountain ranges include the Berkshire Mountains, which extend from western Connecticut through Massachusetts, the Taconic Mountains of Massachusetts, Green Mountains of Vermont, and White Mountains and Mahoosics of New Hampshire and Maine. The entire region was glaciated, and erosion has been a major influence on the landforms present today.

Six forest regions have been identified in New England. Major tree species that characterize some of these regions include pitch pine (*Pinus rigida*), oaks (*Quercus* spp.), eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), red spruce (*Picea rubens*), and balsam fir (*Abies balsamea*). These forest regions, in a general south to north distribution, are pitch pine-oak (on Cape Cod), central hardwoods-hemlock-white pine, transition hardwoods-white pine, northern hardwoods, northern hardwoods-spruce, and spruce-fir (DeGraaf and Yamasaki 2001). American beech (*Fagus grandifolia*), birches (*Betula* spp.), sugar maple (*Acer saccharum*) and several other maples, hickories (*Carya* spp.), ashes (*Fraxinus* spp.), cherries (*Prunus* spp.), and aspens are other major tree species. Disturbance to forest growth and structure is common in New England; DeGraaf and Yamasaki (2001) identify and discuss five major types of disturbances that have altered New England's forest, including windthrow, fire, exotic pests and pathogens, agriculture, and logging.

Much of southern New England is highly urbanized, with some of the highest densities of people in the country. However, substantial portions of the region are still rural. Most of the forest land (some 120 000 km² or >70%) is privately owned by >760 000 different owners and divided into small parcels and woodlots of nonin-

dustrial-private forest (commonly abbreviated as NIPF lands), but there are large privately owned commercial timberlands in the north, particularly in Maine (Birch 1996). Federal land is much less common in the East than the West, but there are two national forests in the region: the Green Mountain National Forest in Vermont and the White Mountain National Forest in New Hampshire and Maine.

METHODS

I reviewed written accounts, both recent and historical, of the Northern Goshawk and related land-use changes in New England. I also summarized information reported from breeding bird atlases, which have been published for all six states. I examined long-term trends in numbers for both breeding and wintering goshawks by querying web databases for the North American Breeding Bird Survey (BBS; <http://www.mp2-pwrc.usgs.gov/bbs/>) and the National Audubon Society's Christmas Bird Counts (CBC; <http://audubon2.org/birds/cbc/hr/graph.html>). Finally, I queried local experts in each state to gather their knowledge on the status and distribution of goshawks. I defined an expert as anyone currently working as a professional biologist with a state or federal agency or a recognized non-governmental organization, who had a focus on raptors, threatened or endangered species, or forest wildlife. I asked a series of eight questions, which addressed issues related to status, distribution, population trends, habitat use, relationship to mature forest and young, early-successional forest, and prey. Questions were sent to biologists in each state and at the Green Mountain and White Mountain National Forests.

RESULTS

Historical and Recent Accounts of New England Forests. Before European settlement, the Northeast was probably a mix of forested and open habitats. Native prairie and forests cleared by Native American activities were common in southern New England, while beaver (*Castor canadensis*) meadows, periodic fires, and hurricanes created a shifting mosaic of forest and open habitats throughout the region (Cronin 1983, DeGraaf and Yamasaki 2001, Lorimer 2001, Parshall and Foster 2002). Interior and northern regions were more heavily forested than coastal sections or lands along major rivers (DeGraaf and Yamasaki 2001).

