THE NORTHERN GOSHAWK: ECOLOGY AND MANAGEMENT

WILLIAM M. BLOCK, MICHAEL L. MORRISON, AND
M. HILDEGARD REISER, EDITORS

Studies in Avian Biology No. 16
A Publication of the Cooper Ornithological Society

Steven M. Speich
18 January 199~~4~~5
Tucson, Arizona

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Proceedings of a Symposium of the
COOPER ORNITHOLOGICAL SOCIETY
Sacramento, California,
14–15 April 1993

Sponsors:
Rocky Mountain Forest and Range Experiment Station, USDA Forest Service
Forest Environment Research, USDA Forest Service
Cooper Ornithological Society

Studies in Avian Biology No. 16
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Cover drawing of Northern Goshawk and snowshoe hare by John Schmitt

STUDIES IN AVIAN BIOLOGY

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Studies in Avian Biology is a series of works too long for *The Condor,* published at irregular intervals by the Cooper Ornithological Society. Manuscripts for consideration should be submitted to the editor. Style and format should follow those of previous issues.

Price $16.00 including postage and handling. All orders cash in advance; make checks payable to Cooper Ornithological Society. Send orders to Walter Wehtje, Assistant Treasurer, Western Foundation of Vertebrate Zoology, 439 Calle San Pablo, Camarillo, CA 93010.

ISBN: 0-935868-76-3

Library of Congress Catalog Card Number: 94-069777
Printed at Allen Press, Inc., Lawrence, Kansas 66044
Issued: 23 November 1994

CONTENTS

SYMPOSIUM OVERVIEW

RESEARCH APPROACHES AND MANAGEMENT CONCEPTS

RESOURCE ECOLOGY

POPULATION ECOLOGY

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Studies in Avian Biology No. 16:1–2, 1994.

Symposium Overview

INTRODUCTION

WILLIAM M. BLOCK, MICHAEL L. MORRISON, AND M. HILDEGARD REISER

Forestry practices conducted since European settlement of North America have come under scrutiny, particularly with respect to their effects on the structure and functioning of ecological systems. Typically, this scrutiny has focused on vertebrate populations. This was especially evident in the case of the Northern Spotted Owl (*Strix occidentalis caurina*). Prior to 1983, numerous researchers working independently were studying the factors responsible for apparent population declines within the range of the owl. Unfortunately, the results of these studies were scattered and as an integrated whole not generally available to decision makers and other researchers. It was not until the 1984 symposium on the Ecology and Management of the Northern Spotted Owl—held 19–23 June 1984 in Arcata, California, as part of the 54th meeting of the Cooper Ornithological Society—that researchers and managers shared their findings, identified critical information gaps, and outlined directions for future research. Even though the debate continues, the initial symposium established the foundation for a concerted research effort in the years following.

The current situation with the Northern Goshawk (*Accipiter gentilis*), a raptor typically dependent on mature forests, bears an uncanny resemblance to that of the Northern Spotted Owl a decade ago. Within the past five years, evidence has arisen to suggest that populations of Northern Goshawks are declining, particularly in the western United States. Presently, the Northern Goshawk is regarded as a management indicator species of specific habitat conditions in many regions of the U.S. Forest Service and is a Forest Service Sensitive Species within the Rocky Mountain and Intermountain regions. The United States Fish and Wildlife Service has been petitioned twice within the past three years to list the goshawk as threatened or endangered under the Endangered Species Act. Likely, a third petition will be filed in the near future.

Although researchers are engaged in studies examining goshawk biology, no comprehensive, integrated research agenda underlies those efforts. Consequently, we felt that it was timely to assemble information on the biology of the Northern Goshawk (especially western populations) to assess our current state of knowledge. Thus, the symposium, The Biology and Management of the Northern Goshawk, was held on 14–15 April 1993 in conjunction with the 63rd annual meeting of the Cooper Ornithological Society in Sacramento, California.

The objectives of the symposium were (1) to assemble researchers and managers from across the country to exchange information and discuss ideas on the biology and management of the Northern Goshawk, and (2) to publish a compendium of current information on goshawk biology and management as a proceedings from the symposium.

We first contacted individuals who were conducting goshawk research. A call for papers was distributed nationally to reach researchers that we failed to contact initially. Our efforts resulted in a symposium that included 31 oral presentations.

Some of the results reported herein are from studies still in progress. Given the experience with the protracted debate over the Northern Spotted Owl, however, we felt that it was timely to publish these proceedings. To guarantee quality in these proceedings, all papers were required to go through a rigorous peer-review process and were held to the standards applied to submissions to *The Condor*. These 22 papers summarize the current state of knowledge on goshawks within the scientific and management communities. Sharing this information will allow researchers to critically evaluate past work, identify knowledge gaps, and develop strategies to focus on those needs in future studies.

These proceedings are presented in three sections. *Research Approaches and Management Concepts* contains overviews of research and management for goshawks, forest management to provide goshawk habitat, and field techniques. *Resource Ecology* focuses largely on habitat use at spatial scales ranging from landscapes to microhabitats. Also included are food habits papers. The section on *Population Ecology* includes papers on reproductive rates, survival rates, turnover, and numerical responses of goshawks to prey abundance.

This collection of papers represents the current state of knowledge on Northern Goshawks. Our intent is for these proceedings to serve as a springboard from which researchers will critically evaluate their work and that of others, and provide direction for future research. Only through such actions can researchers provide the information needed to guide timely and appropriate management for the species.

ACKNOWLEDGMENTS

These proceedings represent the culmination of efforts by numerous people. We thank D. A. Boyce and R. T. Reynolds for helping to identify symposium participants. K. E. Sieving and A. P. Gomez ensured that the symposium ran smoothly with their excellent logistic support. B. Witsell deserves special recognition for help tracking manuscripts through the review process. Special thanks to J. Verner and other members of the local organizing committee of the 63rd meeting for their support of the symposium. J. T. Rotenberry especially deserves credit for ensuring that these proceedings met the high standards of *Studies in Avian Biology* publications. Financial support for the proceedings was provided by the USFS—Rocky Mountain Forest and Range Experiment Station, and USFS—Forest Environment Research.

We also thank the following reviewers who helped improve the quality of the papers contained within these proceedings: M. J. Bechard, J. C. Bednarz, P. Beier, P. H. Bloom, C. E. Bock, T. Bosakowski, D. A. Boyce, J. B. Buchanan, L. A. Brennan, E. L. Bull, D. Call, P. J. Detrich, S. DeStefano, C. B. Edminster, T. C. Edwards, T. C. Erdman, E. D. Forsman, M. R. Fuller, J. L. Ganey, T. L. George, R. T. Graham, T. G. Grubb, L. A. Hall, G. D. Hayward, R. L. Hutto, J. J. Keane, P. L. Kennedy, T. J. Kimmel, W. S. LaHaye, J. F. Lehmkuhl, D. L. Leslie, R. J. Lilieholm, P. N. Manley, R. W. Mannan, J. P. McTague, H. C. Mueller, C. H. Sieg, W. Shepperd, J. N. M. Smith, J. Squires, K. Steenhof, T. J. Tibbitts, K. Titus, J. P. Ward, C. M. White, G. C. White, B. Woodbridge, and C. J. Zabel.

Studies in Avian Biology No. 16:3–11, 1994.

Research Approaches and Management Concepts

NORTHERN GOSHAWK ECOLOGY: EFFECTS OF SCALE AND LEVELS OF BIOLOGICAL ORGANIZATION

JOHN J. KEANE AND MICHAEL L. MORRISON

Abstract. We develop a conceptual framework that addresses the effects of scale and levels of biological organization on ecological studies. We specifically consider Northern Goshawk (*Accipiter gentilis*) ecology relative to this framework. Traditionally, ecological studies have emphasized phenomenological, rather than mechanistic, explanations of ecological phenomena. Emphasis has focused on describing the general patterns of "how" an animal interacts with the environment. Less effort has been directed towards determining "why" we observe particular patterns; that is, what are the basic biological and ecological reasons for the phenomena that we observe? In our study area in the Sierra Nevada, California, we observed both individual and seasonal variation in the size of goshawk home ranges. We are developing an energetics model for goshawks and conducting detailed studies of the prey species used by goshawks. We will use these data to build up from an intensive understanding of the factors influencing an individual to explain the patterns at the more extensive scales. We argue that the intensive and extensive data needs that are required to develop conservation strategies should be based on a mechanistic understanding of the patterns observed. Predictions derived from phenomenological models assume that the conditions on which the model was constructed do not change. However, conservation planning requires quantitative predictions for systems that are often dynamic in both space and time, such as forests managed for timber production. Thus, emphasis should be placed on developing a mechanistic understanding of particular ecological phenomena to improve the predictive ability of conservation planning.

Key Words: *Accipiter gentilis*; conservation planning; home range; levels of biological organization; Northern Goshawk; Sierra Nevada; temporal and spatial scale.

Data needs for conservation planning require intensive and extensive field studies (Verner 1992). Addressing these needs will require studies that are conducted over various spatial and temporal scales and at different levels of biological organization. For example, spatial scales can vary from the microhabitat of a specific foraging site up through the landscape level. Temporal scales can vary from the duration of a foraging bout up through annual and geologic time scales. Additionally, levels of biological organization can vary from individuals through populations, communities, ecosystems, and landscapes. Correspondingly, interpretations of the observations we make will vary depending upon the scale and level of biological organization investigated (O'Neill et al. 1986, Wiens 1989, Gavin 1991, Levin 1992, Morrison et al. 1992). Indeed, differing interpretations of ecological phenomena that result from research conducted at different scales and levels of organization have impeded ecological advancement (Wiens 1986, 1989). Therefore, it is imperative that researchers explicitly identify the scale and level of organization that they study and define the domain to which their results are applicable. Our objectives are to (1) present a conceptual overview that considers the effects of scale and level of biological organization on ecological studies, (2) develop a conceptual framework that addresses Northern Goshawk (*Accipiter gentilis*) ecology, (3) present an example of a study design for investigating goshawk ecology, and (4) make recommendations for future research.

CONCEPTUAL OVERVIEW

The choice of scale and level of organization to be studied depends on the question being asked and should correspond to the natural scales of the phenomenon being studied (O'Neill et al. 1986, Wiens 1989). For example, to determine the geographic breeding range of the Northern Goshawk in California, a researcher would be concerned with a regional spatial scale. Similarly, if the question of interest was related to the daily activity budget of a goshawk, then one would be concerned with detailed observations of individuals. If the question was related to the role of goshawk predation in structuring forest wildlife assemblages, then a community level approach might be most appropriate.

Any phenomenon can be studied from a variety of perspectives at different scales. For example, goshawk nest sites can be studied from a microhabitat perspective that might consider the structure, composition, and stand size of the forest immediately around a nest. Alternatively, goshawk nest sites could also be studied from a perspective that considers the abundance and distribution of suitable nest stands over the landscape. Although these examples are not mutually exclusive, they illustrate the need to define clearly the objectives and scale at which the results will apply.

The questions asked in ecological studies can be fundamentally classified as "how" and "why" questions (Gavin 1991). "How" questions focus on how organisms interact with the environment and address the proximate cause of an observed phenomenon. For example, there are numerous studies on how animals forage, and what types of prey they consume. Alternatively, "why" questions focus on why an organism behaves or is structured as it is and what the effects of these traits are on survival and reproductive success. "Why" questions address ultimate causation (Gavin 1991). Here, we are asking why the animal uses (or selects) the prey that it does—what are the basic, biological and ecological reasons for the phenomenon that we observe?

The question we are fundamentally interested in answering is what determines survival and fitness in an individual (Martin 1992). The acquisition of energy and nutrients is obviously a basic determinant of these parameters—but how do we best measure them? Most studies in wildlife ecology, citing time and budgetary limitations, search for indirect measures of these parameters. Conventionally, researchers have measured a subset of an animal's habitat, usually vegetation, and derive correlative relationships between habitat variables and their use by an animal or the presence (or abundance) of the animal. These studies examine habitat use and describe the habitats irrespective of how they contribute to fitness (i.e., habitat quality). In this paper we adopt the definition of habitat use described by Hutto (1985), as not connotating a conscious choice by an organism, but merely indicating the distribution of individuals through some mechanism.

Ecological studies have traditionally emphasized correlative or phenomenological, rather than mechanistic, explanations of ecological phenomena (Wiens 1992). A pattern is observed and is explained in terms of a theory that predicts a linkage between pattern and process. Whereas the pattern is empirically measured, the explanation of the process is inferential (Wiens 1992). Applications of predictions derived from phenomenological models are constrained by the range of spatial and temporal variation encompassed in the data from which the model was constructed. If a phenomenological model is based on a narrow range of spatial and temporal conditions, then predictions from the model are limited because they assume that conditions do not change and that the phenomena on which the model is constructed adequately represent the underlying causal mechanisms (Koehl 1989). Further, most studies center on a specific scale, usually without reference to any other scale.

We can thus recognize research as a process involving different levels of inquiry and scale along a continuum, from intensive to extensive, and micro- to macro-scale. The finer the resolution of the study (i.e., the finer the scale), the closer we address the ultimate reasons, or "why", an animal is doing what it does. A knowledge of "why" organisms behave as they do, based on an intensive, mechanistic understanding of a phenomenon, should be the ultimate goal of research (Gavin 1991). Correlative, descriptive studies are initially necessary to determine patterns, but should serve as starting points for developing a more mechanistic understanding of a phenomenon. An intensive, mechanistic understanding of "why" individual organisms behave as they do will provide a foundation in which to interpret processes at higher levels of organization (Gavin 1991), and to increase the predictive ability of models developed for conservation planning. However, a mechanistic understanding of cause and effect cannot be inferred from correlative studies. Cause and effect relationships can only be proven through controlled experimental manipulations (Sokal and Rohlf 1981, Morrison et al. 1992). Unfortunately, due to the complex nature of most ecological systems, it is difficult to conduct controlled experimental manipulations. Thus, field researchers are often limited to correlative, descriptive studies.

Conservation planning requires quantitative predictions over relatively long time intervals and often must focus on systems where conditions are dynamic (e.g., changing spatial patterns of forests related to management practices). Thus, the key to successful habitat management is to understand what specific components of a species habitat most directly influence survival and reproduction (Kenward and Widén 1989, Martin 1992, Morrison et al. 1992). As discussed by Martin (1992), fitness parameters provide insight into the evolutionary basis for habitat requirements and choices, the effects on population recruitment and demography, and the life history traits of species and their implications for management. Information on survival and reproduction can be gained from detailed, intensive study of the habitat relationships of individuals. Long term demographic studies of marked individuals can provide measures of survival and reproductive output that can address habitat quality. Similarly, intensive studies of individuals can provide insight into the specific components of a habitat that explain the observed patterns of habitat use. For example, Newton (1986) experimentally determined that the addition of food to female European Sparrowhawks (*Accipiter nisus*) in food-poor areas during the pre-laying period resulted in a significant increase in clutch size and earlier laying dates. Earlier laying dates were associated with higher nest success rates relative to pairs that layed later. Thus, intensive study of individuals can provide direct measures of survival and reproduction that would not be evident from correlative vegetation-abundance studies. Additionally, processes that occur at the level of the individual can produce the patterns observed at higher levels of biological organization (Koehl 1989, Real and Levin 1991).

NORTHERN GOSHAWK ECOLOGY: CONCEPTUAL FRAMEWORK

Rather than fluctuating randomly, raptor populations are usually regulated either by resources (e.g., nest sites, habitat, food supply) and/or human factors (e.g., pollutants, disturbance, persecution) (Newton 1979, 1989a, 1991). There is no present information indicating that pollutants have had a significant effect on goshawk populations in North America (Snyder et al. 1973). The major threat to goshawks is the loss or degradation of mature forests used for nesting and foraging, primarily due to timber harvesting, as well as to livestock grazing in aspen nest stands (Bloom et al. 1986, Reynolds 1989, Reynolds et al. 1992). In this section we consider Northern Goshawk ecology relative to the conceptual overview developed above to identify the knowledge that can be gained from ecological studies at the various scales and levels of inquiry.

At the broadest scale goshawks are associated with forests and woodlands throughout the Holartic (Brown and Amadon 1968). Within North America, goshawks are found in a variety of forested vegetation types (Palmer 1988). Extensive studies conducted at this scale are typically concerned with estimating population density or home range sizes in various vegetation types. For example, Reynolds and Wight (1978) reported the density of nesting goshawks in three study areas in Oregon. Similarly, Crocker-Bedford (1990) reported the density of nesting goshawks on the Kaibab plateau in Arizona. The results of these types of studies are quantitative descriptions of the observed patterns, often explained in terms of an unmeasured factor such as prey abundance or distribution. Thus, these types of studies provide the necessary initial description of the pattern. However, because they are not based on an understanding of the underlying mechanisms, the predictive ability of models derived from these data will be constrained by the amount of spatial and temporal variation encompassed in the data set. If the complete range of conditions have been described, then the model should have some predictability. If the study is time- and site-specific, then the predictability of the model will decrease as conditions change from those upon which the model is based.

Newton et al. (1986) provided an example of an extensive study that incorporated a wide range of spatial and temporal variation. Additionally they measured factors that seemed important in explaining the observed patterns. They determined that the nesting densities of European Sparrowhawks varied between 12 study areas. Additionally, the variation was correlated with variation in prey density, which was related to land productivity, which in turn was associated with elevation and soil type (Newton 1986, 1989a).

Within a vegetation type, researchers typically focus on the use of various plant associations by goshawks relative to their abundance within some spatial area, such as the home range. In this paper we define vegetation type based on structure and general composition (e.g., mixed conifer forest type) and plant association as based on the dominant genera or species (e.g., a stand of white fir [*Abies concolor*] within the mixed conifer forest type). Studies at this scale usually present data as a proportion of time spent within different plant associations. Interpretations of such data are thus based on the scale at which the plant associations are defined. They do not necessarily have any direct relation to why the goshawk is using this vegetation; they are thus describing a pattern rather than addressing the cause for the behavior. The use of plant associations by goshawks could be related to the distribution and abundance of prey, microclimatic factors, concealment from predators, as a buffer from human disturbance, and/or various other factors. Thus, studies that do not address these phenomena at the appropriate level of inquiry relative to the question asked will certainly fail to tell us why goshawks are behaving in the manner that they do.

What we need, then, are studies that explain why the phenomena that we observe occurred. The only way to do this is to determine the ultimate reasons for the behaviors. Such studies require intensive analysis at the scale of the individual. Such an approach has a higher probability of being applicable to a range of plant associations and vegetative types than any other approach. This is because this fine level of inquiry addresses factors that directly influence the survival and fecundity of an individual bird—

habitat selection, energy balance, nutrient status, and the like. Such factors are likely to apply broadly to goshawks across their range; at least within a subspecies, all individuals will fall within a similar range of physiological abilities.

Intensive analyses address the specific, direct causes for a behavior, rather than acting as surrogates of the behavior as is the case for vegetation type. For example, what is the relationship between the size and type of prey available, and the energetic requirements and health of a goshawk? Does a female goshawk require a certain fat level to breed successfully? Such questions likely determine survival and fitness. For example, Kenward and Widén (1989) demonstrated that, given adequate hunting perches, food appeared to be the main factor determining winter habitat use by goshawks in central Sweden. In woodland habitat, goshawks foraged more often along woodland edge zones that were the preferred habitat of their prey, brown hares (*Lepus europeas*) and pheasants (*Phasianus* spp.). In boreal forest habitat, goshawks did not show a preference for edges and tended to hunt more in large patches of mature forest. The main prey in the boreal forest were squirrels (*Sciurus vulgarus*), which were most common and more evenly distributed in mature woodland. By adopting an intensive approach, Kenward and Widén were able to determine the main factor (prey distribution) that influenced habitat use and gain insight into why they observed the patterns of habitat use by goshawks that they did.

STUDY DESIGN: AN EXAMPLE

Currently we are conducting a study of Northern Goshawk ecology in the Lake Tahoe region of the Sierra Nevada, California. Our study area is ca. 1000 km ^{2} and ranges between 1700–2275 m elevation. Forest types at lower elevations range from dry, open stands of Jeffrey pine (*Pinus jeffreyi*) to mixed conifer stands composed of Jeffrey pine and white fir along with various site-specific combinations of sugar pine (*P. lambertiana*), incense cedar (*Calocedrus decurrens*), and red fir (*Abies magnifica*). These forest types are replaced at higher elevations by red fir and white pine (*P. monticola*). Lodgepole pine (*P. contorta*) stands occur on sites with higher soil moisture (Orr and Moffitt 1971).

As discussed above, interpretations of ecological phenomena can vary depending upon the scale and level of biological organization investigated. Thus, our approach is to examine goshawk ecology over a range of extensive and intensive scales and levels of inquiry. For example, at an extensive level we are quantifying the breeding density and home range sizes of goshawks over the landscape. Goshawks in our study area remain on their territories throughout the year, with increased home range sizes in the nonbreeding period. Radio-telemetry data from five pairs of goshawks during 1992 illustrated a range of both individual and seasonal variation in home range sizes (Table 1). Ninety-five percent minimum convex polygon home ranges averaged 18.8 km^2 (range 11.4–29.5) during the breeding period and 83.6 km^2 (range 13.4–154.3) during the nonbreeding period for males, whereas female home ranges averaged 12.8 km^2 (range 6.9–32.8) during the breeding period and 31.8 km^2 (range 12.2–40.1) during the nonbreeding period.

Home range sizes were compared between sexes within each season and within sex between seasons using Mann-Whitney U-tests (Zar 1984). The nonparametric Mann-Whitney U-test was used because the data did not meet the assumptions necessary for a parametric test (Zar 1984). No significant differences in home range size were found for male versus female breeding season ($P = 0.20$), male versus female nonbreeding season ($P = 0.20$), male breeding versus nonbreeding season ($P = 0.10$), and female breeding versus nonbreeding season ($P = 0.05$). However, the results of three of these tests were strongly influenced by an individual data point. For example, the pair #4 female had a breeding season home range of 32.8 km^2, whereas the other four females had breeding home ranges between 6.9–8.4 km^2 (Table 1). This female moved approximately eight km away from the nest area during the post-fledging period of the nesting cycle for 2–3 weeks and returned to the nest area just as the one fledgling was dispersing. The other females moved out of the immediate nest area but continued to return for prey deliveries during the post-fledging, pre-dispersal period (Keane, unpubl. data). Thus, the tests comparing male versus female breeding season and female breeding versus nonbreeding season were influenced by this data point. When this data point was excluded from the analyses, significant differences were found for both male versus female breeding season ($P = 0.02$) and female breeding versus nonbreeding season ($P = 0.02$) comparisons.

Therefore, other than for the pair #4 female, males had larger home ranges than females in the breeding season and females had larger home ranges in the nonbreeding season than in the breeding season. Similarly, the test for male breeding versus nonbreeding season home range size was strongly influenced by the pair #3 male, who decreased his home range size in the nonbreeding period (Table 1). We are not sure of the reasons why this was observed. The other four males increased home range size in the nonbreeding period (Table 1). If the nonbreeding season value for the pair #3 male is excluded from the analysis, then males had larger nonbreeding than breeding season home ranges (P = 0.02).

In summary, males had larger breeding season home ranges than females, except for the pair #4 female. There were no significant differences in home range size between sex during the nonbreeding season. All individuals except one (pair #3 male) increased home range size in the nonbreeding period. Although females increased home range size in the nonbreeding period, they continued to return to, and center, their activities near the nest area (Keane, unpubl. data).

To understand why we observe the patterns of home range and habitat use that we do, we are adopting an intensive approach to identify the factors that influence individuals. Our goal is to understand the energy requirements of individual goshawks, their diets, and the distribution, abundance, and habitat relationships of prey in the study area to be able to build up from the intensive level to explain the patterns observed at the extensive scales and levels of inquiry.

We are attempting to construct a model of goshawk energetics to estimate the energy required both for survival and for breeding. Three methods that have been used to estimate energy requirements are time-budget models (Walsberg 1983), allometric scaling models (Nagy 1987), and the doubly-labeled water technique (Nagy 1987, Tatner and Bryant 1989). Time-budget models are based on determining the proportion of time spent by an organism in various activities and then summing the energetic cost of each activity to yield an estimate of energy expenditure. Allometric scaling models predict energy demands based on body mass, diet, and habitat. The doubly-labeled water method measures metabolic rate by determining the turnover rate of hydrogen and oxygen isotopes, injected in the form of water, through water and CO_2 loss from the organism.

Time-budget models can provide accurate measures of energy expenditure, but require the use of measured energy equivalents for each of the various activities, as well as detailed knowledge of the thermal environment around the organism (Weathers et al. 1984, Buttemer et al. 1986, Nagy 1989). Time-budget models that do not empirically determine energy equivalents for each activity, and use estimates derived from the literature, are subject to errors of 20–40%, which may be no better than the rough approximations available from allometric models (Weathers et al. 1984). We plan to measure time-activity budgets (Widén 1984) and to use the doubly-labeled water technique to measure the energetic requirements of breeding adult Northern Goshawks. This information, along with the caloric value of the various prey species, will enable us to estimate the amount of food necessary to support a pair of breeding goshawks.

TABLE 1. ESTIMATED SIZE (KM^2) OF HOME RANGES FOR FIVE MALE AND FIVE FEMALE NORTHERN GOSHAWKS IN THE LAKE TAHOE REGION, CALIFORNIA, DURING THE BREEDING AND NONBREEDING SEASONS, 1992–1993. HOME RANGE SIZES ESTIMATED AS MINIMUM CONVEX POLYGONS FROM RADIO TELEMETRY DATA. BREEDING: JUNE–15 AUGUST 1992; NONBREEDING: 15 AUGUST 1992–MARCH 1993

		Season			
		Breeding		Nonbreeding	
Pair no.	Sex	95%	100%	95%	100%
1	Male	15.6	22.8	39.4	164.2
	Female	8.4	10.1	37.1	42.4
2	Male	21.9	36.7	154.2	160.7
	Female	8.3	13.7	40.1	97.2
3	Male	15.8	25.6	13.4	58.1
	Female	6.9	9.2	38.5	90.3
4	Male	29.5	33.7	96.1	129.3
	Female	32.8	36.4	12.2[1]	29.5
5	Male	11.4	19.6	114.8	148.8
	Female	7.8	9.7	31.3	42.6

[1] Contact was lost with this individual on 22 December 1992.

In addition to measuring energetic requirements, we are conducting inventories of the prey species to measure their distribution, abundance, and habitat relationships. On six sites within goshawk home ranges on our study area we have established a grid of sample points 300 m apart along transect lines in the various plant associations present. About 300 points have been established throughout the study area. We are conducting monthly point counts to measure bird and Douglas squirrel (*Tamiasciurus douglasii*) abundance at about 175 of the sample points, chosen to represent the range of plant associations present. We also are studying the foraging behavior of avian prey species of goshawks to quantify their microhabitat use patterns. Small mammal live-trapping is being used to sample squirrel and chipmunk distribution, abundance, and habitat relationships. Pellet counts are being used to determine relative abundance and distribution of snowshoe hares (*Lepus americana*).

Data on prey abundance, distribution, and habitat relationships will be compared with data on home range size and foraging habitat use to determine if they explain the patterns that we observe. For example, changes in prey abundance could be the reason why goshawks expand home ranges in the nonbreeding season. Similarly, prey abundance could explain the use of the various plant associations, as well as annual variation in goshawk productivity. However, it must be noted that measures of prey abundance and distribution do not necessarily provide a direct measure of prey availability (Hutto 1990). Hutto (1990) concluded that a fundamental obstacle to understanding the relationship between habitat use and food availability requires identifying the possible constraints on what subset of habitats and foods it is possible for a bird to use. By constructing an energetics model for goshawks we will be able to determine caloric needs and possible energetic constraints that influence goshawk ecology.

FUTURE DIRECTIONS IN GOSHAWK RESEARCH

We concur with Verner (1992) that both intensive and extensive field studies are needed to provide the critical data needed for conservation planning. We suggest that, rather than trying to synthesize the results of numerous time- and scale-specific studies at sometime in the future, coordinated efforts and funding be directed into a smaller number of more comprehensive studies that consider goshawk ecology over both intensive and extensive scales and levels of inquiry. Explicit within this approach would be a clear definition of goals and objectives that would serve to standardize procedures both within and between studies. Over the long term, this approach would increase efficiency in terms of funding expenditure and the generation of the critical data needed for conservation planning.

Integrating across scales and levels of organization would be a primary objective of this approach. At the landscape level, recent work indicates the importance of considering demographic rates (mortality, fecundity, dispersal, etc.) relative to the amount, configuration, and dynamics of habitat (e.g., Van Horne 1983, Gilpin 1987, Lande 1987, Pulliam 1988, Harrison 1991, Howe et al. 1991, Pulliam and Danielson 1991). A fundamental question at the population level is to determine the factor or interaction of factors that limit population density or size. As noted by Newton (1991), two populations can have identical demographic schedules even though they can differ significantly in density or size. Given that the probability of extinction due to chance is inversely related to population size (Goodman 1987), it is important to understand the factor or factors that limit population size. For example, Widén (1989) summarized the results of several studies of goshawk nest density and found that densities were higher in areas with greater food availability. He concluded that the evidence strongly indicated that goshawks are normally limited by food availability and that foraging habitat may be more important than nesting habitat for goshawks in boreal forests. Similarly, Doyle and Smith (this volume) documented the importance of annual variation in food availability on goshawk reproduction in boreal forests. Thus, a knowledge of the external factors that limit population size is required if the goal of a particular conservation strategy is to implement management practices to increase population size (Newton 1991). It must be clearly noted that higher levels of organization, such as "populations", are often artifacts constructed by researchers for management purposes. In some cases populations can be defined based on demographic data, particularly in relatively more isolated areas such as the goshawk population on the Kaibab Plateau (Reynolds et al. this volume). However, often the area used to define a "population" is determined by administrative or geographic convenience. For example, we might refer to the goshawk "population" of a specific ranger district without knowledge of immigration or emigration rates.

Studies of variation in demographic rates related to habitat variation clearly indicate the importance of considering the relationship between fitness and habitat quality (Van Horne 1983, Pulliam 1988). As discussed previously, detailed studies of individuals can provide insight into the factors that influence fitness and can be used to interpret processes observed at more extensive scales. At the individual level, the spatial scale of the nesting area and foraging areas are important determinants of fitness. For example, Newton (1989b) documented that territory quality was a major factor associated with lifetime reproductive success in sparrowhawks. Individuals on high quality territories exhibited increased longevity, which resulted in increased lifetime reproductive success relative to individuals on lower quality territories.

Detailed, long-term investigations of individuals are also necessary to determine relationships between habitat quality and fitness. For example, Schnell (1958) and Boal and Mannan (this volume) provide detailed dietary studies from individual pairs of nesting goshawks. Similarly, Widén (1989) investigated habitat use by goshawks in relation to forest structure and prey abundance. Regarding nesting habitat, Woodbridge and Detrich (this volume) addressed habitat quality through a study of marked individuals that considered long-term territory occupancy rates across time and spatial scales that ranged from nest trees to nest stand size to clusters of nest stands.

To implement the approach we advocate would require initiating a long term demographic study of marked individuals. Within this demographic framework, intensive studies of individuals could be conducted that address the factors that influence fitness. This is the approach we have taken in our study of goshawk ecology in the Sierra Nevada. Similarly, Reynolds et al. (this volume) have taken this approach for their study of goshawk ecology on the Kaibab Plateau in Arizona. Based on an understanding of goshawk ecology over a variety of scales and levels of organization it might then be feasible to conduct especially insightful experimental manipulations. Silvicultural prescriptions could then be evaluated in an adaptive management context (Walters 1986, Walters and Holling 1990, Irwin and Wigley 1993) as to their effect on goshawk foraging and nesting habitat at the individual level and to their effect on the population at the landscape level. The results from studies such as that we outline would yield the extensive level data necessary for demographic analyses, as well as, provide the intensive level data needed to understand why goshawks do what they do.

It might be argued that, despite the apparent merits of the approach we outline, funding seldom will be available to support these kinds of intensive studies. Most wildlife research dollars traditionally support graduate students for 1–3 years of work. We argue that it would be better for such students to determine the factors that ultimately relate to survival and reproduction of only a few pairs of goshawks than it would be to produce yet another study of home range that is time- and site-specific. The former addresses ultimate causation and can build towards a more thorough understanding of goshawk biology, whereas the latter provides only a broad-scale, time- and site-specific description of a pattern and must speculate as to the cause and effect relationships.

In conclusion, there is an increased demand for critical data to design conservation plans for the Northern Goshawk. Rather than reinventing the wheel, goshawk researchers should reap the benefits of the valuable lessons learned in conservation planning for the Northern Spotted Owl (*Strix occidentalis caurina*) (Thomas et al. 1990, Carey et al. 1992, Verner 1992, Verner et al. 1992, Harrison et al. 1993), specifically, that the data most vitally needed for conservation planning require both intensive and extensive field studies. In meeting these data demands, researchers should strive to understand the causal mechanisms underlying the patterns observed.

ACKNOWLEDGMENTS

Our study is supported by the California Tahoe Conservancy and California Park Service. We are grateful to G. Walter for assistance and initiation of the study. B. McBride, L. Oechsli, A. Scales, D. Schaffe, and D. Ward provided field assistance during the first year of the project. We gratefully acknowledge the continued assistance of M. Sureda and T. Tennant. Computer services and logistical support have been provided by the Department of Avian Sciences at the University of California, Davis, and the Department of Environmental Science, Policy, and Management at the University of California, Berkeley. We also thank E. Burkett of the California Department of Fish and Game and R. Harris and K. Erwin of the Lake Tahoe Basin Management Unit, United States Forest Service, for permit approvals. W. Block, R. Hutto, and T. Kimmel provided constructive, critical reviews of an earlier draft.

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Studies in Avian Biology No. 16:12–17, 1994.

SUSTAINING FOREST HABITAT FOR THE NORTHERN GOSHAWK: A QUESTION OF SCALE

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Abstract. The nest area, post-fledging family area, and foraging area are critical home range components for maintaining Northern Goshawk (*Accipiter gentilis*) populations. Each of these forest components has a specific purpose in the life history of the Northern Goshawk and each contains several important attributes, ranging from forest structure to forest floor characteristics. The way in which home range components in a forest regenerate, develop, and die is highly variable, both temporally and spatially. Therefore, forests need to be regenerated and tended to ensure that a portion of a goshawk's home range is in old forests indefinitely. This can be best accomplished by analyzing and managing large tracts of forests as sustainable ecological units rather than managing smaller tracts of forests as individual home ranges.

Key Words: Accipiter gentilis; ecosystem analysis; forest management; home ranges; Northern Goshawk; sustainability; vegetative structural stage.

The Northern Goshawk (*Accipiter gentilis*) is a top-level consumer that occupies many forest types in the western United States. However, in some localities there are indications that populations are declining because of habitat loss due to tree harvesting (Herron et al. 1985, Crocker-Bedford 1990). Because little information exists on the number of breeding pairs in these forests, it is prudent to identify and conserve goshawk habitat to prevent populations from declining or individuals from becoming isolated. The identification and conservation of every goshawk home range is important (Reynolds et al. 1992). Forest management recommendations that sustain forest composition and structure necessary for goshawk habitat have been developed (Reynolds et al. 1992). These recommendations were primarily for use in the southwestern United States but they are being adapted for use in other areas of the West.

The nesting home range of goshawks contains three components: the nest area, the post-fledging family area, and the foraging area, each with its individual characteristics and management requirements. Forest management recommendations for the goshawk were developed on the premise that considerable information was available on nesting habitats (Schnell 1958, Reynolds and Meslow 1984). Throughout the western United States goshawks are known to nest and hunt successfully in a wide variety of forest types and structures (Fischer 1986, Kenward and Widén 1989), indicating that foraging habitat may be as closely tied to prey availability as to forest structure or composition. Another important component of goshawk habitat is the area surrounding the nest that is used by fledglings until they are no longer dependent on the adults for food. This intensively used area has been termed the post-fledging family area or PFA (Reynolds et al. 1992). If goshawks winter on or near their nesting home ranges, it should be possible to maintain goshawk populations by maintaining these three habitat components. This paper describes the difficulties of implementing the goshawk recommendations (Reynolds et al. 1992) and provides suggestions for analyzing and managing sustainable ecological units rather than individual goshawk home ranges.

NESTING HOME RANGE COMPONENTS

Nest areas have been thoroughly studied and are readily identified by vegetation structure (Reynolds et al. 1982, Reynolds 1983). Nest areas include one or more forest stands, several nests, and several landform characteristics. The size and shape of nest areas depend on topography, and on the availability of dense patches of large trees ranging in size from 8 to 12 ha. Within a given forest type, characteristics of nest areas can vary depending on forest productivity (defined as the amount of vegetation a site can support and how quickly it accumulates). Nest areas within highly productive forests have more trees and denser canopies than nest areas in less productive forests. Similarly, tree ages in a nest area can be highly variable, depending on forest type. For example, aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*) are much shorter-lived than western hemlock (*Tsuga heterophylla*) or western redcedar (*Thuja plicata*).

Surrounding the nest area is the PFA and foraging area mosaic. The PFA is a 170-ha (range = 120–240 ha) mosaic of large trees, large snags, midaged forests, small openings with a herbaceous understory, and large, downed logs. The foraging area is 2200 ha (range = 2000–2400 ha)

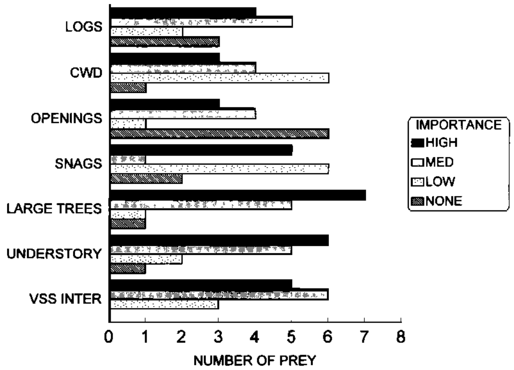

FIGURE 1. Relative importance of special habitat attributes for maintaining sustainable populations of 14 selected northern goshawk prey (Reynolds et al. 1992). Logs = downed logs >45 cm in diameter; CWD = coarse woody debris >7.5 cm in diameter; opening = breaks in forest canopy; snags = dead trees >45 cm in diameter and >9 m tall; large trees = live trees > 45 cm in diameter; understory = presence of herbaceous and shrubby species; VSS inter = interspersion of vegetative structural stages.

of forest that provides the food base for nesting goshawks. This area contains the habitat for larger birds and mammals that serve as prey. A wide variety of these animals are found in the diets of goshawks. They vary from mourning doves (*Zenaida macroura*) and Steller's jays (*Cyanocitta stelleri*) to chipmunks (*Tamias* spp.) and red squirrels (*Tamiasciurus hudsonicus*). The foraging area provides conditions for these animals to thrive, and also provides opportunities for the goshawk to hunt and capture them.

The foraging area is similar in structure to the PFA, with large trees, openings, snags, and downed logs interspersed throughout. An important component of both the PFA and foraging area is the development of hypogeous (underground) fungi, whose fruiting bodies provide food for many small animals. Many of these fungi are also ectomycorrhizal symbionts that play an important role in the uptake of water and nutrients by forest plants. Moreover, these organisms have a positive relationship with the amount of organic materials (e.g., humus, decayed wood) in the forest floor and surface mineral soils (Harvey et al. 1987). Therefore, maintaining ectomycorrhizae habitat through forest management practices will contribute to both the maintenance of forest vegetation and populations of small animals in both the PFA and foraging area.

RECOMMENDED FOREST CONDITIONS

Goshawks prey on over 50 species of birds and mammals throughout their western range. Reynolds et al. (1992) selected 14 prey species that were of particular importance to the goshawk in the Southwest. Using the habitat characteristics associated with high, medium, and low populations of these 14 species, they summarized the importance of snags, downed logs, woody debris, openings, large trees, understory vegetation, and interspersion of forest vegetative structural stages (VSS) in goshawk foraging areas. VSS is a generalized description of forest age and tree size (diameter) from seedling to old forests (see Thomas et al. 1979, Reynolds et al. 1992 for further discussion on forest structural stages). The six VSS for southwestern forests were defined as grass/forb/shrub, seedling, young forest, midaged forest, mature forest, and old forest. Large trees, understory herb and shrub development, and the interspersion of the VSS were the most important characteristics for maintaining high and medium populations of goshawk prey (Fig. 1).

Also important to the prey are the amount and characteristics of the VSS in the foraging area. Reynolds et al. (1992) determined that midaged to old forests were the most important of the VSS for maintaining medium and high populations of goshawk prey (Fig. 2). The prey needed to maintain medium and high populations of goshawks required a minimum of a 2800 ha landscape of midaged, mature, and old forests, interspersed with openings and patches of small trees (saplings and young trees). This analysis showed the importance of VSS, but did not quantify the distribution of the VSS needed in the PFA and foraging area.

DISTRIBUTION OF VSS

The structure of naturally occurring forests depends on the rate of regeneration, growth, and mortality of forest vegetation and all of the interactions affecting these processes. In western hemlock and similar forest types, it usually takes less than 3 years for new seedings to become established after a disturbance (Haig et al. 1941). Trees may take more than 25 years, however, to become established in some ponderosa pine (*Pinus ponderosa*) forests (Pearson 1950). Forest growth is also highly variable, depending on forest type, site quality, and forest density (Schmidt 1988, Edminster et al. 1991). Natural life expectancy can be as brief as 10 years for Gambel oak (*Quercus gambelii*) to more than 450 years for Engelmann spruce (*Picea engelmannii*), even though 80-year-old Gambel oak and 600-year-old Engelmann spruce have been reported (Brotherson et al. 1983, Alexander and Shepperd 1990). Fire, insects, and diseases also play important roles in the longevity of western forests.

Although late-seral and old forests are preferred for goshawk habitat, forest vegetation is not constant but is dynamic and ever changing. Moreover, trees are mortal. They die, regenerate, and grow, making it impossible to maintain all, or even a majority of a forest in late-seral and old stages. Because of the dynamic nature of forests, transitional structural stages must be present to continuously replace these old forests. Therefore, to sustain goshawk habitat in southwestern ponderosa pine forests, approximately 10 percent of the forest needs to be regenerated every 20 years. This assumes 20 years for tree establishment and a moderate level of forest density control occurring naturally by either fire, wind, snow, or by human management. Because of tree growth rates, approximately 19% can be maintained as young forest, 17% as midaged forest, 20% as mature forest, and 24% as old forest in which trees over 200 years old may exist (Bassett et al., this volume).

In shorter-lived lodgepole pine and aspen forests or in a western hemlock forest where longevity is longer the VSS distribution required to sustain these forests would be different than those required for a ponderosa pine forest. Because the VSS distribution required to perpetuate a forest varies by forest type and density, Reynolds et al. (1992) generalized the distribution of VSS for forests in the Southwest. These generalized VSS distributions are 10% in regeneration openings, 10% in saplings, 10% in young forests, 20% in midaged forests, 20% in mature forests, and 20% in old forests. Therefore, the distribution of VSS for sustaining goshawk habitat in the Southwest was not related to the goshawk or its prey, but was based on the forest productivity, dynamics, and biological limitations.

Combining the habitat attributes (e.g., snags, downed logs) (Fig. 1) and the desired VSS distribution (Fig. 2), a desired forest structure for maintaining a prey base for goshawks was determined. This information, in combination with the knowledge of the nesting habitat preferred by the goshawk, led to recommended management and forest conditions for the nesting home range components of nest, PFA, and foraging areas (Reynolds et al. 1992).

SUSTAINING GOSHAWK HABITAT

Because of the suspected loss of goshawk habitat (Crocker-Bedford 1990), sustaining the recommended VSS distribution is the management objective for most areas that contain goshawks. Present forest conditions can be compared to the desired distribution of VSS for each nesting home range, and appropriate management strategies can be developed to sustain the desired forest structure. For example, if the present conditions of a foraging area in a single-species forest (e.g., ponderosa pine) had an excess of mature and old forest compared to the desired VSS distribution, regeneration could be planned to ensure a continual movement of trees through the VSS (Fig. 3). Alternatively, if young and midaged forests were in excess, these VSS could be thinned, freeing them to grow into the mature and old forest size-classes (Fig. 3). These examples of management options for sustaining goshawk habitat are for single-species forests with relatively simple structures.

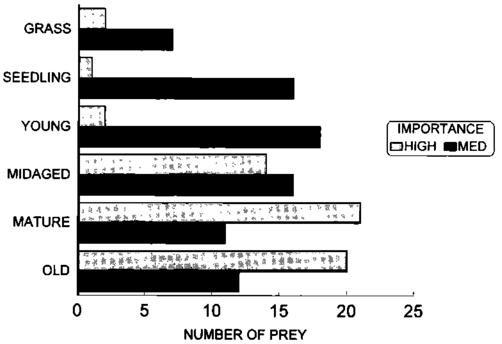

FIGURE 2. Relative importance of vegetative structural stages for habitat of selected prey species (Reynolds et al. 1992). The VSS were defined as grass = grass/forb/shrub and trees <2.5 cm in diameter; seedling = 2.6–13 cm trees; young = 14–30 cm trees; midaged = 31–46 cm trees; mature = 47–61 cm trees; old = >62 cm trees.

During the past 200 years most of the forests of the Southwest have been influenced by fire suppression, timber harvest, and grazing by both domestic animals and wildlife (Dieterich 1983, Brawn and Balda 1988, Stein 1988). These influences have affected forest successional processes, creating forests that often have high tree densities, multiple forest canopies, and species compositions outside the range of natural variability, making them susceptible to disease and insect attack, and to forest replacing wildfires (Habeck and Mutch, 1973). If the recommended VSS distribution for the goshawk is applied based on the proportion of the foraging area in the various vegetative structural stages without regard to species composition, treatments could create an unstable forest environment. For example, if the present forest conditions showed an excess of mature and old ponderosa pine over a smaller size class of white fir (*Abies concolor*) and there was a shortage of midaged and young trees compared to the desired forest structure, the preferred treatment could be to remove the large ponderosa pine, making the distribution conform to the desired VSS. But the consequences of these actions would be a justification to harvest the large trees, creating a forest prone

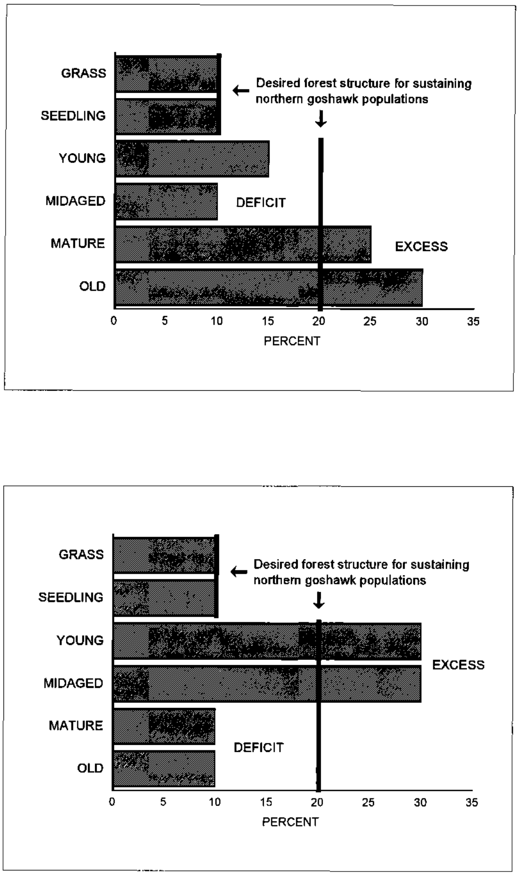

FIGURE 3. The top figure illustrates the distribution of the vegetative structural stages (VSS) for a hypothetical goshawk foraging area compared to the desired distribution as presented by Reynolds et al. (1992). The example shows an excess of trees in the mature and old-forest classes and a deficit in the young and midaged forest classes. Management activities in a forest with this structure could be designed to develop more young and midaged forests through regenerating a portion of the mature and old classes. The lower figure illustrates a forest structure that would benefit from thinning of the young and midaged VSS encouraging the development of mature and old VSS.

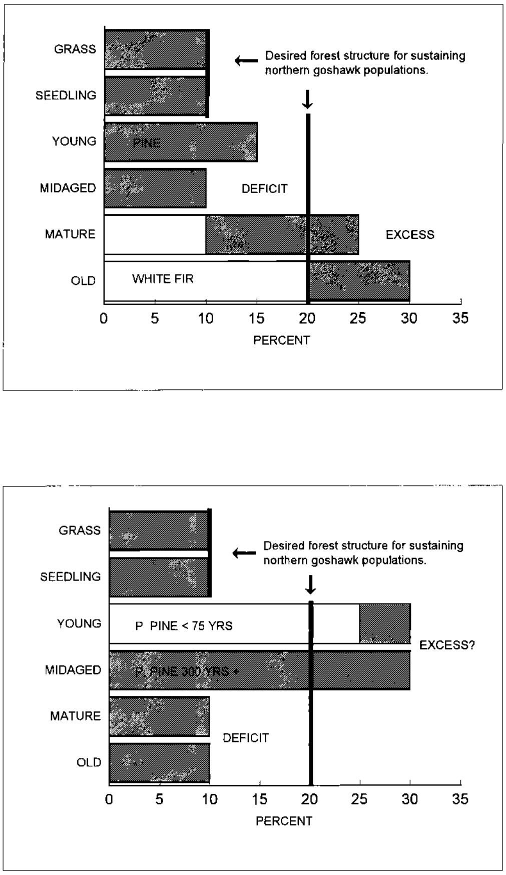

FIGURE 4. The distribution of the vegetative structural stages (VSS) for a hypothetical goshawk foraging area compared to the desired distribution as presented by Reynolds et al. (1992). The top example shows an excess of trees in the mature and old forest classes but a portion of these classes are white fir, a species prone to disease and insect attack. If the ponderosa pine were removed, leaving these trees, an undesirable and unstable forest susceptible to insect and disease attack and stand replacing fires would result. The bottom example shows an excess of trees in the young and midaged VSS but a portion of the trees are older than the life expectancy for ponderosa pine. If these trees were thinned, they probably would not grow to become large old trees.

to insect and disease attack, overcrowding, catastrophic wildfire, and other changes outside the range of natural variability (Habeck 1990) (Fig. 4).

In addition, the VSS classes are based on tree diameter and assume a good correlation between tree diameter and age, (e.g., the larger the tree is, the older it is). This is not always the case, as tree growth can stagnate when forest densities remain high for long periods (50 years or more). Small-diameter lodgepole pine, ponderosa pine, western hemlock, and western redcedar trees can easily be old (Pearson 1950, Lotan and Perry 1983, Graham 1988). If the VSS distribution had an excess of "young and midaged" trees that were actually old, thinning these old trees in the expectation they will become large old trees would not sustain the desired forest (Fig. 4)

Goshawks are habitat generalists and live in a variety of forest types such as aspen, lodgepole pine, ponderosa pine, western hemlock, western redcedar, Douglas-fir (*Pseudotsuga menziesii*), and several other western forest types. For example, the VSS distribution for maintaining a lodgepole forest might contain 5% in openings, and because of the biological limitations of this forest type only 10% might be maintained in old forests. To insure that at least 440 ha of a foraging area is always in old forests, a larger amount of younger and midaged transitional vegetation structures would be needed, increasing the total size of the foraging area. Therefore, forest type, length of the regeneration period, tree growth rate, and tree longevity will dictate how much area is required to insure enough old forest is available to supply the prey base for a goshawk family.

SPATIAL ARRANGEMENT OF FORAGING AREAS

Reynolds et al. (1992) recognized that the extent of overlap between foraging areas for adjacent pairs of goshawks is unknown. When PFAs are closely arranged, it is impossible to establish separate 2200-ha foraging areas for each PFA. In this situation, managers tend to reduce the size of the foraging areas but continue to prescribe a balanced VSS distribution on areas as small as 600 ha. This approach simplifies the application and verification of the VSS recommendations, but does not consider that the rationale for the VSS distribution is to regenerate and provide transitional vegetation structures to maintain a large component of old forests in each foraging area. Also, this approach divides the forest into small, discrete units that may be isolated from other portions of the forest limiting the ability for goshawks to forage for food. In addition, there is probably some physical, biological, or climatic reason why the nest areas were clustered.

A better approach to managing adjacent nest areas and associated foraging areas that overlap is to group them into larger management units, balancing the VSS distribution for the entire unit, yet maintaining the integrity of the recommendations. For example, if three nest areas were grouped, a 7000-ha unit might be formed; six nest areas could be grouped to form a 12,000-ha unit. These management units could be variable in size with boundaries defined by vegetation changes, physiographic differences, or some other well-defined structural division. This approach would be better than trying to manage an ever-changing forest of small, potentially fragmented foraging areas.

FOREST DYNAMICS

The forests of the West are changing every day. In the 10,000 years since the Pleistocene, over 2000 fires could have burned in a ponderosa pine forest if the fire return interval was five years, and over 20 forest-replacing fires could have occurred if the interval was 500 years. Surface fire intervals in much of the ponderosa pine and lodgepole pine forests were less than five years, but in the lodgepole pine forests stand replacement fires occurred every 40 to 100 years (Arno 1980). Likewise, the sizes of forest patches caused by fires varied, as did such things as the frequency of large scale bark beetle epidemics. To a limited extent, the natural range of these processes can be determined for many western forests. By understanding the range of natural conditions to which the goshawk, its prey, and all of the other plants and animals in an ecosystem are adapted, better management strategies can be devised. Not only will they sustain the goshawk but they may also perpetuate the ecosystem components associated with the goshawk.

ECOSYSTEM ANALYSIS

Instead of managing goshawk home ranges or even groups of goshawk home ranges, it would be more ecologically sound to develop management strategies for large geographic areas (approximately 100,000 ha). The goshawk recommendations produced by Reynolds et al. (1992) were an attempt to manage forests on a landscape level, but they have been criticized for not considering many of the other animals and plants in the ecosystems of the Southwest.

Determining the historical variation of vegetation structures for large geographic areas in the Southwest and comparing them to the existing conditions might offer a rational, ecological method of planning management of these forests. This comparison could consider abiotic and biotic components at various scales (e.g., watershed to river basin) and time period (e.g., 100 years in the past to 100 years in the future). Using these types of coarse filter analyses the Nature Conservancy has estimated that 85 to 90 percent of the species might be saved this way (Hunter et al. 1988).

Therefore, instead of analyzing 2200-ha goshawk foraging areas independently or grouping home ranges, it would be more ecologically sound to manage and analyze landscapes. Small 2200-ha forest landscape units would not contain many ecosystem processes and are not large enough to contain the natural range of variation of insect outbreaks or stand-replacing fires. Also, the 2200-ha foraging areas may be too small to support a goshawk family year-round. Therefore, if the goshawk is going to be sustained in the West, more than nesting home ranges need to be considered. Entire ecological units need to be analyzed and managed across vegetation types, land ownership, and political boundaries.

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Studies in Avian Biology No. 16:18–23, 1994.

ASSESSMENT OF GOSHAWK NEST AREA HABITAT USING STAND DENSITY INDEX

ROBERT J. LILIEHOLM, JAMES N. LONG, AND SUSAN PATLA

Abstract. The manipulation of stand density to create a specified stand structure in the future represents a powerful tool in wildlife habitat management. Controlling stand density, and ultimately stand structure, through initial tree spacing and/or subsequent thinning is critical to achieving many specific stand management objectives. Indices of relative stand density, based on average tree size (e.g., mean weight, volume, height, or diameter) and stand density (e.g., trees per hectare) are useful in characterizing current and future stand structure. This paper describes Reineke's stand density index (SDI), and demonstrates its application to the management of Northern Goshawk (*Accipiter gentilis*) nest area habitat.

Key Words: *Accipiter gentilis*; Douglas-fir; Northern Goshawk; *Pseudotsuga menziesii;* Reineke's stand density index; thinning; wildlife.

Setting aside specific habitat for threatened, endangered, and sensitive wildlife is often only a temporary protection measure because plant communities are dynamic and change over time. Furthermore, natural disturbances such as fire and hurricanes often transcend protected area boundaries. While maintaining existing suitable habitat is an important component of species management, increasing populations or providing for the long-term viability of a species requires that suitable habitat be created and/or maintained in the landscape in anticipation of succession and natural disturbance. Because suitable habitat may require decades or even centuries to develop, proactive management requires careful planning that considers how plant community structure changes through time and how such changes affect habitat suitability.

Northern Goshawks (*Accipiter gentilis*), the largest of the North American *Accipiter* hawks, occur across the northern hemisphere in coniferous and mixed forests (Wattel 1981). The goshawk is a species of increasing concern due to possible population declines, and the association of nesting goshawks with late successional forest (Shuster 1980, Hayward and Escano 1989, Reynolds 1989, Crocker-Bedford 1990) indicates a potential sensitivity to management practices that alter existing mature and old-growth forest. As a result, managers need recommendations on how to create and maintain suitable nesting habitat as part of broader habitat management strategies for maintaining goshawk populations.

Silviculturists routinely control stand density to influence tree species composition, stand structure, tree bole shape, rate of tree diameter growth, and stand growth (Daniel et al. 1979). Although these factors are important for meeting objectives of producing timber commodities, they may also be important determinants for producing wildlife habitat.

In studies of wildlife habitat, stand basal area (per-hectare cross-sectional area of the trees in a stand measured at breast height, 1.3 m above the ground) is often used as a measure of stand density. Basal area, however, is of limited use in characterizing stand structure because it fails to convey information on the relationship between tree density and tree size (Daniel et al. 1979, Wilson 1979). McTague and Patton (1989) found that stand basal area, by itself, describes wildlife cover poorly and suggested Reineke's (1933) stand density index (SDI) as a potentially better tool. Smith and Long (1987) used SDI to characterize the structure of lodgepole pine stands for elk hiding and summer thermal cover guidelines. Moore and Deiter (1992) found SDI to be a better predictor of understory forage production in ponderosa pine (*Pinus ponderosa*) stands than basal area. Lilieholm et al. (1993) used SDI to integrate timber and goshawk habitat objectives in the management of Douglas-fir stands.

This paper describes the use of SDI as a method to assess goshawk nest area habitat and guide management practices intended to create forest stand structures similar to those found in nest areas. While other factors such as slope, aspect, distance to water, nest area size and spacing, and foraging habitat must also be considered (Hennessy 1978, Shuster 1980, Reynolds 1983), this approach recognizes the importance of controlling stand structure as a necessary condition of nesting habitat. Indeed, Newton (1986) found stand structure and density to be the most important factors determining stand suitability for nesting goshawks.

