LAND COVER AND TOPOGRAPHIC EFFECTS ON CAVITY-NESTING OWL OCCURRENCE AND THE ROLE OF SPECIES INTERACTIONS IN STRUCTURING CAVITY-NESTING OWL COMMUNITIES

by

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DEDICATION

I dedicate this thesis to my wonderful family and friends.

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ABSTRACT

Relatively little is known about the distribution, abundance, and population trends of many species of owls. Frequently, studies that describe owl distributions are accomplished by modeling characteristics of the habitat such as land cover and topographic features. However, the potential to model owl distributions as a function of species interactions has been largely unexplored. I investigated how habitat characteristics as well as species interactions shape owl distributions in the Western United States. Using occurrence data collected between 2009 and 2010 in the Boise National Forest, Idaho, I developed species distribution models for Flammulated Owls (*Otus flammeolus*) and Northern Saw-whet Owls (*Aegolius acadicus*) and spatially applied these models in a Geographic Information System to delineate habitat suitability. I considered land cover and topographic variables by selecting the best representative spatial scale from 0.4-km, 1-km, or 3-km-radius plots centered on point-count locations (N = 150). Flammulated Owls occupied 27 (18 %) point-count locations and occurred in areas with a higher proportion of Douglas-fir (*Pseudotsuga menziesii*) at the 0.4-km scale, less diverse land cover composition at the 1-km scale, and they associated with south-facing aspects at the 3-km scale. Saw-whet Owls occupied 45 (30%) point- count locations and were associated with relatively flat landscapes at the 0.4-km scale and locations containing larger proportions of non-forested area. At the 1-km and 3-km scales, Saw-whet Owls occurred in areas with south-facing aspects and those containing a higher proportion of ponderosa pine (*Pinus ponderosa*), respectively. To investigate the role of species interactions in determining owl distributions, I examined patterns of co-occurrence between woodpeckers (woodpeckers excavate cavities in living and dead trees, which provide nesting sites for secondary cavity nesters such as owls) and sympatric cavity-nesting owls using two-species occupancy models. Specifically, I tested the hypothesis that cavity-nesting owl occupancy was conditional on the presence of one or more common species of woodpecker: Hairy Woodpeckers (*Picoides villosus*), Lewis's Woodpeckers (*Melanerpes lewis*), Northern Flickers (*Colaptes auratus*), Pileated Woodpeckers (*Dryocopus pileatus*), and Red-naped Sapsuckers (*Sphyrapicus nuchalis*). Additionally, I examined the pattern of co-occurrence between cavity-nesting owl species to help understand the nature of their possible competitive interactions. As snags may also be an important component of cavity-nesting owl occurrence, I modeled owl occupancy as a function of snag number and density and pattern of species co-occurrence while accounting for imperfect detection (i.e., the possibility that an individual may go undetected during surveying even when present). The average number of snags per hectare (12.5 ± 0.2, N = 150) and mean diameter at breast height of snags (35.17 cm ± 0.08, N = 150) had no effect on cavity-nesting owl occupancy. There was no support for the hypothesis that cavity-nesting owl occupancy was conditional on the presence of woodpeckers. Likewise, presence of Saw-whet Owls neither excluded nor facilitated Flammulated Owl occupancy. Thus despite the possible value in understanding the occupancy of the nocturnal owl community by examining the diurnal woodpecker community, relationships between woodpeckers and either Flammulated Owls or Saw-whet Owls do not appear strong enough to warrant such an approach.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS v

ABSTRACT.. vii

LIST OF TABLES xii

LIST OF FIGURES xiv

GENERAL INTRODUCTION 1

- Background 2
- Overview of Chapters 3
- Literature Cited 5

CHAPTER ONE: FACTORS INFLUENCING SITE OCCUPANCY OF CAVITYNESTING OWLS IN THE BOISE NATIONAL FOREST, IDAHO: A SPATIAL APPLICATION USING GIS 7

- Abstract 7
- Introduction 8
- Study Area 10
- Methods 11
  - Field Methods 11
  - Survey Protocol 12
  - Landscape Scale Measurements 13
  - Statistical Analysis 15
  - Model Selection and Spatial Implementation 16

Model Performance 17

Results 18

    Surveys 18

    Variable Surveys 18

    Model Selection 19

    Probability of Occupancy and Detection 20

    Spatial Implementation of GIS 20

    Model Performance 21

Discussion 22

    Probability of Detecting Cavity-Nesting Owls 22

    Habitat Modeling for Flammulated Owls 23

    Habitat Modeling for Saw-whet Owls 26

    Summary and Conclusions 28

Literature Cited 29

CHAPTER TWO: PATTERNS OF CO-OCCURRENCE BETWEEN CAVITYNESTING OWLS AND WOODPECKERS IN THE BOISE NATIONAL FOREST, IDAHO 46

Abstract 46

Introduction 47

Study Area 51

Methods 52

    Field Methods 52

    Nocturnal Survey Protocol for Owls 53

    Diurnal Survey Protocol for Woodpeckers 54

Snag Measurements 54

Probability of Detection 55

Statistical Analysis 55

Results 59

Nocturnal Surveys 59

Diurnal Surveys 59

Co-occurrence Patterns 60

Species Interactions Between Owls and Woodpeckers 60

Species Interactions Between Owls 61

Effect of Snags on Owl Occupancy 61

Discussion 62

Species Interactions Between Owls and Woodpeckers 63

Species Interactions Between Owls 65

Effect of Snags on Owl Occupancy 66

Conclusions 68

Literature Cited 69

APPENDIX A 88

AIC Model Selection Results for Flammulated Owls

APPENDIX B 90

AIC Model Selection Results for Northern Saw-whet Owls

APPENDIX C 93

Occurrence Data for Owls and Woodpeckers

LIST OF TABLES

Table 1.1 Landscape measurements of land cover and topography evaluated as potential predictor variables for Flammulated Owl and Northern Saw-whet Owl occupancy in the Boise National Forest, Idaho 36

Table 1.2 Results of AICc-based model selection for the top 12 models examining habitat associations of Flammulated Owls out of a total set of 42 models 37

Table 1.3 Results of AICc-based model selection for the top 25 models examining habitat associations of Northern Saw-whet Owls out of a total set of 63 models 38

Table 1.4 Relative importance (w+) of individual variables for single season occupancy models for Flammulated and Northern Saw-whet Owls .. 39

Table 1.5 List of threshold values and discriminatory power from models predicting probability of site occupancy for Flammulated Owls and Northern Saw-whet Owls 40

Table 1.6 Classification of occupied and unoccupied sites by the final model for Flammulated Owls from an independent data set collected by Boise State University and the National Forest Service from the Boise National Forest during 2005 and 2006 41

Table 2.1 Parameters used in the conditional two-species model and their descriptions 74

Table 2.2 Constraints used for the conditional two-species models to test for occupancy and probability of detection for species B conditional or unconditional on the presence of species A 75

Table 2.3 Naïve estimates of co-occurrence patterns for sympatric cavity-nesting owls and woodpeckers in the Boise National Forest, Idaho 76

Table 2.4 Relative support (w+) measured as the summed Akaike weights for conditional two-species occupancy models where occupancy of Flammulated Owls and Northern Saw-whet Owls is conditional (C) or unconditional (U) of woodpecker presence 77

Table 2.5 Model selection results for two-species occupancy models fit to Flammulated Owl and woodpecker detection data from 150 point-count locations in the Boise National Forest, Idaho, in 2009 and 2010 78

Table 2.6 Model selection results for two-species occupancy models fit to Northern Saw-whet Owl and woodpecker detection data from 150 point-count locations in the Boise National Forest, Idaho, in 2009 and 2010 80

Table 2.7 Model-averaged occupancy estimates (ψ) and 95% confidence intervals for Flammulated Owls and Northern Saw-whet Owls when woodpeckers were present (ψBA) and absent (ψBa) 82

Table 2.8 Relative Support (w+) for different formulations of the conditional two-species occupancy model where Flammulated Owl occupancy and detection probability was either conditional (C) or unconditional (U) of Northern Saw-whet Owl occupancy 83

Table 2.9 Model selection results for two-species occupancy models fit to Flammulated Owl and Northern Saw-whet Owl detection data from 150 point-count locations in the Boise National Forest, Idaho, in 2009 and 2010 84

LIST OF FIGURES

Figure 1.1 Vicinity map showing the location of the Boise National Forest in southwestern Idaho and point-count locations (N = 150) for cavity-nesting owls 42

Figure 1.2 Broadcast sequence for cavity-nesting owls surveyed in the Boise National Forest, Idaho, 2009-2010 43

Figure 1.3 Maps depicting probability of occurrence for (a) Flammulated Owls and (b) Northern Saw-whet Owls in the Boise National Forest, Idaho, based on data collected from 2009-2010 44

Figure 1.4 By overlaying the spatial projections generated where 50, 75, and 100 percent of occupied sites were correctly classified, habitat suitability maps were produced for Flammulated Owls and Northern Saw-whet Owls in the Boise National Forest, Idaho 45

Figure 2.1 Vicinity map showing the location of the Boise National Forest in southwestern Idaho and point-count locations (N = 150) for cavity-nesting owls 85

Figure 2.2 Broadcast sequence for cavity-nesting owls (a) and woodpeckers (b) surveyed in the Boise National Forest, Idaho, 2009-2010 86

Figure 2.3 Two utility poles containing cavities excavated by woodpeckers 87

GENERAL INTRODUCTION

This thesis consists of two chapters describing results of my research on landscape-level habitat associations and community interactions of three cavity-nesting owls: Boreal Owls (*Aegolius funereus*), Flammulated Owls (*Otus flammeolus*), and Northern Saw-whet Owls (*A. acadicus*). My objectives were to: (1) model the effect of land cover and topographic features on cavity-nesting owl site occupancy, (2) spatially depict the probability of occupancy in a geographic information system, (3) determine whether interspecific interactions influence site occupancy, and (4) assess the effect of snag characteristics on cavity-nesting owl occupancy. I carried out fieldwork from February – June of 2009 and 2010 in the Boise National Forest (BNF), which is located in southwestern Idaho. The BNF is approximately 10,600 km^2 in size and has a diversity of habitats influenced by forestry, fire, recreation, and other factors under a multiple-use mandate for land management. The habitat association and co-occurrence data I collected will serve as a reference in future studies seeking to understand site occupancy for cavity-nesting owls. Cavity-nesting birds are susceptible to anthropogenic changes (Imbeau et al. 2001). Therefore, information contained in this thesis should be of interest to forest managers who guide restoration and management of public or private lands suitable for owls as well as ornithologists and other scientists interested in the biology of cavity-nesting owls and the factors that shape their community structure.

Background

With the exception of a small number of species of conservation concern, little is known about the distribution, abundance, and population trends of North American owls (Takats et al. 2001, Duncan 2003). Understanding cavity-nesting forest owls in particular poses special challenges because of their small size, secretive behavior, and, in some cases, rarity. Therefore, knowledge of their occurrence and distribution is needed. Species occurrence and distributions are affected by a range of factors including land cover, topography, and species interactions (Franklin 2009). Generally, studies that describe owl distributions and occurrence are accomplished by modeling characteristics of the habitat. Larger, landscape-level studies of owl-habitat relationships are useful as they can be modeled within a geographic information system (GIS) to create spatial representations of the probability of occupancy for species of wildlife. However, the potential to model species distributions as a function of species interactions has been largely unexplored (but see Heikkinen et al. 2007). For instance, we know that species interactions play an important role in shaping the distribution and occurrence of cavity-nesting owls (Martin and Eadie 1999). Cavity-nesting owls engage in both facilitation interactions with woodpeckers (woodpeckers excavate cavities in living and dead trees, which provide nesting sites for secondary cavity nesters such as owls; Martin and Eadie 1999, Virkkala 2006) as well as competitive interactions with sympatric owl species (McCallum 1994, Vrezec and Tome 2004, Rasmussen et al. 2008). New advances in occupancy modeling now allow for such species interaction to be assessed along with identifying important habitat characteristics that explain owl occurrence. Furthermore, as owls in particular can be logistically difficult to monitor because nighttime surveys are required, there is potential benefit in identifying possible surrogate species (e.g., woodpeckers) whose occupancy may provide an index of owl occurrence or abundance.

Overview of Chapters

In Chapter One, I developed occupancy models to evaluate the landscape-level habitat associations of Boreal Owls, Flammulated Owls, and Northern Saw-whet Owls (hereafter Saw-whet Owls) in the BNF. I modeled owl occurrence using land cover and topographic variables by selecting the best representative scale (400-m, 1-km, or 3-km-radius plots centered on point-count locations) for each owl species. As I ultimately detected no Boreal Owls, I developed predictive habitat models for Flammulated Owls and Saw-whet Owls and incorporated these results into a GIS to create spatial maps depicting suitable habitat for each.

Flammulated Owls occurred in areas with lower diversity in land cover composition at the 1-km scale and a higher proportion of Douglas-fir forest at the 0.4-km scale. At the 3-km scale, Flammulated Owls tended to occur on more south-facing aspects. At the 1-km scale, Saw-whet Owls occupied locations containing larger proportions of non-forested area situated on more southerly-facing aspects. At the 3-km and 1-km scales, areas containing a higher proportion of ponderosa pine and Douglas-fir, respectively, were more frequently occupied by Saw-whet Owls. Saw-whet Owls also occurred in relatively flat landscapes (low terrain ruggedness) at the 0.4-km scale. An independent data set confirmed that the final occupancy models I developed accurately distinguished between occupied and unoccupied sites for Flammulated Owls ($\chi^2 = 26.03$, d.f. = 3, $P < 0.0001$). External validation of the Saw-whet Owl model was not possible as an independent set of occurrence data for this species in the BNF was not available.

I examined patterns of co-occurrence between woodpeckers and sympatric cavity-nesting owls in Chapter Two using two-species occupancy models. As cavity-nesting owls require natural cavities or, more commonly, cavities that woodpeckers create for nesting and shelter (Martin et al. 2004), their occurrence may be dependent on the presence of primary cavity excavators (i.e., woodpeckers). Specifically, I tested the hypothesis that cavity-nesting owl occupancy was conditional on the presence of one or more common species of woodpecker: Hairy Woodpeckers (*Picoides villosus*), Lewis's Woodpeckers (*Melanerpes lewis*), Northern Flickers (*Colaptes auratus*), Pileated Woodpeckers (*Dryocopus pileatus*), and Red-naped Sapsuckers (*Sphyrapicus nuchalis*). Additionally, I examined the pattern of co-occurrence between cavity-nesting owl species to help understand the nature of their possible competitive interactions.

I surveyed for owls during nighttime hours and returned to these same locations during daytime hours to conduct surveys for woodpeckers. As snags may also be an important component of cavity-nesting owl occurrence, I modeled owl occupancy as a function of snag number and density and pattern of species co-occurrence while accounting for imperfect detection (i.e., the possibility that an individual may go undetected during surveying even when present).

The average number of snags per hectare (12.5 ± 0.2, N = 150) and mean diameter at breast height of snags (35.17 cm ± 0.08, N = 150) had no effect on cavity-nesting owl occupancy. There was no support for the hypothesis that cavity-nesting owl occupancy was conditional on the presence of woodpeckers. Likewise, Saw-whet Owl presence neither excluded nor facilitated Flammulated Owl occupancy (i.e., they occurred independently of one another). Therefore, despite the potential value in understanding the occupancy of the nocturnal owl community by examining the diurnal woodpecker community, relationships between woodpeckers and either Flammulated Owls or Saw-whet Owls do not appear strong enough to warrant such an approach.

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CHAPTER ONE: FACTORS INFLUENCING SITE OCCUPANCY OF CAVITY-NESTING FOREST OWLS IN THE BOISE NATIONAL FOREST, IDAHO: A SPATIAL APPLICATION USING GIS

Abstract

Developing effective management plans requires an understanding of species distribution and the factors affecting their occurrence. Spatially explicit models depicting the probability of species occupancy therefore offer a useful conservation tool for land managers. These models can be generated from remotely sensed data of land cover type, composition, and other topographic features. However, knowledge of the scale at which these factors act to influence occupancy is often lacking. I examined landscape-level habitat associations of Flammulated Owls (*Otus flammeolus*) and Northern Saw-whet Owls (*Aegolius acadicus*) in the Boise National Forest, located in southern Idaho. I considered land cover and topographic variables by selecting the best representative spatial scale from 0.4-km, 1-km, or 3-km-radius plots centered on point-count locations (N = 150). Using occurrence data collected between 2009 and 2010, I developed habitat models for Flammulated Owls and Saw-whet Owls and incorporated these results into a geographic information system (GIS) to create a spatial map depicting suitable habitat. Flammulated Owls (N = 27 occupied point-count locations) occurred in areas with a higher proportion of Douglas-fir (*Pseudotsuga menziesii*) at the 0.4-km scale and less diverse land cover composition at the 1-km scale. At the 3-km scale, Flammulated Owls

tended to occur on south-facing aspects. Saw-whet Owls (N = 45 occupied point-count locations) were found in relatively flat landscapes (i.e., low terrain ruggedness) at the 0.4-km scale. At the 1-km scale, Saw-whet Owls occupied locations containing larger proportions of non-forested area and with more southerly aspects. At the 3-km scale, areas containing a higher proportion of ponderosa pine (*Pinus ponderosa*) were more frequently occupied by Saw-whet Owls. An independent data set confirmed that the final model accurately distinguished between occupied and unoccupied sites for Flammulated Owls (^{2} = 26.03, d.f. = 3, $P < 0.0001$). External validation of the Saw-whet Owl model was not possible as occurrence data for this species were not available. Land managers can use these models to guide future surveys or management focused on owls.

Introduction

Relatively little is known about the distribution, abundance, and population trends of many species of owls, partly because of their nocturnal habit (Takats et al. 2001, Duncan 2003). Managing for cavity-nesting forest owls in particular frequently poses special challenges because of their small size, secretive behavior, and, in some cases, rarity. Forest specialists, such as cavity-nesting owls (Cannings 1987, Hayward and Hayward 1993, Hayward and Verner 1994), may also be more vulnerable to habitat perturbations (Imbeau et al. 2001).

Much of conservation depends upon maintaining habitat for wildlife (Tapia et al. 2007), so a thorough understanding of how land cover and topographic factors affect cavity-nesting owl populations is essential. Studies of wildlife-habitat relationships at large scales are particularly useful as they can be modeled within a geographic information system (GIS) to create a spatial representation of the probability of occupancy for a given species. These predictive habitat models have been applied to a diverse array of wildlife including marine and terrestrial invertebrates (Stensgaard et al. 2006, Mykra et al. 2008), fishes (Hayer et al. 2008, Schismenou et al. 2008), amphibians (Dillard et al. 2008), mammals (Best et al. 2007, Sawyer et al. 2007), and birds (Rodriguez-Estrella 2007, Hamer et al. 2008, Rojas-Soto et al. 2008). For avian species, predictive habitat models have identified habitat associations (Martínez and Zuberogoitia 2004, Groce and Morrison 2010), highlighted suitable but unoccupied habitat (Gibson et al. 2004, Russell et al. 2007), predicted effects of habitat manipulations (Doherty et al. 2008, Grossman et al. 2008), and helped interpret ecological relationships among species (Hayward and Garton 1988, MacKenzie et al. 2004, Richmond et al. 2010).

One important step is to identify at what scale wildlife species respond to habitat characteristics, as ecological processes are influenced by factors acting across a range of scales (Cushman and McGarigal 2002, Holland et al. 2004). In this report, I use the term scale to refer to the spatial extent (i.e., the physical area over which one wishes to draw inferences) as defined by Turner et al. (2001). Analysis on multiple scales often achieves greater understanding than studies focused on a single scale. Furthermore, it is possible that different species respond to factors of their environment at varying spatial scales (Holland et al. 2004). Hence, knowledge of the scale at which habitat selection occurs is valuable for modeling species occurrence (Doherty et al. 2008).

