Distribution of Picoides woodpeckers in relation to habitat disturbance within the Yellowstone area
by Nancy Jean Hoffman

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management
Montana State University

Abstract:
Forest structure characterized as old-growth (large diameter trees, snags, down and decaying wood/logs) supports the highest density and diversity of cavity-nesting birds. Prior to the 20th century, forested habitats within the Intermountain West have been shaped by natural disturbances. Subsequently, forests were largely shaped by silvicultural practices and widespread road networks. Broad-scale changes in landscape pattern and patch-scale changes in forest composition and structure may have strong impacts on woodpeckers and snag-dependent avian species. Extensive forest harvest practices along the eastern boundary of the Targhee National Forest, large-scale fires along the adjacent western boundary of Yellowstone National Park, and a diversity of resident, woodpecker species provided an excellent opportunity to improve understanding of, and management practices of, Picoides species. The objectives of this study were to determine the distribution of active nest-tree cavities of four Picoides species in three lodgepole pine strata (undisturbed, human disturbed, and naturally disturbed) and to estimate habitat characteristics of nest sites used by Picoides species. We (i.e., field crews and I) searched for active cavities along 1,500-m transects within each stratum and sampled vegetation within three plot types (i.e., cavity sites, associated random sites, and truly random sites) during two consecutive field seasons (May -September, 1995 and 1996). In each year, active cavities were more likely to be found in the postfire lodgepole pine stratum than in the two other strata (i.e., undisturbed and human disturbed). Within the postfire lodgepole pine stratum, Three-toed and Black-backed woodpeckers were each 0.17 (e -1.77) [90% CI =0.02 (e -3 73) to 0.77 (e -0.26), P =.04] times as likely to be found nesting than were Hairy Woodpeckers in 1995. In contrast, within the postfire lodgepole pine stratum in 1996, neither Three-toed Woodpeckers (P = 1.00) nor Black-backed Woodpeckers (P =0.52) were more likely to be found nesting than were Hairy Woodpeckers. Size, condition, and quantity of down woody debris differentiated among nest sites of the three Picoides species. Because I found burned habitat more likely to be used by Picoides species than human disturbed or undisturbed habitat and because forest isolates no longer have the capacity for fire events of representative scale and intensity, I believe there are implications affecting the persistence of the species and their ability to track postfire habitat within the region. Thus, there is a need to consider the frequency, intensity, and juxtaposition of fire over the regional landscape when considering the viability of these rare species.

DISTRIBUTION OF *PICOIDES* WOODPECKERS IN RELATION TO HABITAT DISTURBANCE WITHIN THE YELLOWSTONE AREA

by

Nancy Jean Hoffman

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Fish and Wildlife Management

MONTANA STATE UNIVERSITY-BOZEMAN
Bozeman, Montana

August 1997

APPROVAL

of a thesis submitted by

Nancy Jean Hoffman

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

Jay Rotella Jay Rotella 8/4/97
(Signature) Date

Approved for the Department of Biology

Ernest Vyse E R Vyse Aug 4/97
(Signature) Date

Approved for the College of Graduate Studies

Robert L. Brown R L Brown 8/8/97
(Signature) Date

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a master's degree at Montana State University-Bozeman, I agree that the Library shall make it available to borrowers under rules of the Library.

If I have indicated my intention to copyright this thesis by including a copyright notice page, copying is allowable only for scholarly purposes, consistent with "fair use" as prescribed by U.S. Copyright Law. Requests for permission for extended quotation from or reproduction of this thesis in whole or in parts may be granted only by the copyright holder.

Signature________________________

Date 4 August 1997

ACKNOWLEDGMENTS

This research was funded through a Challenge Cost Share Agreement. The cooperators include: Idaho Department of Fish and Game; Intermountain Region, USFS; Montana Department of Fish, Wildlife, and Parks; Montana State University; Targhee National Forest; U.S. Fish and Wildlife Service; Yellowstone Ecosystem Studies; and Yellowstone National Park. A personal thank you to the folks that helped with knowledge, logistics, field support, and moral support. Drs. Andy Hansen and Al Zale provided guidance as my committee members. Dr. Jay Rotella served as my graduate committee chair and provided guidance, assistance in data analysis, editing, and moral support. A big thanks to Drs. Steve Cherry and Marty Hamilton from the Statistics Department, and Dr. Mark Taper from the Biology Department for their brain power, optimistic attitudes and patience. I appreciate and cherish the support of my field crews, friends, family, fellow graduate students, Luna and peanut-head. Hopefully, the woodpeckers will benefit from this research.

TABLE OF CONTENTS

Page

LIST OF TABLES vii

LIST OF FIGURES viii

ABSTRACT ix

INTRODUCTION 1

STUDY AREA 6

METHODS 10
- Sampling Design 10
- Data Collection 12
  - Nest Searching 12
  - Vegetative Sampling 13
- Data Analysis 16
  - Distribution of Nests Among Strata 16
  - Interspecific Comparisons of Cavity Plots 17
  - Intraspecific Comparisons of Occupied and Unoccupied Habitats 21

RESULTS 23
- Interspecific Nest Site Distribution Among Strata 24
- Interspecific Comparisons of Cavity Plots 29
  - Hairy Woodpecker versus Three-toed Woodpecker 29
  - Hairy Woodpecker versus Black-backed Woodpecker 30
  - Black-backed Woodpecker versus Three-toed Woodpecker . . . 30
  - Simultaneous Comparisons of All Three Woodpecker Species . 31
- Intraspecific Comparisons of Occupied and Unoccupied Habitat 35
  - Hairy Woodpecker Cavity Plots versus Random Plots 35
  - Hairy Woodpecker Cavity Plots versus Associated Plots 35
  - Three-toed Woodpecker Cavity Plots versus Random Plots . . . 36
  - Three-toed Woodpecker Cavity Plots versus Associated Plots . 36
  - Black-backed Woodpecker Cavity Plots versus Random Plots . 37

TABLE OF CONTENTS--continued

Page

Black-backed Woodpecker Cavity Plots versus Associated Plots 37
Simultaneous Comparisons of All Plot Types 38

DISCUSSION 42
Interspecific Comparisons of Cavity Plots 44
Intraspecific Comparisons of Occupied and Unoccupied Habitat 47
Scope and Limitations 50

MANAGEMENT AND RESEARCH IMPLICATIONS 53

LITERATURE CITED 57

APPENDIX A 68

APPENDIX B 72

LIST OF TABLES

Table

Page

1. Four *a priori* logistic regression models using vegetation characteristics to differentiate among cavity, associated, and random plots 19

2. Number of quadrats (1500 m x 1500 m) containing active nest-cavities within three strata of lodgepole pine 25

3. Distributions of *Picoides* species among three strata of lodgepole pine habitat 26

4. Habitat characteristics of cavity plots among three *Picoides* species 69

5. Description of vegetation variables measured at cavity, associated, and random 11.3-m radius plots 73

LIST OF FIGURES

Figure

Page

1. Shaded relief of northwestern portion of the Greater Yellowstone Area . 7
2. Active cavity-nest sites of three *Picoides* species overlaid on quadrat grid (1500 m x 1500 m) 9
3. Arrangement of cavity plots (CP), associated plots (AP), and random plots (RP) 15
4. Proportion of quadrats within three strata that contained nests of Three-toed (TTWO), Black-backed (BBWO), and Hairy (HAWO) woodpeckers 28
5. Box-notch plots of scores on discriminant function 1 for cavity plots of three species of *Picoides* 33
6. Scores and 90% confidence ellipses of the means on discriminant functions 1 and 2 for cavity plots of three species of *Picoides* 34
7. Box-notch plots of scores on discriminant function 1 for cavity, associated, and random plots of three species of *Picoides* 40
8. 90% confidence ellipses of the means on discriminant functions 1 and 2 for cavity, associated, and random plots for three species of *Picoides* . 41

ABSTRACT

Forest structure characterized as old-growth (large diameter trees, snags, down and decaying wood/logs) supports the highest density and diversity of cavity-nesting birds. Prior to the 20th century, forested habitats within the Intermountain West have been shaped by natural disturbances. Subsequently, forests were largely shaped by silvicultural practices and widespread road networks. Broad-scale changes in landscape pattern and patch-scale changes in forest composition and structure may have strong impacts on woodpeckers and snag-dependent avian species. Extensive forest harvest practices along the eastern boundary of the Targhee National Forest, large-scale fires along the adjacent western boundary of Yellowstone National Park, and a diversity of resident, woodpecker species provided an excellent opportunity to improve understanding of, and management practices of, *Picoides* species. The objectives of this study were to determine the distribution of active nest-tree cavities of four *Picoides* species in three lodgepole pine strata (undisturbed, human disturbed, and naturally disturbed) and to estimate habitat characteristics of nest sites used by *Picoides* species. We (i.e., field crews and I) searched for active cavities along 1,500-m transects within each stratum and sampled vegetation within three plot types (i.e., cavity sites, associated random sites, and truly random sites) during two consecutive field seasons (May - September, 1995 and 1996). In each year, active cavities were more likely to be found in the postfire lodgepole pine stratum than in the two other strata (i.e., undisturbed and human disturbed). Within the postfire lodgepole pine stratum, Three-toed and Black-backed woodpeckers were each 0.17 ($e^{-1.77}$) [90% CI =0.02 ($e^{-3.73}$) to 0.77 ($e^{-0.26}$), $\underline{P}$ =.04] times as likely to be found nesting than were Hairy Woodpeckers in 1995. In contrast, within the postfire lodgepole pine stratum in 1996, neither Three-toed Woodpeckers ($\underline{P}$ =1.00) nor Black-backed Woodpeckers ($\underline{P}$ =0.52) were more likely to be found nesting than were Hairy Woodpeckers. Size, condition, and quantity of down woody debris differentiated among nest sites of the three *Picoides* species. Because I found burned habitat more likely to be used by *Picoides* species than human disturbed or undisturbed habitat and because forest isolates no longer have the capacity for fire events of representative scale and intensity, I believe there are implications affecting the persistence of the species and their ability to track postfire habitat within the region. Thus, there is a need to consider the frequency, intensity, and juxtaposition of fire over the regional landscape when considering the viability of these rare species.

INTRODUCTION

Prior to the 20th century, vegetation of the central Rocky Mountains (Intermountain West) was influenced by natural disturbances (fire, insects, avalanches, disease, floods)(Amman 1991, Baker 1992, Arno 1993). Fires and mountain pine beetle (*Dendroctus spp.*) irruptions were the most common natural disturbances in lodgepole pine (*Pinus contorta*)/subalpine fir (*Abies lasiocarpa*) dominated forests (Arno 1993, Gara et al. 1985, Lotan et al. 1985). However, beginning early in the 20th century, fire suppression and silvicultural practices played an increasing role as disturbance agents. These "human" disturbances altered the intensity and frequency of natural disturbances (Hejl 1994, Hutto 1995, Thompson et al. 1995). These land-management practices may degrade or destroy woodpecker habitat by removing potential nesting and foraging substrates and altering primary structural characteristics of the forest.

Because of concern regarding broad-scale alterations of forested landscapes, numerous studies of woodpeckers and other cavity-nesters have been conducted in a variety of forested habitats [Douglas fir (*Pseudotsuga menziesii*), Western larch (*Larix occidentalis*), ponderosa pine (*Pinus ponderosa*), and aspen (*Populus tremuloides*)]. However, assemblages of birds within lodgepole pine forests have been scarcely studied despite recent broad-scale changes in the spatial and structural characteristics of lodgepole pine forests. In fact, they are among the least studied forest avifaunas in North America (Hein 1980).

Lodgepole pine is distributed broadly throughout the Intermountain West. Mountain pine beetle epidemics, large fuel accumulations, and stand replacement fires are a normal sequence for unmanaged lodgepole pine ecosystems (McGregor and Cole 1985). Although forest managers may view mountain pine beetles as highly destructive to forests, these beetles play an integral role in the historic cycle of fire and lodgepole pine re-invasion that has maintained lodgepole pine forests. The natural cycle creates diverse landscapes that contain a mosaic of forest age classes with variable species composition. In addition, the landscape of the Intermountain West has historically been dominated by even-aged, pure stands of lodgepole pine forests (Lotan and Perry 1983).

Lodgepole pine forests on federal, state, and private lands adjacent to Yellowstone National Park have been intensively managed since mountain pine beetle outbreaks during the 1970's. Clearcutting and deadwood removal have greatly reduced fuel accumulation. Thus, normal lodgepole pine stand dynamics have been altered. Accelerated harvest of dead standing and down trees has affected about 50,000 hectares of habitat distributed along the western boundary of Yellowstone National Park and the Targhee National Forest.

Broad-scale changes in landscape pattern, and patch-scale changes in forest composition and structure, may affect woodpeckers in lodgepole pine forests. Forest management activities have removed trees of the size and condition selected for by both mountain pine beetles and cavity-dependent avian species (Cole and Amman 1969, Bull 1983). Large-scale removal of dying, dead, and down trees that serve as susceptible hosts for insects and foraging habitat for woodpeckers adversely affects the abundance and diversity of a variety of cavity-nesters (Jackson 1979, Thomas 1979, Conner and Rudolph 1991, Hutto 1995). Because of altered disturbance regimes, woodpeckers as a group may have declined in abundance (Angelstam and Mikusiński 1994). Based on forest changes and bird-habitat relations, Hejl (1994) speculated that Black-backed (*Picoides arctus*), Downy (*P. pubescens*), Hairy (*P. villosus*), and Three-toed (*P. tridactylus*) woodpeckers have declined over the past 100 years.

Black-backed and Three-toed woodpeckers are of special concern due to lack of information regarding their populations within the region and concern that the species may be habitat specialists that depend on disturbance. Woodpeckers depend on key habitat traits (e.g., diameter of tree, decay and/or disease level, basal area, tree species, and canopy cover) for excavation and foraging (Jackson 1979, Miller and Miller 1980, Taylor and Barmore 1980, McClelland and Schmidt 1992, Caton 1996). Forest structure characterized as old growth (e.g., large diameter trees, snags, a high incidence of broken tops and diseases, and down and decaying wood/logs) supports the highest density and diversity of cavity-nesters (McClelland and Schmidt 1992).

Significant positive correlations exist between snag density and the abundance of primary cavity-nesters (i.e., species that create their own holes for nesting) in North American coniferous forests (Rapheal and White 1984, McComb et al. 1986, Carey et al. 1991). However, researchers disagree about whether or not removing trees affects *Picoides* species. Miller and Bock (1972) suggested that interspecific interactions may increase as the density of trees suitable for nesting declines. However, Lawrence (1967) reported that no intraspecific conflicts occurred among Hairy Woodpeckers in Ontario even when the birds nested in very close proximity. Miller and Miller (1980) suggested that birds may use substandard trees when densities of suitable trees are low, which increases susceptibility of woodpeckers to predation and other hazards. Given the lack of data, studies of how woodpeckers respond to human and natural disturbance are needed in the Intermountain West.