MODELING THE DEVELOPMENT OF FOREST STRUCTURE WITH STAND DENSITY INDEX

Controlling stand density through initial tree spacing and/or subsequent thinning is critical to

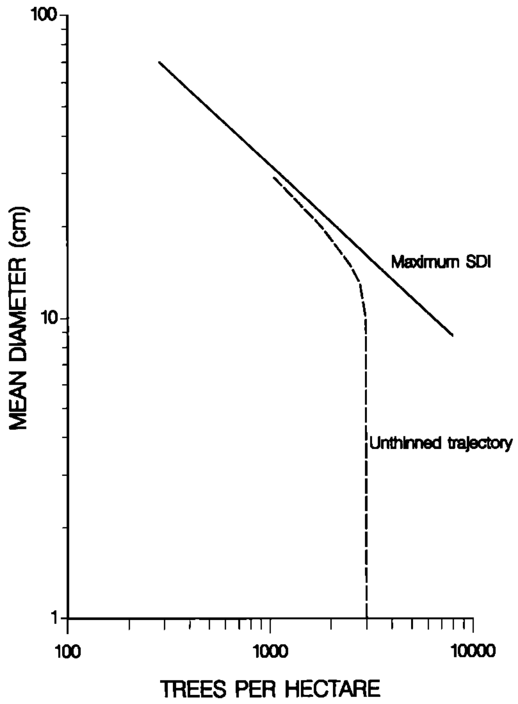

FIGURE 1. Relationship between mean tree size and density on log-log scales. The dashed line represents changing mean size and density for a hypothetical self-thinning Douglas-fir stand.

achieving many stand management objectives. Various indexes of relative density have been developed to characterize current and future stand structure. Typically these expressions of relative density integrate average tree size (e.g., mean weight, volume, height, or diameter) and stand density (e.g., trees per hectare) (Curtis 1971, Drew and Flewelling 1979, Wilson 1979).

One widely used index of relative density is SDI. SDI represents a quantitative measure of stand density that is based entirely on average tree size and density (Long 1985, Long and Daniel 1990). SDI expresses the density in trees per hectare (TPH) that a stand would have if its quadratic mean stand diameter (DBH_Q) were 25 cm. SDI is calculated as:

$$SDI = TPH(DBH_Q/25)^{1.6}$$

A similar relationship between mean size and density is observed for many herbaceous and tree species and is commonly referred to as the "−3/2 power law" in the forest ecology literature. Plotting quadratic mean diameter and trees per hectare on log-log scales reveals a maximum size–density line with a slope of approximately −0.625 (the solid line in Fig. 1). The dashed line on the diagram traces the development of an individual hypothetical stand through time. The stand begins its development near the horizontal axis of Figure 1. Note that the newly established stand has a high stocking rate (3000 TPH) and small average diameter (1 cm). As the stand develops and individual trees grow, mean size increases. As the stand continues to grow, competition-induced mortality results in decreased stocking, indicated by the movement of the trajectory upward and to the left (i.e., continued increase in mean size and decreasing density with the onset of self-thinning).

The size–density relationship described above is largely independent of site quality and stand age. While the slope of the maximum density line is assumed to be constant, its level or distance from the origin will vary for different tree species. For example, the maximum size–density lines for shade-tolerant species are typically higher than those of shade-intolerant species, and the maximum size–density lines for coniferous species are typically higher than those of hardwood species (White and Harper 1970).

Because SDI is largely independent of site quality, stand age, and stand development history, it can be used to compare the relative densities of different stands of the same species directly (Daniel et al. 1979). Density comparisons between stands of different species can be made with $SDI_{\%MAX}$, a ratio of the observed SDI and the maximum SDI (SDI_{MAX}) for the species:

$$SDI_{\%MAX} = [SDI/SDI_{MAX}] \cdot 100$$

Three threshold $SDI_{\%MAX}$ values are commonly used to guide stand management prescriptions (Long 1985). An $SDI_{\%MAX}$ of 25% approximates the onset of inter-tree competition, canopy closure, and the beginning of self-pruning (i.e., the death of branches in the lower crown). An $SDI_{\%MAX}$ of 35% approximates the lower limit of full site occupancy. An $SDI_{\%MAX}$ of 60% is associated with substantially reduced tree vigor and the onset of tree mortality induced by inter-tree competition (Fig. 2).

Silviculturists can use these thresholds to design treatments to guide stand development to meet various stand management objectives. For example, a density management regime could be designed to capture the volume production potential of a site by keeping a stand above the $SDI_{\%MAX}$ of 25% (i.e., full site occupancy) and below the $SDI_{\%MAX}$ of 60% to avoid competition-induced mortality (Long 1985).

In addition, a wide variety of stand structures could be developed using SDI as a guide. For example, a Douglas-fir (*Pseudotsuga menziesii*) stand currently having a DBH_Q of 1 cm and 3000 TPH will follow a typical self-thinning trajectory if left undisturbed (Fig. 3). An alternative stand

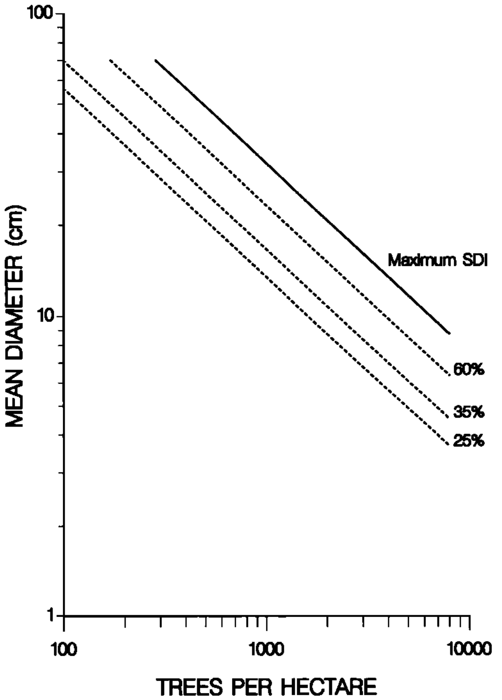

FIGURE 2. Relative density lines indicating 25%, 35%, 60% and 100% of the maximum stand density.

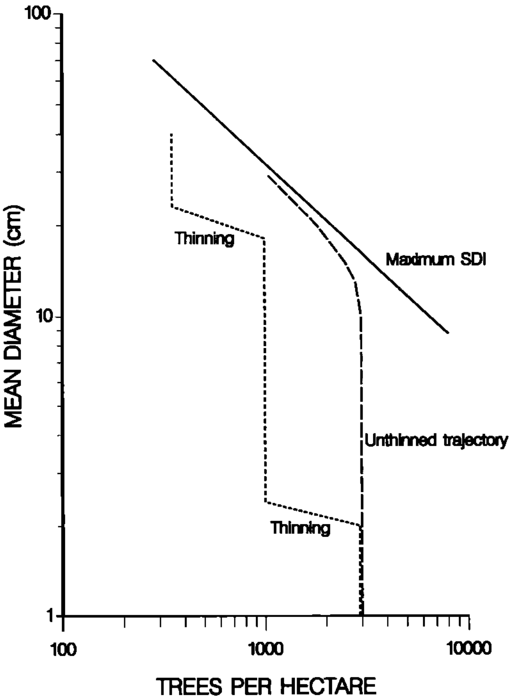

FIGURE 3. Two hypothetical stand density management regimes for Douglas-fir: one represents a natural, unthinned regime; the other includes two planned thinnings.

development trajectory would result from a thinning treatment that reduces density to 1000 TPH, followed by a later thinning that reduces density to 325 TPH. These two density management regimes will lead to fundamentally different future stand structures. For example, the unthinned regime will result in a stand with many relatively small diameter, slow growing trees with small live crowns. In contrast, the thinning regime will result in a stand with relatively large, deep crowned, fast growing trees.

APPLICATIONS TO GOSHAWK NEST AREA REQUIREMENTS

While goshawks nest in many forest types, the vegetative structure and topographic-context of nest areas are relatively consistent (Hayward and Escano 1989), with nests typically built in mature stands and located in trees ranging from 20–75 cm DBH (Eng and Gullion 1962, McGowan 1975, Reynolds 1975, Moore 1980, McCarthy et al. 1989).

A typical nest area is a 8–10 ha forested area of similar structure surrounding the nest tree (Reynolds et al. 1992). Stand densities average 450 TPH and range from 270 to 1530 TPH (Reynolds et al. 1982), and canopy cover ranges from 40 to 89 percent, with the higher portion of the range preferred (Hennessy 1978, Moore 1980, Shuster 1980, Hall 1982, Hayward and Escano 1989, McCarthy et al. 1989). Nest sites typically have an open understory, although variable conditions have been reported (Reynolds et al. 1982, Crocker-Bedford and Chaney 1988).

To apply SDI to the management of goshawk nest area habitat, it is first necessary to describe the range of stand structural conditions that are considered to be suitable nesting habitat. For example, Figure 4 shows data from 31 goshawk nest areas in Douglas-fir forests on the Targhee National Forest in Idaho. Nest area data are based on a 20-m radium plot centered on the nest tree; SDI calculations are based on trees greater than 17.8 cm DBH. The DBH_Q of the nest areas ranged from 25–47 cm. The lower limit of this range could be used to establish a minimum DBH_Q for goshawk nesting habitat in these forests. Similarly, the nest areas all lie between $SDI_{\%MAX}$ limits of 23 and 60, suggesting a range of relative densities for habitat based on stand structure.

Once an appropriate range of stand structures describing nest area attributes for a given forest type and area have been delineated, minimum DBH_Q and upper and lower levels of SDI could guide management practices to ensure the continual availability of stands suitable for nesting

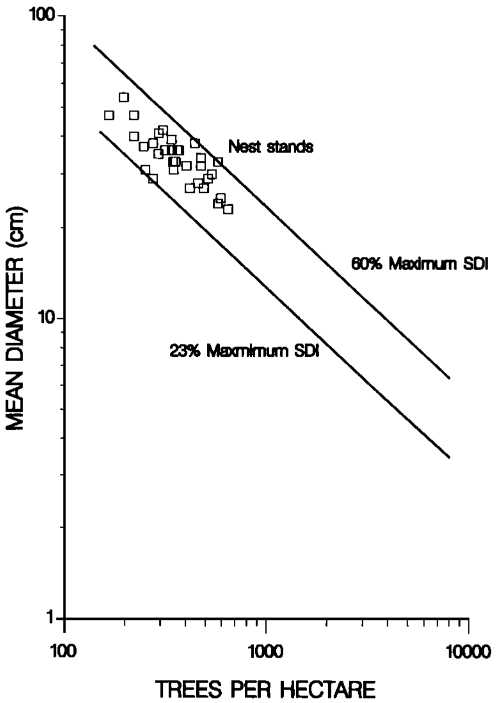

FIGURE 4. Goshawk nest stand data for Douglas-fir stands in southeastern Idaho. The data are bounded by lines representing 23% and 60% of the maximum SDI, which correspond to the minimum and maximum observed relative stand densities.

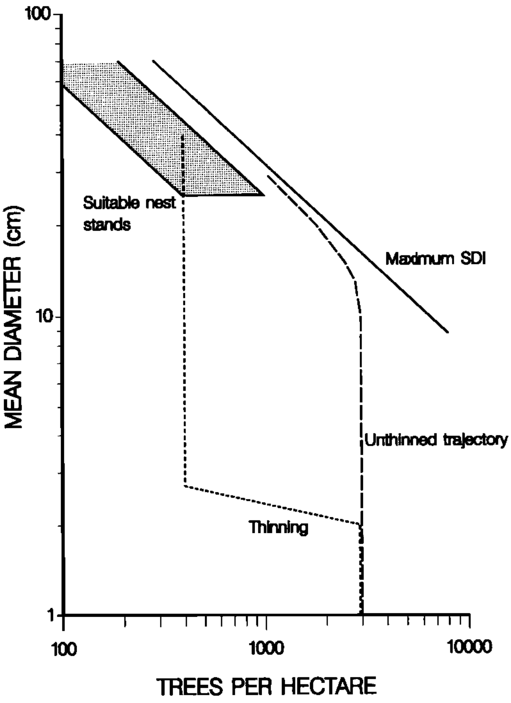

FIGURE 5. Two hypothetical stand density management regimes for Douglas-fir. The shaded area denotes target goshawk nest area structure.

goshawks. For example, management regimes for Douglas-fir forests similar to those found on the Targhee could be developed using the data presented above. If the stand has no artificial or natural stocking control (e.g., thinning, fire, snow, wind), it will result in a typical self-thinning trajectory and will probably fail to provide structure suitable for goshawk nesting (Fig. 5). By thinning the stand at an early age, the stand will likely develop with diameters and relative densities that will provide goshawk nesting habitat. Subsequent thinnings could be used to maintain the stand within this range of suitable relative densities as described in Lilieholm et al. (1993).

An additional result of early thinning is that it will promote rapid individual tree growth, which can substantially reduce the time required for the stand to achieve the minimum DBH_Q (McCarter and Long 1986). For example, assuming a moderately productive forest with a site index of 25 m, the unthinned alternative may require nearly 90 years to achieve a DBH_Q of 25 cm. In contrast, the lower relative densities associated with the thinning alternative would result in a DBH_Q of 25 cm when the stand was about 65 years old.

DISCUSSION

One of the fundamental concepts in silviculture is that site occupancy must be at least broadly related to the size and number of trees on a unit area, and that a given degree of site occupancy can result from either many small trees or fewer large trees. SDI is one of several commonly used expressions of relative density that effectively integrates mean size and density (e.g., Curtis 1982, West 1982). The ecological importance and silvicultural utility of expressions of relative density such as SDI rest on the proposition that stands with the same relative density, regardless of differences in age, site quality, or mean size and density, have equal levels of competition, site occupancy, and other important population-level attributes such as crown closure, self-pruning, and differentiation of crown classes (Reineke 1933, Curtis 1970, Drew and Flewelling 1979, Smith and Long 1987).

An important aspect of habitat management is the design and implementation of strategies to achieve desired future stand conditions. Depending on the specific requirements of species and the objectives of management, desired future conditions may represent a wide range of stand structures. Designing effective and efficient silvicultural prescriptions requires accurate predictions about future stand development. SDI allows characterization of important elements of both current and future stand structure. The mean tree size and density of stands representing suitable habitat (e.g., active goshawk nest areas) can be used as target stand structures and models of desired future condition.

The manipulation of stand density to create a specified stand structure in the future represents a powerful tool in wildlife habitat management. This certainly appears to be true for goshawks, given the importance of stand structure in determining nest area suitability. Thinning can be used to place a dense young stand on a trajectory designed to produce a target DBH_Q and SDI (Fig. 5). This sort of management strategy could be effective in increasing the amount of suitable habitat or even providing it in areas where none currently exists. Implicit in this argument is the assumption that the important elements of stand structure are not directly dependent on stand age (e.g., goshawks respond to tree size and density rather than a stand's actual age).

The method presented provides necessary but probably not sufficient habitat requirements for nesting goshawks, since providing stand structure suitable for nesting is but one of several habitat needs. Other important considerations include the availability of foraging habitat and possibly water, human disturbance, nest predation, topographic location and features, and intra and inter-specific competition for nests and nesting areas (see, for example, Shuster 1977, Hennessy 1978, Call 1979, Jones 1979, Reynolds 1983, Hayward and Escano 1989, Crocker-Bedford 1990, and Reynolds et al. 1992). Biological constraints may influence applications as well. For example, increased risk of bark beetle attacks above certain combinations of diameter and stand density would affect the range of trajectories considered (Cochran 1992).

The spatial and temporal distribution of nest areas must also be considered. For example, planning for potential goshawk nest areas should include alternate nesting sites because goshawks seldom use the same nest tree in consecutive years, but rather rotate between two or three alternate nests located either within the same stand or in other stands (Crocker-Bedford and Chaney 1988). Reynolds et al. (1992) suggest the provision of at least three suitable nest areas within each goshawk home range. Furthermore, to provide future nesting opportunities, managers must ensure that potential goshawk nest areas are at various stages of development so that as nest areas grow out of suitability or are otherwise lost, new areas are ready to take their place. In this role, SDI may also be useful in extending stand structure to mosaics of small groups within home ranges and even nest areas (Long and Daniel 1990, Cochran 1992).

ACKNOWLEDGMENTS

This is Journal Paper No. 4456 of the Utah Agricultural Experiment Station, Utah State University, Logan.

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Studies in Avian Biology No. 16:24–30, 1994.

NORTHERN GOSHAWK BROADCAST SURVEYS: HAWK RESPONSE VARIABLES AND SURVEY COST

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Abstract. We examined responses of Northern Goshawks (*Accipter gentilis*) to taped broadcast calls of conspecifics in tree-harvest areas and around alternate goshawk nests on Kaibab National Forest, Arizona, in 1991 and 1992. Forest areas totaling 476 km^2 were systematically surveyed for goshawks. Ninety responses by adult and juvenile goshawks were elicited and 15 active nests were located. No difference in response rates between sexes was detected. Adult males, however, tended to approach the broadcaster without vocalizing, whereas adult females approached while vocalizing. Our success in finding active nests after getting responses from females was greater than after male responses. Goshawks responded more often to broadcasts during the nestling (2.0 responses/100 stations) than fledgling (1.0 responses/100 stations) period. During the fledgling period, adults were more likely to respond to broadcasts than juveniles. Total costs associated with our surveys for goshawks were $58–82 per km^2 and $4.15–5.80 per broadcast station, depending on salaries.

Key Words: *Accipiter gentilis*; broadcast surveys; Kaibab Plateau; Northern Goshawk; vocalization.

In the southwestern United States, Northern Goshawks (*Accipiter gentilis*) use ponderosa pine (*Pinus ponderosa*), mixed coniferous-deciduous forests, spruce-fir, and pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodlands. These forests are subject to structural and compositional changes due to plant growth and succession, and to various natural (e.g., fire) and anthropogenic (e.g., tree harvest, grazing) disturbances that may affect goshawk reproductive success (Reynolds 1983, 1989; Crocker-Bedford 1990, Reynolds et al. 1992). In 1982 the Southwestern Region of the USDA Forest Service designated the goshawk as a sensitive species. Reynolds et al. (1992) suggested habitat-management strategies for both goshawks and their prey in ponderosa pine and mixed-species forests. The first step in the management of habitat for goshawks is locating their nests.

Broadcasting of raptor vocalizations has been used to locate goshawk nests (Kimmel and Yahner 1990, Mosher et al. 1990, Kennedy and Stahlecker 1993). Broadcasts elicit vocal and/or visual cues of raptors, which can then be followed with nest searches. During the 1991–1992 breeding seasons we conducted broadcast surveys for goshawks on 12 proposed tree-harvest areas on the North Kaibab Ranger District (NKRD) in northern Arizona.

METHODS

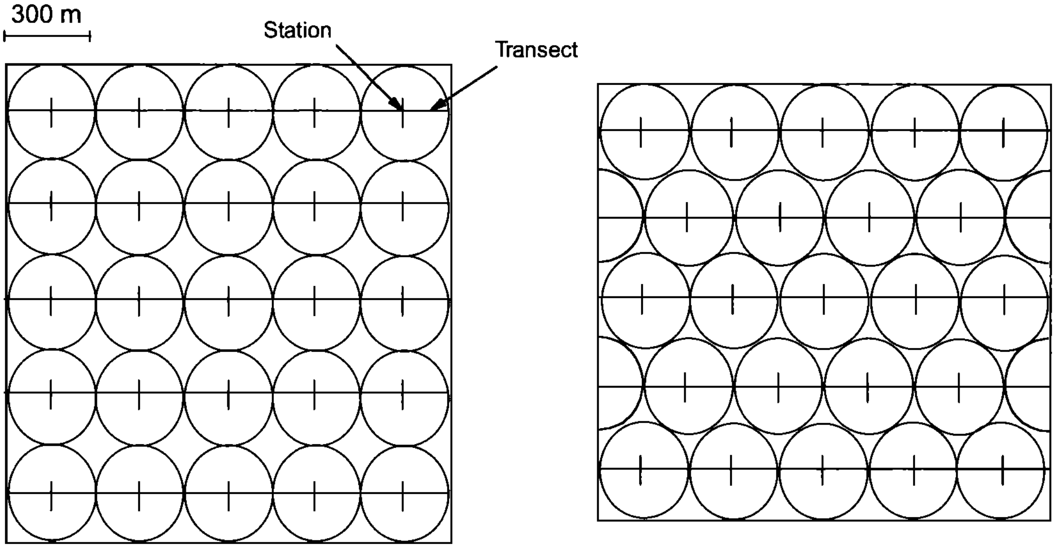
SURVEY AREA

Areas surveyed for goshawks were on the Kaibab Plateau, Coconino County, Arizona. The Plateau is bounded by escarpments and steep slopes that descend into the Grand Canyon of the Colorado River on the south side and desert scrublands elsewhere. Forested areas on the NKRD, which encompasses the northern portion of the Plateau, total approximately 3000 km^2 (Rassmussen 1941). Forests on the Kaibab Plateau consist of a band of pinyon-juniper (1103 km^2) at elevations between 1830–2075 m, ponderosa pine forests (624 km^2) between 2075–2500 m elevation, and mixed-conifer forests (*Abies concolor, Picea engelmannii, Populus tremuloides, Pseudotsuga menziesii*) (605 km^2) above 2500 m (Rasmussen 1941). A complete description of the study area was provided in Reynolds et al. (this volume).

BROADCASTS

We used a modification of the Kennedy and Stahlecker (unpubl. data) broadcast protocol to survey for goshawks. Goshawk vocalizations were broadcast from stations established on parallel transects, and their responses were followed by searches for active nests (containing eggs or young). Responses were classified as (1) vocalization only, (2) sighting only, or (3) vocalization and sighting. We used cassette players (1991 surveys) and portable, long-range callers (1992 surveys) to broadcast goshawk vocalizations. Cassettes were played at a volume that produced a sound audible to the human ear at a minimum of 150 m from the source. Rain, winds exceeding 20 km/h, and occasional vehicle traffic resulted in delay or termination of the survey effort because of the interference with response detection.

Surveys were only conducted during the nestling and fledgling periods when goshawk response rates to broadcasts are highest (Kennedy and Stahlecker 1993). Alarm calls were used during the nestling period and food-begging calls during the fledgling period. For broadcast transects, boundaries of all tree-harvest areas were transcribed onto 7.5-min USGS quadrangle maps. Transects were then drawn with an east-west or north-south orientation depending on topography and accessibility, with both ends of all transects extended 800 m beyond the harvest area boundaries. Distances between transects and stations, as described in Kennedy and Stahlecker (unpubl. data), were modified to increase the theoretical coverage of broadcasts from 78.5 to 90.6% of surveyed areas (Fig. 1). Modifications were that parallel transects were 260 m (vs. 300 m) apart;



A. 25 STATIONS, 1500 X1500 m, 78.5% COVERAGE

B. 25 STATIONS, 1300 X 1500 m, 90.6% COVERAGE

FIGURE 1. Theoretical area of coverage (circles) using (A) Kennedy and Stahlecker's (unpubl. data) transect and station layout, vs. (B) the modified layout used in this study.

and broadcast stations were 300 m (vs. 150 m) apart on each transect and were staggered by 150 m on adjacent transects.

All broadcast stations within 800 m of active nests were deleted from the survey effort. In addition, we did not survey stations in large, treeless openings (diameter > 400 m), on sheer canyon walls, or in stands of Gambel's oak (*Quercus gambelii*), New Mexican locust (*Robinia neomexicana*), or pinyon pine-Rocky Mountain juniper (*J. scopulorum*) that did not contain large ponderosa pine.

Prior to surveys, broadcast personnel were trained in the broadcast technique, field methods, and identification of the calls and physical characteristics of goshawks, Cooper's (*A. cooperii*), Sharp-shinned (*A. striatus*), and Red-tailed (*Buteo jamaicensis*) hawks, and goshawk mimics (e.g., *Cyanocitta* spp.). Observers used the 7.5-min USGS maps with marked transects and stations in the field. At each station, the surveyor broadcasted three times in three directions. First, the surveyor rotated 60° right or left (determined randomly) from the direction of travel, played the taped goshawk vocalization for 10 sec, and then listened and searched in all directions for hawk responses for 30 sec. The broadcast and observation procedures were then repeated two more times after rotating 120° from the previous broadcast. Broadcasts were conducted from 3 June to 12 August between 08:00 and 16:30 MDT.

To avoid misidentifying broadcasts of co-workers, surveyors worked at least two transects apart. When they elicited a response, the following were noted: transect, station, habitat, time, species, sex and age of the hawk, response type, bearing, and estimated initial distance to the responding hawk. All goshawk, and Cooper's, Sharp-shinned, and Red-tailed hawk vocalizations and sightings detected between stations were also recorded. All responses by *Accipiter* spp. were immediately followed with a search for nests within a 200-m radius of the response. Responses by the same species at consecutive stations on a transect were treated as one response.

In 1992, broadcast surveys outside timber harvest areas were conducted within 2 km of three goshawk nests that were active in 1991 but inactive in 1992 to search for alternate nests. An alternate nest is one of several nests used within a goshawk's home range (Reynolds and Wight 1978). In each area, transect and station layout and the protocol described above were used.

Hawk Responses

Chi-square goodness of fit tests (Ott 1984) were used to test the frequency of goshawk responses between sexes, ages (adult, juvenile), nesting stages (nestling, fledgling) (weighted by the number of stations surveyed during stage), and type of vocalizations broadcasted (alarm, food-begging) (weighted by number of stations surveyed with that vocalization) against the null hypothesis of equal frequencies between categories. During 1992 the alarm call was inadvertently used during the first nine days of the fledgling stage. To determine the effect of this, we performed simultaneous tests (Goodman 1964) of response rates to (1) alarm call use (2110 stations) during the nestling stage, (2) alarm call use (1058 stations) during the fledgling stage, and (3) food-begging call use (3681 stations) during the fledgling stage, after standardizing by number of stations surveyed in each category. We also tested whether the success of finding a goshawk nest in follow-up nest searches was independent of the hawk's sex and response type. To examine trends in response parameters, Fisher's Exact test (Proc FREQ; SAS Institute 1987) was used in multi-way comparisons of (1) response type (vocal non-approach, silent approach, vocal approach) by sex, by age, by nesting stage, and by type of broadcast vocalization; and (2) sex of the responder by nesting stage, and by type of vocalization broadcast. We did not test for differences in goshawk response frequency among times of day. Kimmel and Yahner (1990) found that response rates were independent of time of day.

Among-species comparisons of responses of goshawks, and Cooper's, Sharp-shinned, and Red-tailed hawks included the frequency of response type, habitat in which the response occurred, and mean distance from broadcast station to responding individual. In multi-species comparisons, Fisher's Exact Test (Proc FREQ; SAS Institute 1987) was used to test for differences among frequencies of response variables, and the Kruskal-Wallis Test (Proc NPAR1WAY; SAS Institute 1987) was used to test for differences in mean response distances among species.

SURVEY EFFORT AND ASSOCIATED COSTS

We estimated the effort (surveyor-hours) and costs of using the broadcast survey procedure only during 1992 broadcast surveys. Our estimates included preparing survey maps, training, commuting, conducting surveys, daily data transcription to master 7.5-min maps, testing and maintaining equipment, data entry, checking and analysis, and reporting of results. Expenses are based on salaries, vehicle rents and mileage, and equipment costs and maintenance.

RESULTS

In 1991 we surveyed proposed tree-harvest sites (total area = 183.7 km^2) in the Big Burro, Jack, Jolly, Burnt Saddle-Sowat, Lookout Canyon, Paris, and Stina areas. In 1992 we surveyed proposed tree-harvest sites (total area = 219.5 km^2 + 45.2 km^2 beyond harvest boundaries) in the West Lake, Holy Rock, Road Hollow, Lost Canyon, and Taters areas. A total of 6477 stations were covered requiring 1579 hours of survey time. An additional 27.8 km^2 (391 stations) were covered during surveys for alternate nests.

HAWK RESPONSES

In 1991, 41 goshawk responses were detected during broadcast surveys (2749 broadcast stations, 676 survey-hours) on the seven tree-harvest areas, resulting in 1.5 responses per 100 stations surveyed, 0.2 responses per km^2 surveyed, and 1 response per 16.5 hours of survey time. In 1992 surveys (3728 stations, 903 survey-hours) 48 goshawk responses were detected on five tree-harvest areas, resulting in 1.3 goshawk responses per 100 stations surveyed, 0.2 responses per km^2 surveyed, and 1 response for every 18.8 hours of survey time. One goshawk response was recorded during the 1992 surveys for alternate nests.

TABLE 1. FREQUENCY OF ADULT NORTHERN GOSHAWK RESPONSES BY SEX TO DIFFERENT BROADCAST VOCALIZATIONS AND DURING DIFFERENT NESTING STAGES IN BROADCAST SURVEYS ON THE KAIBAB PLATEAU, ARIZONA, 1991–1992

Variable	Responses	
	Male	Female
Vocalization broadcast		
Alarm call	21	15
Food-begging call	6	6
Nesting stage		
Nestling	15	11
Fledgling	12	10

Six and nine active goshawk nests were located during broadcast surveys in 1991 and 1992, respectively. In each year, one of these nests had already been found by a non-broadcast surveyor (Reynolds et al., this volume), but was found again by a naive broadcast surveyor. Thus, one nest was found for every 458 stations covered, 30.6 km^2 surveyed, and 112.7 survey hours in 1991; in 1992, one nest was found for every 414 stations, 29.4 km^2, and 100.3 survey hours. In addition, the number of Cooper's and Sharp-shinned hawk responses during 1991 and 1992 were 14 and 8, and 15 and 6, respectively. Two Cooper's and six Sharp-shinned hawk, and two Cooper's and three Sharp-shinned hawk nests were found during follow-up searches in 1991 and 1992, respectively.

Mean estimated hatching and fledging dates at goshawk nests were 8 June and 17 July in 1991, and 1 June and 5 July in 1992, respectively. In 1991 broadcasting occurred during 18 days (37 surveyor-days) of the nestling period and 31 days (86 surveyor-days) of the fledgling period. In 1992 broadcasting occurred during 19 days (77 surveyor-days) of the nestling period and 26 days (117 surveyor-days) of the fledgling period. Broadcasts of the goshawk alarm call were replaced by broadcasts of the food-begging call on 22 July 1991 and 16 July 1992, coinciding with the latest egg-hatching dates of 24 July 1991 and 15 July 1992.

There was no significant difference in response frequency between adult male and female goshawks ($\chi^2 = 0.75$, df = 1, $P = 0.386$) during 1991 and 1992 broadcast surveys. Furthermore, the frequency of response by sex (in 32 cases the sex could not be determined) was not affected by the type of vocalization broadcasted (N = 48, Fisher's Exact test, P = 0.741) or stage of nesting (N = 48, Fisher's Exact test, P = 1.000) (Table 1).

TABLE 2. FREQUENCY OF NORTHERN GOSHAWK RESPONSE TYPES BY SEX, AGE, NESTING STAGE, AND BROADCAST TYPE DURING BROADCAST SURVEYS FOR NORTHERN GOSHAWKS ON THE KAIBAB PLATEAU, ARIZONA, 1991–1992. N = NUMBER OF STATIONS SURVEYED

	Response type		
Variable	Vocal non-approach	Silent approach	Vocal approach
Sex			
Male	1	17	8
Female	3	3	15
Age			
Adult	4	12	11
Juvenile	9	0	3
Nesting stage			
Nestling (N = 2129)	9	15	17
Fledgling (N = 4739)	18	13	14
Vocalization broadcasted			
Alarm call (N = 3168)	12	23	23
Food-begging call (N = 3700)	15	5	8

Response type, however, differed between the sexes (N = 47, Fisher's Exact test, P = 0.001) (Table 2); males often approached silently, whereas females most often approached and vocalized. More active nests were found in follow-up searches to responses by females (N = 8 nests of 21 responses) than males (N = 3 nests of 27 responses) (N = 48, Fisher's Exact test, P = 0.040).

During the fledgling stage, adults responded to broadcasts more often than juvenile hawks ($\chi^2 = 7.05$, df = 1, P = 0.008; N = 29 and 12 responses, respectively). Also, adults were more likely to approach the broadcaster (either vocalizing or silent) than juveniles (N = 93, Fisher's Exact test, $P < 0.001$) (Table 2).

During both years, more stations were surveyed during the fledgling (4739 stations) than the nestling (2129 stations) stage. After adjusting for these differences, goshawks responded more often during the nestling stage (42 responses per 2129 stations) than the fledgling stage (48 responses per 4739 stations) ($\chi^2 = 10.33$, df = 1, P = 0.001), whereas response type was independent of nesting stage (N = 86, Fisher's Exact test, P = 0.202) (Table 2).

The number of stations surveyed with the alarm and food-begging calls also varied (alarm call = 3168 stations, food-begging call = 3700 stations). After adjustment, goshawks responded more often to the alarm (N = 59 responses/effort) than food-begging (N = 31 responses/effort) call ($\chi^2 = 13.69$, df = 1, $P < 0.001$). Response type (4 of 90 responses were unclassified) was not independent of the type of call broadcasted (N = 86, Fisher's Exact test, P = 0.008) (Table 2). Alarm calls more commonly elicited a silent approach or vocal approach, whereas food-begging calls more often elicited vocalization with no approach. More nests were found during follow-up searches to vocal approaches (N = 31 nests) than to vocal non-approaches (N = 27 nests) or silent approaches (N = 28 nests) alone (N = 86, Fisher's Exact test, P = 0.029).

The overall chi-square among the three categories of call-use by nesting stage (alarm call during the nestling stage, alarm call during the fledgling stage, and food-begging call during the fledgling stage) was significant ($\chi^2 = 14.90$, df = 2, P = 0.013). Response rates were significantly higher using the alarm call during the nestling stage than using the food-begging call during the fledgling stage. However, goshawk response rates using the alarm call during the fledgling period were not significantly different from using the food-begging call during the fledgling period, nor did the former differ from using the alarm call during the nestling period.

Overall, the frequency of response types among the three species of *Accipiter* did not differ (N = 123, Fisher's Exact test, P = 0.208), nor did they differ between any *Accipiter* and Red-tailed Hawks (Fisher's Exact test, $P > 0.016$, Bonferroni significance level, for all pairwise tests). However, when responses were partitioned by habitat (ponderosa pine, mixed-conifer forests), the frequency of responses among all species differed (N = 210, Fisher's Exact test, P = 0.014) (Table 3). Goshawk and Cooper's and Red-tailed hawks responded more often in ponderosa pine forest, whereas Sharp-shinned Hawks responded more often in mixed-conifer forests. Mean response distance was not equal among species (P

TABLE 3. FREQUENCY OF NORTHERN GOSHAWK, COOPER'S HAWK, SHARP-SHINNED HAWK, AND RED-TAILED HAWK RESPONSES BY HABITAT DURING BROADCAST SURVEYS ON THE KAIBAB PLATEAU, ARIZONA, 1991–1992

	Species			
Habitat	Northern Goshawk	Cooper's Hawk	Sharp-shinned Hawk	Red-tailed Hawk
Ponderosa pine	50	17	5	62
Mixed-conifer	38	7	9	22

< 0.001); Red-tailed Hawks responded at distances greater than any of the *Accipiter* ($P < 0.016$, Bonferroni significance level, in all pairwise tests) (Table 4). Response distances did not differ among the *Accipiter* species ($P = 0.492$).

SURVEY EFFORTS AND ASSOCIATED COSTS

In 194 surveyor-days during 1992, observers surveyed 3728 stations (265 km^2 of transects) for a mean survey effort of 19.3 (SD = 6.8) stations per day. Of the 4832 established stations (343 km^2), 1104 stations (78.4 km^2) were not surveyed because they occurred in non-forested habitat or were within 800 m of an active goshawk nest.

Eleven observers spent 0.5–10.0 h ($\bar{X} = 4.7$ h, SD = 1.7) per day surveying for a total survey time of 903.1 h. Mean time required to broadcast, observe, and travel to the next station was 14.5 min per station. A mean of 8.4 h per day (SD = 1.7, total time = 1627 h) per observer was required to broadcast, commute to and from survey sites, update master survey maps, and test and maintain equipment. An additional 184 surveyor-hours were required for training personnel and 252 h were required on pre- and post-season tasks such as preparing survey maps, selecting personnel, data entry and verification, analysis, and report writing. Total personnel costs to complete broadcast surveys of the five tree-harvest areas surveyed in 1992 ranged from \$4.15–5.80 per station and \$58.50–81.85 per km^2 (\$151.40–211.95/mi^2) depending on salary (Appendix). Vehicle and equipment costs were \$1.90 per station and \$26.70 per km^2 (\$69.30/mi^2) surveyed.

DISCUSSION

HAWK RESPONSES

Response rates of goshawks to broadcasts did not differ between the sexes, but male and female behaviors differed when responding. As measured by their intensity of vocalization, females responded more aggressively than males. Males appeared to be more inquisitive than aggressive in their initial response, often approaching and retreating silently. The probability of finding a nest during follow-up searches to female responses was greater than for male responses. Females are more likely to be in the vicinity of their nests during early stages of brood-rearing whereas males are more likely to be away from nests foraging. However, because of potential bias in the misidentification of sex, and because males will respond from their nests, we recommend that equal effort be given to follow-up searches to responses by either sex.

Contrary to Kimmel and Yahner's (1990) report that no difference occurred in response rates between nesting stages, we found that goshawk responses rates were higher during the nestling than fledgling stage. No difference in response rates to the alarm and food-begging calls during the fledgling stage was detected during our surveys. Kennedy and Stahlecker (1993), however, detected fewer responses using the alarm call vs. the food-begging call during this period.

During the fledgling stage, adult response type (silent and vocal approaches to the observer) differed from juvenile response type (vocal non-approaches). This difference may reflect the inability of fledglings to fly well and a reluctance to leave the nest area. Juveniles vocally responded with both alarm and food-begging calls.

Response type to the calls broadcasted (alarm, food-begging), when both nesting stages were combined, differed. More approaches, with and without vocalization, were tallied in response to the alarm call whereas more vocalizations without approach were tallied to the food-begging

TABLE 4. MEAN INITIAL-RESPONSES DISTANCE, STANDARD DEVIATION, AND NUMBERS OF NORTHERN GOSHAWK, COOPER'S HAWK, SHARP-SHINNED HAWK, AND RED-TAILED HAWK RESPONSES TO BROADCAST SURVEYS ON THE KAIBAB PLATEAU, ARIZONA, 1991–1992

	Species			
Variable	Northern Goshawk	Cooper's Hawk	Sharp-shinned Hawk	Red-tailed Hawk
Mean response distance (m)	95.4	75.8	77.0	148.1
SD	87.5	71.1	73.5	121.3
No. of observations	90	26	14	89

call. This pattern reflects the tendency of adults to respond to the alarm call and juveniles to the food-begging call. A high number of vocal responses without approach were also tallied by Kennedy and Stahlecker (1993) during the fledgling stage.

Forests surveyed during 1991 and 1992 were primarily ponderosa pine and mixed-conifer. A greater proportion of goshawk, and Cooper's and Red-tailed hawk responses to goshawks vocalizations were obtained in ponderosa pine than in mixed-conifer forests. For Sharp-shinned Hawks, a greater proportion of responses were obtained in mixed-conifer forest. Mixed-conifer forests are often more structurally and floristically diverse than ponderosa pine forests and probably provide greater hiding cover for Sharp-shinned Hawk nests and higher densities of their prey. Initial response distance to broadcasts was greater for Red-tailed Hawks than any of the *Accipiter* spp. Red-tailed Hawks soar more often than the *Accipiter* and are easier to detect at greater distances.

We think that the Kennedy and Stahlecker (1993) protocol (with modifications described herein) is an effective means of locating goshawk, and Cooper's and Sharp-shinned hawk nests. Blind tests of the efficacy of the broadcast-survey method need to be conducted to determine the proportion of nests missed and the number of survey visits required to achieve an acceptable level of detection. Until such tests are performed, guidelines for surveying proposed tree-harvest areas should require two or more visits in separate years to increase the probability of goshawk detection. Tests of the efficacy of using goshawk vocalizations versus those of congeners to find Cooper's, Sharp-shinned, and Red-tailed hawk nests should be pursued.

SURVEY EFFORT AND ASSOCIATED COSTS

Estimates of cost/effort of locating goshawk nests using methods similar to Kennedy and Stahlecker (1993) were not available for comparison with our estimates. Costs associated with surveying for goshawks (personnel, vehicle, and equipment) vary depending on survey effort and size of the survey area. If finding all goshawk nests is the objective of surveys, effort should not be compromised in order to cover larger areas.

ACKNOWLEDGMENTS

We thank S. T. Bedard, K. L. Boden, P. C. Clark, S. E. Dudley, J. G. Dudley, M. W. Gavin, K. J. Kalin, D. Z. Rubinoff, D. S. Strait, and D. J. Worthington for their hard work in the field. Thanks to the Arizona Game and Fish Department for providing J. T. Driscoll, B. S. Heslin, T. L. Kelley, T. L. Moore, T. J. Rice, and L. E. Schultz to help with surveys. J. G. Dudley provided valuable input in modifying the Kennedy and Stahlecker broadcast design. For statistical advice, we thank R. M. King and J. E. Janssen. We also thank P. H. Bloom, D. Call, and L. G. Eskew for their valuable reviews of the manuscript. Funding, technical assistance, and housing were graciously provided by the North Kaibab Ranger District, USDA Forest Service.

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APPENDIX. PERSONNEL COSTS FOR CONDUCTING NORTHERN GOSHAWK BROADCAST SURVEYS PER BROADCAST STATION AND AREA, ON THE KAIBAB PLATEAU, ARIZONA, IN 1992

Variable	Personnel salary level $7.50/hour	$8.50/hour	$10.50/hour
	Survey time only		
Per station[1]	$ 1.80	$ 2.05	$ 2.54
Per km^2 [2]	$ 25.60	$ 29.00	$ 35.80
Per mile^2 [3]	$ 66.30	$ 75.10	$ 92.80
	All survey-related tasks[4]		
Per station	$ 4.15	$ 4.70	$ 5.80
Per km^2	$ 58.50	$ 66.25	$ 81.85
Per mile^2	$151.40	$171.60	$211.95

[1] Costs determined over 3728 stations that required 903 surveyor-hours of broadcasting.

[2] Costs determined over 264.7 km^2 that required 903 surveyor-hours of broadcasting.

[3] Costs determined over 102.2 mi^2 that required 903 surveyor-hours of broadcasting.

[4] Costs determined over 2063 h required to survey 3728 stations (or 264.7 km^2, or 102.2 mi^2), prepare survey maps, train, travel daily to and from survey sites, conduct surveys, update of "master" survey maps (area covered daily), test and maintain equipment, enter, error-check and analyze data, and report results.

Studies in Avian Biology No. 16:32–40, 1994.

A PHOTOGRAPHIC AND BEHAVIORAL GUIDE TO AGING NESTLING NORTHERN GOSHAWKS

CLINT W. BOAL

Abstract. Observations of behavioral and morphological development of nestling Northern Goshawks (*Accipiter gentilis*) were collected during three nesting seasons at 20 goshawk nests in northern Arizona. A photographic record of a single nestling goshawk's development was made. I combined descriptions of age-specific behaviors exhibited by nestlings with descriptions and photographs of nestling morphological development to construct an aging guide for nestling Northern Goshawks. Adult goshawk behaviors that relate to nestling age are also provided.

Key Words: *Accipiter gentilis*; age guide; nestling development; nestling behavior; Northern Goshawk.

Accurate estimates of the ages of nestling raptors are important for scheduling banding (Fyfe and Olendorff 1976) and assessing productivity (Moritsch 1983a, b; Steenhof 1987, Young and Kochert 1987). Photographic guides to morphological changes that occur as nestlings age have been developed for Prairie Falcons (*Falco mexicanus*), Red-tailed Hawks (*Buteo jamaicensis*), and Ferruginous Hawks (*B. regalis*) (Moritsch 1983a, b; 1985), but are unavailable for most species.

Because the behavior of young raptors is correlated with age (e.g., Ellis 1979), descriptions of age-specific behaviors coupled with pictorial and verbal descriptions of morphological changes provide a more robust guide to aging nestling raptors. In addition, the behavior of the adult female changes with the age of nestlings and may be useful in evaluating nestling ages.

Schnell (1958) provided a written description of the development of nestling Northern Goshawks (*Accipiter gentilis*) at a single nest. Observations of nestling development from several nests may provide a better understanding of the age ranges over which behavioral ontogeny occurs. I provide a photographic and behavioral guide to estimating the age of nestling Northern Goshawks.

STUDY AREA AND METHODS

The study was conducted on the North Kaibab Ranger District (NKRD), Kaibab National Forest, Coconino County, Arizona. The NKRD is an area of approximately 259,000 ha located on the Kaibab Plateau in northern Arizona. A detailed description of the study area is provided in Boal and Mannan (this volume).

Nest observations were conducted at 20 Northern Goshawk nests on the NKRD during the nesting seasons of 1990, 1991, and 1992. Information on the morphological and behavioral development of nestling goshawks was collected during 1539 hours of observation ($\bar{X}$ = 76.8 hour/nest ± 19.3 [SD]). These observations were made from blinds located on the ground or in trees a mean distance of 53 m (±17.6) from the nest trees. Observation periods began in the afternoon and continued until sundown, resuming at dawn until the time of initiation the previous day.

Photographs used in this guide are of the largest of 3 nestlings in a nest that was not part of my study, but was being used in a concurrent telemetry study (Bright-Smith and Mannan, this volume). I estimated the date of hatching as 20 June, based on behaviors exhibited by the nestlings and the adult female. I took photographs at 5-day intervals, starting with 5 days of age and continuing until 20 days of age.

At 18 days the adult female disappeared from the nesting area. Radio telemetry indicated the adult male goshawk remained in the nest area during the following

TABLE 1. GLOSSARY OF TERMS USED IN TEXT AND FIGURES

Auricular	The area of the invisible ear opening just posterior to the eye
Brancher	A young raptor that has left the nest but not the nest tree
Coverts	Small contour feathers of the wings and tail
Crown	The top of the head
Fledge	When a young bird leaves the nest tree of its own volition for the first time
Nape	The back of the head below the occipital portion of the skull
Pin feather	A growing feather that is encased in sheathing
Primaries	The outer flight feathers of the wing
Rapid peering	Rapid movement and readjustment of the head while visually focusing on an object
Remiges	Primary and secondary wing feathers
Rectrices	Tail feathers
Scapulars	Feathers located in the shoulder region
Secondaries	Inner flight feathers of the wing
Sheathing	Wax-like keratinous material that encases and protects newly developing feathers
Talons	The feet and claws of a hawk

days, but nest observations revealed that he did not care for the nestlings. At 20 days of age, the largest nestling, a male, attacked his siblings. He killed and cannibalized one sibling and forced the other to leave the nest and fall to its death (Boal and Bacorn, in press). The surviving nestling was removed from the nest and transferred to a wildlife rehabilitator for care. A photographic record was continued during captivity at 2-day intervals from 25 days of age to 39 days of age. Photographs of this bird were combined with the observational data from the other nests to provide this guide.

Table 1 contains a glossary defining morphological and behavioral terms used in describing ages of nestlings.

RESULTS

When a goshawk nest area is entered by humans during the first 5 days following hatching, adult females show a strong tendency to remain on their nests. Afterwards, females typically flush from nests, perch in nearby trees while vocalizing, and possibly make low passes at intruders. Adult male goshawks are rarely seen in the nest area except during food deliveries. After delivering food to the female away from the nest, males will often visit the nest briefly during the first 10 days following hatching.

It is difficult to determine the presence of nestlings prior to approximately 4 days old. At about 4 days of age nestlings begin attempting to defecate over the nest rim, and their presence is evidenced by minute specks of white excrement on the nest rim but not on the ground below the nest (Fig. 1). At about 9 days white-wash globs will be present on the branches and the ground below the nest (Fig. 2).

Nestlings remain totally white in their first natal down until 14–17 days when the gray second natal down and flight pin feathers begin to appear (Fig. 3). Scapular and covert feathers start emerging between 19 and 22 days (Fig. 4). Rapid and noticeable feather development begins at 24–26 days. At this age, scapular and covert feathers are visible, and the auricular area is covered with small black feathers (Fig. 5). At 28–30 days, dark feathers appear along the nape, but the crown is still downy. Feathering is also apparent along the

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FIGURE 1 (*top left*). Goshawks at 4–7 days post-hatching. *Morphological Characteristics:* Nestlings are small (approximately 13 cm long) and covered in white natal down. *Behavioral Characteristics:* Nestlings lie prostrate and usually out of view below the nest rim. Occasionally the tops of their heads may be seen, especially when the female is feeding them. Nestlings are poorly coordinated and move by scooting motions with the body in contact with the substrate. Nestlings may give whistle-like beg calls during feeding. Nestling hawks are able to excrete over the nest rim starting at 4–5 days old. Small dime-sized specks of white excrement may be visible on the sticks of the nest or against the tree trunk, but usually not on the ground. The adult female is almost continuously present and always broods the nestlings at night. She tends to remain motionless on the nest rather than flush and give the alarm call when the nest is approached.

FIGURE 2 (*bottom left*). Goshawk at 9–12 days post-hatching. *Morphological Characteristics:* Nestlings are 15–18 cm long and covered in white down. *Behavioral Characteristics:* Nestlings are most often lying in the nest cup out of view. Primary movements are to position themselves to be fed or to defecate over the nest rim. Movements are by scooting motions. Nestlings possess good head coordination when feeding, but are weak and often use their wings for balance and support when moving. Nestlings are able to excrete with greater power. Whitewash specks are numerous and obvious on the ground and branches below the nest. The adult female is usually present and broods the nestlings at night. She tends to flush from the nest and give the alarm call when the nest is approached.

FIGURE 3 (*top right*). Goshawk at 14–17 days post-hatching. *Morphological Characteristics:* Nestlings are approximately 20–23 cm long and have molted into their second natal down, which has a gray, woolly appearance. Auricular area is still downy. Pin feather development of the remiges and rectrices is apparent, especially when the wings are extended upward. As much as 1 cm of the feather may have erupted from the pin feather sheaths. *Behavioral Characteristics:* Nestlings are able to walk on their tarso-metatarsus while extending their wings for balance. They may stand for brief moments and look about the nest area. Nestlings begin making preening motions at their breast and wings.

FIGURE 4 (*bottom right*). Goshawk at 19–22 days post-hatching. *Morphological Characteristics:* Auricular area behind and below the eye is developing as a dark patch of small feathers. Remiges and rectrices are erupting from pin sheaths and contrast markedly with the body down. Greater coverts, upper tail coverts, and scapular feathers are starting to emerge and appear as dark dots against the body down. Close observations of the ventral feather tracts reveal dark pins beneath the down. *Behavioral Characteristics:* Nestlings can walk on their feet and usually do not use their wings for balance. They will stand for longer periods and preen. Nestlings rapidly flap their wings for short periods (3–5 seconds), especially following feeding. Nestlings may attempt to peck their own bites of food when the female is feeding them.

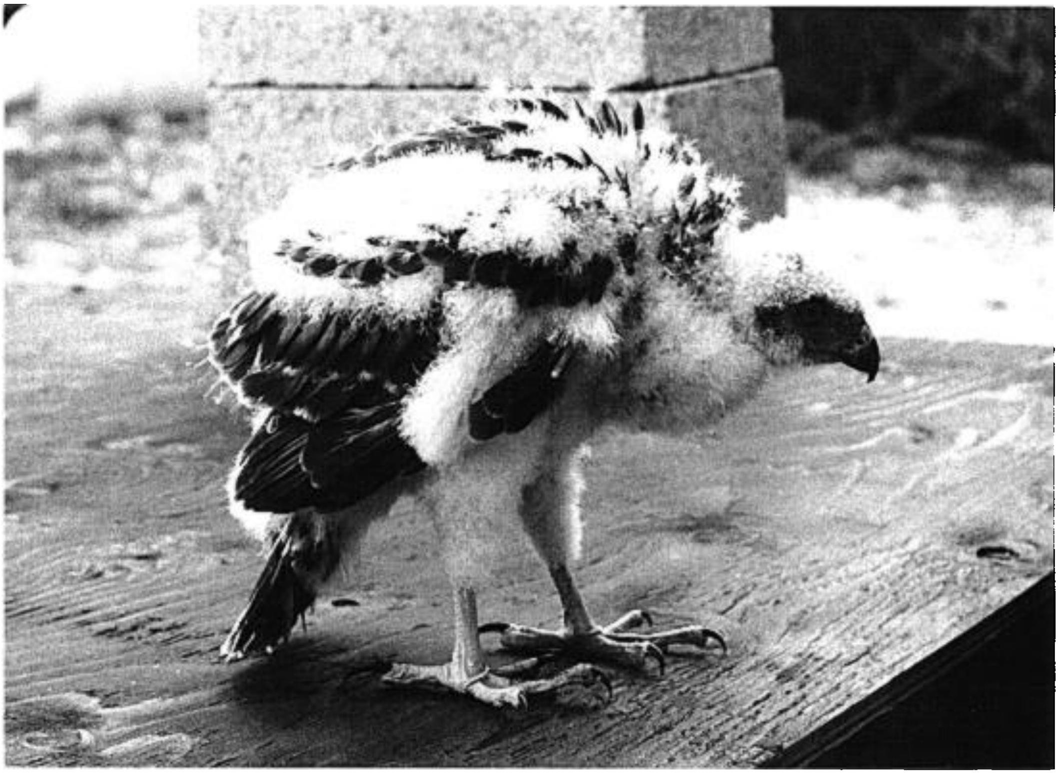

FIGURE 5. Goshawk at 24–26 days post-hatching. *Morphological Characteristics:* Auricular area is now covered with small black feathers. The head and neck are still downy, but sheathed feathers may be seen beneath the down. Scapular feathers and wing coverts are visible and contrast against the natal down. Feathers of the ventral tracts start emerging and under tail coverts may also appear. Nestlings are approximately ½ adult size. *Behavioral Characteristics:* Nestlings stand on the nest rim and observe the nest surroundings. They spend a great deal of time preening and wing flapping. Nestlings start stretching their feet and legs and making fists of the talons. They may start grabbing nest twigs with their feet. Nestlings may successfully feed themselves if the food has no skin or has been opened up by an adult. The adult female is usually in the nest area but does not brood or shelter nestlings at night except during wet or unseasonably cold weather.

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FIGURE 6 (*top right*). Goshawk at 28–30 days post-hatching. *Morphological Characteristics:* Dark feathers emerge along the nape, but the crown is still downy. Covert and scapular feathers fill in the upper wing and back areas. Breast feathers are filling in along the ventral tracts but the middle of the breast and belly is still downy. The under and upper tail coverts and legs are predominately downy, but a few feathers may be present. *Behavioral Characteristics:* Nestlings spend much of their time preening, and begin scratching their heads with their talons. Foot grabbing of nest twigs and other objects increases. Nestlings are very attentive to their surroundings and pay attention to adults exchanging prey away from the nest. Rapid peering and sleeping while standing are new behaviors exhibited during this stage. The adult female is rarely at the nest but is in the nest area and becomes defensive when the nest area is entered.

FIGURE 7 (*bottom right*). Goshawk at 32–34 days post-hatching. *Morphological Characteristics:* Dark feathers have emerged on the crown and are beginning to emerge at the corner of the mouth. The back and dorsal side of wings are 90% feathered. The breast is filling in with feather growth but is still downy in the center and on the belly. The undertail coverts have filled in and feathers will be emerging on the thighs. The underwing area is still downy. Rectrices are about ⅔ adult length. *Behavioral Characteristics:* Nestlings readily feed themselves when the female is not present and may fight aggressively over food. Nestlings will vigorously beat their wings while hopping and running across the nest. Nestlings may start branching at about 34–35 days.

sides of the breast (Fig. 6). At 32–34 days dark feathers emerge on the crown, and feathering of the legs is visible (Fig. 7). Body feathering is nearly completed at 36–38 days, but downy areas persist on the sides of the neck (Fig. 8). At 40 days the only visible down is along the underside of the wings (Fig. 9).

DISCUSSION

Moss (1979) described weight gain in nestling sparrowhawks (*A. nisus*) as being initially slow for 4–6 days, followed by a 10-day period of rapid weight gain, and then a return to slow weight gain. Though the periods will vary with different species, this is the general pattern of growth in nestling raptors. Food shortages can depress weight gain in nestling raptors (Newton 1986). Food deprivation during the 18–20 day age period may have affected negatively the growth and development of the photographed nestling. However, I estimate the nestling goshawk experienced food deprivation near the end of the rapid weight gain period (Moss 1979). Potential depression of the nestlings' development may have been minimized by the timing of the food shortage and the constant food supply provided by the rehabilitator. Fault bars, a likely side effect of food deprivation and stress, were not observed in the nestlings' rectrices after feather growth was complete (C. Van Cleeve, Icarus Foundation, pers. comm.). The photographic record agrees with the observational data of nestling development collected at the other nests used in this study.

Reported fledging ages of nestling goshawks are variable. Reynolds and Wight (1978) found that nestling goshawks in Oregon fledged at 34–37 days. Newton (1979) reported goshawks fledged at 40–43 days, and Brown and Amadon (1968) reported nestlings fledging as late as 45 days. Variation in fledging ages may be related to nestling condition, geographical location, or different definitions of branching and fledging. I define 'branching' as when a nestling leaves the nest but remains in the nest tree, and 'fledging' as when a nestling first leaves the nest tree on its own volition. Reynolds and Wight (1978) found that male nestlings develop and fledge earlier than females. In northern Arizona, male nestlings usually fledged at about 38 days (range = 36–40 days), whereas female nestlings fledged at 39–42 days.

ACKNOWLEDGMENTS

I am grateful to B. Baker, B. Bibles, E. Bibles, R. Brown, M. Collins, N. Karnovsky, R. W. Mannan, and E. Steadman for assisting with nest observations. I thank J. Dawson, S. Joy, M. Kochert, R. Lehman, D. Leslie, R. W. Mannan, R. Reynolds, D. Smith, H. Snyder, and K. Steenhof for providing thoughtful and constructive reviews of this manuscript. I also thank C. Van Cleeve for caring for the nestling and assisting with the photographic record. This material was collected during a study funded by a challenge-cost-share agreement between the University of Arizona and the USDA Forest Service, Southwest Region. Additional funding was provided by Kaibab Industries, the Arizona Wildlife Federation, and the Arizona Falconer's Association.

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FIGURE 8 (*top left*). Goshawk at 36–38 days post-hatching. *Morphological Characteristics:* Nestling bodies are approximately 90% feathered, but downy areas remain along the side of the neck, in the thighs, and in the underwing covert area. Usually a tuft of down remains just above the cere on the otherwise feathered head. Rectrices are approximately ¾ full length. *Behavioral Characteristics:* All nestlings will be branching and some of the males may fledge from the nest tree. Nestlings/fledglings will fight aggressively over food at the nest but will still accept being fed by the adult female. Nestlings/fledglings will food beg for long periods.