The history of New England since the time of European settlement embodies major and constant anthropogenic change (Hall et al. 2002). Foster et al. (2002) characterized these changes to the New England landscape as a continual transformation involving deforestation, intensive agriculture, farm abandonment, reforestation, and human population increase. Land was first cleared slowly for settlements and agriculture until the 1750s, after which the pace accelerated until 75% of the arable

land in central and southern New England was in pasture and crops by the first half of the 1800s (DeGraaf and Yamasaki 2001). Many of the largest trees, such as eastern white pines, were cut to provide masts for ships, first for the British navy before the Revolutionary War and then for the U.S. navy after the war (Walker 1999). Around 1910, the last major logging occurred when primarily white pines were harvested. These sites grew into hardwoods and supported large populations of Ruffed Grouse (*Bonasa umbellus*) during the 1920s and 1930s (DeGraaf and Yamasaki 2001). Today, about 65% of southern New England and >90% of northern New England are forested (DeGraaf and Yamasaki 2001). Each year the age and extent of forest in southern and central New England increases (Brooks and Birch 1988, DeGraaf and Yamasaki 2001).

Today, the evolution of the New England landscape is marked at least partially by what is no longer there. Remnants of what may be called old-growth forest make up <1% of the forests of New England (Davis 1996, Cogbill et al. 2002). Thus, the woodlands of the Northeast could be described as multiply-regrown forests of medium-sized and medium- to mature-age (40–100 yr) trees. Old-growth or virgin forest remnants remain in small and scattered amounts, but are essentially ecologically extinct, while open grasslands, shrubby habitats, or young invasive forest types have given way to altered disturbance regimes and woody plant succession (Lorimer 2001). A dominant canopy and major mast-producing tree species, the American chestnut (*Castanea dentata*), was eliminated as a canopy tree by the chestnut blight (*Cryphonectria parasitica*), introduced from Europe in the early 1900s (Paillet 2002). American chestnuts still exist in the woodlands of New England and elsewhere, but never achieve maturity and survive today only in the form of sprouts originating from trees or seedlings that were established before the arrival of the blight (Paillet 2002). The hemlock woolly adelgid (*Adelges tsugae*), an aphid-like insect from Japan, has already caused the loss of large numbers of eastern hemlock trees in southern New England, and is migrating north, threatening the existence of this long-lived, shade tolerant species (Orwig et al. 2002). Changes due to direct mortality as well as increased logging, which is occurring at a greater rate because of the threat of the loss of trees, have led to thinning canopies (Kizlinski et

al. 2002) and changes in avian communities (Tingley et al. 2002).

Many large mammals, such as elk (*Cervus elaphus*) and caribou (*Rangifer tarandus*), have been extirpated, as have some major predators, such as wolves (*Canis lupus*) and mountain lions (*Puma concolor*; DeGraaf and Yamasaki 2001). Wolves were extirpated around 1900, and soon afterwards coyotes (*Canis latrans*) began colonizing the region from the Midwest (Parker 1995). Passenger Pigeons (*Ectopistes migratorius*), whose numbers quite possibly ranged in the billions and were likely a major prey item for goshawks and other raptors, went extinct at the turn of the 19th century (Blockstein 2002). By sheer numbers alone, their impact was a major driving force on the characteristics of eastern forests (Ellsworth and McComb 2003). During this recent history, other wildlife species have either increased their range or have become more common, such as moose (*Alces alces*), beaver, coyote, fisher (*Martes pennanti*), Wild Turkey (*Meleagris gallopavo*), Mourning Dove (*Zenaidura macroura*), and others (DeGraaf and Yamasaki 2001: 13).

Historical Accounts for the Northern Goshawk. In New England, nesting habitat of Northern Goshawks decreased as forests were cleared for settlement and agriculture (Bent 1937, DeGraaf and Yamasaki 2001). This was an obvious change in habitat for the goshawk, but equally important may have been the extinction of the Passenger Pigeon, which was likely important prey for goshawks (Bent 1937). Thus, the Northern Goshawk may have been a rare nesting species in New England at the turn of the 19th to the 20th century (Bevier 1994). It was called a casual species in summer (Forbush 1925–29), very rare (Bagg and Eliot 1937), and a rare and irregular winter resident (Sage et al. 1913).