Another consideration for modeling species occurrence is when there is imperfect detection (MacKenzie et al. 2002). When not considered, imperfect detection can lead to spurious conclusions regarding habitat use (MacKenzie 2006). Occupancy models (MacKenzie et al. 2005) are capable of estimating detection probability from detection histories established from multiple visits to survey sites. Habitat models are then adjusted for imperfect detection leading to a more precise understanding of species occurrence (MacKenzie et al. 2005).

My goal was to explore land cover and topographic factors affecting occurrence of cavity-nesting forest owls in the Boise National Forest (BNF) and to develop spatial predictions of their distribution. I focused on three owl species: Boreal Owls (*Aegolius funereus*), Flammulated Owls (*Otus flammeolus*), and Northern Saw-whet Owls (*A. acadicus*). My objectives were to: (1) evaluate the best scale at which habitat characteristics explained cavity-nesting owl occupancy, (2) develop a model of probability of occurrence for cavity-nesting owls adjusted for imperfect detection, and (3) spatially depict model results in a GIS for the BNF.

Study Area

I studied cavity-nesting owls within the BNF (Fig. 1.1), which is approximately 10,600 km^2 in size and is administered through six USDA Forest Service Ranger Districts in southern Idaho. The mountainous landscape developed through the uplifting, faulting, and stream cutting of the highly erodible Idaho Batholith, which is a large geological formation encompassing much of the region (Alt and Hyndman 1989). Elevation in the study area ranges from 870 - 3250 m. The Boise and Payette Rivers along with the South and Middle Fork drainages of the Salmon River form the major river systems in the BNF. Forest cover is dominated by conifers with deciduous trees composing less than 1% of the total area. Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) predominate at lower to mid elevations, with smaller amounts of grand fir (*Abies grandis*) occurring in the northern portion of the study area (Steele et al. 1981). At higher elevations, subalpine fir (*A. lasiocarpa*), Engelmann spruce (*Picea engelmanii*), and lodgepole pine (*P. contorta*) constitute the main canopy species (Steele et al. 1981). Shrubs such as ninebark (*Physocarpus malvaceus*), snowberry (*Symphoricarpos* sp.), serviceberry (*Amelanchier anlifolia*), rose (*Rose* sp.), huckleberry (*Vaccinium* sp.), and chokecherry (*Prunus virginiana*) are common in the forest understory, with ceanothus (*Ceanothus velutinus*), bitterbrush (*Purshia tridentata*), and sagebrush (*Artemesia tridentata*) occurring on drier, south-facing aspects (Steele et al. 1981). Deciduous tree and shrub species occur mainly in riparian and drainage areas and include aspen (*Populus tremuloides*), black cottonwood (*Populus trichocarpa*), willows (*Salix* sp.), as well as dogwood (*Cornus sericea*), cascara (*Rhamnus purshiana*), thimbleberry (*Rubus parviflorus*), and others (Steele et al. 1981).

Methods

Field Methods

From February to May 2009-2010, I conducted point-count surveys for Boreal Owls, Flammulated Owls, and Northern Saw-whet Owls (hereafter Saw-whet Owls) using audio broadcasts of owl vocalizations (Takats et al. 2001). Other cavity-nesting owls occur in my study area and include Northern Pygmy-Owls (*Glaucidium gnoma*) and Western Screech-Owls (*Megascops kennicottii*); however, I did not include them in my study because of their diurnal habit and low abundance in higher elevation forested sites, respectively. I continued surveys targeting only Flammulated Owls in June of both years because they are migratory and frequently do not arrive on the breeding grounds until May (McCallum 1994, Powers et al. 1996, Barnes 2007). Additionally, previous research suggests detectability of Flammulated Owls is highest during June (Barnes and

Belthoff 2008). During the month of June, only the Flammulated Owl vocalization was played.

Using GIS, I randomly selected point-count locations (N = 82 in 2008 and 68 in 2009) in regions of the study area that were within skiing, snowshoeing, or walking distance from a plowed road during winter and within six broad forest cover classes: aspen, Douglas-fir, ponderosa pine, lodgepole pine, mixed conifer, and riparian. Ultimately, I pooled data from both years for analyses (N = 150 point-count locations; Fig. 1.1). The most common forest types were Douglas-fir and ponderosa pine, so I placed proportionately more point-count locations in these forest cover classes. Point-count locations were ≥ 800 m apart to decrease the chances of counting the same owl at multiple points.

Survey Protocol

Each point-count consisted of an initial 3-min. listening period, followed by a series of broadcasts of owl vocalizations, which I initially obtained from commercially available recordings (Righter and Keller 1999, Stokes and Stokes 2007). The recordings were of male owls giving vocalizations most frequently associated with territorial display. I broadcasted Flammulated Owl and Boreal Owl vocalizations with adjusted audio output to 90–110 db (Fuller and Mosher 1987) at 1 m using an NX3 Fox Pro Wildlife Caller (FOXPRO Inc., Lewiston, PA). As in Guidelines of Nocturnal Owl Monitoring (Takats et al. 2001), I broadcasted for the smaller Flammulated Owls first to avoid attracting larger Boreal Owls or Saw-whet Owls (Fig. 1.2). As Saw-whet Owls routinely respond to vocalizations of other species (Takats et al. 2001, Kissling et al. 2010, pers. observ.), I was able to detect them through their responses to the Boreal Owl and/or Flammulated Owl calls rather than including broadcasts of Saw-whet Owl calls in the protocol. I broadcasted individual recordings of Boreal Owls or Flammulated Owls for 30 sec. while rotating the Wildlife Caller 360˚. A 1-min. listening period followed each 30 sec. broadcast, and I repeated this broadcast-listening sequence once for each owl species before proceeding to the next largest species in the sequence (Fig. 1.2). Thus, I spent approximately 10 min. at each point-count location documenting the occurrence of the three species of owls. Surveys began at least 30 min. after sunset. I avoided surveying on nights with average wind speeds >15 km/h or persistent precipitation when weather could have affected my ability to detect owls or altered their responsiveness.

I visited each point-count location three times and surveyed for Boreal Owls, Flammulated Owls, and Saw-whet Owls and one to three additional times for Flammulated Owls. I indexed background noise levels during each point-count visit on a scale ranging from 1 (quiet) to 4 (noisy) as in Takats et al. (2001). I used the resulting detection history generated from the multiple visits along with an index of noise during each visit to calculate the probability of a species being detected. As I detected no Boreal Owls, my analyses of owl occupancy ultimately focused on Flammulated Owls and Saw-whet Owls only.

Landscape Scale Measurements

I used tools in ArcMap 9.3 (ESRI 2008) to characterize land cover and topographic features at three different scales: 0.4-km (area = 50 ha), 1-km (area = 314 ha), and 3-km-radius (area = 942 ha) plots centered on each point-count location. I used a 0.4-km buffer distance to approximate home range sizes for Flammulated Owls (Linkhart 1984, Goggans 1986, Barnes 2007) and Saw-whet Owls (Forbes and Warner

1974, Hayward and Garton 1988), and used 1- and 3-km radii to investigate if and how features at larger scales influenced occupancy.

Land cover variables I chose to assess were derived from USDA Forest Service raster layers specific to the BNF. I measured *Douglas-fir* and *ponderosa* as percent cover. To obtain the variable *non-forest*, I combined the land cover layers grassland, meadows, sagebrush-steppe, and shrub-land. *Canopy* cover was originally a categorical variable where 1 = 0-10% cover, 2 = 11-40% cover, 3 = 41-70% cover, and 4 = 71-100% cover. I assigned the midpoint value of the above *canopy* categories to grid cells and averaged these values over the 0.4-km, 1-km, and 3-km-radius plots. I also included *diversity* of the landscape by calculating a Shannon diversity index that reflected the number and type of cover classes from grid cells based on aspen (*Populus tremuloides*), barren, Douglas-fir, grand-fir, lodgepole pine, mixed conifer, non-forest, ponderosa pine, sub-alpine fir, riparian, and white bark pine (*P. albicaulis*) by their relative extent within BNF.

I derived the topographic variables *aspect* and *terrain ruggedness index* (*TRI*) from 30-m resolution digital elevation model (http://seamless.usgs.gov) using spatial analysis tools in ArcMap 9.3. As *aspect* had a circular distribution, I calculated the cosine of aspect for each grid cell to constrain values between 1 (more north facing) and -1 (more south facing) and modeled it as a linear variable. *TRI* represents the topographic heterogeneity of an area expressed as the amount of elevation difference between adjacent cells in a digital elevation model (Riley et al. 1999); values of “0” represent flat terrain, while values approaching 18 represent extremely rugged terrain. Measurements for both land cover and topography variables were averaged from 30-m resolution raster (grid cell) layers over approximately 558, 3488, and 10464 grid cells for 0.4-km, 1-km, and 3-km-radius plots, respectively.

Statistical Analysis

I employed occupancy models (MacKenzie et al. 2002), which adjust logistic regressions of occurrence data for imperfect detection, using the software program PRESENCE (Hines 2006). I estimated occupancy probability (ψ) and detection probability (p) as well as the influence of land cover and topography covariates on these parameters for both Flammulated Owls and Saw-whet Owls. Data for land cover and topography were normalized prior to analysis to ultimately allow comparison of relative strength of beta coefficients. I used the land cover variables *Douglas-fir*, *ponderosa*, *non-forest*, *canopy*, and *diversity* as well as the topographic variables *aspect* and *TRI* to model ψ. To model p, I used the resulting detection history generated from multiple site visits along with an index of noise for each visit. I used univariate, single-season models in program PRESENCE along with AIC model selection (Burnham and Anderson 2002) to identify the scale (i.e., 0.4-km, 1-km, or 3-km radius) that best described Flammulated Owl and Saw-whet Owl occurrence for each variable. Once I identified the best scale for each variable, I removed from the set those variables whose best model had beta coefficients had 75% confidence intervals that overlapped zero (i.e., corresponding to lack of effect in logistic regression) to further narrow candidate variables. I ultimately ran single-season occupancy models using all possible combinations of remaining variables to estimate ψ in program PRESENCE. To avoid over-fitting occupancy models, I restricted the number of predictor variables to approximately 10% of the sites occupied by each species (Hosmer and Lemeshow 2000). I considered my effective sample size to be the number of sites where a species was detected. Moreover, I did not include variables that were highly collinear (Spearman rank correlations > 0.70). All models also included the variable *noise* to account for its potential influence on *p* and adjust estimates of ψ.

Model Selection and Spatial Implementation

I used AIC_c and the associated model weights to assess model strength of candidate models for Flammulated Owls and Saw-whet Owls. When there was model selection uncertainty, I used averaged coefficients from models with a cumulative AIC_c weight of 0.95 (Burnham and Anderson 2002). I recalculated model weights to sum to 1.0 for models in the final candidate set. When model averaging, I set coefficients to zero for variables not included in a model.

I applied the model-averaged results in a GIS to map the probability of site occupancy for Flammulated Owls and Saw-whet Owls. However, in resource management practice, the information presented as species presence/absence may be more applicable than probability estimates (Liu et al 2005, Jiménez-Valverde and Lobo 2007). I selected probability thresholds (Fielding and Bell 1997) above which grid cells represent either species presence or absence. By adopting several threshold cutoffs, where 50%, 75%, and 100% of occupied point-count locations were correctly classified (model sensitivity) by the model, I was able to create spatial projections where probability of owl occupancy was binned into four categories, which may represent a relative index of suitable habitat (see Russell et al. 2007).

Model Performance

Creating a map of species presence/absence is also needed for evaluating model performance by examining the agreement between model predictions and actual observations (Pearce and Ferrier 2000, Jiménez-Valverde and Lobo 2007). To assess goodness-of-fit of the final models, I calculated the area under the curve (AUC) of the receiver operating characteristic (ROC). The ROC curve evaluates the relationship between the number of true positives (correctly classified occupied sites) and the number of false positives (sites classified incorrectly as occupied) at different threshold probabilities (Pearce and Ferrier 2000). AUC is the summed area underneath the ROC curve and provides an index of the model's ability to differentiate between observations of owl occurrence and non-occurrence. Values for AUC range from 0.5 – 1.0, where 0.5 is interpreted as a random prediction, while values > 0.5 suggest performance better than random. Swets (1988) suggests that AUC values of 0.5 – 0.7 reflect relatively poor model performance, 0.7 – 0.9 reflects moderate performance, and ≥ 0.9 is excellent model performance.

I also assessed accuracy of the final Flammulated Owl model by determining how well it predicted presence/absence for an independent sample of 182 point-count locations in the Rock Creek watershed and the Miller Creek and Lick Creek drainages of the BNF, which were previously surveyed for Flammulated Owls by Boise State University (BSU) and the USDA Forest Service personnel during 2005-2006 (see Barnes 2007). This independent dataset consisted of an equal number of occupied and unoccupied sites (N = 91 for each), which were separated by 0.5 km from other sites and at which Flammulated Owl occurrence was assessed using point-count methods that combined broadcast of vocalizations and silent listening periods (Barnes 2007) similar to mine. I classified the independent sites as high, moderate, low, or least suitable and assessed the accuracy of occupancy classification using contingency analysis conducted in SAS version 9.2 (SAS Institute, Inc. 2008). I was not able to evaluate model performance for the final Saw-whet Owl model as no independent data set of owl occurrence was available for my study area.

Results

Surveys

During 2009-2010, I conducted 702 visits to 150 point-count locations to determine owl occupancy. These visits produced 113 detections of two species of cavity-nesting owls. While no Boreal Owls were located, I detected Flammulated Owls and Saw-whet Owls at 27 and 45 point-count locations, respectively. Flammulated Owls and Saw-whet Owls co-occurred at eight point-count locations, with at least one species being detected at 64 separate point-count locations (42.7% of locations). I also encountered Barred Owls (*Strix varia*; N = 2 point-count locations), Great Horned Owls (*Bubo virginianus*; N = 20), Long-eared Owls (*Asio otus*; N = 1), Northern Pygmy-Owls (*Glaucidium gnoma*; N = 1), and Western Screech-Owls (*Megascops kennicottii*; N = 2).

Variable Selection

I examined the relationships among seven land cover and topographic variables (*aspect, canopy, diversity, Douglas-fir, non-forest, ponderosa,* and *TRI*) and occupancy of cavity-nesting owls as determined by point-count surveys. The best scale for *Douglas-fir, non-forest,* and *ponderosa* were similar for both species of owl, while the best scale for the remaining variables differed between species (Table 1.1). For Flammulated Owls, none of the variables were correlated at their best scale. The variables *diversity* and *ponderosa* were highly correlated ($|r| > 0.73$, $p < 0.001$) for Saw-whet Owls; thus, I only included *ponderosa* in subsequent modeling of Saw-whet Owls. I chose to retain *ponderosa* because ponderosa pine is a major timber species throughout the western United States (Smith et al. 2009), including Idaho, so knowledge of its importance to native wildlife is valuable for conservation and management planning in the BNF. For Flammulated Owls, the 75% confidence intervals for the beta estimates included zero for *TRI* (Table 1.1), so I dismissed *TRI* from subsequent modeling. No variables at their best scale had 75% confidence intervals overlapping zero for Saw-whet Owls (Table 1.1).

Model Selection

For Flammulated Owls, I developed a set of 42 occupancy models using all possible combinations of the six remaining variables (Appendix A). Similarly, I developed a set of 63 models for Saw-whet Owls using all possible combinations of the six variables that remained for this species (Appendix B). From the candidate model set, the best approximating models for Flammulated Owls and Saw-whet Owls included 12 models (Table 1.2) and 25 models (Table 1.3), respectively. As there was no clear top model in either case, I model-averaged parameter estimates over the best approximating models. From each model-averaged subset, I obtained parameter estimates for final predictive habitat models and determined the probability of occupancy and detection for each owl species. From the model-averaged sets, I ranked models according to their AIC_c differences (ΔAIC_c) and AIC_c weights (w) from best to worst (Tables 1.2 and 1.3). For Flammulated Owls, the cumulative sum of the Akaike weights across all models for which a particular variable occurred, or relative importance (w_+), was high for both *diversity* and *Douglas-fir* (Table 1.4). The importance of *aspect* was moderate, while *canopy*, *non-forest*, and *ponderosa* each had relative importance weights of < 0.10 (Table 1.4) and were therefore poorly supported.

There was also lack of support for any one Saw-whet Owl model (Table 1.3) as top approximating models had low Akaike weights ($w < 0.15$) and small differences in AIC_c values ($\Delta AIC < 2.0$). The variables *aspect* and *non-forest* stood out as being substantially more important (Table 1.4). The remaining five variables received low to moderate support, with w_+ ranging from 0.22 (*canopy*) to 0.63 (*ponderosa*; Table 1.4).

Probability of Occupancy and Detection

Flammulated Owls had a model-averaged probability of site occupancy (ψ) of 0.22 ± 0.03, while Saw-whet Owls were more likely to occur ($\psi = 0.40 \pm 0.01$). Mean probability of detection as adjusted for ambient noise was high for Flammulated and Saw-whet Owls ($p = 0.93 \pm 0.05$ and 0.77 ± 0.08, respectively). Noise had a negative effect on detectability for both Flammulated Owls (odds ratio = 0.18, 95% CI = 0.09 – 0.42) and Saw-whet Owls (odds ratio = 0.34, 95% CI = 0.20 – 0.58), and neither species of owl was detected where noise indexes were > 3.

Spatial Implementation in GIS

For Flammulated Owls, I applied the final model-averaged logistic regression equation $Y = -1.286 - 2.544\,(aspect) + 0.064\,(canopy) - 1.209\,(diversity) + 0.994\,(Douglas\text{-}fir) - 0.021\,(non\text{-}forest) + 0.013\,(ponderosa)$ in a GIS (Fig. 1.3a). Similarly, I implemented the final model-averaged results for Saw-whet Owls using the logistic regression equation $Y = -0.387 - 0.496\,(aspect) - 0.048\,(canopy) + 0.273\,(Douglas\text{-}fir) + 0.915\,(non\text{-}forest) + 0.323\,(ponderosa) - 0.268\,(TRI)$ using GIS (Fig. 1.3b). For these maps of probability of occupancy, I applied three threshold cutoffs to generate a map of relative habitat suitability for both species. Maps of relative habitat suitability showed the potential for Flammulated Owls and Saw-whet Owls to occupy a large proportion of the BNF (Fig. 1.4a and 1.4b). For Flammulated Owls, the map of habitat suitability (Fig. 1.4a) tended to contain large areas of both highly suitable (2,744 km^2) and least suitable (4,555 km^2) habitat, while regions of moderate (1,192 km^2) and low (1,771 km^2) suitability habitat were less abundant. The map for Saw-whet Owls (Fig. 1.4b) differed in that the majority of the BNF was predicted to be of moderate (4,557 km^2) or low (3,836 km^2) suitability, while areas of least (1,569 km^2) and high (297 km^2) suitability were more scarce.

Model Performance

The ability of the final models to distinguish between occupied and unoccupied sites was moderate for both species. The AUC was 0.71 and 0.70 for Flammulated Owls and Saw-whet Owls, respectively. For one to correctly identify 100% of the occurrence observations, large numbers (>75%) of non-occurrence sites would be incorrectly classified for both Flammulated Owls and Saw-whet Owls (Table 1.5). For both owl species, the overall percentage of correctly classified occupied and unoccupied point-count locations was highest when I applied models using a sensitivity of 50% (Table 1.5). At this level, 70% of the total point-count locations sampled out of 150 would be correctly classified as occupied or unoccupied for Flammulated Owls, and 69% would be correctly classified for Saw-whet Owls (Table 1.5).