FIGURE 9 (*bottom left*). Goshawk at greater than 40 days post-hatching. *Morphological Characteristics:* Nestlings/fledglings appear fully feathered, but downy areas persist along underwing covets. This is only visible when the wings are spread. The crop will also appear downy when the bird is gorged. Rectrices are still slightly short of full length. *Behavioral Characteristics:* Males should be fledged and females will usually fledge by 42 days old. Fledglings can often be located when they food beg from different locations in the nest stand. At about 45 days the adults will begin providing food at locations away from the nest.

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Studies in Avian Biology No. 16:41–45, 1994.

INFLUENCE OF SITE QUALITY AND STAND DENSITY ON GOSHAWK HABITAT IN SOUTHWESTERN FORESTS

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RUSSELL T. GRAHAM, AND RICHARD T. REYNOLDS

Abstract. Current management guidelines for the Northern Goshawk (*Accipiter gentilis*) in the Southwest call for a mosaic habitat consisting of approximately 10 percent of the forest area in grass-forb/shrubs, 10 percent in 2.5–12.7 cm trees, 20 percent in 12.7–30.5 cm trees, 20 percent in 30.5–45.7 cm trees, 20 percent in 45.7–61.0 cm trees, and 20 percent in 61.0 cm and greater trees. This habitat mosaic was conceived as convenient categories to describe a generally balanced, ecologically sustainable, forest ecosystem. In reality, however, the vegetative structural percentages vary. We describe how differences in site quality and stand density affect vegetative structural stage percentage and forest age.

Key Words: *Accipiter gentilis*; forest regulation; Northern goshawk; site quality; stand density, SDI; vegetative structural stages.

A goshawk scientific committee developed recommendations for managing the Northern Goshawk (*Accipiter gentilis*) in the southwestern United States (Reynolds et al. 1992). These recommendations focused on developing and maintaining forest conditions to provide habitat for sustaining goshawks and their key prey species. The recommendations defined size, location, stand structure, woody debris, and soil condition requirements for nest, post-fledging family, and foraging areas. Stand structure included such properties as the proportion and distribution of six different diameter classes or vegetative structural stages (VSS), and number of large (>46 cm) trees, snags, and down logs per ha.

Reynolds et al. (1992) recommended a mosaic of vegetative structural stages interspersed throughout the post-fledging family and foraging areas in small, less than 1.7 ha patches to form a balanced, ecologically sustainable, uneven-aged forest. Vegetative structural stage is a generalized description of forest structure and age based on the majority of trees in a specific diameter class within the forest (Table 1). The mosaic included patches ranging from grass-forb/shrub to old forests, with a high priority on sustaining as much as 40 percent of the area in mature and old forests. The recommended average proportion was about 10 percent of the goshawk management area (14,820 ha) in grass-forb/shrubs, 10 percent in 2.5–12.7 cm (1–5 in.) trees, 20 percent in 12.7–30.5 cm (5–12 in) trees, 20 percent in 30.5–45.7 cm (12–18 in) trees, 20 percent in 45.7–61.0 cm (18–24 in) trees, and 20 percent in 61.0 cm (24 in) and greater trees.

In this paper, we examine how differences in site quality and stand density influence VSS percentage and forest age. This paper also describes the impacts of varying VSS proportions within goshawk management areas to goshawk habitat and their key prey species.

FOREST DEVELOPMENT

Reynolds et al.'s (1992) recommended VSS and forest mosaic can be approached by traditional, even-aged area regulation. Area regulation consists of dividing the forested post-fledging family and foraging areas into as many ≤1.7 ha patches as there are years in the expected life of a forest (forest age) and regenerating an equal percentage of the forest each entry period (Smith 1986). The entry period could vary from 10 to 20 years depending upon existing forest conditions.

Three basic principles apply to area regulation. First, structural stages become important to sustain a forest over time, even where the desired condition is to have large, old trees. Second, new trees must be established at regular intervals to sustain the desired structural stages in a forest through time. Third, forests are dynamic. Trees regenerate and grow at different rates and die at different ages, resulting in a forest that is constantly changing over time (Oliver and Larson 1990).

Four variables that affect VSS distribution and forest age are: (1) length of stand establishment period, (2) site quality, (3) stand density, and (4) tree longevity.

STAND ESTABLISHMENT

Length of stand establishment varies by species, regeneration method (natural or planting), amount and kind of forest floor disturbance, and climatic variation. The observed stand establishment period (or years in VSS 1) for ponderosa pine (*Pinus ponderosa*) forests can range from 15 years on a highly productive site to 30 years on

TABLE 1. VEGETATIVE STRUCTURAL STAGES AND THEIR DIAMETERS

Vegetative structural stage	Forest description	Diameters[1] (cm)
1	Grass-forb/Shrub Opening	0–2.5
2	Seedling/Sapling	2.5–12.7
3	Young	12.7–30.5
4	Mid-aged	30.5–45.7
5	Mature	45.7–61.0
6	Old	>61.0+

[1] Tree diameter measured at 1.4 m above ground level.

a poor site. Generally, south- to west-facing, dryer slopes with shallow soils require the longest seedling establishment period; north-facing, more mesic sites with deeper soils require the least time. Under similar topographic and soil conditions, sites where annual precipitation is usually less require more time than when moisture is more plentiful.

SITE QUALITY

Site quality influences tree growth and varies greatly in the Southwest. Site quality denotes the relative productivity of a site for a particular tree species (Ford-Robertson 1971). Factors that influence site quality include soil characteristics, mineral composition, slope, aspect, microclimate, and tree species (Daniel et al. 1979). Site index is useful to help quantify site quality, and refers to the average height of dominant and codominant trees in a stand at an arbitrarily chosen age. Minor (1964) developed site index curves for ponderosa pine in northern Arizona, measuring age at 1.4 meters above ground level using a chosen base age of 100 years. For example, a site index of 70 (a tree 21.3 m [70 ft] tall at 100 years of age at 1.4 m above ground level) is considered about average for ponderosa pine in the Southwest. Thus, the length of time required for trees in each VSS is a function of site quality and stand density (Table 2).

A forest growth simulator model (Edminster et al. 1991) was used to project diameter growth per decade (Table 2) for two key stand densities: (1) Stand density index (SDI) 113 (25% of maximum SDI 450 for ponderosa pine); and (2) 157 SDI (35% of maximum SDI). The first level is considered to be the onset of competition between trees, whereas the second is the lower limit of full site occupancy (Long and Daniel 1990). Stand density index is the number of trees at an average stand density of 25.4 cm (10 in) (Daniel et al. 1979, Lilliholm et al., this volume).

During modeling, the growth of 500 ponderosa pine seedlings and 4 large reserve trees (trees > 46 cm dbh) were simulated over a 320-year period at SDIs of 113 and 157. Four reserve trees were allowed to die (snag creation) at stand age 30, and thereafter thinning from below, to the specified SDI, was allowed at 20-year intervals, starting at stand age 40 years.

Generally, seeding/sapling and young trees have a faster diameter growth rate than mature and old trees (Table 2). The time it took for a tree to move through one VSS ranged from 11 to 59 years for 25% maximum SDI, and from 11 to 95 years for 35% maximum SDI depending on the site quality and VSS. Also, it takes longer to grow through a stage on the low productivity sites than on high productivity sites; the exception was VSS 3 on average and high sites.

STAND DENSITY

Stand density influences tree diameter growth. On sites with the same site quality, tree diameter growth will vary with different management intensities. For example, the number of years in VSS 4, 5, and 6 are longer for the higher stand density (35% SDI) than for the lower stand density (25% SDI). The growth simulator model showed no differences in number of years for VSS 2. The seedling establishment period for low (30 years), average (20 years), and high (15 years) site quality was assumed to be equal for the two densities.

Stand density and site quality also influence VSS percentage and the time required to achieve the desired forest structure for goshawks and their prey species (Tables 3 and 4). One desired forest structure condition is to maintain 40% of the goshawk post-fledging family and foraging areas in VSS 5 and 6 to sustain moderate to high populations of key prey species. These older age classes maintain the most species at an abundant population level (10 of 12 species found in ponderosa pine forests: i.e., woodpeckers, chipmunks, tassel-eared squirrels) (Reynolds et al. 1992). Since forest stands reach VSS 5 and 6 from 30 to 70 years earlier in stands with lower density (25% SDI), the desired forest structure could be maintained for a longer period of time. Older-aged stands (>200 years) are also more frequently used as goshawk nest sites. Because nest sites have a higher density of large trees, these areas should be managed for even higher density stands (43% SDI).

Actual VSS percentage varies from the recommended 10-10-20-20-20-20 (Reynolds et al. 1992). For example, the VSS percentage for a low quality site with 25% SDI is 12-9-18-17-23-21 and for a high quality site with 25% SDI, VSS is 9-6-22-19-22-22 (Table 3).

TABLE 2. ESTIMATED DIAMETER GROWTH AND NUMBER OF YEARS IN EACH VEGETATIVE STRUCTURAL STAGE (VSS) FOR DIFFERENT QUALITY PONDEROSA PINE SITES AND STAND DENSITIES IN THE SOUTHWEST

		Stand density[2]			
		Diameter growth per decade (cm)		Approximate years in each VSS	
Vegetative structural stages	Site quality[1]	25% Max SDI	35% Max SDI	25% Max SDI	35% Max SDI
1	Low	Seedling	Seedling	30	30
	Average	estabishment	establishment	20	20
	High	period	period	15	15
2	Low	4.32	4.32	24	24
	Average	6.86	6.86	15	15
	High	9.40	9.40	11	11
3	Low	3.68	3.05	48	58
	Average	4.83	4.32	37	41
	High	4.75	4.24	37	42
4	Low	3.48	2.79	44	55
	Average	4.06	3.25	38	47
	High	4.83	3.63	32	42
5	Low	2.59	1.60	59	95
	Average	3.63	2.44	42	63
	High	3.99	2.97	38	51
6	Low	1.52	1.27	—[3]	—[3]
	Average	2.08	1.70		
	High	2.52	2.08		

[1] Site quality (Minor 1964). Low = 50 SI (SI = site index – dominant tree height at 100 years), Average = 70 SI, High = 90 SI.

[2] Stand density index (SDI) is the number of trees of average stand diameter of 25.4 cm. 25% max SDI = onset of competition; 35% max SDI = lower limit of full site occupancy.

[3] Years in VSS 6 depends on the selected forest age.

TREE LONGEVITY

Tree longevity influences forest life expectancy and forest age required to achieve desired forest structure. The lifespan of trees varies within and between species. For example, the oldest known living ponderosa pine tree in the Southwest was found to be 742 years old (Swetnam and Brown 1992), whereas the average life expectancy of most ponderosa pine is closer to 200 years or less (Pearson 1950, White 1985, Covington and Moore 1991). Life expectancy for Engelmann spruce (*Picea engelmannii*) ranges from 250–450 years (Alexander and Shepperd 1990). The life expectancy of the typical tree would be more appropriate to set targets for sustaining forests then the age of the oldest tree. Tree species and

TABLE 3. ESTIMATED DIAMETER GROWTH, YEARS IN VEGETATIVE STRUCTURAL STAGE, ACCUMULATED AGE, AND PERCENT OF LANDSCAPE IN EACH VSS FOR PONDEROSA PINE ON LOW, AVERAGE, AND HIGH QUALITY SITES WHERE STAND DENSITY IS 113 SDI (25% MAX SDI)[1]

		Vegetative structure stages					
Site quality		VSS 1	VSS 2	VSS 3	VSS 4	VSS 5	VSS 6[2]
Low (50 SI)	Diameter growth/decade	0	4.32	3.68	3.48	2.59	1.52
	Years (Acc-years)[3]	30 (30)	24 (54)	48 (102)	44 (146)	59 (205)	55 (260)
	% in VSS	12	9	18	17	23	21
Average (70 SI)	Diameter growth/decade	0	6.86	4.83	4.06	3.63	2.08
	Years (Acc-years)[3]	20 (20)	15 (35)	37 (72)	38 (110)	42 (152)	48 (200)
	% in VSS	10	8	18	19	21	24
High (90 SI)	Diameter growth/decade	0	9.40	4.75	4.83	3.99	2.52
	Years (Acc-years)[3]	15 (15)	11 (26)	37 (63)	32 (95)	38 (133)	37 (170)
	% in VSS	9	6	22	19	22	22

[1] Maximum stand density index for ponderosa pine is 450.

[2] Number of years in VSS 6 is determined by selecting a growth period that is approximately 20% of forest age.

[3] Number of years in VSS and accumulated years.

TABLE 4. ESTIMATED DIAMETER GROWTH, YEARS IN VEGETATIVE STRUCTURAL STAGE, ACCUMULATED AGE, AND PERCENT OF LANDSCAPE IN EACH VSS FOR PONDEROSA PINE ON LOW, AVERAGE, AND HIGH QUALITY SITES WHERE STAND DENSITY IS 157 SDI (35% MAX SDI)[1]

		Vegetative structural stages					
Site quality		VSS 1	VSS 2	VSS 3	VSS 4	VSS 5	VSS 6[2]
Low (50 SI)	Diameter growth/decade	0	4.32	3.05	2.79	1.60	1.27
	Years (Acc-years)[3]	30 (30)	24 (54)	58 (112)	55 (167)	95 (262)	65 (327)
	% in VSS	9	7	18	17	29	20
Average (70 SI)	Diameter growth/decade	0	6.86	4.32	3.25	2.44	1.70
	Years (Acc-years)[3]	20 (20)	15 (35)	41 (76)	47 (123)	63 (186)	44 (230)
	% in VSS	9	7	18	20	27	19
High (90 SI)	Diameter growth/decade	0	9.40	4.24	3.63	2.97	2.08
	Years (Acc-years)[3]	15 (15)	11 (26)	42 (68)	42 (110)	51 (161)	39 (200)
	% in VSS	7	6	21	21	25	20

[1] Maximum stand density index for ponderosa pine is 450.

[2] Number of years in VSS 6 is determined by selecting a growth period that is approximately 20% of forest age.

[3] Number of years in VSS and accumulated years.

longevity must be considered when considering an older forest age.

By decreasing or increasing forest age, VSS percentage is changed. For example, if the forest age on the low productive site was lowered from 327 to 250 years, the VSS percentage would change from 9-7-18-17-29-20 to 12-10-23-22-33-0 (Table 4). VSS 6 may not be achievable if a 327-year forest age is not ecologically sustainable. This should not influence goshawks, given the average life expectancy of ponderosa pine and that sites with low productivity (SI ≤ 50) account for only 2.3% (N = 4 national forests) of ponderosa pine stands in the Southwest (USDA 1993). Planning for forest ages less than 200 years, however, could negatively impact goshawks and their prey populations. Regardless of site quality or stand density index (25% or 35%), forests less than 200 years will not provide for the older classes (VSS 5 and 6) (Tables 3 and 4). Suitable goshawk nesting habitat is commonly composed of older trees (>200 years) in the VSS 5 and 6. Prey species like the Red-naped Sapsucker (*Sphyrapicus nuchalis*) and Williamson's Sapsucker (*Sphyrapicus thyroideus*) would lose 66% of the forest structure conditions that maintain high populations (Reynolds et al. 1992). Forests without VSS 5 and 6 would also not provide the large snags that are used by other nesting-cavity prey species.

SUSTAINING GOSHAWK HABITAT

Not all structural stages are equally important for the goshawk and its prey species, but all structural stages are equally important for a forest to become established and to sustain itself from the grass-forb/shrub stage (VSS 1) with seedlings through the old forest stage (VSS 6). The traditional area even-aged method of regulating a forest can be applied successfully to sustain a forest with the mosaic of VSS that will meet the habitat needs of the goshawk and its key prey species.

Of 12 goshawk prey species found in ponderosa pine forests, openings (VSS 1) are of no importance to 5 prey species (i.e., sapsuckers, tassel-eared squirrel), and important to 1 prey species (cottontail) for maintaining high populations. For only 1 prey species (tassel-eared squirrel) found in the ponderosa pine forests younger-aged forests (VSS 3) are important, and only when larger,

TABLE 5. APPROXIMATE PERCENT IN EACH VEGETATIVE STRUCTURAL STAGE (VSS) AND FOREST AGE THAT CAN BE EXPECTED TO OCCUR IN GOSHAWK POST-FLEDGING FAMILY AND FORAGING AREAS OF AVERAGE SITE QUALITY FOR PONDEROSA PINE FOREST TYPE AND MANAGEMENT INTENSITIES (REYNOLDS ET AL. 1992)

Management intensity	Percent in each vegetative structural stage						Forest age (years)
	VSS 1	VSS 2	VSS 3	VSS 4	VSS 5	VSS 6	
No management[1]	10	10	80	0	0	0	200
Minimal	9	13	20	17	20	21	233
Moderate	10	10	19	17	20	24	204
Intensive	10	8	18	17	21	26	194

[1] Unthinned ponderosa pine stand at Fort Valley Experimental Forest (Reynolds et al. 1992). An unthinned stand, using GENGYM growth and yield model, never grew beyond VSS 3 with a 200-year forest age (Ronco et al. 1985, Edminster et al. 1991).

older trees are available for nesting and seed sources (Reynolds et al. 1992).

Under varying management options, VSS percentages never attain 10-10-20-20-20-20. The youngest forest age (shorter time span) occurs under intensive management; oldest forest age (longest time span) occurs under minimal management (Table 5). Minimal management level is characterized by trees that are significantly competing with one another. When management intensities are at moderate and intensive levels, trees develop without significant competition. Without management, however, unthinned ponderosa pine stands of average site quality are unlikely to grow beyond the young forest structural stage (VSS 3), even after 200 years (Ronco et al. 1985, Edminster et al. 1991).

To provide the desired forest conditions of large old trees over 40% of the goshawk management area and small forest openings for prey species and tree regeneration, entry periods for management activities (i.e., harvesting, fire, etc.) would need to be about every 20 years for the moderate level. An expected level of management intensity (stand density) must be determined prior to establishing the desired VSS proportions and forest age.

The recommended 10-10-20-20-20-20 VSS percentage is now being considered as a hard-and-fast rule by those implementing and reviewing timber sale projects. However, the 10-10-20-20-20-20 distribution was intended to describe approximate percentages of each VSS throughout the post-fledging family and foraging areas to sustain suitable goshawk habitat (Reynolds et al. 1992). The achievable VSS percentage should be determined by considering existing local factors that influence forest establishment and growth, expected management intensity, and tree longevity.

ACKNOWLEDGMENTS

We would like to thank the following reviewers: W. M. Block, R. M. Jeffers, M. Johnson, M. J. Larson, R. J. Lilieholm, C. O. Minor, and M. L. Morrison.

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Resource Ecology

MACROHABITAT SELECTION BY NESTING NORTHERN GOSHAWKS: IMPLICATIONS FOR MANAGING EASTERN FORESTS

THOMAS BOSAKOWSKI AND ROBERT SPEISER

Abstract. Macrohabitat data from 16 Northern Goshawk (*Accipiter gentilis*) nest sites and 70 random sites in the New York–New Jersey Highlands were analyzed. Variables included distances to human habitation, paved road, water, wetlands, and forest openings, elevation, and slope, slope location, and slope aspect. Univariate tests revealed that macrohabitat was important to nest site selection in goshawks, since several variables were significantly different than random sites (distance to human habitation, paved roads, and elevation). In addition, slope aspect data revealed that nesting on southern aspects (SW, S, SE) was avoided. A full-model discriminant function analysis (DFA) was used to determine the extent of overlap between random sites and nest sites. The DFA was able to correctly classify 69% of nest sites and 79% of random sites, further demonstrating that macrohabitat plays an important role in nest site selection. A management model using stepwise DFA revealed that distance to paved road and elevation were the most important discriminating variables. These variables indicated that the goshawk may be an area-sensitive species, since smaller forest tracts bounded by paved roads were not used for nesting.

Key Words: *Accipiter gentilis*; area sensitive species; discriminant function analysis; macrohabitat; nest site selection; Northern Goshawk.

Most habitat studies of Northern Goshawks (*Accipiter gentilis*) in western Northern America have emphasized microhabitat features of the nest site, such as basal area, stand densities, canopy cover, or shrub cover (Hennesey 1978, Reynolds et al. 1982, Hall 1984, Moore and Henny 1983, Crocker-Bedford and Chaney 1988, Kennedy 1988, Hayward and Escano 1989). In the eastern deciduous forest biome, Speiser and Bosakowski (1987) found that macrohabitat (landscape level) features were also important parameters in nest site selection of Northern Goshawks when compared to random sites. Macrohabitat was also found to be an important component of nest site selection for Red-tailed (*Buteo jamaicensis*) (Speiser and Bosakowski 1988) and Red-shouldered hawks (*B. lineatus*) (Bosakowski et al. 1992a). In the East, wilderness forests are typically much smaller and are impacted more by highways, rights-of-way, and suburban development. As such, the suitability of nest sites may be highly influenced by the presence of these macro features of the environment. Thus, management plans based on microhabitat alone may include many unsuitable areas for nesting.

In this paper, we present an analysis of goshawk nest sites in the Northeast to determine which macrohabitat features are important components of nest site selection.

STUDY AREA AND METHODS

The study area was in the Highlands Physiographic Province of northern New Jersey and southeastern New York (315,780 ha) and was described in detail in Speiser and Bosakowski (1987) and Bosakowski et al. (1992b). Goshawk nests were located in the study area from 1976–1989. In addition to our own searches, we pursued all reports of possible goshawk nesting from *Records of New Jersey Birds*, local naturalists, and forestry personnel.

Habitat data were collected as described in Bosakowski et al. (1992b) for 16 Northern Goshawk nests and for 70 random sites described in Speiser and Bosakowski (1988). Macrohabitat variables included distances to human habitation, paved road, water, wetland (>0.5 ha), and forest opening (>1 ha), and elevation, slope (over a 150-m baseline centered through the site), slope location rating (0 = no slope, 1 = lower slope, 2 = middle slope, 3 = upper slope) and slope aspect (8 classes).

All data were analyzed on a personal computer using NCSS software version 5.03 (Number Cruncher Statistical Software, Kaysville, Utah). Univariate tests were run separately for each variable comparing nest sites and random sites with an F-test and t-test. An unequal variance t-test was used (Winer 1971) when F-test results indicated significant differences in variance ($P < 0.05$). All variables were tested for normality using the test described by D'Agostino (1990). Random site variables were found to be non-normal, so all data were square root-transformed. This transformation normalized the data set prior to multivariate analysis.

The first stage in model building was to construct a correlation matrix to determine any problems of collinearity among variables. Titus and Mosher (1981) used a cut-off value of $r < 0.6$ to eliminate multicollinearity. Because the highest simple correlation in this study was only 0.54, all variables were retained for inclusion in a full-model discriminant function analysis (DFA). Discriminant scores were automatically

TABLE 1. MACROHABITAT VARIABLES FROM RANDOM SITES AND NEST SITES OF NORTHERN GOSHAWKS WITH UNIVARIATE COMPARISONS

	Random site (N = 70)		Nest site (N = 16)			
	$\bar{X}$	SD	$\bar{X}$	SD	F-test P value	t-test P value
Distance to (m)						
Paved road	501.9	± 452.7	1170.6	± 652.3	0.079	0.000
Human habitation	730.1	± 516.5	1052.2	± 634.7	0.314	0.034
Water source	250.8	± 201.9	212.2	± 106.2	0.004	0.288
Wetland	564.2	± 552.0	326.8	± 370.0	0.080	0.084
Forest opening	238.1	± 210.0	263.8	± 116.8	0.008	0.508
Elevation (m)	273.1	± 84.2	342.9	± 62.8	0.155	0.003
Slope (degrees)	8.67	± 5.84	9.50	± 8.15	0.108	0.637
Slope location (rank 0–3)	1.14	± 1.12	1.06	± 0.77	0.074	0.786

rescaled to a probability scale (0–1) by the NCSS program and were plotted to show the extent of group separation.

RESULTS

STATISTICAL RESULTS

Nest sites and random sites were significantly different for several macrohabitat variables (Table 1). Distance to paved road, distance to human habitation, and elevation were significantly different when comparing means. Unequal variances were found for distance to water and distance to forest opening, with nest sites showing lower variation in each case. Goshawks nested in all but southern aspects (SW, S, SE) (Fig. 1), resulting in a significantly different distribution from random sites (Kolmogorov-Smirnov Test, 2-tailed, $D = 0.875$, $P < 0.05$).

FULL-MODEL DISCRIMINANT FUNCTION ANALYSIS

Full-model DFA of the macrohabitat variables correctly classified 78.6% of the random sites and 68.8% of the goshawk nest sites. Conversely, there were 15 misclassified random sites (21.4%) and 5 misclassified nest sites (31.3%) (Table 2). Discriminant scores from all sites were plotted to show the pattern of separation between the groups as well as to demonstrate the pattern of overlap that resulted in misclassified sites (Fig. 2).

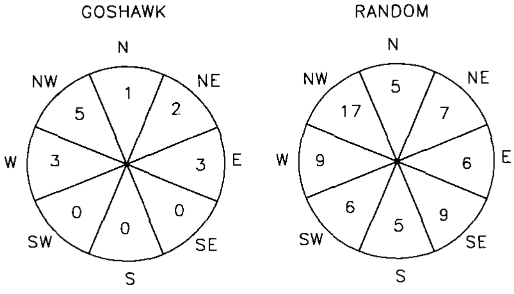

FIGURE 1. Slope aspects of Northern Goshawk nest sites and random sites. No aspect was determined for two nest sites and six random sites on level ground.

MANAGEMENT MODEL

Following the suggestion of Mosher et al. (1986), we also used a stepwise DFA to determine the most important discriminating variables in habitat selection. This test revealed that two of the original eight variables retained nearly the same Wilks' lambda value (Table 3), and that the prediction (classification) accuracy was also nearly the same. In this case, the nest site predictions remained the same, but one less random site was misclassified as a nest site.

DISCUSSION

Our results with discriminant models showed that goshawks do not select macrohabitat at random, as the majority of nest sites and random sites were correctly classified. Since random sites should include the whole spectrum of available habitat (suitable, marginal, and unsuitable habitat), a certain degree of overlap is expected between random site data and nest site data (Fig. 3). This overlap region includes all of the sites that the models had difficulty segregating between random and nest sites, which are typically known as misclassified sites (Fig. 2). Thus, the misclassified random sites included habitat that was both suitable and marginal for goshawk nesting, whereas the misclassified nest sites represented sites with marginal habitat for goshawks.

Overall, these results suggest that goshawks are selecting certain macrohabitat features for nesting in eastern forests, which means that nest site selection is not based entirely on forest stand

TABLE 2. SUMMARY OF FULL-MODEL DISCRIMINANT FUNCTION ANALYSIS OF SQUARE ROOT-TRANSFORMED MACROHABITAT VARIABLES FROM NORTHERN GOSHAWK NEST SITES AND RANDOM SITES

	Canonical coefficients		
Variables	Random site	Nest site	F-Prob
Distance to			
Paved road	0.286	0.427	<0.001
Human habitation	0.088	0.080	0.858
Water source	0.206	0.179	0.669
Wetland	0.329	0.316	0.727
Forest opening	0.029	0.097	0.308
Elevation	2.544	2.870	0.031
Slope	1.236	0.968	0.370
Slope location	−2.085	−1.992	0.440
(Constant)	−30.80	−39.69	
Wilks' Lambda = 0.7065			

characteristics. Additional investigations of Red-tailed Hawks (Speiser and Bosakowski 1988) and Red-shouldered Hawks (Bosakowski et al. 1992a) in the same study area also showed significant macrohabitat selection by these sympatric raptors, albeit each species exhibited different macrohabitat preferences. For the goshawk, this selectivity results in only a fraction of the total study area that is suitable macrohabitat for nesting, an important point for management and conservation in eastern forests. If the avoidance of southern aspects for nesting that we noted for 16 nests is verified with larger sample sizes, it may be possible to eliminate approximately 37.5% of management areas from future nest searches or habitat management.

The remote nature of goshawk nest sites was characterized by significantly longer distances to paved roads and human habitation. Higher elevations were also selected, possibly because the largest wilderness areas occurred only at higher elevations in the study area. These results indi-

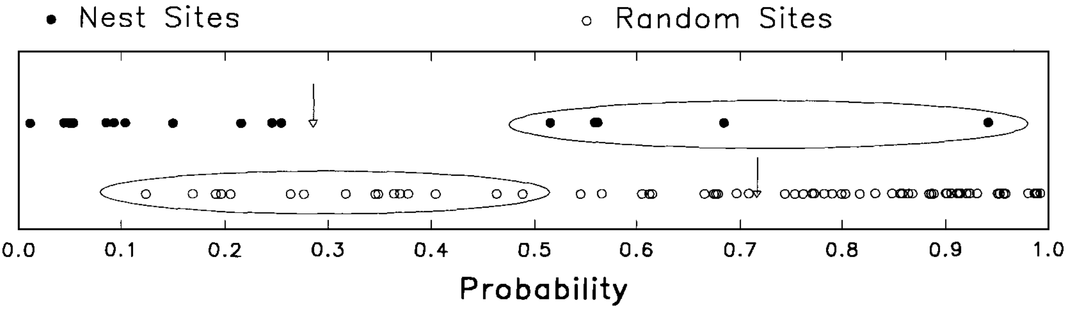

FIGURE 2. Discriminant score distribution for full-model DFA macrohabitat model of nest sites (N = 16) and random sites (N = 70). Data indicate probability of a site being a random site with arrows indicating group means. Circled sites represent the misclassified sites.

TABLE 3. SUMMARY OF STEPWISE DISCRIMINANT FUNCTION ANALYSIS (MANAGEMENT MODEL) OF SQUARE ROOT-TRANSFORMED MACROHABITAT VARIABLES FROM NORTHERN GOSHAWK NEST SITES AND RANDOM SITES

	Canonical coefficients		
Variables	Random site	Nest site	F-Prob
Distance to paved road	8.06	11.84	<0.001
Elevation	114.2	119.7	0.004
(Constant)	−144.7	−167.5	
Wilks' Lambda = 0.7253			

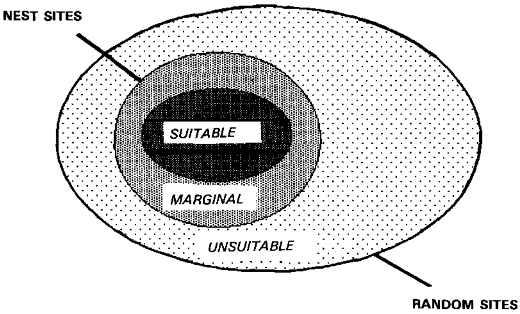

FIGURE 3. Random site and nest site domains for discriminant models in relation to habitat suitability.

cate that the goshawk is an area sensitive species, requiring large blocks of forested habitat since the study area was very nearly covered by contiguous forest. Robbins et al. (1989) demonstrated that area sensitivity was a phenomenon for many breeding bird species in the eastern deciduous forest. In our study, goshawks rarely nested in smaller forest tracts, which underscores the important effect of macrohabitat on breeding bird occurrence in eastern forests. In eastern forests this effect appears to stem from encroaching urbanization.

As a management model for eastern forests, the stepwise DFA indicated that only two of the original eight variables (distance to paved road and elevation) are needed to predict suitable macrohabitat for nesting goshawks. This reduction in the number of variables could speed the search for suitable macrohabitat and managers could apply these two variables to a sampling grid-system of random points on study area maps. With the advent of Geographic Information Systems and digital elevation models, rapid identification of suitable nesting areas is now possible and there may be less need to eliminate variables from consideration. Once suitable macrohabitat blocks have been identified, it would be prudent to conserve these areas from logging and development to preserve mature and old-growth stands which are preferred for nesting (Speiser and Bosakowski 1987).

ACKNOWLEDGMENTS

Part of the field work was funded by grants from the New Jersey Audubon Society and Fyke Nature Association. We would also like to thank D. Smith, L. George, and an anonymous reviewer for comments on the manuscript.

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LARGE-AREA GOSHAWK HABITAT MODELING IN DIXIE NATIONAL FOREST USING VEGETATION AND ELEVATION DATA

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Abstract. To expedite the evaluation of potential Northern Goshawk (*Accipiter gentilis*) habitat in Dixie National Forest, Utah, four computer models were designed to delineate areas where there was high probability of finding goshawk nest sites. Digital elevation data and vegetation class information derived from satellite imagery was acquired from the USDA Forest Service. These data were used to determine diagnostic elevation and vegetation characteristics for 30 known nesting sites and their associated post fledgling family areas (PFA). The first model, using elevation class as the only discriminator, located 95% of the known goshawk nest sites within 50% of the Forest. Using vegetation class in lieu of elevation, the second model located the same number of nest sites within 37% of the Forest. The third model employed vegetation and elevation class concurrently. The amount of Forest delineated to account for 95% of the goshawk nest sites dropped to 19%. By adding PFA information to the vegetation and elevation data, the fourth model reduced the area of search to only 14% of the Forest.

Key Words: *Accipiter gentilis*; habitat modeling.

The Northern Goshawk's (*Accipiter gentilis*) breeding habitat consists of mature forest patches used for prey acquisition and nesting. The decline of some local goshawk populations (Crocker-Bedford 1990) has led to a Category 2 listing by the US Department of Interior (1991).

Searching for goshawk nests through large patches of mature forests is time consuming and laborious. Any model that could delimit potential goshawk nest sites within a study area based on readily available, accurate, and inexpensive data would be a valuable management tool. In this paper, we present four models for predicting potential goshawk nesting site habitat in Dixie National Forest, Utah. These models evaluate potential nesting territory habitat by manipulating digital elevation data and a digital vegetation map.

METHODS

STUDY AREA

The Dixie National Forest encompasses 801,000 hectares in south central Utah. Vegetation distribution in the Forest is complex, but is determined primarily by elevation, slope, and aspect. Pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) are prevalent below 2400 m elevation, whereas ponderosa pine (*Pinus ponderosa*) is the most common tree between 2400 and 3050 m. A mixture of spruce (*Picea* ssp.) and fir (*Abies* ssp.) predominates above 3050 m. Patches of quaking aspen (*Populus tremuloides*) are scattered throughout the forest, but cover only about 1% of the total area.

DATA COLLECTION

We conducted field work within the study area 13 June–27 August, 1991 and 17 May–28 August, 1992. We verified previously located goshawk nests and searched for previously undiscovered nests within areas thought to be suitable goshawk habitat. We surveyed areas within the study region using at least one of three different methods. Some areas were surveyed following the call playback protocol of Kennedy and Stahlecker (1993). Where the forest patch was long and thin (<300 m wide) the playback protocol was adjusted by bending the transect line to permit us to remain on the hypothetical center-line of the strip. As a third alternative, we would walk slowly through suspected habitat, listening for goshawk vocalizations while looking for plucking perches, nests, or other indicators of goshawks.

Active goshawk nests were easily identified, whereas

TABLE 1. ELEVATION CLASSES WITHIN THE DIXIE NATIONAL FOREST STUDY AREA. ALL LOCATED GOSHAWK NEST SITES WERE FOUND BETWEEN 2350–3100 M

Elevation class	Number of known goshawk nest sites within elevation class	Study area within elevation class (%)
<1300	0	1.2
1300–1450	0	1.1
1450–1600	0	2.1
1600–1750	0	4.0
1750–1900	0	6.7
1900–2050	0	8.2
2050–2200	0	13.3
2200–2350	0	14.9
2350–2500	3	14.8
2500–2650	13	9.9
2650–2800	4	8.7
2800–2950	5	6.0
2950–3100	5	5.1
3100–3250	0	2.2
>3250	0	2.0
Total	30	

TABLE 2. VEGETATION CLASSES WITHIN THE DIXIE NATIONAL FOREST STUDY AREA. WITH EXCEPTION OF PONDEROSA PINE/JUNIPER TRANSITION, GOSHAWK NESTS WERE FOUND WITHIN ALL VEGETATION CLASSES

Vegetation class	Number of known goshawk nest sites within vegetation class	Study area composed of vegetation (%)
Aspen	1	1.1
Aspen/conifer	2	4.4
Pinyon pine/juniper	4	14.8
Ponderosa pine (high density)	6	4.7
Mixed conifer (low density)	1	3.4
Mixed conifer (high density)	8	7.9
Nonforested	3	55.3
Ponderosa pine (low density)	3	3.9
Ponderosa pine/mixed conifer transition	2	2.7
Ponderosa pine/juniper transition	0	1.8
Total	30	

inactive goshawk nests were distinguished from other species' nests by the estimated size of the nest, size of the nesting tree, height of the tree, local canopy cover within a 100-m radius of the tree, and size of the sticks used in the nest construction. Whereas heights and canopy cover were measured with a clinometer and densiometer respectively, we estimated the size of the nest and its sticks visually. When these criteria suggested a goshawk nest, we would examine the immediate area for definitive evidence of occupancy such as feathers, plucking perches, egg shell fragments, and prey remains. If a goshawk nest was found, its location was recorded using a Magellan Nav 5000 global positioning unit (GPU).

GIS DATA BASE

Maps of elevation and vegetation were provided by the USDA Forest Service (USFS) for potential goshawk nesting habitat elevation. Already in digitized grid-cell (i.e., raster) format, these maps were imported into an Intergraph geographic information system (GIS). Both data sets of 796,770 grid cells covered the entire Dixie National Forest and adjacent areas with a grid cell resolution of 120 m. The elevation map divided the study area into 15 equal elevation classes of 150 vertical meters. Table 1 presents the 15 elevation classes, the proportion of study area belonging to each, and number of located nest sites found within each class. The second digitized map contained ten broad vegetation community classes derived from USFS analysis of Landsat satellite imagery (Table 2).

CONSTRUCTING THE PFA VEGETATION FREQUENCY MAPS

The models we created were designed to discriminate between known goshawk nest sites and surrounding areas. Given the data sets provided, we decided to base this discrimination on three factors: (1) the dominant vegetation class of the nest site itself, (2) the elevation class of the nest site, and (3) the vegetation community composition within the post-fledgling family area (PFA). Where unconstrained by lakes or other landscape features, this PFA was originally defined as the 242.8 hectare (600 acre) circular zone centered on a nesting site (Reynolds et al. 1992). However, because of software limitations and the finite 120 meter grid cell size, a square PFA was assumed in this analysis.

Determining the PFA vegetation community composition for a cell was a multiple step process. As shown

TABLE 3. AVERAGE VEGETATION COMMUNITY CHARACTERISTICS OF POST FLEDGLING FAMILY AREAS (PFA) FOR 30 NEST SITES

	Number of cells within PFA possessing vegetation class (N = 30 nest site PFAs)	
Vegetation class	$\bar{X}$ (cells)	SD
Aspen	4.21	6.57
Aspen/conifer	24.12	22.35
Pinyon pine/juniper	10.70	12.79
Ponderosa pine (high density)	28.67	25.21
Mixed conifer (low density)	6.24	12.88
Mixed conifer (high density)	36.30	32.26
Nonforested	29.48	25.82
Ponderosa pine (low density)	7.30	8.81
Ponderosa pine/mixed conifer transition	15.21	11.95
Ponderosa pine/juniper transition	3.64	8.70

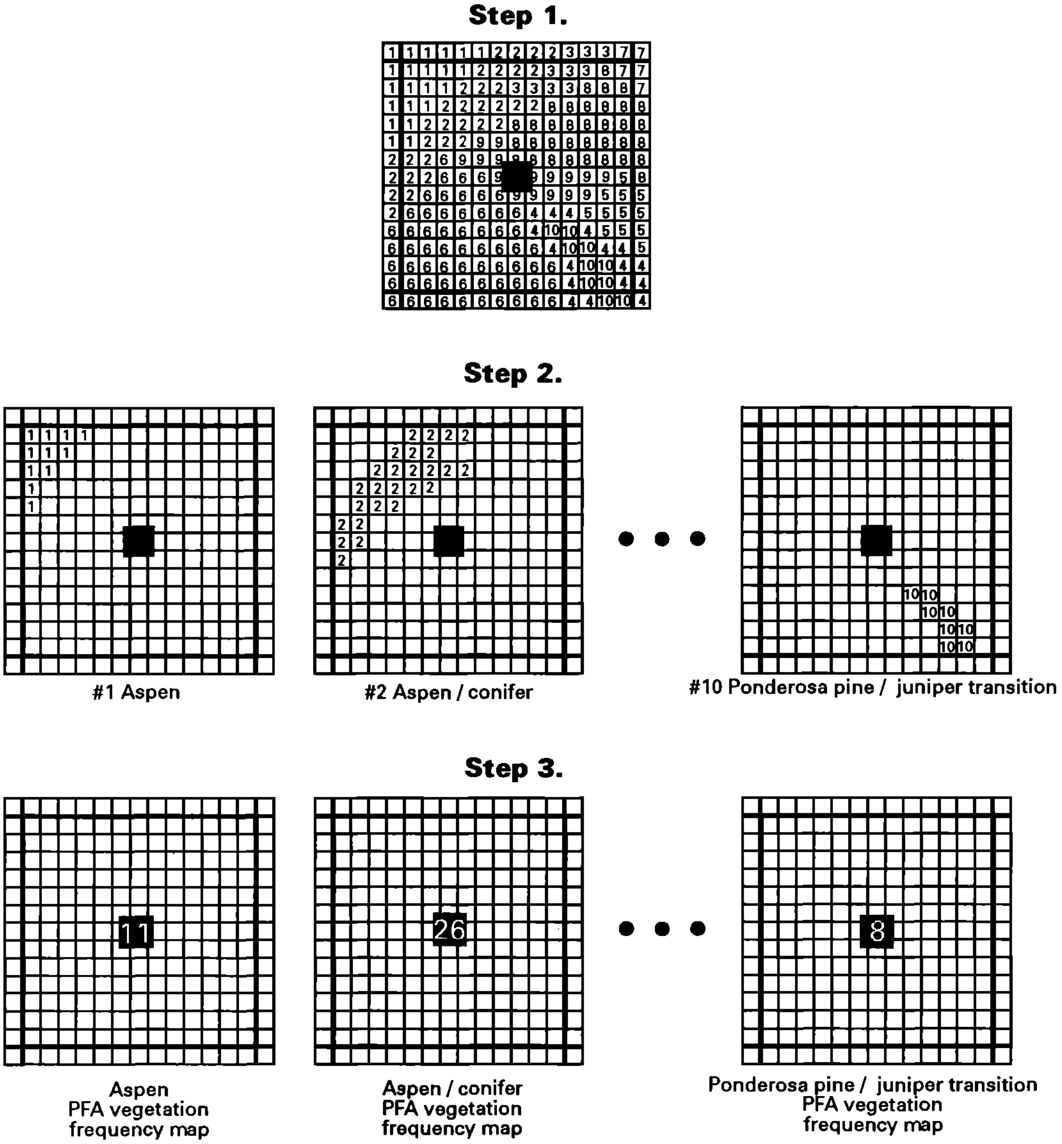

FIGURE 1. PFA value calculation for a single cell in the vegetation map is a three step process. In performing this calculation for every cell in the study area, the "sliding window" is placed over each cell successively, and the three step process is repeated. Step 1: A sliding window defining the PFA is centered over a cell in the original map. Step 2: The cells for each vegetation class are isolated within the sliding window and counted. Step 3: The counts are placed in the PFA frequency map cells which correspond to the center of the sliding window.

in Figure 1, a "sliding window" defining the 242.8 hectare PFA was centered over the cell's location on the digital vegetation map. The cells for each of the ten vegetation classes within the sliding window were then counted. The resulting counts for each of the ten vegetation classes were next placed into new PFA frequency maps at the cell location corresponding to the center of the window (Fig. 1, Step 3). To map the PFA vegetation community composition for the entire study area, this process was repeated for each of the 796,770 cells defining the Forest. The result of this process was ten PFA frequency maps, one corresponding to each vegetation class. Once completed, we located the 30 nest sites on the PFA vegetation frequency maps. The PFA composition of the 30 nest sites is summarized in Table 3.

TABLE 4. ORDER OF SEARCH ACCORDING TO MODEL I. ORDER IS DETERMINED BY RANKING OBSERVED – EXPECTED DIFFERENCES FROM HIGH TO LOW

		Known goshawk nest sites (N = 30)	
Order of search	Elevation class	Observed	Observed minus expected
1	2500–2650	13	10.05
2	2950–3100	5	3.49
3	2800–2950	5	3.21
4	2650–2800	4	1.38
5	1300–1450	0	−0.33
6	<1300	0	−0.36
7	>3250	0	−0.59
8	1450–1600	0	−0.64
9	3100–3250	0	−0.65
10	1600–1750	0	−1.21
11	2350–2500	3	−1.45
12	1750–1900	0	−2.00
13	1900–2050	0	−2.46
14	2050–2200	0	−3.98
15	2200–2350	0	−4.46

BUILDING THE MODELS

We built four models of goshawk nesting site location based on differences between observed and expected distributions of nest sites within different categories of elevation and vegetation (e.g., Fienberg 1980). Model I was based on elevation, Model II on vegetation classes, and Model III on both. Model IV used the PFA vegetation community composition in addition to elevation and vegetation. This model used a heuristic approach that combined the observed–expected differences with similarity measures used in cluster analysis. The interested reader should consult Spath (1980, 1985) for a discussion of these measures.

Based on the null hypothesis that no relationship existed between goshawk nest site location and elevation class, Model I predicts the percentage of the 30 goshawk nest sites located within an elevation class to be equal to the percentage of the study area covered by the class. Subtracting the number of goshawk nesting sites expected in an elevation class from the number observed and ranking the differences from high to low, the elevation classes are ordered in a sequence that, when used for field work, would maximize the number of goshawk nest sites found while minimizing the area searched (Table 4). This assumes that the 30 nest sites and their distribution were representative of all nest sites still not found in the Forest. The logic for the model predicted only on vegetation (Model II) was identical (Table 5).

The correlation between the ten vegetation classes and 15 elevation classes was low, producing a Goodman and Kruskal's τ_b (Blalock 1979) of only 0.26. Because of this, Model III incorporated both factors. The ten elevation classes where no goshawk nest sites were found (see Table 1) were discarded from further consideration, and every remaining possible combination of vegetation and elevation in the study area was determined from the digital maps. The number of goshawk nest sites observed and expected in each combination of elevation and vegetation was also determined by simple inspection of the maps. As before, the differences produced when subtracting the expected from the observed nest site count for each combination were sorted to generate an orderly search sequence. This model is represented by Table 6.

Whereas the first three models were based on probability, Model IV used a new heuristic approach. We devised a fourth model because the simple models based on elevation and vegetation did not incorporate PFA characteristics and all the models appeared to delimit too much of the forest to be of practical value.

Given our experience with the previous models, we defined three broad probability classes based on the combined categories of vegetation and elevation used in Model III. Class 1 consisted of areas where the observed–expected difference was positive or zero. These were locations where odds of finding goshawk nest sites would be no worse than expected. Class 2 consisted of those areas where nest sites were observed, but where

TABLE 5. ORDER OF SEARCH ACCORDING TO MODEL II. ORDER IS DETERMINED BY RANKING OBSERVED – EXPECTED DIFFERENCES FROM HIGH TO LOW

		Known goshawk nest sites (N = 30)	
Order of search	Vegetation class	Observed	Observed minus expected
1	Mixed conifer (high density)	8	5.63
2	Ponderosa pine (high density)	6	4.58
3	Ponderosa pine (low density)	3	1.83
4	Ponderosa pine/mixed conifer transition	2	1.19
5	Aspen/conifer	2	0.69
6	Aspen	1	0.67
7	Mixed conifer (low density)	1	−0.03
8	Pinyon pine/juniper	4	−0.45
9	Ponderosa pine/juniper transition	0	−0.53
10	Nonforested	3	−13.60

TABLE 6. Order of Search According to Model III. Order is Determined by Ranking Observed − Expected Differences from High to Low. LD = Low Density; HD = High Density; Trans. = Transition

Order of search	Known goshawk nest sites (N = 30)		Nesting site vegetation class	Elevation class (m)
	Observed	Observed minus expected		
1	4	3.21	Ponderosa pine (HD)	2500–2650
2	2	1.62	Mixed conifer (HD)	2500–2650
3	3	1.31	Pinyon pine/juniper	2500–2650
4	1	0.87	Aspen	2950–3100
5	2	0.84	Mixed conifer (HD)	2800–2950
6	1	0.80	Ponderosa pine/mixed conifer trans.	2800–2950
7	1	0.78	Mixed conifer (HD)	2350–2500
8	1	0.76	Ponderosa pine (LD)	2650–2800
9	1	0.74	Ponderosa pine (LD)	2500–2650
10	1	0.67	Aspen/conifer	2800–2950
11	1	0.66	Ponderosa pine (LD)	2950–3100
12	1	0.63	Ponderosa pine/mixed conifer trans.	2650–2800
13	1	0.59	Mixed conifer (LD)	2800–2950
14	1	0.53	Nonforested	2950–3100
15	1	0.52	Aspen/conifer	2500–2650
16	1	0.49	Mixed conifer (HD)	2650–2800
17	2	0.46	Mixed conifer (HD)	2950–3100
18	1	0.32	Ponderosa pine (HD)	2650–2800
19	1	0.23	Ponderosa pine (HD)	2350–2500
20	0	−0.05	Aspen	2350–2500
21	0	−0.07	Mixed conifer (LD)	2350–2500
22	0	−0.08	Ponderosa pine/mixed conifer trans.	2950–3100
23	0	−0.09	Aspen	2500–2650
24	0	−0.12	Mixed conifer (LD)	2500–2650
25	2	−0.12	Nonforested	2500–2650
26	0	−0.15	Aspen	2650–2800
27	0	−0.18	Mixed conifer (LD)	2650–2800
28	0	−0.20	Aspen	2800–2950
29	0	−0.26	Aspen/conifer	2950–3100
30	0	−0.32	Aspen/conifer	2350–2500
31	0	−0.40	Ponderosa pine/mixed conifer trans.	2350–2500
32	0	−0.45	Mixed conifer (LD)	2950–3100
33	0	−0.45	Ponderosa pine (LD)	2800–2950
34	0	−0.47	Ponderosa pine/mixed conifer trans.	2500–2650
35	0	−0.48	Ponderosa pine (LD)	2350–2500
36	0	−0.52	Aspen/conifer	2650–2800
37	0	−1.02	Nonforested	2800–2950
38	0	−1.11	Ponderosa pine/juniper trans.	2650–2800
39	1	−1.49	Pinyon pine/juniper	2350–2500
40	0	−1.72	Nonforested	2650–2800
41	0	−4.83	Nonforested	2350–2500

the observed–expected difference was negative. These were areas where observation indicated that the probability of finding goshawk was greater than zero, but where the odds were less than expected, given the area to be searched. Class 3 consisted of areas where nest sites were not observed.

We used the PFA information to stratify areas belonging to each of the three probability classes. The goal of this refinement was to determine areas within each probability class that had PFA characteristics closely resembling the PFA characteristics of the nest sites. In preparation for this step, the average PFA vegetation frequency counts were determined for cells in the study area belonging to each of the three probability classes individually (Table 7). The cell counts for each vegetation class were then standardized using the mean and standard deviation of cell counts across the three combined classes (Table 7).

Using this prepared standardized PFA information, an algorithm was utilized to assign each grid cell in the map to a predicted "nest site similarity class". The algorithm generated three indicators for every cell in the study area. The first indicator placed the cell into either Class 1, Class 2, or Class 3, depending on the

TABLE 7. VEGETATION COMPOSITION OF POST FLEDGLING FAMILY AREAS (PFA) FOR THREE BROAD PROBABILITY CLASSES AND NEST SITES USED IN MODEL IV. VALUES USED TO NORMALIZE FREQUENCIES ARE ALSO SHOWN

	Mean grid cell frequency				Normalizing values (pooled classes 1 through 3)	
PFA vegetation class component	Class 1 (cells)	Class 2 (cells)	Class 3 (cells)	Nest sites (cells)	$\bar{X}$ (cells)	SD
Aspen	5.1	0.7	4.2	4.4	3.4	12.69
Aspen/conifer	12.4	4.7	14.4	24.7	10.7	13.59
Pinyon pine/juniper	12.1	40.3	18.0	10.3	23.1	31.87
Ponderosa pine (high density)	11.6	10.3	15.0	30.8	12.4	15.51
Mixed conifer (low density)	10.0	1.3	9.7	6.6	7.2	14.42
Mixed conifer (high density)	19.4	3.2	38.7	39.0	21.4	31.80
Nonforested	53.1	85.8	36.4	24.2	57.3	42.44
Ponderosa pine (low density)	10.6	7.8	10.6	7.3	9.7	11.95
Ponderosa pine/mixed conifer transition	8.4	5.9	10.5	15.9	8.4	8.76
Ponderosa pine/juniper transition	10.3	1.5	6.8	4.0	6.3	12.21

observed–expected difference associated with the cell's vegetation and elevation class. The second indicator was the observed–expected difference itself, rounded off to an integer. The third was a "flag" that indicated whether the cell had PFA vegetation composition characteristics similar to one of the 30 nest sites, or more similar to the average PFAs of either Class 1, Class 2, or Class 3 (see Table 7). Euclidean distance was used to measure similarity; the smaller the Euclidean distance the greater the similarity. Table 8 shows the search order built from these indicators.

RESULTS

Table 9 shows the results of the four models for the entire Forest. The model based on vegetation class requires 49.6% of the forest to be searched to account for 95% of the known nest sites (i.e., 28.5 nests) whereas the elevation-based model requires only 37.0% of the forest be searched to account for the same number. The third model, which takes into consideration both

TABLE 8. ORDER OF SEARCH ACCORDING TO MODEL IV. MODEL LOGIC IS CAPABLE OF PRODUCING MORE CLASSES, BUT ONLY THE FIRST 20 ARE SHOWN IN THE TABLE. (PFA = POST FLEDGLING FAMILY AREA)

Order of search	Known goshawk nest sites observed (N = 30)	Probability class	PFA vegetation composition most similar to	Rounded observed − expected difference[1]
1	4	Class 1	Nest site	3
2	2	Class 1	Nest site	2
3	15	Class 1	Nest site	1
4	4	Class 1	Nest site	0
5	0	Class 1	Class 1	3
6	0	Class 1	Class 1	2
7	1	Class 1	Class 1	1
8	1	Class 1	Class 1	0
9	2	Class 2	Nest site	0
10	1	Class 2	Nest site	−1
11	0	Class 2	Class 1	0
12	0	Class 2	Class 1	−1
13	0	Class 3	Nest site	0
14	0	Class 3	Nest site	−1
15	0	Class 3	Nest site	−2
16	0	Class 3	Nest site	−5
17	0	Class 3	Class 1	0
18	0	Class 3	Class 1	−1
19	0	Class 3	Class 1	−2
20	0	Class 3	Class 1	−5

[1] Values are missing from sequence because they were not obtained in this study area.

TABLE 9. MODEL RESULTS SHOWING HOW MUCH OF THE FOREST REQUIRES SEARCHING TO LOCATE A SPECIFIC NUMBER OF KNOWN GOSHAWK NEST SITES

	Model I—based on elevation			Model II—based on vegetation			Model III—based on vegetation and elevation			Model IV—based on vegetation, elevation, and PFA composition		
Search order	Goshawk nest sites observed (N = 30)	Study area searched (%)	Cumulative study area searched (%)	Goshawk nest sites observed (N = 30)	Study area searched (%)	Cumulative study area searched (%)	Goshawk nest sites observed (N = 30)	Study area searched (%)	Cumulative study area searched (%)	Goshawk nest sites observed (N = 30)	Study area searched (%)	Cumulative study area searched (%)
1	13	9.9	9.9	8	7.9	7.9	4	1.2	1.2	4	0.9	0.9
2	5	5.1	14.9	6	4.7	12.6	2	0.6	1.8	2	0.4	1.2
3	5	6.0	20.9	3	3.9	16.5	3	2.5	4.3	15	6.2	7.4
4	4	8.7	29.6	2	2.7	19.2	1	0.2	4.5	4	4.4	11.8
5	0	1.1	30.7	2	4.4	23.6	2	1.7	6.2	0	0.1	11.9
6	0	1.2	32.0	1	1.1	24.7	1	0.3	6.5	0	0.1	12.0
7	0	2.0	33.9	1	3.4	28.1	1	0.3	6.8	1	0.7	12.7
8	0	2.1	36.0	4	14.8	42.9	1	0.4	7.2	1	0.3	13.0
9	0	2.2	38.1	0	1.8	44.7	1	0.4	7.6	2	0.9	13.9
10	0	4.0	42.2	3	55.3		1	0.5	8.0	1	0.7	14.6
11	3	14.8	57.0				1	0.5	8.5	0	0.2	14.8
12	0	6.7	63.6				1	0.6	9.1	0	<0.1	14.8
13	0	8.2	71.9				1	0.6	9.7	0	4.4	19.2
14	0	13.3	85.1				1	0.7	10.4	0	2.7	22.0
15	0	14.9					1	0.7	11.1	0	1.2	23.0
16							1	0.8	11.9	0	1.0	24.0
17							2	2.3	14.2	0	0.4	24.4
18							1	1.0	15.2	0	0.4	24.8
19							1	1.2	16.3	0	0.2	25.0
20							0	0.1	16.4	0	0.1	25.1[2]
21							0	0.1	16.5			
22							0	0.1	16.6			
23							0	0.1	16.8			
24							0	0.2	16.9			
25							2	3.2	20.1[1]			

[1] Search order continues to 41 (see Table 6). One goshawk nest site would be placed in search order position 39 with a corresponding cumulative forest area value of 92.4%.

[2] List continues, but all known goshawk nests sites have been accounted for.

cell elevation and vegetation class concurrently, provides a much more efficient map product; only 19.3% of the forest needs to be searched to locate 95% of the goshawk nest sites. The fourth model, which added the PFA information to the other two criteria, was the best performer. In this case 95% of the nest sites are found within only 13.7% of the forest.

DISCUSSION

We learned several things from the four models. We learned that elevation class was a more efficient predictor of goshawk nest sites than was vegetation class. We learned that vegetation class or elevation class alone were less efficient predictors of goshawk nest site location than was the combination of the two. We also learned that the vegetation composition of the PFA provides a small improvement in the model efficiency when employed as a predictor in a heuristic fashion.

Based on the results of the second and third models, the most important vegetation classes for search are apparently the high density mixed conifer and all the ponderosa pine classes. Ignoring any other factor, 63% of the goshawk nest sites are located within these classes, and their density is greater than expected given the area required to search. Nearly half the known goshawk nest sites are also between 2500 and 2650 m. A nesting site search of this elevation zone has good probability of success as well. If we were limited to searching a small acreage zone with the highest probability of success, we would select high density ponderosa pine and mixed conifer between 2500–2650 m; 20% of the known goshawk nest sites are located in this small percentage (4.8%) of forest.