The Targhee National Forest (TNF) adjacent to Yellowstone National

Park (YNP) contains a diversity of primary cavity-nesters. Large tracts of lodgepole pine forest under various disturbance regimes are closely juxtaposed and provide opportunity to study the dynamics of woodpeckers in areas of naturally- and human-disturbed lodgepole pine. Knowledge of factors that limit species abundance is necessary to formulate effective management guidelines and to predict the effects of habitat alteration (Waters et al. 1990).

I designed this study to: (1) determine the nesting distributions of four *Picoides* species (Three-toed Woodpecker, Black-backed Woodpecker, Downy Woodpecker, and Hairy Woodpecker) in three lodgepole pine strata (i.e., undisturbed, human disturbed, and naturally disturbed), (2) estimate habitat characteristics of nest sites used by *Picoides* species, and (3) develop management recommendations for maintaining nesting habitat for *Picoides* species.

STUDY AREA

The study area straddled the southern portion of the western boundary of Yellowstone National Park and extended about six kilometers east and west of the Targhee National Forest-Yellowstone National Park boundary (44° 22' N, 111° 12' W; 44° 26' N, 111° 06 W) (Fig. 1). Island Park (TNF), within Fremont County, Idaho, and Bechler Meadows (YNP), within Teton County, Wyoming, represented the northern and southern limits of the study area (44° 22' N, 111° 12' W; 44° 10' N, 111° 07 W), respectively.

The study area encompassed about 9,500 ha on the Ashton and Island Park districts of the Targhee National Forest and about 15,100 ha on the Yellowstone National Park (Fig. 1). About 3,400 ha were within the 1994 Robinson Creek burn, a mosaic of burned and unburned forest resulting from a fire that varied in intensity, which was located in the southwest corner of Yellowstone National Park. The remaining 11,700 ha within Yellowstone National Park were located north and south of the 1994 Robinson Creek burn and south of the 1988 North Fork burn along the southern portion of the west boundary of Yellowstone National Park .

The study area was dominated by rhyolite soils and rhyolitic ash-flow tuff. Glacial till derived from rhyolite and basalt with andesite rock fragments

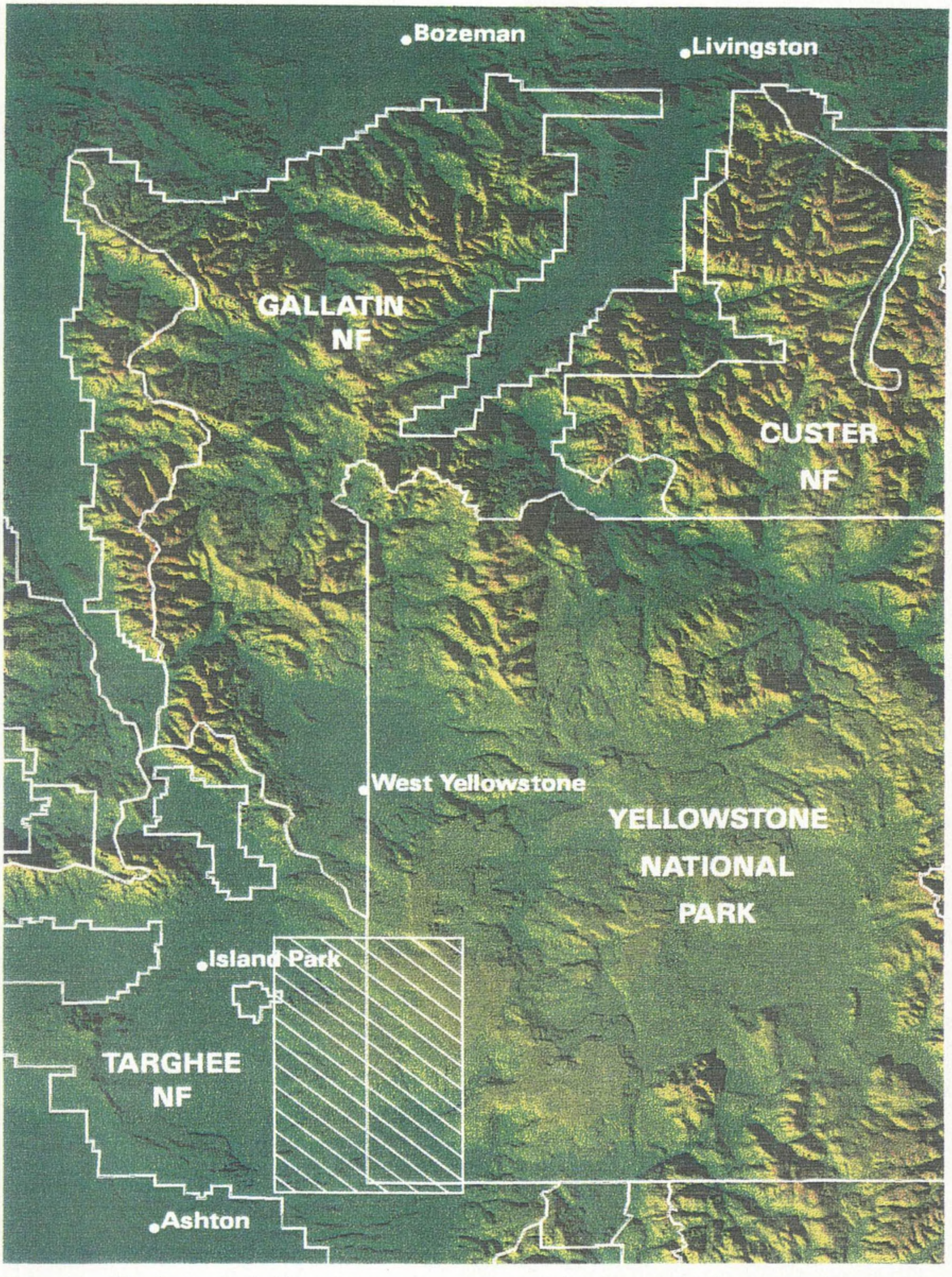


Figure 1. Shaded relief of northwestern portion of the Greater Yellowstone Area, with study area highlighted in white hatching.

also occurred at lower levels throughout the study area. The high-elevation southwest plateaus (1,830 m to 2,500 m) were generally flat to rolling terrain, moderately dissected by river gorges and intermittent streams (Rodman et al. 1996). Lodgepole pine dominated the study area, with scattered patches of aspen, Douglas-fir, and subalpine fir. The forested landscape of the Targhee National Forest resembled a patchwork of delineated various single-aged stands (i.e., seedling, sapling, pole, mature, overmature) that were relatively uniform in shape. Yellowstone National Park's forested landscape was a matrix of stands that blended naturally from pole-aged through overmature stands (Fig. 2).

The Bechler Meadows weather station, located in the southwest corner of Yellowstone National Park, reported annual means of 101.6 cm of precipitation, >508 cm of snow fall, and air temperature of -0.56 °C from 1951-1980 (Martner 1986). Mean annual temperature and precipitation (1995-1996) during woodpecker breeding (June), nesting (June-July), and fledgling (July -September) periods were: 12.22 °C and 6.05 cm, 13.75 °C and 5.31 cm, and 12.87 °C and 3.81 cm, respectively (National Weather Service, unpubl. data).

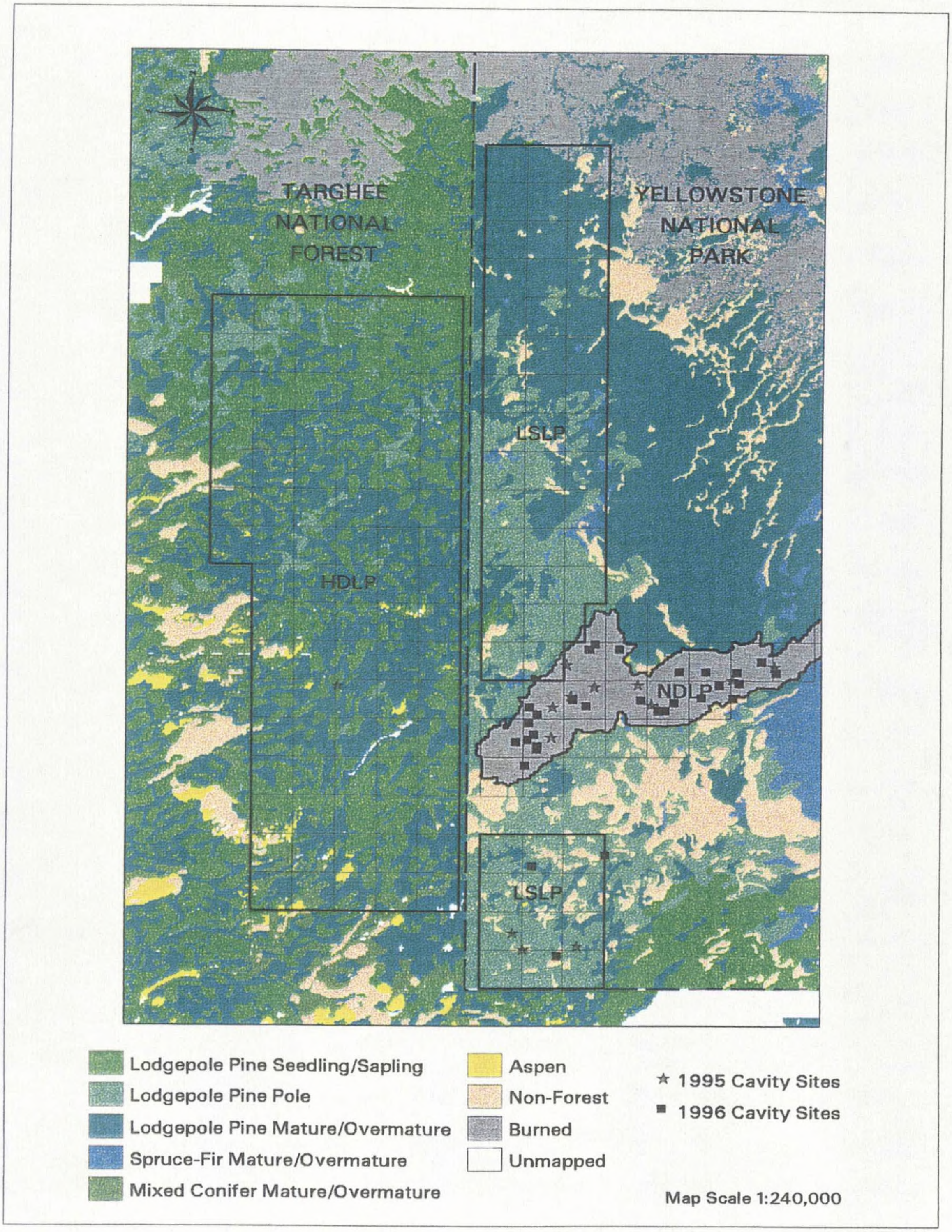


Figure 2. Active cavity-nest sites of three *Picoides* species overlaid on quadrat grid (1500m X 1500m) used for sampling nest sites in three disturbance strata (HDLP = human-disturbed, NDLP = naturally disturbed, LSLP = undisturbed) of lodgepole pine in the Targhee National Forest and Yellowstone National Park, 1995-1996 (Robinson Creek burn is outlined in black).

METHODS

I gridded the study area into 160 sampling units (1,500 m x 1,500 m quadrats) that were categorized into three strata: (1) human-disturbed lodgepole pine dominated habitat that had been clearcut logged (87 quadrats), (2) naturally disturbed lodgepole pine dominated habitat that experienced a recent wildfire (17 quadrats within the Bechler Meadows area of Yellowstone National Park), and (3) late seral lodgepole pine dominated habitat (undisturbed) that had neither been burned nor managed by silvicultural practices (56 quadrats) (Fig. 2). I measured distribution of cavity-nests among these three strata and investigated vegetative characteristics of cavity plots, associated plots, and random plots.

Sampling Design

I conducted field studies in lodgepole pine dominated habitat within each of the three disturbance strata: (1) human disturbed lodgepole pine (total available area=9,500 ha), (2) naturally disturbed lodgepole pine (total available area=3,400 ha), and (3) LSLP (total available area=11,700 ha). To delineate sampling units (225-ha quadrats), I gridded the study area into quadrats and determined which quadrats met the criteria for being in one of the three strata of interest. Criteria for quadrats to be sampled, were (1) accessible terrain (cliffs, lakes) and land ownership (private, state, closed/open management area), (2) elevation within the assumed elevational range of *Picoides* species, (3) lodgepole pine of pole size or larger, and (4) ≥60% percent lodgepole pine coverage per quadrat.

I chose units for sampling in 1995 by stratified, systematic, random sampling (Scheaffer et al. 1990). The number of quadrats sampled in each stratum was based on availability of habitat and logistical constraints (time and size of field crews). In 1995, I had a crew of three people and chose 20 of 43 quadrats in human disturbed lodgepole pine, 21 of 52 quadrats in undisturbed lodgepole pine, and 15 of 15 quadrats in naturally disturbed lodgepole pine. In 1996, because of the restricted number of available quadrats in naturally disturbed lodgepole pine, I re-sampled the same 15 quadrats that were surveyed in 1995. Re-sampling naturally disturbed lodgepole pine quadrats meant that the human disturbed lodgepole pine and undisturbed lodgepole pine had to be re-sampled in proportion to the number of quadrats found with and without active cavity-nests during the 1995 survey. Therefore, in human disturbed lodgepole pine and undisturbed lodgepole pine, I used proportional allocation sampling (Scheaffer et al. 1990) of the initial list of quadrats available. I had a crew of five in 1996 and consequently surveyed

22, 15, and 22 quadrats within human disturbed lodgepole pine, naturally disturbed lodgepole pine, and undisturbed lodgepole pine, respectively (Fig. 2). I re-sampled 11 and eight of the quadrats sampled in 1995 in human disturbed lodgepole pine and undisturbed lodgepole pine, respectively.

Data Collection

Nest Searching

Universal Transverse Mercator (UTM) coordinates were identified for each quadrat to be sampled. These UTM coordinate points were located on the ground using a global positioning system (GPS). In 1995 and 1996, crews searched quadrats for active cavity-nest trees of *Picoides* species in the three strata from mid-May through late June, which has been reported as an approximate time period to sample breeding woodpeckers, (Goggans et al. 1987, Toone 1992).