When tested against the independent sample of 182 point-count locations from Barnes (2007), the final predictive model for Flammulated Owls accurately distinguished between suitable and unsuitable habitat ($\chi^2 = 26.03$, d.f. = 3, $P<0.0001$). Most occupied sites (53 of 91) were in areas of highly suitable habitat, while no occupied sites occurred in areas the final predictive model classified as unsuitable (Table 1.6).

Discussion

Applying predictive habitat models in GIS has become a common tool to project the probability of species occurrence across large spatial scales (Guisan and Zimmermann 2000). I explored the influence of several land cover and topographic variables on the occupancy of Flammulated Owls and Saw-whet Owls and determined the best spatial scale at which these variables operate. Considering the scale at which species respond most strongly is important because (1) we often know little about the scale at which a species responds to characteristics of their environment, (2) different species may respond to their environments in different ways (Block and Brennan 1993).

Probability of Detecting Cavity-Nesting Owls

Similar to Barnes and Belthoff (2008), I found that the probability of detecting a Flammulated Owl was high ($p = 0.93$). Saw-whet Owls also had a relatively high detection probability ($p = 0.77$). Groce and Morrison (2010) reported much lower detection probabilities ($p= 0.28$, SE = 0.04) for Saw-whet Owls in the Lake Tahoe Basin of the central Sierra Nevada, California. However, their study occurred from mid-May through July in 2006 and mid-March through July in 2007, during which time owls may be somewhat less responsive to conspecific calls (Rasmussen et al. 2008).

Detectability of both Flammulated Owls and Saw-whet Owls decreased when noise indexes exceeded 2.0. Kissling et al. (2010) reported similar effects of noise on detectability of Saw-whet Owls in southeastern Alaska, where noise levels ≥ 3 reduced detection probabilities by about two-thirds. Many of my point-count surveys were conducted during springtime when snowmelt in nearby creeks, streams, and rivers contributed to higher values of the noise index. This was especially true of points that were located closer to large rivers (e.g., Boise and Payette River systems). Higher noise could have reduced my ability to detect owls or their response to broadcast vocalizations. It is also possible that noise affected owl occupancy if owls avoided noise from streams and rivers. In fact, I observed patterns similar to those identified by Barnes (2007) in that neither species of owl occurred where noise index was > 3. Auditory sense is important in both owl species for detecting potential predators, communication with mates and offspring, and foraging. As such, owls may completely avoid areas of high noise.

Habitat Modeling for Flammulated Owls

The habitat suitability model I derived for Flammulated Owls was successful at predicting owl occurrence, especially when distinguishing occupancy in highly suitable and not suitable habitat. Both *diversity* and *Douglas-fir* were important factors that contributed to Flammulated Owl occupancy. *Diversity* at the 1-km scale had a strong negative relationship with owl occurrence. *Diversity* was a variable that I calculated using 11 land cover classes of which nine were forested and two were non-forested classes. Low diversity would be a result of either (1) a small number of land cover classes around a point-count location, or (2) a larger number of land cover classes but with a small number predominating. Indeed, most sites that Flammulated Owls occupied consisted primarily of Douglas-fir, ponderosa pine, or a combination of these two land cover classes. Lower occupancy in high diversity landscapes could be a reflection of

Flammulated Owls selecting more for relatively contiguous tracts of forest consisting of only a small number of cover classes.

There was an equally strong tendency for Flammulated Owls to occupy areas with a high proportion of Douglas-fir within 0.4 km of point-count locations. Howie and Ritchey (1987) found that owls favored Douglas-fir forest in British Columbia. Douglas-fir was also the dominant tree species associated with the occurrence of Flammulated Owls in south-central British Colombia (Christie and van Woudenberg 1997). Mature stands of Douglas-fir forest may present the favorable park-like stands and open forest physiognomy of primary importance to these owls (McCallum 1994). Given that *diversity* at the 1-km scale was an important predictor, Flammulated Owls may be likely to occupy patches of Doulas-fir (0.4-km scale) surrounded by a matrix of relatively homogenous cover types more likely to be forest than non-forest.

Barnes (2007) noted that Flammulated Owls were more likely to occupy east-facing and south-facing aspects within the Rock Creek watershed and the Miller and Lick Creek drainages within the BNF. Bull et al. (1990) found a similar pattern for Flammulated Owls in northeastern Oregon. While model-averaged estimates of aspect from my study conducted throughout a larger number of drainages in the BNF were only moderately supported, they corroborated these findings and suggest that Flammulated Owls occupied areas with more southerly-facing aspects. South-facing aspects in colder regions such as Idaho and Oregon may experience earlier release of snow pack thereby creating favorable conditions for arthropod prey, which Flammulated owls require. The physiological demands of thermoregulation may also restrict these small owls to areas that experience warmer temperatures early in the breeding season when the greatest cold stress occurs (McCallum 1994).

Ponderosa was a poor predictor of Flammulated Owl occupancy despite previous research indicating a strong association between these two (Goggans 1986, Reynolds and Linkhart 1987, Bull et al. 1990, Linkhart et al. 1998). One possibility is that Flammulated Owl selection for ponderosa pine is occurring on a smaller spatial scale than the ones I studied. However, other studies have found Flammulated Owls in a variety of other forest types including aspen, lodgepole pine, subalpine fir, and Douglas-fir (Powers et al. 1996, Marti 1997, Oleyar 2000). The current physiognomy of many ponderosa pine forests may also be unsuitable for Flammulated Owls because of fire suppression, cattle grazing, and timber harvesting (Wisdom et al. 2000). Efforts in the BNF to restore ponderosa pine to its pre-settlement physiognomy are currently underway (L. Nutt, pers. comm.), but their effects on wildlife populations, including the response of Flammulated Owls, has yet to be fully determined.

Although forest openings appear to be an important component of Flammulated Owl habitat based on previous literature (Hayward and Verner 1994, McCallum 1994), the final predictive habitat model for Flammulated Owls indicated a lack of support for the land cover variable *non-forest*. My landscape-level approach may have been too coarse to detect the effects of non-forest should the importance of non-forest have been operating on a smaller spatial scale. This seems possible as Barnes (2007) found that owls frequently foraged in small (< 0.5 ha), open clearings within the BNF. Likewise, Bull et al. (1990) reported that more than half of known nest trees located in northeastern Oregon occurred within 30 m of a 1-ha opening. Commonly taken prey such as orthopterans and lepidopterans (Goggans 1986) may be more abundant in forest openings and along forest edges.

There was moderate support in the final model set for the predictor variable *canopy*, which indicated that Flammulated Owl occupancy increased with increasing canopy. This makes sense as Flammulated Owls are forest specialists. Flammulated Owl selection for intermediate levels of canopy cover has been well documented (Goggans 1986, Bull et al. 1990, Moore and Fredrick 1991, Barnes 2007). Several of these authors also observed that a multi-layered structural component of canopy cover was also important (Goggans 1986, Bull et al. 1990, Moore and Fredrick 1991).

Habitat Modeling for Saw-whet Owls

The final predictive habitat model for Saw-whet Owls performed well and indicated that the majority of the BNF is of moderate suitability for this species. Model-averaged results indicated *non-forest* at the 1-km scale had a strong positive influence on Saw-whet Owl occupancy. Saw-whet Owls frequently hunt in forest openings, along forest edges (Hayward and Garton 1988), and in sagebrush and bitterbrush habitats (Cannings 1987, Marks and Doremus 1988). Hinam and Clair (2008) suggest that low levels of forest loss, which will result in larger proportions of non-forested areas, may benefit Saw-whet Owls by increasing small rodent populations. Therefore, a higher proportion of non-forested grassland and shrub-land within 1 km of occupied point-count locations may represent areas of suitable foraging habitat.

Aspect also had high importance in explaining Saw-whet Owl occupancy, and model coefficients indicated that Saw-whet Owl occupancy increased with increasing southerly aspects when considered at the 1-km scale. Land with a south-facing aspect within the study area may warm more quickly in April and May, as many north-facing areas are still bound with snow during this time period (pers. observ.). This may provide greater access to microtine rodents at a time when owls are brooding and rearing young (Cannings 1987). Similar to Flammulated Owls, Saw-whet Owls are small in size and therefore may also derive thermoregulatory benefits especially in the early portion of their breeding period from south facing aspects where temperatures are warmer.

Saw-whet Owl occupancy was positively related to both *ponderosa* at the 3-km scale and to *Douglas-fir* at the 1-km scale. In the western portions of their range, Saw-whet Owls occupy a variety of conifer forests with ponderosa pine, Douglas-fir, grand fir, western larch (*Larix occidentalis*), and western redcedar (*Thuja plicata*) hosting the densest populations of birds (Hayward and Garton 1988, Rasmussen et al. 2008). Thus, Saw-whet Owls are typically more general in their habitat use (Rasmussen et al. 2008) than many other forest dwelling owl species. Grossman et al. (2008) found that Saw-whet Owls occupy a variety of landscapes with the amount of forested area ranging between 16% and 100% within 0.8 km-radius plots. Therefore, in addition to occupying areas with a component of non-forest, Saw-whet Owls nonetheless require forested areas to meet life history needs, including nesting, roosting, and seeking shelter. Their positive relationship with *ponderosa* and *Douglas-fir* may also reflect the relatively higher abundance of these two forest types in the BNF.

The ruggedness of terrain (*TRI*) had a negative influence on Saw-whet Owl occupancy, and this indicates that owls occupied areas that exhibited fewer changes in elevation. Saw-whet Owls rely on their auditory ability to detect prey owing primarily to their asymmetrically located ears (Frost et al. 1989). It is possible that rugged terrain presents sub-optimal conditions for foraging as sounds may be deflected more frequently under these conditions. Alternatively, highly rugged areas may also provide greater opportunities for prey to find cover or more easily evade capture by owls.

Finally, I found that Saw-whet Owl occupancy had a weak but negative relationship with *canopy* cover, which also may have been related to the importance of non-forested areas for Saw-whet Owl foraging. Likewise, Groce and Morrison (2010) found that open canopy was influential for Saw-whet Owl occupancy in Nevada. However, they also noted that scale is important in that open canopy was more relevant at the size of Saw-whet Owls territories (e.g., 20-ha plots) rather than larger scales such as those I measured and also found important (e.g., 1-km radius).

Summary and Conclusions

Flammulated Owls occupied habitats with lower land cover diversity and more southerly-facing aspects at the 1-km scale and with higher proportions of Douglas-fir forest at the 0.4-km scale. Higher occupancy in low diversity landscapes may be best described as areas having relatively contiguous tracts of forest consisting mostly of xeric Douglas-fir and a small number of other land cover classes. Flammulated Owls also occupied areas with higher proportions of ponderosa pine forest at the 3-km scale, lower amounts non-forest at the 1-km scale, and higher canopy cover at the 0.4-km scale. Saw-whet Owls occupied areas with larger amounts of non-forest situated on south-facing aspects at the 1-km scale. There was also moderate support for increasing Saw-whet Owl occupancy in relation to increasing ponderosa pine at the 3-km scale and Douglas-fir at the 0.4-km scale. At the 0.4-km scale, Saw-whet Owls also tended to occupy flatter landscapes (i.e., low terrain ruggedness) and to a lesser extent areas with more open canopy cover.

In addition to increasing understanding of the land cover and topographic variables associated with owl occurrence, the models I developed allowed projections for spatially explicit maps of Flammulated Owl and Saw-whet Owl occupancy in a GIS. These spatially explicit models (maps) provide land managers with a pragmatic tool with which to identify suitable habitat for owls and to help inform land use decisions or restoration in the BNF. Generating multiple habitat suitability maps where 50%, 75%, and 100% of occupied point-count locations were correctly classified by the models will allow land managers to be more flexible in how they allocate management efforts. For instance, if it is not possible for logistical, financial, or other reasons to focus on all suitable owl habitat, then one's efforts can concentrate only on habitat predicted to be most suitable (i.e., 50% sensitivity) for Flammulated Owls and Saw-whet Owls. On the other hand, if the goal is to conserve habitat for these owl species in all regions where they are likely to occur, then a scenario using the 100% sensitivity map I provided can be used to guide management efforts. Furthermore, land managers responsible for maintaining or improving habitat for cavity-nesting owls can use these models to target areas for habitat restoration.

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Table 1. Landscape measurements of land cover type, composition, and topography evaluated as potential predictor variables for Flammulated Owl and Northern Saw-whet Owl occupancy in the Boise National Forest, Idaho, during 2009 and 2010. AIC$_c$ and model weights (w) were used to identify the best scale at which selection occurred for individual variables over 0.4-km, 1-km, and 3-km-radius plots. Calculated 75% confidence intervals of the beta coefficients are shown for the each variable at its best scale. The best scale for each variable is the top row of each individual landscape measurement and highlighted in gray.

	Flammulated Owls						Northern Saw-whet Owls					
Landscape Measurement	Radius (km)	AIC$_c$	W	β	Lower 75% CI	Upper 75% CI	Radius (km)	AIC$_c$	w	β	Lower 75% CI	Upper 75% CI
Douglas-fir	0.4	182.65	0.60	0.554	0.307	0.801	0.4	360.94	0.52	0.245	0.026	0.464
	1	183.96	0.31				1	362.45	0.24			
	3	186.61	0.08				3	362.46	0.24			
Non-forest	1	185.99	0.54	-0.488	-0.791	-0.186	1	357.81	0.65	0.469	0.199	0.738
	0.4	186.89	0.35				3	359.50	0.28			
	3	189.15	0.11				0.4	362.21	0.07			
Ponderosa Pine	3	187.07	0.59	0.352	0.113	0.591	3	360.58	0.45	0.286	0.0512	0.521
	1	188.68	0.26				1	361.50	0.28			
	0.4	189.82	0.15				0.4	361.59	0.27			
Canopy Cover	0.4	185.77	0.58	0.288	0.193	0.718	1	360.44	0.50	-0.306	-0.552	-0.060
	1	186.83	0.34				0.4	361.68	0.27			
	3	189.77	0.08				3	361.98	0.23			
Diversity	1	179.50	0.50	-0.721	-0.997	-0.446	3	358.58	0.68	-0.405	-0.645	-0.165
	0.4	180.21	0.35				0.4	361.20	0.18			
	3	181.98	0.15				1	361.84	0.13			
Aspect	3	184.39	0.82	-3.321	-6.472	-0.170	1	360.21	0.57	-0.384	-0.703	-0.0647
	1	188.49	0.11				0.4	361.85	0.25			
	0.4	189.13	0.08				3	362.61	0.17			
TRI[a]	3	189.00	0.37	-0.212	-0.465	0.0414	0.4	355.53	0.93	-0.545	-0.795	-0.296
	1	189.08	0.35				1	362.02	0.036			
	0.4	189.56	0.28				3	362.08	0.035			

[a] TRI = index or terrain ruggedness derived from a digital elevation model.

Table 1.2. Results of AIC_c-based model selection for the top 12 models examining habitat associations of Flammulated Owls out of a total set of 42 models. Top-performing models accounted for > 0.95 Akaike weight from the model set and were used in calculating model-averaged coefficients for occupancy (ψ) and detectability (p) and their associated covariates (see Appendix A for the entire model set and additional model details). Akaike weights have been adjusted to reflect relative weight within the model-averaged set of 12 models.

Model	K^a	$\Delta AIC_c{}^b$	w^c
ψ(aspect, diversity, Douglas-fir), p(noise)	6	0.00	0.385
ψ(diversity, Douglas-fir), p(noise)	5	0.62	0.282
ψ(canopy, diversity, Douglas-fir), p(noise)	6	2.84	0.093
ψ(diversity, Douglas-fir, non-forest), p(noise)	6	3.23	0.077
ψ(diversity, Douglas-fir, ponderosa), p(noise)	6	3.96	0.053
ψ(aspect, canopy, diversity), p(noise)	6	5.05	0.031
ψ(canopy, diversity), p(noise)	5	5.50	0.025
ψ(aspect, diversity), p(noise)	5	5.70	0.022
ψ(aspect, Douglas-fir, ponderosa), p(noise)	6	6.84	0.013
ψ(aspect, diversity, ponderosa), p(noise)	6	8.11	0.007
ψ(Douglas-fir, ponderosa), p(noise)	5	8.22	0.006
ψ(aspect, diversity, non-forest), p(noise)	6	8.28	0.006

[a] The number of estimated parameters.

[b] The relative difference in AIC values.

[c] AIC model weight.

Table 1.3. Results of AIC_c-based model selection for the top 25 models examining habitat associations of Northern Saw-whet Owls out of a total set of 63 models. Top-performing models accounted for > 0.95 Akaike weight from the model set and were used in calculating model-averaged coefficients for occupancy (ψ) and detectability (p) parameters and their associated covariates (see Appendix B for the entire model set and additional model details). Akaike weights have been adjusted to reflect relative weight within the model-averaged set of 25 models.

Model	K^a	$\Delta AIC_c{}^b$	w^c
ψ(aspect, Douglas-fir, non-forest, ponderosa, TRI*), *p*(Noise)	8	0.00	0.142
ψ(aspect, Douglas-fir, non-forest, ponderosa), *p*(noise)	7	0.11	0.134
ψ(aspect, Douglas-fir, non-forest, TRI), *p*(noise)	7	0.92	0.090
ψ(aspect, non-forest, ponderosa), *p*(noise)	6	1.27	0.075
ψ(aspect, non-forest, TRI), *p*(noise)	6	1.53	0.066
ψ(aspect, non-forest, ponderosa, TRI), *p*(noise)	7	1.72	0.060
ψ(Douglas-fir, non-forest, ponderosa, TRI), *p*(noise)	7	1.94	0.054
ψ(aspect, canopy, Douglas-fir, non-forest, ponderosa), *p*(noise)	8	2.54	0.040
ψ(aspect, canopy, Douglas-fir, non-forest, TRI), *p*(noise)	8	2.59	0.039
ψ(aspect, non-forest), *p*(noise)	5	3.01	0.032
ψ(Douglas-fir, non-forest, ponderosa), *p*(noise)	6	3.04	0.031
ψ(aspect, Douglas-fir, non-forest), *p*(noise)	6	3.57	0.024
ψ(Douglas-fir, non-forest, TRI), *p*(noise)	6	3.63	0.023
ψ(aspect, canopy, non-forest, TRI), *p*(noise)	7	3.63	0.023
ψ(aspect, canopy, Douglas-fir, non-forest), *p*(noise)	7	3.70	0.022
ψ(aspect, canopy, non-forest, ponderosa), *p*(noise)	7	3.77	0.022
ψ(aspect, canopy, non-forest), *p*(noise)	6	3.86	0.021
ψ(non-forest, ponderosa, TRI), *p*(noise)	6	4.24	0.017
ψ(non-forest, ponderosa), *p*(noise)	5	4.31	0.016
ψ(non-forest, TRI), *p*(noise)	5	4.46	0.015
ψ(aspect, canopy, non-forest, ponderosa, TRI), *p*(noise)	8	4.60	0.014
ψ(canopy, Douglas-fir, non-forest, ponderosa, TRI), *p*(noise)	8	4.74	0.013
ψ(canopy, Douglas-fir, non-forest, TRI), *p*(noise)	7	5.20	0.011
ψ(canopy, Douglas-fir, non-forest, ponderosa), *p*(noise)	7	5.25	0.010
ψ(canopy, non-forest, TRI), *p*(noise)	6	6.35	0.006

[a] The number of estimated parameters.

[b] The relative difference in AIC values.

[c] AIC model weight.

*TRI = index or terrain ruggedness derived from a digital elevation model.

Table 1.4. Relative importance (w_+) of individual variables for single-season occupancy models for Flammulated and Northern Saw-whet Owls occupancy covariates calculated by summing the cumulative Akaike weights across all models for which a particular variable occurred.