Although the fourth model places 95% of the known goshawk nest sites within 13.7% of the forest, the model can be improved; nest site slope, aspect, and proximity to water will be variables added in the near future. We expect this information will more completely delimit the high priority search areas.

We are also verifying the model using two methods: ground verification and simulation. To facilitate ground verification, the computer will select random locations within the classes defined by Model IV (see Table 8). To insure adequate coverage, these locations will be allocated proportionally among the spatial areas of each class. We will then visit each in turn and search for goshawk nests using the methods described previously. Nest-finding success rates will then be compared to expected random occurrence rates and evaluated statistically for agreement. Furthermore, nest sites that were located after the modeling process was initiated will be used to validate the predictive value of the model. We will also attempt to verify the models using bootstrap simulation processes described by Willmott et al. (1985). These computationally intensive simulation methods allow for the inclusion of all the training data while withholding half for verification. Estimates of bias and standard error are produced as well.

Should verification prove our fourth model to be sufficiently accurate, it may be possible to predict the goshawk population within the Dixie National Forest and establish confidence intervals for that prediction. Application of this modeling process in forests with different attributes should be attempted and compared to the results obtained within this study area.

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Studies in Avian Biology No. 16:58–65, 1994.

HABITAT USE BY BREEDING MALE NORTHERN GOSHAWKS IN NORTHERN ARIZONA

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Abstract. We radio-tagged and followed five and nine male Northern Goshawks (*Accipiter gentilis*) during the breeding seasons of 1991 and 1992, respectively, to evaluate their use of different forest conditions in managed ponderosa pine (*Pinus ponderosa*) forests in northern Arizona. Sufficient data for habitat analyses were collected for 11 birds located a total of 734 times. Mean size of the home ranges was 1758 ha (SD = 500 ha, range 896–2528 ha) calculated by the minimum convex polygon method, and 1530 ha (SD = 477 ha, range 859–2321 ha) calculated by the 95% harmonic mean method. We compared use (i.e., number of hawk locations) of several categories of forest conditions to the availability (i.e., % of area of home range) of these categories for three different overlays (canopy closure, edge, and diversity) generated from LANDSAT data. Most (≥6) of the 11 birds used the categories in the three overlays approximately in proportion to their availability. Six of the 11 birds used at least one category on one of the overlays nonrandomly. Of these, three hawks used forests with relatively closed canopies more than expected; three used areas with relatively open canopies less than expected; four used woodland >200 m from edge more than expected; and one used areas with a high diversity of categories less than expected. When the categories of canopy closure were ranked for each bird on the basis of relative preference, average rank of preference increased with increasing canopy closure.

Key Words: *Accipiter gentilis*; habitat use; home range; LANDSAT imagery; Northern Goshawk.

Efforts to maintain habitat for the Northern Goshawk (*Accipiter gentilis*) in managed forests in western North America have focused on retaining stands of relatively large, old trees for nesting sites (Reynolds 1987). More complete conservation strategies for goshawks also need to address environments used for other activities, such as foraging (Reynolds 1983, Crocker-Bedford 1990). Current recommendations for managing forests for Northern Goshawks in the southwestern U.S. call not only for maintaining nest stands, but also for developing forest environments that support a variety of their prey species in a 2430 ha-area surrounding each nest (Reynolds et al. 1992).

Information from North America about the kinds of forest conditions used by foraging goshawks is limited. Fisher and Murphy (1986) radio-tracked a breeding pair of goshawks in Utah and concluded that the male occupied habitat nonrandomly by foraging predominantly in mature stands of Douglas-fir–white fir (*Pseudotsuga menziesii-Abies concolor*) forest. Austin (1993) radio-tracked ten goshawks (five males and five females) in northern California and found that they occupied meadows and stands of seedlings and saplings less than expected, and mature forest stands (dominant trees ≥ 52 cm in diameter at breast height, canopy closure ≥40%) more than expected, based on availability.

Kenward (1982) found that the European goshawk (*A. g. gentilis*) spent a disproportionately large amount of time in woodlands during the breeding season in agricultural areas of England and Sweden. In Sweden, goshawks used woodlands within 200 m of edge but avoided both unbroken woodland and extensive open areas (Kenward 1982). Widén (1989) radio-tracked goshawks in an intensely managed boreal forest in Sweden that contained a patchwork of stands of differing ages. Widén (1989) found that males and females both foraged in relatively large (>40 ha) tracts of forest >60 years of age.

Our objective in this study was to compare the availability and use of different forest conditions within the home ranges (Johnson 1980) of nesting male goshawks during the breeding season. Our statistical null hypothesis was that male goshawks used forest conditions within their home ranges randomly.

METHODS

STUDY AREA

The study was conducted on the North Kaibab Ranger District (NKRD), Kaibab National Forest, on the Kaibab Plateau in northern Arizona. The district encompasses ca. 259,000 ha and is located north of Grand Canyon National Park. Elevation of the NKRD ranges from 1060 to 2800 m. Topography of the plateau is typified by gentle slopes interspersed with shallow to deep drainages. Vegetation on the plateau is characterized by mixed-conifer forest (white fir, blue spruce [*Picea pungens*], Douglas-fir, and quaking aspen [*Populus tremuloides*]) at the highest elevations, ponderosa pine forest between 2075–2500 m, and pinyon-juniper-oak woodland (*Pinus edulis-Juniperus* spp.-*Quercus* spp.) at lower elevations. A detailed description of the plateau is given by Rasmussen (1941). We selected hawks to study that nested in areas dominated by ponderosa pine (about 99,200 ha on the plateau).

TELEMETRY

Personnel from the USDA Forest Service and Arizona Game and Fish Department had located nests of goshawks throughout the Kaibab Plateau prior to this study. We chose hawks to study based on four criteria: sex of the bird, topography and roads in the area around the nest, and forest type. Only males were studied because they provide between 80% and 90% of the prey consumed by the nestlings and because females spend the first half of the nestling period on or near the nest (Schnell 1958, Snyder and Wiley 1976, Reynolds and Meslow 1984, Kennedy 1991). Males were chosen from nests in areas that were relatively flat (although all areas were transversed by drainages), were dominated by ponderosa pine, and had a good system of roads. Flat areas with good roads were chosen to allow easy access to an entire home range. The hawks studied were not chosen randomly and therefore their use of forest conditions may not reflect that of the population of goshawks on the plateau.

Birds were trapped with falling-end Swedish goshawk traps (Kenward and Marcstrom 1983) and dhogaza traps (Clark 1981, Bloom 1987). Captured goshawks were banded with a US Fish and Wildlife Service band and a color band, and fitted with a two-stage radio transmitter (model TW-2 from BIOTRACK). The transmitters had posture-sensitive activity switches, weighed around 10 g, (less than 2% of the body weight of the birds), and were attached to tail feathers (Kenward 1978).

We located marked birds from 13 June–10 August 1991 and 8 June–9 August 1992. Monitoring began at least 36 hours after the radios were attached to allow the birds to become accustomed to the transmitter. During 1991, we tracked birds for one 4-hour period a day and attempted to locate the birds every half hour during this period. We rotated the 4-hour period so that each bird was monitored at different times of the day. In 1992, we attempted to locate each bird twice a day. Locations were obtained so that they were evenly distributed among all daylight hours. The change in data collection was made to maximize the number of statistically independent locations (Schoener 1981, Swihart and Slade 1985a) we could collect.

Locations were obtained by one of two methods: triangulation and direct observation. All observations of marked birds were recorded directly onto US Geological Survey (USGS) topographic maps. For locations obtained by triangulation, two observers with hand-held yagi antennas approached the bird until the sound of the signal at a specified gain value became distorted (ca. 50–200 m away). The observers then took positions which gave an angle to the bird between the two observers of 45–135 degrees. The observers then recorded the bearing to the bird and mapped their location on 7.5″ USGS topographic maps with the aid of a compass and by pacing to identifiable topographic features. Location of the bird was assumed to be where the two bearings crossed. Actions were coordinated between the observers with hand-held radios. Activity switches on the transmitters allowed observers to avoid attempting to triangulate on moving birds. Observers did not approach within 200 m of the nest while radiotracking because the presence of humans near the nest caused the male to remain in the area, disrupting his normal activities.

ESTIMATION OF LOCATION ERROR

We estimated the error associated with triangulations by following a protocol similar to that described by White and Garrott (1990) for estimating error of locations from airplanes. Transmitters were placed in a variety of topographic positions, stand conditions, and microsites to simulate locations of goshawks. Microsites included brush piles, logs, snags, and tree branches 0–10 m from the ground. The locations of the "test" transmitters were mapped by pacing and/or triangulating from known locations and visible topographic features. The error associated with the mapped locations of the test transmitters was small because they were placed near features that were clearly identifiable on topographic maps.

A pair of observers who did not place the test transmitter then located it by triangulation, following the procedure outlined above. Locations based on triangulation were converted to Universal Transverse Mercator (UTM) coordinates. The UTM coordinates of the triangulated position were then compared to the UTM coordinates of the position mapped by the team placing the transmitter. The distance between the triangulated position and the mapped position was then calculated and considered the error associated with location of that test transmitter. This distance incorporates error associated with triangulation and error associated with mapping the location of the observers. An average error for test transmitters was calculated for each year. We assumed that the average error associated with the location of the test transmitters was similar to the error associated with the location of hawks. Distances also were calculated from each observer to the triangulated location of the test transmitters and the hawks.

HOME RANGE

Sizes of home ranges were calculated using the minimum convex polygon (MCP) (Mohr 1947) and harmonic mean (HM) (Dixon and Chapman 1980) methods. All data, regardless of the time interval between consecutive locations, were used for the MCP calculations because this method does not require statistically independent locations (Swihart and Slade 1985b). For 1991, HM home ranges were calculated with a subset of the data that was not autocorrelated. We selected the subset by calculating the time to independence to the nearest 15 min using the Schoener ratio (Schoener 1981, Swihart and Slade 1985a), and then selecting locations that were separated by the minimum time to independence for each bird (60–135 min). All data for 1992 were used to calculate HM home ranges because the time between locations was much greater than the maximum time to independence determined in 1991. The grid size used in the calculation of harmonic mean home ranges was larger than the average error associated with the locations. Area-observation curves (Odum and Kuenzler 1955) were generated for each home range to ensure that the average increase in home range size was below 5% for the last ten locations recorded (Fuller and Snow 1988).

HABITAT CATEGORIES

Digital elevation data (DEM) for the Kaibab Plateau were obtained from the USDA Forest Service, Kaibab National Forest. These data were used to create a slope map for the study area so that we could examine goshawk use of topographic positions. The slope map was classified into seven slope categories (1 = 0–2%, 2 = 3–5%, 3 = 6–10%, 4 = 11–15%, 5 = 16–20%, 6 = 21–25%, and 7 = >26%).

Satellite imagery from LANDSAT 5 was obtained from 22 June 1991. This scene included no cloud cover over the study area. We used the satellite imagery to identify forest conditions within the home ranges of the goshawks we studied. Our general approach was to classify the imagery and then assess what the classes represented with aerial photographs. We allowed the computer to search for "natural" groupings of spectral properties (i.e., an unsupervised classification [Jensen 1986:215]) produced by the reflectance in bands 3, 4, and 5. This procedure was conducted in the Geographical Resources Analysis Support System (GRASS) with a maximum likelihood discriminant analysis classifier. Cell size was 30-m by 30-m for all analyses.

Fifteen classes with different spectral signatures were delineated. We overlaid a map of the 15 classes on a sample of aerial photographs taken in July 1991 (scale 1:8000) to ascertain visually what the classes represented in terms of forest conditions. We found that, with one exception, the classes (1–15) corresponded to a continuum of increasing forest density. Our relatively small sample of hawk locations prevented us from evaluating use of 15 different classes so we lumped the classes into five categories that broadly represented the following forest conditions: (1) bare ground or occasional trees, (2) open savannah-like conditions, (3) open overstory with a dense deciduous understory (this category was the exception mentioned above and was distinguished primarily on the basis of vegetative composition), (4) moderate overstory, and (5) dense overstory.

We then used the aerial photos to define each of the five categories on the basis of canopy closure and to estimate how consistently measures of canopy closure separated the five categories. We chose canopy closure to define the categories because this measure appeared to reflect a major difference among the categories and could be estimated from aerial photos. For each home range for which aerial photos were available (N = 7), one photo was randomly chosen for examination. We first outlined the areas of all five categories on the seven photos. We then estimated canopy closure by measuring the amount of intercept of tree crowns along 199 lines each 20 mm long. The lines were randomly placed on the photos with the restrictions that they fall within the boundary of one category and not be within 2.5 cm of the edge of the photos. The later restriction was to reduce the effects of lens distortion. We used a single eyepiece magnifier (7× lens) with a 20-mm bar scale on an attached reticle to make the measurements. Canopy closure was calculated as the percent of the 20-mm line intercepted by tree crowns.

The five categories were defined to maximize the percent of line estimates in each category that would be correctly classified. Definitions were (1) 0–15% canopy closure (CC); (2) 15–33% CC; (3) <33% ponderosa pine canopy closure with a dense understory of aspen, oak, or locust; (4) 34–55% CC; and (5) >55% CC.

TABLE 1. ACCURACY MATRIX FOR THE CLASSIFICATION OF LANDSAT IMAGERY INTO CANOPY CLOSURE CATEGORIES WITHIN NORTHERN GOSHAWK HOME RANGES ON THE KAIBAB PLATEAU, NORTHERN ARIZONA, 1991–1992. TABLE COMPARES AGREEMENT AMONG CATEGORIES IDENTIFIED IN AN UNSUPERVISED CLASSIFICATION OF LANDSAT IMAGERY AND MEASUREMENTS OF CANOPY CLOSURE MADE ON AERIAL PHOTOS

LANDSAT categories		Aerial photo canopy closure			
		<15%	15–33%	34–55%	>55%
<15%	31[1]	0.84	0.13	0.03	0.00
15–33%	52	0.13	0.72	0.15	0.00
34–55%	47	0.00	0.19	0.79	0.02
>55%	69, 37[2]	0.00	0.03	0.14	0.83

[1] Number of canopy closure estimates used to calculate percentages.

[2] Number of canopy closure estimates used to calculate percentages and number of stands of dense seedlings/saplings measured.

The accuracy of defining the five categories on the basis of canopy closure was estimated as the percent of the total number of line estimates for each category that fell in the ranges given above. One problem we noted was that dense, pure stands (>0.36 ha) of seedlings and small trees were classified as >55% CC. We measured the area of the dense, young stands on the sample of aerial photographs to obtain an estimate of how much they contributed to the total area of the >55% CC category (N = 37 patches totalling 40.0 ha) and added this to percent misclassification. Based on these estimates, we determined that measures of canopy closure from aerial photographs accurately defined 84% of the <15% CC category, 72% of the 15–33% CC, 79% of the 34–55% CC, and 83% of the >55% CC (Table 1). The category with <33% ponderosa pine overstory with an understory of oak, locust, or aspen occurred too rarely to assess accuracy adequately or to use in statistical analyses, so it was lumped with the 15–33% CC category.

Because measures of canopy closure from aerial photographs likely overestimate canopy closure on the ground (Brunnell and Vales 1989), we made some preliminary measurements on the ground to quantify the potential bias. Sixty-nine transects, each 100 m long, were laid out in areas representing four categories (17 in the <15% CC, 34–55% CC, and >55% CC categories, and 18 in the 15–33% CC category). Areas sampled and position of the transects were chosen randomly. Canopy closure was estimated along the transects by determining the percent of each transect that was covered by crowns of overstory trees (i.e., crown intercept). Preliminary measurements on the ground confirmed that our canopy closure categories represented areas with increasing canopy closure, but suggested that our measurements from aerial photographs overestimated canopy closure (measurements of canopy closure from the ground: <15% CC, $\bar{X}$ = 4.1%, range = 0–11.8%; 15–33% CC, $\bar{X}$ = 15.4%, range = 0–32.1%; 34–55% CC, $\bar{X}$ = 34.7%, range = 17.4–49.7%; >55% CC, $\bar{X}$ = 48.3%, range = 22.2–78.2%).

The map of canopy closure categories (i.e., canopy closure overlay) was used as a base map to create a habitat diversity overlay, a basic habitat overlay, and an edge overlay. The diversity map was created by performing a 5 × 5 cell neighborhood analysis on the canopy closure overlay. Each cell was approximately 30 m on a side so this analysis counted the number of different canopy closure categories found in a 2.25-ha square centered on a cell. Areas that were uniform (1 CC category), or had low (2 CC categories), moderate (3 CC categories), or high (4 or 5 CC categories) diversity were outlined on the diversity overlay.

The basic habitat overlay (HAB) was created by a two-step process. First an overlay was made by smoothing the original canopy closure overlay from the LANDSAT data. Smoothing consisted of two iterations of a 3 × 3 cell neighborhood analysis in which each cell of the new overlay was assigned the value of the most commonly occurring class in the 9-cell neighborhood. The smoothed overlay was then combined with a map from the USDA Forest Service that showed areas that were dominated by pinyon-juniper woodland. The resulting map (HAB) was equivalent to the smoothed habitat map except that all pinyon-juniper woodland was assigned a new value. The area of pinyon-juniper was too small to allow its inclusion in the statistical analyses, so based on its average canopy closure it was lumped with the 15–33% CC category.

The HAB overlay was used as the starting point to create the edge overlay. The 34–55% CC and >55% CC categories from the HAB overlay were lumped as "woodland" and the remainder of the classes were lumped as "open areas." The edge overlay was created by defining five new categories: open areas, woodland within 50 m of an open area, woodland 50–100 m from an open area, woodland 100–200 m from an open area, and woodland >200 m from an open area.

ANALYSIS OF HABITAT USE

We included all independent locations of goshawks that were perched or observed flying below the canopy in the analyses of habitat use. We do not know what portion of the locations represented foraging behavior because we could not determine what the birds were doing in most instances. We assumed that our data would reflect the relative value of the categories for foraging. We made this assumption because we collected data during the nestling and fledgling periods, when foraging demands are highest and males must capture prey for the female and nestlings in addition to satisfying their own needs.

Analyses of use versus availability were conducted for each bird at two scales for each overlay, and then trends in relative preference among all birds were evaluated for each overlay. For the first scale, we compared the number of hawk locations in each habitat category (i.e., use) to the number expected if the hawks were using the categories randomly (i.e., based on the availability of the categories in the MCP home range). Second, we compared the area of each habitat category in 90-m radius circles centered on the locations of birds (i.e., used) to the area of each category available (i.e., expected) in the MCP home range. A radius of 90 m was chosen for three biological reasons and one practical reason. First, information from Europe suggests that *A. g. gentilis* may forage near edges (Kenward 1982) and we did not want to throw out all locations near edges (e.g., Call et al. 1992). Second, for some overlays, as many as three or four habitat categories occurred within 90 m of a hawk location and, given the error associated with triangulations, assigning all the weight to one category could bias the results. Third, goshawks do not forage only at a single point but scan the surrounding area for potential prey. This idea is supported by Kenward (1982), who found that attack flights averaged 54 m from perch to prey in woodland and 103 m in open areas. Finally, the value of 90 m was chosen because it was an even multiple of the 30-m cell size.

A chi-square goodness of fit test was used to test use vs. availability for the habitat and slope categories for individual birds, as discussed by Thomas and Taylor (1990). When chi-square tests were significant ($P < 0.05$), Bonferoni 95% confidence intervals were calculated to determine which categories differed from expected (Neu et al. 1974). For the 90-m circle analyses, the observed value for the chi-square test was calculated for a habitat category by summing the proportion of the area of each circle that was in that habitat category.

Patterns of habitat preference among all birds were evaluated by averaging the rank preferences of all hawks for each habitat category (i.e., a Friedman's test [Ott 1988]) as discussed by Alldredge and Ratti (1992) and Conover (1980) with one modification. Instead of testing the rank of the difference between the percent used and the percent available for each category, as done by Alldredge and Ratti (1992), we tested the rank of the relative preference (Chesson 1983) for each category. We used relative preference, as defined below, because it accounted for differences in availability of each habitat category among birds, and allowed us to compare the ranks of relative preferences among birds with different home ranges.

Relative preference (RP) was defined for each bird as follows:

$$RP = \frac{O_i/E_i}{\sum_{i=1}^{n} (O_i/E_i)},$$

where O_i = the observed proportional use of habitat category i, E_i = the expected proportional use of habitat category i, and n = the number of habitat categories used by one bird.

The resulting preference values have a range of 0 to 1 and sum to 1 for each bird. These values were ranked for each bird so that the least "preferred" habitat was given a value of 1 and the most "preferred" a value of 4 or 5 depending on the number of habitat categories. Mean ranks were then compared among habitat categories. When the Friedman's test was significant (i.e., a difference among mean ranks was detected), Fisher's least significant difference was calculated to determine which mean rankings differed significantly. For the remainder of the paper when we discuss which habitats are most or least preferred we shall be referring explicitly to the relative preference as defined above.

TABLE 2. SIZE OF HOME RANGE AS CALCULATED BY THE MINIMUM CONVEX POLYGON (MCP) AND HARMONIC MEAN (HM) METHODS, AND AVERAGE PERCENT INCREASE FOR THE LAST 10 LOCATIONS IN AREA-OBSERVATION CURVES (A/O%) FOR 11 MALE NORTHERN GOSHAWKS ON THE KAIBAB PLATEAU, NORTHERN ARIZONA, 1991–1992

			MCP home range		95% HM home range[1]	
Bird	Year studied	A/O (%)	Size (ha)	N	Size (ha)	N
66	1991	0.0	2444	86	2322	55
136	1991	3.3	1502	87	1041	39
141	1991	4.1	2528	59	1939	47
223	1992	3.7	1450	36	1020	35
237	1991	0.2	1630	42	1279	40
273	1992	0.0	1454	80	1191	80
274	1991	0.2	1478	68	1889	45
285	1992	0.3	2139	84	1903	79
333	1992	0.0	2190	59	1559	59
339	1992	2.8	897	60	860	60
342	1992	0.1	1623	73	1830	72
191	1992	68.4[2]	431	13	518	13
239	1992	NA[3]	14	9	393	9
292	1992	5.3	178	32	1439	32

[1] Sample sizes in this column are also sample sizes used for habitat analyses.

[2] Birds with % A/O >5.0 were not included in results of home range or habitat portion of this study.

[3] Not applicable.

TABLE 3. RANKS OF RELATIVE PREFERENCE OF FOUR CANOPY CLOSURE CATEGORIES FOR 11 MALE NORTHERN GOSHAWKS DURING BREEDING SEASONS OF 1991–1992 ON THE KAIBAB PLATEAU, NORTHERN ARIZONA (1 = LEAST PREFERRED AND 4 = MOST PREFERRED)

	Percent canopy closure[1]			
Bird	<15%	15–33%	34–55%	>55%
66	1/1	3/3	2/2	4/4
136	1/1	3/3	2/2	4/4
141	1/1	3/2	2/3	4/4
223	2/2	1/1	3/3	4/4
237	1/1	3/3	4/2	2/4
273	1/1	2/2	4/4	3/3
274	1.5/2	1.5/1	3/3	4/4
285	1/1	2/2	3/3	4/4
333	3/1	2/3	1/2	4/4
339	3/3	2/1	1/2	4/4
342	1/1	2/2	4/4	3/3

[1] Ranks are presented for locations/90-m circle.

RESULTS

ERROR

The average error associated with triangulations was 98.3 m (N = 48 test transmitters, SD = 134.0) in 1991, and 68.5 m (N = 116 test transmitters, SD = 58.2) in 1992, probably because the observers were better trained in 1992. In 1991, observers were significantly closer to test transmitters when they took bearings ($\bar{X}_t$ = 80.3 m, SD = 60.9) than they were to birds when they took bearings ($\bar{X}_b$ = 183.6 m, SD = 145.3, $P < 0.001$), but in 1992 there was no difference in this distance ($\bar{X}_t$ = 158.8, SD = 84.5, $\bar{X}_b$ = 162.9, SD = 82.6, $P > 0.5$). The average error associated with the locations was less than the numbers given above because 45.7% of the locations were determined from direct observations.

HOME RANGE

Transmitters were attached to five birds in 1991 and nine birds in 1992. Twelve of the 14 marked birds successfully fledged young in the year they were studied. Area-observation curves indicated that we obtained a sufficient number of locations to calculate home ranges for 11 birds (Table 2).

The average size of the MCP home ranges for the 11 birds was 1758 ha (SD = 500, range 896–2528; Table 2). The average size of the 95% HM home ranges was 1530 ha (SD = 477, range 859–2321; Table 2).

HABITAT USE

The number of locations used for the habitat analyses for each bird was the same as the number of locations used to calculate the 95% HM home-ranges ($\bar{X}$ = 55.5, SD = 16.0, range 35–80; Table 2).

Slope

There was no preference for slope among the birds studied. Only one of the 22 tests on individual birds showed any difference between use and availability of slope categories.

Locations

Eight of the 11 birds used the canopy closure categories in proportion to their occurrence, whereas the remaining three birds used areas with >55% CC more than expected and areas with <15% CC less than expected ($P < 0.02$). One of these birds also used areas with 34–55% CC less than expected. Six of the 11 birds used the edge categories randomly, and the remaining five birds used them nonrandomly. Four of these five birds used open areas (all areas with <34% CC) less than expected, one used areas between 50–100 m from edge less than expected, one used areas between 100–200 m from edge more than expected, and two used areas >200 m from edge more than expected ($P < 0.05$). Only one of the 11 birds used the diversity categories nonrandomly and this bird used areas of high diversity less than expected.

Mean rank of relative preference of the canopy closure categories increased with increasing canopy closure (T_2 = 9.28, df_1 = 3, df_2 = 30, P <

TABLE 4. MEAN RANK OF RELATIVE PREFERENCE OF FOUR CANOPY CLOSURE CATEGORIES FOR 11 MALE NORTHERN GOSHAWKS DURING THE BREEDING SEASONS OF 1991–1992 ON THE KAIBAB PLATEAU, NORTHERN ARIZONA

Analysis	Percent canopy closure				N	P[1]
	<15%	15–33%	34–55%	>55%		
90-m circles	1.36A	2.09B	2.73C	3.82D	11	0.001
Locations	1.50A	2.23AB	2.64B	3.64C	11	0.001

[1] Friedman test of ranks of relative preference. Differences between means followed by same letter were not significant (Fisher's least significant difference).

0.001; Tables 3, 4). No difference in relative preference was shown for woodland with regard to distance from open areas, but open areas (<34% CC) were preferred less than woodland (areas with ≥34% CC) ($T_2 = 6.56$, $df_1 = 4$, $df_2 = 40$, $P < 0.001$; Table 5). There was also no difference in relative preference for the diversity categories ($T_2 = 2.45$, $df_1 = 3$, $df_2 = 30$, $P > 0.1$).

90-m radius circles

Only one bird used areas with >15% CC less than expected ($P < 0.02$). Only three birds occupied edge categories nonrandomly. Two used open areas less than expected and one used woodland >200 m from edge more than expected ($P < 0.05$). Only one bird used areas of high diversity less than expected.

Mean rank of relative preference of the canopy closure categories increased with increasing canopy closure ($T_2 = 18.50$, $df_1 = 3$, $df_2 = 30$, $P < 0.001$; Tables 3, 4). There was no clear pattern in relative preference for woodland categories with respect to distance from open areas, but open areas were preferred less than woodland areas ($T_2 = 10.49$, $df_1 = 4$, $df_2 = 40$, $P < 0.001$; Table 5). There was no difference in preference among the categories of the diversity overlay ($T_2 = 1.36$, $df_1 = 3$, $df_2 = 30$, $P > 0.25$).

DISCUSSION

HOME RANGE

The sizes of home ranges found in this study are intermediate compared with those found by Eng and Gullion (1962) in Minnesota (one male, 1272 ha), Kennedy (unpubl. data) in New Mexico (three males, $\bar{X} = 2106$, range 1696–2837 ha), and Austin (1993) in California (five males, $\bar{X} = 2425$ ha, range 1083–3902). However, comparisons among these studies should be done with caution because the hawks were tracked for different periods of time and/or different methods were used to calculate home range size.

HABITAT USE

The main pattern we found in the use of forest conditions by goshawks was that mean rank of relative preference of all hawks increased with increasing canopy closure. Potential explanations for this trend are the availability of prey (Kenward 1982, Reynolds et al. 1992) and the morphological adaptations of goshawks that presumably make them well adapted for hunting in forests. Fisher and Murphy (1986) and Austin (1993) also found that goshawks used forests with closed canopies more than open woodlands or meadows.

The pattern of use of canopy closure categories suggested by the ranking of relative preferences was not significant in most hawks when analyzed individually. The following factors may have reduced our ability to detect significant habitat preferences at the individual bird level: (1) goshawks were more easily observed in open areas than in forests and about half of our locations were direct observations; (2) goshawks were more easily located when they were near roads (usually relatively open areas near edges); (3) our sample of locations for each bird was relatively small; (4) some individuals may not have strong habitat

TABLE 5. MEAN RANK OF RELATIVE PREFERENCE FOR DISTANCE FROM OPEN AREAS (<34% CANOPY CLOSURE) FOR 11 MALE NORTHERN GOSHAWKS DURING THE BREEDING SEASONS OF 1991–1992 ON THE KAIBAB PLATEAU, NORTHERN ARIZONA

Analysis	Woodland distance from open areas					N	P[1]
	Open	0–50 m	>200 m	50–100 m	100–100 m		
90-m circles	1.09A	2.91B	3.45BC	3.59BC	3.95C	11	0.001
Locations	1.27A	3.18B	3.23B	3.54B	3.73B	11	0.001

[1] Friedman test of ranks of relative preference. Differences between means followed by same letter were not significant (Fisher's least significant difference).

preferences within their home ranges; and (5) goshawks may select habitat on the basis of conditions we did not measure. Significant trends at the individual bird level also may have been obscured by the error associated with our locations, the uncertainty about what the birds were doing when we located them, and the error introduced when we smoothed the basic habitat overlay. Smoothing results in small patches potentially being misclassified.

MANAGEMENT RECOMMENDATIONS

Tree harvest methods that create large areas with sparse tree cover are potentially detrimental to Northern Goshawks, especially if the percent of open forests (<34% CC as measured from aerial photos) in a home range is greater than 35% (the mean found in this study). Therefore, in areas being managed for Northern Goshawks, selection cuts and other harvest methods that leave a substantial portion of the canopy intact should be favored. Reynolds et al. (1992) recommended maintaining 40% canopy closure over 60% of a proposed foraging area (2187 ha) for each pair of nesting goshawks. We can not directly evaluate the specific values recommended by Reynolds et al. (1992) because we made our measurements of canopy closure from aerial photos, but our findings support the general idea of maintaining relatively high canopy closure over a significant portion of areas managed for foraging goshawks.

Our investigation examined only males during the breeding season. Much information on habitat use is needed, especially on females, immatures, and wintering males before a more complete assessment of goshawk habitat requirements can be made. Future researchers should be aware that, as Kenward (1982) and Reynolds et al. (1992) suggested, goshawk habitat selection may be a function of habitat selection by prey species. For this reason, detailed diet analyses should be done in conjunction with studies of habitat use and prey availability if we are to understand more fully the requirements of the Northern Goshawk.

ACKNOWLEDGMENTS

We thank A. Duerr, J. Bacorn, D. Wotherspoon, T. Ashbeck, M. Miller and M. McGrath for hours of grueling labor, and R. Reynolds, S. Joy, D. Leslie, and crew for help trapping birds. We are indebted to C. Boal for his help, suggestions, and support throughout the entire course of this study. Special thanks to R. Bright for all her help in the field and at home. This work was funded by the UDSA Forest Service, Rocky Mountain Forest and Range Experiment Station and the University of Arizona. Partial support for D. Smith was provided by an NSF graduate student fellowship. The Arizona Game and Fish Department provided housing during the last field season.

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HOME RANGES AND HABITATS OF NORTHERN GOSHAWKS IN EASTERN CALIFORNIA

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Abstract. We conducted a 3-summer telemetry study of nesting Northern Goshawks (*Accipiter gentilis*) (N = 10) to determine stand structure, landscape patterns, and geographic features that characterize home ranges. We subdivided home range use into two phases of the breeding season, the nestling phase and post-fledging phase, because home ranges of adult males and females showed significant expansion after the young had fledged. Nearly all birds incorporated areas into their home ranges that were spatially distant from the nest stand, which resulted in higher vegetative diversity within the nestling-phase home ranges than would be expected from random home range placement. Home range locations used by perched goshawks were similar to nest sites, and both had greater canopy cover, greater basal area, and more trees per ha than a random sample from the study area. Thus, perched goshawks tended to be in well-canopied stands with large trees that were in proximity to a variety of vegetation types and seral stages. Nest sites were significantly closer to water sources than random study area points, and home range configurations were influenced by the location of water. Goshawk management strategies should include the potential home range as well as the nest site. Our data suggest that a goshawk can incorporate vegetation types and water sources as far as 3.5 km from the nest stand into its home range. Within this potential use area, emphasis should be placed on creating or maintaining vegetative diversity. Mature forests should be retained around water sources, along forest-open edges, and throughout the potential foraging area.

Key Words: *Accipiter gentilis*; adaptive kernel; habitat use; home range; Northern Goshawk.

Much of the current knowledge of habitat use by the Northern Goshawk (*Accipiter gentilis*) has been taken from nest sites (e.g., Reynolds et al. 1982, Moore and Henny 1983, Kennedy 1988, Patla 1990). Little is known about habitat characteristics that define the rest of the home range, that is, the area used by individuals for foraging and resting as well as for care of young. Prior to the development of goshawk management recommendations for the southwestern United States (Reynolds et al. 1992), goshawk management in timber resource areas was generally limited to the retention of an uncut buffer of mature timber around nest sites, ranging from a recommended 8 ha (Reynolds et al. 1982) to 49 ha (Fowler 1988).

The emphasis placed on nest sites is justified because the nest or a nearby alternate nest is used by goshawks for many years (Palmer 1988). Protection of the nest and alternate nests provides a reasonable long-term management strategy. However, even though a nest site is protected, the remainder of the home range is frequently subjected to habitat alteration. If certain habitat components are needed by breeding goshawks in areas other than the immediate nest sites, then habitat alterations could eventually cause the decline of this species even though nest sites are protected.

Our study was prompted by the need to provide better management guidelines for goshawk home ranges within areas of timber management on the Inyo National Forest in eastern California. Beginning in 1979, goshawk nests on the Inyo National Forest were protected from timber harvests by delineating a 16-ha buffer around each known nest when the boundaries of each sale were mapped. This area was enlarged for all sales after 1987 to meet the guidelines of the Inyo National Forest Land Management Plan, which called for either a 40.5-ha buffer around the nest or two 20-ha buffers around the currently occupied nest and an alternate nest. One of our concerns was whether small, isolated buffers were sufficient to meet the needs of nesting goshawks, or whether other components within the home ranges needed to be considered. We needed to know where goshawks foraged in relation to their nests and what habitats were used for foraging, in order to make meaningful recommendations for extending management over areas larger than the nest buffers.

We investigated goshawk home range use at the microhabitat and landscape level. At the microhabitat level, we focused on the forest stand structure associated with goshawk telemetry locations within their home ranges. Other studies have shown that nest sites are typically in stands with large trees and dense canopies (e.g., Hall 1984, Speiser and Bosakowski 1987, Hayward and Escano 1989). We wanted to determine whether these conditions were also characteristic of areas used within home ranges.

At the landscape level, we were interested in vegetation patterns and landscape features that might influence the size, location, and configuration of home ranges. In particular, we wanted to determine whether home ranges were influenced by the location of large blocks of mature timber, the amount of vegetative diversity, the availability of interior habitat or habitat edge, the location of open areas, and the presence of water.

The objectives of our study were (1) to determine stand structure, landscape patterns and key geographic features that influence the size, location, and configuration of goshawk home ranges; and (2) to develop management recommendations focused on home range management rather than nest site management.

METHODS

STUDY AREA

The study area is approximately 440 km^2 of forested habitat on the Inyo National Forest, located east of Yosemite National Park near the California–Nevada border. Elevations range from 2000–2700 m. Extensive tracts of Jeffrey pine (*Pinus jeffreyi*) are interspersed with stands of lodgepole pine (*Pinus contorta*), big sagebrush (*Artemisia tridentata*), aspen (*Populus tremuloides*), and pumice flats sparsely vegetated with grasses and forbs. Red fir (*Abies magnifica*) is the dominant vegetation within the narrow elevational band of 2600–2700 m along the eastern Sierra slope. Red fir is also found in Jeffrey pine and lodgepole pine stands on many north- and east-facing slopes.

Most stands in the study area have 1–3 age classes of trees and a shrub or grass-sedge understory. The dominant ground vegetation in Jeffrey pine stands is bitterbrush (*Purshia tridentata*). A sparse cover of grasses (*Sitanion hystrix, Stipa occidentalis*) and sedge (*Carex rossii*) occur in lodgepole pine stands. Forest canopies tend to be open due to xeric conditions imposed by poor soils and climate (20–40 cm annual rainfall).

Much of the landscape has been modified by timber harvests, mostly through the removal of large diameter overstory trees, leaving mid-seral stage stands. Clearcuts are uncommon and are restricted to patches <16 ha.

For the purpose of this paper, older seral stages of timber will be referred to as "old growth." A formal old growth definition has not been developed for the Inyo National Forest, but old growth Jeffrey pine is typically >250 years old, with ocular-estimate canopy closures rarely >40%. Lodgepole pine old growth is >200 years old, with canopy closures between 30–50%. Red fir old growth is >250 years old, with canopy closures between 35–60%. Timber compartment stands identified as old growth on the Inyo National Forest (Inyo National Forest unpubl. stand record cards) are mostly 15–60 ha in size except for the 486-ha Indiana Summit Research Natural Area, managed for old growth Jeffrey pine, and a 900-ha tract of red fir, lodgepole pine, and white fir (*Abies concolor*).

HOME RANGES

Home range and habitat use data were derived from radiotelemetered goshawks during the summer seasons of 1986–1988. We captured goshawks using a dho-gaza with a Great Horned Owl (*Bubo virginianus*) lure in the vicinity of active nests (Hamerstrom 1963, Bloom et al. 1992). Each goshawk was banded with a US Fish and Wildlife Service leg band. Radio transmitters were attached to the backs of the birds with teflon tubing fitted around the wings. The 28-g transmitters had a life expectancy of 7 months.

We created a grid overlay for 1:24,000-scale USGS maps of the study area and used the grid coordinates in calculating goshawk locations. The spacing of 1 mm between grid lines corresponded to 26 m on the ground. Telemetry locations were obtained by two observers using Telonics 2A (Mesa, Arizona) and Advanced Telemetry Systems (Isanti, Minnesota) receivers and 5-element yagi antennae mounted in two truck beds. Simultaneous bearings were taken from two locations, and the estimated location of the bird was calculated by triangulation (White and Garrott 1990) using the two bearings and the known grid coordinates of the observers. We took bearings on each goshawk at 15-min intervals for 1.5 hr. Each bird was monitored every 2–3 days at a randomly selected time between 08:00–14:00.

To determine errors associated with location estimates, the observers estimated the location of a transmitter placed at 20 random locations by an independent party. The observers were on average 718 ± 368 (SD) m from the transmitter during these tests, and the mean error in location was 102 ± 66 m. The error associated with estimation of goshawk locations may have been somewhat lower, since during monitoring the observers were on average closer to the goshawks ($\bar{X} = 465 \pm 292$ m) than to the test transmitter. By proportional extrapolation, the mean error in estimating goshawk locations was 66 m.

Home ranges were calculated using an adaptive kernel method (Worton 1989) developed by J. Baldwin (USDA Forest Service, Pacific Southwest Experiment Station, Berkeley, California, pers. comm.). This method is based on Anderson's (1982) definition of home range: the probability of finding an animal at a particular location on a geometric plane, given a bivariate probability density function for that animal. The kernel method is a non-parametric technique that estimates the probability density function from a data set of known locations, using a data smoothing function similar to the Fourier transformation employed by Anderson (1982). The adaptive kernel method differs from the Fourier transformation and from fixed kernel methods in that the magnitude of the smoothing parameter is changed depending on the concentration of data points. Areas with a low concentration of points have less weight than frequently used areas, thereby rounding off finger-like extensions of the home range that are caused by a few location points (Worton 1989). All of these methods calculate a three-dimensional volume for the bivariate probability function from which contours can be selected that represent a given percentage of the volume, or a given percentage of the sample points. For the adaptive kernel method, our contours were constructed to represent a percentage of the sample points.

Contour intervals that represented 95% and 50% of each goshawk telemetry data set were constructed at the 1:24,000 scale and traced onto mylar overlays of the study area. We calculated home range estimates for the entire monitoring period from late June to mid September. However, we found that these home range estimates were misleading because they included areas that were not used by the adults until the young had fledged. Also, these estimates masked information on home range shifts and range expansion that occurred after the young had fledged. A division of the monitoring period into two phases, nestling and post-fledging, provided a more sensitive discrimination of home range use, and separated the restricted, nest-oriented home ranges of the earlier period from the broader areas used later in the breeding season. Since observations at the nests indicated that all young had fledged by the end of July, we used 1 August to delineate the two periods and calculated nestling-phase and post-fledging-phase home range estimates for each bird.

LANDSCAPE PATTERNS

Landscape patterns were compared between nestling-phase home ranges, post-fledging-phase home ranges, and a random sample of artificial home ranges within the study area. Artificial home ranges were created by placing a circle with an area of 9.04 km^2 at random points within all available habitat of the study area. The centers of the artificial home ranges were grid coordinates that were generated randomly from the entire study area. The size of the circle corresponded to the mean size of the 95% polygons for the nestling-phase and post-fledging-phase home ranges. Within each randomly-placed circle and within the 95% contour of each home range, we recorded the number of vegetation types per km^2, total number of vegetation units (patches) per km^2, percent of home range in inventoried old growth, length of forest-open edge per km^2, distance to water, and distance to a forest opening greater than 20 ha. Vegetation types were qualitatively differentiated on the basis of the most abundant overstory and understory species (Mueller-Dubois and Ellenberg 1974) and seral stage (Mayer and Laudenslayer 1988). Vegetation boundaries were delineated using aerial photogrammetry and were field verified. Old growth acreages were derived from a comprehensive old growth inventory conducted on Inyo National Forest in 1989-1990 (Inyo National Forest, unpubl. data).

All distance measurements were taken from 1:24,000 orthophotos with a map wheel. Since the home range polygons were not circular, we developed the following criteria for selecting the point from which distances to water and forest openings were measured. For nestling-phase home ranges, distances were measured from the nest, whether or not the nest was the geometric center of the range. If the range contained other polygons besides the polygon containing the nest, we measured distances from the center of the other polygons and averaged the values. The center of each polygon was the midpoint of the longest axis bisecting the polygon. For post-fledging-phase home ranges, we measured distances from the center of the 50% contour located inside the 95% contour. In the majority of cases, the home range was a cluster of 2–3 polygons, so 2–3 distance measures were taken and averaged.

We noted whether home ranges encompassed or were in proximity to human developments, but did not quantify these relationships. Principal developments were the town of Mammoth Lakes (pop. 10,000), highways, developed campgrounds, and major dirt roads.

STAND STRUCTURE

As a means of evaluating stand structure used within home ranges and at nests, we collected data at three types of sites: nest sites, sites within the home ranges other than nest sites, and sites located at random within the study area. The nest site data included the nests of the radio-tracked birds and all other known goshawk nests within the study area. The home range data set was a stratified random sample of all radio telemetry locations other than nest sites for the three summer seasons of study. We stratified the data to ensure that some locations were derived from all ten birds that were monitored. The sample was taken from the entire monitoring period. Random sites were selected by generating random x,y coordinates from the study area grid overlay.

Plot size used to measure stand structure variables was 0.04 ha. At each nest we collected data at five plots to include local variation in stand structure parameters. One plot was centered on the nest tree and the remaining plots were located 30 m from the tree in each of the cardinal directions.

Home range telemetry points were located in the field using the estimated grid locations placed over the study area map. We began collecting data at home range locations prior to selecting a method for determining the error associated with estimation of these points. We assumed that our error ranged from 25–75 m from the true locations of the birds and collected data at two plots at random distances between 25–75 m from the calculated telemetry location. The stand structure values obtained from both plots were then averaged. These distances proved to be close to the 66 m error that we calculated later. The two points also helped capture some of the variation found within the forest stands. Time constraints did not permit collecting data at more than two plots per location. We located the random sites in the field and collected data in the same manner as at home range sites, using two plots located 25–75 m from each random point.

Habitat parameters collected in each plot for all three site types were used to assess stand density and the amount of standing and down dead material. These included number of trees in five diameter classes (1–15 cm, 16–27 cm, 28–45 cm, 46–61 cm, and >62 cm), basal area, percent canopy cover, percent slope, aspect, and number of snags and down logs within each plot. Basal area data were collected with a 20-factor basal area prism. Percent canopy cover was the average of four ocular estimates made within the major quarters of each circular plot. Percent slope was taken with a clinometer. At nest sites we also took data on nest tree diameter at breast height (dbh) (cm), nest tree height (m), and height of nest (m) within the tree. The dbh measurements were taken with a logger's tape. Tree and nest heights were derived from a clinometer reading taken at a known distance from the tree bole.

Prior to statistical analyses, all variables were examined for normality and transformed when appro-

TABLE 1. SELECTED LANDSCAPE ATTRIBUTES FOR GOSHAWK NESTLING-PHASE RANGES, POST-FLEDGING RANGES, AND RANDOM CIRCLES WITHIN THE STUDY AREA

	Nestling-phase ranges		Post-fledging ranges		Random	
Landscape attribute	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
No. of veg types/km	1.4	1.2	0.8	0.8	0.6	0.2
No. of patches/km	2.3	0.9	1.7	0.5	1.2	0.4
Km edge/km	1.1	0.7	1.2	0.3	0.9	0.4
Dist. to water (km)	1.2	0.9	2.2	1.2	2.7	1.2
Dist. to openings >20 ha (km)	0.7	0.6	0.6	0.3	0.7	0.6
Proportion of range in old growth	0.17	0.29	0.09	0.12	0.09	0.09

priate. The square root transformation was applied to all count data, and an arcsine square root transformation was done for canopy closure proportions. Normal probability plots for the transformed data were linear, indicating that the transformations were appropriate. Univariate ANOVA procedures were used to test for stand structure and landscape level differences. We used Tukey's studentized range tests to determine which group or groups were responsible for any significant differences detected with the ANOVA tests.

RESULTS

We radio tracked eight females and two males over the three summer seasons of the project: two females and one male in 1986, three females in 1987, and three females and one male in 1988. These ten adults were associated with six territories. Two of the territories were monitored twice, but with different females and alternate nests. The male in 1986 was the mate of a monitored female in the same year, and the male in 1988 was associated with the nest used by a monitored female in 1987. A female from 1987 was recaptured and followed again in 1988 but the second year of data was omitted from all statistical analyses and home range estimates. The number of telemetry locations per bird ranged from 35-56 during the nestling phase ($\bar{X}$ = 44 ± 7) and from 48–107 locations during the post-fledging phase ($\bar{X}$ = 64 ± 18). For the entire monitoring period, the mean number of telemetry locations was 108 ± 17 per bird.

HOME RANGES

All home range estimates presented are for the areas of the 95% polygons. Home ranges for all ten adults for the entire monitoring period averaged 15.5 ± 8.9 km^2. The seven female home ranges averaged 13.4 ± 8.1 km^2, and the two male ranges were 17.9 km^2 and 30.1 km^2.

After approximately 1 August, we noted a significant range expansion (one-tailed paired-sample t-test, t = 2.4, df = 9, P = 0.04). This expansion was not correlated with the number of telemetry points associated with each bird (adjusted r^2 = 0.12). All but one female expanded their home ranges. Female home ranges increased from a mean of 5.2 ± 3.9 km^2 (range = 0.7–7.8 km^2) during the nestling phase to 10.2 ± 8.2 km^2 after the young had fledged (range = 1.1–24.6 km^2). The two males also expanded their ranges, from 3.4 km^2 to 16.2 km^2, and from 9.5 km^2 to 28.4 km^2. One female's range decreased from 7.8 km^2 during the nesting period to 1.1 km^2 after the young had fledged.

Four of the ten goshawks showed complete range shifts after the young fledged. The most extreme case was the shift of one female to an area 9 km from her nest. Her post-nesting range had roughly a 90% overlap with another radio-tracked female. The female who did not expand her range shifted her area of use by approximately 6 km to the vicinity of a playing field. This female exhibited the same range shift in two consecutive breeding seasons.

In relationship to human activities other than timber harvests, the 50% polygon for one nesting range included a 20-unit campground. Three of the post-nesting ranges were divided by a 4-lane highway, and one post-nesting range included a playing field adjacent to the town of Mammoth Lakes.

LANDSCAPE PATTERNS

We compared landscape patterns between three groups: nestling-phase home ranges (N = 10), post-fledging-phase home ranges (N = 10) and randomly-placed circles (N = 10). Using ANOVA and α = 0.1, we detected significant differences in the number of vegetation types per km^2 between the 3 groups (F = 2.53, df = 29, P = 0.1). A Tukey's studentized range test at α = 0.1 indicated that nestling-phase home ranges had on average a greater number of vegetation types per km^2 than the random circles. The mean number of vegetation types per km^2 for post-fledging phase ranges was less than that found in nestling-phase home ranges and greater than that found in random circles, but was not statistically different from either of these groups (Table 1). There was no significant difference in the number of patches per km^2 (F = 2.29, df = 27, P = 0.12), although we noted a trend similar to that found with vegetation types; nestling-phase home ranges had the greatest number of patches per km^2 and random circles had the lowest number (Table 1). As measured by these two variables, goshawk home ranges during the nestling phase appeared to contain more vegetative interspersion than would be expected if their ranges had been located at random in the study area. After the young had fledged, home ranges tended to maintain higher vegetative diversity than expected.

The configurations of nearly all home ranges supported this conclusion, since seven out of the ten monitored birds had areas of concentrated use that were spatially distant from the nest stand during the nestling phase (Fig. 1). These areas were disjunct polygons of the 95% home range area and contained vegetation types and seral stages that were not present in the polygon around the nest.

For two birds, this additional polygon included a large pumice flat (a different pumice flat for each bird). In four cases, the second polygon added seral stages of Jeffrey pine that were not present within the nesting polygon, and in the remaining case, the second polygon added riparian vegetation.

During the post-fledging phase, eight of the ten birds had disjunct home ranges at the 95% level. There were three instances where the additional clusters of telemetry points were associated with water sources and riparian vegetation, two which added extensive edge along large pumice flats, one that added old growth not present in the nest polygon, one that added moderately stocked young forest, and one that added a baseball field adjacent to mature forest.

One female selected a vegetatively diverse area approximately 3.5 km east of her nest rather than including more of the available old growth that surrounded her nest. This caused her post-nesting range to be two disjunct use areas divided by a 4-lane highway (Fig. 2). The majority of telemetry points for this female were along a forest-pumice flat edge and in the adjacent stand of old growth. There were no other active goshawk territories within the old growth around her nest that might have caused her to forage elsewhere. However, her range overlapped that of a second monitored female who used the same pumice flat and surrounding forest.

These disjunct polygons were not an artifact of our monitoring method of taking six consecutive readings per day. When we calculated the home ranges using one location per day, we ob-

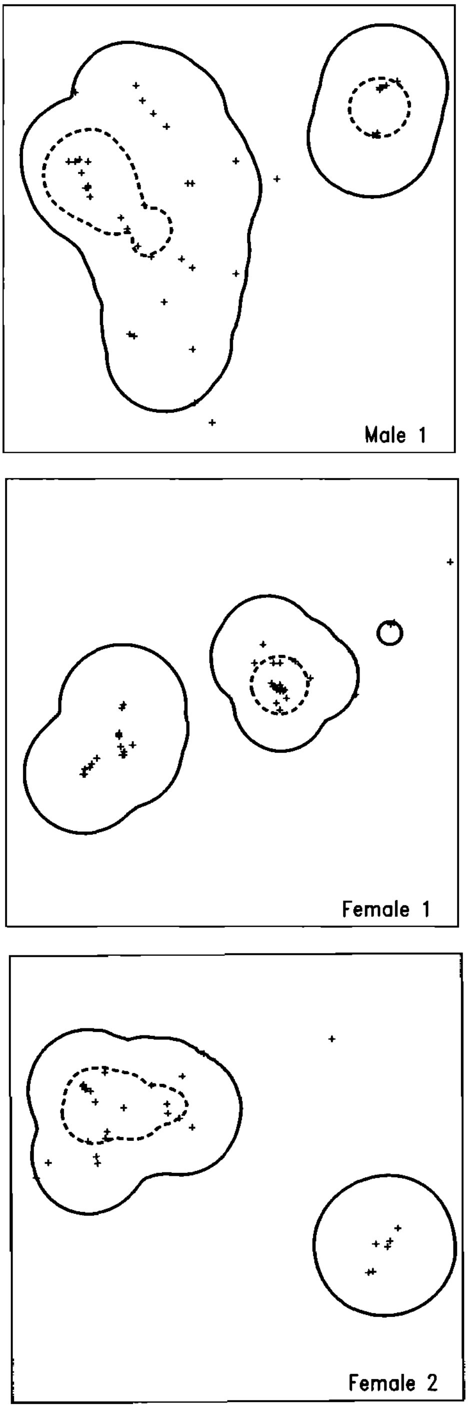

FIGURE 1. Examples of three goshawk nestling-phase home ranges from eastern California, showing clustering of telemetry points and disjunct polygons representing 95% (solid lines) and 50% (dashed lines) of telemetry locations.

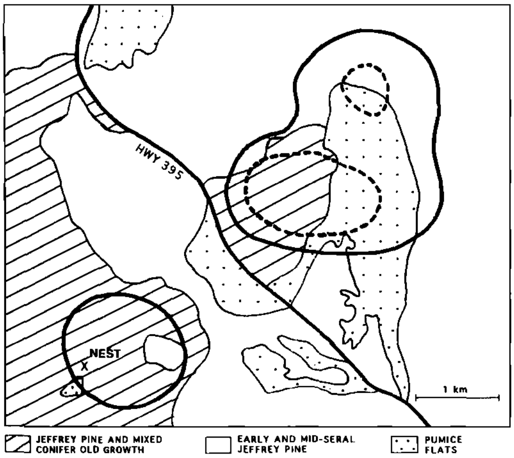

FIGURE 2. Post-fledging phase home range of a female goshawk in eastern California, showing selection for forest edge along a large pumice flat. The solid and dashed lines encompass 95% and 50% of the telemetry locations, respectively.

served polygons that maintained the same spatial arrangement and similar configuration as the home range estimates generated from six consecutive locations per day.

We also detected significant differences between the three groups in the distance to water ($F = 3.22$, $df = 29$, $P = 0.06$). The nests were on average closer to permanent water sources (springs and small streams) than were the centers of the post-fledging ranges or the artificial home range circles (Table 1). Six birds had water within the polygon containing the nest, and in one case, the home range polygon was extremely elongated to include a spring located 3.5 km from the nest (Fig. 3). In this case, 50% of the locations were divided between the nest stand and this spring. One female did not use the permanent water within her nest polygon, presumably because it flowed through open meadows, but she consistently used a water source 3.3 km from her nest in mature Jeffrey pine, thereby creating a second polygon that defined her home range at the 95% level (Fig. 4).

STAND STRUCTURE

We collected stand structure data at 20 nests, 63 home range sites (telemetry locations), and 102 random sites within the study area. The nest data set included three situations where data were collected on more than one nest in a territory (alternate nests). The inclusion of these nests may affect the assumption of independence. We included these nests because they were not in the same vegetation polygon as the active nest and our banding records indicated they were used by different females.

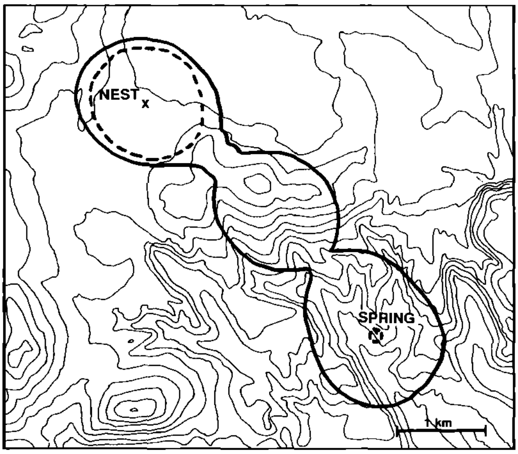

FIGURE 3. Nestling-phase home range of a female goshawk in eastern California, showing elongation of the home range to include the nearest source of water, 3.5 km from the nest. The solid and dashed lines encompass 95% and 50% of the telemetry locations, respectively. Note that a portion of the 50% contour is around the spring.

Five of the eight variables examined with ANOVAs were significantly different at $\alpha = 0.05$: basal area ($F = 47.74$, $df = 184$, $P < 0.01$), canopy cover ($F = 31.66$, $df = 184$, $P < 0.01$, pole-sized trees 16–27 cm dbh ($F = 11.55$, $df = 184$,

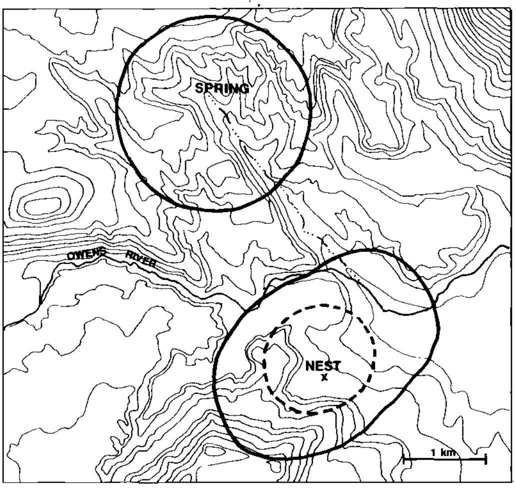

FIGURE 4. Nestling-phase home range of a female goshawk in eastern California, showing use of a water source located approximately 3.3 km north of the nest. The solid and dashed lines encompass 95% and 50% of the telemetry locations, respectively.

TABLE 2. STAND STRUCTURE VARIABLES FOR GOSHAWK NEST SITES, USE SITES WITHIN HOME RANGES, AND RANDOM SITES WITHIN THE STUDY AREA

Variable	Nest sites		Home ranges		Random	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Basal area (m^2/ha)[1]	37	9	39	12	26	13
Canopy cover (%)[1]	31	13	34	16	21	15
Slope (%)	12	11	7	9	10	13
Timber class (trees/ha)[2]						
1	16.1	11.6	11.6	11.0	10.1	10.1
2[1]	6.9	7.9	6.5	5.2	4.2	3.8
3	3.5	1.8	3.4	2.7	2.6	2.8
4[1]	1.8	1.0	1.7	1.5	1.0	1.0
5[1]	1.3	0.7	1.2	1.2	0.8	1.0

[1] Indicates differences in mean values between random sites and the two goshawk data sets (alpha = .05/3) using Tukey's studentized t-test.