Observers (2-4 field assistants/year and myself) searched for active cavities in each selected quadrat using standard surveying methods for woodpeckers (Goggans et al. 1987, Toone 1992, Saab 1994). To ensure thorough coverage of each quadrat and to provide reference points, 7-8, 1,500-m transects equally spaced 200 m apart were oriented along north-south axes in each quadrat. Observers conducted nest searches within each quadrat by walking circuitous paths along each transect. Observers walked within 100 m of all habitat within each quadrat (Toone 1992, Saab 1994). During surveys, observers walked slowly along each line transect and stopped every 500 m for 3-5 minutes to listen and watch for cavity-nesters. At every 500-m interval, field personnel played a tape-recorded drumming of a Three-toed Woodpecker for 30 seconds and then listened for 30 seconds for vocalizations of *Picoides* species (Toone 1992, Joy et al. 1993). When observers heard vocalizations and/or saw woodpecker species and/or a freshly excavated cavity or fresh wood chips at the trunk of a tree, they recorded the location and *Picoides* species, if applicable (Goggans et al. 1988, Bull et al. 1990). The status of each nest-cavity suspected of being active was confirmed at a later date. A cavity was considered active if the observer noted exchange of incubation duty between mates or heard or saw young in the cavity. To minimize effects of observer variability, each observer conducted surveys in each stratum (Ralph et al. 1993).

Vegetative Sampling

To characterize vegetative features (structure and composition) of nest sites, I sampled vegetation on 11.3-m radius (0.04 ha) plots that were centered on cavity-nest trees (CP). I measured micro-habitat features, within each plot, that may be critical for predicting habitat use and occurrence of *Picoides* species

(Bull et al. 1986, Ralph et al. 1993, Saab 1994, A. J. Hansen unpubl.). Vegetation measurements collected at each plot included: (1) landscape features: slope position, aspect, distance to water, distance to clearing; (2) stand composition and structure: average canopy cover, percent ground cover (coniferous, deciduous, and herbaceous), average diameter of down woody debris, origin of down woody debris, decay class for down woody debris, tree/snag counts, tree species; and (3) cavity tree characteristics: percent of bark and branches on tree, tree height, tree species, tree diameter.

To compare characteristics of sites used and nonused for nesting, I also measured vegetative features at two types of randomly located plots: (1) an associated plot (AP) located ≥365 m and ≤1,500 m from the nest site (this method placed the plot within the average home range [214 ha] of a Three-toed Woodpecker pair but outside the nest fidelity radius [91-365 m] [Goggans et al. 1988]) and (2) a plot randomly (RP) placed within the same disturbance stratum (i.e., human disturbed, naturally disturbed, or undisturbed) as that of the cavity plot (Saab 1994) (Fig. 3).

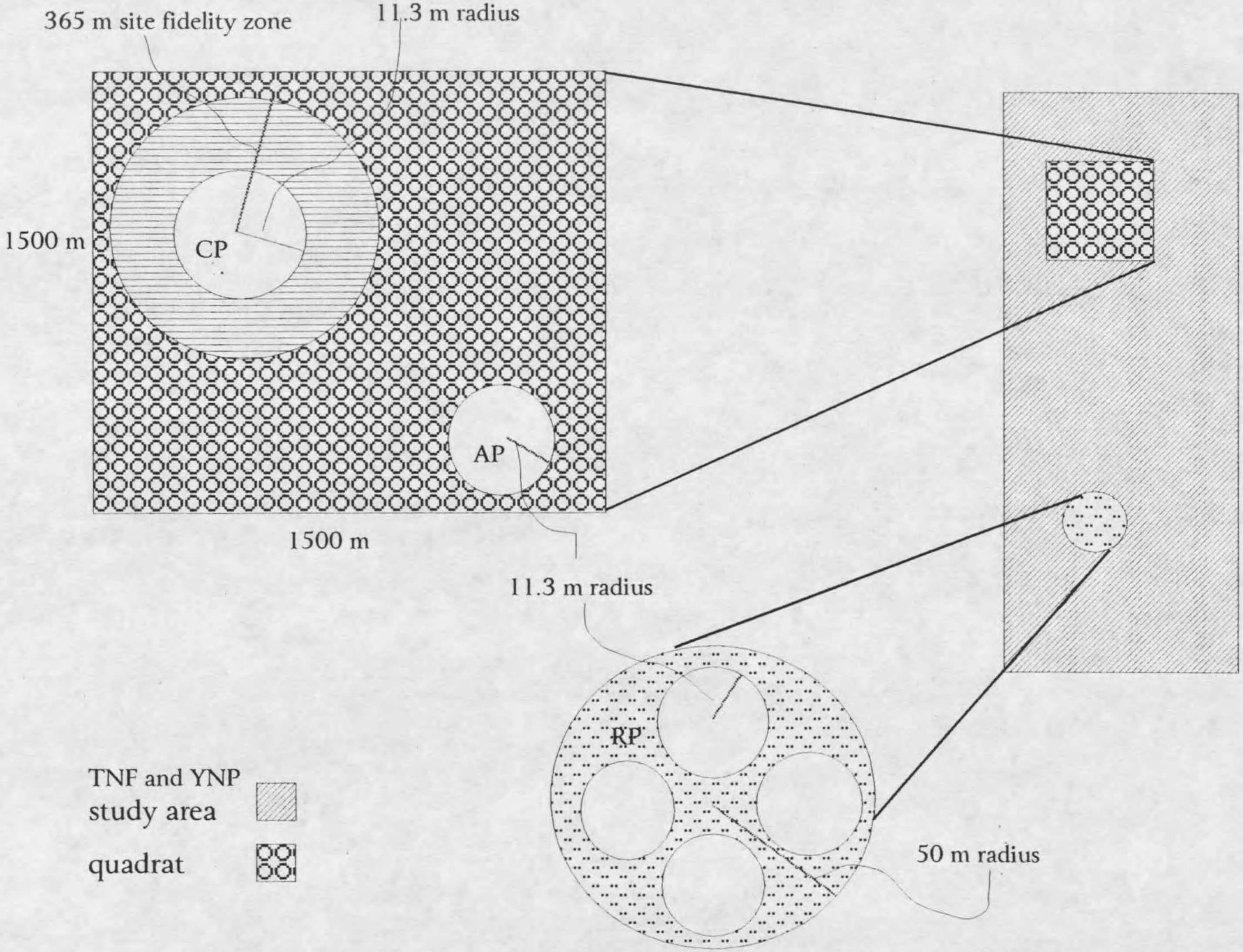


Figure 3. Arrangement of cavity plots (CP), associated plots (AP), and random plots (RP) within Targhee National Forest and Yellowstone National Park.

Data Analysis

Distribution Of Nests Among Strata

To test whether *Picoides* species were distributed similarly among the three strata, I performed exact logistic regression analysis. I used program LogXact (Cytel 1993) and presence/absence data collected for each quadrat sampled. I used exact logistic regression rather than conventional logistic regression because my data contained zero cell counts and other cells with values less than five (Cytel 1993). I used program LogXact (Cytel 1993) to perform conditional exact inference on the parameters of the logistic regression model, analyze main effects (stratum and species), and evaluate interactions between species and strata. The likelihood of finding nest-cavities in postfire and human disturbed habitat was based on comparisons to the likelihood of finding active woodpecker nest-cavities in undisturbed lodgepole pine which was held constant over both years. The likelihood of a nest-cavity belonging to Three-toed or Black-backed woodpeckers was based on comparisons to the likelihood of a nest-cavity belonging to Hairy Woodpeckers which was held constant over both years.

Interspecific Comparisons of Cavity Plots

I used a combination of multivariate and univariate techniques to compare vegetative characteristics of cavity plots among species. Because I obtained relatively small samples of cavities for each species in each year (see Results), I combined 1995 and 1996 data for these and the remaining analyses of vegetation data. The two years were combined because vegetative structure and composition were not confounded by year effects. Observations of active cavity-nest sites may not be independent because 1995 quadrats were re-sampled (11 in human disturbed and eight in undisturbed lodgepole pine habitat) in 1996. Therefore, the assumptions of independence may have been violated for the following multivariate logistic regression and MANOVA analyses. I used MANOVA analysis to determine main effect differences and individual differences among mean values which could not be analyzed with multivariate logistic regression.

I first developed four *a priori* multivariate logistic regression models (Table 1) based on biological knowledge of the species and published literature. Because most woodpecker literature on cavity-nest sites concentrated on cavity-nest tree conditions and live and dead standing tree densities surrounding the nest tree, and because I observed woodpeckers foraging on down woody debris, I chose to look at alternative microhabitat variables within cavity and random plots (e.g., condition, size, and quantity of down woody debris, canopy cover, and distance to water). I used PROC LOGISTIC to evaluate each model (SAS Institute, Inc. 1990) and chose the best model based on Akaike's information criteria (AIC) (Akaike 1973, Burnham and Anderson 1992). AIC values provided an evaluation of model fit, emphasized parsimony, and have been suggested for selection among models in a likelihood context (Burnham and Anderson 1992). All models whose AIC values were within two units of the AIC value for the most parsimonious model were considered part of a confidence list of models and evaluated (Burnham and Anderson 1992). When the null model was in the confidence list the *a priori* models were not evaluated further, because they were no more parsimonious than the null model.

Table 1. Four *a priori* logistic regression models using vegetation characteristics to differentiate among cavity, associated, and random plots of different *Picoides* species on the Targhee National Forest and Yellowstone National Park.

Model Number	Logit[a]
1	$\alpha + \beta_1 AVCC^{b} + \beta_2 AVGDBH \leq 4^{c} + \beta_3 AVGDDBH5^{d}$
2	$\alpha + \beta_1 AVCC + \beta_2 AVGDDBH5 + \beta_3 DISH20^{e}$
3	$\alpha + \beta_1 AVCC + \beta_2 AVGDBH \leq 4 + \beta_3 AVGDDBH5 + \beta_4 AVGDKS^{f} + \beta_5 AVGDKR^{g}$
4	$\alpha + \beta_1 AVCC + \beta_2 AVGDBH \leq 4$

[a] Logit of the equation estimating probability of occurrence of woodpeckers where the equation is $e^{logit}/1 + e^{logit}$.

[b] Average canopy cover (%).

[c] Average number of down woody debris 8 to < 24 cm in diameter.

[d] Average number of down woody debris 24 to < 39 cm in diameter.

[e] Distance to water (m).

[f] Solid decay class of down woody debris (count).

[g] Rotten decay class of down woody debris (count).

I performed multivariate analysis of variance (MANOVA) (Manly 1995, Scheiner 1993) to test whether vegetation characteristics of nest sites differed among three species groups (i.e., Black-backed Woodpeckers, Three-toed Woodpeckers, Hairy Woodpeckers). The power of MANOVA decreases as the number of dependent variables increases and sample size decreases (Scheiner 1993). Because of my small sample sizes I limited my analysis to only microhabitat variables which I thought were lacking in published literature. I used MANOVA (Statistica 1994, SYSTAT, Inc. 1992) to analyze eight explanatory variables: (1) distance to water, (2) average percentage of canopy cover, (3) average number of pieces of down woody debris 8 to 23.99 cm in diameter, (4) average number of pieces of naturally occurring down woody debris, (5) average number of pieces of burned down woody debris, (6) average number of pieces of solid down woody debris, (7) average number of pieces of rotten down woody debris, and (8) average number of live and dead trees (all species) 24 to 38.99 cm in diameter. To determine significance of the MANOVA, I calculated a multivariate F-statistic value (Wilks' Lambda), which is quite robust to possible differences among species-specific variances for explanatory variables (i.e., multicollinearity). I also tested the resulting discriminant function axes for significance and tested for relationships among species-specific (i.e., group) means. Additionally, I calculated a univariate F-statistic for each variable and evaluated the significance of univariate F-statistics by comparing them to values generated by Rice's (1990) sequential-Bonferroni-correction method. Rice's sequential-Bonferroni-correction method was used to control Type I error rates when assessing significance of results and is less conservative than traditional Bonferroni corrections. Variables with significant F-statistics were identified as dependent variables that contributed to a significant overall effect, if one existed.

I generated projections (scores) off the discriminant function axes and 90% confidence ellipses of the means (see Results) to visually interpret each species-specific group. Distributions of species-specific groups (notched-box plots) were generated for significant discriminant functions (see Results).

Intraspecific Comparisons of Occupied and Unoccupied Habitats

I used the four *a priori* models used in intraspecific analyses (see above) to evaluate vegetative differences among plot types (i.e., cavity plot, associated plot, random plot) for each species. I again used PROC LOGISTIC for all logistic regression analyses (SAS Institute, Inc. 1990) and chose the best model on the basis of AIC values (Akaike 1973, Burnham and Anderson 1992). In this analysis, I conducted a total of six multivariate logistic regressions because there were three species and two plot-type contrasts (i.e., cavity plot vs. associated plot, cavity plot vs. random plot) per species.

I conducted exploratory analyses of how vegetative characteristics differed among plot types for each species using MANOVA (Scheiner 1993, Manly 1995) (SYSTAT, Inc. 1992, Statistica 1994,). I analyzed the eight variables used in interspecific analysis (see above) using six contrasts (i.e., cavity plot vs. associated plot, cavity plot vs. random plot for each species). I again calculated a multivariate F-statistic value (Wilk's Lambda), tested the resulting discriminant function axes for significance, calculated a univariate F-statistic for each variable, and evaluated the significance of univariate F-statistics by comparing them to values generated by Rice's (1990) method.

I generated 90% confidence ellipses of the means on discriminant function axes (see Results) to visually interpret the interaction of the six contrasts. Distributions of the groups on the significant discriminant function axis (notched-box plots) were generated (see Results). Given my small sample sizes, I considered results significant at $\underline{P} \leq 0.10$ in all statistical analyses to achieve a better balance of Type I and Type II errors.

RESULTS

We surveyed 56 quadrats in 1995 and 59 quadrats in 1996. Of the 115 quadrats surveyed, 28 contained active nest-cavities (14 quadrats in each year) (Table 2). I found 14 active nest-cavities in 1995 and 30 active nest-cavities in 1996 (Table 3), which included cavities of Three-toed Woodpeckers, Black-backed Woodpeckers, and Hairy Woodpeckers. Thirty-four quadrats sampled in 1995 were re-sampled in 1996. No quadrat had the same number of species and/or composition of cavity-nesting species present in both years, which indicated that data from 1996 for the re-sampled quadrats provided new information. Three out of eight quadrats in the undisturbed stratum changed activity status between years (two changed from active to non-active and one changed from non-active to active). One out of 11 quadrats in the human disturbed stratum changed activity status between years (active to non-active). Eight out of 15 quadrats in the naturally disturbed stratum changed activity status between years (one changed from active to non-active and seven changed from non-active to active). Eight out of 15 in the naturally disturbed stratum changed species composition between years.

Hairy Woodpecker nest sites were predominately located within aspen stands scattered throughout the lodgepole pine dominate forest. Thirteen of

17 Hairy Woodpecker cavities were in aspen trees. Neither Black-backed nor Three-toed woodpeckers nested in aspen trees. No Downy Woodpeckers were observed. Vegetation sampling was conducted for each active nest-cavity (n=44) and for associated (n=44) and random plots (n=44).