Flammulated Owls				Northern Saw-whet Owls			
Variable	Scale (km)	*N*	w_+	Variable	Scale(km)	*N*	w_+
Diversity	1	10	0.98	Non-forest	1	25	1
Douglas-fir	0.4	7	0.91	Aspect	1	15	0.80
Aspect	3	6	0.46	Douglas-fir	0.4	13	0.63
Ponderosa	3	4	0.08	Ponderosa	3	13	0.63
Non-forest	1	2	0.08	TRI	0.4	14	0.57
Canopy	0.4	3	0.06	Canopy	1	11	0.22
TRI	*	*	*	Diversity	*	*	*

Note: *N* is the number of models in which a variable appeared; w_+ is the relative importance weight, which is the summed Akaike weights for all models sharing a similar model structure; * represents a variable eliminated during the variable reduction procedure.

Table 1.5. List of threshold values and discriminatory power from models predicting probability of site occupancy for Flammulated Owls and Northern Saw-whet Owls in the Boise National Forest, Idaho, 2009-2010. Sensitivity (%) is the percentage occupied sites that would be correctly identified if the corresponding threshold value was used while specificity (%) denotes the percentage unoccupied sites that would be correctly identified. Classification (%) is the number of total sites correctly identified from the sample for a given threshold value.

Species	Sensitivity (%)	Specificity (%)	Classification (%)	Threshold Value
Flammulated Owls	100	23	36	0.296
	75	59	62	0.476
	50	75	70	0.577
Northern Saw-whet Owls	100	17	42	0.005
	75	56	62	0.023
	50	77	69	0.038

Note: A threshold value is the predicted value above which a location is classified as occupied and below which location is classified as unoccupied.

Table 1.6. Results of Flammulated Owl model validation whereby sites from an independent data set collected by Boise State University and the National Forest Service from the Boise National Forest during 2005 and 2006 were classified using the final model. The final model successfully discriminated between occupied and unoccupied sites (^{2} = 26.03, d.f. = 3, $P < 0.0001$).

Habitat Suitability	Occupied	Unoccupied
High	53	35
Moderate	13	13
Low	25	21
Least	0	22

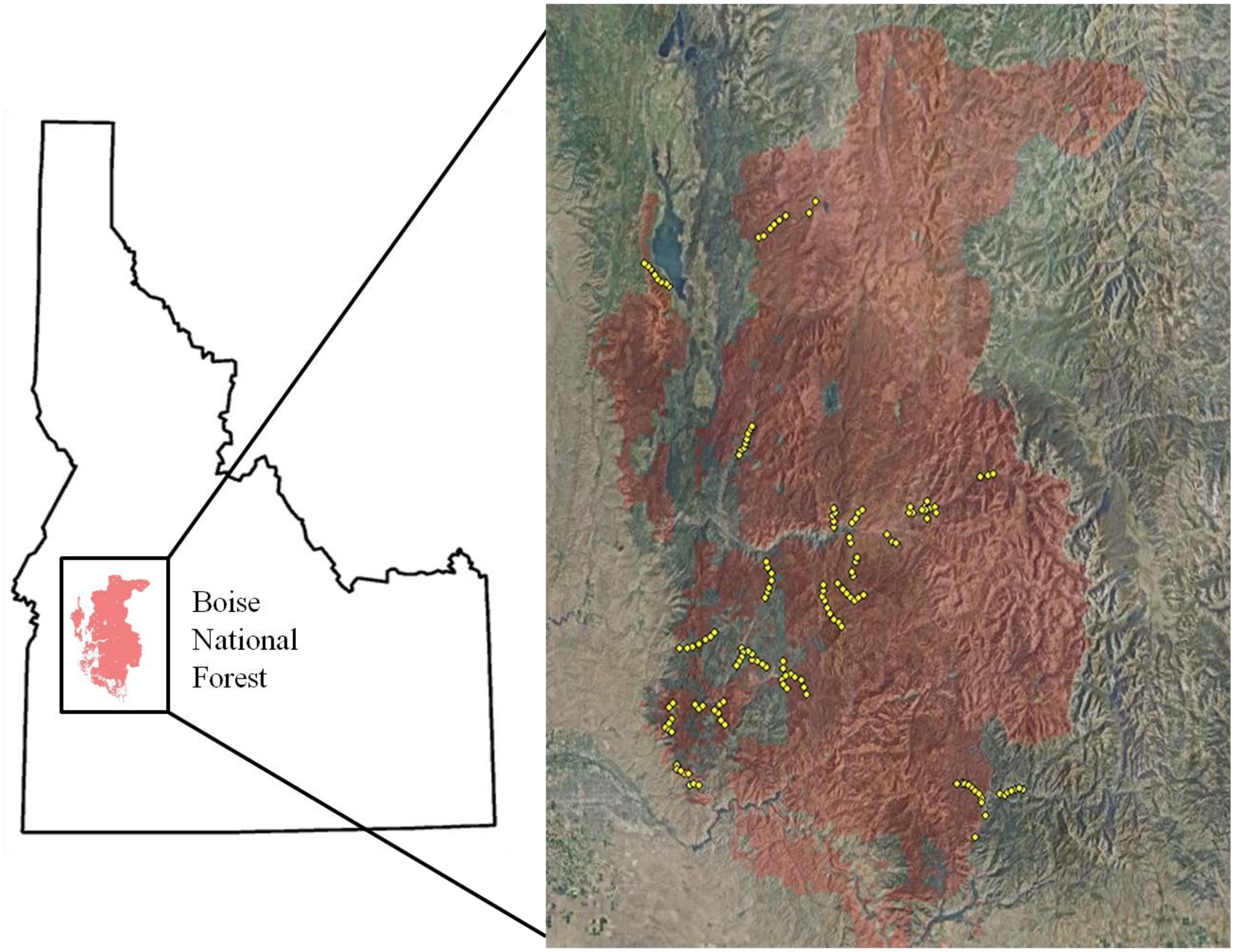

Figure 1.1. Vicinity map showing the location of the Boise National Forest in southwestern Idaho and point-count locations (N = 150) for cavity-nesting owls. Point-count locations were spaced ≥ 800m apart and were located in portions of Boise National Forest that were accessible by road during winter months.

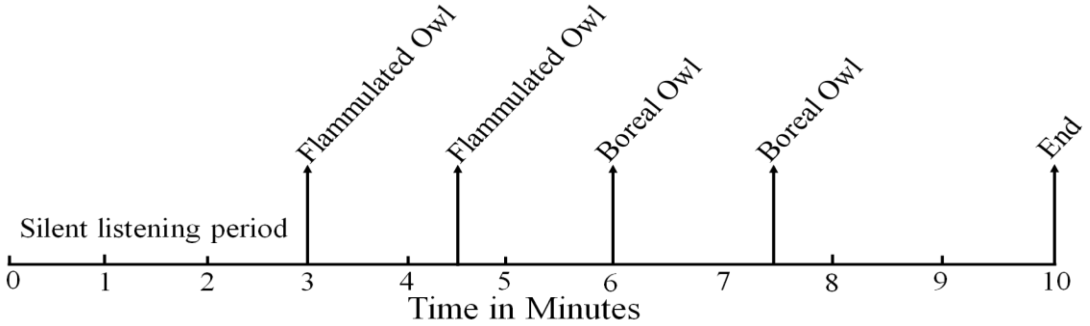

Figure 1.2. Broadcast sequence for cavity-nesting owls surveyed in the Boise National Forest, Idaho, 2009-2010. Point-counts for owls began with 3 min. of silent listening followed by 30 sec. of Flammulated Owl broadcasts and another 1 min. of silent listening. This broadcast-listening sequence was repeated once before replicating the process using Boreal Owl broadcasts.

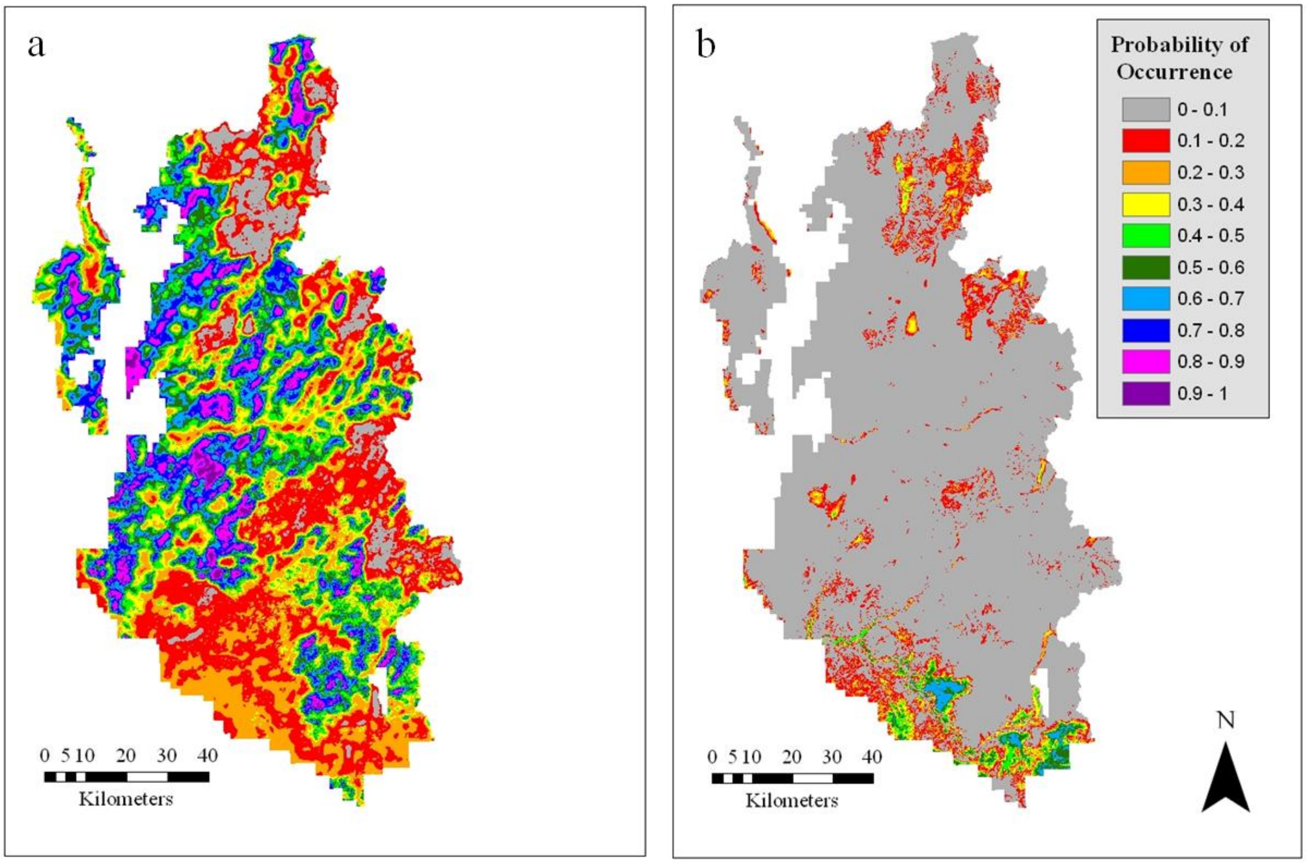

Figure 1.3. Maps depicting probability of occurrence for (a) Flammulated Owls and (b) Northern Saw-whet Owls in the Boise National Forest, Idaho, based on data collected from 2009-2010. Maps were generated from model-averaged coefficients for the predictor variables Douglas-fir, non-forest, ponderosa pine, percent canopy cover, land cover diversity, aspect, and a terrain ruggedness index.

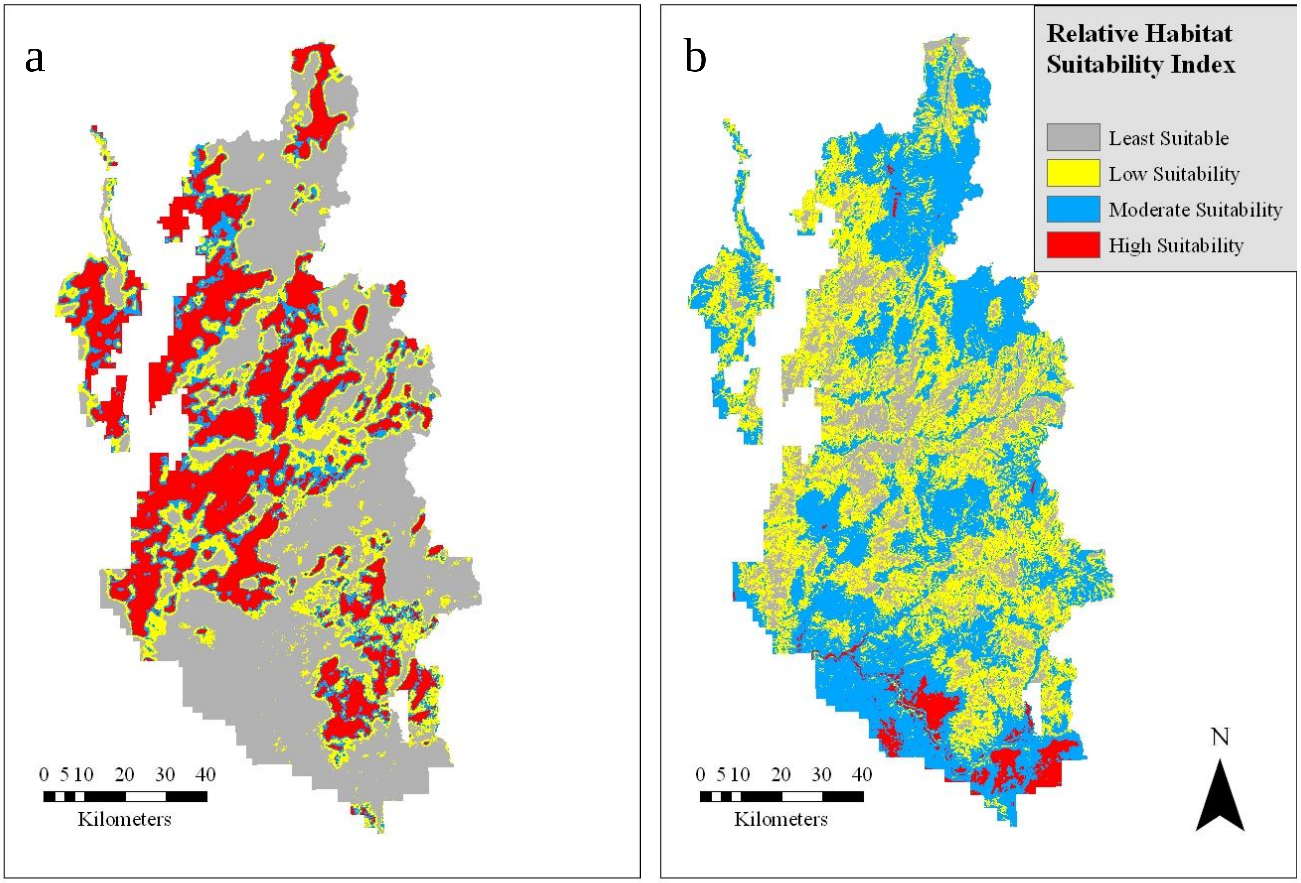

Figure 1.4. By overlaying the spatial projections generated where 50, 75, and 100 percent of occupied sites were correctly classified, habitat suitability maps were produced for (a) Flammulated Owls and (b) Northern Saw-whet Owls in the Boise National Forest, Idaho. High suitability habitat was defined by regions where 50% of occupied sites were correctly classified. Moderate suitability habitat is that area added outside of the high suitability habitat when 75% of occupied sites are modeled. Low suitability habitat is the additional area outside of moderate suitability added when 100% of occupied sites are modeled. All of these areas together represent suitable habitat in the BNF. Areas outside of the high, moderate, and low suitability projections are considered unsuitable.

CHAPTER TWO: PATTERNS OF CO-OCCURRENCE BETWEEN CAVITY-NESTING OWLS AND WOODPECKERS IN THE BOISE NATIONAL FOREST, IDAHO

Abstract

Boreal Owls (*Aegolius funereus*), Flammulated Owls (*Otus flammeolus*), and Northern Saw-whet Owls (*A. acadicus*) are small, secondary cavity-nesting birds that require cavities that woodpeckers create for nesting and shelter. I investigated co-occurrence between woodpeckers and sympatric cavity-nesting owls in the Boise National Forest, Idaho. Specifically, I tested the hypothesis that owl occupancy was conditional on the presence of one or more common species of woodpecker. Moreover, I examined the pattern of co-occurrence between cavity-nesting owl species to help understand the nature of their possible competitive interactions. I located owls by broadcasting conspecific vocalizations during nighttime hours at point-count locations (N = 150) during 2009 and 2010. I surveyed for Hairy Woodpeckers (*Picoides villosus*), Lewis's Woodpeckers (*Melanerpes lewis*), Northern Flickers (*Colaptes auratus*), Pileated Woodpeckers (*Dryocopus pileatus*), and Red-naped Sapsuckers (*Sphyrapicus nuchalis*) at these same locations during daylight hours in a similar manner while broadcasting their respective woodpecker vocalizations. As no Boreal Owls or Lewis's Woodpeckers were detected, my analyses focused on relationships among the remaining owl and woodpecker species. I modeled occupancy as a function of snag number, diameter at breast height, and species co-occurrence while accounting for imperfect detection (i.e., the possibility that an individual may go undetected during surveying when present) using the software program PRESENCE. Average number of snags per hectare (12.5 ± 0.2, N = 150) and mean diameter at breast height of snags (35.17 cm ± 0.08, N = 150) had no effect on cavity-nesting owl occurrence. There was no support for the hypothesis that cavity-nesting owl occupancy was conditional on the presence of woodpeckers. Likewise, presence of Northern Saw-whet Owls neither excluded nor facilitated Flammulated Owl occurrence (i.e., they occurred independently of one another). Therefore, despite the potential value in understanding the nocturnal owl community by examining the diurnal woodpecker community, relationships between woodpeckers and Flammulated Owls and Northern Saw-whet Owls do not appear strong enough to warrant such an approach.

Introduction

Avian communities are structured by a combination of resources (e.g., food and nest sites) and species interactions within the community (Davis 1973, Vrezec and Tome 2004a, Virkkala 2006). Understanding the factors affecting site occupancy and their influence on avian distributions requires knowledge of which species interact and the nature of such interactions. In forested ecosystems, for example, obligate, secondary cavity-nesting birds form part of a distinct avian community ideal for investigating how biological interactions affect site occupancy, as their interactions revolve around the creation of, and subsequent competition for, nest sites (Martin and Eadie 1999). For example, secondary cavity-nesting birds may engage in facilitation (i.e., formation of a nesting cavity by one species that is required by another animal) and competition (i.e., competing with other members of the community for nest holes). Members of this community can be classified as primary, weak, or secondary cavity nesters (Martin and Eadie 1999). Primary cavity nesters, such as woodpeckers, create cavities for nesting and roosting, thereby making cavities available to other members of the avian community once the woodpeckers vacate them. Nuthatches and chickadees represent weak cavity excavators that may excavate their own cavities, but they often use those created by primary cavity nesters. Secondary cavity-nesting birds, including many passerines, waterfowl, and birds of prey, such as owls, are unable to excavate their own nest sites and so rely upon the formation of natural cavities or, more frequently, those created by primary cavity nesters (Martin and Eadie 1999, Martin et al. 2004).

Secondary cavity nesters may also engage in interspecific competition for available food resources and nest holes. Competition can manifest itself as the partial or complete displacement of one species by another or by one species reducing reproductive success and survival of another species when sympatric (Gill 1995). Interspecific competition increases as species become more similar in their ecological roles (Morin 1999). Thus, in cases where competition exists, two species with overlapping diets or those requiring a similar habitat resource may not be able to coexist. Interspecific competition is an important factor explaining owl community composition in Finland where density of breeding birds is lowered and clutch initiation is delayed for Tengmalm's (Boreal) Owls (*Aegolius funereus*) within 2 km of Ural Owl (*Strix uralensis*) territories (Hakkarainen and Korpimäki 1996). Similarly, competitive exclusion is a significant factor explaining altitudinal segregation between Tawny Owls (*Strix aluco*) and Ural Owls in central Slovenia (Vrezec 2003, Vrezec and Tome 2004b). Playback experiments further supported evidence of competition between these two species of owls as Ural Owls responded aggressively to broadcasts of both conspecific and Tawny Owl vocalizations (Vrh 2006).