[2] Timber classes correspond to the following dbh sizes: timber class 1: 1–15 cm; timber class 2: 15–27 cm; timber class 3: 28–45 cm; timber class 4: 46–61 cm; timber class 5: >62 cm.

$P < 0.01$), and the two largest tree diameter classes ($F = 18.42$ and $F = 47.74$, $df = 184$, $P < 0.01$). Goshawk nest sites and the surrounding home range telemetry points had greater basal area, more canopy cover, and more trees in these three diameter classes than the random plots in the study area (Table 2). For all of the above variables, the Tukey's test for differences among means separated the random plots from the home range telemetry plots and the nest sites ($df = 27$, $P < 0.05$) but did not distinguish between the home range plots and the nest sites. Forest structure selected by goshawks within their foraging ranges was similar to forest structure within the nest stands, and both differed significantly from random plots.

NEST TREE CHARACTERISTICS

Goshawk nests were in lodgepole pine, Jeffrey pine, and red fir, with a mean tree height of 28.0 ± 6.73 m and a mean dbh of 87.2 ± 27.2 cm. The average diameter was within the largest diameter class used in this study and was therefore in the upper range of tree diameters found within the study area. The mean nest height was 11.6 ± 2.33 m. Canopy cover immediately around the nest tree averaged 29% ± 12.6%.

DISCUSSION AND MANAGEMENT IMPLICATIONS

Goshawk home ranges in our area tended to be located in areas with high vegetative and seral diversity, especially during the nestling phase. The disjunct nature of many of the home ranges appeared to increase the number of vegetation types incorporated into the birds' foraging areas. By using areas that were geographically removed from their nest stands, goshawks were able to include vegetation types and patterns that were generally uncommon, such as riparian vegetation, wet meadows, and old growth stands adjacent to meadows or pumice flats.

Nest sites and telemetry locations were associated with forest stands that had higher basal area, more canopy cover, and more trees per ha than the study area average. The telemetry locations were not necessarily foraging locations, because bearings were taken when the signals were stationary, and represented times when the birds were perched. Our telemetry data indicated that perched goshawks tended to be found in well-canopied stands with large trees. These locations may have provided hunting perches, thermal cooling, or protective cover.

The proximity of these locations to a variety of vegetation types and seral stages may have been related to prey availability. Reynolds et al. (1992) reported a medium to high degree of vegetative interspersion for 13 of 14 selected goshawk prey species. Although we lack dietary information for our monitored goshawks, 12 of the prey discussed in Reynolds et al. (1992) are found in our area. The selection of areas with high diversity corresponds to the degree of interspersion used by common goshawk prey species.

Goshawk home ranges in our area were influenced by the location of permanent springs and small streams. The value of water for goshawks has been variously reported in the literature. Speiser and Bosakowski (1987) found no significant difference in the proximity of water to goshawk nests and random plots, and Crocker-Bedford and Chaney (1988) reported that only 8 out of 43 nests were <1 km from water. Other studies have reported distances of <275 m (Shuster 1980), <600 m (Reynolds et al. 1982), and <1 km (Kennedy 1988).

In areas where permanent streams and springs are uncommon, it may be difficult for all nesting goshawks to establish territories in proximity to water. In these situations, the nearest available well-canopied water source should be viewed as potentially within the range of active nests that are not near water. Our study indicated that goshawks could incorporate water sources into their home ranges from as far as 3.5 km away.

Goshawks nested in stands that were substantially more open than those used in other geographic areas. The mean canopy closure of 29% at nest sites is far below the values of 88%, 81%, 79%, 63% and 60% found in northwestern California (Hall 1984), northern California (Saunders 1982), northern Arizona (Crocker-Bedford and Chaney 1988), northwestern Utah (Hennessy 1978), and eastern Oregon (Reynolds et al. 1982), respectively. Dissimilar methods in measuring canopy cover may account for some of the difference.

Regardless of the absolute values, goshawks in our study selected stands that were denser than the average available, both for nesting and foraging, as measured by basal area, canopy closure, and the number of trees in all five diameter classes. Although absolute values may not be applicable to all geographic areas used by goshawks, the selection for stands with the most canopy cover and largest diameter trees can be translated to the site potential for different regions.

Goshawk management that focuses solely on nest sites assumes that goshawks are not selective in their use of habitats other than nest location. Yet our study indicates that goshawks select areas that are vegetatively diverse for foraging, including numerous aggregations of mature trees for nest stands and perch sites. Timber harvests on the Inyo National Forest typically remove the overstory, but numerous aggregations of mature timber are left for archeological site protection, deer hiding cover, snag recruitment, and riparian habitat. Although goshawk management is primarily limited to nest site buffers, these other management actions have resulted in the retention of mature timber and more vegetative diversity than would be expected under most prescriptions using overstory removal. All goshawk territories associated with timber sales have been active for approximately two-thirds of the years since the harvests, based on our nesting records over the past 14 years. Typically these territories have produced 2–3 young per nest.

Timber harvests can be compatible with goshawk conservation if key features such as permanent water sources, well-canopied stands of mature trees, and mature forest edge are provided within potential goshawk home ranges. Home range configurations cannot be determined with telemetry, but our data suggest that vegetation types and water sources as far as 3.5 km from the nest stand can be viewed as potential foraging range, especially if these features are not present near the nest.

An effective goshawk conservation strategy would consider the potential home range associated with each nest site. Within this area, emphasis should be placed on creating or maintaining vegetative diversity, retaining mature timber around permanent water sources and along forest-open edges, and ensuring that a portion of the range provides forest stands that have structural attributes similar to those found at the nest site for each particular geographic area. These mature stands would provide adequate perch sites near or within selected foraging areas. We recommend that timber harvests be designed to create a juxtaposition of seral stages, including mature forests, rather than leaving large tracts of homogeneous, mid-seral stage stands.

ACKNOWLEDGMENTS

Field work for this study was funded by Inyo National Forest. We gratefully acknowledge P. Bloom, R. Anderson, and L. Spiegel for their help in capturing the goshawks, D. Ritzman, T. Mark, K. Erwin, and M. Palchak for assisting with field work, J. Baldwin for running the home range analyses, and J. Baldwin and S. Durham for statistical counseling. We thank B. Woodbridge, P. Kennedy, and J. Baldwin for review of earlier drafts of this manuscript.

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POST-FLEDGING AREAS IN NORTHERN GOSHAWK HOME RANGES

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JAMES A. GESSAMAN

Abstract. In 1984, 1986 and 1988, we studied the movement patterns of eight (4 in 1984, 2 in 1986, 2 in 1988) Northern Goshawks (*Accipiter gentilis*) nesting in the Jemez Mountains of north-central New Mexico to estimate nesting season home range size and identify areas of concentrated use, particularly those areas used by the family after fledging until the young are independent (post-fledging areas [PFAs]). Female home ranges were significantly ($P = 0.025$) smaller ($\bar{X} = 569.3 \pm 473.1$ ha [SD]; $N = 5$) than male range sizes ($\bar{X} = 2106.3 \pm 634.5$ ha; $N = 3$). Core areas were approximately 32% of the home range area ($\bar{X} = 348.2 \pm 321.6$ ha). Female core areas were significantly ($P = 0.025$) smaller ($\bar{X} = 167.9 \pm 128.5$ ha) than male core areas ($\bar{X} = 648.7 \pm 334.9$ ha). We monitored the movement patterns of 16 juveniles from six nests that were fitted with transmitters at 21 days of age during 1992. During the early fledgling-dependency period (week 1–4 after fledging) 88.1% of the juveniles' locations ($N = 193$) occurred within 200 m of the nest and 99.5% of the locations occurred within 800 m of the nest. However, during the last four weeks of the fledgling-dependency period only 34.3% of the locations ($N = 108$) were within 200 m and 75.9% of the locations were within 800 m of the nest (a 167.9-ha circle would have a radius of 731.5 m). These observations support the existence of a PFA in north-central New Mexico and suggest that nesting habitat include both the nest site and a PFA.

Key Words: *Accipiter gentilis*; habitat management; harmonic mean; home range; Northern Goshawk; post-fledging area.

Much of our knowledge of raptor habitat use is restricted to nest sites. This is especially true for forest-dwelling species, whose activities away from the nest site are difficult to observe. The Northern Goshawk (*Accipiter gentilis*) occurs in a wide variety of forest types throughout North America and Eurasia (Kenward 1982, Speiser and Bosakowski 1987, Hayward and Escano 1989, Widén 1989). Although goshawk populations in Europe appear to be increasing (Bijlsma 1989), concern exists about its population status in North America, particularly in timber harvest areas (Reynolds et al. 1992). Prior to the publication of the management recommendations for the southwestern U.S. (Reynolds et al. 1992), management of goshawk habitat in North America was limited to establishing <20-ha protective buffers around nest sites (Reynolds 1983). Nest sites are a focal point for the goshawk's activities associated with courtship, incubation and the nestling stage. However, many goshawk activities critical to recruitment and survival—foraging, parental care of fledglings and roost sites—may occur away from the nest site and these activity areas need to be considered in goshawk management plans.

Currently, the only reliable way to identify goshawk activity areas (or areas of concentrated use) is to use radio-telemetry methods combined with home range estimators. This type of analysis requires considerable care to minimize the well known problems that can arise with this approach (White and Garrott 1990). Using these techniques, goshawk home range size and foraging habitat have been described for wintering birds in Europe (Kenward and Widén 1989, Widén 1989). Little radio-telemetry data are available for North American birds. Thus, little information is available on nesting season home range and areas of concentrated use within this home range.

The aim of our study was to estimate nesting season home range size and identify areas of concentrated use, particularly those areas used by the family after fledging until the young are independent (post-fledging areas [PFAs]). In addition, we evaluate the movement patterns of fledgling goshawks to determine if the PFA described by Reynolds et al. (1992) represents the area used by the fledglings until independence.

METHODS

STUDY AREA

The study examined goshawk activity areas within approximately 650,000 ha of forested lands in the Jemez Mountains in north-central New Mexico. The Jemez Mountains were formed by volcanic activity and are dissected by steep-walled canyons formed by the erosion of volcanic tuff. Elevations ranged from 1200–3900 m. The average annual precipitation is 45 cm, 75% of which occurs from May through October. Ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and white fir (*Abies concolor*) are the most prevalent forest types found over the study area. Subalpine grassland, spruce-fir, pinyon-juniper, juniper-grassland, and riparian woodlands are also present (see Kennedy [1988] for a more detailed study area

TABLE 1. DURATION OF TRACKING PERIOD AND NUMBER OF SEPARATE LOCATIONS OF RADIO-TAGGED ADULT NORTHERN GOSHAWKS IN NORTH-CENTRAL NEW MEXICO

Hawk no.	Tracking period	Hours tracking[1]	No. of locations[2]	No. of samples
Male1[3]	6/13/84–8/28/84	44.2	62	12
Female1[3]	6/06/84–8/11/84	27.5	57	10
Female2	6/08/84–8/03/84	30.6	46	10
Female3	7/13/84–8/18/84	21.8	69	7
Male2	7/23/86–10/25/86	94.2	184	18
Female4	7/25/86–9/22/86	36.4	157	9
Male3[3]	6/16/88–8/19/88	57.6	100	14
Female5[3]	6/09/88–5/16/89	183.6	367[4]	57

[1] Does not include time spent in radio-tracking periods during which birds could not be located.

[2] Numbers of locations used to estimate home range; does not include locations that did not meet the 0.5-h separation criteria and had a measurement accuracy of <250 m.

[3] The mate of this bird was radio-tagged.

[4] 174 of these 367 locations were used to estimate nesting season home range (6/9/88–9/30/88) and 193 locations were used to estimate winter home range (10/1/88–5/16/89) (P. L. Kennedy, unpubl. data).

description). The USDA Forest Service, Santa Fe National Forest; USDI National Park Service, Bandelier National Monument; and Los Alamos National Laboratory manage these lands.

ADULTS

We captured adult goshawks at the nest during the nestling period (mid-June to mid-July) with a dho-gaza net using a live Great Horned Owl (*Bubo virginianus*) as the lure (Bloom 1987). All hawks were in adult plumage and their sex was determined by morphometric measurements. Eight hawks were captured, banded and affixed with a tail-mount (N = 6, Biotrack, Inc., Dorset, UK) or back-pack type (N = 2, L&L Electronics, Mahomet, IL, USA) transmitter (Kenward 1987) that weighed <3% of their body weight (tail-mounts = 15 g and back-packs = 20 g). All transmitters had posture-monitoring switches (Kenward 1987) to detect flight and non-flight behavior.

We began monitoring the marked birds 1–2 days after capture. Hawks were monitored simultaneously by a minimum of two observers on the ground using a mobile null peak system (Kenward 1987, Equipment manufactured by Televilt HB, Storå, Sweden and Custom Electronics, Urbana, IL, USA). Yagi antennae were used to obtain a general location of the bird from a distance and the null peak antennae were used to acquire more accurate bearings once an observer was within 0.4 km of the bird. Two to three bearings were made on perched birds simultaneously by 2–3 observers on foot or in a car. Observer locations were plotted on U.S. Geological Survey (USGS) 7.5-minute quadrangle maps. Bird location and the measurement error associated with each location was estimated from these field data using program FIXX (G. A. Rinker, pers. comm.). FIXX is a program to triangulate and analyze radio-telemetry data as described in the Appendix.

We monitored four hawks in 1984, two hawks in 1986 and two hawks in 1988 (Table 1). Each bird was monitored continuously for a 2–6 hour period, a minimum of once per week, until transmitters were molted or failed (5 weeks to 11 months after attachment; Table 1). The beginning of each sampling period was systematically selected from four periods of the day (05:00–09:00, 09:00–13:00, 13:00–17:00, and 17:00–21:00) to ensure diurnal coverage throughout the season. Since the same bird was not monitored for more than one year, there is no measure of within-bird variation.

During each sample period, the signal of a systematically chosen bird was continuously monitored. Perching and flight bouts were timed to the nearest second. After every flight we attempted to record the bird's location. We defined a flight as a period when the fast pulse lasted at least 5 sec. This definition was determined by monitoring the behavior of trained falconry birds temporarily equipped with transmitters and by spending several hours simultaneously radio tracking and visually observing birds near nests. With some training, field personnel could consistently identify flights by changes in volume and pitch of the signal combined with a signal direction change (Kenward 1987).

We used the harmonic mean (HM) method in Program HOME RANGE (Samuel et al. 1985b) to delineate size and shape of each goshawk's home range. We chose this home range estimator because it (1) is nonparametric, (2) is not as sensitive to number of locations as are other estimators, and (3) is commonly used to estimate home range size of raptors. Details on this estimator and its limitations are described in White and Garrott (1990).

We identified the boundaries of the home range of each bird with the 75% and 95% isopleths. The 75% and 95% contours define the area in which we expect to find a hawk 75% and 95% of the time, respectively. We identified core areas using the method described by Samuel et al. (1985a), where the core area is defined as the portion of the hawk's home range that exceeds an equal-use pattern. This was done by comparing the observed use pattern within the home range with that expected from a uniform pattern of use using the core area analysis in Program HOME RANGE (Samuel et al. 1985b). The difference in ordered cumulative distribution functions was tested with a one-sided Kolmogorov goodness-of-fit procedure (Daniel 1978). Core areas were identified by outlining those areas within the home range where use exceeded that expected from a uniform distribution.

A nesting season (brood rearing) home range was estimated for all birds and a winter home range was estimated for one bird that was monitored for 11 months. This bird's nesting home range was based on data collected from the time of attachment until 30 September 1988, and the winter home range was based on the remaining locations (Table 1). Only locations that were separated by a minimum of 0.5 hour and had a measurement error of ≤250 m (see Appendix for details on estimating measurement errors of the birds' locations) were used in the HM calculations. The accuracy stipulation resulted in censoring approximately 25% of the locations that met the 0.5 h separation criteria. Measurement error was used primarily as an aid in discarding inaccurate locations; these errors were not used to calculate the total error associated with the home range estimates.

FLEDGLINGS

Examination of female home range characteristics suggests a PFA exists that surrounds the nest site and is substantially larger than the nest site. If the fledglings restricted their activity to the nest site, we would expect most of their locations to be within 178.5 m of the nest (the radius of a 10-ha circle). If a PFA exists and is approximately 168 ha (average female core area), we would expect the fledglings to occur at any distance from the nest tree up to 731.5 m from the nest. To account for mapping error we rounded these distances to 200 m and 800 m, respectively in the analysis of the fledgling location data.

To determine the areas used by juveniles after fledging ($\bar{X}$ = 42 days of age; J. M. Ward and P. L. Kennedy, unpubl. data) and until independence ($\bar{X}$ = 92 days of age, J. M. Ward and P. L. Kennedy, unpubl. data), we monitored the movement patterns of 16 juveniles from six nests that were fitted with tarsal-mounted transmitters (Advanced Telemetry Systems, Inc., Isanti, MN) at 21–25 days of age during 1992. We defined independence as the first time a juvenile spends more than three consecutive days at least 2 km from the nest. This is comparable to the definitions of independence used by Marquiss and Newton (1981) and Kenward et al. (1993a) for European Sparrowhawks (*A. nisus*) and goshawks, respectively. These juveniles were from the same population but were not offspring of the radio-tagged adults. Only one of the six nests used in this phase of the study was used previously by the radio-tagged adults.

The tarsal-mounted transmitters weighed 9 g, had mortality switches, and were designed to drop off after three months. After transmitter attachment, the birds were located every 2–3 days by one or two observers from the ground or from the air with the same telemetry equipment used for the adults. One location was obtained for each bird during each sampling period. Each bird was monitored until (1) the transmitter failed, (2) the transmitter detached from the tarsus, (3) the bird died, (4) the bird left the study area, or (5) the study was terminated (14 October 1992). Unlike the adults in which the majority of locations were obtained via triangulation, most (82.7%) of the juvenile locations were based on visual or auditory observations of the birds at close range (≤75 m). The measurement accuracy of the juvenile triangulated locations was not estimated.

To evaluate the area used by the fledglings, we measured the linear distance from the nest to each location and assumed the locations represented radii of circles around the nest. Using radii to estimate the fledglings' area of use assumes that space is used in a uniform circular fashion. We did not use the harmonic mean estimator to estimate home range size for the fledglings because <20 locations were obtained for the majority of the fledglings. Locations obtained after the birds were independent were not included in any analyses.

STATISTICAL ANALYSES

The areas defined by the 95% and core area contours were analyzed for gender differences using a Kruskal-Wallis test (CoHort Software 1990). To evaluate the influence of our sampling design on the area estimates, we used linear regression (CoHort Software 1990) to see if there was a significant positive relationship between home range size and the number of sample periods.

A Chi-square analysis (PROC FREQ; SAS Institute, Inc. 1989) was used to determine if the distance fledglings traveled from the nest varied with age. Observations were categorized into four, 2-week age classes and six distance categories (0–50 m, 51–100 m, 101–200 m, 201–400 m, 401–800 m, and >800 m) for this analysis. This analysis is based on movement data collected on 15 of the 16 fledglings (Table 2). This analysis treats juveniles as the experimental unit and not nests; consequently it assumes that juvenile movements are independent of the movements of their siblings, which may or may not be realistic. For all hypothesis tests, P ≤ 0.05 was considered significant.

RESULTS

ADULTS

We monitored each hawk from 21.8–83.6 hours for a total of 325.9 hours for all eight hawks. The number of locations used to estimate each hawk's nesting home range varied from 46–184 ($\bar{X}$ = 106 ± 57 [SD]) (Table 1). The home range size did not increase with increasing numbers of sample periods (r = 0.2, P = 0.64). Based on observed reproductive behavior, all hawks were territorial adult breeders. We simultaneously tracked both members of two mated pairs (Male1–Female1 and Male3–Female5). In addition, Female4 and Female5 were breeders on the same territory in 1986 and 1988, respectively.

Female nesting home ranges (N = 5), as defined by the 95% HM contour, varied in size from 95–1292 ha ($\bar{X}$ = 569 ± 473). Female home ranges were significantly (H = 5, df = 1, P = 0.025) smaller than male home ranges (N = 3) which ranged from 1698 to 2837 ha ($\bar{X}$ = 2106 ± 635). The females' 75% HM contour averaged 340 ± 288 ha and the males' 75% HM contour averaged 1273 ± 400 ha.

Goshawk home ranges varied in shape and size and in the number of core areas (Fig. 1). All birds had a core area that included the nest site but two birds had additional core areas that did not include the nest site (Fig. 1B). Only the core areas

TABLE 2. SUMMARY OF RADIO-TELEMETRY INFORMATION FOR NORTHERN GOSHAWK OFFSPRING IN NORTH-CENTRAL NEW MEXICO IN 1992

Bird	Sex	Tracking period	Fledgling age[1] (weeks)	Transmitter life (days)
GARC1	Male	6/9/92–7/11/92[2]	8	33
GARC2	Male	6/9/92–7/15/92[3]	9	37
GARC3	Female	6/9/92–6/21/92[3,8]	5	13
GUAJ1	Male	6/10/92–10/5/92[4]	20	118
GUAJ2	Female	6/10/92–10/14/92[5]	22	127
GUAJ3	Male	6/10/92–9/11/92[6]	17	94
BARL1	Female	6/11/92–9/21/92[4]	18	103
BARL2	Male	6/11/92–9/11/92[7]	17	93
BARL3	Male	6/11/92–10/9/92[4]	21	121
SJ1	Female	6/17/92–10/9/92[4]	20	115
SJ2	Male	6/17/92–8/14/92[3]	12	59
SJ3	Male	6/17/92–7/23/92[3]	9	37
BAC1	Male	6/18/92–10/14/92[5]	21	119
BAC2	Female	6/18/92–9/17/92[6]	17	92
STAB1	Male	6/19/92–8/26/92[4]	13	69
STAB2	Female	6/19/92–9/26/92[6]	18	100

[1] Age of the bird when we obtained the last location.

[2] Bird died.

[3] Transmitter failure (bird seen but signal not picked up).

[4] Transmitter failed or bird dispersed.

[5] Bird tracked until end of study (10/14/92); still in study area at time the study was completed.

[6] Transmitter dropped.

[7] Bird recaptured at Manzano Mountain migration station by HawkWatch International personnel, approximately 150 km SE of the nest site in New Mexico.

[8] Due to small number of locations obtained on this bird, it was not included in Table 3 and the statistical analyses described in text.

that included the nest were used in the statistical analyses. The females' core areas averaged 168 ± 129 ha and were significantly ($H = 5$, $df = 1$, $P = 0.025$) smaller than the males' core areas ($\bar{X} = 649 \pm 335$ ha). The core areas for all adults averaged 31.8% (±3.2) of the total home range area and 60.3% (±7.4) of the utilization volume.

All observations of fledglings occurred within the females' core areas centered around the nest, overlapping extensively with the core areas of mated pairs (qualitatively determined by visual inspection of home range plots). Females were observed regularly perching and roosting near fledglings throughout their core area, and prey deliveries to fledglings from both adults also occurred in this area (P. L. Kennedy, unpubl. data). We suggest the female's core area represents a concentrated-use area for the family from fledging until the young are independent (PFA). Males were observed perching, roosting and hunting in their core areas (the areas not included in the PFA).

FLEDGLINGS

We obtained radio-telemetry information on 16 goshawk offspring ranging from 5 to 22 weeks post-fledging (Table 2). Approximately 69% of the fledgling locations ($N = 301$) occurred within 200 m of the nest and 91.0% of the locations occurred within 800 m of the nest (Table 3). About 83% of these observations ($N = 259$) were visual or auditory observations and the remaining 17% ($N = 52$) were obtained from triangulation on the ground or from aerial surveys. The maximum distance from the nest recorded for a fledgling was 8.8 km. The mean (SD) distances from the nest by week post-fledging were: Week 1, 11.8 m (32.2 m), Week 2, 47.4 m (147.0 m), Week 3, 50.4 m (93.7 m), Week 4, 164.6 m (101.8 m), Week 5, 302.0 m (443.3 m), Week 6, 547.7 m (655.5 m), Week 7, 1330.6 m (2402.7 m), and Week 8, 1955.6 m (1858.5 m). Fledglings moved gradually further away from the nest site with time ($\chi^2 = 226$, $P < 0.001$). During the first four weeks of the fledgling-dependency period, 88.1% ($N = 193$) of the locations occurred within 200 m of the nest and 99.5% of the locations occurred within 800 m of the nest. During the last four weeks only 34.3% of the locations ($N = 108$) were within 200 m of the nest and 75.9% of the locations were within 800 m of the nest.

DISCUSSION

NESTING SEASON HOME RANGE

Similar to other home range estimates for nesting raptors (Becker and Sieg 1987, Bloom et al. 1993, Squires et al. 1993), the nesting ranges of the goshawks in this study varied extensively. This variation can be attributed to variation in

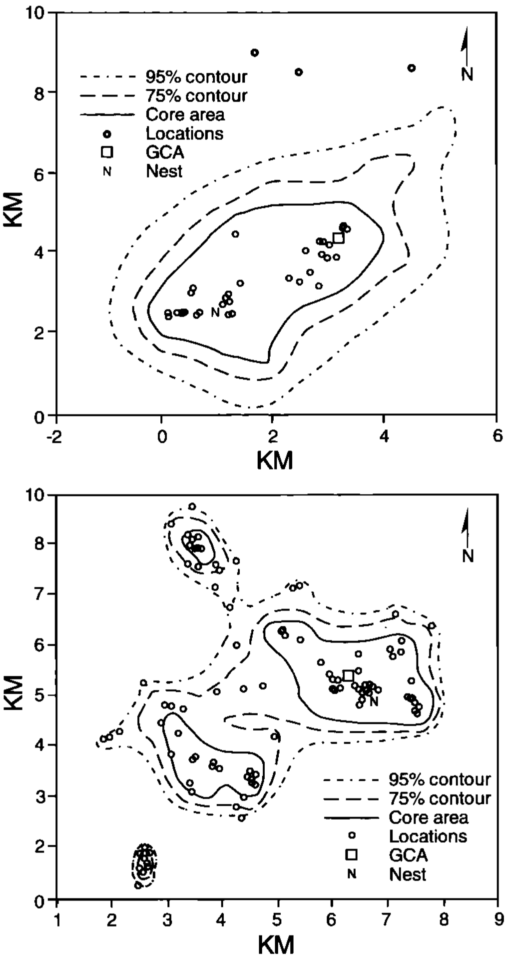

FIGURE 1. Examples of home ranges of male nesting northern goshawks. The axes of the plots reflect the distance from the central point in the study area (0,0) which was arbitrarily chosen as the southwest corner of a USGS 7.5-minute quadrangle. (*Top*) This is an example of a bird (Male1) with one core area, and (*bottom*) a bird (Male2) with multiple core areas. GCA is the geometric center of activity.

(1) sexual differences in parental care strategies, (2) the experience of the bird with its territory, (3) hunting efficiencies, (4) food requirements (which vary by brood size), and (5) food availability within the territory. Goshawk range size is predicted to decrease with increasing food availability and this relationship is probably a function of the distributions of habitat types in the home range. We do not have information on the habitat distributions within the home ranges of the eight hawks so we cannot evaluate the influence of habitat on home range size in this study area.

The home range sizes in this study were within the range of sizes reported by other investigators who estimated goshawk nesting ranges with a variety of other techniques besides radio-telemetry (Kramer 1955, Eng and Guillion 1962, Brüll 1964, van Beusekom 1972, Reynolds 1983). Home range estimates for hawks from European and North American populations range from 1980 to 3202 ha. Although these estimates are remarkably close to the estimates in this study, generalizations are difficult, and may not be meaningful because of differences in methodologies.

POST-FLEDGING AREAS

Home range is an estimate of the area normally used by an animal (White and Garrott 1990). In raptor home range studies, the area within the home range boundary minus the nest site is assumed to represent the adult's foraging area (see Marquiss and Newton 1981, Becker and Sieg 1987, and Squires et al. 1993 as examples). Our results suggest that the nest site is not large enough to encompass all of the other activities associated with brood rearing. In goshawk home ranges in the Jemez Mountains of north-central New Mexico, family activities during the second half of the fledgling-dependency period extend beyond the 10-ha nest site into an area referred to as the PFA (Reynolds et al. 1992).

The PFA surrounds and includes the nest site (see Fig. 9 in Reynolds et al. [1992]) and is estimated to be 168 ha for goshawks nesting in this study area. This size estimate is based on the average core area of the five adult females and the movement data of the 15 fledglings monitored in this study. During the first four weeks of the fledgling-dependency period most of the young hawks' movements occurred in the nest site. However, from four weeks post-fledging until independence the juveniles regularly occurred outside the nest site up to 800–1000 m from the nest. Similarly, Kenward et al. (1993a) observed fledgling European goshawks abruptly increasing the distance they traveled from the nest when they were 3–4 weeks past fledging. Before that age, fledglings were almost always observed within 400 m of the nest. From 3–4 weeks post-fledging until independence (approximately 25 days later) the juveniles frequently occurred up to 1000 m from the nest. Based on these results, we think the average female core area is a reasonable approximation of the area used by the fledglings during the second half of the fledgling-dependency period.

Although we estimate the PFA to average 168 ha in this study area, it probably varies in size as a result of variation in food availability. Kenward et al. (1993b) observed that distances moved

TABLE 3. NUMBER OF OBSERVATIONS (N = 301) OF YOUNG NORTHERN GOSHAWKS (N = 15) AT DIFFERENT DISTANCES FROM THE NEST (N = 5) DURING THE POST-FLEDGING DEPENDENCY PERIOD IN NORTH-CENTRAL NEW MEXICO, 1992

Distance from nest (m)	Weeks after fledging							
	1	2	3	4	5	6	7	8
0–49	38	40	23	4	2	0	0	0
50–99	5	6	15	5	3	2	0	1
100–199	2	8	5	19	10	9	8	2
200–399	0	2	1	16	11	13	1	1
400–799	0	0	1	2	1	8	6	4
≥800	0	1	0	0	2	9	6	9
Total	45	57	45	46	29	41	21	17
Percent of birds in post-fledging area[1]	100	98.2	100	100	93.1	78.0	71.4	47.1

[1] Percentage of observations <800 m from nest.

by juvenile European goshawks after independence were significantly shorter in areas of high food availability as compared to areas of low food availability. Presumably pre-independence movements would demonstrate a similar pattern if juveniles initiate self-feeding prior to independence.

The exact significance of the PFA is unknown, but it may be an area of very high prey availability as compared to other areas within the home range of the nesting pair. As suggested by Kennedy (1988), goshawk nest sites may be selected because they are central points within a localized area of high food availability within the home range of a nesting pair. A PFA of high prey availability would provide more hunting opportunities for young hawks while they are learning to hunt. As noted by Reynolds et al. (1992), the PFA may also be an area that provides additional cover for the inexperienced juveniles to use for avoiding predators and for concealment while learning how to approach prey.

FORAGING AREAS

The 95% HM contour area is an overestimate of the foraging area of goshawks in this study area because a bird only uses portions of the home range in its normal activities. However, until better information is available on the location of specific foraging areas, we estimate the male's foraging area to be 2090 ha (2100 ha minus the 10-ha nest site) and the female's foraging area to be 560 ha (570 ha minus 10 ha). The nest site area is not included in the foraging area because the adults rarely hunt in this area (P. L. Kennedy, unpubl. data). The male's foraging area is larger in size because of his role as primary food provider during brood rearing. Female goshawks in this area were rarely observed hunting until the young were close to fledging and even after the females began hunting, they did not provision the young as frequently as the male (Kennedy 1991).

The core areas were not excluded from the foraging area estimates because we have no information to suggest that the adults do not hunt in these areas of concentrated use. In fact, our observations suggest the male's core area (excluding the nest site) represents preferred hunting areas used by him throughout brood rearing and the female's core area includes hunting areas she regularly uses after the young fledge.

MANAGEMENT IMPLICATIONS

We concur with management guidelines developed by Reynolds et al. (1992) that management of goshawk nesting habitat in the southwestern U.S. should include the three components of the goshawk home range: nest site, PFA, and foraging area. In north-central New Mexico the sizes of these areas are estimated to be 10 ha, 168 ha and 2090 ha, respectively. Nest sites need to be managed to provide habitat for the breeding activities that occur from courtship through fledging. The PFA needs to be managed to provide sufficient cover and prey for the fledglings, and the foraging area should be managed for enhancing prey populations exploited by the adults.

The forest conditions needed to provide these areas in the southwestern U.S. and management guidelines for maintaining these conditions are discussed in detail in Reynolds et al. (1992). Because of the preliminary nature of our results, we suggest the acreages presented in this study only be used as guides in the absence of site-specific data on goshawk activity areas.

ACKNOWLEDGMENTS

This study was financially supported by Los Alamos National Laboratory's National Environmental Research Park, New Mexico Department of Game and Fish Share With Wildlife Program, USDA Forest Service Region 3, and USDA Forest Service, Santa Fe National Forest. The senior author was on an Associated Western University Graduate Fellowship during 1986–1989. D. Clark, D. Crowe, T. Dean, A. Ebinger, D. H. Fisher, Jr., T. Johnson, D. Kimmey, J. Lavy, J. Leon, J. Longmire, L. Morgan, J. Morrison, D. Ponton, M. Siders. D. Sinton, and R. Warren provided invaluable assistance in locating nests, trapping and banding goshawks and radio-tracking. We thank F. J. Barnes, K. Bostick, D. A. Boyce, Jr., D. DeLorenzo, D. H. Fisher, Jr., T. Hakonson, J. P. Hubbard, B. McKinney, M. Orr, and R. T. Reynolds for their administrative support. T. Dean and O. B. Myers assisted with database development and graphics. Comments from G. Hayward and an anonymous reviewer improved the manuscript substantially.

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APPENDIX

Bird locations are triangulated using the known positions of two observers and their simultaneous measurements of bearing direction to the bird. The coordinates (x_0,y_0) of the bird are given in terms of the coordinates (x_1,y_1) and (x_2,y_2) of the two observers and the measured bearing angles θ_1 and θ_2 as

$$x_0 = \frac{y_2 - y_1 + x_1\cot\theta_1 - x_2\cot\theta_2}{\cot\theta_1 - \cot\theta_2}$$

$$y_0 = \frac{x_2 - x_1 + y_1\tan\theta_1 - y_2\tan\theta_2}{\tan\theta_1 - \tan\theta_2}, \qquad \text{(A1)}$$

where θ_1 and θ_2 are measured clockwise from a convenient common origin (e.g., magnetic north). We assume that the observer coordinates are known exactly, and that the bearing angles are each subject to uncorrelated uncertainties of magnitude $\delta\theta_1 = \delta\theta_2 = \delta\theta$. These assumptions lead to uncertainties in the computed bird coordinates of magnitude

$$(\delta x_0)^2 \cong \left(\frac{\partial x_0}{\partial\theta_1}\delta\theta_1\right)^2 + \left(\frac{\partial x_0}{\partial\theta_2}\delta\theta_2\right)^2$$
$$= \frac{(x_0 - x_1)^2\sin^4\theta_2 + (x_0 - x_2)^2\sin^4\theta_1}{\sin^2\theta_1\sin^2\theta_2\sin^2(\theta_2 - \theta_1)}(\delta\theta)^2$$

$$(\delta y_0)^2 \cong \left(\frac{\partial y_0}{\partial\theta_1}\delta\theta_1\right)^2 + \left(\frac{\partial y_0}{\partial\theta_2}\delta\theta_2\right)^2$$
$$= \frac{(y_0 - y_1)^2\cos^4\theta_2 + (y_0 - y_2)^2\cos^4\theta_1}{\cos^2\theta_1\cos^2\theta_2\sin^2(\theta_2 - \theta_1)}(\delta\theta)^2. \qquad \text{(A2)}$$

The standard bearing uncertainty $\delta\theta$ is estimated by analyzing the errors in repeated observations of known transmitter locations. To estimate $\delta\theta$ in this study, we attempted to determine the direction to a transmitter placed at 50 random locations by an independent assistant. The standard deviation of differences between observed and true bearings was 5°. Visual observations (approximately 20% of the total) were assumed to have $\delta\theta = 0$. If the true field errors are constant, independent of location and observer, and well-represented by our adopted value of $\delta\theta$, then our procedure yields results equivalent to repeated measurement and statistical analysis of the actual field bearings (White and Garrott 1990). Our procedure is more efficient than attempting to obtain statistical samples for every field observation. In the present context, it yields better results because it is rarely possible to make a statistically significant number of repetitions in the field.

Studies in Avian Biology No. 16:83–87, 1994.

TERRITORY OCCUPANCY AND HABITAT PATCH SIZE OF NORTHERN GOSHAWKS IN THE SOUTHERN CASCADES OF CALIFORNIA

BRIAN WOODBRIDGE AND PHILLIP J. DETRICH

Abstract. We monitored annual occupancy of forest patches by nesting Northern Goshawks (*Accipiter gentilis*) in the southern Cascades Mountains in northern California. Goshawks typically used 3–9 alternate nests distributed among 1–5 different forest stands ranging from 4.1 to 115 hectares in size, and showed low fidelity to individual nest trees or stands. Mean distance between alternate nests was 273 ± 68.6 m. Alternate nests and nest stands were grouped into nest stand clusters, which for monitoring purposes were the equivalent of territories. Nest stand clusters ranged from 10 to 114 hectares in size, and were occupied 74% (±5.5) of years monitored. Occupancy of nest stand clusters by nesting goshawks was positively correlated with cluster area, with occupancy of clusters <20 ha typically <50%. Reproductive success was not correlated with habitat area. Two patterns of territory occupancy were distinguishable; traditional territories (23) where nesting by goshawks was predictable within finite nest clusters and ephemeral territories (5) where alternate nests were widely scattered and sporadically used. Despite extensive timber harvesting and forest fragmentation within our study area, goshawks occurred at relatively high densities (0.57–1.07 territories per 1000 ha). However, most goshawk territories were associated with the larger remaining patches of mature forest, and occupancy of these patches was positively associated with patch area.

Key Words: *Accipiter gentilis*; forest fragmentation; nesting habitat; Northern Goshawk; territory occupancy.

Habitat suitability for an animal is a function of the structural characteristics and spatial arrangement of habitat patches, as well as the presence of predators, competitors and adequate food resources (Cody 1981). Fragmentation of habitat can influence habitat suitability even if the structure of the remaining habitat patches remains unchanged (Temple and Wilcox 1986). Assessing the effects of habitat fragmentation on large, mobile species such as birds of prey is further complicated by these species' use of multiple patches in a landscape, often using different types of patches to fulfill different life requisites (e.g., nesting versus foraging or cover) (Harris and Kangas 1988).

The structural attributes of forest stands used for nesting by Northern Goshawks (*Accipiter gentilis*) have been described in a variety of forest ecosystems in North America, including eastern deciduous (Speiser and Bosakowski 1987) and western coniferous (Reynolds et al. 1982, Hall 1984, Crocker-Bedford and Chaney 1988, Hayward and Escano 1989) forests, and Great Basin shrubsteppe communities (White and Lloyd 1965, Younk and Bechard, this volume). Although conducted in different communities, these studies and others (summarized in Reynolds 1989, Reynolds et al. 1992) found that a number of structural features were common to goshawk nest stands in most areas. Nest stands are typically composed of large, densely spaced trees, with higher canopy closure and more open understories than the surrounding landscape. The majority of these studies, however, did not consider spatial relationships such as size and distribution of habitat patches, and none used long-term patterns of occupancy of habitat patches by nesting goshawks to assess habitat quality.

Estimates of stand size given by Reynolds (1983) were based on measurement of areas of intensified activity adjacent to nests (nest areas) and did not necessarily reflect the actual size of the forest stands used for nesting. Crocker-Bedford (1990) described the spacing and occupancy of alternate nests within goshawk territories (nest clusters) and reported a relationship between the size of unharvested buffers surrounding nest sites and subsequent occupancy by nesting goshawks. Kennedy (1991) used the movements of radio-marked goshawk family groups to define the post-fledging family area (PFA), an area of concentrated use by the family group after the young left the nest. It is not clear, however, how PFAs were differentiated from nest stands or clusters of nest stands. Estimating the relationship between patch size of nesting habitat and overall territory quality is further complicated when the effects of foraging habitat quality are considered (Crocker-Bedford 1990, Reynolds et al. 1992).

In this study we describe spatial patterns of habitat use by nesting Northern Goshawks at four levels of resolution: nest trees, nest stands, territories (clusters of nest stands), and spacing between territories. At each level we compare spatial attributes to rates of occupancy by nesting goshawks.

STUDY AREA AND METHODS

This study took place in the southern Cascades Mountains of northern California, on the Goosenest Ranger District of the Klamath National Forest. The area was composed of three major forest types. Sierran Montane Forest and Upper Montane Forest (Küchler 1977) occurred at higher elevations and were dominated by red fir (*Abies magnifica*), white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), and incense cedar (*Calocedrus decurrens*). Lower elevation forests were comprised primarily of Northern Yellow Pine Forest (Küchler 1977), dominated by ponderosa pine and white fir. Most of the study area was between 1400 m and 2330 m elevation and was relatively dry, with most precipitation falling as snow in winter. The area had a long history of timber harvest, with intensive harvesting occurring as early as 1900 (Laudenslayer and Darr 1990). The resulting forest landscape occurred as scattered patches of unmanaged mature forest dispersed in a matrix of thinned or regenerated stands. Suppression of natural fire within this ecosystem resulted in increased density of fire-susceptible conifer species such as white fir in areas formerly dominated by fire resistant species (ponderosa pine, incense cedar; Biswell 1989, Laudenslayer et al. 1989).

We surveyed for nesting northern goshawks each spring and summer from 1984 to 1992. Our initial sample of territories was derived from Forest Service records and survey transects conducted in areas of potential goshawk habitat. In 1988 we began using broadcast of taped conspecific alarm calls along established transects (Fuller and Moser 1981, Rosenfield et al. 1985, Kennedy and Stahlecker 1993) within two 12,000 hectare survey blocks. We returned annually to all known territories to determine occupancy and reproductive success. We intensively surveyed an area of 1.6 km radius surrounding each previously active nest to locate alternate nest sites. Terminology proposed by Postupalsky (1974) and Steenhof and Kochert (1982) was used to define occupancy and nesting success of goshawk territories. We defined nest productivity as the number of large (minimum 5 week old) nestlings. Each year that a given territory was monitored was termed a territory-year. Alternate nests within territories were typically clumped and could be distinguished from adjacent territories. However, in cases where alternate nests were widely spaced we used simultaneous occupancy of both adjacent territories to distinguish between them. We measured distances between the geometric centers of nest clusters at adjacent territories to estimate nearest-neighbor distances. Locations of occupied nests, alternate nests, and habitat boundaries were mapped each year on aerial photographs (scale 1:13,000).

We defined nest stands as patches of forest that were homogeneous in composition, age, and structure relative to the surrounding forest (Spurr and Barnes 1980) and were used for nesting. Boundaries of most stands were the result of forest management activities and natural features such as meadows and lava flows, and were clearly distinguishable on aerial photographs. Areas of nest stands were measured directly from aerial photographs with a Numonics digital planimeter. We classified a stand as occupied if goshawks built a nest or reused an existing nest within it. We calculated occupancy rates for individual stands by dividing the number of years the stand was occupied by the total number of years the stand was monitored.

Nest stand clusters were defined as the aggregate area of all stands within a territory that were used for nesting, and for monitoring purposes were the equivalent of territories. Nest stand clusters were considered occupied if goshawks attempted to nest, exhibited defensive behavior, or were sighted repeatedly within them. The occupancy rate of each cluster was calculated by dividing the number of years the cluster was monitored by the total number of years the cluster was monitored.

Comparisons of stand and nest cluster size with occupancy rates were made using the Spearman Rank Correlation (Zar 1984). Only stands (N = 71) or clusters (N = 23) with >5 years of monitoring were used in statistical comparisons. We found that five years of monitoring was sufficient to delineate the area of most nest stand clusters. Mean values in the text are presented with standard errors (±SE).

RESULTS

MONITORING

We monitored 141 territory-years at 28 goshawk territories within the study area. Occupancy by at least one adult goshawk was confirmed in 100 (71%) of monitored territory-years, and breeding attempts were observed in 89 (63%). Rates of occupancy and breeding were likely underestimated due to the secretive behavior (Kennedy and Stahlecker 1993) and annual movements of nesting goshawks observed in this study. The sample of monitored territories increased each year of the study, from 18 in 1984 to 28 in 1992. Six territories were monitored for over 10 years, 17 were monitored 5–9, and five were monitored ≤4 years.

Productivity for 84 nesting attempts averaged 1.93 young per attempt (range = 0–4). Eighty-seven percent of observed nesting attempts were successful. Primary causes of nest failure included failed incubation (cause unknown = 7), severe spring storms (2), and predation by Great Horned Owls (2; *Bubo virginianus*). Brood size was reduced in nine successful nest attempts when nestlings fell from the nest or were killed by siblings. Nest success and productivity were probably overestimated because nesting attempts failing prior to the nestling stage and mortalities occurring after fledging were less likely to be detected.

OCCUPANCY OF NEST TREES

Territories typically contained more than one nest, most having from 3 to 9. Many of these inactive alternate nests were not observed to be used by goshawks during the study. The mean number of nests actually used during the study was 2.6 (±0.42, range = 1–5) per territory. The reoccupancy rate of individual nest trees was low. Only 37 of 85 (44%) nest attempts were in nests

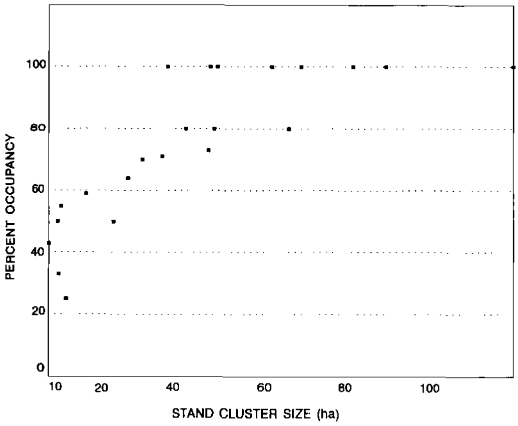

FIGURE 1. Correlation of percent occupancy of goshawk nest stand clusters versus cluster size for 26 territories in the southern Cascades of California, 1984–1992.

used the previous year. The average reoccupancy rate of individual nests at 26 territories over at least 5 years was 49% (±11%). Reoccupancy of alternate nests was highly variable; at some territories goshawks did not re-use the same nest twice in 4–7 years, whereas others used a single nest for 2–6 years and then moved to or built another.

Distribution of Alternate Nests

Spacing and distribution of alternate nests varied widely among territories. Nests in most territories were clumped in two or three adjacent stands, whereas others contained nests scattered in stands up to 2.1 km apart. The mean distance between alternate nests in 65 nest attempts in this study was 273 (±68.6) m, (range = 30–2066 m). This estimate of nest spacing was conservative in that it included only movements actually observed between years. Longer movements were more difficult to detect and were likely underrepresented.

Use of Nest Stands

Goshawk territories typically contained 1–5 different forest stands used for nesting ($\bar{X}$ = 2.4 ± 0.7). Stands used for nesting ranged from 4.1 to 115 hectares in size ($\bar{X}$ = 27.8 ± 5.3 ha, N = 71 stands).

At territories with at least five successive years of monitoring, individual nest stands were occupied by nesting goshawks an average of 46% (±6%) of the years monitored (N = 71). The maximum distance recorded between nest stands was 1.8 km. However, over 85% of alternate nest stands were less than 0.7 km apart ($\bar{X}$ = 0.52 ± 0.11 km, N = 71 stands). Occupancy rates of individual nest stands were positively correlated with stand size (r_S = 0.85, P = 0.001). Smaller stands (<10 ha) typically contained 1–2 nests and were only occasionally occupied by goshawks, whereas larger stands (>20 ha) often contained several nests and were occupied in a high proportion of territory-years.

Nest Stand Clusters

Nest stand clusters ranged from 10.5 to 114 ha in size ($\bar{X}$ = 41.7 ± 5.89, N = 26 territories). The mean occupancy rate of nest stand clusters was 0.74 (±0.055, N = 26). Occupancy rates of 23 nest stand clusters with at least five years of monitoring was positively correlated with cluster size (r_S = 0.88, P = 0.008). Occupancy rates of clusters of <20 hectares were typically <50%. At approximately 40 ha occupancy rose to 75–80%, and was nearly 100% for stand clusters >61 ha (Fig. 1). We found no significant relationship between stand cluster size and productivity (r_S = 0.052, P = 0.819). The mean number of young produced per occupied territory (minimum five year average) was relatively uniform among territories.

Territory Spacing and Density

Nearest-neighbor distances for 21 goshawk territories within intensive survey blocks ranged from 1.3 to 6.1 km, averaging 3.25 ± 0.34 km. Spacing appeared to be reduced around landscape features such as meadows and riparian systems, where goshawk territories were clumped. Eleven territories were located within a 10,230 ha block of Sierran Montane Forest yielding a density of 1.07 territories per 1000 ha, compared with 0.575 territories per 1000 ha in a 10,440 ha block of Upper Montane Forest.

DISCUSSION

Territory use by goshawks in this study was characterized by alternate use of nest sites up to 2.1 km apart, and low fidelity to any particular nest site. Over time the number of nest sites recorded in most territories increased, as did the area of habitat containing them. From 4 to 6 years of monitoring were required to define the actual area used for nesting within most territories. The resulting area of nesting habitat (nest stand cluster) was considerably larger than area estimates derived from a single year (Crocker-Bedford 1990), or measurement of activity centers surrounding individual nests (Reynolds 1983).

Comparison of nest habitat area in this study with results of other studies is complicated by differences in terminology and basic study design. Measurements of nest stands and stand clusters in this study were made using physical boundaries of nest stands. It is likely that only a small portion of each stand is actually used for nesting in a given year. Reynolds et al. (1992) proposed a hierarchy of spatial components comprising goshawk home ranges: nest area, post fledging family area, and foraging area. Each of these components was based on measurement of goshawk activity and cannot be estimated without radio-telemetry. Estimates of nest habitat area based on observations of nest-tending activities (Reynolds 1983) overlook the possibility that selection of nest sites by goshawks is based at least partially on patch size. Our observations of reduced occupancy in smaller stands suggest that patch size may be an important factor determining quality of nesting habitat.

The post fledging family areas (PFA) described by Kennedy (1991) may be somewhat analogous to nest stand clusters in that the PFA is a larger area encompassing at least one nest site. It is not clear whether the PFAs studied by Kennedy (1991) contained all known nest sites within each territory, or if goshawk pairs moved outside of PFA boundaries in subsequent years. This relationship could be assessed by comparison of PFA boundaries with the distribution of alternate nest sites and the boundaries of nest stands, particularly over a number of years.

Alternate nest sites within most territories appeared as clusters, spatially distinct from nest clusters at neighboring territories. At five territories (18%), however, alternate nests were very widely spaced and territory boundaries were less distinct. Maximum distances between alternate nests at these territories were similar to minimum distances between simultaneously occupied neighboring territories.

Mean occupancy rates of habitat components increased as spatial scale increased from nest trees to nest stands and nest stand clusters. Annual movements of nesting goshawks may have reduced our ability to detect some nest attempts in remote nest sites, resulting in underestimation of occupancy at larger scales (nest stand clusters). Patterns of occupancy at goshawk territories fell into two categories: traditional territories (23), where nesting by goshawks was predictable and typically occurred within finite nest clusters; and ephemeral territories (5), where nesting was sporadic and nest sites were widely distributed. Ephemeral territories were occupied in less than three of five years and appeared to be associated with highly fragmented areas of lodgepole pine and mixed pine stands where extensive tree mortality due to bark beetles (*Dendroctonus* spp.) had occurred. Changes in stand structure in these areas may have resulted in increased density or vulnerability of prey and attracted goshawk pairs to nest in areas where little mature forest habitat was available.

Although occupancy of nest stand clusters was clearly correlated with cluster size, other factors may have affected occupancy of specific clusters by nesting goshawks. Reduction and fragmentation of mature forest habitat may favor early successional competitors and predators such as Red-tailed Hawks (*Buteo jamaicensis*) and Great Horned Owls (Moore and Henny 1983, Johnson 1993) and reduce occupancy by goshawks (Crocker-Bedford 1990). Occupancy of traditional goshawk nests or nest stands by Great Horned Owls, Long-eared Owls (*Asio otus*), Northern Spotted Owls (*Strix occidentalis caurina*), Red-tailed Hawks and Cooper's Hawks (*Accipiter cooperi*) was recorded in this study, but was not associated with territory abandonment by goshawks. In three instances, however, goshawks moved outside of their traditional nest cluster after it was occupied by Northern Spotted Owls.

Despite intensive timber harvest and fragmentation of mature forest, our study area supported high densities of nesting goshawks. Goshawk territories, however, were associated with the larger remaining patches of mature forest, and territory occupancy was positively correlated with the size of nesting habitat patches.

Several factors may act to mitigate the effects of timber harvest and forest fragmentation on goshawk habitat quality in our study area. Timber harvests occurring after the early 1960s typically consisted of commercial thinning, shelterwood, and sanitation prescriptions, resulting in less distinction between harvested areas and remaining mature forest than in large clearcut regimes. Golden-mantled Ground Squirrels (*Spermophilus lateralis*), a primary prey species for goshawks in the southern Cascades (Woodbridge, unpubl. data), are abundant in open habitats (Ingles 1965) and were frequently observed in previously harvested areas. This prey resource could act to offset losses of prey species associated with mature forest. Finally, effects of forest fragmentation on goshawk populations may be less important in forest ecosystems such as the southern Cascades that are naturally fragmented by topography, xeric conditions, and wildfire. Comparison of our results with data collected in different forest ecosystems may provide insights into the relative importance of nesting habitat area.

ACKNOWLEDGMENTS

We thank B. Allison, T. Seager, K. Finley, A. Strassler, and the numerous student interns who performed the majority of fieldwork over the past six years. Comments by S. DeStefano, L. Rissler, T. Filliater, and three anonymous reviewers greatly improved earlier drafts of this manuscript. The Goosenest Ranger District of the Klamath National Forest provided financial and logistical support for our studies.

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Studies in Avian Biology No. 16:88–91, 1994.

DENSITY AND PRODUCTIVITY OF NORTHERN GOSHAWKS: IMPLICATIONS FOR MONITORING AND MANAGEMENT

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E. CHARLES MESLOW

Abstract. We studied Northern Goshawk (*Accipiter gentilis*) breeding populations on five study areas on the Fremont, Malheur, and Wallowa-Whitman National Forests in eastern Oregon during 1992 and 1993. We found 50 active territories, with average densities of 0.07 active territories per 100 ha (SE = 0.15, N = 3 study sites) in 1992 and 0.06 (SE = 0.15, N = 5 sites) in 1993. However, densities were variable both between years and among areas within each year, and no consistent patterns were seen based on forest cover type. Productivity (number of young fledged per nest) was also variable between years and among study sites within the same year. Current USDA Forest Service management for goshawks emphasizes reducing tree harvest around specific nest sites or post-fledging family areas (PFAs). Our data, however, show that numbers of nesting goshawks are variable among years, and not all breeding sites will be discovered in a single year of survey. We recommend multiple-year surveys for nesting birds and habitat management on a landscape rather than "per nest" basis.

Key Words: *Accipiter gentilis*; breeding; nesting; Northern Goshawk; Oregon.

Timber harvesting has been implicated as a factor in reducing the number and altering the distribution of nest sites of Northern Goshawks (*Accipiter gentilis*) throughout much of the forested western United States (Reynolds et al. 1982, Crocker-Bedford 1990, Ward et al. 1992). In Oregon, this concern has led the Oregon Department of Fish and Wildlife to place the Northern Goshawk on the state's list of sensitive species.

In the Pacific Northwest, scientific research and public attention has focused on forest ecosystems and wildlife populations on the west side of the Cascade Mountain Range, largely due to concern for the status of Northern Spotted Owls (*Strix occidentalis caurina*). Interest is growing, however, in east-side forest issues, such as timber harvest, forest health, and wildlife habitat. The Northern Goshawk has been identified as a species of special concern and is being considered as a potential indicator of the health of mature ponderosa pine (*Pinus ponderosa*) and mixed conifer forests in eastern Oregon (Marshall 1992).

We studied goshawk populations in eastern Oregon to determine the distribution, density, and productivity of nests in major forest types, describe diet, and make recommendations for goshawk management and monitoring of breeding populations.

METHODS

STUDY SITES

Research took place on three National Forests in eastern Oregon: the Fremont, Malheur, and Wallowa-Whitman. These Forests were located across eastern Oregon and represented a wide spectrum of forest types. Mixed conifer forest (including combinations of ponderosa pine, Douglas-fir [*Pseudotsuga menziesii*], western larch [*Larix occidentalis*], incense-cedar [*Calocedrus decurrens*], sugar pine [*Pinus lambertiana*], and firs [*Abies* spp.]) and forest stands with a large component of ponderosa pine were found on all three Forests. In addition, large expanses of lodgepole pine (*Pinus contorta*) were present on the Fremont National Forest. Topography on all Forests ranged from gently sloping ridges to steep-walled drainages, with elevations between 900–2000 m. Natural openings, such as wet meadows, grasslands, and burns, were distributed throughout the study sites. Partial cuts (shelterwood, overstory removal, commercial thinning) and some clear-cutting were the major tree harvesting practices.

Five survey areas (called Density Study Areas [DSA]) were established on the three National Forests and ranged from 11,500 to 15,500 ha. Two DSAs were located on the Fremont National Forest: the Paisley DSA contained mostly lodgepole pine (80%), with some ponderosa pine (15%) and mixed conifers (5%); the Bly DSA was primarily mixed conifer (70%) and ponderosa pine (30%). Two DSAs were located on the Malheur National Forest: Bear Valley East DSA was dominated by ponderosa pine, with about 25% of the area covered by islands of lodgepole pine and mixed conifers; Bear Valley West DSA was mostly mixed conifer, with about 25% of the area in ponderosa pine. The Spring Creek DSA on the Wallowa-Whitman National Forest was comprised of mixed conifer stands.

SURVEYS

We used survey protocol recommended by Woodbridge (pers. comm.) and Kennedy and Stahlecker (1993) to search for all nesting goshawks within the five DSAs. Survey stations were about 300 m apart and were set up on roads and trails and along transects through roadless areas to obtain complete coverage of each DSA. From mid-May to early August, taped goshawk calls were broadcast through a megaphone (modified Realistic® model 32-2030 coupled to a Sony® walkman model WMA53). Responses to the taped calls and incidental sightings of goshawks were followed by intensive searches to locate nests. Nest locations were marked on topographic maps and aerial photographs.