Interspecific Nest Site Distribution Among Strata

Data from the 1995 and 1996 field seasons were analyzed separately due to the interaction between years found in exact logistic regression analysis which indicated that the effect of year was more influential in creating changes in species distributions among strata than were the main effects (habitat and/or species).

Table 2. Number of quadrats (1,500 m X 1,500 m) containing active nest-cavities in three strata of lodgepole pine within the Targhee National Forest and Yellowstone National Park, 1995 and 1996.

		Habitat Type (Stratum)[a]								
		Human Disturbed			Natural Disturbed			Late Seral		
			Quadrats with cavities			Quadrats with cavities			Quadrats with cavities	
Species[b]	Year	Quadrats Sampled	n	%	Quadrats Sampled	n	%	Quadrats Sampled	n	%
TTWO	1995	20	0	0	15	2	0.13	21	0	0
	1996	22	0	0	15	7	0.47	22	0	0
BBWO	1995	20	0	0	15	1	0.07	20	1	0.05
	1996	22	0	0	15	10	0.67	22	0	0
HAWO	1995	20	1	0.05	15	6	0.40	21	2	0.10
	1996	22	0	0	15	4	0.27	22	3	0.14
Total	Both	42	1	0.02	30	21	0.70	43	6	0.14

[a] Lodgepole pine habitats were: human disturbed (HDLP-managed), natural disturbed (NDLP-burned), and late seral (LSLP-un-managed)

[b] Species were: Three-toed Woodpecker, Black-backed Woodpecker, and Hairy Woodpecker

Table 3. Distributions of *Picoides* species among three strata of lodgepole pine habitat within the Targhee National Forest and Yellowstone National Park, 1995-1996.

		Habitat Type (Stratum)[a]					
		HDLP		NDLP		LSLP	
Species[b]	year	n[c]	%[d]	n	%	n	%
TTWO	1995	0	0	2	100	0	0
	1996	0	0	9	100	0	0
BBWO	1995	0	0	1	50	1	50
	1996	0	0	13	100	0	0
HAWO	1995	1	10	7	70	2	20
	1996	0	0	4	57	3	43
All	Both	1	2	36	84	6	14

[a] Strata were human disturbed lodgepole pine (HDLP), naturally disturbed lodgepole pine (NDLP), and late seral lodgepole pine (LSLP).

[b] Species were Three-toed Woodpecker, Black-backed Woodpecker, and Hairy Woodpecker.

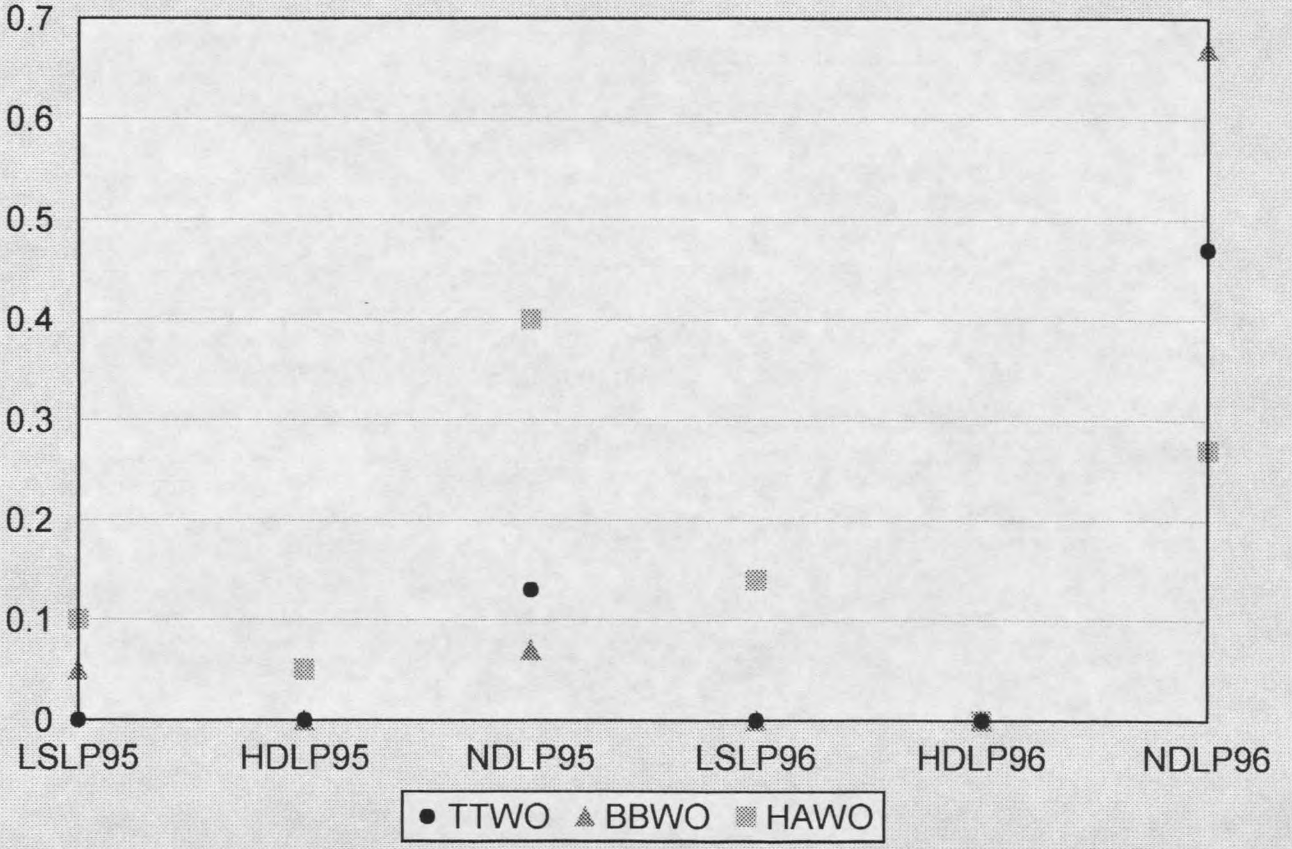
[c] Number of active cavity-nests found for each species in each stratum.

[d] Species- and year-specific percentages of stratum containing an active cavity.

When all *Picoides* species were considered together, nests were not distributed evenly among the three strata in 1995 (P =0.02) or in 1996 (P ≤0.001). In 1995, active cavities were 5.47 ($e^{1.70}$) times more likely to be found in the postfire lodgepole pine stratum (naturally disturbed) than in the undisturbed (un-managed) lodgepole pine stratum [90% CI =1.45 ($e^{0.37}$) to 26.05 ($e^{3.26}$), P =0.02]. In 1996, active cavities were 17.46 ($e^{2.86}$) times more likely to be found in the postfire lodgepole pine stratum than in the human disturbed (clearcut) lodgepole pine stratum [90% CI =5.47 ($e^{1.70}$) to 74.44 ($e^{4.31}$), P ≤0.001]. Cavity plots were not more likely to be found in the human disturbed stratum than in the undisturbed stratum in either year (1995, P =0.65; 1996, P =0.24).

Within the postfire lodgepole pine stratum, Three-toed and Black-backed woodpeckers were each 0.17 ($e^{-1.77}$) [90% CI =0.02 ($e^{-3.73}$) to 0.77 ($e^{-0.26}$), P =.04] times as likely to be found nesting than were Hairy Woodpeckers in 1995. In contrast, within the postfire lodgepole pine stratum in 1996, neither Three-toed Woodpeckers (P =1.00) nor Black-backed Woodpeckers (P =0.52) were more likely to be found nesting than were Hairy Woodpeckers. In postfire lodgepole pine habitat in 1995, nests of Hairy Woodpeckers (n =7) were more abundant than nests of Three-toed Woodpeckers (n =2), which were more abundant than nests of Black-backed Woodpeckers (n =1) (Fig 4). In 1996, the graded response was reversed: I found 13 Black-backed

Figure 4 Proportion of quadrats within three strata that contained nests of Three-toed (TTWO), Black-backed (BBWO), and Hairy woodpeckers (HAWO) on the Targhee National Forest and Yellowstone National Park, 1995 and 1996.



Woodpecker nests, nine Three-toed Woodpecker nests, and four Hairy Woodpecker nests (Fig. 4).

Interspecific Comparisons of Cavity Plots

Hairy Woodpecker versus Three-toed Woodpecker

Logistic regression, predicting the probability of a cavity plot being that of a Three-toed Woodpecker, indicated that a model containing canopy cover (AVCC), small, down woody debris, (8 - 23.99 cm in diameter, AVGDBH≤4), down woody debris of dbh class 5 (24 - 38.99 cm in diameter, AVGDDBH5), solid downed wood (AVGDKS), and rotten downed wood (AVGDKR) was the most parsimonious model for differentiating between Three-toed Woodpecker and Hairy Woodpecker cavity plots (AIC =35.93, AIC_{NULL} =39.52, Table 4). This model contained coefficients different from zero (Wald chi-square, P ≤0.10; beta for AVGDBH≤4 =-6.66, SE =4.10; beta for AVGDDBH5 = -4.90, SE =2.30; beta for AVGDKR =1.84, SE =1.06), had an adequate fit to the data (Hosmer-Lemeshow goodness-of-fit test, P =0.64), was significantly better than the null model (P =0.02), and had an R^2 of 0.38. When all possible pairs of response values were examined, 84.0% of the observations with the lower observed value also had a lower predicted value (16.0% of the pairs were discordant; n =187 possible pairs). AIC values for two other models [model 1: AVCC, AVGDBH≤4, and AVGDDBH5; and model 2: AVCC, AVGDBH≤4, and distance to water (DISH2O)] were within two units of the most parsimonious model. Therefore, they were considered part of a confidence list and evaluated. Both of these models contained down woody debris in dbh class 5 ($\underline{P}$ =0.07, beta =-1.86, SE =1.03; $\underline{P}$ =0.07, beta =-1.80, SE =0.99 in the two models, respectively). All three models in the confidence set contained down woody debris in dbh class 5 and indicated that sites with less downed wood of 24 - 38.99 cm in diameter were more likely to be used by nesting Three-toed Woodpeckers than by Hairy Woodpeckers.

Hairy Woodpecker versus Black-backed Woodpecker

None of the four *a priori* models (AIC ≥46.48) (Table 1) used to differentiate between Black-backed Woodpecker and Hairy Woodpecker cavity plots was more parsimonious than the null model (AIC_{NULL} =46.24). Therefore, I did not evaluate *a priori* models further. Thus, I did not detect differences in the vegetative characteristics of Black-backed Woodpecker and Hairy Woodpecker cavity plots.

Black-backed Woodpecker versus Three-toed Woodpecker

The four *a priori* models were not used to differentiate between Black-backed Woodpecker and Three-toed Woodpecker cavity plots. However, a comparison of the previous two contrasts (Hairy Woodpecker versus Three-toed Woodpecker and Hairy Woodpecker versus Black-backed Woodpecker) indicates that sites with less down woody debris were more likely to be used by nesting Three-toed Woodpeckers than by Black-backed and/or Hairy woodpeckers. In addition, models considered part of the confidence list indicated that Three-toed Woodpecker cavity sites were differentiated from those of Black-backed Woodpeckers by the decay level of down wood, distance to water, and amount of canopy cover.

Simultaneous Comparisons of All Three Woodpecker Species

Species-specific vegetation characteristics of cavity plots varied significantly (Wilks' Lambda, $\underline{P} \approx 0.03$; Pillai-Bartlett Trace, $\underline{P} \approx 0.04$) among the three *Picoides* species. However, results of univariate tests were not significant when compared to Rice's adjusted significance levels ($\underline{P} > 0.10$). Thus, only when all eight variables were considered together were differences indicated among cavity plots used by different species (i.e., groups). Two discriminant functions (i.e., axes) combined explained 100% of the variation among the three groups. The first discriminant function represented a gradient from low to high amounts of 8 - 23.99 cm in diameter down woody debris. The first axis was significant ($\underline{P} < 0.001$) and explained the majority of the variation (84%) in the data. The second axis representing a gradient from rotten to solid, naturally occurring down woody debris, was not significant (P =0.29), and explained 16% of the variation in the data. Species-specific means for Three-toed Woodpecker and Black-backed Woodpecker cavity plots occupied different, yet slightly overlapping positions along the first axis, whereas the mean for Hairy Woodpecker cavity plots was distinct (Fig. 5). Confidence ellipses (90%) for the three species indicated that: (1) Black-backed and Three-toed woodpeckers were associated with sites containing low amounts of small down woody debris and high levels of naturally fallen, solid woody debris; (2) Three-toed Woodpeckers tended to be associated with high levels of naturally fallen, rotten woody debris; and (3) Hairy Woodpeckers were associated with high amounts of small down woody debris and low levels of solid, naturally fallen woody debris (Fig. 6).

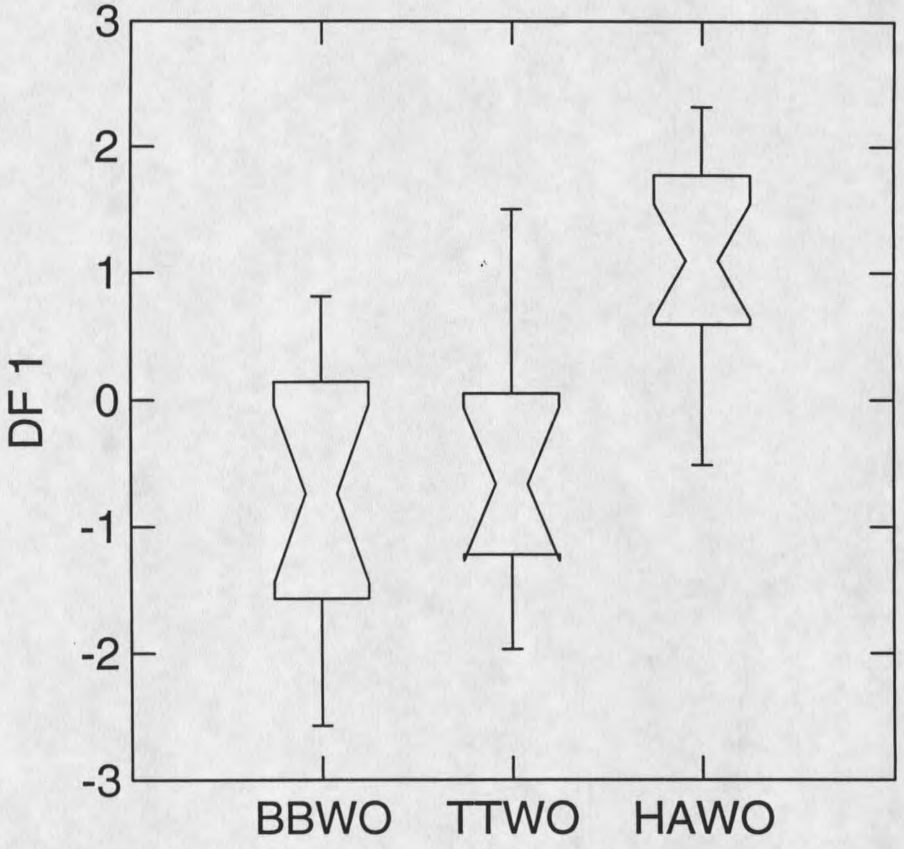


Figure 5. Box-notch plots of scores on discriminant function 1 for cavity plots of three species of *Picoides* within three strata of lodgepole pine habitat in the Targhee National Forest and Yellowstone National Park, 1995-1996.