Nest holes that secondary cavity nesters use are frequently in standing dead trees (i.e., snags) or in live trees with decay (Martin et al. 2004). Thus, the abundance and quality of snags in which birds can make cavities may affect the degree to which facilitation occurs. Likewise, competition may be strongest between species with similar ecological roles (Root 1967) and, consequently, should increase with the amount of overlap in the use of a limited resource (Gill 1995). For secondary cavity nesters, this means competition should occur more between species requiring similarly sized cavities.

I was interested in the relationships between primary cavity excavators (woodpeckers) and those forest owls that make use of such cavities for nesting. My study focused on Boreal Owls, Flammulated Owls (*Otus flammeolus*), and Northern Saw-whet Owls (*Aegolius acadicus*), each of which is an obligate cavity nester that requires forested habitats to roost and reproduce. Although the geographic ranges of these nocturnal cavity-nesting owls overlap, their interactions remain poorly understood (but see Hayward and Garton 1988), and if and how woodpeckers shape the owl community remains unknown. Cavity-nesting owl species may be selecting among the available cavities for nesting, so one can ask if certain woodpeckers are preferred cavity excavators and expect more overlap in occupancy between owls and that species. Flammulated Owls use cavities excavated by a variety of species, including Acorn Woodpeckers (*Melanerpes formicivorus*), Northern Flickers (*Colaptes auratus*), Pileated Woodpeckers (*Dryocopus pileatus*), and Red-naped Sapsuckers (*Sphyrapicus nuchalis*; McCallum and

Gelbach 1988, Bull et al. 1990, McCallum 1994, Arsenault 2004), while Northern Saw-whet Owls (hereafter Saw-whet Owls) and Boreal Owls often use cavities excavated by Northern Flickers and Pileated Woodpeckers (Dudley pers. comm., Hayward and Hayward 1993, Priestley 2008, Rasmussen et al. 2008).

In this study, I investigated the distribution of cavity-nesting owls and woodpeckers, their patterns of co-occurrence, and the effect of snag characteristics on owl occupancy. In addition to increasing our knowledge of how biological interactions shape avian communities, my study also highlights the importance of understanding the strength of species interactions for management planning (MacKenzie et al. 2004, Halme et al. 2009). If woodpeckers ultimately are a necessary element in facilitating nesting opportunities for secondary cavity-nesting owls, then single species approaches to management and monitoring may not be as effective as those that focus on biological interactions among species. Furthermore, if woodpeckers ultimately are good predictors of the nocturnal owl community, forest managers may be able to use existing data from Christmas bird counts, breeding bird surveys, or other surveys focused on diurnal bird distributions to understand and manage for the nocturnal owl community.

My goal was to determine whether interspecies interactions affect the occurrence of Boreal Owls, Flammulated Owls, and Saw-whet Owls and to investigate the potential habitat characteristics contributing to site occupancy for these cavity-nesting owl species. Specifically, I (1) tested for evidence of facilitation between woodpeckers and owls, (2) assessed patterns of co-occurrence and exclusion among cavity-nesting owls, and (3) examined the influence of snag characteristics on cavity-nesting owl occupancy.

Study Area

I studied cavity-nesting owls within the Boise National Forest (BNF), which is approximately 10,600 km^2 in size and is located in southern Idaho (Fig 2.1a). Elevation in the study area ranges from 870–3250 m. The Boise and Payette Rivers along with the South and Middle Fork drainages of the Salmon River form the major river systems in the BNF. Forest cover is dominated by conifers as deciduous trees compose less than 1% of the total forest cover. Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) predominate at lower to mid elevations, with smaller amounts of grand fir (*Abies grandis*) occurring in the northern portion of the study area (Steele et al. 1981). At higher elevations, subalpine fir (*A. lasiocarpa*), Engelmann spruce (*Picea engelmanii*), and lodgepole pine (*P. contorta*) constitute the main canopy species (Steele et al. 1981). Shrubs such as ninebark (*Physocarpus malvaceus*), snowberry (*Symphoricarpos* sp.), serviceberry (*Amelanchier anlifolia*), rose (*Rose* sp.), huckleberry (*Vaccinium* sp.), and chokecherry (*Prunus virginiana*) are common in the forest understory, with ceanothus (*Ceanothus velutinus*), bitterbrush (*Purshia tridentata*), and sagebrush (*Artemesia tridentata*) occurring on dryer, south facing slopes (Steele et al. 1981). Riparian and drainage areas support aspen (*Populus tremuloides*), black cottonwood (*P. trichocarpa*), willows (*Salix* sp.), dogwood (*Cornus sericea*), cascara (*Rhamnus purshiana*), thimbleberry (*Rubus parviflorus*), and other deciduous tree or shrub species (Steele et al. 1981).

Methods

Field Methods

Using a stratified random approach in a geographic information system (GIS), I selected point-count locations (N = 82 in 2009 and N = 68 different locations in 2010) that were accessible during winter either by driving, skiing, or snowshoeing and within six broad forest cover classes: aspen, Douglas-fir, ponderosa pine, lodgepole pine, mixed conifer, and riparian. Ultimately, I pooled data from both years for analyses (N = 150 point-count locations; Fig. 2.2b).The most common forest types were Douglas-fir and ponderosa pine, so I placed proportionately more point-count locations in these forest cover classes. Each point-count location was separated by a minimum of 800 m to help reduce the chances of counting the same owl or woodpecker at multiple locations.

I timed my surveys for owls and woodpeckers to overlap with their respective breeding periods. Thus, from mid-February to mid-May of 2009 and 2010, I conducted point-count surveys for cavity-nesting owls using audio broadcasts of owl vocalizations to increase their detectability (Takats et al. 2001). I anticipated few if any Flammulated Owl detections during this time period because of their migratory habit and information from previous studies concerning their arrival timing (Powers et al. 1996, Barnes 2007). Therefore, I continued surveys targeting Flammulated Owls only into June of both years. June is also when detectability of Flammulated Owls is at its peak (Barnes and Belthoff 2008). While other cavity-nesting owls occur in this area (Northern Pygmy-Owls, *Glaucidium gnoma*; Western Screech-Owls, *Megascops kennicottii*), I did not consider them because of their diurnal habit or low abundance in higher-elevation forested sites, respectively. I surveyed for woodpeckers between May and June of 2009 and 2010, which is when these species are breeding and their detectability is high (Dudley pers. comm.).

Nocturnal Survey Protocol for Owls

Each survey consisted of an initial 3-min. listening period followed by a series of broadcasts of territorial owl songs (obtained from commercially available recordings). I broadcasted Flammulated Owl and Boreal Owl vocalizations with audio output adjusted to 90–110 dB (Fuller and Mosher 1987) at 1 m using an NX3 Fox Pro Wildlife Caller (FOXPRO Inc., Lewiston, PA). As in Guidelines of Nocturnal Owl Monitoring (Takats et al. 2001), I broadcasted for the smaller Flammulated Owls first to avoid attracting larger Boreal Owls or Saw-whet Owls. As Saw-whet Owls routinely respond to calls of other species (Takats et al. 2001, Kissling et al. 2010, pers. observ.), I documented their vocal responses to the Boreal or Flammulated Owl calls rather than including broadcasts of Saw-whet Owl calls. I broadcasted individual recordings of each of the above owls for 30 sec. (Fig. 2.2a) while rotating the Wildlife Caller 360˚. A 1-min. listening period followed each 30 sec. broadcast, and I repeated this broadcast-listening sequence once for Flammulated Owls before proceeding to the Boreal Owl sequence (Fig. 2.2a). Thus, I spent approximately 10 min. at each point-count location recording occurrence of the three species of owls. Surveys began at least 30 min. after sunset. I avoided surveying on nights with average wind speeds > 15 km/h or persistent precipitation as such weather could have affected my capability to detect owls or altered their responses to broadcasts. As I detected no Boreal Owls, my analyses of owl occurrence ultimately focused on Flammulated Owls and Saw-whet Owls only.

Diurnal Survey Protocol for Woodpeckers

Beginning 30 min. after sunrise, I conducted point-counts for Hairy Woodpeckers, Lewis's Woodpeckers, Northern Flickers, Pileated Woodpeckers, and Red-naped Sapsuckers at each of the point-count locations previously surveyed for owls. Following Martin and Eadie (1999), I played 15 sec. of broadcasts followed by 30 sec. listening periods and repeated this for each species (Fig. 2.2b). As there was no concern for larger species preying on smaller species as there was for owls, the order in which I presented woodpecker broadcasts was randomly assigned prior to each point-count survey. As point-count surveys ultimately detected no Lewis's woodpeckers, my analyses focused on the remaining four species of woodpeckers.

Snag Abundance and Measurements

Using methods similar to Bate et al. (1999), I estimated the number of snags per hectare and the diameter at breast height (dbh) of snags along belt transects established at each point-count location. I established four, 10-m-wide transects of 100 m, 200 m, 300 m, and 400 m in length centered on each point-count location. The four transects emanated in random directions from point-count locations with the constraint that each transect occurred in a separate quadrant defined by the four cardinal directions. Within each belt transect, I counted and measured the dbh of all snags that were (1) > 15 cm dbh, (2) > 2 m in height, and (3) capable of serving as a nest tree for an owl or woodpecker (i.e., no excessive deterioration, snag was not fractured from crown to base, and snag was able to stand without support from surrounding trees). I estimated the abundance of snags and mean dbh of snags within 400 m of each point-count location by extrapolating from the data on snags measured along the four transects.

Probability of Detection

To account for imperfect detection of species (i.e., false negatives), I visited point-count locations three times for Saw-whet Owls and one to three times for Flammulated Owls. Similarly, I visited point-count locations two to three times each to conduct woodpecker surveys. As detection of owls may be influenced by noise, I indexed background noise levels during each point-count visit on a scale ranging from 1 (quiet) to 4 (noisy) as described by Takats et al. (2001). I used the resulting detection history generated from multiple site visits along with an index of noise for each point-count location during sampling to calculate the detection probability (p) for models considering the co-occurrence of cavity-nesting owls with woodpeckers and Flammulated Owls with Saw-whet Owls to more accurately estimate occupancy (MacKenzie et al. 2002).

Statistical Analyses

I used the occupancy-modeling software program PRESENCE (MacKenzie et al. 2002) and conditional two-species models (Richmond et al. 2010) to adjust logistic regressions of occurrence data for imperfect detection and to assess patterns of co-occurrence within the cavity-nesting avian community. These models provide unbiased estimates for probability of site occupancy and allow inclusion of occupancy covariates in understanding patterns of co-occurrence between species. Richmond et al. (2010) reported model parameterizations that were designed to examine cases of competitive exclusion, whereby the probability of a subordinate species (species B) occupying a site is estimated conditional on the presence of a dominant species (Species A; Table 2.1). I expanded this technique and applied this model parameterization in a new way to explore facilitative interactions between the above mentioned cavity-nesting owls and woodpeckers, as well as to test for evidence of competitive exclusion between two cavity-nesting owls (Flammulated Owls and Saw-whet Owls).

The effect of the dominant species on the probability of site occupancy (ψ) of the subordinate species can be tested explicitly by comparing model performance when the presence of species B is conditional on the presence of species A (i.e., ψ^{BA} and ψ^{Ba} are estimated independently; Table 2.2) and when the presence of species B is unconditional of the occupancy state of species A (i.e., $\psi^{BA} = \psi^{Ba}$; Table 2.2). As woodpeckers create the majority of cavities occupied by Flammulated Owls (McCallum 1994) and Saw-whet Owls (Rasmussen et al. 2008), I predicted that Flammulated Owl and Saw-whet Owl occupancy would depend on the presence of woodpeckers. To test for facilitation between woodpeckers and owls, I considered cases where occupancy of owls (subordinate) was conditional upon the presence of woodpeckers (dominant). I did this for the aforementioned woodpecker species individually and with woodpeckers as a group (i.e., owl occupancy conditional on the presence of a member of any woodpecker species). As cavity-nesting owls and woodpeckers separate their periods of activity temporally, I had no reason to believe that the presence of woodpeckers would affect the probability of detecting a nocturnal cavity-nesting owl. Nor would the presence of a cavity-nesting owl affect the detectability of a diurnal woodpecker (i.e., species detection probabilities were estimated independently). Thus, I did not consider models where species detection probability was conditional on the presence or absence of the other species for woodpecker and owl dyads ($p^A = r^A$ and $p^B = r^{BA} = r^{Ba}$; Table 2.2). For each dyad of owls and woodpeckers, in Program PRESENCE, I considered the effective sample size to be the number of sites where the owl species was detected.

For modeling, I considered Saw-whet Owls to be dominant over Flammulated Owls because Saw-whet Owls breed earlier than Flammulated Owls and are thereby able to select available nesting cavities at a time when Flammulated Owls likely are still on their wintering grounds (McCallum 1994, Rasmussen et al. 2008). Therefore, I predicted a negative relationship between the occupancy of Saw-whet Owls and Flammulated Owls on the basis of competition over limited nest holes. I also tested for evidence of an effect of Saw-whet Owl occupancy on the detectability of Flammulated Owls by comparing model performance when the probability of detection for Flammulated Owls was dependent versus independent of Saw-whet Owl occupancy (i.e., p^B estimated separately from $r^{BA} = r^{Ba}$ compared to $p^B = r^{BA} = r^{Ba}$; Table 2.2). I predicted that Saw-whet Owl presence would not affect detectability of Flammulated Owls because Saw-whet Owls initiate breeding earlier, are generally less vocal at the time Flammulated Owl surveys were conducted, and likely do not pose a predatory threat to Flammulated Owls (Cannings 1987, Rasmussen et al. 2008, pers. observ.). As Flammulated Owls are generally absent from my study area until early May (McCallum 1994, Barnes 2007, pers. observ.), I did not test for an effect of Flammulated Owl occupancy on Saw-whet Owl detectability. I used an effective sample size equivalent to the number of sites where Flammulated Owls were detected to examine the effect of possible competition between cavity-nesting owls.

I developed a set of eight and 16 candidate models for dyads (i.e., two-species combinations to assess the extent and nature of species interactions) of cavity-nesting owls and woodpeckers and cavity-nesting owls to examine the following potential effects: (1) woodpecker presence on Flammulated Owl and Saw-whet Owl occupancy, (2) Saw-whet Owl presence on Flammulated Owl occupancy and detectability, and (3) snag characteristics on the occupancy of both cavity-nesting owl species. Models of woodpecker and cavity-nesting owls included estimates of p as a function of noise during time of survey and considered occupancy of Flammulated Owls and Saw-whet Owl (species B) conditional or unconditional of the presence of woodpeckers (species A). Models also included all possible combinations of owl occupancy dependent or independent of the number of snags per hectare and snag dbh. As I was mainly concerned with the effects of snag characteristics on owl occupancy, snag characteristics were used as occupancy covariates for only cavity-nesting owls. The dyad of cavity-nesting owls considered the previously mentioned model structures as well as detection probability of Flammulated Owls (species B) conditional and unconditional of Saw-whet Owl (species A) presence.

For species dyads, I determined whether presence of species A had an effect on the occurrence of species B by assessing model performance using AIC (Burnham and Anderson 2002) corrected for small sample size (AIC_c) and by comparing the parameter estimates for ψ^{BA} and ψ^{Ba}. If occurrence of species B depends on the occupancy status (presence or absence) of species A, then ψ^{BA} and ψ^{Ba} will differ from one another. To examine this, I compared 95% confidence intervals of model-averaged estimates of ψ^{BA} and ψ^{Ba} using only those models in which both parameters were present (i.e., model structures where occupancy of species B is conditional on occupancy of species A). I used a similar approach to determine whether the presence of Saw-whet Owl occurrence affected Flammulated Owl detectability by comparing estimates of p^{B} and r^{BA} and their associated 95% confidence intervals. All means are presented below with their standard error.

Results

Nocturnal Surveys

During 2009 and 2010, I conducted 720 visits to 150 point-count locations, which produced 113 detections of two species of cavity-nesting owls. There were no Boreal Owls detected during the point-counts. I detected Flammulated Owls and Saw-whet Owls at 27 and 45 point-count locations (Table 3; Appendix 2.1), respectively, with at least one of these species of owl detected at 64 point-count locations (42.7% of locations). Point-count surveys conducted during June yielded no new Saw-whet Owls detections. In addition to the focal species, I also detected Barred Owls (*Strix varia*; N = 2 point-count locations), Great Horned Owls (*Bubo virginianus*; N = 20), Long-eared Owls (*Asio otus*; N = 1), Northern Pygmy Owls (N = 1), and Western Screech-Owls (N = 2).

Diurnal Surveys

I conducted 373 point-count surveys for woodpeckers at 150 locations and recorded 153 detections of four woodpecker species. Woodpeckers occurred at 79 (51.7%) point-count locations, with more than one species of woodpecker at 27 (18.0% of occupied sites). Northern Flickers were most frequent, followed by Hairy Woodpeckers, Red-naped Sapsuckers, and Pileated Woodpeckers, respectively (Table 2.3). Two Williamson’s Sapsuckers (*Sphyrapicus thyroideus*), a Downy Woodpecker

(*Picoides pubescens*), and White-Headed Woodpecker (*Picoides albolarvatus*) were also detected, but I excluded these species from analyses because of their rarity.

Co-occurrence Patterns

As a group, woodpeckers co-occurred more frequently with Flammulated Owls than they did with Saw-whet Owls (Table 2.3). Both species of owls co-occurred most frequently with Northern Flickers, while Pileated Woodpeckers were the least commonly co-occurring woodpecker (Table 2.3). Flammulated Owls and Saw-whet Owls co-occurred at eight point-count locations (5% of point-count locations, Table 2.3).

Species Interactions Between Owls and Woodpeckers

Contrary to my prediction, the presence of woodpeckers did not affect cavity-nesting owl occupancy. Models that assumed Flammulated Owl occupancy was unconditional on woodpecker presence received moderate to strong support (Table 2.4), with cumulative Akaike weights ranging from 0.64 – 0.85. There was a similar lack of relationship between Saw-whet Owl occupancy and woodpecker presence. Models that assumed no effect of woodpecker presence on the probability of Saw-whet Owl occupancy had cumulative Akaike weights ranging from 0.53 – 0.76 (Table 2.4). For both owl species, occupancy unconditional of woodpecker presence was the top ranking model for all species dyads (Table 2.5 and 2.6). Likewise, 95% confidence intervals of ψ^{BA} (woodpecker present) and ψ^{Ba} (woodpecker absent) overlapped for all woodpecker-owl dyads, which indicate that the probability of cavity-nesting owl occurrence was not conditional on the occupancy state of woodpeckers (Table 2.7).

Species Interactions Between Owls

Saw-whet Owl presence did not affect the probability of Flammulated Owl occupancy (Table 2.8). Models that assumed Flammulated Owl occupancy was unconditional on the occupancy state of Saw-whet Owls received stronger support than models that assumed a subordinate-dominant relationship between these species (Table 2.9). For Flammulated Owls, I detected no difference between models where occupancy was estimated as conditional or unconditional of Saw-whet Owl presence. The model-averaged estimates for ψ^{BA} and ψ^{Ba} were 0.47 (95% CI = 0.416-0.532) and 0.49 (95% CI = 0.450-0.530), respectively, indicating that occupancy of Flammulated Owls was unconditional of Saw-whet Owl occurrence.