TABLE 1. Number and Density of Northern Goshawk Nesting Territories on the Fremont, Malheur, and Wallowa-Whitman National Forests in Eastern Oregon, 1992–1993

			1992				1993			
Forest	DSA	Primary forest cover	Area (ha)	Known nests	Active territories	Density (active terr./100 ha)	Area (ha)	Known nests	Active territories	Density (active terr./100 ha)
Fremont	Paisley	Lodgepole	8780	3	4	0.046	12,960	6	8	0.062
	Bly	Mixed conifer/ponderosa					10,627	3	4	0.038
Malheur	Bear Valley East	Ponderosa/mixed conifer	9046	6	8	0.088	9046	6	6	0.066
	Bear Valley West	Mixed conifer/ponderosa					10,519	8	9	0.086
Wallowa-Whitman	Spring Creek	Mixed conifer	11,396	7	8	0.070	11,396	3	3	0.026

The Paisley, Bear Valley East, and Spring Creek DSAs were surveyed in 1992 and 1993. The Bly and Bear Valley West DSAs were surveyed in 1993 only. In some cases, there was evidence of nesting goshawks (responses by birds to taped calls, repeated observations of defensive adults in an area) but the nest was not found. We included them in our calculations of breeding densities.

Productivity of nests was determined by visiting nest sites in late July and counting nestlings either just before or just after fledging. Nesting phenology dates were based on back-dating from estimated weekly development of juveniles based on plumage characteristics and fledging dates. Prey remains and goshawk pellets were collected under nest trees and at plucking posts and were placed in labeled plastic bags and stored frozen for analysis at a later date.

RESULTS

We found a total of 20 active territories in 1992 and 30 in 1993 (Table 1). Overall density averaged 0.07 active territories per 100 ha (SE = 0.15, N = 3) in 1992 and 0.06 per 100 ha (SE = 0.15, N = 5) in 1993. Densities were variable both between years and among areas within each year. No consistent patterns were seen based on forest cover type (i.e., DSAs dominated by lodgepole pine, ponderosa pine, or mixed conifers).

There was a decreasing trend in productivity (number of young per active territory) from the Fremont National Forest in the south to the Wallowa-Whitman National Forest in the north in 1992 (Table 2). This trend was repeated in 1993, when the Paisley and Bly DSAs on the Fremont and the Bear Valley East and Bear Valley West DSAs on the Malheur were combined ($\bar{X}$ = 1.56 young per nest, SE = 1.15, N = 9 nests for Fremont; $\bar{X}$ = 1.00, SE = 0.96, N = 13 for Malheur; $\bar{X}$ = 0.67, SE = 0.76, N = 3 for Wallowa-Whitman). In some cases, however, productivity was variable between years (e.g., Bear Valley East DSA) and between DSAs on the same Forest (Table 2). Nesting phenology was similar among Forests, with eggs laid in late April to early May, eggs hatched during late May to mid-June, and young fledged from late June to mid-July.

Totals of 119 and 101 prey items were identified in 1992 and 1993, respectively (Table 3). Avian and mammalian species made up 100% of identifiable prey remains. Both percent composition and percent biomass indicated that mammalian prey was more prevalent on the Fremont and Malheur National Forests, whereas avian prey was proportionally larger on the Wallowa-Whitman. However, our sample of prey remains for the Wallowa-Whitman was very low in 1993 because few pairs of goshawks nested.

DISCUSSION

Our estimates of density of goshawk breeding sites in eastern Oregon are probably minimums

TABLE 2. PRODUCTIVITY (NUMBER OF FLEDGLINGS PER KNOWN NEST SITE) OF NORTHERN GOSHAWKS ON THREE NATIONAL FORESTS IN EASTERN OREGON, 1992–1993

		1992			1993		
Forest	Density study area	$\bar{X}$	SE	N	$\bar{X}$	SE	N
Fremont	Paisley	2.2	0.75	6	2.2	1.08	6
	Bly				0.3	0.76	3
Malheur	Bear Valley East	1.9	0.57	10	0.3	0.72	6
	Bear Valley West				1.6	0.89	7
Wallowa-Whitman	Spring Creek	1.0	0.71	9	0.7	0.76	3

because we may not have found all active territories (Kennedy and Stahlecker 1993). In addition, nest failures early in the breeding season would have precluded us from detecting some active territories. However, our use of survey protocol recommended by Woodbridge (pers. comm.) and Kennedy and Stahlecker (1993) allowed us to obtain complete coverage of all five DSAs with equal effort, and to survey all forest types and seral stages for goshawk nests. Thus, we believe that our estimates of density are relatively accurate and directly comparable among the five study sites.

There was a substantial reduction in numbers of active territories from 1992 to 1993 on the Spring Creek DSA. This trend was also noted elsewhere on the Wallowa-Whitman National Forest (A. Blumton, pers. comm.) and adjacent Boise-Cascade Company lands (M. McGrath, R. Riggs, pers. comm.). This drop in breeding activity may have been due to cold, wet spring weather in northeastern Oregon. Densities of active goshawk territories also varied between DSAs on the same Forest, especially the Paisley and Bly DSAs on the Fremont.

There was a latitudinal trend in productivity, with higher numbers of juveniles fledged from south to north. This may have been a function of diet, as higher proportions of mammals were found in prey remains on the Fremont and Malheur than the Wallowa-Whitman. Bull and Hohman (*this volume*) reported similar productivity and diet results during 1992 from their study area on the Wallowa-Whitman National Forest. A relationship between high productivity and proportionally more mammalian species in the diet is speculative, however, and additional data on diet and productivity are required to draw conclusions.

Current USDA Forest Service management for Northern Goshawks in Region 6 (Oregon and Washington) calls for establishing protected zones around some nest sites (nest sites in areas under current timber harvest contracts are often exempt), where no or reduced timber harvest would take place. These zones are of variable size and often are on the order of 2–12 ha (5–30 acres). More recently, managers have been directed to protect a larger area around goshawk nest sites corresponding to the post-fledging family area (PFA).

Either of these approaches necessitate finding active goshawk breeding sites, and promotes management on a "per nest" basis. Our data show that not all sites are active in all years, and thus searching for goshawk nests in a single season in preparation for potential timber sales could easily overlook territories. This variability between years in nest site use by goshawks could be due to a poor breeding year because of inclement spring weather or some other environmental variable, as we believed happened in northeastern Oregon in 1993. Also, use of alternate nest sites by goshawks or early nest failure

TABLE 3. PERCENT COMPOSITION AND PERCENT BIOMASS OF PREY REMAINS COLLECTED AT NESTS AND PLUCKING SITES OF NORTHERN GOSHAWKS ON THE FREMONT, MALHEUR, AND WALLOWA-WHITMAN NATIONAL FORESTS IN EASTERN OREGON, 1992–1993

	1992					1993				
		Composition (%)		Biomass (%)			Composition (%)		Biomass (%)	
Forest	N[1]	Birds	Mammals	Birds	Mammals	N[1]	Birds	Mammals	Birds	Mammals
Fremont	49	49	51	34	66	47	53	47	27	73
Malheur	44	34	66	16	84	50	60	40	37	63
Wallowa-Whitman	26	62	38	64	36	4	50	50	51	49

[1] N = number of separate prey remains or goshawk pellets examined.

also influences the ability of surveyors to locate all nest sites.

Because of the variability in nest site use by goshawks, we recommend as an absolute minimum that surveys be conducted for at least two, and preferably three or four years in an area before allowing timber harvest. An alternative to the per-nest management approach would be to manage forest habitat on more of a landscape scale. Management plans, such as suggested by Reynolds et al. (1992), consider other forest-dependent species and promote management at a more holistic level. We believe that similar landscape-level recommendations are appropriate to other diurnal and nocturnal raptors.

ACKNOWLEDGMENTS

Funding for this project was provided by the Oregon Department of Fish and Wildlife's Nongame Wildlife Program, U.S. Fish and Wildlife Service, Center for Analysis of Environmental Change of Oregon State University, and USDA Forest Service. We thank C. Carstarphen, R. L. Llewellyn, J. Maurer, M. A. McLeod, C. Schelz, K. H. Schmidt, C. A. Wolfe, and S. A. Wolfe for working hard in the field, and G. Keister, M. Henjum, C. Carey, and C. Puchy of the Oregon Department of Fish and Wildlife and S. Egeline, R. Haines, T. Hershey, T. Schommer, G. Silovsky, and B. Woodbridge of the USDA Forest Service for their important insights and input. We also thank T. Cutler and T. Church for analyzing all prey remains, L. Alexander, B. J. Verts, and L. Carroway for assistance in prey identification, and P. Beier and L. Hall for reviewing the manuscript. This project would not have been possible without the interest, assistance, and dedication of a very large number of wildlife biologists and wildlife technicians of the USDA Forest Service.

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Studies in Avian Biology No. 16:92–96, 1994.

NESTING HABITAT OF *ACCIPITER* HAWKS: IS BODY SIZE A CONSISTENT PREDICTOR OF NEST HABITAT CHARACTERISTICS?

MELISSA S. SIDERS AND PATRICIA L. KENNEDY

Abstract. In western coniferous forests a general correlation of accipiter size and structural size of nesting stands and nest trees used by sympatric *Accipiter* species has been reported. In this paper we review the literature to evaluate the following predictions: accipiter hawks consistently use nesting habitat in which their body size is (1) positively correlated with nest tree height, and average stand tree diameter, and (2) inversely correlated with average stand tree density and stand % canopy closure. We include in this review summary habitat data collected at 42 Northern Goshawk (*Accipiter gentilis*), 52 Cooper's Hawk (*A. cooperii*), and 16 Sharp-shinned Hawk (*A. striatus*) nest sites in the Jemez Mountains of north-central New Mexico. From our review of the literature, stand % canopy closure, and nest tree height did not consistently follow the expected pattern. Average stand tree density and average stand tree diameter consistently supported the body size predictions. However in several studies, stand densities of goshawk and Cooper's Hawk stands were not significantly different. In addition, there seems to be much variation between studies for mean values for all of the parameters, and the ranges of the mean values overlap among species. This is probably indicative of both habitat variation between study areas and differences in methodology. This review of accipiter habitat studies supports Kennedy's (1988) hypothesis that the correlation between accipiter size and nest stand and nest site structural size is not a widespread phenomenon for all vegetation parameters and may not be adequate for predicting suitable accipiter nesting habitat in all areas.

Key Words: Accipiter cooperii; Accipiter gentilis; Accipiter striatus; Cooper's Hawk; nesting habitat; Northern Goshawk; Sharp-shinned Hawk.

The three North American *Accipiter* species (Northern Goshawk [*A. gentilis*], Cooper's Hawk [*A. cooperii*] and Sharp-shinned Hawk [*A. striatus*]) are sympatric predators in many forested areas in North America (Palmer 1988:304–378, Reynolds 1989). In western coniferous forests Reynolds et al. (1982), Moore and Henny (1983) and Fischer (1986) reported a general correlation of accipiter size and tree size (used as an index of successional stage) of nesting stands and nest trees used by sympatric *Accipiter* species. Kennedy (1988) also observed this correlation for nest tree size and accipiter size in New Mexico. However, in the northeastern U.S., Bosakowski et al. (1992) found Cooper's Hawks nesting in trees with greater diameter than goshawks. In addition, Kennedy (1988) and Bosakowski et al. (1992) found no significant differences for basal area (BA), tree densities, or mean diameter at breast height (dbh) between goshawk and Cooper's Hawk nesting stands in their study areas.

There are two plausible explanations for these equivocal results: (1) a correlation between accipiter size and nest stand and nest tree sizes is not a widespread phenomenon; or (2) a strong correlation does exist but it cannot be detected because of small sample sizes (goshawk N = 11, Cooper's Hawk N = 12 [Kennedy 1988]; goshawk N = 16, Cooper's Hawk N = 19 [Bosakowski et al. 1992]). Our primary study objective is to review the literature to determine if accipiters consistently use nesting habitat in which their body size is positively correlated with nest tree height and average stand tree diameter and inversely correlated with tree density and % canopy closure. We include in this review summary habitat data collected at 42 goshawk, 52 Cooper's Hawk, and 16 Sharp-shinned Hawk nest sites in north-central New Mexico during 1992 and 1993 (Siders and Kennedy, unpubl. data). These data were collected in the same area studied by Kennedy (1988), and thus allow us to determine if her results are maintained when sample sizes of goshawks and Cooper's Hawks are more than doubled and Sharp-shinned Hawk nest sites are included.

APPROACH

In our literature review, we tried to include all published studies, M.S. theses, and Ph.D. dissertations on accipiter nesting habitat characteristics within the United States. We included habitat studies of single *Accipiter* species if the study was conducted in an area where the species was probably nesting sympatrically with congeners. To be included in this review, a study had to have data on one or more of the following parameters: average stand tree density, average stand tree diameter, average stand % canopy closure, and average nest tree height. Of these studies, coniferous forest habitat was the predominant forest cover type, with Bosakowski et al. (1992) and Joy (1990) as the only predominantly deciduous forest cover type for goshawk and Cooper's Hawk.

In reviewing the literature, we encountered various definitions of nest site and/or nest stand, indicating

TABLE 1. COMPARISON OF *Accipiter* NEST STAND TREE DENSITY (TREES/HA) AMONG U.S. STUDIES

Location	Northern Goshawk (N)	Cooper's Hawk (N)	Sharp-shinned Hawk (N)	Source
California, N	749.0 (12)			Saunders (1982)
California, NW	427.0 (10)			Hall (1984)
Missouri		1137.8 (33)	1370.0 (15)	Wiggers and Kritz (1991)
Montana–Idaho	1135.0 (17)			Hayward and Escano (1989)
New Mexico	959.3 (11)	723.9 (12)		Kennedy (1988)
New Mexico	1054.8 (42)	1129.0 (52)	1815.6 (16)	Siders and Kennedy (unpubl. data)
New York–New Jersey	540.1 (16)	633.4 (19)		Bosakowski et al. (1992)
Oregon, E	482.0 (7)	1159.0 (5)	1594.0 (5)	Reynolds et al. (1982)
Oregon, E	1007.4 (34)	1802.5 (31)	2312.0 (15)	Moore and Henny (1983)
Oregon, NW		656.0 (4)	1296.0[1] (3)	Reynolds et al. (1982)
			652.0[2] (2)	Reynolds et al. (1982)[3]
Utah	720.0 (10)	1900.0 (17)	4003.0 (9)	Fischer (1986)
Minimum	427.0	656.0	652.0	
Maximum	1135.0	1802.5	2312.3	

[1] Second growth stands.

[2] Old growth stands.

[3] Goshawk and Cooper's hawk nest stands were not separated into second growth and old growth.

differences in the usage of these terms. We defined a nest stand as the area surrounding a nest tree, including vegetation and topographic features used by a nesting pair during the entire nesting season, exclusive of foraging areas (Reynolds et al. 1982). We defined a nest site as the actual tree in which the nest was placed. In compiling the data from other studies, these definitions were used to avoid confusing nest site and nest stand level comparisons.

In addition to the literature, we included in this comparison unpublished data from our ongoing research on accipiter habitat in the Jemez Mountains and adjacent Pajarito Plateau in north-central New Mexico. In the 1992 and 1993 nesting seasons, we collected habitat data at all known goshawk (N = 42), Cooper's Hawk (N = 52) and Sharp-shinned Hawk (N = 16) nest stands that had not been drastically altered by timber harvest or other disturbance since the sites were identified as active. Each of these nest sites had been occupied (minimally, hawks observed constructing nests during courtship) at least once between 1984–1993.

To estimate the four vegetative parameters of interest, we established 0.08-ha (corrected for slope) circular plots around nest trees. On each plot we measured nest tree height and diameter at breast height (dbh) of all trees ($\geq$2.54 cm dbh) using standard forest measurement techniques (Wenger 1984). To determine % canopy closure, we divided the plot into four quadrants using the four cardinal directions for quadrant boundaries. We measured % canopy closure using a convex spherical densiometer (Lemmon 1956, 1957). Four canopy closure measurements were taken (facing NE, SE, SW, and NW) at each of five locations (center, and at one-half the radius of the plot to the NE, SE, SW, or NW) and averaged for each stand. We determined stand tree density by counting all trees ($\geq$2.54 cm dbh) within the 0.08-ha plot (converting this value to number of trees per ha).

In this comparison, we present mean values of nest tree height, stand tree density, stand tree diameter, and stand % canopy closure for each species in each study. We compared these data qualitatively to determine if accipiters consistently use nesting habitat in which their body size is positively correlated with nest tree height and average stand tree diameter and inversely correlated with average stand tree density and stand % canopy closure. The database cannot be evaluated statistically because sampling techniques and plot sizes varied between studies.

RESULTS AND DISCUSSION

Accipiter nest habitat studies in the U.S. indicate that there is a trend of increasing average stand tree density with increasing accipiter body size (Table 1). However, in three studies (Kennedy 1988, Bosakowski et al. 1992, Siders and Kennedy, unpubl. data) average stand densities for goshawk and Cooper's Hawk stands were not significantly different. It is also interesting to note that Kennedy's average stand densities are lower than the average stand densities we recorded. This is probably due to her small sample sizes and the inclusion of a few riparian cottonwood (*Populus fremontii*) nest stands, which typically have lower stand densities.

This potential effect of sample size on descriptions of accipiter nesting habitat characteristics is also evident in the two studies conducted in the same area in eastern Oregon (Reynolds et al. 1982, Moore and Henny 1983). Both of these studies appear to differentiate between goshawks and Cooper's Hawks by roughly a factor of two in stand density, and between Cooper's Hawks and Sharp-shinned Hawks by 25–30% differences in stand density. Yet, similar to the two New Mexico studies, stand densities for the study with larger sample sizes (Moore and Henny 1983) consistently report larger stand densities than the

TABLE 2. COMPARISON OF *Accipiter* NEST STAND AVERAGE CANOPY CLOSURE (%) AMONG U.S. STUDIES

Location	Northern Goshawk (N)	Cooper's Hawk (N)	Sharp-shinned Hawk (N)	Source
California, N	76.9 (12)			Saunders (1982)
California, NW	94.0 (10)			Hall (1984)
Colorado	95.0 (2)	95.0 (4)	94.0 (14)	Joy (1990)
Missouri		80.9 (31)	82.3 (14)	Wiggers and Kritz (1991)
New Mexico	65.7 (42)	61.6 (52)	77.5 (16)	Siders and Kennedy (unpubl. data)
New York–New Jersey	90.0 (16)	88.7 (19)		Bosakowski et al. (1992)
Oregon, E	59.8 (7)	64.0 (5)	68.3 (5)	Reynolds et al. (1982)
Oregon, NW		75.0 (4)	80.3[1] (3)	Reynolds et al. (1982)
			89.7[2] (2)	Reynolds et al. (1982)[3]
Utah	68.4 (10)	83.1 (17)	81.6 (9)	Fischer (1986)
Minimum	59.8	61.6	68.3	
Maximum	95.0	95.2	97.9	

[1] Second growth stands
[2] Old growth stands
[3] Goshawk and Cooper's hawk nest stands were not separated into second growth and old growth.

study with the smaller sample sizes (Reynolds et al. 1982).

The relationship between stand % canopy closure and accipiter body size is unclear (Table 2). For all three species, average % canopy closure varied from approximately 60% to 95% throughout the range of the studies. In some studies stand % canopy closure was inversely related to body size (Reynolds et al. 1982, Wiggers and Kritz 1991), but in other studies this was not the case. In the eastern U.S., Bosakowski et al. (1992) found goshawks and Cooper's Hawks nesting in stands with similar % canopy closures. In Colorado, Joy (1990) found that all three species were using stands with similar % canopy closures. In Utah, Fischer (1986) found Cooper's Hawks and Sharp-shinned Hawks using stands with similar % canopy closures but with higher % canopy closures than stands used by goshawks. In our study, Cooper's Hawks used stands with more open canopies than did the goshawk which nested in more open stands than did Sharp-shinned Hawks. The values for goshawk and Sharp-shinned Hawk stands in our study are within the range of previously recorded averages for this variable, but the Cooper's Hawk value is the lowest reported stand % canopy closure.

The data on average stand tree diameter supports the prediction that this parameter is positively correlated with accipiter body size (Table 3). The range in stand tree diameters for goshawks was almost a factor of two greater than the reported ranges of its congeners. This is a result of Hall's (1984) study in northwestern California where she reported average stand diameters of 46.0 cm. In contrast, average stand tree diameters for the goshawk and Cooper's Hawk nest stands in our study are the lowest reported

TABLE 3. COMPARISON OF *Accipiter* NEST STAND AVERAGE TREE DIAMETER (DBH-CM) AMONG U.S. STUDIES

Location	Northern Goshawk (N)	Cooper's Hawk (N)	Sharp-shinned Hawk (N)	Source
California, N	27.0 (12)			Saunders (1982)
California, NW	46.0 (10)			Hall (1984)
Missouri		21.8 (33)	20.8 (15)	Wiggers and Kritz (1991)
New Mexico	22.0 (11)	20.0 (12)		Kennedy (1988)
New Mexico	14.8 (42)	13.5 (52)	12.5 (16)	Siders and Kennedy (unpubl. data)
Oregon, E	27.4 (7)	21.3 (5)	18.3 (5)	Reynolds et al. (1982)
Oregon, E	22.1 (34)	15.0 (31)	12.9 (15)	Moore and Henny (1983)
Oregon, NW		24.4 (4)	21.3[1] (3)	Reynolds et al. (1982)
			27.4[2] (2)	Reynolds et al. (1982)[3]
Utah	27.5 (10)	14.7 (17)	10.0 (9)	Fischer (1986)
Minimum	14.8	13.5	10.0	
Maximum	46.0	24.4	27.4	

[1] Second growth stands.
[2] Old growth stands.
[3] Goshawk and Cooper's hawk nest stands were not separated into second growth and old growth.

TABLE 4. Comparison of *Accipiter* Nest Site Average Nest Tree Height (m) among U.S. Studies

Location	Northern Goshawk (N)	Cooper's Hawk (N)	Sharp-shinned Hawk (N)	Source
California, N	34.4 (13)			Saunders (1982)
California, NW	43.0 (12)			Hall (1984)
Colorado	26.0 (2)	23.0 (4)	19.0 (14)	Joy (1990)
Montana–Idaho	26.0 (17)			Hayward and Escano (1989)
New Mexico	25.9 (11)	24.1 (12)		Kennedy (1988)
New Mexico	28.6 (42)	20.8 (52)	15.9 (16)	Siders and Kennedy (unpubl. data)
New York–New Jersey	24.1 (16)	25.2 (19)		Bosakowski et al. (1992)
Oregon, E	33.5 (22)	22.6 (15)	11.0 (10)	Reynolds et al. (1982)
Oregon, NW		22.3 (18)	27.1[1] (6)	Reynolds et al. (1982)
South Dakota	18.3 (21)			Bartelt (1974)
Utah	22.4 (10)	12.2 (17)	8.5 (9)	Fischer (1986)
Minimum	18.3	12.2	8.5	
Maximum	43.0	24.1	27.1	

[1] Second growth stands.

values. In addition, average stand diameter for the three species in our study area are not significantly different (Siders and Kennedy, unpubl. data). We cannot evaluate how much of these differences in nest stand parameters between our study and other studies can be attributed to differences in methodology and/or habitat variation.

Most of the studies that included nest tree height found that the taller nest trees were used by the larger species and the shorter nest trees were used by the smaller species (Reynolds et al. 1982 for eastern Oregon, Fischer 1986, Kennedy 1988, Joy 1990, Siders and Kennedy, unpubl data), but not in all cases (Reynolds et al. 1982 for northwestern Oregon) (Table 4). Similar to stand tree diameters, mean nest tree heights were more variable for goshawks than their congeners.

The goshawk, Cooper's Hawk, and Sharp-shinned Hawk are morphologically similar species at three different sizes. Studies that compare habitat characteristics of all three *Accipiter* species are few, and some of these studies have indicated a relationship between the size of the species and the size of elements of its habitat. However, from our review of the literature, not all habitat characteristics follow this pattern for all studies. Stand % canopy closure did not follow the expected pattern in four studies. Stand density trends did follow the expected pattern in most studies; however, differences between goshawk and Cooper's Hawk stands were non-significant in three studies. Nest tree height did not follow the expected pattern in northwestern Oregon (Reynolds et al. 1982). Average stand tree diameter was the only parameter that consistently supported the prediction of increasing habitat scale with increasing body size. In addition, there seems to be much variation among studies for mean values for all the parameters, and the ranges of the mean values overlap between species. This is probably indicative of both habitat variation among study areas and differences in methodology, particularly sample size. Our review of accipiter habitat studies supports Kennedy's (1988) hypothesis that the correlation between accipiter size and nest stand and nest site structural size is not a widespread phenomenon for all vegetation parameters and may not be adequate for predicting suitable accipiter nesting habitat in all areas.

ACKNOWLEDGMENTS

This project was funded by the USDA Forest Service, Region 3, and the Santa Fe National Forest. R. Hoffer and R. Reynolds were invaluable in the development of this research. W. McKinney, J. Peterson, and D. Lentz of the Jemez Ranger District were especially helpful and supportive of this project. Los Alamos National Laboratory provided access to many of the lower elevation Cooper's Hawk nest sites. Special thanks go to the 1992 and 1993 inventory crews, A. Alexander, K. Colfer, J. DeLong, V. Dreitz, J. Moore, and D. Sinton, for their diligent efforts at finding nest sites and assistance in vegetation data collection. O. Myers, J. Ward, and J. Fair were indispensable in their helpful suggestions for this project's design, implementation, and analysis. We also thank two anonymous reviewers who helped improve this manuscript.

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Studies in Avian Biology No. 16:97–102, 1994.

NORTHERN GOSHAWK DIETS IN PONDEROSA PINE FORESTS ON THE KAIBAB PLATEAU

CLINT W. BOAL AND R. WILLIAM MANNAN

Abstract. We recorded 385 prey deliveries at a mean delivery rate of 0.25/hr at 20 Northern Goshawk (*Accipiter gentilis*) nests in ponderosa pine (*Pinus ponderosa*) forests on the North Kaibab Ranger District (NKRD), Kaibab National Forest, Arizona, 1990–1992. Golden-mantled ground squirrels (*Spermophilus lateralis*) and cottontail rabbits (*Sylvilagus* spp.) were the most common mammalian prey species (41%). Steller's Jays (*Cyanocitta stelleri*) and Northern Flickers (*Colaptes auratus*) were the most common avian prey species (16%). Mammals and birds accounted for 76% and 24% of the observed prey, respectively. Mammals accounted for 94% of the biomass used by Northern Goshawks, and cottontail rabbits made up the greatest proportion of the biomass (26%). Goshawks on the NKRD fed slightly less equitably upon different prey taxa than goshawks in California, New Mexico, and Oregon, but size of prey taken by goshawks varied little among geographic locations.

Key Words: *Accipiter gentilis*; Arizona; diet; Northern Goshawk; ponderosa pine.

Habitat alteration by timber harvesting is one of the most significant factors affecting Northern Goshawk (*Accipiter gentilis*) populations (Reynolds 1989). Timber harvesting alters the structure of vegetation in mature forests and may reduce the suitability of stands as nest sites for goshawks (Reynolds 1983). Timber harvesting may also influence prey populations by changing the structure and composition of vegetation in areas where goshawks forage (Moore and Henny 1983). For example, densities of Kaibab squirrels (*Sciurus aberti kaibabensis*) are lower in harvested stands of ponderosa pine (*Pinus ponderosa*) than in uncut stands (Patton et al. 1985), red squirrels (*Tamiasciurus hudsonicus*) decrease up to 80% following thinning (Sullivan and Moses 1986), and golden-mantled ground squirrels (*Spermophilus lateralis*) increase in numbers following timber harvesting (Tevis 1956).

Populations of Northern Goshawks on the North Kaibab Ranger District and elsewhere in the western United States may be declining (Bloom et al. 1986, Kennedy, unpubl. data, Crocker-Bedford 1990, Zinn and Tibbitts, unpubl. data, Reynolds et al. 1992), although the evidence is equivocal. Prey abundance influences the reproductive success of raptors (Newton 1979). Northern Goshawks generally nest in areas with high prey densities (Hantage 1980, Kenward and Widén 1989, Kennedy 1988), and in years when availability of prey is low they experience nest failures (Hantage 1980). Other studies also suggest that the abundance of prey has an important influence on goshawk populations. Schnell (1958) found that days of increased food consumption by nestlings did not correspond with an increased delivery rate of prey, suggesting that foraging rate was controlled by prey abundance rather than food requirements. Wikman and Linden (1981) observed that goshawk numbers declined and brood sizes decreased in response to a reduction in grouse (Tetraoninae), their principal prey species, despite adequate available nesting habitat. Finally, sizes of goshawk ranges are inversely related to prey availability (Kenward 1982).

Northern Goshawks are opportunistic foragers with diets reflecting the diversity of available prey species (Opdam 1975, Widén et al. 1987, Kenward and Widén 1989, Kennedy 1991). Diet information is a principal component of management plans, but goshawk prey varies regionally. Diet studies of individual goshawk populations are necessary to understand their food habits on a regional scale (Storer 1966, Kenward and Widén 1989). Little diet information exists for goshawks in the southwestern United States, and our objective was to document the diet of Northern Goshawks during the breeding season on the Kaibab Plateau, 1990–1992.

STUDY AREA AND METHODS

The study area was on the North Kaibab Ranger District (NKRD), Kaibab National Forest, Coconino County, Arizona. The NKRD is approximately 259,000 ha located on the Kaibab Plateau, and is situated along the northern border of Grand Canyon National Park. The Kaibab Plateau ranges from 923 to 2830 m in elevation. The topography of the Plateau is typified by gentle slopes interspersed with shallow to deep drainages. The Plateau descends to sage flats on the north, east, and west sides, and is bounded by the Grand Canyon to the south. Ponderosa pine forests are found between 2075 and 2500 m elevation and comprise approximately 99,200 ha of the District.

All goshawk nests observed in this study were in stands of ponderosa pine or stands dominated by ponderosa pine. Other overstory trees include quaking aspen (*Populus tremuloids*) and white fir (*Abies concolor*). Gambel's oak (*Quercus gambelii*), New Mexico locust (*Robinia neomexicana*), and Utah juniper (*Juniperus* *osteosperma*) were common understory species found along drainages and slopes in all stands.

We observed eight Northern Goshawk pairs each year in 1990 and 1991, and six pairs in 1992. One pair failed each year, and we obtained insufficient data from the failures in 1990 and 1991 to include them in our analyses. We collected dietary data for the remaining 20 nesting goshawk pairs during 1539 hours of observation ($\bar{X}$ = 76.8 hour/nest ± 19.3 SD); we did not study any nesting pair for more than one successful breeding season.

REPRODUCTIVE SUCCESS

We documented nest site productivity for all nests observed in this study. We estimated hatching and fledging dates when not actually observed and we attempted to date and identify causes of nestling mortalities.

PREY DELIVERIES

We determined food habits by directly observing prey brought to the nest by adult goshawks. Observations at the nest are considered the least biased and most accurate way to assess diet of diurnal raptors (Errington 1930, 1932; Mader 1975; Snyder and Wiley 1976; Zeisemer 1981; Marti 1987; Mersmann et al. 1992; Bielefeldt et al. 1992). The technique, however, does have weaknesses, including: (1) it requires considerable time; (2) the probability of identifying different prey types is not always equal because the prey often are plucked, decapitated, or skinned prior to delivery to the nest; and (3) no information can be collected about the items consumed by adults away from the nest.

We located active goshawk nests from mid-May to early June by visiting historic nest sites in ponderosa pine forests on the NKRD. The only constraints on our selection of nesting pairs to study were that the pair had not been used in previous years of the study, and the nest was situated in such a way that it could be observed from ground or tree blinds. The order of nest observations was randomly selected during the first rotation, and followed the initial order during following rotations until fledging except when the nest failed or weather prevented access to nest sites. We began observations at each nest in the afternoon and continued until sundown, resuming at dawn until the time of initiation the previous day. We observed the nests from cloth blinds located on the ground or in trees a mean distance of 53 m (±17.6 SD) from the nest trees. Blinds were constructed over a 2–3 day period to decrease disturbance to the nesting pair (Fyfe and Olendorff 1976, Marti 1987). We initiated our observations during late incubation or early nestling stages. Approximately 5–7 days after fledging we discontinued observations because prey deliveries often occurred away from the nest.

We identified prey deliveries to species with binoculars and 15–45× spotting scopes. We tabulated the identified prey and used an Analysis of Variance for Ranked Data test (Winer 1971) to investigate variance among nests. We used chi-square tests (Sokal and Rohlf 1981) to examine changes in diet composition on basis of mammal and avian prey, and individual species for which there were sufficient samples, through the nesting season.

We categorized prey into a priori size classes based on Storer's (1966) cubic function size class system. We calculated the mean weights for adult mammalian species from the collection weight of museum specimens in the University of Arizona mammal collection; museum specimens were from various regions throughout their ranges in Arizona. We only used adult weights when calculating average mammal biomass. Weights for adult avian species were taken from Dunning (1984). Estimates of avian weights for the age classes of nestling-fledgling, subadult, and unknown age were computed following Bielefeldt et al. (1992).

We categorized unidentified mammals as being small or large and assigned them the average weight of identified mammals occurring in size classes 1–12 ($\bar{X}$ = 164.8 g ± 61.4 SD) for small mammals, and size classes 13–20 ($\bar{X}$ = 676.4 g ± 42.2 SD) for large mammals. We categorized unidentified avian prey as small, medium, or large and assigned them the average weight of identified birds occurring in size classes 1–3 ($\bar{X}$ = 19.8 g ± 0 SD), 4–6 ($\bar{X}$ = 45.6 g ± 14.1 SD), and 7–8 ($\bar{X}$ = 96.7 g ± 7.2 SD), respectively. We also noted when prey was cached or retrieved from a cache, and excluded the cache retrievals from diet assessment (Johnson 1981).

PREY REMAINS

Goshawks often remove plumage and pelage from their prey in the nest area or at the nest structure. We collected prey remains (i.e., feathers, fur, skin, skeletal parts) found in the nest area following each observation period. We also removed prey remains from nests whenever nest trees were climbed to band nestlings.

We cataloged prey remains to nest number and date of recovery on a master list. We packaged samples and assigned each a random identification number to alleviate observer bias when identifying remains. The master list was referred to only after remains were identified.

We reconstructed mammalian and avian remains following Reynolds and Meslow (1984). Remains were identified by comparison to specimens held in the University of Arizona mammal and avian collections. We excluded single feathers from analysis as they may have come from molting birds.

DIET BREADTH

We examined regional variation in diet breadth between Northern Goshawks in Arizona (this study), California (Bloom et al. 1986), New Mexico (Kennedy 1991), and Oregon (Reynolds and Meslow 1984). We used Levins' (1968) equation

$$B = 1/\sum P_i^2$$

to calculate diet breadths for the niche dimensions of prey taxon and prey size. The value P_i is the proportion of prey in each category, and B ranges from 1 to n, n being the number of categories. If B equals n, prey are used equally from all categories. On the other hand, if B is close to 1, the diet breadth is narrower and categories of prey are not used equally. The number of categories varied among studies. To compare diet

TABLE 1. SPECIES CONTRIBUTING $\geq 5.0\%$ OF THE IDENTIFIED PREY DELIVERED TO NORTHERN GOSHAWK NESTS, NORTH KAIBAB RANGER DISTRICT, KAIBAB NATIONAL FOREST, ARIZONA, 1990–1992

Species	N	Percent observed	Percent biomass
Golden-mantled ground squirrel	86	28.0	14.9
Cottontail rabbit	41	13.3	26.1
Chipmunk	38	12.4	2.0
Steller's Jay	33	10.7	2.7
Red squirrel	31	10.1	5.8
Tassel-eared squirrel	26	8.5	15.0
Rock squirrel	18	5.9	9.8
Northern Flicker	16	5.2	1.5
Total	289	94.1	77.8

breadths among regions we standardized diet breadth values with the equation

$$B_{\text{standard}} = (B - 1)/(n - 1)$$

(Reynolds and Meslow 1984), which allows diet breadths to be compared on a scale of 0 to 1, the larger the value corresponding to increasing breadth of diet.

RESULTS

REPRODUCTIVE SUCCESS

Goshawks had a nestling rate of 2.4 ± 0.7 SD and 2.6 ± 0.5 SD nestlings per active (reached at least incubation) and successful (fledged young) nest, respectively. Forty-two of 53 nestlings survived to fledge, with a fledging rate of 1.9 ± 1.0 SD and 2.2 ± 0.7 SD fledglings per active and successful nest, respectively. We identified Great Horned Owl (*Bubo virginianus*) predation as the principal cause of nestling mortality (45.4%; N = 5) at our study nests, and a likely factor in some of the unidentified causes of death (36.4%; N = 4). The other identified cause of nestling mortality was falling from the nest (18.2%; N = 2).

PREY DELIVERIES

We observed a mean delivery rate of 0.25 prey items/hour, and identified 370 (97%) of the prey items to class. Only mammals (76%) and birds (24%) were delivered to the nest. We identified 241 (89.2%) of the mammal prey items to at least genus. We identified 59 (65.6%) of the avian prey to species, and six to the Family *Picadae* (6.7%); seven mammalian genera and eight avian genera were represented in goshawk diets.

There was no difference in the mean prey rank between nests ($\chi^2 = 5.0$, df = 19, P = 0.99) for prey species contributing $\geq 5.0\%$ of the diet. Thus, we pooled the data from all nests to characterize the diet of the goshawk population. Mammalian prey contributing $\geq 5.0\%$ of the identifiable prey were golden-mantled ground squirrels, cottontail rabbits (*Sylvilagus* spp.), chipmunks (*Tamias* spp.), red squirrels, tassel-eared squirrels (*Sciurus aberti*), and rock squirrels (*Spermophilus variegatus*) (Table 1). Steller's Jays (*Cyanocitta stelleri*) and Northern Flickers (*Colaptes auratus*) were the only avian species contributing $\geq 5.0\%$ of identifiable prey (Table 1).

We found no significant difference in the proportions of mammal and avian prey taken through the nesting season ($\chi^2 = 8.9$, df = 4, P = 0.06) over 10 day intervals. Neither were there significant differences through the nesting season in the proportions of the three most frequent goshawk prey, golden-mantled ground squirrels ($\chi^2 = 14.9$, df = 9, P = 0.09) over 5 day intervals, or cottontail rabbits ($\chi^2 = 4.1$, df = 4, P = 0.39) and chipmunks ($\chi^2 = 5.6$, df = 4, P = 0.23) over 10 day intervals. Insufficient samples prevented analysis of cottontail rabbit and chipmunk use over five day intervals.

PREY BIOMASS

We used only prey delivered to the nest when computing biomass of goshawk prey. Mammals accounted for 94% and birds accounted for 6% of the biomass in goshawk diets. Only mammals contributed $\geq 5.0\%$ of the biomass, with cottontail rabbits, golden-mantled ground squirrels, and tassel-eared squirrels accounting for most of the biomass (Table 1).

PREY REMAINS

Mammals accounted for 47.5% and birds accounted for 52.5% of the remains collected (N = 179) at the 20 study nests. Cottontail rabbits (N = 49), Steller's Jays (N = 47), and Northern Flickers (N = 22), the three species represented most frequently in remains, accounted for 65.6% of all remains.

DIET BREADTH

Though goshawks from different regions have similar diet breadth, the goshawks on the NKRD use the available prey slightly less equitably than goshawks in the other regions (Table 2). Size class of prey used by goshawks on the NKRD was also

TABLE 2. STANDARDIZED FOOD NICHE BREADTH OF BREEDING NORTHERN GOSHAWKS IN ARIZONA, CALIFORNIA, NEW MEXICO, AND OREGON BASED ON NUMBER OF PREY GENERA

		Food niche breadth		
	Nests	Prey genera[1] (total no. genera)	Size class (total no. classes)	Source
Direct observation				
Arizona	20	0.32 (15)	0.33 (9)	This study
New Mexico	8	0.62 (9)	0.47 (6)	Kennedy (1991)
Prey remains				
Arizona	20	0.29 (18)	0.25 (11)	This study
California	114	0.41 (21)	0.30 (12)	Bloom et al. (1986)
New Mexico	8	0.36 (22)	0.39 (10)	Kennedy (1991)
Oregon	4	0.42 (30)	0.38 (14)	Reynolds and Meslow (1984)

[1] We pooled *Sphyrapicus* and *Picoides* due to difficulty in distinguishing between them during direct observations.

similar to the goshawks from other regions (Table 2).

DISCUSSION

REPRODUCTION

We studied nests that were active and in late incubation or early nestling stages. Thus, our data on reproduction do not take into account goshawk nests that failed prior to reaching at least late incubation. Nor did we determine the frequency of failed eggs in successful nests. Though it is uncommon for accipiters to experience reproductive losses early in the breeding cycle (Snyder and Wiley 1976), there is a potential bias in our observed rate of 1.9 fledglings per active nest.

Nestling goshawks in successful nests on the NKRD have a high probability (84%) of fledging. Mortality at our study nests appeared to be related to factors other than food availability. For example, Great Horned Owl predation was the single greatest factor contributing to nestling mortality. Only one of the three nesting failures we observed was due to factors other than predation. Eggs in this nest failed to hatch in 1990, but the same nest produced 2–3 young in the following years. One possible cause of the failure was disturbance by a slash cutting crew operating within 100 m of the nest for ≥2 days during incubation. This disturbance may have kept the female away from the nest long enough to allow the eggs to chill.

Our data suggest that food availability was not limiting goshawk productivity at the active nests we studied in ponderosa pine forests on the NKRD during 1990–1992.

PREY FREQUENCY AND BIOMASS

Northern Goshawks purportedly possess an inherent inclination to prey on avian species (Sutton 1925). This suspected proclivity has been supported by numerous studies of diet during the breeding season in which avian prey accounted for ≥55% of the diet (Meng 1959, Opdam 1975, Reynolds and Meslow 1984, Bloom et al. 1986, Widén et al. 1987). These studies used the indirect methods of pellet analysis and/or prey remains identification to determine goshawk diets. Many early anecdotal accounts of goshawk nesting behavior, however, suggest that goshawks take a greater proportion of mammals than these studies indicate (Sutton 1925, Gromme 1935, Dixon and Dixon 1938).

Our data, based on direct observations, indicate a 3:1 mammal to avian ratio in the diets of goshawks in our study on the NKRD. To our knowledge, this is the largest proportion of mammals reported in the diet of a breeding goshawk population. In addition, mammals accounted for 94% of the biomass due to the larger body size of most mammalian prey compared to avian prey. The high use of mammalian prey may be a phenomena associated with the forest structure and available prey found in our study area, or it may be common to the species across its range but only apparent through direct methods of diet analysis (Boal and Mannan, unpubl. data).

Reynolds et al. (1992) recommended that habitat for Northern Goshawks be managed for the 14 prey species that are consistently used by goshawks. Although preliminary information from our study was part of the database used to develop the management recommendations, our final results further support this aspect of the recommendations. All 14 of the listed species occurred in goshawk diets on the NKRD. In addition, six of the seven species accounting for ≥5% of the goshawk diets on the NKRD are among the 14 listed prey species in the management recommendations. The single exception is rock squirrels, which the recommendations list as a potential prey species for which importance is unknown (Reynolds et al. 1992).

Goshawks on the NKRD use the available prey less equitably than is reported elsewhere. This is probably a reflection of predation on golden-mantled ground squirrels at a rate of >2:1 over any other species. Ground squirrels are undoubtedly an important part of goshawk diet during the nesting season. A dependence upon one prey species could conceivably lead to a decline in a predator population if that prey species declined (Dymond 1947, Craighead and Craighead 1956, McGowan 1975, Newton 1979). We think this is unlikely on the NKRD because the prey base of goshawks, though inequitably used, is varied (≥19 species) and is likely to buffer affects of individual prey species fluctuations. The inequitable pattern of predation may be a functional response to the most abundant or available prey species, which appears to have been the golden-mantled ground squirrel during this study. It is possible that during periods when ground squirrels are less abundant, goshawks shift to other species that may be more abundant. Long-term studies of goshawk diet and long-term monitoring of the abundance of prey populations will be necessary to address this issue.

ACKNOWLEDGMENTS

We thank B. Baker, B. Bibles, E. Bibles, R. Brown, M. Collins, N. Karnovsky, and E. Steadman for assistance with the field work; D. Smith for his help and logistical support with our concurrent studies; and R. Reynolds and his crews for assistance and logistical coordination of our concurrent studies. V. Meretsky provided much appreciated guidance with the statistical analysis. The North Kaibab Ranger District and the Arizona Game and Fish Department provided housing and logistical support. P. Krausman, W. Shaw, and two anonymous reviewers provided many valuable suggestions on the manuscript. This study was funded by a challenge-cost-share agreement between the USDA Forest Service, Southwestern Region, and the University of Arizona. Additional funding was provided by Kaibab Forest Products, the Arizona Wildlife Federation's Michael Halle Award, and the Arizona Falconer's Association.

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Studies in Avian Biology No. 16:103–105, 1994.

Population Ecology

BREEDING BIOLOGY OF NORTHERN GOSHAWKS IN NORTHEASTERN OREGON

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Abstract. Ten of 25 historical Northern Goshawk (*Accipiter gentilis*) nest stands in Wallowa County had active nests in 1992. Young fledged at 10 of 12 nests at an average of 1.4 young per successful nesting attempt, or 1.2 young for all nests. Incubation occurred in late April and May, and nestlings were present in June and July. The earliest and latest fledging dates were 22 June and 27 July; the mean fledging date was 8 July. All nests were in old growth or remnant old-growth stands; however, most of the stands searched were old growth. Nest trees averaged 65 cm diameter at breast height and 34 m tall. Diet determined from prey remains consisted of 58.5% birds and 41.5% mammals.

Key Words: *Accipiter gentilis*; breeding biology; Northern Goshawk; northeastern Oregon.

The Northern Goshawk (*Accipiter gentilis*) has generated interest throughout the western United States because there is concern that populations and reproduction of this species are declining (Reynolds et al. 1992). In addition, the Northern Goshawk has been designated as a Management Indicator Species, and the National Forest Management Act regulations require that such species be monitored. Therefore, site specific information on breeding biology is needed to monitor populations of this species. Our objectives were (1) to search historical goshawk nest sites to ascertain how many still had active goshawk nests, and (2) to determine nesting chronology, nest habitat characteristics, and diet during the breeding season.

METHODS

STUDY AREA

The study was concentrated in 42 stands that ranged in size from 10 to 109 ha; these stands were contained within a 350,000-ha area on the Wallowa Valley Ranger District and adjacent portions of the Eagle Cap Ranger District and Hells Canyon Natural Recreation Area, Wallowa County, northeastern Oregon. The study areas were a mixture of stands including ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), grand fir (*Abies grandis*), and Engelmann spruce (*Picea engelmannii*). Elevations within the study areas range from 1200 m to 1800 m, and topography varies from flat to steep canyons.

NEST LOCATION AND HABITAT

To locate active Northern Goshawk nests, we searched 25 historical goshawk nest stands and 17 additional stands containing old growth. A historical nest stand was one where goshawks had nested at least once in the last 20 years based on records kept by the Wallowa Valley Ranger District. Additional sites were selected on the basis of having a stand with >12 trees/ha that were >50 cm dbh, with >60% canopy closure, and >10 ha in size. Stand boundaries were delineated by changes in successional stages. Only the blocks of forest that met the criteria listed above were searched.

Searches for nests were conducted between 16 April and 17 July 1992; however, the majority of the search effort occurred in May and June. We used a silent search and a broadcast of taped calls to search for nests. We searched 75% of the stands with the silent search technique where we walked through the stand looking for nest platforms, white-wash, prey remains, and goshawks. Approximately one person-day was spent searching stands >40 ha in size, and one-half a person-day was spent in smaller stands.

In the remainder of the stands we broadcast adult alarm calls (Kennedy and Stahlecker 1993) at stations about 400 m apart. This distance was used because we determined that the tape could be heard 200 m away. At each station, three calls were broadcast; each call was 10-sec long and 1-min apart. The speaker was oriented at 60°, 180°, and 300° during the calls. We did not use broadcast calls more extensively because the majority of our searching was done when the birds were presumed to be incubating, and birds are not likely to respond to calls during this period (Kennedy and Stahlecker 1993).

Active nest trees (terms defined in Reynolds et al. 1992) were revisited every 1–2 weeks to determine nesting chronology. If there was evidence of occupancy by goshawks (e.g., birds seen, prey remains, white-wash) but no nest was found, the stand was revisited in 2–4 weeks.

At each active nest tree, we recorded tree species, condition (live or dead), diameter at breast height (dbh), and height; exposure of nest (north = 316–45°, east = 46–135°, south = 136–225°, west = 226–315°); and height of nest above ground. In 1 ha around the nest tree, forest type, logging activity, successional stage, canopy closure, landform, slope aspect, and gradient were measured. We climbed seven of the nest trees and recorded: length, width, and depth of the nest structure; depth of the nest cup; and distance of the nest from the bole of the tree.

Forest type was classified using Johnson and Clausnitzer (1992): (1) ponderosa pine, (2) Douglas-fir, or (3) grand fir. Logging activity was classified as high-graded (logging where only the valuable trees are removed, but the majority of the stand is left), selective (partial overstory removal), and clearcuts and shelterwoods. Clearcuts and shelterwood harvests were combined because neither silvicultural technique leaves habitat structure usable for nesting for many decades. Successional stages were defined as (1) young, trees <30 cm dbh; (2) mature, most trees 30–50 cm dbh; (3) old growth, >12 trees/ha that were >50 cm dbh, >60% canopy closure, and >1 canopy layer; and (4) remnant, some trees >50 cm dbh in the stand but not enough to classify as old growth. Canopy closure was measured with a spherical densiometer. Slope gradient was measured with a clinometer.

Diet and Plucking Posts

We searched for prey remains and pellets within 0.3 km of each nest. All prey remains found in one day of searching at each nest were combined to reduce the chance of counting the same prey item twice (Reynolds and Meslow 1984); however, this method may underestimate common prey types relative to rare prey types (C. Zabel, pers. comm.). Prey remains were identified later with the assistance of skull keys and museum collections.

Places where prey remains were found were called plucking posts. We recorded type of perch (e.g., log, stump, branch), perch height, distance from the nest, tree species, dbh, and condition (live or dead) at each plucking post.

RESULTS

Nesting

Of 25 historical sites searched, 23 had suitable habitat and two had been logged. Ten of the 25 sites had active nests in 1992. Two other active nests were found in the additional 17 stands searched.

The 12 active nests were located between 10 April and 15 July. Five nests were found with defensive adults, three with incubating females, three with nestlings, and one with fledglings. The two nests that failed were found when adults were defensive, and incubating females were seen on the nests before they failed.

Incubation typically started in late April and early May. Nestlings were present in June and early July. The mean fledging date was 8 July among five nests where we knew approximate dates. The earliest fledging date was about 22 June, and the latest was 27 July.

Juveniles fledged from 83% of the nests. Fourteen young fledged from the 10 nests, for an average of 1.4 young produced per successful nest or 1.2 young per nesting attempt. At least two young died before fledging; we could not determine if additional young died because we did not climb to the nests until young were ready to fledge.

Ten of the 12 nest trees were in old-growth stands that either had not been logged or had been high-graded in the past. The remaining two nest trees were in stands that had only remnants of old growth because they had been partially logged. Nine nest trees were in a grand fir forest type, two were in a Douglas-fir type, and one was in a western larch-lodgepole pine-spruce type. The average canopy closure was 81% (SD = 6.9%). Nine nest trees were on the lower third of a slope, and the remainder were at midslope. Slope gradient averaged 31% (SD = 21.2%). Nine nest trees were on a north- or east-facing slope. The average distance from the nest to the nearest water was 70 m (SD = 72.0). None of the nests were >200 m from water. Stands containing an active nest averaged 43 ha (SD = 34.0) in size.

Seven nest trees were Douglas-fir, three were western larch, and two were grand fir. All but two of the trees were alive. Average dbh and height of the nest trees were 65 cm (SD = 23.5) and 34 m (SD = 7.3), respectively. Average nest height was 15 m (SD = 3.3). Aspect of the nest on the tree was south or west at 10 nests and north or east at two nests.

The actual nest platform averaged 94 cm (SD = 18.5) in length, 66 cm (SD = 20.3) in width, and 36 cm (SD = 12.4) in depth. The depression inside the nest averaged 24 cm (SD = 7.0) in length, 21 cm (SD = 4.0) in width, and 8 cm (SD = 7.6) in depth.

Diet and Plucking Posts

We identified 94 prey items collected at nine nests; 58.5% were birds and 41.5% were mammals (Table 1). We collected between one and 32 prey items at each nest. American Robins comprised the majority (29%) of the birds found, and snowshoe hares comprised the majority (33%) of the mammals.

Forty-three plucking posts were found around nest sites; 51% were in trees, 33% on logs, 14% on stumps, and 2% on rocks. Of the standing trees, 63% were live and the remainder dead. Mean dbh and perch height of the standing trees were 32 cm (range = 8–75 cm) and 2.1 m (range = 0.8–4 m), respectively. The type of perch at these trees was a leaning tree trunk (55%), a branch (32%), or the top of the trunk where it had broken off (13%). Logs used as plucking posts averaged 59 cm in diameter (range = 16–110 cm). Perching height on logs averaged 0.5 m (range = 0.2–1.0 m) above the ground because logs were elevated. Three of the plucking posts on stumps were western larch; the remainder could not be identified. Mean diameter and perching height of stumps were 67 cm (range = 40–90 cm) and 0.6 m (range = 0.3–1.0 m), respectively.

Plucking posts typically were clustered around the nest tree, although we did not search >0.3 km from the nest. The distance between nests

TABLE 1. PREY REMAINS AND FREQUENCY (%) COLLECTED AT NINE NORTHERN GOSHAWK NEST SITES IN WALLOWA COUNTY, OREGON, 1992

Prey	N[1]	Birds or mammals (%)	Total (%)
Birds			
American Robin (*Turdus migratorius*)[2]	16	29.0	17.0
Northern Flicker (*Colaptes auratus*)	8	14.6	8.5
Western Meadowlark (*Sturnella neglecta*)	7	12.7	7.5
Western Tanager (*Piranga ludoviciana*)	4	7.3	4.3
Clark's Nutcracker (*Nucifraga columbiana*)	4	7.3	4.3
Steller's Jay (*Cyanocitta stelleri*)	3	5.5	3.2
Gray Jay (*Perisoreus canadensis*)	3	5.5	3.2
Hairy Woodpecker (*Picoides villosus*)[3]	3	5.5	3.2
Ruffed Grouse (*Bonasa umbellus*)	2	3.6	2.0
Dark-eyed Junco (*Junco hyemalis*)	2	3.6	2.0
Long-eared Owl (*Asio otus*)	1	1.8	1.1
Black-headed Grosbeak (*Pheucticus melanocephalus*)	1	1.8	1.1
Northern Goshawk (*Accipiter gentilis*)[4]	1	1.8	1.1
Total	55	100.0	58.5
Mammals			
Snowshoe hare (*Lepus americanus*)	13	33.3	13.8
Ground squirrels[5]	12	30.8	12.8
Red squirrel (*Tamiasciurus hudsonicus*)	11	28.2	11.7
Yellow pine chipmunk (*Tamius amoenus*)	3	7.7	3.2
Total	39	100.0	41.5

[1] Represents number of individuals.
[2] Also may have included Varied Thrush (*Ixoreus naevius*).
[3] Also may have included sapsuckers.
[4] Remains of a nestling were found in pellets at the base of a nest.
[5] Columbian ground squirrels (*Spermophilus columbianus*) comprised 33% of these; the remainder could not be identified to species.

and plucking posts averaged 42 m (range = 7–200 m).

DISCUSSION

We found active nests in ten of the 23 historical nest stands that we considered still suitable. Adult Northern Goshawks were seen in two suitable stands where we did not find nests. Consequently, about half the suitable stands we searched had nests or adults. Because we subjectively selected our stands, our findings do not necessarily indicate a preference for old growth. However, all the goshawk nests we located were in large-diameter trees, which are characteristic of old-growth stands.

The nesting pairs were productive with 83% of the nests successful and an average of 1.2 young fledged per nesting attempt. Similarly, Reynolds and Wight (1978) reported 1.7 young fledged per nesting attempt in Oregon during 1969–1974. The diet we determined from prey remains was similar to that reported by Reynolds and Meslow (1984) in Oregon (55% birds and 45% mammals).

ACKNOWLEDGMENTS

We thank P. Talbot for assistance with field work. R. Anderson, K. Martin, and other employees at the Wallowa Valley Ranger District provided additional assistance. J. Crawford, L. Alexander, and E. Forsman assisted with prey identification, and the Department of Fisheries and Wildlife at Oregon State University allowed us to use their museum collection. B. Jackson and L. Goebel kindly allowed us to observe an active nest on their land. Funding was provided by the USDA Forest Service, Pacific Northwest Region—Fish and Wildlife, Pacific Northwest Research Station, and Wallowa Valley Ranger Station.

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NEST PRODUCTIVITY, FIDELITY, AND SPACING OF NORTHERN GOSHAWKS IN ARIZONA

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Abstract. Distribution of nests, nest success and productivity, mate and site fidelity, and diets of Northern Goshawks (*Accipiter gentilis*) were examined on the Kaibab Plateau, Arizona, in 1991–1992. A total of 98 nest attempts was studied, 92 in the Kaibab National Forest and six in Grand Canyon National Park. Of 36 nests in which eggs were laid in 1991, 34 produced young ($\bar{X}$ = 2.15 young/successful nest) and of 59 nests in which eggs were laid in 1992, 49 produced young ($\bar{X}$ = 2.16 young/successful nest). In 1991, 49 adults were banded at nests, including both adults at 21 nests. In 1992 both adults were recaptured at 10 of these 21 nests. At six (60% of 10) of these nests, both adults remained paired and five produced the same or more fledglings in 1992. Three (6% of 49) nesting hawks banded in 1991 moved to new territories in 1992 and each fledged one more young in 1992 than in 1991. The proportion of nesting adults banded in 1991 that were replaced by new hawks at 1992 nests was 23%. In 1992, nine (9.7% of 93) nesting hawks were classed as "young-adult" based on plumage characteristics; young-adults produced significantly fewer fledglings than full adults.

Mean distance between nearest neighboring nests in 1992 was 3.0 km (range = 1.6–6.4 km, N = 59 nests). Alternate nests were used between years in 17 of 34 territories; mean distance between the original and alternate nests was 266.4 m (SD = 157.0 m). Diets in 1991 were composed of 62% mammals and 38% birds by number, and 84% mammals and 16% birds by biomass.