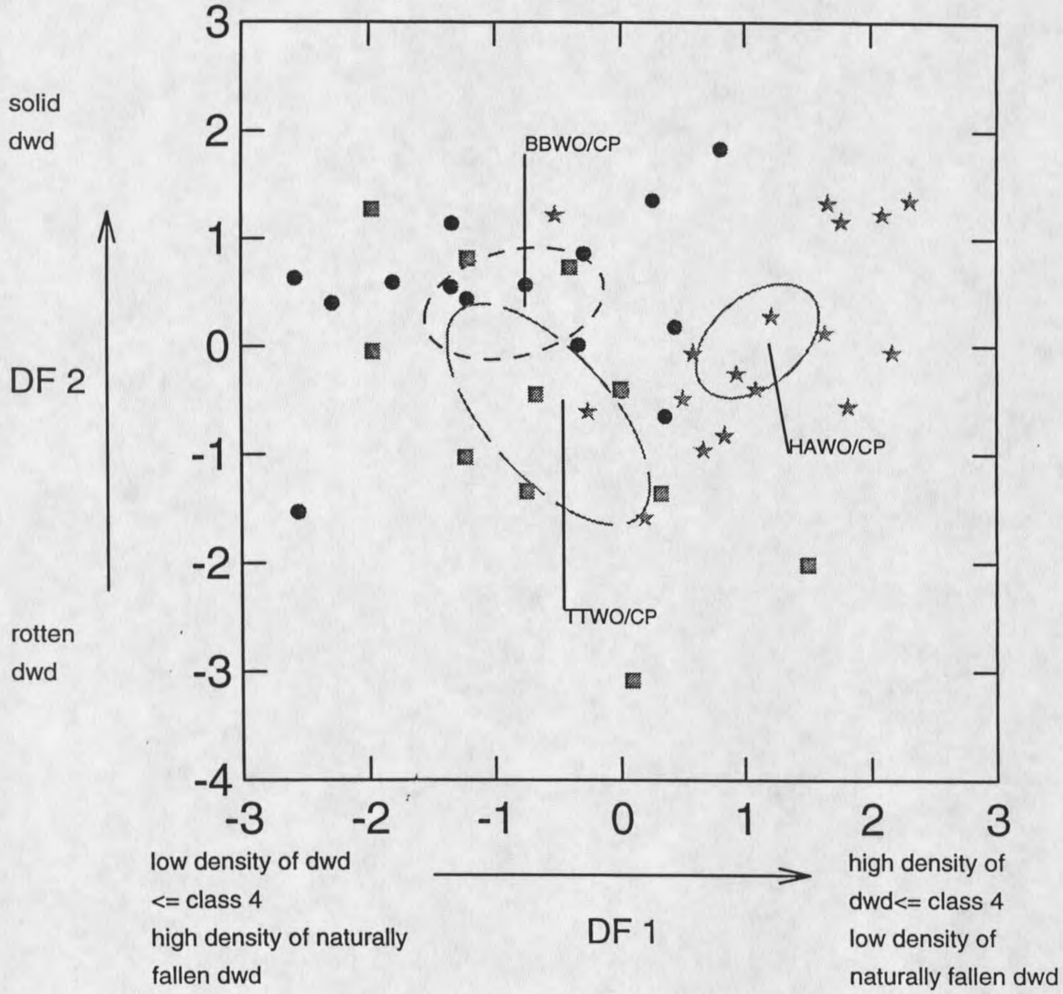


Figure 6. Scores and 90% confidence ellipses of the means on discriminant functions 1 and 2 for cavity plots for three species of *Picoides* within the Targhee National Forest and Yellowstone National Park, 1995-1996.

Intraspecific Comparisons of Occupied and Unoccupied Habitats

Hairy Woodpecker Cavity Plots versus Random Plots

Logistic regression indicated that a model (Model 1, Table 1) containing canopy cover (AVGCC), small, down woody debris (AVGDBH≤4), and down woody debris in dbh class 5 (AVGDDBH5) was the most parsimonious model for differentiating between Hairy Woodpecker cavity plots and random plots (AIC =73.44). However, this model was not more parsimonious than the null model (AIC_{NULL} =73.52). Therefore, this model and other *a priori* models were not evaluated further. Thus, I did not detect differences in the vegetative characteristics of Hairy Woodpecker cavity plots and random plots.

Hairy Woodpecker Cavity Plots versus Associated Plots

Logistic regression performed on four *a priori* models indicated that the model (Model 3, Table 1) containing canopy cover (AVGCC), small, down woody debris (AVGDBH≤4), down woody debris in dbh class 5 (AVGDDBH5), solid downed wood (AVGDKS), and rotten downed wood (AVGDKR) was the most parsimonious model at predicting differences between Hairy Woodpecker cavity plots and associated plots (AIC =47.76). However, this model was not more parsimonious than the null model (AIC_{NULL}

=49.13). Therefore, I did not evaluate *a priori* models further. Thus, I did not detect differences in the vegetative characteristics of Hairy Woodpecker cavity plots and associated plots.

Three-toed Woodpecker Cavity Plots versus Random Plots

Logistic regression indicated that the model (Model 3, Table 1) containing canopy cover (AVGCC), small, down woody debris (AVGDBH≤4), down woody debris in dbh class 5 (AVGDDBH5), solid downed wood (AVGDKS), and rotten downed wood (AVGDKR) was the most parsimonious (AIC =56.26). However, this model was not more parsimonious than the null model (AIC_{NULL} =56.59) at predicting differences between Three-toed Woodpecker cavity plots and random plots. Therefore, I did not evaluate *a priori* models further. Thus, I did not detect differences in the vegetative characteristics of Three-toed Woodpecker cavity plots and random plots.

Three-toed Woodpecker Cavity Plots versus Associated Plots

Logistic regression indicated that a model (Model 2, Table 1) containing canopy cover (AVGCC), down woody debris in dbh class 5 (AVGDDBH5), and distance to water (DISH2O) was the most parsimonious model for differentiating between Three-toed Woodpecker cavity plots and associated plots (AIC = 27.51, AIC_{NULL} =32.50). No other model was in the confidence list (AIC $\geq$30.78). The most parsimonious model contained one coefficient different from zero (Wald chi-square, $\underline{P} \leq 0.10$; beta for DISH2O =-0.007, SE =0.004), had an adequate fit to the data (Hosmer-Lemeshow goodness-of-fit test, $\underline{P} = 0.52$), was significantly better than the null model ($\underline{P} = 0.01$), and had a R^2 value of 0.39. When all possible pairs of response values were examined, 86.0% of observations with the lower observed value also had a lower predicted value (14.0% of pairs were discordant, $\underline{n} = 121$ possible pairs). Thus, according to the most parsimonious model, Three-toed Woodpecker cavity plots were closer to water than were associated plots.

Black-backed Woodpecker Cavity Plots versus Random Plots

None of the four *a priori* models (AIC $\geq$71.09) (Table 1) used to differentiate between Black-backed Woodpeckers cavity plots and random plots was more parsimonious than the null model ($AIC_{NULL} = 68.31$). Therefore, I did not evaluate *a priori* models further. Thus, I did not detect differences in the vegetative characteristics of Black-backed Woodpecker cavity plots and random plots.

Black-backed Woodpecker Cavity Plots versus Associated Plots

None of the four *a priori* models (AIC $\geq$46.91) (Table 1) used to differentiate between Black-backed Woodpecker cavity plots and associated plots was more parsimonious than the null model (AIC_{NULL} =43.59). Therefore, I did not evaluate *a priori* models further. Thus, I did not detect differences in the vegetative characteristics of Black-backed Woodpecker cavity plots and associated plots.

Simultaneous Comparisons of All Plot Types

MANOVA indicated that species-specific vegetative characteristics of cavity plots and associated plots and random plots varied significantly (Wilks' Lambda and Pillai-Bartlett Trace, $\underline{P} = 0.06$; respectively) among the three *Picoides* species. However, results of univariate test were not significant when compared to Rice's adjusted significance levels ($\underline{P} > 0.10$). Thus, only when all eight variables were considered together were differences indicated among the seven groups. To evaluate main effect differences, I interpreted the discriminant functions that explain the variation among vegetative characteristics of Three-toed Woodpecker cavity plots and associated plots, Black-backed Woodpecker cavity plots and associated plots, Hairy Woodpecker cavity plots and associated plots, and random plots compared to species-specific plots. Two discriminant functions (i.e., axes) explained 70% of the variation among the groups. The first discriminant function represented a gradient from low to high amounts of small, down woody debris and a gradient from low to high amounts of naturally occurring down woody debris. The first axis was significant (P =0.01) and explained nearly half of the variation (46%) in the data (Fig. 7). The second axis represented a gradient from low to high amounts of small, down woody debris and a gradient from low to high numbers of live and dead trees (all species) 24 - 38.99 cm in diameter, was not significant (P ≤0.10), and explained 24% of the variation in the data. Confidence ellipses (90%) for the seven groups' means (Fig. 8) indicated that Three-toed Woodpecker cavity plots were associated with high amounts of naturally fallen woody debris, low amounts of small, down woody debris, and a highly variable number of trees in dbh class 5. Three-toed Woodpecker cavity plots differed (Wilks' Lambda test, P =0.10) from associated plots by having fewer small, down woody debris and fewer trees in dbh class 5. Three-toed Woodpecker and Black-backed Woodpecker cavity plots had (Wilks' Lambda test, P =0.09; 0.007, respectively) less small, down woody debris and more naturally fallen down woody debris than random plots.

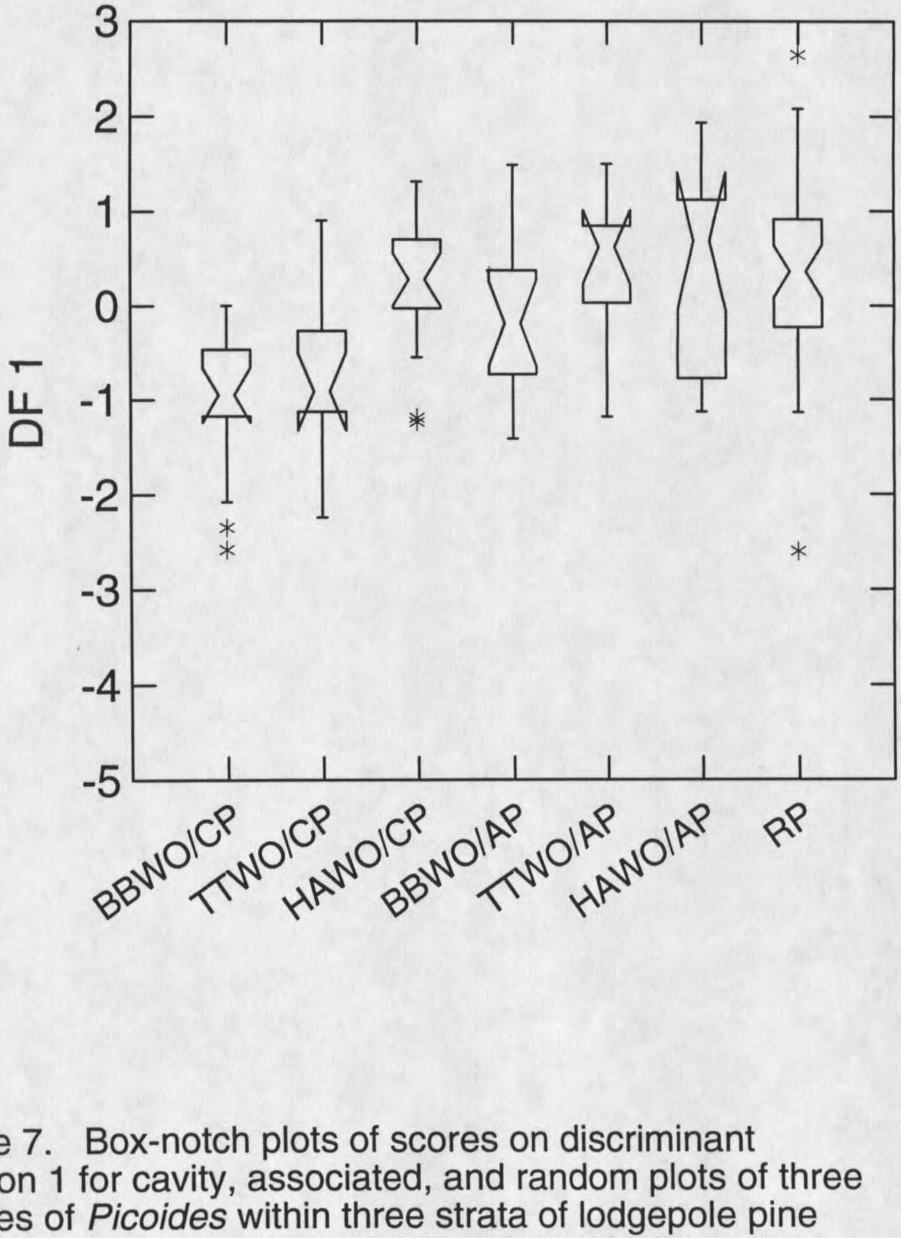


Figure 7. Box-notch plots of scores on discriminant function 1 for cavity, associated, and random plots of three species of *Picoides* within three strata of lodgepole pine habitat in the Targhee National Forest and Yellowstone National Park, 1995-1996.