As expected, Flammulated Owl detection probability was not affected by Saw-whet Owl presence (Table 2.8). Models that assumed an independent relationship between occupancy and detection probabilities outperformed those where Flammulated Owl detectability was conditional on the presence of Saw-whet Owls (Table 2.9). The model-averaged probability of detection for Flammulated Owls did not differ when Saw-whet Owls were absent ($p = 0.69$, 95% CI = 0.498-0.874) as compared to when Saw-whet Owls were present ($p = 0.53$, 95% CI = 0.465-0.534).

Effect of Snags on Owl Occupancy

The number of snags per hectare for occupied versus unoccupied sites was 11.07 ± 0.05 and 12.78 ± 0.17 for Flammulated Owls (N = 27 occupied sites) and 8.6 ± 0.05 and 14.1 ± 0.18 for Saw-whet Owls (N = 45 occupied sites), respectively. For Flammulated Owls, the average snag dbh was 36.10 ± 0.06 cm in occupied sites and

34.95 ± 0.08 cm in unoccupied sites. Snags at point-count locations with and without Saw-whet Owls averaged 38 ± 0.08 and 34 ± 0.08 cm in dbh, respectively.

Model selection results for dyads of owls and woodpeckers indicated that the number of snags per hectare and average snag dbh were not strong predictors of cavity-nesting owl occupancy. For Flammulated Owls, neither the number of snags per hectare nor snag dbh entered into models within two ΔAIC_c of the best approximating model (Table 2.5). Although both snag covariates were in all of the best approximating models for Saw-whet Owls (Table 2.6), 95% confidence intervals for model-averaged beta coefficients of snags per hectare and snag dbh overlapped zero for all species dyads.

Discussion

Conditional two-species occupancy models offer a useful tool for drawing inferences about the interactions between species in cases where direct observation of species interactions are difficult, such as those of small, secretive, and nocturnal cavity-nesting owls. In this study, I explored the occurrence patterns for two species that potentially compete with one another: Flammulated Owls and Saw-whet Owls. I also investigated the spatial distribution of these owls and the woodpeckers with which they may share a potentially facilitative relationship. While several studies have examined the strength of competitive interactions using two-species occupancy models (see MacKenzie et al. 2004, Luiselli 2006, Bailey et al. 2009, Richmond et al. 2010), mine may be the first that simultaneously incorporated detection probabilities and occupancy covariates to assess the strength of a potential facilitation interaction (i.e., woodpeckers excavating cavities for use by cavity-nesting owls). In addition, previous parameterizations of the two-species model (MacKenzie et al. 2004) often precluded the use of habitat covariates (see Richmond et al. 2010 for further discussion of these limitations). In comparison, the conditional two-species occupancy model parameterization that both Richmond et al. (2010) and I used was able to concurrently model habitat covariates (e.g., snag characteristics) while assessing the effect of species A's presence on probability of occupancy of species B, which helped distinguish between co-occurrence patterns resulting from interspecific interactions and those that may have been a product of species responding to similar habitat preferences (e.g., species-specific responses to the number of snag per hectare and dbh).

Species Interactions Between Owls and Woodpeckers

After accounting for imperfect detection, there was no evidence that the presence of woodpeckers affected the occupancy of either Flammulated Owls or Saw-whet Owls. One possibility for the lack of a relationship is that it may take time to develop. That is, there may be a number of years necessary before cavities are vacated by woodpeckers or before owls locate them. For example, occupancy of artificial nest boxes typically increases in the years following initial nest box deployment (e.g., American Kestrels, *Falco sparverius*; Beasley and Parrish 2009, Steenhof and Peterson 2009; Barn Owls, *Tyto alba*; Marti et al. 1979, Great Crested Flycatchers, *Myiarchus crinitus*; White and Seginak 2000, Vaux's Swifts, *Chaetura vauxi*; Bull 2003, Western Screech-Owls; Marks and Doremus 2000, and Wood Ducks, *Aix sponsa*; Ransom and Frentress 2007) until a point of saturation in the density of nesting birds is reached. One may expect to see this trend of an initial increase followed by a plateau in the number of occupied nest boxes as a consequence of a species' increased probability of encountering boxes over time. Thus, there may be a lag period associated with the presence of woodpeckers and site occupancy of owls. Such an effect could also result from an overall increase in a species' population. However, given that the majority of forest dwelling vertebrates in the northwestern United States are suspected of being stable or in decline (Manley et al. 2004), this latter scenario seems less likely.

Alternatively, if the available pool of useable cavities for Flammulated Owls and Saw-whet Owls are not all used, the presence of woodpeckers at a point-count location may not be a good predictor for the probability of cavity-nesting owl occurrence. Woodpeckers, specifically Northern Flickers (Wiebe and Moore 2008), only occasionally reuse nest holes for breeding while cavity reuse among secondary cavity-nesting owls (McCallum 1994, Rasmussen et al. 2008) and other birds is common. Thus, if woodpeckers excavate more cavities than are used by cavity-nesting owls, a surplus of cavities may be available. For instance, Bonar (2000) found Pileated Woodpeckers in the Pacific Northwest produce more cavities than secondary-cavity nesters use. However, patterns such as those Bonar (2000) described depend on habitats containing the necessary components (e.g., appropriate snags or trees) for creating suitable cavities. Indeed, the number of suitable cavities becomes a limiting factor in heavily managed landscapes where snags and other standing deadwood have been removed (Newton 1994). While primary excavators provide the majority of cavities secondary cavity-nesting birds use, it is possible that the use of natural cavities (e.g., those created through decay or by broken tree limbs) by Flammulated Owls and Saw-whet Owls may also have contributed to the lack of relationship that I observed.

Imperfect detection of species could also have contributed to the apparent lack of observed facilitation between woodpeckers and owls. Many of my point-count surveys were conducted during springtime when snowmelt in nearby creeks, streams, and rivers contributed to a higher value on the noise index. This was especially true of points that were located closer to large rivers (e.g., Boise and Payette River systems). One potential complication arising from moderate ($p = 0.50 – 0.15$) to low ($p < 0.15$) detection probabilities and a small number of sampling occasions (< 7) is inflation in occupancy estimates (MacKenzie et al. 2002). Detection probabilities for woodpeckers ranged from 0.23 for Pileated Woodpeckers to 0.45 for Northern Flickers. Although poor detection probability was not an issue for Flammulated Owls ($p = 0.68$ and 0.53 when Saw-whet Owls were absent versus present, respectively) and Saw-whet Owls ($p = 0.85$), probabilities of detection for woodpeckers were lower. Lower probabilities of detection for woodpeckers therefore may make patterns of co-occurrence with owls difficult to detect.

Species Interactions Between Owls

Model selection results as well as comparison of the parameter estimates ψ^{BA} and ψ^{Ba} provided no support for the predicted negative relationship in occupancy of the two species of owl. Thus, there was no evidence that Saw-whet Owls excluded the smaller Flammulated Owls through competition. These results contrast with studies of owls in which large- and medium-sized species appear to out-compete small species for space or resources in forest systems (Hakkarainen and Korpimäki 1996, Vrezec 2003, Vrezec and Tome 2004b). My prediction was based on studies reporting that similar primary cavity excavators (Northern Flickers and Pileated Woodpeckers) were preferred cavity creators for Flammulated Owls (McCallum and Gelbach 1988, Bull et al. 1990, McCallum 1994, Arsenault 2004) and Saw-whet Owls (Hayward and Hayward 1993, Priestley 2008, Rasmussen et al. 2008). However, Flammulated Owls and Saw-whet Owls differ in their body size and in the size of cavities they typically use for nesting. As such, the smaller Flammulated Owl may occupy cavities created by smaller primary cavity nesters (e.g., Hairy Woodpeckers and Red-naped Sapsuckers). However, if there is a surplus of available cavities (as indicated by such studies as Bonar 2000), then competition over nest sites may not be common between these species.

It is almost certain that competition over food does not occur as Saw-whet Owls consume primarily woodland mice (*Peromyscus* sp.), voles (*Microtus* sp.), and small numbers of migrating passerines (Grove 1985, Cannings 1987, Marks and Dormeus 1988), while Flammulated Owls are almost exclusively insectivorous (McCallum 1994). While my results suggest no negative association (i.e., competitive exclusion) between Flammulated Owls and Saw-whet Owls, interestingly they also provide no evidence of a positive relationship between the two species; instead, their occurrence was independent of one another.

There was no evidence for an effect of Saw-whet Owl presence on the detectability of Flammulated Owls. This is perhaps not surprising as Saw-whet Owls establish breeding territories earlier, vocalize less frequently at the time Flammulated Owls arrive on the study area, and likely prey infrequently, if at all, on Flammulated Owls (Cannings 1987, Rasmussen et al. 2008, Groce and Morrison 2010).

Effect of Snags on Owl Occupancy

Although snags may be a necessary component of cavity-nesting owl habitat (Martin and Eadie 1999), I found no effect of the snag dbh or number of snags on Flammulated Owl or Saw-whet Owl occupancy. Although model selection results from dyads of Saw-whet Owls and woodpeckers suggest snag characteristics provide information on Saw-whet Owl occurrence, the model-averaged coefficients and their associated 95% confidence intervals indicated that these covariates had relatively little influence on owl occupancy. It is possible that woodpecker presence and snags have a synergistic effect on owl occupancy. That is, snag characteristics may become an important element to Saw-whet Owl occurrence when considering the presence of woodpeckers. My study cannot confirm this as I could not consider models containing interactions between these factors because of the need to minimize the number of model parameters driven by effective sample size.

It is possible that the effects of snags may be acting on a smaller spatial scale than I measured. Groce and Morrison (2010) also assessed the effect of snags over a large spatial scale (250 m-radius around survey locations) and found no relationship between snag dbh in sites used and not used by Saw-whet Owls in Nevada. Assessments of snag characteristics are often done on a much smaller scale by comparing the number of snags immediately around a known nest site to a randomly selected location (Martin et al. 2004, Russell et al. 2007). As I did not specifically locate owl nest sites, I sampled snags over a much larger area. Important snag characteristics that I did not measure such as snag condition (e.g., state of decay), nest height, and cavity dimensions may ultimately drive cavity selection (Newton 1994, Martin et al. 2004). Thus, availability of species-appropriate cavities and snags may be a limiting factor for cavity-nesting owls.

Another interesting possibility is that utility poles may be serving the same role as snags (Fig. 2.3). I frequently observed cavities in utility poles that were located throughout the BNF and close to my point-count locations, although they were not considered in snag surveys. For instance, in one region of the BNF, I counted 13 consecutive utility poles that each contained woodpecker cavities. Although the effects of utility poles on birds are generally considered to be negative (i.e., causing electrocutions, collisions, and indirect impacts through habitat loss and edge effects, Blue 1996), they offer benefits to birds as well. Utility poles can provide hunting perches, roosting sites, and nesting substrates (Blue 1996). Woodpecker use of utility poles is also well documented and is almost always presented in a negative context (i.e., causing extensive damage and reducing life expectancy of poles; Dennis 1964, Stemmerman 1988, Harness 2004). However, the presence of woodpecker cavities in utility poles may help offset some of the negative effects involved in erecting such structures and could provide nest sites for many secondary cavity-nesting birds, perhaps even owls.

Conclusions

If there were a strong relationship between the occupancy of woodpeckers and cavity-nesting owls, then it would be possible for avian biologists or land managers to understand the occurrence of the nocturnal species simply by characterizing the diurnal woodpecker community. This would obviate the need for nighttime surveys, which frequently present challenging logistics. However, my results indicated that relationships between woodpeckers and both Flammulated Owls and Saw-whet Owls are not strong enough to warrant such an approach. The apparent lack of an association between woodpeckers and owls should be interpreted carefully as species interactions may be acting on a different temporal scale than those of which I made observations. Specifically, there may be a lag effect between the presence of woodpeckers and occupancy of cavity-nesting owls. My findings also indicated that the presence of Saw-whet Owls neither excluded nor facilitated Flammulated Owl occupancy. While both woodpeckers and sympatric owls appeared to coexist across a wide variety of forest types, it is also possible that additional species-specific habitat covariates may help reveal an effect of any of the woodpeckers and occupancy of either Flammulated Owls or Saw-whet Owls. Future research could focus on expanding two-species occupancy models to more complex multispecies communities (Richmond et al. 2010). Such models would further improve our ability to examine the influence of species interactions on the distribution and site occupancy of wildlife.

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Table 2.1. Parameters used in the conditional two-species model and their descriptions.

Parameter	Description
ψ^{A}	Probability of occupancy for species A, regardless of the occupancy state of species B.
ψ^{BA}	Probability of occupancy for species B, given species A is present.
ψ^{Ba}	Probability of occupancy for species B, given species A is absent.
p^{A}	Probability of detection for species A, given species B is absent.
p^{B}	Probability of detection for species B, given species A is absent.
r^{A}	Probability of detection for species A, given both species are present.
r^{BA}	Probability of detection for species B, given both species are present and species A is detected.
r^{Ba}	Probability of detection for species B, given both species are present and species A is not detected.

Table 2.2. Constraints used for the conditional two-species models to test for occupancy and probability of detection for species B conditional or unconditional on the presence of species A.

Testing	Constraints Imposed
ψ Conditional	$\psi^{BA} \neq \psi^{Ba}$
ψ Unconditional	$\psi^{BA} = \psi^{Ba}$
p Conditional	$p^{A} = r^{A}$ and $p^{B} \neq r^{BA}$
p Unconditional	$p^{A} = r^{A}$ and $p^{B} = r^{BA}$

Table 2.3. Naïve estimates of co-occurrence patterns for sympatric cavity-nesting owls and woodpeckers in the Boise National Forest, Idaho. Number of point-count locations out of 150 where species were detected is shown in parentheses. Values represent the percentage of point-count locations occupied by Flammulated Owls and Northern Saw-whet Owls that were also occupied by sympatric cavity-nesting owls or woodpeckers.

	Flammulated Owls	Northern Saw-whet Owls
Species	% Occupied	% Occupied
Flammulated Owls (27)	-	11
Northern Saw-whet Owls (45)	19	-
Hairy Woodpecker (29)	41	27
Northern Flicker (43)	48	40
Pileated Woodpecker (14)	11	13
Red-naped Sapsucker (27)	26	29
Woodpeckers (79)	75	66

Table 2.4. Relative support (w_+) measured as the summed Akaike weights for conditional two-species occupancy models where occupancy of Flammulated Owls and Northern Saw-whet Owls is conditional (C) or unconditional (U) of woodpecker presence.

	Flammulated Owls		Northern Saw-whet Owls	
Species	C	U	C	U
Hairy Woodpecker	0.363	0.636	0.396	0.604
Northern Flicker	0.185	0.815	0.245	0.755
Pileated Woodpecker	0.210	0.790	0.269	0.731
Red-naped Sapsucker	0.151	0.849	0.268	0.732
Woodpeckers	0.265	0.735	0.473	0.528

Notes: Relative importance (w_+) of conditional and unconditional model structures for ψ were summed for four models in a set of eight.

Table 2.5. Model selection results for two-species occupancy models fit to Flammulated Owl and woodpecker detection data from 150 point-count locations in the Boise National Forest, Idaho, in 2009 and 2010. The terms in parentheses represent the sources of variation in the model parameters for occupancy (ψ) of owls only and detection probability (p) of both species; “dbh” indicates models that were fit using average diameter at breast of snags, “snag#” denotes models fit using average number of snags per hectare, and “noise” indicates models where detection probability differed by the amount of ambient noise during surveying. Models estimated Flammulated Owl occupancy unconditional (U) or conditional (C) of woodpecker presence. All models include separate estimates (U) of detection probability for each species.

Species Dyads	Model	K^a	ΔAIC_c^b	w^c
Hairy Woodpeckers	ψ(U), p(U, noise)	5	0.00	0.431
	ψ(C), p(U, noise)	6	1.07	0.252
	ψ(U, dbh), p(U, noise)	6	2.91	0.100
	ψ(U, snag#), p(U, noise)	6	3.20	0.087
	ψ(C, dbh), p(U, noise)	7	3.90	0.061
	ψ(C, snag#), p(U, noise)	7	4.69	0.041
	ψ(U, dbh, snag#), p(U, noise)	7	6.45	0.017
	ψ(C, dbh, snag#), p(U, noise)	8	7.95	0.008
Northern Flickers	ψ(U), p(U, noise)	5	0.00	0.554
	ψ(C), p(U, noise)	6	2.85	0.133
	ψ(U, dbh), p(U, noise)	6	2.95	0.126
	ψ(U, snag#), p(U, noise)	6	3.21	0.111
	ψ(C, dbh), p(U, noise)	7	6.14	0.026
	ψ(C, snag#), p(U, noise)	7	6.40	0.023
	ψ(U, dbh, snag#), p(U, noise)	7	6.50	0.022
	ψ(C, dbh, snag#), p(U, noise)	8	10.11	0.004
Pileated Woodpeckers	ψ(U), p(U, noise)	5	0.00	0.527
	ψ(C), p(U, noise)	6	2.54	0.148
	ψ(U, dbh), p(U, noise)	6	2.79	0.130
	ψ(U, snag#), p(U, noise)	6	3.17	0.108
	ψ(C, dbh), p(U, noise)	7	5.58	0.032
	ψ(C, snag#), p(U, noise)	7	6.09	0.025
	ψ(U, dbh, snag#), p(U, noise)	7	6.28	0.023
	ψ(C, dbh, snag#), p(U, noise)	8	9.47	0.005
Red-naped Sapsuckers	ψ(U), p(U, noise)	5	0.00	0.578
	ψ(U, dbh), p(U, noise)	6	2.95	0.132
	ψ(U, snag#), p(U, noise)	6	3.2	0.117
	ψ(C), p(U, noise)	6	3.34	0.109
	ψ(U, dbh, snag#), p(U, noise)	7	6.51	0.022
	ψ(C, dbh), p(U, noise)	7	6.60	0.021
	ψ(C, snag#), p(U, noise)	7	6.89	0.018
	ψ(C, dbh, snag#), p(U, noise)	8	10.58	0.003
Woodpeckers	ψ(U), p(U, noise)	5	0.00	0.505
	ψ(C), p(U, noise)	6	1.92	0.193
	ψ(U, dbh), p(U, noise)	6	3.04	0.110
	ψ(U, snag#), p(U, noise)	6	3.22	0.101
	ψ(C, dbh), p(U, noise)	7	5.4	0.034

ψ(C, snag#), *p*(U, noise)	7	5.43	0.033
ψ(U, dbh, snag#), *p*(U, noise)	7	6.62	0.018
ψ(C, dbh, snag#), *p*(U, noise)	8	9.35	0.005

[a] The number of estimated parameters.

[b] The relative difference in AIC$_c$ values.

[c] AIC$_c$ model weight.

Table 2.6. Model selection results for two-species occupancy models fit to Northern Saw-whet Owl and woodpecker detection data from 150 point-count locations in the Boise National Forest, Idaho, in 2009 and 2010. The terms in parentheses represent the sources of variation in the model parameters for occupancy (ψ) of owls only and detection probability (*p*) of both species; "dbh" indicates models that were fit using average diameter at breast of snags, "snag#" denotes models fit using average number of snags per hectare, and "noise" indicates models where detection probability differed by the amount of ambient noise during surveying. Models estimated Northern Saw-whet Owl occupancy unconditional (U) or conditional (C) of woodpecker presence. All models included separate estimates (U) of detection probability for each species.