Key Words: *Accipiter gentilis*; Kaibab Plateau; mate and territory fidelity; morphometrics; Northern Goshawk; population; productivity.

The Northern Goshawk (*Accipiter gentilis*) is holarctic in distribution. The North American subspecies (*A. g. atricapillus*) occurs from the northeastern United States across the boreal forests of Canada to Alaska and southward through the montane forests of western United States to northern Mexico (Wattel 1973). The Northern Goshawk nests in most of the coniferous, deciduous, and mixed coniferous-deciduous forests that occur within its range. Northern Goshawks prey on 20 or more species of birds and mammals within nesting home ranges of 15–31 km^2 (Schnell 1958, Meng 1959, Reynolds 1983, Reynolds and Meslow 1984, Bright-Smith and Mannan, this volume).

The Northern Goshawk is listed as a "sensitive species" by the USDA Forest Service Southwestern Region because of potential threats of forest management (e.g., tree harvests, fire suppression, and grazing) to the hawk's nesting and foraging habitats (Reynolds et al. 1982, Herron et al. 1985, Bloom et al. 1986, Reynolds 1989, Crocker-Bedford 1990, Reynolds et al. 1992). In fact, several authors (Herron et al. 1985, Bloom et al. 1986, and Crocker-Bedford 1990) suggest that Northern Goshawk populations have recently declined in Nevada, California, and Arizona due to habitat loss. Crocker-Bedford (1990), for example, estimated that there were 260 pairs of Northern Goshawks on the 120,000 ha North Kaibab Ranger District before timber harvesting began in the 1950s. By 1972, following "light partial" tree harvesting over most of his study area, the number of pairs declined to 130, and to probably half of that in 1988 after the introduction of a more intensive harvesting (Crocker-Bedford 1990).

In 1991 we began a long-term study of individual and population responses of Northern Goshawks to tree harvest and other forest management practices on the Kaibab Plateau. Our objective is to determine the effects of management by measuring Northern Goshawk response variables (e.g., distribution and density of nests, nest success and productivity, diets and prey populations, mate and territory fidelity, time budgets, home range characteristics, and mortality factors) to changes in habitat resulting from forest management. Here we report on nest dispersion, nest success and productivity, mate and territory fidelity, morphometrics, and diets of Northern Goshawks on the Kaibab Plateau in 1991–1992.

METHODS

STUDY AREA

The study area encompassed the coniferous forests on the Kaibab Plateau in northern Arizona. The Kaibab Plateau is an oval-shaped (95 km × 55 km), limestone plateau that rises from a shrubsteppe plain (elevation 1750 m) to a maximum elevation of 2800 m (Rasmussen 1941). It is bounded by escarpments and steep slopes that descend into the Grand Canyon of the Colorado River on its southern half and by more gentle slopes that descend to the shrubsteppe plain on its northern half. Total area covered by forests in the study area, including the Grand Canyon National Park

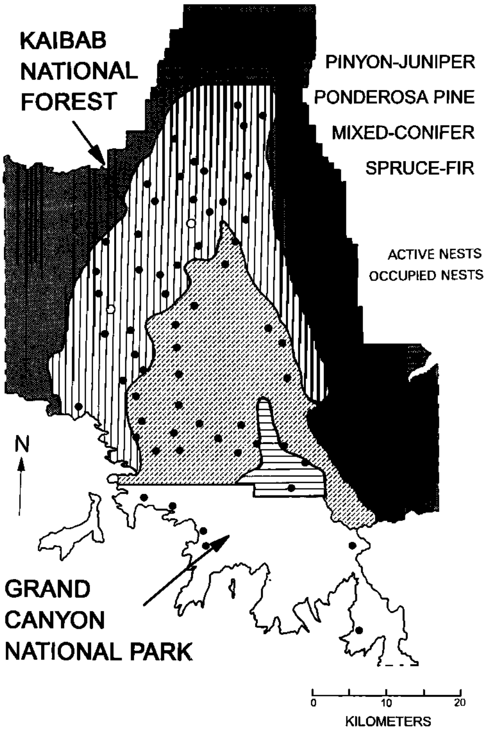

FIGURE 1. Forest types and nest locations of Northern Goshawk on the Kaibab Plateau, including the North Kaibab Ranger District and the Grand Canyon National Park, in 1992 (forest types in the National Park not mapped).

and North Kaibab Ranger District, is about 320,600 ha. Pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodlands occur at lower elevations (1830–2075 m) on the Plateau and occupy about 176,000 ha. Ponderosa pine (*Pinus ponderosa*) forests occur between 2075–2500 m elevation and occupy about 99,200 ha, and mixed-conifer forests (*P. ponderosa, Abies concolor, Pseudotsuga menziesii, Picea engelmannii,* and *Populus tremuloides*) occur above 2500 m, occupying about 45,400 ha (Rasmussen 1941) (Fig. 1). Annual precipitation averages 67.5 cm, with winter snowpacks of 2.5–3.0 m. Mid to late summers are characterized by frequent (2–4 per week) thunderstorms and heavy showers.

The Kaibab Plateau was isolated from established railroad heads in the late 1800s and early 1900s. Thus, forests on the Kaibab Plateau were not subjected to the heavy logging that typically occurred in montane areas on the Colorado Plateau and elsewhere in the southwestern United States during this period (Pearson 1950, Laudenslayer et al. 1989, J. Hanson, pers. comm.). Organized tree harvests did not begin on the Kaibab Ranger District until 1923 and were limited to single-tree cutting to remove dead and dying trees (sanitation cutting) (Burnett 1991). In the late 1960s clear-cutting began in the mixed-conifer forests (total = 922 ha) but was discontinued in the early 1970s; single-tree cutting in ponderosa pine continued through the mid-1980s. Intensive management at the forest stand level began in the mid-1980s with even-aged silvicultural treatments in the pine and mixed-conifer forests; these even-aged treatments continued until 1991. From the 1940s to 1990, the total volume of wood removed from the Ranger District increased by a factor of 5, from 9077 to 48,412 boardfeet per ha (1992 Kaibab National Forest Timber Atlas, J. Ellenwood, pers. comm.). While the early sanitation cutting occurred over much of the North Kaibab Ranger District, the application of stand level management beginning in 1986 resulted in a reduction of the total area harvested (1986–1991) to 12,632 ha, about 14% of the Ranger District (1992 Kaibab National Forest Timber Atlas, J. Ellenwood, pers. comm.).

The suppression of naturally frequent ground fires on the Kaibab Plateau since the 1910s has resulted in an increase in the number of small trees ($\leq$29.4 cm in diameter at breast height) per ha by a factor of almost eight in ponderosa pine forests and by a factor of 11 in mixed-conifer forests (1992 Kaibab National Forest Timber Atlas, J. Ellenwood, pers. comm.). In 1991, due to concerns for the Northern Goshawk population on the Plateau, the focus of management shifted from the level of the stand to small (0.1–1.6 ha) groups of trees combined with an area-wide thinning of the small, understory trees (Reynolds et al. 1992). The objective of this management was to move the ponderosa pine and mixed-conifer forests on the Ranger District toward the species composition and structure that existed prior to fire suppression and intensive tree harvests (Reynolds et al. 1992).

NESTS, MORPHOMETRICS, DIETS, AND MOVEMENTS

To locate active (containing eggs or young) Northern Goshawk nests, we visited all previously documented nests (Goshawk Nest Records, 1990–1992, Arizona Game and Fish Department, Phoenix, Arizona, and North Kaibab Ranger District, Fredonia, Arizona), searched for new nests on foot (Reynolds 1982), and used a vocalization broadcast technique (Joy et al. *this volume*). Each year nest visits and searches were begun in May and continued through August. Broadcast surveys were conducted daily between 08:00 and 16:30 MDT (Joy et al. *this volume*). All nests of Northern Goshawks, and their potential competitors and predators, Cooper's (*A. cooperii*), Sharp-shinned (*A. striatus*), and Red-tailed (*Buteo jamaicensis*) hawks, and Great Horned Owl (*Bubo virginianus*) found were recorded on 7.5-minute USGS topographic maps. We used the Universal Transverse Mercator (UTM) coordinates of all nests to determine the distances between alternate Northern Goshawk nests (nests used in subsequent years by a pair) and to calculate nearest-neighbor distances among nests. Nearest-neighbor distances were the straight-line distances between each active nest and its closest neighbor. Calculation of nearest-neighbor distance included duplicate measures between reciprocal nearest neighbors (Diggle 1983).

The fates of nests (successful = fledged $\geq$1 young) and nest productivity (number of fledglings produced) were determined by weekly visits to nests. Adults were captured at nests in dho-gaza traps baited with live Great Horned Owls (Bloom 1987). Away from nests,

TABLE 1. Number of Nests of *Accipiter* Found on the Kaibab Plateau, 1991–1992

Year	Species	Nest search technique: Visits to historic nests	Broadcast survey	Foot search	Total
1991	Northern Goshawk	28	5	4	37
	Cooper's Hawk	0	3	4	7
	Sharp-shinned Hawk	0	7	1	8
1992	Northern Goshawk	40	8	13	61
	Cooper's Hawk	5	2	1	8
	Sharp-shinned Hawk	3	3	2	8

adults and juveniles were captured with 5–6 "falling-end" Swedish goshawk traps (Kenward and Marcström 1983) that were baited with domestic pigeons (*Columba livia*) and placed at about 1 km intervals. Swedish goshawk traps were also placed at nests to capture fledglings. All hawks were fitted with U.S. Fish and Wildlife Service aluminum leg bands and anodized aluminum color leg bands with unique alpha-numeric codes. Bands were read from blinds in nest areas or when the hawks were recaptured. Age classes (immature, young-adult, or adult) were determined by plumage characteristics (Bond and Stabler 1941, Stabler 1943) and sex by body mass (see below). Morphometrics of adults included body mass, wing chord, tail, tarsometatarsal length, and condition (good, moderate, or poor based on breast muscle assessment).

Accipiter remove pelage and plumage from their vertebrate prey in the nesting area and on the nest itself. In addition, these hawks regurgitate pellets that contain keratinous body parts of prey. On each visit to a nest, all prey remains and pellets were completely collected. During identification, remains in a day's collection from a nest were lumped and reconstructed by matching the remiges, rectrices, and bills of birds, and the fur, skull parts, and feet of mammals (Reynolds and Meslow 1984). This procedure estimates the minimum number of individuals of each species in a collection (Reynolds and Meslow 1984). Estimates of body mass of birds and mammals in diets were from the literature and museum specimens. We assigned the mass of young prey to be one-half of their adult mass. The mass of prey that could be identified only to genus was determined by averaging mass of all members of that genus in our study area (Reynolds and Meslow 1984). Prey remains collected in 1992 have not been identified and we present only the 1991 diet data.

To determine post-fledging movements and dispersal of Northern Goshawks, 13 adults and 15 fledglings were fitted with tail-mounted (Kenward 1978) and backpack (Kenward 1985) transmitters weighing 6 g ($\leq$0.8% of body mass). We attempted to locate radio-tagged adults and juveniles once a week from the ground in late summer and early fall and from aircraft during winter (2 flights/year).

RESULTS

Nest Numbers, Nest Productivity, and Morphometrics

A total of 37 occupied Northern Goshawk nests (nests at which adults were observed on two or more occasions during a breeding season) were located on National Forest lands on the Kaibab Plateau in 1991; 28 (76%) of these were located during visits to historic nests, five (13%) during broadcast surveys, and four (11%) during foot searches (Table 1). Active nests of seven Cooper's Hawks and eight Sharp-shinned Hawks were also located during searches and broadcast surveys. In 1992, 61 occupied Northern Goshawk nests were found, 55 nests on National Forest and six on National Park lands. Of these 61 nests, 40 (66%) were found during visits to historic nest areas (including 1991 nests), eight (13%) during broadcast surveys, and 13 (21%) during foot surveys. Three additional Cooper's Hawk nests and five additional Sharp-shinned Hawk nests were found (Table 1).

Of the 2-year total of 98 occupied Northern Goshawk nests, 83 pairs (85%) fledged young, three pairs (3%) either did not lay a clutch or lost their clutch in early incubation, six clutches (6%) were lost during incubation, and six (6%) nests failed during the nestling period. Among active nests there was no significant difference in the rate of nest failure in the two years (one of 34 [5.6%] nests failed in 1991 and 10 of 59 [16.7%] nests failed in 1992) (Fisher's exact test, N = 93, P = 0.13), nor were there significant differences in the mean number of young fledged in the two years per occupied (Fisher's exact test, N = 98, P = 0.26), active (Fisher's exact test, N = 95, P = 0.23), or successful (Fisher's exact test, N = 83, P = 0.44) nests (Table 2). For both years modal brood size was two, with one fledgling produced at 13 successful nests (16%), two at 44 nests (53%), and three at 26 nests (31%). All but three (8%) of the 37 occupied nests (or alternate nests) in 1991 were reoccupied in 1992. Broadcast and foot searches for active, alternate nests within 2 km of these three nests in 1992 were unsuccessful.

Nestling Northern Goshawks fledged between 7–25 July and eggs hatched between 31 May and 16 June. Assuming a 30–32 day incubation period (Reynolds and Wight 1978), egg-laying occurred in late April and early May. Combining

TABLE 2. FLEDGLINGS PRODUCED PER OCCUPIED, ACTIVE, AND SUCCESSFUL NORTHERN GOSHAWK NESTS ON THE KAIBAB PLATEAU, 1991–1992

	1991			1992		
	$\bar{X}$	SD	N	$\bar{X}$	SD	N
No./occupied nest	2.0	0.83	37	1.7	1.08	61
No./active nest	2.0	0.77	36	1.8	1.05	59
No./successful nest	2.2	0.61	34	2.2	0.72	49

years, the sex ratio of nestlings just prior to fledging for 23 broods was 23 males to 27 females, not significantly different from a 1:1 ratio (Fisher's exact test, N = 50, P = 0.58).

In 1991–1992 we captured and banded 76 fledglings (hatching year), one second-year hawk (after hatching year), and 93 adults (44 males, 49 females). Three (6.8%) males and six (12.2%) females were in the young-adult plumage class (after second year). All of these young adults nested in 1992, and each was paired to an adult hawk. The mean number of fledglings produced by the young-adult females ($\bar{X}$ = 1.0 fledglings, SD = 0.89, N = 6) was not significantly different from the mean produced by the young-adult males ($\bar{X}$ = 1.3 fledglings, SD = 1.33, N = 3) (Fisher's exact test, N = 9, P = 0.71). However, the production of fledglings at active nests of young-adult to adult pairings was significantly less than the production of fledglings at active nests of adult-to-adult pairs ($\bar{X}$ = 1.1 fledglings, SD = 0.9 vs. $\bar{X}$ = 2.3 fledglings, SD = 0.8, N = 21) (Fisher's exact test, N = 30, P = 0.01).

All but four adults were captured with dhogaza nets. The exceptions (three males, one female) were captured in Swedish traps (98 trap-hours/capture). Four juveniles (one male, three females) were also captured in Swedish traps (77 trap-hours/hawk). There were no significant differences between years in the frequency of adults trapped with either method in the three condition classes (Fisher's exact test: males, N = 50, P = 1.00; females, N = 63, P = 0.51). There was a total of three nesting adult males (one in 1991, two in 1992) and five adult females (two in 1991, three in 1992) in the "poor condition" class. All hawks in poor condition were paired with birds in "moderate" or "good" condition. Mean number of fledglings produced per successful nest of pairs with a hawk in poor condition ($\bar{X}$ = 2.3 fledglings, SD = 0.52, N = 6 pairs) and pairs in which both adults were in moderate to good condition ($\bar{X}$ = 2.2 fledglings, SD = 0.73, N = 38) were not significantly different (Fisher's exact test, N = 44, P = 0.62). Also, nest success of pairs with a hawk in poor condition (six of eight pairs, 75%) did not differ from pairs in which both adults were in moderate to good condition (38 of 40 pairs, 95%) (Fisher's exact test, N = 48, P = 0.12).

Overlap between the sexes occurred for all morphometrics (body mass, wing chord, tail length, tarsometatarsal length) except body mass (Table 3). Mean wing chord and tail length were larger and mass smaller for Northern Goshawks on the Kaibab Plateau than for migrating birds in Wisconsin (Mueller et al. 1976). However, variation in all morphological measurements from hawks on the Kaibab Plateau was less than for Northern Goshawks in Wisconsin. Wing chords of Northern Goshawks on the Kaibab Plateau were also longer than for adults of the

TABLE 3. MEASUREMENTS OF BODY MASS, TAIL, WING, AND TARSOMETATARSUS LENGTH OF ADULT NORTHERN GOSHAWKS ON THE KAIBAB PLATEAU, 1991–1992

Variable	$\bar{X}$	SD	Max.	Min.	N
		Males			
Mass (g)	704.4	32.7	774.0	631.0	45
Tail (cm)	23.5	1.1	28.7	21.3	45
Wing (cm)	34.2	0.7	36.2	32.4	45
Tarsometatarsus (mm)	81.4	3.5	87.7	73.8	45
		Females			
Mass (g)	985.5	51.9	1100.0	907.0	49
Tail (cm)	27.7	0.9	29.0	24.7	49
Wing (cm)	37.3	0.9	38.9	35.0	49
Tarsometatarsus (mm)	88.2	4.4	94.9	79.1	49

subspecies *A. g. laingi* reported by Johnson (1989).

MATE FIDELITY, TERRITORY FIDELITY, AND NEST PRODUCTIVITY

Both members of pairs were banded at 21 nests in 1991. In 1992, both sexes were recaptured at 10 of the 21 nests. At six of the 10 nests both sexes remained paired, at two nests one of the original pair was replaced by a new hawk (one new male, one new female), and at two nests both members of the original pair were replaced by new hawks (at one of these nests both replacement hawks had been banded in 1991 at two different nests).

In 1992, all (six) banded pairs that renested on their 1991 territory (in the same or alternate nest, see below) successfully fledged young in 1991 ($\bar{X}$ = 1.8 fledglings, SD = 0.8), and all but one of these pairs produced the same (two pairs) or more (three pairs) fledglings in 1992 ($\bar{X}$ = 2.3 fledglings, SD = 0.5). The exception produced three fledglings in 1991 and two in 1992. In addition there were ten other nests at which only one adult (either the 1991-banded adult or its replacement) was captured in 1992. At these ten nests, one male and none of the females were replaced. Productivity at the nest where replacement occurred decreased from three to zero fledglings in 1992. Of the females, four produced the same number of fledglings in both years, three produced more in 1992, and two produced less in 1992 (one failed). The overall replacement rate of banded hawks at nests from 1991 to 1992 was 23% (seven replacements for 30 previously banded hawks captured or recaptured in 1992).

Of three banded hawks that moved from their 1991 territory to nest elsewhere in 1992, each fledged two young in 1991 and three young in 1992. In two of these cases, the hawks moved to nests in territories adjacent to their original (male RO, 3.5 km; female EB, 2.6 km). In the third case, female (AH) moved 9.2 km over two territories to pair with male RO.

DISTANCES BETWEEN NEAREST-NEIGHBOR AND ALTERNATE NESTS

Nearest-neighbor distances among a collection of nests provides an estimate of the distribution of those nests. Mean distance between 59 nearest neighboring nests in 1992 was 3 km (SD = 834.2 m, range = 6417–1573 m), and 47% of the nests were within 2.0–3.5 km of each other (Fig. 2). Although by the end of the 1992 season only 50% of the forest on the Kaibab Plateau was searched for Northern Goshawk nests, we think the nearest-neighbor distance is representative of the Plateau. Nest searches were systematically conducted in contiguous areas that expanded (and joined) from the northwest toward the southeast of the Plateau, and few nests were likely to have been missed within this area. Two isolated Northern Goshawk nests in the Grand Canyon National Park, discovered in non-systematic nest searches (B. S. Heslin and J. T. Driscoll, unpubl. data), were excluded from the analysis.

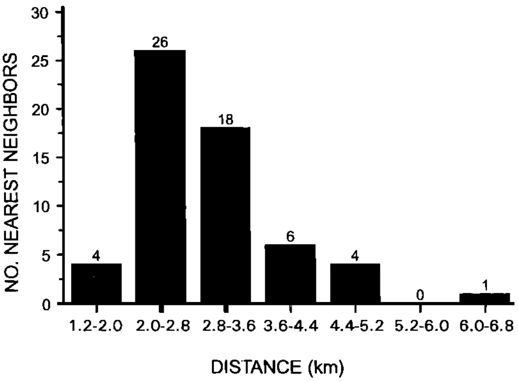

FIGURE 2. Number of occupied Northern Goshawk nests by nearest-neighbor distance in 1992 ($\bar{X}$ = 2.97 ± 0.83 km, N = 59 nests).

Pairs of Northern Goshawks often use alternate nests in different years (Reynolds and Wight 1978, Reynolds 1983). Four pairs of nesting Northern Goshawks banded in 1991 moved a mean distance of 485 m (SD = 130 m, range = 326–635 m) to alternate nests in 1992. In addition, three nesting females banded in 1991 (males not banded) moved a mean distance of 194 m (SD = 50 m, range = 142–241 m) to alternate nests in 1992. Finally, ten unbanded pairs (we presumed one or both sexes to be the same hawks in both years) moved a mean distance of 201 m (SD = 99 m, range = 100–425 m) to alternate nests in 1992. Combining these, the mean distance from 1991 nests to 1992 alternate nests was 266 m (SD = 157 m) (Fig. 3).

DIETS

A total of 121 prey items, representing 11 species of birds and eight species of mammals, was identified in prey remains collected at nests in 1991 (Table 4). In descending order of frequency, the most commonly taken species included cottontail rabbit, tassel-eared squirrel, Steller's Jay, red squirrel, black-tailed jackrabbit, and Northern Flicker. By biomass, the most important of the mammals were the cottontail rabbit, tassel-eared squirrel, red squirrel, and jackrabbit and, among birds, Steller's Jay, Northern Flicker, and Williamson's Sapsucker. Overall, mammals con-

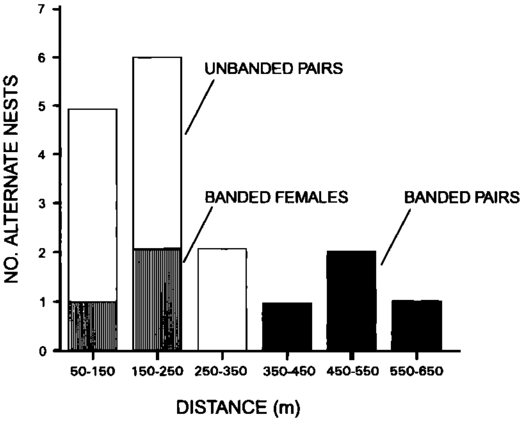

FIGURE 3. Distance between 1991 nests and 1992 alternate nests of Northern Goshawks on the Kaibab Plateau for banded pairs, unbanded pairs, and pairs in which only females were banded.

tributed 62% of number of prey items, while birds contributed 38%.

POST-BREEDING MOVEMENTS

Fifteen fledglings were fitted with radio-transmitters in 1991–1992. Dispersal of fledglings from nest areas began in mid August and was completed by late August. Two radio-tagged fledglings in 1991 and four in 1992 could not be relocated after dispersing from nests and two other transmitters, lost by the fledglings, were recovered from the pinyon-juniper woodland on the north end of the Plateau. Five fledglings (two in 1991, three in 1992) were relocated from aircraft one or more times in November and December, and one fledgling was relocated during a March 1993 flight, all on the Plateau. One radio-tagged fledgling was found dead in October 1992, approximately 8 km southeast of Flagstaff, Arizona, a distance of 160 km from its birthplace.

In July and August of 1991 and 1992, five adults (all males) and four adults (two males, two females) were fitted with transmitters, respectively. All adults except one remained on their nesting territories through late October. The exception was a female who left her nesting territory in late August 1992 and spent two weeks in pinyon/juniper woodland on the north end of the Plateau, 13 km north of her nest. The female was relocated in the woodland habitat for two weeks before disappearing. She was again relocated on the Plateau during a March 1993 flight. None of the five males radio-tagged in 1991 were relocated after October 1991, probably because of transmitter failure. Of the other radio-tagged adults, two were relocated from aircraft during a flight in December, both on the Plateau.

TABLE 4. FREQUENCY AND % OF TOTAL BIRDS AND MAMMALS IN DIETS OF NORTHERN GOSHAWKS ON THE KAIBAB PLATEAU IN 1991

Species	Frequency	%
Birds		
Cyanocitta stelleri Steller's Jay	17	37.0
Colaptes auratus Northern Flicker	11	23.9
Sphyrapicus thyroideus Williamson's Sapsucker	7	15.2
Accipiter gentilis Northern Goshawk	3	6.5
Turdus migratorius American Robin	1	2.2
Buteo jamaicensis Red-tailed Hawk	1	2.2
Dendragopus obscurus Blue Grouse	1	2.2
Corvus brachyrhynchos American Crow	1	2.2
Sitta pygmaea Pygmy Nuthatch	1	2.2
Siala mexicana Western Bluebird	1	2.2
Unknown Emberizidae	1	2.2
Unknown bird	1	2.2
Mammals		
Sylvilagus spp. Unknown rabbit	22	29.3
Sciurus aberti Abert's Squirrel	13	17.3
Lepus californicus Black-tailed Jackrabbit	11	14.7
Tamiasciurus hudsonicus Red Squirrel	11	14.7
Unknown Sciuridae	6	8.0
Spermophilus lateralis Mantled Ground Squirrel	5	6.7
Spermophilus variegatus Rock Squirrel	4	5.3
Eutamius dorsalis Cliff Chipmunk	1	1.3
Eutamius umbrinus Uinta Chipmunk	1	1.3
Eutamias spp. Unknown chipmunk	1	1.3

DISCUSSION

For the North American *Accipiter* species, habitat quality can be regarded as a measure of the abundance and distribution of the structural and floristic elements of forests and woodlands that provide nesting opportunities, hunting perches, and protective cover as well as the accessibility to, and abundance of, suitably-sized prey. Habitat quality can be reflected in a hawk's physical condition (body mass), its nesting success and productivity, its degree of fidelity to territory and mate, the size of its home ranges, and population densities of the hawk and its prey (McGowan 1975; Newton 1976, 1986; Moss 1979; Geer 1981; Newton and Marquiss 1981, 1982; Marquiss and Newton 1982). In many raptors, the age of breeding individuals confounds the investigation of habitat quality because age may affect nesting success and productivity. For example, in European Sparrowhawks (*A. nisus*), the number of young produced per nest attempt increases from yearling-to-yearling pairs, through yearling-to-adult pairs, to adult-to-adult pairs (Newton 1986). Furthermore, individuals of some species can improve their annual reproductive performance by pairing with older, more experienced birds and by moving, with or without a previous mate, to territories of higher quality (Newton 1986, Reynolds and Linkhart 1987).

The mean number of young fledged per active nest on the Kaibab Plateau in 1991–1992 was within the range of values (0.69–3.0 young/nest attempt) for the Northern Goshawk in other areas of western North America, including Alaska (see Reynolds 1989 for review). Although the nest failure rate of pairs in which one adult was in poor condition was not statistically higher than for pairs in which both adults were in moderate or good condition, we anticipate that further sampling will demonstrate that physical condition affects nesting success. Additionally, production of fledglings was significantly related to age of nesting adults; younger hawks produced fewer fledglings. Returning to the same territory and pairing with the same mate in most cases resulted in the same or higher production of fledglings. A few adults, however, increased their production of fledglings after changing territories and mates.

The spacing of Northern Goshawk nests has only been determined for a few areas. On the Kaibab Plateau, the mean distance to nearest nests (3.0 km) was slightly less than half the nearest-nest distance (5.6 km) among four Northern Goshawk nests in Oregon (Reynolds and Wight 1978) and among European Goshawk nests (*A. g. gentilis*) in Sweden (5.5 km) (Hoglund 1964). The Oregon data, however, consist of a small sample of nests and, when compared to the Kaibab data, the nearest-neighbor distance is biased upward because duplicate measures between reciprocal nearest neighbors in Oregon were not used (Reynolds and Wight 1978). Nevertheless, nests of Northern Goshawks on the Kaibab Plateau appear to occur at a density higher than reported for other populations of the subspecies (see Reynolds 1989 for review).

ACKNOWLEDGMENTS

We thank S. Bedard, K. Boden, P. Clark, S. Dudley, J. Dudley, M. Gavin, K. Kalin, T. Kelley, D. Rubinoff, L. Schultz, T. Rice, D. Strait, and D. Worthington for their invaluable help in finding, capturing, and banding Northern Goshawks. G. Beatty, J. Driscoll, B. Heslin and crews of Arizona Game and Fish Department, D. Laing and S. MacVean of North Kaibab Ranger District, and C. Boal and D. Smith of the University of Arizona and their crews helped with broadcasts, nest searches, nest visits, and capturing and banding of goshawks. R. W. Mannan of the University of Arizona provided a Great Horned Owl and P. L. Kennedy of Colorado State University advised us on broadcast survey. Arizona Game and Fish Department provided aircraft flights and personnel for the location of radio-tagged hawks in both years; thanks especially to J. Goodwin and R. Miller. Support for various aspects of this study came from numerous people in the USDA Forest Service, Southwestern Regional Office, especially S. Boyce and L. Fisher, and the North Kaibab Ranger District, especially R. Brown and D. Garcia.

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Studies in Avian Biology No. 16:114–118, 1994.

APPROACHES TO INVESTIGATING FOOD LIMITATION HYPOTHESES IN RAPTOR POPULATIONS: AN EXAMPLE USING THE NORTHERN GOSHAWK

JOHANNA M. WARD AND PATRICIA L. KENNEDY

Abstract. Food supplementation experiments have been used to demonstrate that food limits reproductive success and recruitment of a given animal population. Of the experiments that have been conducted on terrestrial vertebrates, few have been conducted on raptors. Hence, correlative evidence supporting a relationship between food availability and breeding densities of raptors may not be conclusive. We discuss the strengths and weaknesses of past supplementation experiments and detail an experiment designed to investigate this relationship for a Northern Goshawk (*Accipiter gentilis*) population in northern New Mexico. Our experiment illustrates that food supplementation experiments can be conducted on raptors throughout brood-rearing to rigorously test hypotheses concerning the effect of food availability on raptor demographics.

Key Words: Accipiter gentilis; dispersal; experimental design; food supplementation; juvenile survival; nestling size; Northern Goshawk.

It is commonly assumed that food often limits the reproductive success and thus, recruitment of animals into a breeding population (Lack 1954; Newton 1980, 1991). To test this relationship rigorously, a multitude of supplemental feeding experiments have been conducted on terrestrial vertebrates, including nesting birds, and have successfully increased at least one breeding parameter (Boutin 1990). Nearly all of the avian supplemental feeding experiments have been conducted on herbivores (seed eaters) and omnivores (insect and seed eaters) and have examined the influence of food on clutch size and hatching success where supplemental feeding was discontinued after hatching. Advanced laying date and/or increased clutch size as a result of supplemental food have been reported (Yom-Tov 1974, Newton and Marquiss 1981, Dijkstra et al. 1982, Hochachka and Boag 1987, Arcese and Smith 1988) and some experiments demonstrated an increase in nestling and fledgling survival as a result of supplemented diets (Yom-Tov 1974, Hansen 1987, Simons and Martin 1991). However, results of the studies have been variable, and very few studies have been conducted with non-passerines such as raptors. Newton (1980, 1991) noted that only correlative relationships between food abundance and raptor densities have been established. As a result, current evidence supporting a relationship between food availability and breeding densities of raptors is not conclusive.

Another limitation of past avian supplementation experiments is that only three studies have initiated supplemental feeding after hatching (Hochachka and Boag 1987, Simons and Martin 1991, Kenward et al. 1993), so knowledge about the effects of additional food on the post-hatching period and particularly its influence on offspring growth, survival and recruitment is scarce for all birds, and nonexistent for raptors. In three experiments on raptors (Newton and Marquiss 1981, Dijkstra et al. 1982, Hansen 1987), birds were not provided additional food after hatching. Since Boutin's (1990) review, Kenward et al. (1993) conducted a study examining causes of dispersal, providing excess food to goshawk young from three weeks post-fledging until independence (a period of ca. 30 days).

The transition from dependent fledgling to independent juvenile is assumed to be one of the most critical periods for avian survival (Richner 1992). High avian juvenile mortality rates attributed to starvation have been reported during this time (Southern 1970, Hirons et al. 1979, Newton et al. 1982, Korpimäki 1988, Sullivan 1989). Further, both Newton et al. (1982) and Sullivan (1989) speculated that adequate food may be available to the young during the fledgling dependency period, but that juveniles may starve because they are inexperienced and inefficient foragers.

Most of the aforementioned studies were controlled experiments; however, most failed to measure the magnitude of the treatment, supplying unquantified amounts of excess food (but see Yom-Tov 1974, Hogstedt 1981, Dijkstra et al. 1982, Hansen 1987, Hochachka and Boag 1987, Kenward et al. 1993). We believe it is important to quantify the treatment to know how much excess food needs to be provided to yield a true treatment effect. There further exists a need for experimentation on a larger spatial scale over longer periods of time (Boutin 1990).

We are currently examining the potential effects of increased food availability on (1) the size of nestling Northern Goshawks (*Accipiter gentilis*), (2) the time of goshawk fledging, (3) the

TABLE 1. ESTIMATES OF AGE-SPECIFIC ENERGY REQUIREMENTS FOR JUVENILE NORTHERN GOSHAWKS (KELLY AND KENNEDY 1993:TABLE A2.1). AVERAGE AGE OF DISPERSAL FOR TREATMENT JUVENILE GOSHAWKS WAS 12 WEEKS; FOOD SUPPLEMENTATION ENDED AT 22 WEEKS

Age (weeks)	Formula[1]	Energetic requirement (kJ/day)	No. of quail required/ day[2]	Total no. of quail required
0–2	$0.3E^{*n}$	239.1	0.3	4.2
3–5	E^{*n}	797.0	1.0	21.0
6–7	$0.7E^{*n}$	557.9	0.7	9.8
8–22	$0.5E^{*n}$	398.5	0.5	45.5

[1] E^{*n} = peak energy expenditure of an altricial nestling.

[2] Assimilated energy intake of 150 g quail = 792 kJ (based on methods in Kennedy [1991]).

time of goshawk dispersal, and (4) juvenile goshawk survival. In this paper, we discuss our experimental design as an example of an approach that can be used to evaluate the influence of increased food availability on post-hatching reproductive success and juvenile survival in raptors.

METHODS

STUDY AREA

The experiment was conducted from mid-April to mid-October during the 1992 breeding season and is ongoing for 1993, on a goshawk population in the Jemez Mountains and the adjacent Pajarito Plateau in north-central New Mexico. The majority of the goshawk nests in this area were on land managed by the USDA Forest Service, Santa Fe National Forest. The study area elevation ranges from 1200–3900 m, and the average elevation of the goshawk nests was 2493 m. The mountains are characterized by steep terrain dominated by typical southwestern montane habitat types such as ponderosa pine (*Pinus ponderosa*) and mixed-conifer forests. The Pajarito Plateau, a table-like extension of the eastern flank of the Jemez Mountains, is cut into numerous, narrow, finger-like mesas by southeast-trending, intermittent streams. The mesas are dominated by pinyon-juniper woodland. The drainages contain riparian habitats dominated by ponderosa pine or cottonwood (*Populus* spp.) stands and flow into the Rio Grande. See Kennedy (1988) for a detailed description of the study area.

ENERGETIC CALCULATIONS

To maximize the effect of the treatment, we designed the experiment to supply at least 100% of the broods' (excluding adults) energy requirements at treatment nests. Kennedy (1991) developed an allometric equation describing the relationship between peak energy expenditure of altricial nestlings (E^{*n}, measured in Watts) and adult biomass (M, measured in g), where $E^{*n} = 53.578M^{0.757}$. We used this equation to determine the peak energy expenditure for a nestling goshawk. Peak energy expenditure of nestling males and females was estimated to be 730 kJ/day (where M = 800 g) and 864 kJ/day (where M = 1000 g), respectively. The average of these two estimates, 797 kJ/day, was used as the estimate of E^{*n}. The energetic requirements for young goshawks over the rest of the breeding season can then be calculated as a percentage of E^{*n}. The age-specific energetic requirements are not yet known for the goshawk. However, energetic requirements have been estimated for the Cooper's Hawk (*Accipiter cooperi*), a smaller accipiter that also breeds in the study area (Kelly and Kennedy 1993). We used a modification of the method described by Kelly and Kennedy (1993:Table A2.1) to estimate the age-specific energetic requirements for nestling goshawks (Table 1).

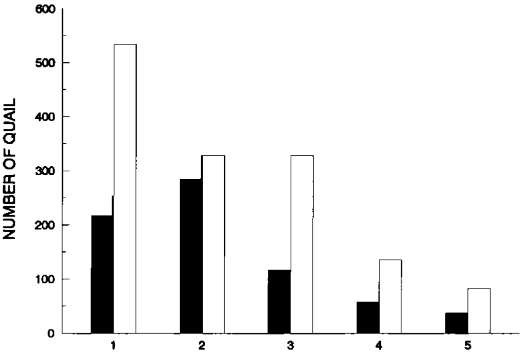

FIGURE 1. Number of quail required (solid bars) to meet 100% of the energetic requirements of the treatment goshawk broods (based on brood size and sex ratio), and the number of quail provided (open bars) at each treatment nest (1–5) during the 1992 experiment.

The treatment broods were supplemented with Japanese quail (*Coturnix* sp.) that weighed 120–150 g. The assimilated energy of one 150-g quail is estimated to be about 792 kJ (based on methods used by Kennedy [1991] to estimate assimilated energy of avian prey). According to the age-specific energy requirement calculations, one goshawk offspring required 73.5 quail to meet its daily energy requirements from hatching until mid-October. To maximize the treatment effect, we put out as many quail as the brood would take in addition to the amount provided to meet 100% of the offsprings' estimated energetic requirements. Hence the amount provided at each nest varied with how much excess food the birds would take, and with the number of young at each nest (Fig. 1).

FOOD SUPPLEMENTATION

Twelve of 14 known nest sites were active in 1992; six of the 12 active goshawk nests were randomly assigned as treatments and the remaining six were controls. Sixteen active nests were located in 1993, with eight randomly assigned as treatments and eight as controls. We observed the behavior of the incubating adult bird to determine date of hatching. After hatching, the adult bird on the nest would remain relatively still, except for frequent jerking motions caused by the newly hatched young. It is likely that the hatchlings do not cause this behavior until they are a few days old. However, since we used the same behavior protocol to determine date of hatching at all nests, any error in age estimation should be equal for all nests.

Food supplementation began the day after hatching was observed (late April) and ended when most birds had dispersed (mid-October). When Newton and Marquiss (1981) provided extra food to sparrowhawks (*Accipiter nisus*), they placed food on or near a regularly used plucking post, and the birds could not remove the food. We modified this technique, placing quail on a podium about 1.5 m tall, located within 10 m of the active nest where the incubating adults could always see the food while on the nest. To entice the birds to take the supplemental food, we initially provided daily 1–2 live quail tethered to the podium. After the live quail were regularly taken, we provided dead quail every other day. In all cases, the quail could be removed by the hawk from the podium. To avoid attracting potential nocturnal predators such as the Great Horned Owl (*Bubo virginianus*), each feeding podium had a motorized cover activated by a solar cell that covered the food by sunset and exposed it by sunrise the following morning. Feeding podiums were also placed at control nests, and were visited every other day to equalize the amount of disturbance at each nest. Each treatment podium was observed 2–3 times during the experiment from sunrise to sunset from a blind approximately 15 m from the feeding podium to verify that the adults, and later, the juvenile goshawks from that territory, were taking the quail. Individual birds were identified by unique alpha-numeric coded color bands.

DATA COLLECTION

Size of nestling goshawks

Morphometric measurements were taken for culmen and hallux length, tarsometatarsus width and length, and weight on 29 21-day-old nestling goshawks (16 controls, 13 treatments) in 1992, and 13 nestling goshawks (10 treatments, 3 controls) in 1993. A single observer (JMW) collected all measurements to eliminate observer variability in measurement technique.

Time of fledging and dispersal

When the morphometric measurements were taken, tarsal-mounted transmitters with mortality switches (Advanced Telemetry Systems, Inc., Isanti, MN) were attached to the nestling goshawks. To minimize the impact of transmitter attachment to the offspring, the transmitters were designed to drop off after 3–4 months. After transmitter attachment, the birds were relocated at least once every two days either from the ground or from an airplane. By mid-October the majority of the juvenile birds could not be relocated because they had dispersed, or their transmitter had dropped off or failed prematurely, and the experiment was terminated.

Fledging was defined a priori as the first observation of young perching on a branch (we assume the same fledging date for all young in a nest), and dispersal was defined a priori as the first time a juvenile spent more than a week at least two km away from the nest. Kenward et al. (1993) used a similar definition of dispersal for goshawks in Sweden, defining dispersal as the first day that a hawk was not within 1.5 km of the nest and did not return for at least two days.

RESULTS AND DISCUSSION

The food supplementation experiment was successful, with all treatment birds eating quail. None of the adult birds ate immediately, but all ate within 3–5 days after the experiment was initiated. Adult females and fledgling goshawks were observed taking quail at every treatment nest. However, adult males were never observed taking quail from the podium. In 1992, when the experiment was terminated in mid-October, both adult females and juvenile birds were still taking the supplemental food. On several occasions while delivering quail, we observed goshawks perching on the podium. We also regularly observed molted adult feathers at the base of the podium, and quail feathers were frequently observed at goshawk plucking posts and at the base of frequently used perches. Although we recorded the number of quail taken from the podium, we do not know how many of these quail were eaten by the young and by the adults. Since both parents continued to hunt and were rarely seen in the nest stand during the fledgling-dependency period, we surmise that the young ate most of the quail during this period. The amount of quail eaten varied by nest, which we expected because parental care, habitat quality, and the number of offspring differed at each nest. In 1992, the family that ate the most quail had three offspring and removed 86% of the supplemented quail, whereas the family that consumed the fewest number of quail had one offspring and ate only 22% of the quail.

On several occasions, the podiums were knocked over by black bears (*Ursus americanus*) but the bears did not regularly take quail. There was no evidence of other mammalian predators taking quail. At two of the treatments, Gray Jays (*Perisoreus canadensis*) and Steller's Jays (*Cyanocitta stelleri*) regularly picked at the quail. Also, yellowjackets (Hymenoptera: Vespidae) were an unexpected consumer, sometimes eating the entire quail and leaving only the skeleton. We never observed other avian predators taking food from the podium, which was not surprising since goshawks are such vigorous defenders of their territories. If this technique is used for a less aggressive species or in areas where other consumers are more of a problem, the podium may have to be modified (e.g., metal sheeting placed around the base) to prevent consumption of the supplemental food by other animals.

Although our experiment is an improvement on past supplemental feeding studies (for reasons stated in the introduction), our design also had some flaws that should be corrected in future experiments. Our sample size is probably not large enough to provide meaningful comparisons of survival of treatment versus control offspring, a common problem in raptor studies. Also, when calculating the energetic requirements of the offspring, the requirements of the adults should be accounted for if the excess food is available to the adults. Another weakness of our experiment is measuring offspring's morphometrics at only one age, the expected time of maximum growth (Kennedy 1991). It is possible that significant differences may be found in the mass of treatment versus control offspring after they reach independence, when the controls have to capture their food and the treatments are still being supplemented. Finally, the fates of goshawk offspring need to be monitored for a longer period of time. We chose tarsal-mounted transmitters because we thought backpack transmitters would adversely affect survival, a parameter we were measuring. The drawback of tarsal-mounts is their short battery life (about 4 months). We suggest using Kenward et al.'s (1993) approach of recapturing fledglings prior to independence and replacing the tarsal-mounted transmitters with backpacks.

This experiment demonstrates the feasibility of conducting food supplementation experiments on birds of prey. We hope our work will encourage other raptor researchers to employ rigorous experiments to demonstrate causality when investigating questions about birds of prey, rather than observational studies that only describe correlative relationships. Possible future research regarding the question of raptor population regulation and food availability may be to conduct an experiment for one part of the breeding season (e.g., courtship) at some nests and another part of the breeding season (e.g., fledgling-dependency period) at other nests during the same year. This would determine if food is limiting during all of the breeding season or only for a portion of it. Other useful experiments would be to provide excess food during the winter when food availability may have a greater influence on raptor survival than during the breeding season. Experimental manipulations of food availability are logistically challenging, but we believe they are necessary to answer conclusively questions regarding food limitation and population regulation in birds of prey.

ACKNOWLEDGMENTS

We thank T. Dean for his tireless efforts in data collection. We are also indebted to J. Fair, O. Myers, S. Skagen, M. Siders, and G. White for their invaluable advice on experimental design. B. Booth designed and constructed the mechanical feeding boxes. C. Akin, J. Fretwell, A. Lindstrom, and C. Mansfield helped us locate dispersing birds from the air. A. Alexander, D. Clark, K. Colfer, T. Dean, J. Lavy, J. Morrison, J. Moore, M. Siders, and D. Sinton located many of the nests used in this experiment. D. A. Boyce, D. Fisher, B. McKinney, J. Peterson, M. Orr, and R. Reynolds provided logistical support. L. Hall, S. Skagen, J. Smith, and G. White provided constructive criticism on the manuscript. This research was supported by the USDA Forest Service, Region 3, Rocky Mountain Forest and Range Experiment Station, and the Santa Fe National Forest. This research was approved by the Animal Care and Use Committee at Colorado State University.

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Studies in Avian Biology No. 16:119–121, 1994.

BREEDING ECOLOGY OF THE NORTHERN GOSHAWK IN HIGH-ELEVATION ASPEN FORESTS OF NORTHERN NEVADA

JAMES V. YOUNK AND MARC J. BECHARD

Abstract. We examined the habitat requirements of Northern Goshawks (*Accipiter gentilis*) nesting in small, isolated aspen (*Populus tremuloides*) stands in high-elevation, shrubsteppe habitat in northern Nevada. We found 14 and 22 occupied goshawk nests in 1991 and 1992, respectively. Nests were in aspen stands consisting of mature trees with a closed canopy and little understory cover. All were located near water and most were in north- or east-facing stands situated on variable slopes (4–39%). Fourteen breeding pairs fledged 18 young in 1991 and 22 breeding pairs fledged 61 young in 1992 for an average productivity of 2.2 young/occupied nest. Nest observations from blinds indicated that Belding's ground squirrels (*Spermophilus beldingi*) were the primary prey item, followed by various species of birds that were taken in the latter half of the breeding season after ground squirrels had estivated.

Key Words: *Accipiter gentilis*; *Artemisia*; aspen; Belding's ground squirrel; Northern Goshawk; *Populus tremuloides*; *Spermophilus beldingi*.

In the western U.S., the Northern Goshawk (*Accipiter gentilis*) typically nests in mature coniferous forests dominated by ponderosa pines (*Pinus ponderosa*), Douglas-firs (*Pseudotsuga menziesii*), and white firs (*Abies concolor*) (Palmer 1988, Johnsgard 1990). In drier areas of the west such as the Great Basin, goshawks also nest in high-elevation shrubsteppe habitats supporting small, highly fragmented stands of aspen trees (*Populus tremuloides*). Very little information is available on the habitat requirements of goshawks in these shrubsteppe habitats.

METHODS

The study was conducted in the Independence and Bull Run Mountain ranges between the Idaho–Nevada border and a point approximately 50 km north of Elko, Nevada. The ranges are ca. 150 km long and vary from 10 to 30 km in width. Elevations range from 1700 m on the adjacent plain to over 3000 m on the highest peaks. Vegetation is predominately open sagebrush (*Artemisia* spp.) with conifers (*Pinus albicaulis, P. flexilis* and *Abies lasiocarpa*) above 2500 m and aspen (*Populus tremuloides*) growing in riparian areas (Loope 1969). Most of the range is publicly owned and administered by the USDA Forest Service.

We conducted helicopter surveys for all raptor nests in the study area in April of 1991 and 1992 prior to emergence of aspen catkins. In addition, we searched stands of aspens or mixed aspen/conifer that either had a history of occupancy by breeding goshawks or appeared to be suitable nesting habitat. Searches were concentrated in the southern portion of the study area in 1991 but were extended in 1992 to include the northern portion where higher elevations created a shift from aspen to conifer habitat. A nest was classified as occupied if a raptor was seen in the vicinity of a nest structure or if there was evidence of fresh nesting material in nests. Locations of all occupied nests seen from the helicopter were recorded using a Loran C unit and later transcribed onto U.S.G.S. 7.5 min. topographical maps of the region. A nest or nest structure was the platform of sticks on which eggs were laid, and a nesting stand was the stand of trees that contained the nest.

During May and June we checked all goshawk nests on foot to verify occupancy and to determine if eggs had been laid. An occupied nest was defined as a nest where territorial defense, courtship, or a goshawk was seen. Evidence of egg laying included the presence of eggs or young in the nest, or any field sign indicating that eggs were laid (e.g., adults in incubating posture, egg shell fragments in fresh nesting material). Characteristics of aspen stands used by breeding pairs of goshawks were also recorded. Measurements of slope, elevation, aspect, and distances to nearest water were obtained from Geographic Information System (GIS) maps that were developed from data previously collected by USDA Forest Service personnel. We used diameter at breast height (dbh) tapes and increment borers to obtain measurements on sizes and ages of nest trees.

In 1992, we observed eight pairs of goshawks throughout the nesting period from blinds to obtain information on diet and nesting behavior. Blinds were built with lumber and white canvas and placed 30–50 m from a nest tree. Observation periods lasted 3–5 hours and were scheduled to incorporate all times of the day. By continuously recording activities at the nest, observers monitored the types of food that were delivered to nests, the number of food deliveries per hour, and the time spent away from the nesting area by both sexes.

In 1992, adult goshawks were also captured in nest areas in June using a live Great Horned Owl (*Bubo virginianus*) and dho-gaza net. Adults were aged in the hand using plumage characteristics (B. Woodbridge, pers. comm.), and banded with green (male) and blue (female) alpha-numeric, anodized aluminum bands on the left leg and U.S. Fish and Wildlife Service aluminum bands on the right.

RESULTS

In 1991, 123 nest structures were found during helicopter surveys and goshawks were seen at or near ten of these nests. In 1992, only 66 nest

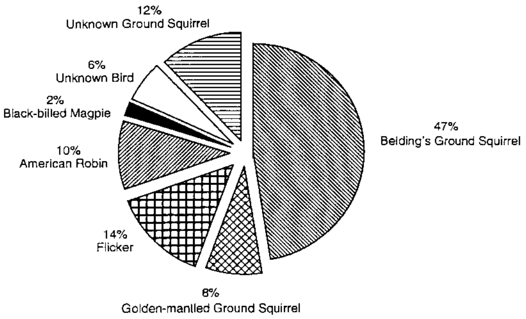

FIGURE 1. Frequency of occurrence of prey species in the diet of Northern Goshawks nesting in shrubsteppe habitats of northern Nevada.

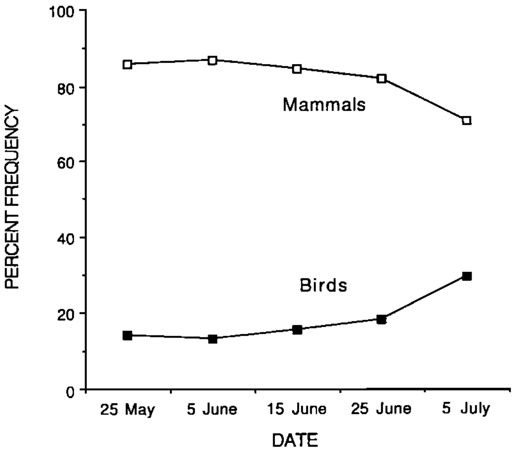

FIGURE 2. Seasonal variation in the frequency of occurrence of prey species in the diets of Northern Goshawks nesting in shrubsteppe habitats of northern Nevada.

structures were found and goshawks were seen at only six of these nests. Subsequent ground searches showed 14 and 22 of the nests to be occupied by goshawks in 1991 and 1992, respectively. The 1992 survey resulted in 11 new goshawk nest sites not located in 1991. Although the 1992 helicopter survey covered conifer forests, and these areas were searched on foot, no goshawks were found nesting there.

All goshawk nest stands had similar characteristics. Mean stand elevation was 2119 m (range 1975–2386 m). Aspens used as nest trees usually had the largest dbh in the stand ($\bar{X}$ = 29 ± 3.8 [SE] cm) and averaged ca. 60 years of age based on core samples. Nest stands were relatively open with a park-like appearance and little understory cover. Although nest stands were small ($\bar{X}$ = 24.9 ± 21.9 ha), the terrain was not steep ($\bar{X}$ slope = 19.4 ± 8.3%) and slopes generally faced north or east. Water, such as a stream or spring, was also usually present within 100 m ($\bar{X}$ = 91 ± 129 m).

Breeding began in April. By backdating from known-aged nestlings and using an incubation period of 33 days, we estimated that egg laying was completed on average by 1 May. We did not observe eggs so could not calculate egg hatchability, but the modal brood size was 3 young. Productivity increased significantly (t-test, $P < 0.05$) from a mean of 1.2 young/breeding pair in 1991 to a mean of 2.8 young/breeding pair in 1992. Young also fledged significantly earlier in 1992 ($\bar{X}$ = 1 July ± 5 days) than in 1991 ($\bar{X}$ = 11 July ± 8 days), possibly because of a very cold and wet spring in 1991.

All 22 adult females and 15 of 22 males were trapped and color marked in 1992. Aging in the hand showed that 11 of the 22 females were in second-year plumage, and none showed 1-year-old plumage characteristics (B. Woodbridge, pers. comm.). We expected the younger females to be less productive, but this was not the case (2.54 vs. 3.0 young per nest). Two-year-old females did fledge young at a significantly later date than older birds (means of 28 June vs. 5 July, t-test, $P < 0.01$). Based on the plumage of birds observed with binoculars in 1991, 5 of 14 breeding females were 1 year of age. We did not trap adults in 1991, so no yearly comparison of 2- and 3+-year-old birds could be made. In both years, only one breeding male was estimated to be less than 3 years of age.

Based on the frequency of occurrence of prey delivered to nests, observations from blinds showed that goshawks ate mostly Belding's ground squirrels (*Spermophilus beldingi*) (Fig. 1). Ground squirrels were delivered by males on 24 of the 51 observed prey deliveries. We did not collect prey remains from plucking posts because goshawks were found to pluck birds and not ground squirrels. Instead, ground squirrels were brought directly to the nest. Mean rate of prey delivery was 0.31 prey item per hour. This was comparable to delivery rates reported by Boal and Mannan (*this volume*). As the nesting season progressed and ground squirrels began to estivate, we observed a shift in the types of prey that were delivered. After 1 July, males began to bring in more birds such as American Robins (*Turdus migratorius*) and Northern Flickers (*Colaptes auratus*) (Fig. 2).

DISCUSSION

In high-elevation shrubsteppe habitats, goshawks nest in small, widely-spaced stands of mature aspen trees that grow along creeks and drainages. These aspen stands are located primarily on north or east-facing slopes. The tree in which the nest is built averages 60 years of age. The canopy is mostly closed and the understory is open with little cover. Understory cover is probably limited by livestock that use the stands for grazing and shading during the hot summer months.

Helicopter surveys were effective in surveying this type of habitat for nesting goshawks. These surveys are best conducted when the ground is snow-covered and prior to aspen catkin emergence. Lack of snow and early catkin emergence made survey conditions less favorable in 1992. As a result, the number of adults seen in the vicinity of nests was reduced from ten in 1991 to six in 1992. Also, the lack of contrasting snow cover lowered the visibility of nest structures in trees.

Nest observations indicated that female goshawks remained almost continuously in the vicinity of nests, even when young approached fledging age. Male goshawks did almost all the hunting. Many authors state that the female begins to hunt as the young get older (Palmer 1988, Johnsgard 1990). We did not observe this. Females were never seen to leave the immediate vicinity of the nest, even when the young were near fledging.

In 1992, 11 of 22 breeding females were in "sub-adult" plumage of 2-year-old birds (Bent 1937, Johnsgard 1990). We expected to find subadult females less successful than older females in rearing young, but found no difference. No females in 1-year-old plumage bred in 1992, but 5 of 14 breeding females observed in 1991 were in first-year plumage. In Alaska, younger birds bred during years of increasing prey abundance that follow a sharp decline in both prey and goshawk numbers (McGowan 1975). Apparently it is when populations of their preferred food, snowshoe hares (*Lepus americanus*), are increasing that younger females are recruited into the breeding population. A similar increase in the population of the preferred food of goshawks in northern Nevada may have accounted for the large number of one-year-old females that bred in 1991.

Our results indicated that the collection of prey remains from plucking posts to determine goshawk diets may be highly biased when they are feeding on mammals as opposed to birds. We observed that males delivering ground squirrels to nests brought them in unplucked. They did, however, pluck birds at plucking posts. This indicates that, in places where goshawks feed heavily on small mammals, dietary studies must focus on both prey at nests and plucking posts to develop an unbiased estimate of the diets of these birds.

ACKNOWLEDGMENTS

We would like to thank S. Anderson, J. Bokich, P. Bradley, M. Kochert, K. McAdoo, R. Reynolds, and J. Warder for help in the course of this study. We would also like to thank field assistants E. Ellsworth, M. Shipman, and C. Younk. The study was funded in part by Boise State University, Humboldt National Forest, Independence Mining Company, and Nevada Department of Wildlife.

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Studies in Avian Biology No. 16:122–129, 1994.

POPULATION RESPONSES OF NORTHERN GOSHAWKS TO THE 10-YEAR CYCLE IN NUMBERS OF SNOWSHOE HARES

FRANK I. DOYLE AND JAMES M. N. SMITH

Abstract. We studied the abundance, diet, and migratory status of Northern Goshawks (*Accipiter gentilis*) at Kluane, southwest Yukon, Canada, from 1987 to 1993. This period spanned a local increase, peak, and decline in numbers of snowshoe hares (*Lepus americanus*). Goshawk sightings increased from 1988 to 1991, the year after hares reached peak densities, and about 40 pairs of goshawks occupied the 400 km² study area in 1990. As hare numbers fell, goshawk numbers dropped, birds became more nomadic, and their mortality increased within the study area. Goshawks nested mainly in mature but small spruce trees (*Picea glauca*). In the breeding season, male goshawks preyed heavily on hares, arctic ground squirrels (*Spermophilus parryi*), red squirrels (*Tamiasciurus hudsonicus*), and took some Spruce Grouse (*Dendragapus canadensis*) and Willow Ptarmigan (*Lagopus lagopus*). Hares made up 56% of the biomass of prey killed from 1989 to 1991. No successful breeding by goshawks was noted in 1992, after hare numbers declined to low levels. Data from mortality-sensing radio transmitters fitted to hares showed that goshawks accounted for about 10% (summer) to 17% (winter) of mortalities of radio-collared hares from fall 1988 to spring 1993. The number of breeding attempts located and the reproductive success of breeding pairs increased with hare densities. Pairs breeding at the hare peak fledged 2.8 young per nest. We suggest that this population of goshawks is resident year-round during periods of high hare numbers, because snowshoe hares are available as food in winter. In periods of low hare abundance, goshawks become more nomadic in spring, summer, and fall, and virtually disappear from the Kluane area in winter.