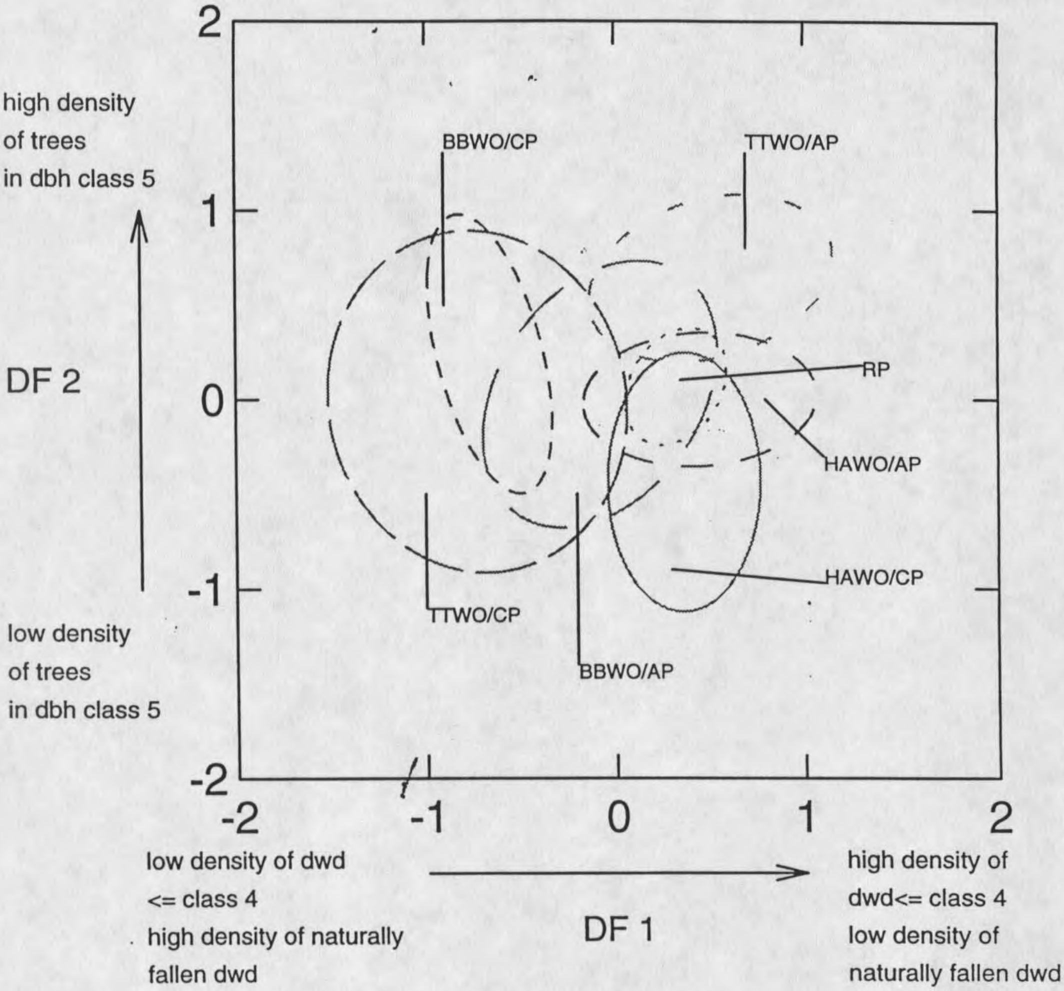


Figure 8. 90% confidence ellipses of the means on discriminant functions 1 and 2 for cavity, associated and random plots for three species of *Picoides* within the Targhee National Forest and Yellowstone National Park, 1995-1996.

DISCUSSION

Cavity nests of *Picoides* species were more likely to be found in naturally disturbed forest than in undisturbed and human disturbed forests. These results are consistent with findings of previous studies that concluded cavity-nesters, specifically Three-toed and Black-backed woodpeckers, were more abundant in recently disturbed habitat than in mature/overmature coniferous forests (Van Tyne 1926, Blackford 1955, West and Spiers 1958, Koplin 1969, Niemi 1978, Apfelbaum and Haney 1981, Yunick 1985, Villard and Beninger 1993, Villard 1994, Hutto 1995, Caton 1996, Schulte 1996, E. C. Murphy and W. H. Lehnhausen, unpubl. data). Furthermore, I found that Three-toed and Black-backed woodpeckers were more likely to be found nesting in postfire habitat than were Hairy Woodpeckers. This result is supported by previous studies that found both Three-toed Woodpeckers and Black-backed Woodpeckers readily occupied postfire habitat (Wickman 1965, Koplin 1969, Angelstam and Mikusiński 1994, Blackford 1955, Hutto 1995, Caton 1996, E. C. Murphy and W. H. Lehnhausen, unpubl. data).

Three-toed, Black-backed, and Hairy woodpeckers concentrate locally in response to the superabundant prey base that is sometimes created by fire-damaged trees (Van Tyne 1926, Short 1982, Yunick 1985, E. C. Murphy and

W. H. Lehnhausen, unpubl. data). Bark beetles and wood borers (Scolytidae and Cerambycidae, respectively), which are key food items for Three-toed and Black-backed woodpeckers (Beal 1911, E. C. Murphy and W. H. Lehnhausen, unpubl. data), frequently occur in large numbers in areas where tree mortality occurs as a result of fire. Although dynamics of insect invasions are not well understood (Evans 1971, Amman and Ryan 1991, Lavigne et. al 1992), insects are typically thought to infest fire-injured conifers within two years following a fire (Amman and Ryan 1991). A possible time lag to postfire insect irruptions may explain why I found twice as many nests in the naturally disturbed habitat in 1996 as in 1995.

Although three *Picoides* species localized within the naturally disturbed habitat, temporal responses to postfire habitat were not consistent among *Picoides* species. Species-specific densities fluctuated among *Picoides* species during the 1995 and 1996 breeding seasons. Hairy Woodpecker densities within postfire habitat were highest in 1995, followed by Three-toed and Black-backed woodpeckers, respectively. This observed pattern was reversed in 1996. Other researchers (Baldwin 1960, Crockett and Hansley 1978, Taylor and Barmore 1980, E. C. Murphy and W. H. Lehnhausen, unpubl. data) witnessed similar temporally graded responses in abundances of Hairy, Three-toed, and Black-backed woodpeckers in postfire habitat.

The observed graded response may have been the result of species-specific differences in foraging adaptations. Hairy Woodpeckers are generalists that use a variety foraging substrates and techniques and feed primarily on insects in wood (Short 1971, Kisiel 1972). Hairy Woodpeckers may not be as adept at excavating deeply into wood as Black-backed Woodpeckers. In fact, Hairy Woodpeckers have been known to forage in holes previously excavated by Black-backed Woodpeckers (Villard and Beninger 1993). In contrast, Black-backed and Three-toed woodpeckers are more site-specific foragers with more specialized foraging techniques (Spring 1965, Hogstad 1970, Hogstad 1977, Villard and Beninger 1993, Villard 1994, E. C. Murphy and W. H. Lehnhausen, unpubl. data). Compared to Hairy Woodpeckers, Black-backed Woodpeckers forage on larger substrates and excavate deeper into wood (Spring 1965, Kisiel 1972). In contrast, Three-toed Woodpeckers predominantly forage by scaling or flaking bark off trees to uncover insects in and/or just beneath the tree's bark (Koplin 1969, Villard 1994, E. C. Murphy and W. H. Lehnhausen, unpubl. data).

Interspecific Comparisons of Cavity Plots

Interspecific comparisons of vegetative structure at cavity sites indicated that size, condition (i.e., decay level and origin), and quantity of down woody debris differentiated among nest sites of *Picoides* species. Black-backed and Three-toed woodpeckers nested on sites with higher densities of solid, naturally fallen down woody debris (i.e., >24 cm in diameter) and lower densities of small-diameter down woody debris than did Hairy Woodpeckers. These results provide further evidence that Three-toed and Black-backed woodpeckers are more likely to use mature/overmature forest habitat. Mature/overmature forests may provide several features (large trees and dead, dying, and down wood) that Black-backed and Three-toed woodpeckers use for nesting and foraging (Goggans et al. 1987, Marshall 1992, Angelstam and Mikusiński 1994). Alternatively, high densities of solid, naturally fallen wood may have been remnants of the mountain pine beetle infestation that occurred within the Yellowstone area in the 1970's; adult mountain pine beetles generally attack and kill proportionately more large-diameter than small-diameter trees (Cole and Amman 1969, Amman 1977, Lester 1980). I speculate that pre-fire densities of small-diameter down woody debris within mature/overmature forest habitat would have been reduced by the 1994 Robinson Creek fire. The low density of small-diameter down woody debris on sites occupied by Three-toed and Black-backed woodpeckers was a function of pre-fire conditions and fire severity which created site conditions suitable for use by these two *Picoides* species.

Although many characteristics of nest-sites were similar for Three-toed and Black-backed woodpeckers, rotten, naturally fallen down woody debris differentiated between their nest sites. Therefore, I concur with Kilham (1966) and Short (1974) who reported that Black-backed Woodpeckers use more open, drier sites within mature/overmature forests. Additionally, Black-backed Woodpecker nest sites may have been located on steeper terrain where downed wood on south slopes is more prone to drying (Bull et al. 1986, Goggans et al. 1987, Barrett 1994). My results also corroborate those of other researchers (Short 1974, Yunick 1985, Bull et al. 1986, Wesolowski and Tomialojc 1986, Goggans et al. 1987, Angelstam and Mikusiński 1994) who found that Three-toed Woodpeckers use flat to gently sloping terrain and wet to swampy areas within mature/overmature forests.

Biogeographical histories of Three-toed and Black-backed woodpeckers may explain why these two similar species partition habitat in the observed manner. Although the two species are sympatric in boreal and montane forests of North America, the range of Three-toed Woodpeckers continues across the Palearctic. Three-toed Woodpeckers are thought to have evolved circumboreally with spruce (*Picea*) forests, while Black-backed Woodpeckers are thought to have evolved in closed boreal and montane coniferous forests of North America (Bock and Bock 1974). Accordingly, Wesolowski and

Tomialojc (1986) suggested that use of wet, coniferous forests by Three-toed Woodpeckers may approximate habitat use in cool, boreal forests within more northerly portions of their range.

Cavity sites of Hairy Woodpeckers had higher densities of small-diameter down woody debris (fuels) than cavity sites of Three-toed and Black-backed woodpeckers. Thus, I suspect that Hairy Woodpecker nest sites may have been located in denser, younger-aged forests (pole to mature) and/or sites that experienced fire of a lower intensity than did sites used by Three-toed and Black-backed woodpeckers.

Intraspecific Comparisons of Occupied and Unoccupied Habitats

Intraspecific comparisons of vegetative structure between cavity plots, associated plots, and random plots provided further evidence that Three-toed and Black-backed woodpeckers were more specialized than Hairy Woodpeckers. Three-toed and Black-backed woodpecker nest sites were structurally different from random plots. Previous studies also found that characteristics of Three-toed and Black-backed woodpecker nest sites differed from those of random plots (Lester 1980, Caton 1996). Additionally, characteristics of Three-toed Woodpecker nest sites were closer to water than associated plots were, which suggests that this species may select forest habitat features at a finer scale than do Black-backed Woodpeckers. I am unaware of any other woodpecker studies that compared characteristics of nest sites and associated plots. Thus, it is impossible to determine whether Three-toed Woodpeckers consistently make habitat choices at a finer scale than do Black-backed Woodpeckers.

Habitat on Hairy Woodpecker nest sites was not different from habitat on associated or random plots. This result again suggests that Hairy Woodpeckers are less specialized than the other *Picoides* species I studied. However, in contrast to my findings, other researchers have found that characteristics of Hairy Woodpecker nest sites differed from those of random sample plots (Lester 1980, Harestad and Keisker 1989, Loose and Anderson 1995, Caton 1996). In these previous studies, nest site characteristics (e.g., basal area, burn severity, nest-tree features) that were found to be different were not the same characteristics I used in analyses for this study.

Downy Woodpeckers overlap in habitat distribution with the similar Hairy Woodpecker. However, Hairy, Three-toed, and Black-backed woodpeckers show a stronger preference for mature coniferous forests (Winkler et al. 1995). Finding no Downy Woodpeckers within my study area corroborate those of Hutto (1995b) who found Downy Woodpeckers to be particularly uncommon within the Northern Rocky Mountain region.

Forest isolates within the region no longer have the capacity for fire events that represent scales and intensities typical of the past 500 years (Turner et al. 1993). Thus, my finding that burned habitat was more likely to be used by *Picoides* species has major implications for plans to maintain viable populations of *Picoides* species, especially populations of Three-toed and Black-backed woodpeckers, in the Greater Yellowstone Area. Specifically, my results indicate that we need to consider the frequency, intensity, and juxtaposition of fire over the regional landscape when considering the viability of these rare species. Whereas we do not yet know the dispersal ability of these species, nor do we understand metapopulation dynamics, we do know that naturally disturbed areas are crucial for these *Picoides* species. Further study should be conducted in replicate burns and in areas with beetle-killed tree. In this way, we may be able to identify critical habitat features which attract these woodpeckers, learn more about their dispersal ability, and in time mimic these features at a landscape level to ensure the viability of these uncommon woodpecker species.

Scope and Limitations

This study was limited by the lack of previously existing information regarding distributions (historic and current), minimum-area requirements, demography, fledging success/survival, dispersal rates, and predation/mortality of *Picoides* species in lodgepole pine dominant forests within the Intermountain West. The study was further limited because of the spatial arrangement of available and accessible postfire habitat (≤ 1 year since fire) existing within the Greater Yellowstone Area. Given the limitations mentioned above and logistical constraints of budgets, I chose to focus on distributions of *Picoides* species in three disturbance types of mature lodgepole pine habitat within the southwestern portion of the system. Thus, sampling quadrats were not chosen randomly throughout the Greater Yellowstone Area. Further, all human disturbed, naturally disturbed, and undisturbed quadrats were within an associated single stratum (i.e., burned, clearcut, undisturbed). Thus, portions of my sampling design may be considered pseudoreplication by some (Hurlbert 1984). Although this was unavoidable, I recommend caution when using my results to make inferences for other areas.

Because I knew that *Picoides* species were likely to occur in low densities, I was aware before the study began that I would obtain small sample sizes. I also realized that small samples would yield low statistical power for detecting small intra- and inter-specific differences in habitat use and that real and important effects would likely go undetected. However, given our lack of knowledge, I felt it was reasonable to use attainable sample sizes to at least identify evident features of habitat selection. Given that these species have large home ranges and occur in low densities, it will remain difficult to obtain the large samples needed to detect the subtleties of habitat selection in future studies.

Because the forest structure varied among strata, detectability of *Picoides* species may have varied accordingly. Although visual-detection distance was not monitored, it may have been lower in late-seral forest (i.e., undisturbed) habitat than in burned or clearcut habitat. Thus, actual use of undisturbed habitat may have been greater than indicated by my survey results. Future efforts within undisturbed habitat may require survey transects to be closer together, surveying the area more than once during the breeding season, or a combination of both.

Further knowledge of habitat selection may have been gained by measuring additional landscape metrics (e.g., nearest patch, patch density, patch size) and abiotic variables (e.g., temperature gradients at nest site, site productivity) associated with nest sites and random sites. Unfortunately, logistical constraints prevented me from examining such factors.