In the late 1800s and early 1900s, the goshawk was a rare summer resident in northern New Hampshire (Allen 1903, Hoffman 1904, Foss 1994) and was seen in southern New Hampshire primarily as a winter visitor (Dearborn 1903, Foss 1994). The discovery (or rediscovery) of the first goshawk nest in Massachusetts has been attributed to two officials of the Harvard Forest in Petersham, central Massachusetts, in 1922–23 (Wetherbee 1945). In some winters, goshawks were reported to come out of the north in great numbers to “wreak havoc with the grouse of the county” (Wetherbee 1945: 38). Over 20 skins were reported collected from

1883–1935 (Wetherbee 1945:117–18). In 1945, Wetherbee (1945:23) reported that the “eastern” goshawk was among several species of birds that have “nested in the past but have doubtful nesting status at present.”

Since about 1955, however, there is some evidence that both numbers of nesting pairs and the range of breeding goshawks have increased steadily in New England (DeGraaf and Yamasaki 2001). For example, only three nesting records existed in Vermont before 1933, but now goshawks nest throughout northern New England (Laughlin and Kibbe 1985, DeGraaf and Yamasaki 2001). DeGraaf and Yamasaki (2001) attribute range expansion and an increase in population size to the regrowth of New England forests.

Recent Accounts for the Northern Goshawk. DeGraaf and Yamasaki (2001) list the Northern Goshawk as uncommon to rare, but increasing, in New England. They state that goshawks breed throughout the New England states and winter throughout the region, except for northernmost Maine. The Northern Goshawk was one of 41 breeding bird species that DeGraaf and Yamasaki (2001) listed as having “increased significantly in abundance” in Massachusetts (Veit and Petersen 1993).

State Accounts. The following accounts for each of the six New England states were excerpted from the atlas of breeding birds for each state and other sources as cited.

Connecticut. Bevier (1994) described the goshawk as an uncommon permanent resident and migrant. Nesting concentrated in higher elevations of western Connecticut, where pairs usually occupy a territory throughout the year. They exhibit “flexible habitat selection,” nesting in tracts of mixed northern hardwoods and conifers, especially eastern hemlock and white pine, pure stands of mature white or red pine (*Pinus resinosa*) within more extensive tracts of deciduous woods, wetlands, and second-growth, deciduous stands. Nesting occurs on hillsides, frequently near wetlands and away from human disturbance. Prey brought to nests was mostly squirrels and chipmunks, grouse, songbirds, and waterfowl.

Rhode Island. Enser (1992) reported that historical nesting was unknown. Northern Goshawks may now be the most common nesting Accipiter in Rhode Island, but there are still very few known nests (ca. eight confirmed or possible occurrences in the early 1990s). This species became reestab-

lished in the mid-1950s. They usually breed in isolated areas of coniferous forest, particularly mature stands of hemlock and white pine and also deciduous woodlots.

Massachusetts. Veit and Petersen (1993) listed the goshawk as one of 41 breeding bird species whose numbers have increased significantly since the 1950s, based on Griscom and Snyder's (1955) accounts. The current status is given as an uncommon resident and migrant on the mainland and a rare migrant on the islands of Nantucket and Martha's Vineyard. In 1995, nesting was restricted to western Massachusetts, but now occurs regularly throughout the state, except for Cape Cod and the Islands. Goshawk numbers fluctuate annually, but have been increasing steadily since the mid-1950s, both during the breeding season and in winter.

Vermont. Laughlin and Kibbe (1985) reported that goshawks were found almost statewide, but were largely confined to areas with medium to high relief (e.g., in the Champlain Lowlands along Lake Champlain). All but one record were from the hilly eastern and southern portions of that region.