Species Dyads	Model	K^a	ΔAIC_c^b	w^c
Hairy Woodpeckers	ψ(U, dbh, snag#), *p*(U, noise)	7	0.00	0.373
	ψ(C, dbh, snag#), *p*(U, noise)	8	0.60	0.277
	ψ(U, snag#), *p*(U, noise)	6	1.99	0.138
	ψ(U, dbh), *p*(U, noise)	6	3.36	0.070
	ψ(C, snag#), *p*(U, noise)	7	3.62	0.061
	ψ(C, dbh), *p*(U, noise)	7	4.13	0.047
	ψ(U), *p*(U, noise)	5	5.58	0.023
	ψ(C), *p*(U, noise)	6	7.07	0.011
Northern Flickers	ψ(U, dbh, snag#), *p*(U, noise)	7	0.00	0.463
	ψ(U, snag#), *p*(U, noise)	6	1.95	0.175
	ψ(C, dbh, snag#), *p*(U, noise)	8	2.37	0.142
	ψ(U, dbh), *p*(U, noise)	6	3.30	0.089
	ψ(C, snag#), *p*(U , noise)	7	4.14	0.058
	ψ(C, dbh), *p*(U, noise)	7	5.28	0.033
	ψ(U), *p*(U, noise)	5	5.51	0.029
	ψ(C), *p*(U, noise)	6	7.35	0.012
Pileated Woodpeckers	ψ(U, dbh, snag#), *p*(U, noise)	7	0.00	0.461
	ψ(C, dbh, snag#), *p*(U, noise)	8	1.96	0.173
	ψ(U, snag#), *p*(U, noise)	6	2.07	0.164
	ψ(U, dbh), *p*(U, noise)	6	3.50	0.080
	ψ(C, snag#), p(U, noise)	7	3.89	0.066
	ψ(U), *p*(U, noise)	5	5.77	0.026
	ψ(C, dbh), *p*(U, noise)	7	6.04	0.023
	ψ(C), *p*(U, noise)	6	8.13	0.008
Red-naped Sapsuckers	ψ(U, dbh, snag#), *p*(U, noise)	7	0.00	0.436
	ψ(U, snag#), *p*(U, noise)	6	1.84	0.174
	ψ(C, dbh, snag#), *p*(U, noise)	8	2.65	0.116
	ψ(C, snag#), *p*(U, noise)	7	2.82	0.106
	ψ(U, dbh), *p*(U, noise)	6	3.13	0.091
	ψ (U), *p*(U, noise)	5	5.24	0.032
	ψ(C, dbh), *p*(U, noise)	7	5.61	0.026
	ψ(C), *p*(U, noise)	6	6.21	0.020
Woodpeckers	ψ(U, dbh, snag#), *p*(U, noise)	7	0.00	0.320
	ψ(C, dbh, snag#), *p*(U, noise)	8	0.25	0.283
	ψ(C, snag#), *p*(U, noise)	7	1.69	0.138
	ψ(U, snag#), *p*(U, noise)	6	1.91	0.123
	ψ(U, dbh), *p*(U, noise)	6	3.25	0.063

	ψ(C, dbh), *p*(U, noise)	7	4.33	0.037
	ψ(U), *p*(U, noise)	5	5.43	0.021
	ψ(C), *p*(U, noise)	6	6.02	0.016

[a] The number of estimated parameters.

[b] The relative difference in AIC_c values.

[c] AIC_c model weight.

Table 2.7. Model-averaged occupancy estimates (ψ) and 95% confidence intervals for Flammulated Owls and Northern Saw-whet Owls when woodpeckers were present (ψ^{BA}) and absent (ψ^{Ba}). In all dyads of cavity-nesting-owls and woodpeckers, ψ did not differ with the occupancy status of woodpeckers as indicated by overlapping 95% CIs between ψ^{BA} and ψ^{Ba}.

		Flammulated Owls			Northern Saw-whet Owls		
Species	Woodpecker occupancy status	ψ	Lower 95%	Upper 95%	ψ	Lower	Upper
Hairy Woodpeckers	Present	0.55	0.398	0.692	0.53	0.345	0.720
	Absent	0.44	0.319	0.558	0.42	0.237	0.611
Northern Flickers	Present	0.50	0.444	0.558	0.49	0.427	0.555
	Absent	0.48	0.419	0.538	0.47	0.372	0.541
Pileated Woodpeckers	Present	0.46	0.361	0.562	0.52	0.413	0.619
	Absent	0.51	0.445	0.573	0.46	0.374	0.541
Red-naped Sapsucker	Present	0.49	0.438	0.541	0.50	0.434	0.577
	Absent	0.49	0.446	0.536	0.46	0.378	0.539
Woodpeckers	Present	0.49	0.442	0.551	0.44	0.262	0.607
	Absent	0.42	0.247	0.583	0.34	0.121	0.561

Table 2.8. Relative Support (w_+) for different formulations of the conditional two-species occupancy model where Flammulated Owl occupancy and detection probability was either conditional (C) or unconditional (U) on Northern Saw-whet Owl occupancy.

Effect of Northern Saw-whet occupancy on Flammulated Owl occupancy	Effect of Northern Saw-whet occupancy on Flammulated Owl detection	N	w_+
U	U	4	0.743
C	U	4	0.130
U	C	4	0.110
C	C	4	0.018

Note: N is the number of models and w_+ is the relative importance weight: the summed Akaike weights for all models sharing the same model configuration in the set of 24 models.

Table 2.9. Model selection results for conditional two-species occupancy models fit to Flammulated Owl and Northern Saw-whet Owl detection data from 150 point-count locations in the Boise National Forest, Idaho, in 2009 and 2010. The terms in parentheses represent the sources of variation in the model parameters for occupancy (ψ) and detection probability (p); "dbh" indicates models that were fit using average diameter at breast of snags, "snag#" denotes models fit using average number of snags per hectare, and "noise" indicates models where detection probability differed by the amount of ambient noise during surveying. Parameters were always fit to both species in the pair. Models estimated Flammulated Owl occupancy and detection probability either unconditional (U) or conditional (C) of Northern Saw-whet Owl presence.

Model	K^a	$\Delta AIC_c{}^b$	w^c
ψ(U, snag#), p(U, noise)	7	0.00	0.250
ψ(U), p(U, noise)	5	0.25	0.221
ψ(U, dbh), p(U, noise)	7	0.48	0.197
ψ(U, dbh, snag#), p(U, noise)	9	2.44	0.070
ψ(C), p(U, noise)	6	3.37	0.045
ψ(C, snag#), p(U, noise)	8	3.44	0.044
ψ(U), p(C, noise)	6	3.45	0.044
ψ(U, snag#), p(C, noise)	8	4.09	0.032
ψ(C, dbh), p(U, noise)	8	4.25	0.029
ψ(U, dbh), p(C, noise)	8	4.46	0.026
ψ(C, dbh, snag#), p(U, noise)	10	6.72	0.008
ψ(C), p(C, noise)	7	6.73	0.008
ψ(U, dbh, snag#), p(C, noise)	10	7.59	0.005
ψ(C, snag#), p(C, noise)	9	7.84	0.005
ψ(C, dbh), p(C, noise)	9	8.50	0.003
ψ(C, dbh, snag#), p(C, noise)	11	12.4	0.000

[a] The number of estimated parameters.

[b] The relative difference in AIC_c values.

[c] AIC_c model weight.

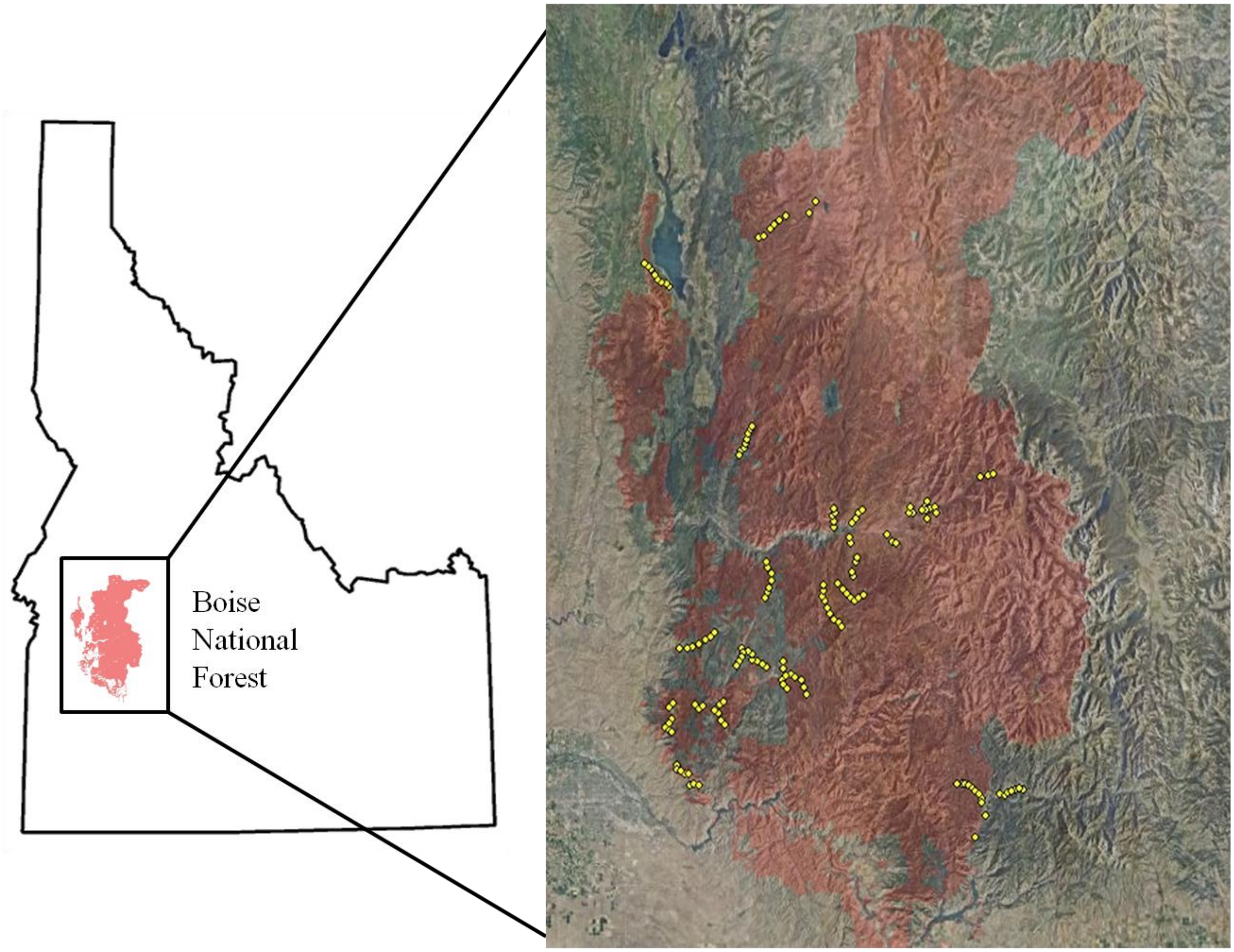

Figure 2.1. Vicinity map showing the location of the Boise National Forest in southwestern Idaho and point-count locations (N = 150) for cavity-nesting owls. Point-count locations were spaced ≥ 800 m apart and were concentrated in portions of Boise National Forest that were accessible by road during winter months.

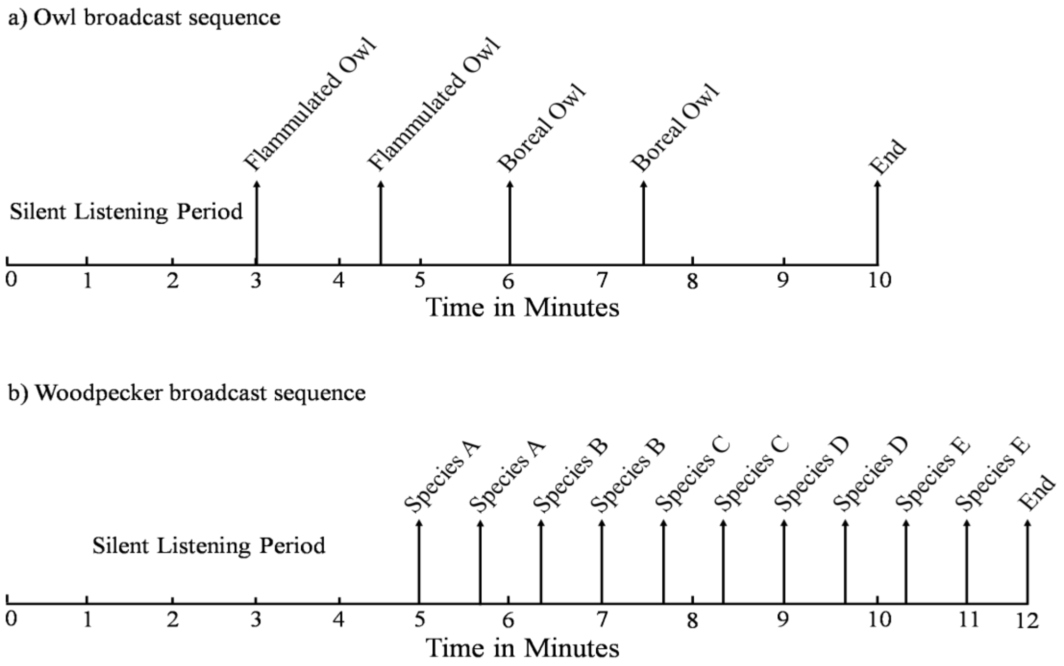

Figure 2.2. Broadcast sequence for (a) cavity-nesting owls and (b) woodpeckers surveyed in the Boise National Forest, Idaho, 2009-2010. Point-counts for owls began with 3 min. of silent listening followed by 30 sec. of Flammulated Owl broadcasts and another 1 min. of listening. This broadcast-listening sequence was repeated once before replicating the process using Boreal Owl vocalizations. Woodpeckers were surveyed in a similar manner beginning with 5 min. silent listening followed by vocalizations of Hairy Woodpeckers, Lewis's Woodpeckers, Northern Flickers, Pileated Woodpeckers, and Red-naped Sapsuckers. Woodpecker broadcasts were played for 15 sec. followed by a 30 sec. listening period, and this was repeated once for each species. The order in which woodpecker broadcasts were played was randomized prior to each survey.

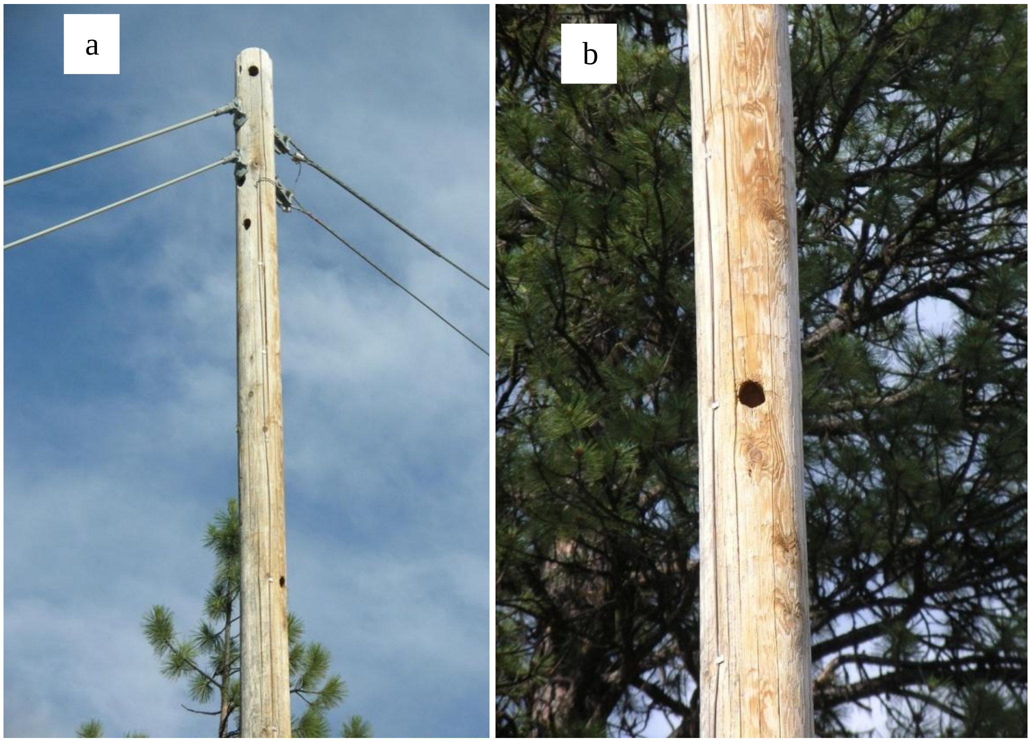

Figure 2.3. Two utility poles containing cavities excavated by woodpeckers. (a) A pole located near Idaho City, Boise County, Idaho occupied by a Northern Flicker (top most cavity). (b) A pole near Featherville, Boise County, Idaho occupied by a Hairy Woodpecker.

APPENDIX A

Appendix A. Results of AIC$_c$-based model selection examining habitat associations of Flammulated Owls.

Model	*K*[a]	ΔAIC$_c$[b]	*w*[c]
ψ(aspect, diversity, Douglas-fir), *p*(noise)	6	0.00	0.367
ψ(diversity, Douglas-fir), *p*(noise)	5	0.62	0.269
ψ(canopy, diversity, Douglas-fir), *p*(noise)	6	2.84	0.088
ψ(diversity, Douglas-fir, non-forest), *p*(noise)	6	3.23	0.073
ψ(diversity, Douglas-fir, ponderosa), *p*(noise)	6	3.96	0.050
ψ(aspect, canopy, diversity), *p*(noise)	6	5.05	0.029
ψ(canopy, diversity), *p*(noise)	5	5.50	0.023
ψ(aspect, diversity), *p*(noise)	5	5.70	0.021
ψ(aspect, Douglas-fir, ponderosa), *p*(noise)	6	6.84	0.012
ψ(aspect, diversity, ponderosa), *p*(noise)	6	8.11	0.006
ψ(Douglas-fir, ponderosa), *p*(noise)	5	8.22	0.006
ψ(aspect, diversity, non-forest), *p*(noise)	6	8.28	0.006
ψ(canopy, diversity, ponderosa), *p*(noise)	6	8.63	0.005
ψ(aspect,), *p*(noise)	5	8.81	0.005
ψ(canopy, diversity, non-forest), *p*(noise)	6	8.83	0.004
ψ(diversity), *p*(noise)	4	8.92	0.004
ψ(aspect), *p*(noise)	4	9.10	0.004
ψ(diversity, non-forest), *p*(noise)	5	9.92	0.003
ψ(canopy, Douglas-fir, ponderosa), *p*(noise)	6	10.08	0.002
ψ(Douglas-fir, non-forest, ponderosa), *p*(noise)	6	10.20	0.002
ψ(aspect, ponderosa), *p*(noise)	5	10.36	0.002
ψ(aspect, non-forest), *p*(noise)	5	10.73	0.002
ψ(aspect, canopy, ponderosa), p(noise)	6	10.77	0.002
ψ(aspect, canopy), *p*(noise)	5	10.85	0.002
ψ(diversity, ponderosa), *p*(noise)	5	11.04	0.002
ψ(aspect, Douglas-fir, non-forest), *p*(noise)	6	11.53	0.001
ψ(canopy, ponderosa), *p*(noise)	5	11.58	0.001
ψ(Douglas-fir), *p*(noise)	4	11.73	0.001
ψ(aspect, canopy, Douglas-fir), *p*(noise)	6	12.00	0.000
ψ(diversity, non-forest, ponderosa), *p*(noise)	6	12.30	0.000
ψ(Douglas-fir, non-forest), *p*(noise)	5	12.47	0.000
ψ(non-forest), *p*(noise)	4	12.56	0.000
ψ(aspect, non-forest, ponderosa), *p*(noise)	6	12.71	0.000
ψ(.), p(noise)	3	13.17	0.000
ψ(canopy), *p*(noise)	4	13.27	0.000
ψ(aspect, canopy, non-forest), *p*(noise)	6	13.68	0.000
ψ(ponderosa), *p*(noise)	4	13.96	0.000
ψ(canopy, Douglas-fir), *p*(noise)	5	14.03	0.000
ψ(non-forest, ponderosa), *p*(noise)	5	14.29	0.000
ψ(canopy, non-forest, ponderosa), *p*(noise)	6	14.85	0.000
ψ(canopy, non-forest), *p*(noise)	5	14.90	0.000
ψ(canopy, Douglas-fir, non-forest), *p*(noise)	6	15.81	0.000

[a] The number of estimated parameters.