MANAGEMENT RECOMMENDATIONS

My management recommendations focus on Three-toed and Black-backed woodpeckers, because Hairy Woodpeckers appear less specialized in their habitat use than Three-toed and Black-backed woodpeckers. Additionally, Three-toed and Black-backed woodpeckers are of concern because they are both listed as Sensitive Species in Region 4 (central and south Idaho, Nevada, Utah, and western Wyoming) and Region 1 (Montana and northern Idaho), respectively, of the U.S.D.A. Forest Service (Sphahr et al. 1991, U.S.D.A. Forest Service 1994).

Three-toed and Black-backed woodpeckers use recently disturbed habitats. Thus, management should ensure that fire, insect, or wind are allowed to regularly disturb habitat throughout space and time. Habitats should be protected for at least three years after disturbance occurs (E. C. Murphy and S. H. Lehnhausen, unpubl. data). Disturbance can be allowed to occur naturally on large reserves or networks of reserves. Where natural disturbance will not be tolerated, managers will need to employ prescribed disturbances. The appropriateness of microhabitat features (e.g., distance to water, density and condition of down woody debris) must be considered when choosing locations for reserves or for prescribed disturbances.

The spatial and temporal dimensions of a system and the target organism(s) must be considered together in any definition of disturbance (Pickett and White 1985). Therefore, when designing disturbance within the Yellowstone area, managers should focus on time and space, severity, juxtaposition, and resilience of the system based on historic record. Additionally, focus should include demography, productivity, and dispersal of, and condition of nesting and foraging habitats (basal area, canopy cover, ground cover vegetation) for Three-toed and Black-backed woodpeckers. Ultimately, designs for disturbance may transpose the system enough to provide a shifting mosaic of habitats which resemble the historic disturbance regime of the Yellowstone system.

Many forests within the Intermoutain West require fire events for their perpetuation on the landscape (Habeck and Mutch 1973). Conditions created by stand-replacement fires are not simulated by traditional timber harvest methods. Usually <10% of wood is consumed during a fire, leaving volumes of standing and downed wood (Foster 1983, Payette et al. 1989). Whereas 85-90% of wood (i.e., in a lodgepole pine dominated stand) is typically removed after clearcutting in the western portion of the Yellowstone area (S. Cassani, U.S. Forest Serv., pers. commun., J. Councilman, U.S. Forest Serv., pers. commun.). Because this study and others have stressed the importance of postfire conditions (i.e., dead and down trees) for woodpeckers, forest managers need to design silvicultural practices (e.g., sanitation, salvage, and clearcut logging) that preserve the dead-wood structure and function and incorporate prescribed burn programs.

In conclusion, I recommend that forest managers within the Greater Yellowstone Area (1) determine distributions and habitat use of Three-toed and Black-backed woodpeckers, (2) inventory and monitor Three-toed and Black-backed woodpeckers, (3) determine intensity, frequency, composition, and configuration of historic fire events, (4) determine silvicultural methods that preserve dead wood in the appropriate configurations and incorporate fire, and (5) delay removal of dead wood from disturbed habitat for ≥ three years after disturbance. The economics of delayed harvest will likely be of special concern to land managers. Specifications for dead lodgepole pine trees that will be used as products vary from very stringent (e.g., power poles) to very lenient (e.g., fuels) (Fahey 1980). When considering the economics of the decision to delay, it is important to consider that while prices paid for live lodgepole pine versus dead account for most of the economic loss (i.e., 2 Common and Better grade lumber was degraded to 3 Common after dead one year), only gradual losses in the value of lumber recovered from dead lodgepole pine occur in the following 2-3 years (i.e., because of checking and eventual rot) (Fahey 1980).

However, given the lack of information on values of variously aged dead wood in the Yellowstone area, local guidelines/measures for evaluating beetle- and fire-killed lodgepole pine for marketable products need to be developed.

LITERATURE CITED

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* B.N. Petran, and F. Csaki, eds. International symposium on information theory, second edition. Adademiai iadi, Budapest, Hungary.

___, 1985. Prediction and entropy. Pages 1-24 *in* A.C. Atkinson, and S. E. Fienberg, eds. A celebration of statistics: the ISI Centenary Volume. Springer-Vaerlag, New York, New York, USA.

Amman, G. D. 1969. Mountain pine beetle emergence in relation to depth of lodgepole pine bark. Research Note INT-96. Ogden, Ut. U.S.D.A. Forest Serv., Intermountain Forest and Range Experiment Stat. 8 p.

___. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems; impact on succession. Pages 3-18 *in* Mattson, W. J., ed. Arthropods in forest ecosystems: proceedings in life sciences. New York: Springer-Verlag.

___, and K. C. Ryan. 1991. Insect infestation of fire-injured trees in the greater Yellowstone area. Research Note INT-398. U.S. For. Serv., Intermountain Research Station, Ogden, Ut. 9 p.

Angelstam, P., and G. Mikusiński. 1994. Woodpecker assemblages in natural and managed boreal and hemiboreal forest — a review. Ann. Zool. Fennici 31: 157-172.

Apfelbaum, S., and A. Haney. 1981. Bird populations before and after wildfire in a great lakes pine forest. Condor 83:347-354.

Arno, S. F., E. D. Reinhardt, and J. H. Scott. 1993. Forest structure and landscape patterns in the subalpine lodgepole pine type: a procedure for quantifying past and present conditions. Gen. Tech. Rep. INT-294. Ogden, Ut: U.S. For. Serv., Intermountain Research Station. 17 p.

Baker, William L. 1992. The landscape ecology of large disturbances in the design and management of nature reserves. Landscape Ecol. 7:181-194.

Baldwin, P. H. 1960. Overwintering of woodpeckers in bark beetle-infested spruce-fir forests in Colorado. 12th Internatl. Ornithol. Congr. Proc., Helsinki (1958):71-84.

___. 1968. Predator-prey relationships of birds and spruce beetles. Proc. Entomol. Soc. Amer. N. Central Branch. 23:90-99.

Barrett, S. W. 1994. Fire regimes on andesitic mountain terrain in northeastern Yellowstone National Park, Wyoming. Int. J. Wildland Fire 4:65-76.

Beal, F. E. L. 1911. Food of the woodpeckers of the United States. U.S. Dept. Of Agri. Biol. Surv. Bull. No. 37 Washington, D.C.

Blackford, J. 1955. Woodpecker concentration in a burned forest. Condor 57:28-30.

Bock C. E., and J. H. Bock. 1974. On the geographical ecology and evolution of the three-toed woodpeckers, Picoides tridactylus and P. arctcus. The American Midl. Naturalist 92:397-405.

Bull, E. L. 1983. Bird response to beetle-killed lodgepole pine. The Murrelet 64:94-96.

___., S. R. Peterson, and J. W. Thomas. 1986. Resource partitioning among woodpeckers in northeastern Oregon. U.S. For. Serv., Pacific Northwest Res. Sta., LaGrande, Oreg. PNW-4444. 19 pp.

___., R. S. Holthausen, and Mark G. Henjum. 1990. Techniques for monitoring pileated woodpeckers. U.S. For. Serv. Gen. Tech. Rep. PNW-GTR-269.

Burnham, K. P., and D. R. Anderson. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. U.S. Fish and Wildlife Serv., Colorado Cooperative Fish and Wildlife Res. Unit, Colorado State Univ., Fort Collins.

Carey, A. B., M. M. Hardt, S. P. Horton, and B. L. Biswell. 1991. Pages 122-142 *in* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords. Wildlife and vegetation of unmanaged Douglas-fir forests.

U.S. For. Serv. Gen. Tech. Rep. PNW-GTR-285.

Cassani, S. personnal communication. U.S. For. Serv. June, 1997.

Caton, E. L. 1996. Effects of fire and salvage logging on the cavity-nesting bird community in northwestern Montana. Ph.D. Thesis, Univ. of Montana, Missoula. 115 pp.

Cole, W. E. and G. D. Amman. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters U.S. For. Serv., Res. note INT-95. Ogden, Ut. 7 p.

Conner, R. N., and D. C. Rudolph. 1991. Forest habitat loss, fragmentation, and red-cockaded woodpecker populations. Wilson Bull. 103:446-457.

Councilman, J. personnal communication. U.S. For. Serv. June, 1997.

Crockett, A. B. and P. L. Hansley. 1978. Apparent response of *Picoides* woodpeckers to outbreaks of the pine bark beetle. Western Birds 9:67-70.

Cytel Software Corporation. 1993. LogXact-Turbo user manual. Cambridge, Ma. 400 pp.

Evans, W. G. 1971. The attraction of insects to forest fires. Pages 115-127. *in* Proc. tall timbers conference on ecological animal control by habitat management. Tall timbers research center. Tallahassee, Fla.

Fahey, T. D. 1980. Beetle-killed pine can be salvaged, but for how long? Forest Indust. 60-61.

___. 1980b. Evaluating dead lodgepole pine for products. Forest Products J. 30:34-39.

Foster, D. R. 1983. The history and pattern of fire in the boreal forest of southeastern Labrador. Can. J. Bot. 61:2459-2471.

Gara R. I., W. R. Littke, J. K. Agee, S. R. Geiszler, J. D. Stuart, and C. H. Driver. 1985. Influence of fires, fungi and mountain pine beetles on development of a lodgepole pine forest in south-central Oregon. Pages

153-162 *in* Baumgartner, D. M., R. G. Krebill, J. T. Arnott, and G. F. Weetman, eds. Lodgepole pine the species and its management. Symposium proceedings. Cooperative Extension Washington State Univ., Pullman.

Goggans, R. R., R. Dixon, and L. C. Seminara. 1987. Habitat use by three-toed and blacked-backed woodpeckers. Oreg. Dept. Fish and Wildl. Nongame Rep. 87-3-02. Oreg. Dept. Fish and Wildl., Bend. 46 pp.

___., ___, and ___. 1989. Habitat use by three-toed and black-backed woodpeckers. U.S. For. Serv., Deschutes National Forest. ODFW Nongame Rep. 87-3-20. xvii+49 pp+34 figures/tables.

Habeck, J. R. and R. W. Mutch. 1973. Fire-dependent forests in the Northern Rocky Mountains. Quater. Resea. 3:408-424.

Hansen, A. J. Avian diversity in the Greater Yellowstone Ecosystem, Montana State Univ., Bozeman. unpubl.

___., T. A. Spies, F. J. Swanson, and J. L. Ohman. 1991. Conserving biodiversity on managed forests: lessons from natural forests. Bioscience 41:382-392.

Harestad, A. S., and D .G. Keisker. 1989. Nest tree use by primary cavity-nesting birds in south central British Columbia. Can. J. Zool. 67:1067-1073.

Harris, M. A. 1982. Habitat use among woodpeckers in forest burns. M.S. Thesis, Univ. of Montana, Missoula.

Harris, R. J. 1985. A primer of multivariate statistics. Second ed. Academic Press, Inc., San Francisco, Calif. 576 pp.

Hein, D. 1980. Management of lodgepole pine for birds. Pages 238-347. *in* DeGraff [DeGraaf], R. M., tech. coord. Workshop preceedings: Management of western forests and grasslands for nongame birds. 1980 February 11-14; Salt Lake City, Ut. Gen. Techn. Rep. INT-86. Ogden, Ut. U.S.D.A. Stat.

Hejl, S. L. 1994. Human-induced changes in bird populations in coniferous forests in western North America during the past 100 years. Studies in Avian Biology 15:232-246.

___., R. L. Hutto, C. R. Preston, and D. M. Finch. 1995. Effects of silvicultural treatments in the Rocky Mountains. Pages 220-244 *in*: Martin, T.E. and D.M. Finch, eds. Ecology and management of neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York.

Hogstad, O. 1970. On the ecology of the three-toed woodpecker *Picoides tridactylus* (L.) outside the breeding season. Nytt Mag. Zool. 18:221-227.

___. 1977. Seasonal change in intersexual niche differentiation of the three-toed woodpecker *Picoides tridactylus*. Ornis Scand. 8:101-111.

Hulbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Mono. 54:187-211.

Hutto, R. L. 1985. Habitat selection by nonbreeding, migratory land birds. Pages 455-476 *in* Cody, M.L., ed. Habitat selection of birds. Academic Press, New York.

___, R. L. 1995. Composition of bird communities following stand-replacement fires in Northern Rocky Mountain (U.S.A.). Cons. Biol. 9:1041-1058.

___, 1995b. Distribution and habitat relationships. U.S. For. Serv. Northern Region Songbird Monitoring Prog. Sec. Rep. U.S. For. Serv., Missoula, Mont.

Jackson, J. A. 1979. Tree species as foraging substrates for insectivorous birds. Pages 69-93 *in* The role of insectivorous birds in forest ecosystems. Edited by J .G. Dickson, R.N. Conner, R. R. Fleet, J. A. Jackson, and J. C. Kroll. Academic Press. San Francisco, Calif. 69-93.

Joy, S. M., R. T. Reynolds, and D. G. Leslie. 1993. Northern goshawk broadcast surveys: Hawk response variables and survey costs. Rocky Mountain Forest and Range Experiment Station, 240 West Prospect Road, Fort Collins, Colo. 80526.

Kilham, L. 1966. Nesting activities of black-backed woodpeckers. Condor 68:308-310.

___. 1970. Feeding behavior of downy woodpeckers I. Preference for paper birches and sexual differences. Auk 87:544-556.

Kisiel, D. S. 1972. Foraging behavior of *Dendrocopos villosus* and *D. pubescens* in eastern New York state. Condor 74:393-398.

Koplin, J. R. 1969. The numerical response of woodpeckers to insect prey in a subalpine forest in Colorado. Condor 71: 436-438.

Lavigne, R. J., J. A. Lockwood, S. R. Shaw, and T. Christiansen. 1992. Insect response to the 1988 fires in Yellowstone National Park. Univ. of Wyo. Nat. Park Serv. Research Center. 243 pp.

Lawrence, (Lousie de Kirdine). 1967. A comparative life-history study of four species of woodpeckers. Ornithol. Monogr: 5:1-156.

Lester, A. N. 1980. Numerical response of woodpeckers and their effect on mortality of mountain pine beetles in lodgepole pine in northwestern Montana. M.S. Thesis, Univ. Of Montana, Missoula. 103 pp.

Loose, S. S. and S. H. Anderson. 1995. Woodpecker habitat use in the forests of southeast Wyoming. J. Field Ornithol. 66:503-514.

Lotan, J. E., J. K. Brown, and L. F. Neuenschwander. 1985. Role of fire in lodgepole forests. Pages 133-152 *in* Baumgartner, D.M., R.G. Krebill, J. T. Arnott, and G. F. Weetman, eds. Lodgepole pine the species and its management. Symposium proceedings. Cooperative Extension. Washington State Univ., Pullman.