New Hampshire. Foss (1994) described the goshawk as much more common in southern New Hampshire in recent decades, while the Cooper's (*Accipiter cooperii*) and Sharp-shinned (*A. striatus*) hawks seem to have made only modest recoveries since the use of DDT was banned in the early 1970s. The goshawk breeds throughout the state, typically in higher elevations, and often nests in deciduous trees, especially white birch (*Betula papyrifera*), red maple (*Acer rubrum*), and black birch (*B. lenta*), but occasionally in white pine. Prey items include grouse, crows, waterfowl, small birds, hares, squirrels, and chipmunks.

Maine. Adamus (1987) reported that the goshawk was somewhat common in the central and southern parts of the state, but less so further north. Confirmed nesting records exist for coastal regions and southern and central Maine. Probable breeding records exist throughout Maine, including the north-central region and along the Canadian border. Goshawks are generally absent in northern Maine during winter (DeGraaf and Yamasaki 2001).

Breeding Bird Surveys and Christmas Bird Counts. Both breeding (from BBS data) and winter (from CBC data) distribution maps show the goshawk present throughout all of New England, but in both cases the number of observations of indi-

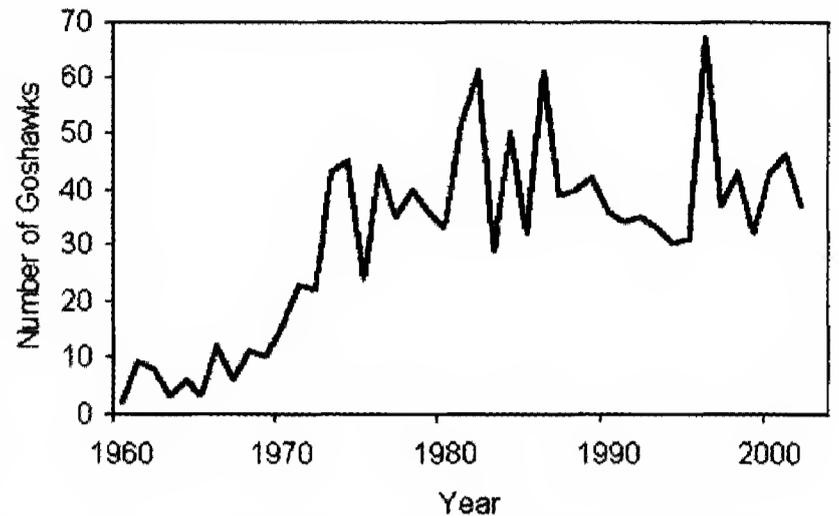


Fig. 1. During the Christmas Bird Count in New England from 1959–60 to 2002–03, counts of Northern Goshawks have shown a long-term increasing trend. Data compiled from National Audubon Society, Inc. web site Christmas Bird Count home page (<http://www.audubon.org/bird/cbc/>) for Connecticut, Rhode Island, Massachusetts, Vermont, New Hampshire, and Maine.

vidual birds is <1 per route (Sauer et al. 2003). In spite of extremely low densities, long-term CBC data show a concurrent long-term increase in sightings of goshawks, but a slight decrease in number of birds observed per unit effort (Fig. 1).

Expert Opinions. Several biologists responded to my questions about goshawks in their state. Not unexpectedly, the distribution of Northern Goshawks in most New England states is somewhat easier to determine, and thus better known, than population status or trends. Breeding bird surveys probably best indicate the distribution of nesting pairs. In general, goshawks can be found in forested areas throughout New England, although densities could be expected to vary among regions (C. Gaughan, S. Melvin, S. Parren, and T. Hodgman pers. comm.). In short, most biologists described the goshawk as uncommon but present, and given naturally low densities of this species, well distributed in forested habitat.

State biologists recognize that information on population trends is lacking. Some have stated that, although it is commonly reported that goshawk numbers may be increasing because of widespread reforestation, there are no definitive data to support this proposal. Goshawk numbers may have decreased in northern Maine during the 1960s through 1980s because of widespread spruce budworm (*Choristoneura fumiferana*) infestations and subsequent increased tree mortality and salvage harvests; however, numbers there may have stabilized in the last decade (T. Hodgman pers.

comm.). It appears that goshawks have expanded south in New Hampshire, suggesting that numbers have increased in the southern part of the state in recent years (C. Gaughan pers. comm.).