Key Words: *Accipiter gentilis*; demography; diet; migration; Northern Goshawk; reproduction; snowshoe hare cycle.

The "10-year cycle" of the northern boreal forest (Keith 1963) is one of the most dramatic ecological events in northern North America. Every 8–11 years, the numbers of snowshoe hares (*Lepus americanus*) rise to a peak, where they dominate the biomass of vertebrates in the boreal forest (Krebs et al. 1986, 1992; S. Boutin et al., unpubl. ms.). Several larger avian predators reproduce well and increase in numbers during the prey bonanza at peak hare densities (Craighead and Craighead 1956, Luttich et al. 1971, McInvaille and Keith 1974, Keith et al. 1977, Adamcik et al. 1978). One of many interesting questions about the 10-year cycle is: how do large raptors respond to the appearance and disappearance of the snowshoe hare from their prey base, at a rate that is rapid relative to their potential lifespan? We studied this question for the Northern Goshawk (*Accipiter gentilis*) at Kluane, Yukon, from 1987 to 1993, during the cyclic rise and fall of snowshoe hare numbers. Our study forms part of a larger experimental project (C. J. Krebs et al. 1992, unpubl. data), on the effects of the rise and fall in hare numbers on the boreal forest food web.

In this paper, we address four specific questions: (1) do numbers of goshawks change as hare numbers rise and fall; (2) does the breeding performance of the goshawk respond to the changing abundance of snowshoe hares; (3) do the diets of goshawks shift from the period of peak hare numbers, to the time when hare numbers are declining; and (4) is this northern population of goshawks migratory?

METHODS

STUDY AREA

We worked at Kluane (60°57′N, 138°12′W) in a 400 km² area of the Shakwak Trench, a broad glacial valley bounded by alpine areas to the northwest and southeast. The part of the valley studied (ca. 30 × 13 km) contains a 30-km stretch of major highway (the Alaska Highway) and about 50 km of secondary roads and tracks. Snowmobile trails in winter generally follow these secondary roads. Most parts of the valley are accessible only on foot. The valley bottom averages about 900 m above sea level and is mostly covered with closed spruce forest, interspersed with shrub thickets, grassy meadows, old burns, eskers, small lakes, marshes, and many ponds.

The dominant tree species is white spruce (*Picea glauca*), with some aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*). The dominant shrubs are gray willow (*Salix glauca*), bog birch (*Betula glandulosa*), and soapberry (*Sherpherdia canadensis*).

We distinguished two main forested habitats: closed spruce forest, with dense stands of spruce and a sparse understory; and open spruce forest, with scattered spruce, occasional clumps of aspen trees, and a dense shrub layer. Trees at Kluane are small (canopy height 8–13 m) because of the proximity to tree line. On the borders of the valley the vegetation changes first to open sub-alpine forest of spruce and dense tall willow (*Salix* spp.) thickets, then to patchy short willows, and finally to open tundra at about 1400 m above sea level. The large Kluane Lake (ca. 300 km²) borders the study area to the northwest. The valley lies in the rain shadow of the St. Elias mountains, and experiences a cold continental climate with only moderate precipitation. Snow depths average about 55 cm by late winter (Krebs et al. 1986).

SURVEY METHODS

We sought information on goshawk numbers in five main ways:

(1) All project field personnel were trained by one of us (FID) to identify local raptors. These observers spent a total 47,276 hours in the study area on foot during both summer and winter and 9777 additional hours driving vehicles on the Alaska Highway and tracks in the study area. At the end of each field day, each worker recorded the numbers of goshawks and other larger animals seen on foot or from a vehicle while in the study area, and the number of foot- or vehicle-hours accumulated each day. We term these observations "seen sheet" data, and expressed them here as goshawk sightings per 100 observer hours.

(2) We designated part of the study area as a 100 km^2 "intensive area." This area was closer to our base camp than the rest of the study area, and thus more easily searched on foot; it also contained most of our sampling plots. The intensive area contained the same sets of habitats and prey species, and had similar vegetation to the remainder of the study area. We searched the intensive area systematically on foot for the presence of breeding goshawks each May and June. From 1990 on, we broadcast tape-recorded goshawk "kakking" calls every 200 m on regularly-spaced transects walked through the intensive area during the nestling period. Kimmel and Yahner (1990) found that such broadcast calls produced responses (calls, flights overhead, or a close approach) from about 50% of breeding pairs tested with single calls broadcast 150 m from known nests. Joy et al. (*this volume*) found somewhat higher levels of response to playbacks of alarm calls by nesting goshawks.

(3) We worked more opportunistically elsewhere in the study area, searching particularly near water (Beebe 1978), near past nest sites, and by broadcasting calls in areas where recent goshawk sightings had been reported. Several parts of the remaining 300 km^2 area contained study plots and a satellite field camp, and these areas were also visited regularly. Ground searches focused primarily on indirect signs of goshawk presence (long streaks of "whitewash" below perches, and prey remains and pellets near plucking sites).

(4) We also searched for nests from a light aircraft in early spring in 1988 and 1989 before leaves appeared on deciduous trees, but while snow was still on the ground (McGowan 1975). This method revealed some nests in deciduous trees. However, we discontinued its use after 1989, when it became clear that most goshawk nests were in white spruce trees and were not visible from the air.

(5) We trapped goshawks using falling-lid traps baited with live rock doves (*Columba livia*) in an inaccessible bottom compartment. Trapped goshawks considered to be likely breeders (adults or yearling females in spring or late winter) were fitted with tail-mounted radio transmitters manufactured by Biotrack Ltd. (Kenward 1978). We monitored the presence of these birds weekly, until they left the study area or molted their transmitters in the fall. In May 1988, we monitored the hunting ranges of a non-breeding adult male and an immature female intensively, using methods outlined by Mech (1983) and Kenward (1987). Bearings were taken from fixed points on the Alaska Highway, and we moved rapidly between points to minimize movements of birds between readings, and spaced the points far enough apart so that successive bearings deviated by 90° or more. We used the program RANGES IV (Kenward 1990) to calculate 95% outer convex polygons for each bird's range.

REPRODUCTIVE SUCCESS AND DIET

When nests were located, they were monitored every 2–5 days until the young left the nest. When a nest was first found, we conducted a careful spiral search around the site to locate the plucking sites used by the male bird. The fallen trees and bowed branches used for plucking prey by the male were then flagged and revisited every 2–4 days. Any non-fresh prey remains were removed and discarded on the first visit, and all fresh prey remains were collected and removed on each subsequent visit. At the end of the breeding season, we collected nest remains, sorted them together with prey remains from plucking sites, and matched parts of each prey (tails, heads, wings, etc.) to establish the minimum number of prey individuals captured per species for each nest. Small mammals (mice, voles) are probably under-represented in data from plucking sites, because these require little preparation, and thus generate few remains.

In 1990, we also watched nests from blinds using a 20–45 power telescope for 68.1 hours, to identify possible biases in the prey remains left at plucking sites. Similar prey items were brought to nests during watches and collected from plucking sites in 1990, but a higher proportion of birds was recorded at plucking sites (54 of 229 items, 23.6%) than in observations at nests (1 of 19 items, 5.3%). Nearly all prey at plucking sites could be identified, but some prey brought to nests were not identifiable. Pellets have yet to be analyzed at the time of writing.

INFORMATION ON GOSHAWK PREY AND PREDATORS

Snowshoe hares, arctic ground squirrels (*Spermophilus parryi*), red squirrels (*Tamiasciurus hudsonicus*), deer mice (*Peromyscus maniculatus*) and voles (*Clethrionomys rutilus, Microtus* spp.) were live-trapped each summer on 2–3 unmanipulated 34-ha plots in the study area. Squirrels and hares were trapped with live traps (Tomahawk Live Trap Co., Tomahawk, WI). Squirrel traps were baited with peanut butter and placed near middens or burrow complexes on 10-ha plots. Hare traps (Tomahawk Live Trap Co.) were placed each April in runways under cover at 50 sites evenly-spaced on four rows of each 34-ha plot. Hare traps were supplied with apple slices and alfalfa cubes. Mice and voles were trapped in Longworth box-and-tunnel traps (Penlon Ltd., Abingdon, Oxfordshire, U.K.), supplied with cotton batting, baited with whole oats, and covered with 20 × 25-cm wooden boards. Fifty Longworth traps were placed at alternate stations on a 10 × 10 grid with 15-m trap spacing, on a 2.8-ha plot nested within each 34-ha plot. Hares were trapped once each April in a 5–6 day trapping period, and other species were trapped twice over three to five days in June and August. Trapped mammals were given numbered metal ear tags (National Band and Tag Co., Newport, KY). Hare densities on the 34-ha plots were calculated by assuming that the effective trapping area of each plot was 60 ha. Weights of juvenile hares were estimated from the length of their right hind foot using an equation provided by M. O'Donoghue (unpubl. data): weight (g) = $-302.2 + 10.2 \times$ RHF (N = 1051, $r^2 = 0.92$). Goshawks did not consume hare feet, and thus these were readily obtained.

Detailed analyses of population changes in other prey species have yet to be completed (S. Boutin et al., unpubl. data), and we report only qualitative trends here. We used numbers of animals trapped to calculate estimates of available adult biomass of each prey species.

A sample of 50–150 trapped hares at any one time was fitted with 40-g mortality-sensing radio collars (made by various manufacturers) on nine 34-ha study plots. When a collared hare was found dead in winter, we could usually (>80% of cases) identify the predator responsible for the kill from tracks, feather-imprints in the snow, and predator hair or feathers (Einarsen 1956). Summer deaths could not be so readily identified because of the absence of tracks, but the way a prey was plucked, and distinctive long streaks of whitewash, identified the goshawk or Red-tailed Hawk (*Buteo jamaicensis*) as the killer. Mortality-sensing radio collars (various manufacturers) were also fitted to 60–100 red squirrels annually from 1989 on, and to 30–100 arctic ground squirrels from 1991 to 1993. Spruce Grouse (*Dendragapus canadensis*) were color-banded and counted on the ground on four sample plots each spring, and ptarmigan (*Lagopus* sp., mostly Willow Ptarmigan [*L. lagopus*]) were counted on transects in the alpine tundra from a light aircraft in spring (late April or early May) from 1990 to 1993. Numbers of passerine birds were estimated in early June using 5-minute point counts at 11 regularly-spaced stations on each of four 34-ha study plots from 1988 to 1992 (Folkard 1990).

The seen sheets yielded estimates of the abundance of several potential predators on goshawks (e.g., Golden [*Aquila chrysaetos*] and Bald [*Haliaeetus leucocephalus*] eagles). The Great Horned Owl (*Bubo virginianus*), the most abundant large predatory bird at Kluane (peak densities of ca. 1 pair per 4 km²), was studied intensively in the valley by C. Rohner (Rohner and Doyle 1992, Rohner, unpubl. data) from 1988 to 1992.

METHODOLOGICAL PROBLEMS

Before presenting and discussing our results, we first comment on some methodological problems encountered in this study. First, there is the issue of biases in our data. We are confident that our seen sheet data provided a reliable index of the relative abundance of goshawks among years, despite some variability in the skill of observers. One of us (FID) was present during the collection of most of the seen sheet data, and his observations correlated well with those of other project workers. Most observers spent thousands of hours in the field and became very familiar with the commoner raptors at Kluane, including goshawks. These data stemmed from extensive field work during all seasons, not just from an intensive period of work during spring and summer. It is possible, however, that seasonal differences in sightings were affected to some degree by skill levels of seasonal workers, and by seasonal shifts in the type of field work. Summer workers were slightly less skilled on average, and they spent more time trapping mammals and sampling vegetation, whereas winter workers mainly did snow tracking. As sightings from vehicles showed similar trends to those on foot, we do not think that biases stemming from the type of work were large.

We are also confident that our methods yielded a useful index of the numbers of breeding birds, particularly after 1989, but we are not confident that we tallied all breeding birds present. Northern Goshawks at Kluane did not often fly above the forest canopy, and were thus hard to detect from the ground or air. When active nests were approached closely, females generally attacked us vigorously, but the rugged terrain and the size of the study area made it impossible to search every nook and cranny thoroughly.

As found by Kimmel and Yahner (1990), calls broadcast near known active nest sites at Kluane produced responses from only about half of the pairs tested. Therefore, our methods underestimated the numbers of breeding pairs, perhaps by about 50 per cent, even in the intensive study area (100 km²). We probably detected an even lower proportion of pairs in 1988 and 1989, before we used broadcast calls.

Data on diets reported here are also likely to be subject to biases. Birds were over-represented at plucking sites, and very small prey may have been taken by males but not brought to plucking sites or nests. Adult hares are too heavy (ca. 1.4 kg) for a male goshawk to carry any distance, and large adult hare remains at plucking sites and nests were probably mostly from kills made by the female hunting from the nest. Diets outside the breeding season must have been radically different from those of nesting birds, because of the much simpler prey base available in winter (hares, red squirrels, voles, small mustelids, corvids, chickadees and finches).

RESULTS AND DISCUSSION

NUMBERS OF HARES AND GOSHAWKS

Hare densities on unmanipulated plots at Kluane rose over six-fold from about 0.2 hare ha^{-1} in the spring of 1987 to a peak of 1.44 hares ha^{-1} in 1990 (Fig. 1). Hare numbers remained near this level in 1991, but declined fifteen-fold to below 0.1 hare ha^{-1} by the spring of 1993 (Fig. 1). No goshawks were sighted in the winter of 1988–1989, after the first spring with high hare numbers, but goshawk numbers increased sharply during the next three winters. The peak number of goshawk sightings in winter occurred just after the onset of the decline in hare numbers (Fig. 1). Rates of responses to broadcast goshawk calls also declined five-fold from 1990 to 1992 (Table 1).

Winter sightings (November–March) of gos-

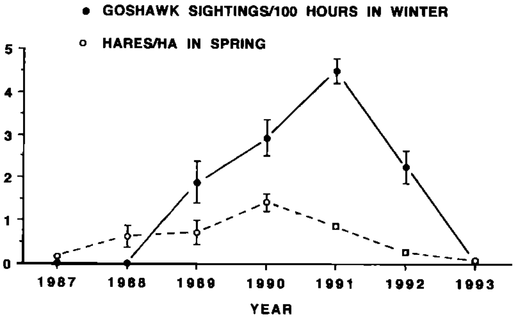

FIGURE 1. Mean number of goshawks sighted per month in winter (November to March), in relation to mean numbers of snowshoe hares live-trapped in spring (mean of two to three plots) at Kluane, Yukon. The bars represent one standard error.

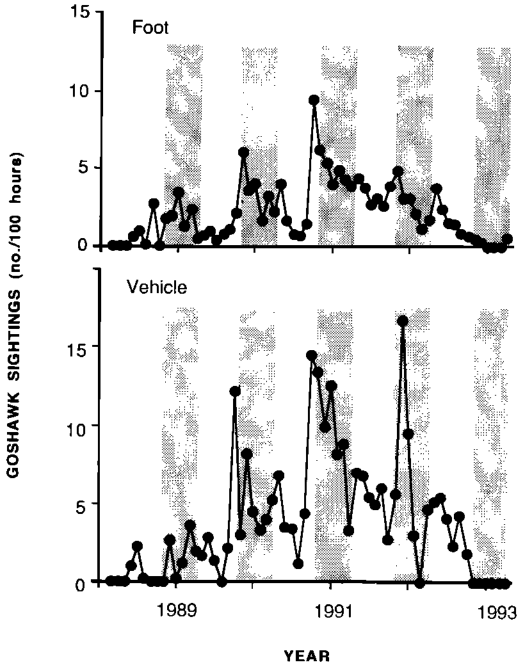

FIGURE 2. Monthly index of sightings (per 100 hours) of Northern Goshawks by observers on foot, and observers in vehicles. Shaded areas display the five winter months (November to March).

hawks were about twice as frequent from both vehicles and on foot (Fig. 2) as sightings in the previous summer (June–August) for the four years beginning in June 1988. However, goshawk numbers declined in the winter of 1991 to 1992, and they almost disappeared from Kluane in the winter of 1992 to 1993 (Fig. 2). An index of goshawk numbers at Rochester, Alberta, declined over four successive winters from 1970 to 1974, as hares declined from a peak (Keith and Rusch 1986).

These data all suggest that Northern Goshawk numbers at Kluane responded strongly to declining hare abundance. Declines in goshawk numbers from 1991 to 1993, however, may also have been affected by trends in other prey species, two of which decreased in numbers at about the same time as did hares. Spruce Grouse and Willow Ptarmigan both declined sharply in numbers from 1990 to 1991 and remained scarce up to 1993 (K. Martin and C. Esser, unpubl. data). In contrast to these declines in step with the decline in hare numbers, numbers of red squirrels declined briefly from 1989 to 1990 in response to a poor crop of spruce cones in 1989, but increased again in 1991 and remained stable thereafter (S. Boutin et al., unpubl. data). Arctic ground squirrel numbers remained relatively stable from 1990 to 1993 (A. Byrom, T. Karels, A. Hubbs, and R. Boonstra, unpubl. data). Mice and voles were scarce near the peak in hare numbers in 1990, but numbers of red-backed voles increased about ten-fold from 1990 to 1992, and remained high in 1993 (R. Boonstra et al., unpubl. data). Numbers of passerine birds in summer remained fairly stable from 1988–1992 (Folkard 1990, N. Folkard and J. Smith, unpubl. data).

Thus, Northern Goshawks at Kluane, like goshawks and other large avian predators at Rochester (McInvaille and Keith 1974, Adamcik et al. 1978, Adamcik and Keith 1978, Keith and Rusch 1986), showed a strong numerical response in step with a cyclic decline in snowshoe hare numbers. Declines in goshawk abundance at Kluane, however, may have been partly due to declines in other prey species as well as hares.

TABLE 1. RESPONSES OF NORTHERN GOSHAWKS TO BROADCAST GOSHAWK ALARM CALLS DURING THE BREEDING SEASON

Year	Total time of playback (min)	Number of nesting pairs responding	Number of birds without known nests responding	Pairs found per 100 minutes of broadcast
1990	2655	10	3	0.38
1991	3005	6	4	0.20
1992	2460	2	1	0.08

NEST SITE CHARACTERISTICS

Several other papers in this volume describe and discuss nest site characteristics of Northern Goshawks in detail. Information is also available from neighboring Alaska (McGowan 1975). We therefore present our information on nest sites for comparison with these other reports.

Six nests were located by reading signs left by goshawks on the ground, seven by broadcasting taped alarm calls (1990–1992 only), and two by tracking radios fitted to breeding birds. The remaining five nests were found by checking previously active nests.

We measured the habitat and stand type of 17 of the active nests located during the study. Eleven of the nests were entirely among mature trees and only two were in stands with >50% immature trees. Nine of the 17 nests were in mixed coniferous/deciduous stands, six were in pure spruce, and two in pure aspen. The mean height of ten nests in spruce trees was 7.4 ± 0.7 (SE) m, and spruce nest trees averaged 10.8 ± 0.4 m. Six nests in aspen averaged 5.8 ± 0.4 m in height (mean tree height 8.3 ± 0.3 m). Nests in deciduous trees were much more readily seen from both ground and air, and we thus may have underestimated the proportion of nests in spruce trees. Nests were not particularly close to water ($\bar{X} = 258 \pm 40$ m). Whereas goshawks often nest near water (e.g., Beebe 1978) to provide the incubating female with a nearby place to bathe and drink, water is readily available throughout the Kluane landscape in late spring and early summer from melting snow in small ponds and streams. Nest sites were clustered across years, with pairs often reusing the same stands of trees and nests.

Goshawk nests in Alaska (McGowan 1975) were in larger deciduous trees (mean height 9.1 m compared to 5.8 m at Kluane). Most nests studied in Alaska were in birch (*Betula papyrifera*), a species not found at Kluane. McGowan, however, did not search for nests in spruce trees. Elsewhere in North America, goshawks sometimes select stands of very large and old trees for nesting (other papers *this volume*). Large trees are rare at Kluane because of the high elevation and latitude, poor soils, and fire history of the Shakwak Valley. Goshawks, like Sparrowhawks (*Accipiter nisus*), are flexible in their choice of nesting trees and nesting habitat (Newton 1986) and do not require particularly large trees for nesting, provided their principal breeding requirements (an adequate prey base, and fairly open flight lanes) are met.

REPRODUCTIVE RESPONSES OF GOSHAWKS TO HARE DENSITY

The numbers of territorial and breeding pairs of goshawks detected changed markedly with hare densities (Table 2). No active nests were located in 1988, despite the presence of two resident birds fitted with radios. At least three pairs bred in 1989, and 11 pairs were located in 1990 at peak hare densities, eight of which bred. Five of the pairs detected in 1990 were in the intensive area, suggesting a minimum density of about 1 pair per 20 km^2. If we assume our index of the number of pairs underestimated the true number by 50% (see methodological problems, above), and if the density of goshawks in the intensive area was the same as in the rest of the study area, there were about 40 pairs of goshawks in the study area in 1990.

TABLE 2. BREEDING PERFORMANCE OF NORTHERN GOSHAWKS AT KLUANE, YUKON, FROM 1988 TO 1992

Year	Number of pairs located	Number of nests located	Mean number of young fledged per pair (SE)	Mean number young fledged per successful nest (SE)
1988	0	0		
1989	3	3	1.3 (0.88)	2.0 (0.35)
1990	11	8	2.8 (0.57)	3.9 (0.37)
1991	7	7	1.3 (0.47)	2.3 (0.25)
1992	3	1	0.0	0.0

Breeding success peaked in 1990, with 2.8 young being produced per pair and 3.9 young per successful pair. There was one nest failure in 1989, and no nest failures in 1990. Four of eight nests were preyed upon during 1991 and 1992. The identity of three of the nest predators was unknown; a fourth was a Great Horned Owl (Rohner and Doyle 1992), and the fifth was a wolverine (*Gulo gulo*). Peaks of sightings of birds each fall (September, October) from 1990 to 1992 suggested the appearance of pulses of newly-independent juveniles in these years.

As hare numbers declined, so did breeding success of goshawks, until in 1992 the single pair detected failed to breed successfully (Table 2, Fig. 3). McGowan (1975) also reported strongly reduced use of traditional nest sites and some reduction in breeding success by goshawks in central Alaska during a decline in hare numbers from 1971 to 1974.

As hare densities changed, the ratio of adult to immature goshawk sightings first declined slightly from 58% adults in 1990 (N = 43) to 49% adults in 1991 (N = 92), and then increased to 70% adults (N = 64) in 1992, and finally to 100% adults (N = 11) in 1993. These data agree with our data from nests in suggesting that reproductive success peaked in 1990, and that there was much less successful reproduction after 1991.

An interesting pattern was a peak in goshawk sightings in the breeding season in 1991, immediately after the onset of the decline in numbers of breeders (Fig. 3). This pattern suggests either (1) a pulse of non-breeding yearlings (see above) raised at peak hare numbers in 1990, (2)

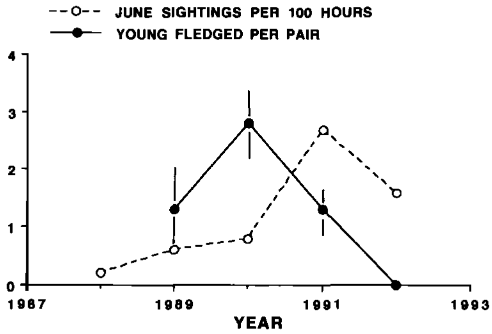

FIGURE 3. Breeding success of Northern Goshawks at Kluane, Yukon (mean number of young fledged per territorial pair), in relation to an index of abundance of goshawks during the breeding season. The bars are one standard error. No data are plotted for 1988, as no breeding pairs of goshawks were detected that year.

an apparent increase caused by non-breeding adult and immature birds ranging more widely in 1991 than in 1990, when they guarded nest areas closely, or (3) increased time spent hunting by goshawks as hare availability declined.

Levels of breeding success attained by goshawks at Kluane during the peak in hare abundance in 1990 equalled or exceeded those reported for southern populations of the species (see other articles *this volume*). Zachel (1985) also found good breeding success for goshawks in nearby Alaska during a snowshoe hare peak in 1979–1981.

In sum, goshawks at Kluane bred frequently and produced many young during the period of high hare density, but reproduced more poorly as hare numbers began to decline, in part because of increasing predation on goshawk eggs and nestlings. Goshawks virtually ceased reproducing after hares and some other prey species became rare in 1992.

Hunting Ranges

Both birds radio-tracked in May 1988 maintained stable ranges throughout the month, with the male using a 95% range of 40.0 km^2 (50 fixes over 30 days) and the female a 95% range of 28.8 km^2 (49 fixes over 30 days). These ranges are 3–4 times larger than values reported by Zachel (1985) for breeding goshawks in Alaska in 1979 and 1980, at approximately the same phase of the previous hare cycle.

Diets at Plucking Sites and Nests

Our main data on diets came from prey remains near nests (Table 3). Medium-sized mammals, particularly hares and squirrels, made up 77% of prey items and over 85% of biomass from 1989 to 1991. Hares accounted for over 55% of the total prey biomass over these three summers. Because of the over-representation of birds at plucking sites (see above), the use of mammals as prey was probably even greater than these estimates imply. Juvenile hares were taken most frequently in 1990, the year when goshawk reproductive success was highest. Ground squirrels were a dominant item in the diet in 1990, a year when red squirrel numbers were low because of poor over-winter survival, but were about as frequent as red squirrels at other times. Spruce Grouse and ptarmigan were also taken frequently from 1989 to 1991. Other birds taken included American Kestrels (*Falco sparverius*), Gray Jays (*Perisoreus canadensis*), and Northern Flickers (*Colaptes auratus*). Diets of goshawks breeding in boreal forest in nearby Alaska also contained about 90% of mammalian prey by biomass (Zachel 1985). At the southern edge of the boreal forest in Alberta, mammals made up 73% of the biomass in goshawk diets (Keith et al. 1977). Goshawks further south in North America generally killed more birds and fewer mammals (Reynolds and Meslow 1984, Bull and Hohmann *this volume*, DeStephano et al. *this volume*), but Boal and Mannan (*this volume*) also found heavy use of mammalian prey. In Europe, birds made up over 85% of prey items (Opdam 1975, Opdam et al. 1977, Widén 1987) and 91% of biomass (Widén 1987). Widén noted greater use of mammals in winter in Sweden, but Opdam et al. (1977) did not find such a switch in the Netherlands and Germany. These differences in the ratio of birds to mammals in goshawk diets probably occur principally because the goshawk is an opportunist, and the availability and relative sizes of avian and mammalian prey differ among sites.

Few data on goshawk diets were available from the summer of 1992, as the only nest found failed soon after the young hatched. These few data suggested a switch from mammals to birds in 1992, after hares had become scarce, and when grouse numbers were also declining from a peak in 1990. Radio-collared adult red squirrels were rarely taken by goshawks or unknown predators in summer or winter, although young-of-the-year with radios were preyed on by raptors in summer (K. Stuart-Smith and S. Boutin, unpubl. data). Goshawks caused a substantial proportion of winter deaths of radio-collared hares (17%), and we suspect that goshawks depended heavily on snowshoe hares as prey in winter. Widén (1987) also found that female goshawks killed mountain hares (*Lepus timidus*) in winter.

Goshawks accounted for about 10% of radio-collared hare mortalities in summer. The summer value is less reliable, because over half the summer kills could not be assigned to a predator

TABLE 3. MINIMUM NUMBERS OF PREY ITEMS (% OF TOTAL ITEMS PER YEAR) FOUND AT 16 NESTS OF NORTHERN GOSHAWKS AT KLUANE, YUKON

Prey species	1989	1990	1991	1992	Biomass (%)[1]
Adult snowshoe hare	13 (14)	32 (14)	16 (20)	1	35.4
Juvenile hare	9 (10)	57 (25)	14 (17)	0	22.7
Red squirrel	31 (34)	10 (4)	17 (21)	0	5.6
Arctic ground squirrel	16 (18)	76 (33)	17 (21)	1	22.0
Northern flying squirrel	1 (1)	0	0	0	0.1
Grouse-ptarmigan	12 (13)	31 (14)	9 (11)	2	12.4
Other birds	8 (9)	23 (10)	8 (10)	5	0.9
Voles-mice	1 (1)	0	0	0	0.01
Total prey items	91	229	81	9	

[1] Biomass (kg) values used: adult hare 1.41, red squirrel 0.24, ground squirrel 0.51, grouse/ptarmigan 0.57, other birds/voles 0.05 kg; for juvenile hares, see text. Samples of nests: 1989 = 3; 1990 = 8; 1991 = 4; 1992 = 1.

species and because some kills in summer may have been made by Red-tailed Hawks. The Northern Goshawk is one of the four most important hare predators at Kluane near peak hare numbers; the others are the lynx (*Lynx canadensis*), the coyote (*Canis latrans*), and the Great Horned Owl. These other three predators typically captured hares in open spruce forest, but 33% of 100 kills attributed to goshawks were in dense forest cover, although this comprised only 18% of habitats in the valley. Goshawks thus can capture hares in dense cover, where they are relatively safe from their other major predators in winter. Goshawks may therefore affect the habitat choices of hares, which generally avoid open areas where risk of predation is high (Hik 1994).

MIGRATORY STATUS OF GOSHAWKS AT KLUANE

Goshawk abundance in winter followed hare densities closely (Figs. 1, 2). Birds were present year-round during the period of high hare numbers from 1989 to 1991, and several birds remained in the summer of 1992. Sightings, however, dropped sharply in the winter of 1992–1993, after hare densities had declined to low levels. The sharp drop in numbers could have been because (1) goshawks migrated from the study area during winter in periods of low hare density, or (2) numbers of resident goshawks declined through mortality. Our data (Fig. 2) did not suggest any obvious fall exodus and spring return of goshawks as hare numbers declined, but we did note a change from resident to transient status of birds trapped before and during the hare decline. Thirteen of 14 birds fitted with radios in 1988 to 1990 remained in the study area for at least one month after capture during the periods of increasing and high hare numbers, but only one of five captured birds did so from 1991 to 1993 during the hare decline ($P = 0.002$, Fisher exact test). Mueller et al. (1977), and T. C. Erdman and D. F. Brinker (unpubl. data) have reported large southward flights of goshawks, including many adult birds, south of Lake Superior in years following declines in snowshoe hare numbers.

Concerning the local mortality hypothesis, no natural deaths of adult or immature goshawks were noted during the period of increasing and high hare densities from summer 1988 to spring 1991, but eight birds (five adults and three immatures) were found dead in either summer 1991 or the following winter, during the hare decline. Five of these were found as carcasses revealed after snow melt in spring, and these birds may have starved. Two birds were killed by Great Horned Owls, and another bird by an unknown raptor. Predation and food shortage thus combined to reduce breeding numbers and reproductive success of goshawks in the hare decline. This supports Rohner and Doyle's (1992) suggestion that strong predator-predator interactions occur in the boreal forest as hares become increasingly scarce. The abundant Great Horned Owl may be a key killer of other smaller predators in these interactions.

In summary, our data suggest that many Northern Goshawks at Kluane are resident during periods of high hare abundance. Declines in goshawk numbers from 1991 to 1993 were due to both increased local morality and increased movements induced by declines in the availability of snowshoe hares as prey, particularly in winter.

CONCLUSIONS

Data from boreal areas (McGowan 1975, Zachel 1985, this study), suggest that four factors characterize goshawk populations in the boreal forest: (1) year-round resident status during periods of high hare numbers; (2) increased nomadism and/or migration during hare declines; (3) increased mortality of adults, immatures, and eggs and nestlings, during declines in hare numbers; and (4) a partial or complete withdrawal of surviving birds from large parts of the boreal forest in winter during periods of low hare numbers.

As reported elsewhere (e.g., Beebe 1978, McGowan 1975, Zachel 1985, Widén 1987), goshawks breeding at high latitudes have broad diets, preying mainly on medium-sized mammals, supplemented by some medium-sized to large birds. Goshawks at Kluane preyed heavily on snowshoe hares in summer and winter from 1989 to 1991, but the few remaining breeders switched to smaller prey in 1992 after hare numbers declined markedly.

ACKNOWLEDGMENTS

Financial support for this work was provided by a Natural Sciences and Engineering Research Council (Canada) Collaborative Special Projects Grant, and by grants from the Metcalfe Foundation and the Northern Sciences Training Program. We thank many project personnel for collecting field data on goshawks, particularly M. O'Donoghue, C. Esser, T. Hucal, V. Nams, C. Rohner, S. Schweiger, and T. Wellicome. R. Boonstra, S. Boutin, A. Byrom, C. Esser, T. Karels, N. Folkard, A. Hubbs, M. O'Donoghue, C. Rohner, and K. Stuart-Smith kindly allowed us to cite their unpublished data on other species. The staff of Kluane Lake Research Station, particularly A., C., and J. Williams, provided considerable logistic help. G. Bortolotti, P. James, and L. Oliphant offered useful advice on methods. C. Rohner and M. Morrison helped improve the text, and L. Schwarzkopf helped with graphics. This paper is publication number 45 of the Kluane Project.

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Studies in Avian Biology No. 16:130–132, 1994.

TERRITORY FIDELITY, MATE FIDELITY, AND MOVEMENTS OF COLOR-MARKED NORTHERN GOSHAWKS IN THE SOUTHERN CASCADES OF CALIFORNIA

PHILLIP J. DETRICH AND BRIAN WOODBRIDGE

Abstract. Eighty adult Northern Goshawks (*Accipiter gentilis*) were marked with color bands during a 9-year period in northern California, and 119 nestlings were banded. Observations in subsequent years located 47% of the adult females and 40% of the adult males. Seventy-two percent of the adults located in consecutive years retained the mate from the previous year. There was no significant difference in mate retention among sexes. Males were significantly more likely to remain in the same territory from year to year than were females. Among hawks located in years subsequent to marking, 18.2% of the females and 23.1% of the males were found breeding in other territories 4–13 km from the location of marking. Two banded nestlings (1.7%) were recaptured as adult female breeders at distances of 16 and 24 km from their natal sites.

Key Words: *Accipiter gentilis*; color-marking; movements; Northern Goshawk; site and mate fidelity.

Since 1983, Northern Goshawks (*Accipiter gentilis*) have been marked on three USDA Forest Service ranger districts (RD) in northern California: the McCloud RD on the Shasta–Trinity National Forest (1983–1989), the Goosenest RD on the Klamath National Forest (1985–1993), and the Devil's Garden RD on the Modoc National Forest (1988–1992). The objectives of this marking were to evaluate mate fidelity and site fidelity, turnover of adults at territories, and movements among territories.

METHODS

Adult Northern Goshawks were captured at nest sites using the dho-gaza with a live Great Horned Owl (*Bubo virginianus*) as a lure (Bloom 1987, Bloom et al. 1992). Adult goshawks were banded with U.S. Fish and Wildlife Service (USFWS) aluminum bands on one leg, and with colored plastic bands with contrasting numerals on the other leg. Goshawks were identified in subsequent years either by re-trapping or by reading color bands with binoculars or spotting scope. The degree of annual follow-up effort varied considerably because of variation in personnel and funding. Typically, each year several hours were spent during the nestling period searching for nests and hawks in each area where nesting had been recorded in the past. In later years, taped goshawk calls were used to locate nests. On the Goosenest RD, standardized belt transects were employed to locate sites, and blinds were built to facilitate reading color bands. Climbers banded nestling goshawks with USFWS bands; nestlings were not marked with color bands. Most nests were climbed while the adult female was held hooded.

We did not reliably locate marked goshawks that did not nest or that failed during incubation, because early in the nesting season access was limited by snow and the goshawks were secretive. Because we were most successful in finding nests and trapping and identifying adults during the nestling period, this study was limited primarily to goshawks that were successful in hatching young.

We used the term "occupancy" to include any year in which a marked adult was found in a territory (including the year of marking). Goshawks that had not yet ended a period of occupancy were not included in calculations of duration of occupancy. We used the term "fidelity" to refer to consecutive years of occupancy or mate retention by marked individuals. A territory was defined as a cluster of nest sites with >1 year of recorded use (Woodbridge and Detrich *this volume*). Occasionally, marked adults were located in a territory even though the nest was not found. Because these adults demonstrated site fidelity, they were included in the analysis. Significance of proportional differences in fidelity to mate and site were analyzed using the log-likelihood ratio (Zar 1984:52).

RESULTS AND DISCUSSION

Through the 1991 season, we color-banded 47 adult females and 33 adult males, and banded 119 nestlings. Results include re-sightings through the 1992 season. Twenty-two females and 13 males were found in years following marking. Thus, 53% of the females and 60% of the males either died or were not found in subsequent years. Two goshawks banded as nestlings were located as breeders in subsequent years. One marked goshawk was found dead. At least one adult was marked in 46 territories. We attempted to locate marked birds in 194 territory-years (i.e., a year subsequent to marking during which searches or observations took place in the territory). Marked females were located in 98 (51%) of these opportunities, and marked males were located in 60 (31%).

OCCUPANCY AND FIDELITY TO MATES AND NEST TERRITORY

Territory occupancy by females ranged from 1 to 7 years, and averaged 1.8 years (SD = 1.3, N = 40). Because of the difficulty of finding nests

TABLE 1. SITE AND MATE FIDELITY AMONG MARKED REPRODUCTIVELY SUCCESSFUL NORTHERN GOSHAWKS IN SUCCESSIVE YEARS IN NORTHERN CALIFORNIA

Pattern	% males (N)	% females (N)	Overall (N)
Same mate	75.0 (12)	69.2 (13)	72.0 (25)
Same nest area	76.5 (17)*	71.4 (49)	73.1 (66)

* Significant difference between sexes (G = 5.2, df = 1, P < 0.025).

TABLE 2. MATE FIDELITY AMONG MARKED REPRODUCTIVELY SUCCESSFUL NORTHERN GOSHAWKS IN SUCCESSIVE YEARS IN THE SAME BREEDING TERRITORY IN NORTHERN CALIFORNIA

Pattern	% males (N)	% females (N)	Overall (N)
Same mate	80.0 (10)	69.2 (13)	73.9 (23)
Different mate	20.0	30.8	26.1

in consecutive years (Woodbridge and Detrich *this volume*), the observed mean occupancy was probably less than the actual.

Territory occupancy by males ranged from 1 to 3 years, and averaged 1.3 years (SD = 0.54, N = 27). The observed occupancy by males was also believed to be lower than the actual rate and cannot be directly compared with that of females because of the greater difficulty in trapping and observing males.

In 18 of 25 instances when mates were identified in consecutive years, the mate from the previous year was retained (Table 1). Mate retention did not differ significantly between sexes (G = 0.8, df = 1, P < 0.40). In 48 of the 66 instances in which adults in a territory were identified in consecutive years, marked adults remained in the territory. Males were significantly more likely to remain in the same territory from year to year than were females (G = 5.2, df = 1, P < 0.025).

Among the 23 adults that remained on the same territory in consecutive years and whose mate was known in those years (Table 2), there was no significant difference in mate retention between sexes (G = 3.6, df = 1) at P < 0.05, but at P < 0.10, males were more likely to retain the same mates than were females, suggesting a tendency in this regard.

Considerable variation was observed among adults that did not retain mates in consecutive years. For instance, in three territories observed for five-year periods, two males and two females bred in three different combinations. Another male bred with three different females in the same territory during a six-year period; one of these females was present in three non-consecutive years.

We remain uncertain as to the effects of our activities on site occupancy and fidelity. Among 17 occupied nests where no trapping or banding occurred, only two were occupied in the following year, indicating a high degree of movement in the undisturbed population. However, because these adults were not marked, fidelity patterns in the undisturbed population could not be determined for comparison.

MOVEMENTS

Among the 22 females located in years subsequent to marking, four (18.2%) were found breeding at a second territory. These movements ranged from 5.5 to 12.9 km (mean = 9.8 km, SD = 2.7). One of these females later returned to the territory where she had been marked; that territory had been occupied by another female during the interim. Among the 13 males located in years subsequent to marking, three (23.1%) were found breeding at a second territory. Their movements ranged from 4.2 to 10.3 km (mean = 6.5 km, SD = 2.7).

The distances to the nearest neighboring territory for most of the adults that moved were not reliably known. However, nearest-neighbor distances in intensively surveyed portions of the study area ranged from 1.3 to 6.1 km (mean = 3.3 km, SD = 0.3) (Woodbridge and Detrich *this volume*). All adult movements among territories were more than two standard deviations greater than the mean nearest-neighbor distance, and thus, it appears that few were likely to involve movements to neighboring territories.

Two of the 119 nestlings banded (1.7%) were recaptured as adult female breeders at distances of 16.1 and 24.2 km from their natal sites. One was captured in the fifth year following banding, the other in the seventh year following banding.

TURNOVER IN TERRITORIES

Analysis of turnover was problematic because of the high rate of attrition of territories (Woodbridge and Detrich *this volume*), movement among territories by both sexes, intermittent use of territories by individuals, and the need for more years for observations of hawks marked in recent years.

In 27 territories occupied in the year following marking of adults, eight (30%) were occupied by new females and six (23%) were occupied by new males. Among the 43 territories with marked females, 16 were occupied by different females during different years. One was occupied by three different females in a 6-year period, and another by four different females in an 8-year period.

Among the 34 territories with marked males, 13 were occupied by different males in different years; one was occupied by three males in an 8-year period.

To our knowledge, there are no published data on Northern Goshawks for comparison with the results of this study. Our data indicate that some previous assumptions about mate fidelity need re-examination, for instance statements by Jones (1979) and Palmer (1988) that goshawks probably mate for life.

Site fidelity reported for the congeneric European Sparrowhawk (*Accipiter nisus*) (Newton and Wyllie 1992) was similar to that found in our study in that about 70–75% of hawks found in successive years were on the same territory. Northern Goshawks on our study area retained mates more frequently than European Sparrowhawks (Newton and Marquiss 1982), which might be partially explained by a presumably higher mortality rate among the smaller sparrowhawks. Movements by male sparrowhawks were often to a neighboring territory, whereas females typically moved further (Newton and Wyllie 1992).

Our data provide only a partial understanding of tendencies and variation within the population studied, despite a substantial sustained effort in the field. Our experience indicates that obtaining complete demographic data for Northern Goshawks will demand efforts far exceeding those expended in the last 10 years on the Northern Spotted Owl (*Strix occidentalis caurina*) (Thomas et al. 1990). Researchers contemplating marking studies of Northern Goshawks must be committed to intensive long-term efforts to obtain adequate data.

ACKNOWLEDGMENTS

We gratefully acknowledge the contributions of B. Allison, R. L. Anderson, L. Andrews, N. Arey, K. Austin, P. Bloom, C. Cheyne, B. Koerner, I. Krell, T. Seager, D. Selby, K. Toner-Phelps, G. Studinski, and the dozens of volunteers who assisted in the field. We also wish to recognize the support and cooperation of the Goosenest RD, Klamath National Forest; the McCloud RD, Shasta–Trinity National Forest; and the Devil's Garden RD, Modoc National Forest. We thank B. Block, T. Erdman, and an anonymous reviewer for constructive comments on the manuscript.

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Studies in Avian Biology No. 16:133–136, 1994.

SURVIVAL OF NORTHERN GOSHAWKS IN THE SOUTHERN CASCADES OF CALIFORNIA

STEPHEN DESTEFANO, BRIAN WOODBRIDGE, AND PHILLIP J. DETRICH

Abstract. From 1983 to 1992, 95 Northern Goshawks (*Accipiter gentilis*) were marked with numbered, colored leg bands in northern California. We used capture-recapture techniques to estimate survival and resighting (or recapture) rates. Low sample size of marked birds and low resighting rates contributed to lack of fit of these data to the capture-recapture model. Survival estimates were generated, but variance was high. There were indications, however, that survival in goshawks varied among years, and survival of females was higher than males. We suggest that researchers interested in estimating survivorship of raptors strive for large numbers of marked birds, high resighting rates, and at least 5 years of data. These recommendations necessitate large study areas, large field crews, and careful consideration of model assumptions and raptor biology.

Key Words: *Accipiter gentilis*; California; capture-recapture; Northern Goshawk; survival.

In many wildlife studies, the presence of animals in certain habitats is often thought to be an indication of the quality of those habitats. Presence of individuals and estimates of relative densities among different habitats, however, may not be adequate to assess habitat quality (Van Horne 1983, Vickery et al. 1992). Other demographic parameters, such as reproductive success and survival, perhaps in conjunction with density, may be important indicators of habitat quality or "habitat fitness" (i.e., the capacity of a habitat to support optimum fecundity and high survival).

Much of the research conducted on Northern Goshawks (*Accipiter gentilis*) has focused on habitat use during the breeding season, often with some associated measure of reproductive success (Reynolds and Wight 1978, Crocker-Bedford 1990). Estimates of survival, however, are difficult to obtain for most species and involve some degree of uncertainty because absence of a marked individual does not necessarily indicate mortality. This is particularly true for studies of marked goshawks because of their low densities, large home ranges, high mobility, and secretive behavior.

Capture-recapture methodology (Cormack 1964, Jolly 1965, Seber 1965) conducted over long periods of time with an adequate sample of marked individuals, each of which has a high probability of being resighted ("visually recaptured"), can overcome these challenges. Capture-recapture models have been developed to account for the uncertainty inherent in survival estimation.

We used capture-recapture techniques to (1) explore the feasibility of calculating survival estimates for goshawks, (2) calculate point estimations and variances of survival, and (3) examine the yearly variation in survivorship and sex-related differences in goshawks. We then make recommendations for studies designed to estimate survival and suggest a cautious approach to interpretation of the results.

STUDY AREA AND METHODS

Northern Goshawks were captured on the Goosenest Ranger District of the Klamath National Forest and adjacent lands on the Shasta–Trinity and Modoc National Forests in the southern Cascades of northern California. The area was dominated by Sierra montane and upper montane forests. The former was comprised of Douglas-fir (*Pseudotsuga menziesii*), incense-cedar (*Calocedrus decurrens*), red fir (*Abies magnifica*), white fir (*A. concolor*), and ponderosa pine (*Pinus ponderosa*), and was interspersed with permanent streams and wet meadows with stands of lodgepole pine (*P. contorta*) and trembling aspen (*Populus tremuloides*). Upper montane forests consisted of pure stands of red fir, white fir, and lodgepole pine with some ponderosa pine. Stream drainages were few and typically dry. Forest seral stages were characterized by small patches of unmanaged mature forest interspersed among varying degrees of managed forest. Dominant silvicultural systems included thinning, shelterwood cuts, and small clearcuts.

Surveys for nests were conducted on 10,440 and 10,230 ha blocks in Sierra montane and upper montane forest types, respectively. We used conspecific alarm and begging tapes to elicit responses from adult and fledgling goshawks and visual clues (feathers, prey remains, nest structures, whitewash) to locate nests (Kimmel and Yahner 1990, Kennedy and Stahlecker 1993). In addition, about 20 nests outside of the study blocks were monitored. Adult goshawks were captured at nests with dho-gaza sets with a live Great Horned Owl (*Bubo virginianus*) as a decoy (Bloom et al. 1992). Adults were marked with uniquely numbered plastic colored leg bands and U.S. Fish and Wildlife Service aluminum leg bands. We used camouflaged blinds and spotting scopes to observe marked adults at nests in subsequent years; some bands were read when adults were re-trapped in subsequent years.

We input capture-resighting data as a capture history matrix, and used program RELEASE for data summarization and goodness-of-fit tests (Burnham et al.

TABLE 1. NUMBER OF FEMALE AND MALE NORTHERN GOSHAWKS BANDED IN THE SOUTHERN CASCADE RANGE, CALIFORNIA, 1983–1992

Year	Female	Male
1983	0	3
1984	2	2
1985	2	6
1986	2	6
1987	8	7
1988	6	6
1989	4	4
1990	2	6
1991	4	2
1992	10	13
Totals	40	55

1987). Goodness-of-fit tests examine the data with a series of χ^2 contingency tables to determine if the data fit the capture-recapture model. In RELEASE, goodness-of-fit has two components that look for differences in survival and recapture rates among cohorts (groups rereleased on different occasions; TEST 2) and subcohorts (individuals with different capture histories; TEST 3). Differences, shown by low P-values, among cohorts or subcohorts indicate lack of fit. We used program SURGE (Lebreton et al. 1992) to derive point estimates and variances of survival. Models used for estimation of survival were based on the Cormack-Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) model $\{\phi, p\}$, where ϕ = survival and p = probability of resighting.

We examined eight models, where ϕ and p were assumed to vary among years (subscript t) and between sexes (subscripts F for female and M for male). Twelve models were used to evaluate the interaction between time and sex. We used Akaike's Information Criteria (AIC), which is a numerical measure based on the deviance and the number of parameters in a model, and the principle of parsimony to select the model that best fit the data with the fewest number of parameters, and was still biologically reasonable (i.e., the "best" model) (Burnham et al. 1987, Lebreton et al. 1992).

RESULTS

We marked 95 adult goshawks with color bands and collected resightings of these marked birds from 1983 to 1992 (Tables 1, 2). For all goshawks (i.e., females and males combined) goodness-of-fit tests indicated that there was a definite lack of fit of the data to the capture-recapture model at the cohort and subcohort levels (χ^2 = 12.9, df = 7, P = 0.07 and χ^2 = 16.6, df = 12, P = 0.16 for TESTS 2 and 3, respectively), and overall fit of the data to the model was inadequate (χ^2 = 29.6, df = 19, P = 0.06 for TEST 2 + TEST 3; Burnham et al. 1987:71–77).

We first examined two sets of nested models to estimate survival (Table 3). Time-specific models revealed that there may be yearly differences in survival of goshawks, as model $\{\phi_t, p\}$ had the lowest AIC value, with $\{\phi_t, p_t\}$ as a competitive model (Likelihood ratio test, χ^2 = 4.67, df = 7, P = 0.70). The model with no time specificity ($\{\phi, p\}$) was not competitive (χ^2 = 30.6, df = 8, P = 0.0002). Survival rates were not estimable in some years because of low sample sizes (Table 4). According to our analysis, survival and resighting probabilities were higher for females than for males, but wide confidence intervals, due mainly to low sample sizes, precluded us from demonstrating a statistical difference (Table 4).

We then examined 12 models where the parameters ϕ and p were allowed to vary as an interaction between time (years) and sex (Table 3). The model $\{\phi_{Ft}, \phi_{Mt}, p\}$ had the lowest AIC value, which indicated that survival varied among years and between sexes (Table 4).

TABLE 2. MARK-RECAPTURE DATA ARRAY FOR NORTHERN GOSHAWKS IN THE SOUTHERN CASCADES, CALIFORNIA, 1983–1992. R_i IS THE NUMBER OF GOSHAWKS MARKED AND RELEASED ON THE iTH OCCASION (OR YEAR OF STUDY), m_{ij} THE NUMBER OF GOSHAWKS MARKED AND RELEASED ON OCCASION i THAT WERE RECAPTURED OR RESIGHTED ON OCCASION j, AND r_i THE TOTAL NUMBER OF GOSHAWKS MARKED AND RELEASED ON OCCASION i THAT WERE LATER RECAPTURED (= Σm_{ij})

		m_{ij} for j =									
i	R_i	2	3	4	5	6	7	8	9	10	r_i
1	3	1	1	0	0	0	0	0	1	0	3
2	5		1	1	1	1	0	0	0	0	4
3	10			6	3	1	0	0	0	0	10
4	15				9	0	0	0	0	0	9
5	28					13	1	0	0	0	14
6	27						7	1	0	0	8
7	16							5	0	0	5
8	14								4	2	6
9	11									3	3

TABLE 3. Capture-recapture Models, where ϕ is Survival Rate and p is Recapture Rate, Used to Estimate Survival in Northern Goshawks in the Southern Cascades of California, 1983–1992. Associated Akaike's Information Criteria (AIC = [2 × No. of Parameters] + Deviance) is Used to Evaluate Related Models; Lowest AIC Value Indicates the Best Model (i.e., the Model with the Fewest Parameters and Fits the Data and is Biologically Reasonable). Subscript t Indicates Time (i.e., Survival and Recapture Rates Estimated for Each Year, 1983–1990); Subscripts F and M Indicate Females and Males, Respectively

Model	No. of parameters	Deviance	AIC
	Time-specific models		
$\{\phi_t, p_t\}$	17	236.53	270.53
$\{\phi_t, p\}$	10	241.20	261.20
$\{\phi, p_t\}$	10	258.08	278.08
$\{\phi, p\}$	2	271.82	275.82
	Sex-specific models		
$\{\phi_F, \phi_M, p_F, p_M\}$	4	268.77	276.77
$\{\phi_F, \phi_M, p_{F+M}\}$	3	269.51	275.51
$\{\phi_{F+M}, p_F, p_M\}$	3	269.43	275.43
$\{\phi_{F+M}, p_{F+M}\}$	2	271.82	275.82
	Time- and sex-specific models		
$\{\phi_{Ft}, \phi_{Mt}, p_{Ft}, p_{Mt}\}$	34	223.21	291.21
$\{\phi_{Ft}, \phi_{Mt}, p_{Ft}, p_M\}$	27	231.69	285.69
$\{\phi_{Ft}, \phi_{Mt}, p_F, p_{Mt}\}$	27	227.40	281.40
$\{\phi_{Ft}, \phi_{Mt}, p_F, p_M\}$	20	235.88	275.88
$\{\phi_{Ft}, \phi_M, p_{Ft}, p_{Mt}\}$	27	234.86	288.86
$\{\phi_F, \phi_{Mt}, p_{Ft}, p_{Mt}\}$	27	236.70	290.70
$\{\phi_F, \phi_M, p_{Ft}, p_{Mt}\}$	20	248.31	288.31
$\{\phi_{Ft}, \phi_M, p_{Ft}, p_M\}$	19	243.81	281.81
$\{\phi_F, \phi_{Mt}, p_F, p_{Mt}\}$	19	248.21	286.21
$\{\phi_{Ft}, \phi_M, p_F, p_{Mt}\}$	20	239.05	279.05
$\{\phi_F, \phi_{Mt}, p_{Ft}, p_M\}$	20	245.14	285.14
$\{\phi_{Ft}, \phi_{Mt}, p\}$	19	236.50	274.50

TABLE 4. Maximum Likelihood Estimates of Survival (ϕ) and Probability of Resighting (P) for Northern Goshawks in the Southern Cascade Range, California, 1983–1992, Based on Capture-recapture Techniques. Numbered Subscripts Indicate the Year for which Survival Is Estimated; Subscripts F Indicate Survival Estimates for Females, M for Males. Estimates Are Shown for Models with the Lowest AIC Values (See Text for Further Explanation)

Model	Parameter	ϕ	SE(ϕ)	P	SE (P)
$\{\phi_t, p\}$	ϕ_{83}	Inest.[1]	Inest.	0.54	0.06
	ϕ_{84}	0.91	0.15		
	ϕ_{85}	Inest.	Inest.		
	ϕ_{86}	0.94	0.12		
	ϕ_{87}	0.71	0.14		
	ϕ_{88}	0.39	0.11		
	ϕ_{89}	0.43	0.14		
	ϕ_{90}	0.58	0.19		
$\{\phi_{Ft}, \phi_{Mt}, p\}$	ϕ_{F83}	Inest.	Inest.	0.54	0.07
	ϕ_{F84}	0.85	0.19		
	ϕ_{F85}	Inest.	Inest.		
	ϕ_{F86}	0.93	0.15		
	ϕ_{F87}	0.80	0.18		
	ϕ_{F88}	0.44	0.15		
	ϕ_{F89}	0.35	0.17		
	ϕ_{F90}	0.81	0.27		
	ϕ_{M83}	Inest.	Inest.		
	ϕ_{M84}	Inest.	Inest.		
	ϕ_{M85}	Inest.	Inest.		
	ϕ_{M86}	0.94	0.30		
	ϕ_{M87}	0.57	0.22		
	ϕ_{M88}	0.31	0.16		
	ϕ_{M89}	0.60	0.31		
	ϕ_{M90}	0.20	0.19		

[1] Parameter inestimable.

DISCUSSION

Much interest has been generated by the estimates of survival and associated population rate of change (λ) generated for the federally listed Northern Spotted Owl (*Strix occidentalis caurina*) (Anderson and Burnham 1992). We were able to calculate survival estimates for goshawks using the same capture-recapture methodology, but these estimates were imprecise due to small samples of marked birds and low resighting rates. In addition, the estimates that were produced were likely biased low because some marked goshawks emigrated off of the study area, and only birds that were associated with successful nests were resighted. These problems contributed to the lack of fit of the data to the capture-recapture model, resulting in low resighting probabilities and biased parameter estimates. However, empirical estimates of survival for goshawks in Arizona by Leslie et al. (pers. comm.) showed that survival may indeed be higher than our estimates, but their data did support the conclusion that female survival is higher than male survival.

We recommend to researchers wishing to estimate ϕ and λ that they strive for large numbers of banded birds, the highest resighting rates possible, and >5 years of data collected over a broad geographic area. Opportunities to coordinate banding and resighting efforts with adjacently located studies should be considered and encouraged. In addition, we recommend that researchers become familiar with all the assumptions of capture-recapture models when planning their study (see Burnham et al. 1987:51–54). Capture and recapture episodes are assumed to be instantaneous, an obviously unrealistic requirement. Confining banding and resighting efforts to as short a time period as possible, however, would move toward fulfilling this assumption. A 1-month capture and resighting period may be realistic for field conditions. Another important assumption is that marks not be lost or misread. Color band loss over time and error in identifying bands needs to be assessed.

Studies such as these will require large field crews and will be expensive. We strongly suggest that the biology of Northern Goshawks, such as their wide-ranging habits and mobility, be considered carefully when designing a study and interpreting results of survival estimation. We believe that these recommendations will be helpful in survival studies of other raptor species as well.

ACKNOWLEDGMENTS

Funding for this project was provided by the USDA Forest Service, the U.S. Fish and Wildlife Service, and the California Department of Fish and Wildlife. We thank the many field assistants who helped capture and band goshawks. Support for computer analyses was provided by the Oregon Cooperative Wildlife Research Unit and Oregon State University. This manuscript benefitted from the thoughtful reviews of J. C. Bednarz, R. J. Steidl, and G. C. White.

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