____, and D. A. Perry. 1983. Ecology and regeneration of lodgepole pine. U.S. For. Serv. Agri. Handb. No. 606. p 12-16.

Manly, B .F. J. 1995. Multivariate statistical methods. Second ed. Chapman and Hall. London. England. 215 pp.

Marshall, D. B. 1992. Status of the black-backed woodpecker in Oregon and Washington. *in* Bibliography of selected literature regarding the management of cavity excavators in eastside habitats: Oregon and Washington. U.S. For. Serv., Pacific Northwest Region. La Grande, Oreg.

Martner, B. E. 1986. Wyoming Climate Atlas. Univ. of Nebraska Press. 432 pp.

McClelland, B. R. 1977. Relationships between hole-nesting birds, forest snags, and decay in western larch - Douglas-fir forests of the northern Rocky Mountains. Ph. D. Diss., Univ. of Montana, Missoula.

___., and J. A. Schmidt. 1992. Old-Growth western larch forests: management implications for cavity-nesting birds. Ecology and management of Larix forests: a look ahead, proceedings of an international symposium. Whitefish, Mont., U.S.A., 1995: p.376. U.S. For. Serv. Gen. Tech. Rep. INT; no. 319.

McComb, W. C., S. A. Bonney, R. M. Sheffield, and N. D. Cost. 1986. Snag resources in Florida: are they sufficient for average populations of primary cavity-nesters? Widl. Soc. Bull. 14:40-48.

McGregor, M. D., and D. M. Cole, editors. 1985. Integrating management strategies for the mountain pine beetle with multiple-resource management of lodgepole pine forests. U.S. Dept. Agri. Gen. tech. rep. INT-174; Ogden, Ut. 57 p.

Miller, A. H., and C. E. Bock. 1972. Natural history of the nuttall woodpecker at the hastings reservation. Condor 74:284-294.

Miller, E. and D. R. Miller. 1980. Snag use by birds Pages 337-356 *in* Proc. workshop: management of Western forests and grasslands for nongame birds. U.S. For. Serv. Gen. tech. rep. INT-86. 535 pp.

Murphy, E. C. and S. H. Lehnhausen. unpubl. Responses of woodpeckers to a fire in interior Alaska: do black-backed woodpeckers require recently burned forests? J. Wildl. Manage.

Natural Weather Serv. unpubl. data. Asheville, N.C.

Neter, J., W. Wasserman, and G.A. Whitman. 1993. Applied Statistics.

Allyn and Bacon. London. 989 pp.

Niemi, G. J. 1978. Breeding birds of burned and unburned areas in northern Minnesota. Loon 50:73-84.

___, and J. M. Hanowski. 1984. Relationships of breeding birds to habitat characteristics in logged areas. J. Wildl. Manage. 48:438-443.

Payetté, S., C. Morneau, L. Sirois, and M. Desponts. 1989. Recent fire history of the northern Quebec biomes. Ecology 70:656-673.

Pickett, S. T. A., and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Acedemic Press, Inc., San Diego, Calif. 472 pp.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Field methods for monitoring landbirds. U.S. For. Serv. Gen. Tech. Rep. PSW-GTR-144.

Raphael, M. G. and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildl. Monogr. 86:1-66.

Renkin, R. A., and D. G. Despain. 1992. Fuel moisture, forest type, and lightning-caused fire in Yellowstone National Park. Canadian Journal of Forest Research 22:37-45.

Rice, W. R. 1990. A consensus combined P-value test and the family-wide significance of component tests. Biometrics 46:303-308.

Rodman, A., H. F. Shovic, and D. Thoma. 1996. Soils of Yellowstone National Park. Yellowstone Center for Resources, Yellowstone National Park, Wyo, YCR-NRSR-96-2.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests in Yellowstone National Park. Ecological Monographs. 52:199-221.

Saab, V. A. 1994. unpubl. Bird responses to stand-replacement fire, fire suppression, and tree thinning with prescribed fire in ponderosa pine/Douglas-fir forests. Intermountain Research Stat. U.S. For. Serv. Boise, Id.

SAS Institute, Inc. 1990. SAS/STAT User's Guide, Release 6.03 Edition. Cary, N. C. SAS Institute, Inc. 1028 pp.

Scheaffer, R. L., W. Mendenhall, and L. Ott. 1990. Elementary survey sampling. Fourth ed. PWS-Kent Publ., Boston, Mass.

Scheiner, S. M. 1993. MANOVA: Multiple response variables and multispecies interactions. Pages 94-112 *in* Scheiner, S. E. and J. Gurevitch, eds. Design and analysis of ecological experiments. Chapman and Hill, New York, N. Y.

Schulte, L. A. 1996. Bird communities of early successional burned and logged forest in northeastern Minnesota. M.S. Thesis, Univ. of Minn., Duluth 61 pp.

Short, L. L. 1971. Systematics and behavior of some North American woodpeckers, Genus *Picoides* (Aves). Bull. of the Amer. Mus. of Natural History 145:63-97.

___. 1974. Habits and interactions of North American three-toed woodpeckers (Picoides arcticus and Picoides tridactylus). Amer. Mus. Novitates. 2547, 42 pp.

___. 1982. Woodpeckers of the world. Delaware Museum of Natural History. Mich. pp. 301-334.

Sphahr, R., L. Armstrong, D. Atwood, and M. Rath. 1991. Threatened, endangered, and sensitive species of the intermountain region. U.S. For. Serv. Fisheries and Wildl. Manage., Intermountain Region.

Spring, L. W. 1965. Climbing and pecking adaptations in some North American woodpeckers. Condor 67:457-488.

Statistica for Windows. 1994. General Conventions and Statistics I. StatSoft, Inc. Tulsa, Ok. 1718 pp.

SYSTAT: Statistics, Version 5.2 Edition. SYSTAT, Inc., 1992. Evanston, Ill. 724 pp.

Taylor, D. L. and W. J. Barmore Jr. 1980. Post-fire succession of avifauna in coniferous forests of Yellowstone and Grand Teton National Parks, Wyoming. Pages 130-145. *in* Management of western forests and grasslands for nongame birds. U.S. For. Serv. Gen. Tech. Rep. INT-86.

Thomas, J. W., editor. 1979. Wildlife habitats in managed forests - the Blue Mountains of Oregon and Washington. U.S. For. Serv. Agri. Handbook. 53, 512 pp.

Thompson, F. R., J. R. Probst, and M. G. Raphael. 1995. Impacts of silviculture: overview and management recommendations. Pages 201-219. *in* Martin, T. E. and D. M. Finch, eds. Ecology and management of neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York.

Toone, Robin A. 1992. General inventory for northern three-toed woodpeckers (*Picoides tridactylus dorsalis*) on the Wasatch Plateau, Ferron and Price Ranger Districts, Manti-La Sal National Forest, Utah. U.S. For. Serv. Region 4 and Utah Natural Heritage Program. Utah Dept. Of Natural Resources, 1636 West North Temple, Suite 316, Salt Lake City, Ut 84116-3193. 32 pp.

Turner, M. G., W. H. Romme, R. H. Gardner, R. V. O'Neill, and T. K. Kratz. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. Landsc. Ecolo. 8:213-227.

U.S.D.A. Forest Service. 1994. Northern region sensitive list(1994). Northern Region. Missoula, Mont. 31 pp.

Van Tyne, J. 1926. An unusual flight of the Arctic three-toed woodpecker. Auk 43:469-474.

Villard, P. 1994. Foraging behavior of black-backed and three-toed woodpeckers during spring and summer in a Canadian boreal forest. Can. J. Zool. 72:1957-1959.

___. and C. W. Beninger. 1993. Foraging behavior of male black-backed and hairy woodpeckers in a forest burn. J. Field Ornithol. 64:71-76.

Waters, J. R., B. R. Noon, and J. Verner. 1990. Lack of nest-site limitation in a cavity nesting bird community. J. Wildl. Manage. 54:239-245.

Weins, J. A. 1989. The ecology of bird communities. Cambridge Studies in Ecology. 1:333-351.

Wesolowski, T. and L. Tomialojc. 1986. The breeding ecology of woodpeckers in a temperate primeval forest - preliminary data. Acta Ornithologica 22:1-22.

West, J. D. and J. M. Speirs. 1958. The 1956-57 invasion of three-toed woodpeckers. Wilson Bull. 71:348-352.

Wickman, B. E. 1965. Black-backed three-toed woodpecker, *Picoides arcticus*, predation on *Monochamus oregonensis*. Pan-Pac. Entomol. 41:162-164.

Wilcox, B. A. and D. D. Murphy. 1985. American Conservation strategy: the effects of fragmentation on extinction. Naturalist. 125:879-887.

Winkler, H. D. A. Christie, and D. Nurney. 1995. Woodpeckers: a guide to the woodpeckers of the world. Houghton Mifflin Comp. New York, N.Y. 406pp.

Yunick, R. P. 1985. A review of recent irruptions of the black-backed woodpecker and three-toed woodpecker in eastern North America. J. Field Ornithol. 56:138-152.

APPENDIX A

Table 4. Habitat characteristics within cavity plots of three *Picoides* species on theTarghee National Forest and Yellowstone National Park, 1995 and 1996.

	Picoides species					
	Black-backed Woodpecker (n = 15)[a]		Three-toed Woodpecker (n = 11)[b]		Hairy Woodpecker (n = 17)[c]	
Habitat Characteristic	Mean	SE	Mean	SE	Mean	SE
Canopy cover (%)	26.28	6.03	27.41	5.87	35.75	4.70
Distance to water (m)	282.73	45.19	185.45	40.90	297.41	70.23
Distance to clearing (m)	185.47	38.70	154.64	42.71	50.47	7.82
Coniferous ground cover (%)						
0 - 1 m (ht)	1.48	0.50	0.73	0.35	0.10	0.07
1 - 2 m (ht)	0.02	0.02	0.00	0.00	0.00	0.00
Decidous ground cover (%)						
0 - 1 m (ht)	3.15	3.00	0.25	0.23	6.70	1.66
1 - 2 m (ht)	0.05	0.05	0.45	0.45	1.01	0.64
Herbaceous ground cover (%)						
0 - 1 m (ht)	14.90	4.10	21.66	5.76	36.54	4.82
1 - 2 m (ht)	0.40	0.25	0.18	0.13	0.44	0.44
Height of cavity tree (m)	32.73	1.94	30.18	2.81	20.22	2.58

Table 4. Continued

	Picoides species					
	Black-backed Woodpecker (n = 15)[a]		Three-toed Woodpecker (n = 11)[b]		Hairy Woodpecker (n = 17)[c]	
Habitat Characteristic	Mean	SE	Mean	SE	Mean	SE
Bark on cavity tree (%)	76.10	5.31	85.63	6.21	91.76	4.26
Cavity tree dbh (cm)	26.76	2.35	27.26	1.72	31.28	2.14
Live and dead trees (all species) in dbh classes 1-9[d] (count)	26.53	2.61	25.45	4.50	37.30	19.53
Live and dead trees ≥ dbh class 5 (count)						
ABLA[e]	3.40	1.51	1.81	0.69	0.41	0.35
PICO[f]	4.00	0.74	3.73	0.98	1.94	0.52
PSME[g]	0.20	0.14	0.09	0.09	0.00	0.00
POTR[h]	0.00	0.00	0.00	0.00	3.18	0.74
Height of tallest tree (m)	34.68	1.66	33.45	2.24	25.02	2.23
dwd[i] in dbh classes 1 - 4	3.75	0.54	3.07	0.33	2.61	0.51

Table 4. Continued

	Picoides species					
	Black-backed Woodpecker (n = 15)[a]		Three-toed Woodpecker (n = 11)[b]		Hairy Woodpecker (n = 17)[c]	
Habitat Characteristic	Mean	SE	Mean	SE	Mean	SE
All tree species in dbh class 5	0.64	0.10	0.72	0.10	0.78	0.13
Naturally fallen dwd	4.16	1.81	2.48	0.85	6.85	1.88
Burned dwd	4.72	1.27	5.31	0.73	2.24	0.69
Solid dwd	11.18	2.27	10.47	1.45	6.82	1.72
Rotten dwd	3.78	0.95	2.50	0.56	3.87	1.16

[a] Number of active cavities found in 1995-1996: NDLP - 1; HDLP - 0; LSLP - 1.

[b] Number of active cavitites found in 1995-1996: NDLP - 2; HDLP - 0; LSLP - 0.

[c] Number of active cavities found in 1995-1996: NDLP - 7; HDLP - 1; LSLP - 2.

[d] 1=2.5-8cm, 2≥8-12cm, 3≥13-15cm, 4≥16-23cm, 5≥24-38cm, 6≥39-53cm, 7≥53-60cm, 8≥60-90cm, 9≥90cm.

[e] subalpin fir species

[f] lodgepole pine species

[g] Douglas-fir species

[h] aspen species

[i] down woody debris

APPENDIX B

Table 5. Description of vegetation variables measured at cavity, associated, and random 11.3-m radius plots within the Targhee National Forest and Yellowstone National Park, 1995-1996.

Habitat Characteristic Variable	Description
SL/Pos.	Slope position (1-valley bottom, 2-concave slope, 3-even slope, 4-convex slope, 5-bench, 6-ridge top)
SL/Loc.	Aspect (1-360 degrees)
DisH20	Distance to water (m)
DisCLE	Distance to clearing (m)
AvgCC	Canopy cover (%)
Avgc 0-1m	Average coniferous ground cover (%)
Avgc 1-2m	Average coniferous ground cover (%)
Avgd 0-1m	Average deciduous ground cover (%)
Avgd 1-2m	Average deciduous ground cover (%)
Avgh 0-1m	Average herbaceous ground cover (%)
Avgh 1-2m	Average herbaceous ground cover (%)
CanLay	Canopy layers (1-3)
AvgN	Natural origin of wood (count)
AvgC	Cut origin of wood (count)
AvgB	Burn origin of wood (count)
AvgBCH	Burned, charred origin of wood (count)
AvgdkS	Solid decay condition of down woody debris (count)
AvgdkR	Rotten decay condition of down woody debris (count)

Table 5. Continued

Habitat Characteristic Variable	Description
Avght	Height classes (m) (1=0-1.5, 2=>1.5-3, 3=>3-10, 4=>10-30, 5=>30)
Avgdk	Decay classes: 1=completely hard as in first or second season downed; no decay; usually with bark and branches intact. 2 =some early decay evident but core mostly hard, as though in the second or third year; most or all bark gone, large branches remaining. 3 =bark gone, outer wood rotten, and easily detached, branches gone. 4 =snag either still intact but easily broken apart or fragmenting; fibrous
Avgdbh	Diameter classes (cm) (1=2.5-8, 2=>8-12, 3=>13-15, 4=>16-23, 5=>24-38, 6=>39-53, 7=>53-60, 8=>60-90, 9>90)