Biologists from the Green and White Mountain National Forests provided responses similar to those of state biologists regarding the status and distribution of Northern Goshawks on their areas (C. Grove and M. Yamasaki pers. comm.). Goshawks are distributed throughout most or all of both Vermont's Green Mountain and New Hampshire and Maine's White Mountain National Forests, certainly as breeders and probably as winter residents, although some birds may be winter migrants from the north. Goshawks are not common, but neither are they considered rare; the term "uncommon breeder" might best describe their status on national forest lands within New England. Forest biologists believe that goshawk numbers are probably stable at some undetermined level, and may even be increasing as suggested by state breeding bird atlas accounts, but again caution that data are lacking and opinions on population trends are speculative. On both the Green and White Mountain National Forests, goshawks nest in mature stands of white pine or mixed spruce-fir and hardwoods. Given the land-use history of New England, many of these stands are essentially regrown mature forest of 80–100 yr. Often there are forest openings, such as roads, trails, and upland openings nearby, but usually nests are away from high levels of human activity. Some additional generalizations of nest sites include gentler slopes at lower elevations (e.g., below 450 m). The Northern Goshawk was listed as a Regional Forester Sensitive Species in 2003 on some national forests in the northern portions of the U.S. Forest Service's Region 9, but not on either the Green or White Mountain National Forest (M. Yamasaki pers. comm.).

DISCUSSION

Foster et al. (2002) characterized six major trajectories of change in the long-term dynamics of wildlife populations in the northeast: (1) many large mammals and birds that declined historically have increased recently, (2) open-land species went from low to high abundance with land clearing, but are in decline today, (3) some species were extirpated, (4) some species have expanded their ranges into the northeast, (5) introduced non-natives have proliferated, and (6) some persistent

species did not exhibit major long-term trends. Likewise, DeGraaf and Yamasaki (2001) identified three major trends in New England's wildlife in the last several decades: (1) forest species are increasing, (2) grassland and shrubland species are declining, and (3) many southern birds are spreading northward into the region. In addition, a few species like Common Ravens (*Corvus corax*) and moose have extended their range southward.

At least some of these statements apply directly or indirectly to the Northern Goshawk in New England. The goshawk was apparently one of those forest species that has increased in numbers in the last half century. This was probable given that at least three quarters of New England's forests were cleared for agriculture and high-graded for timber. The number and distribution of goshawks could have been expected to decline significantly with the amount of forest clearing that occurred in the 18th and 19th centuries. With reforestation occurring during the middle decades of the 20th century, the distribution and number of goshawks likely increased. This presumed long-term decline followed by an increase in numbers of goshawks must be viewed in the proper temporal scale: in decades, if not centuries, of change. More difficult to decipher is whether or not goshawk distribution and numbers are increasing today. Some evidence indicates that this is the case, but empirical data are extremely limited to nonexistent. Thus, it is difficult to speculate on recent (say, the last 20–30 yr) population trends without more definitive data. However, long-term efforts, such as the Christmas Bird Count, indicated a possible increase, or at least stabilization, of goshawk numbers in the region (Fig. 1).

The status of Northern Goshawks is certainly tied to the distribution and condition of mature forest. However, the recent decline of some early-successional-stage species, such as grouse and lagomorphs (Rusch et al. 2000, Litvaitis 2001, Fuller and DeStefano 2003), may influence goshawk distribution and reproduction (Doyle and Smith 1994). Historically, the extirpation of some species, particularly the Passenger Pigeon, have likely altered the suite of available prey species for goshawks, while the expansion of some species, such as some passerines, in New England may provide new prey. Regardless, ubiquitous and intensive anthropogenic change has characterized, and will continue to influence, the region's landscape, vegetation, and wildlife. DeGraaf and Yamasaki (2001:

3) summarized this by stating, "Most species have likely had very different distributions through time. In 50 or 100 years, both the species present and their distributions will be different." This is likely the case for the Northern Goshawk.

The characteristics of topography and forest cover reportedly used by goshawks in New England show similar patterns to other parts of the species' range in North America. Nesting occurs in mature coniferous, deciduous, and mixed forest, typically on gentle rather than steep terrain, in proximity to some forest openings, but mostly away from well-used roads and human habitation. Similar patterns in nesting cover have been reported for other northeastern states (outside of New England). In New Jersey and New York, goshawks selected extensive mature forested areas for nesting, particularly in mixed hardwood-coniferous stands with greater numbers of large trees (>20 cm Diameter Breast Height) and high tree basal area (Allen 1978, Speiser and Bosakowski 1987, Bosakowski and Speiser 1994). Hemlock, pine, and cedar (*Chamaecyparis thyoides*) dominated nest sites, while oaks were less prevalent, although nests were usually in deciduous hardwood trees. Nests were present on gentle slopes or flat terrain, away from southern exposures, small forest tracts, paved roads, and human habitation.

Kenward (1996) speculated that goshawks in North America may face more competition from Red-tailed Hawks (*Buteo jamaicensis*), Red-shouldered Hawks (*B. lineatus*), and Great Horned Owls (*Bubo virginianus*) than goshawks face in Europe with similar raptor species. Red-tailed and Red-shouldered hawks are found throughout New England, except for northernmost Maine for the Red-shouldered Hawk, and are regular breeders (DeGraaf and Yamasaki 2001). Red-shouldered Hawks inhabit mature deciduous-coniferous forest, while Red-tailed Hawks are found in more open habitats (DeGraaf and Yamasaki 2001). Great Horned Owls are uncommon, but widespread, and are found year-round throughout all of New England, occurring in all types of cover (DeGraaf and Yamasaki 2001). Although little is known about the interactions among these raptor species, given the potential for aggressive interactions (Crannell and DeStefano 1992, Rohner and Doyle 1992), this may be an important local influence on the distribution of goshawks in some parts of the region. Broad-scale loss of hemlocks and the conditions of forest cover and canopy closure they create could also

have important and related consequences for several wildlife species, including goshawks.

NEW ENGLAND: A "NATURAL EXPERIMENT"

Keane and Morrison (1994), in the first symposium on the ecology and management of Northern Goshawks, stressed the importance of identifying effects of scale and biological organization in ecological studies. In the same symposium, Graham et al. (1994) recommended that management of goshawks take place in large tracts of forest, which should be viewed as sustainable ecological units rather than smaller tracts or individual goshawk home ranges. Of the potential spatial scales that can be addressed, most forest wildlife biologists stressed the importance of, and need for, studies at large landscape levels (DeStefano 2002).

New England would offer an interesting opportunity to examine how goshawks have responded to a changing landscape. Widespread intensive land clearing and logging have given way to extensive reforestation of second- or multi-growth forest, embodying changes that have taken place over the last 2–3 centuries. Today, small, rare, and widely-dispersed patches of old-growth or virgin forest, altered disturbance regimes including reduced timber harvest, dominant mid-aged forest, loss of early-successional-stage cover, and increases in human densities and development offer an opportunity to see how goshawks have dealt with these changes in the northeast. This investigation would also offer insights into similar developing trends in the western U.S. Well distributed and coordinated monitoring of goshawk populations on randomly selected forested areas in New England, perhaps stratified by state, forest cover type, or ecological region, would be an appropriate approach. Surveys for goshawks could also include other forest raptors and major prey species, given recent emphasis away from single-species approaches and toward biodiversity (DeStefano 2002). However, the extent and effort required would be large, given the large spatial and temporal scales involved.

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