[b] The relative difference in AIC values.

[c] AIC model weight.

APPENDIX B

Appendix B. Results of AIC$_c$-based model selection examining habitat associations of Northern Saw-whet Owls.

Model	K^{a}	$\Delta\mathrm{AIC}_c^{\,b}$	w^{c}
ψ(aspect, Douglas-fir, non-forest, ponderosa, TRI*), *p*(Noise)	8	0.00	0.142
ψ(aspect, Douglas-fir, non-forest, ponderosa), *p*(noise)	7	0.11	0.134
ψ(aspect, Douglas-fir, non-forest, TRI), *p*(noise)	7	0.92	0.090
ψ(aspect, non-forest, ponderosa), *p*(noise)	6	1.27	0.075
ψ(aspect, non-forest, TRI), *p*(noise)	6	1.53	0.066
ψ(aspect, non-forest, ponderosa, TRI), *p*(noise)	7	1.72	0.060
ψ(Douglas-fir, non-forest, ponderosa, TRI), *p*(noise)	7	1.94	0.054
ψ(aspect, canopy, Douglas-fir, non-forest, ponderosa), *p*(noise)	8	2.54	0.040
ψ(aspect, canopy, Douglas-fir, non-forest, TRI), *p*(noise)	8	2.59	0.039
ψ(aspect, non-forest), *p*(noise)	5	3.01	0.032
ψ(Douglas-fir, non-forest, ponderosa), *p*(noise)	6	3.04	0.031
ψ(aspect, Douglas-fir, non-forest), *p*(noise)	6	3.57	0.024
ψ(Douglas-fir, non-forest, TRI), *p*(noise)	6	3.63	0.023
ψ(aspect, canopy, non-forest, TRI), *p*(noise)	7	3.63	0.023
ψ(aspect, canopy, Douglas-fir, non-forest), *p*(noise)	7	3.70	0.022
ψ(aspect, canopy, non-forest, ponderosa), *p*(noise)	7	3.77	0.022
ψ(aspect, canopy, non-forest), *p*(noise)	6	3.86	0.021
ψ(non-forest, ponderosa, TRI), *p*(noise)	6	4.24	0.017
ψ(non-forest, ponderosa), *p*(noise)	5	4.31	0.016
ψ(non-forest, TRI), *p*(noise)	5	4.46	0.015
ψ(aspect, canopy, non-forest, ponderosa, TRI), *p*(noise)	8	4.60	0.014
ψ(canopy, Douglas-fir, non-forest, ponderosa, TRI), *p*(noise)	8	4.74	0.013
ψ(canopy, Douglas-fir, non-forest, TRI), *p*(noise)	7	5.20	0.011
ψ(canopy, Douglas-fir, non-forest, ponderosa), *p*(noise)	7	5.25	0.010
ψ(canopy, non-forest, ponderosa), *p*(noise)	6	6.56	0.005
ψ(non-forest), *p*(noise)	4	6.56	0.005
ψ(canopy, non-forest, ponderosa, TRI), *p*(noise)	7	6.97	0.004
ψ(canopy, non-forest), *p*(noise)	5	7.00	0.004
ψ(canopy, Douglas-fir, non-forest), *p*(noise)	6	7.03	0.004
ψ(Douglas-fir, non-forest), *p*(noise)	5	7.23	0.004
ψ(TRI), *p*(noise)	4	8.92	0.002
ψ(canopy), *p*(noise)	4	9.45	0.001
ψ(aspect, TRI), *p*(noise)	5	9.53	0.001
ψ(ponderosa), *p*(noise)	4	9.64	0.001
ψ(canopy, TRI), *p*(noise)	5	9.69	0.001
ψ(aspect, canopy, Douglas-fir), *p*(noise)	6	10.02	0.001
ψ(Douglas-fir, TRI), *p*(noise)	5	10.04	0.001
ψ(.), *p*(noise)	3	10.06	0.001
ψ(ponderosa, TRI), *p*(noise)	5	10.09	0.001
ψ(aspect, canopy), *p*(noise)	5	10.25	0.001
ψ(aspect), *p*(noise)	4	10.33	0.001
ψ(aspect, canopy, TRI), *p*(noise)	6	10.33	0.001
ψ(canopy, Douglas-fir, TRI), *p*(noise)	6	10.40	0.001
ψ(aspect, ponderosa), *p*(noise)	5	10.44	0.001
ψ(canopy, Douglas-fir), *p*(noise)	5	10.45	0.001
ψ(DOFI, ponderosa), *p*(noise)	5	10.50	0.001

ψ(canopy, ponderosa), *p*(noise)	5	10.56	0.001
ψ(aspect, canopy, Douglas-fir, TRI), *p*(noise)	7	10.68	0.001
ψ(Douglas-fir, ponderosa, TRI), *p*(noise)	6	10.79	0.001
ψ(aspect, Douglas-fir, TRI), *p*(noise)	6	10.90	0.001
ψ(aspect, ponderosa, TRI), *p*(noise)	6	11.08	0.001
ψ(canopy, Douglas-fir, ponderosa), *p*(noise)	6	11.14	0.001
ψ(aspect, canopy, ponderosa), *p*(noise)	6	11.36	0.001
ψ(aspect, Douglas-fir, ponderosa), *p*(noise)	6	11.60	0.000
ψ(canopy, ponderosa, TRI), *p*(noise)	6	11.61	0.000
ψ(Douglas-fir), *p*(noise)	4	11.61	0.000
ψ(aspect, Douglas-fir), *p*(noise)	5	12.10	0.000
ψ(canopy, Douglas-fir, ponderosa, TRI), *p*(noise)	7	12.10	0.000
ψ(aspect, Douglas-fir, ponderosa, TRI), *p*(noise)	7	12.11	0.000
ψ(aspect, canopy, Douglas-fir, ponderosa), *p*(noise)	7	12.25	0.000
ψ(aspect, canopy, ponderosa, TRI), *p*(noise)	7	12.60	0.000
ψ(aspect, canopy, Douglas-fir, ponderosa, TRI), *p*(noise)	8	13.11	0.000

[a] The number of estimated parameters.

[b] The relative difference in AIC values.

[c] AIC model weight.

APPENDIX C

Appendix C. Owl and woodpecker occurrence by species and point-count location (N=150) in the Boise National Forest, Idaho, over 2009 and 2010. Occupied sites are denoted by a 1 while sites where no birds were detected are denoted by 0. In total, I detected targeted owls and woodpeckers at 64 and 79 point-count locations, respectively.

Point-Count Location	UTM Northing	UTM Easting	Survey Year	Flammulated Owls	Northern Saw-whet Owls	Great Horned Owls	*Other	Hairy Woodpeckers	Northern Flickers	Pileated Woodpeckers	Red-naped Sapsuckers	**Other
Banner Ridge 1	618613	4880761	2010	0	0	0	0	0	1	0	0	0
Banner Ridge 2	619594	4879395	2010	0	1	0	0	0	1	0	1	0
Banner Ridge 3	620480	4879312	2010	0	0	0	0	0	0	0	0	0
Bear Creek 1	611050	4883213	2009	0	1	0	0	0	0	0	0	0
Bear Creek 2	611769	4884094	2009	0	1	1	0	0	0	0	0	0
Bear Creek 3	612428	4885026	2009	0	0	0	0	0	0	0	0	0
Bear Creek 4	613117	4885723	2009	0	0	0	0	0	1	0	0	0
Bear Run 1	596141	4856164	2009	1	1	1	0	1	1	0	1	0
Bear Run 2	595949	4854687	2009	1	1	0	0	1	1	0	0	0
Beaver Creek 1	611756	4875486	2009	1	0	0	1	1	0	0	0	0
Beaver Creek 2	612181	4876448	2009	0	0	0	0	0	0	0	0	0
Bogus 1	570532	4843297	2010	1	0	0	0	0	1	0	0	0
Bogus 2	571357	4844069	2010	0	0	0	0	0	1	0	0	0
Bogus 3	571983	4845053	2010	0	1	0	0	0	0	0	1	0
Bogus 4	571327	4847291	2010	1	1	1	0	1	1	0	0	0
Bogus 5	572150	4848088	2010	0	0	0	0	1	1	1	0	0
Bogus Spur 1	571241	4842805	2010	1	0	0	0	1	1	0	0	0

Bogus Spur 2	571994	4842430	2010	1	1	0	0	0	0	1	1	0
Boise Ridge 1	575505	4834282	2010	0	1	0	0	1	0	1	1	0
Boise Ridge 2	574665	4834373	2010	1	0	0	0	1	0	0	0	0
Boise Ridge 3	573975	4834761	2010	0	1	0	0	0	0	0	0	0
Boise Ridge 4	573164	4835216	2010	1	1	0	0	1	0	0	1	0
Boise Ridge 5	572969	4836048	2010	0	1	0	0	1	1	0	1	0
Cascade 1	571465	4929194	2010	0	0	0	0	0	1	0	1	0
Cascade 2	570710	4929662	2010	0	1	0	0	0	1	1	0	0
Cascade 3	569794	4930062	2010	0	0	0	0	0	0	0	0	0
Cascade 4	568948	4930704	2010	0	0	0	0	0	0	1	0	0
Cascade 5	568200	4931360	2010	0	1	0	0	0	2	0	1	0
Cascade 6	567387	4932486	2010	0	0	0	0	1	0	0	0	0
Cascade 7	566834	4933179	2010	0	0	0	0	0	0	0	0	0
Cascade 8	566143	4933710	2010	0	0	0	0	0	1	0	0	0
Centerville 1	592396	4854991	2009	1	0	1	0	1	1	0	0	0
Centerville 2	591661	4855685	2009	1	0	0	1	0	0	0	0	0
Centerville 3	590471	4856166	2009	1	0	0	0	0	0	0	0	0
Centerville 4	589199	4856547	2009	1	0	0	0	1	0	0	1	0
Centerville 5	589283	4857569	2010	1	1	0	0	1	1	0	0	0
Centerville 6	588617	4858198	2010	0	0	0	0	0	1	0	0	0

Crooked Creek 1	610596	4868634	2009	0	0	0	0	0	0	0	0	0
Crooked Creek 2	611400	4867932	2009	0	0	0	0	1	0	0	0	0
Crooked Creek 3	612432	4868497	2009	0	0	0	0	0	0	0	1	0
Crooked Creek 4	613512	4869112	2009	0	1	0	0	0	0	0	0	0
Deadwood 1	607140	4882267	2009	0	0	0	1	0	0	0	0	0
Deadwood 2	606885	4883427	2009	0	0	0	0	0	0	0	0	0
Deadwood 3	606744	4884399	2009	0	0	0	0	1	0	0	0	0
Deadwood 4	607378	4885098	2009	0	0	0	0	0	0	0	0	0
Deadwood 5	606960	4886016	2009	1	0	0	0	0	1	0	0	0
Eight Mile1	626931	4886382	2009	0	0	0	0	1	0	0	0	0
Eight Mile 2	627249	4887392	2009	0	0	0	0	0	0	1	0	0
Feather Road 1	639880	4826147	2010	0	1	1	0	0	0	0	0	1
Feather Road 2	637561	4821872	2010	0	1	0	0	0	0	0	1	0
Featherville 1	642879	4830278	2010	0	0	0	0	0	0	0	0	0
Featherville 2	644046	4830055	2010	0	1	1	0	0	0	0	0	0
Featherville 3	644601	4830644	2010	0	0	1	0	0	0	0	1	0
Featherville 4	645437	4830818	2010	0	0	0	0	0	0	0	0	0
Featherville 5	646331	4831100	2010	0	0	0	0	0	1	0	0	0
Featherville 6	647150	4831411	2010	0	0	0	0	0	0	0	0	0
Featherville 7	647995	4831170	2010	0	0	0	0	0	0	0	0	0

Five Mile 1	623328	4885100	2009	0	1	0	0	0	0	0	0	0
Five Mile 2	623471	4886290	2009	0	0	0	0	0	0	0	0	0
Gold Mile 1	611371	4872598	2009	0	0	0	0	0	0	0	0	0
Gold Mile 2	610979	4873637	2009	0	0	0	0	0	0	0	0	0
Grandjean 1	638717	4891986	2009	0	1	1	0	1	0	0	0	0
Grandjean 2	640313	4892492	2009	0	0	0	0	0	0	0	0	0
Grandjean 3	641551	4892659	2009	0	1	0	0	0	0	0	1	0
Grimes Creek 1	583489	4843756	2009	0	0	1	0	0	0	0	0	0
Grimes Creek 2	582648	4844680	2009	1	0	0	0	0	1	0	0	0
Grimes Creek 3	582141	4846025	2009	0	0	0	0	0	1	0	0	0
Grimes Creek 4	582241	4847830	2009	0	0	1	0	0	0	0	0	0
Grimes Creek 5	583170	4848376	2009	0	0	0	0	0	0	0	0	0
Grimes Creek 6	587186	4858703	2010	1	1	1	0	0	1	0	0	0
Grimes Creek 7	587283	4857763	2010	0	0	0	0	1	1	0	1	0
Grimes Creek 8	587073	4856963	2010	0	0	0	0	0	1	0	0	0
Grimes Creek 9	586538	4856098	2010	0	1	0	0	1	0	0	0	0
Grimes Creek 10	586086	4855414	2010	0	0	0	0	1	0	0	0	0
Grimes Pass 1	592045	4868454	2009	0	1	0	0	0	0	0	0	0
Grimes Pass 2	592649	4869647	2009	0	1	0	0	0	1	0	0	0
Grimes Pass 3	592985	4870533	2009	0	0	0	0	0	0	0	0	0

Grimes Pass 4	593414	4871768	2009	1	0	0	0	0	0	0	0	0
Grimes Pass 5	593430	4873260	2009	0	0	0	0	0	0	0	1	0
Grimes Pass 6	592750	4874315	2009	0	0	0	0	0	0	0	1	0
Grimes Pass 7	592509	4875620	2009	0	0	0	0	0	0	0	1	0
Harris Creek 1	581177	4861754	2009	0	0	0	0	0	0	0	0	0
Harris Creek 2	580319	4860816	2009	0	1	0	0	0	1	0	1	0
Harris Creek 3	579162	4860485	2009	0	0	1	0	0	0	0	0	0
Harris Creek 4	577709	4859587	2009	0	0	1	0	0	0	0	0	0
Harris Creek 5	576401	4859101	2009	0	0	0	0	0	0	0	0	0
Harris Creek 6	575213	4858788	2009	0	0	0	0	0	0	0	0	0
Harris Creek 7	573616	4858670	2009	0	0	0	0	0	0	0	0	0
Kettle Creek	624270	4885097	2009	0	0	0	0	0	0	1	0	0
Forest Service 1	609878	4869492	2009	0	0	1	0	0	0	0	0	0
Forest Service 2	609127	4870275	2009	0	1	0	0	0	0	0	0	0
Forest Service 3	607794	4871329	2009	0	0	0	0	0	0	0	0	0
Forest Service 4	581292	4846694	2009	0	0	0	0	0	0	0	0	0
Forest Service 5	578758	4847412	2009	1	0	0	0	0	0	0	0	0
Forest Service 6	577781	4846811	2009	0	0	0	0	1	0	0	0	0
Forest Service 7	577074	4847765	2009	0	0	0	0	0	0	0	0	0
North Fork 1	586402	4896399	2010	0	1	0	0	0	1	0	0	0

North Fork 2	586773	4897116	2010	0	1	0	0	0	0	0	0	0
North Fork 3	587550	4897756	2010	0	0	0	0	0	0	1	0	0
North Fork 4	587804	4898643	2010	0	1	0	0	0	0	0	0	0
North Fork 5	588074	4899492	2010	0	1	0	0	0	0	0	0	0
North Fork 6	588576	4900410	2010	0	1	0	0	0	1	0	0	0
North Fork 7	589085	4901282	2010	0	0	0	0	0	0	0	0	0
North Fork 8	589448	4902054	2010	0	1	0	0	1	1	0	0	0
Pine Creek 1	595816	4852621	2010	0	0	1	0	0	1	0	1	0
Pine Creek 2	596087	4851681	2010	0	0	0	0	1	1	0	1	0
Pine Creek 3	596827	4850937	2010	0	1	0	0	1	1	0	0	0
Rabbit Creek 1	597626	4853589	2009	0	0	0	0	0	0	0	0	0
Rabbit Creek 2	598668	4853196	2009	0	0	0	0	0	1	0	0	0
Rabbit Creek 3	600010	4852403	2009	0	0	0	0	0	0	0	0	0
Rabbit Creek 4	600456	4851124	2009	0	0	0	0	0	0	0	0	0
Rabbit Creek 5	601083	4849753	2009	1	0	0	0	0	0	0	0	0
Rabbit Creek 6	596506	4853263	2009	0	1	0	0	0	1	0	1	0
Rock Creek 1	610549	4879191	2009	1	0	0	0	0	1	0	0	0
Rock Creek 2	610346	4880327	2009	1	0	0	0	0	0	0	0	0
Rocky Canyon 1	575881	4832078	2010	0	1	0	0	0	0	1	0	0
Rocky Canyon 2	576733	4832366	2010	1	1	0	0	0	0	1	0	0

Rocky Canyon 3	577700	4832008	2010	1	0	0	0	0	0	0	0	0
Summit 1	606078	4865478	2009	0	0	0	0	0	0	0	0	0
Summit 2	605617	4866513	2009	0	0	0	0	0	0	0	0	0
Summit 3	604939	4867979	2009	0	0	0	0	0	0	0	0	0
Summit 4	604583	4868732	2009	0	0	0	0	0	0	0	0	0
Summit 5	604727	4869882	2009	0	0	0	0	0	0	0	0	0
Summit 6	604817	4871110	2009	0	0	0	0	0	0	1	0	0
Sunset 1	607115	4864314	2009	1	0	0	0	0	0	0	1	1
Sunset 2	608044	4863628	2009	1	1	0	0	0	1	0	1	1
Sunset 3	608613	4862786	2009	1	0	1	0	1	0	0	0	0
Ten Mile 1	627909	4885936	2010	0	1	0	0	1	0	0	0	0
Ten Mile 2	629001	4886174	2010	0	1	0	0	0	0	0	0	0
Ten Mile 3	629168	4885130	2010	0	0	0	0	1	0	0	0	0
Ten Mile 4	627084	4885551	2010	0	0	1	0	0	0	0	0	0
Ten Mile 5	627131	4883959	2010	0	0	0	0	0	1	0	0	0
Ten Mile 6	626161	4885590	2010	0	1	0	0	0	1	0	0	0
Trinity 1	639085	4829616	2010	0	1	0	0	0	0	0	0	0
Trinity 2	638402	4830244	2010	0	0	0	0	0	0	0	0	0
Trinity 3	637635	4830842	2010	0	0	0	0	0	0	0	0	0
Trinity 4	637014	4831428	2010	0	0	1	0	0	0	0	0	0

Trinity 5	636350	4832015	2010	0	0	0	0	0	0	0	0	0
Trinity 6	635505	4832318	2010	0	0	0	0	0	0	0	0	0
Trinity 7	634699	4832173	2010	0	1	0	0	0	0	0	0	0
Trinity 8	633566	4832309	2010	0	0	1	0	0	0	0	0	0
Wagon Trail	639156	4828649	2010	1	0	0	0	0	0	1	1	0
Warm Lake 1	590750	4938620	2009	0	0	0	0	0	0	0	1	0
Warm Lake 2	591846	4939111	2009	0	1	0	0	0	0	1	0	0
Warm Lake 3	593160	4940424	2009	0	0	0	1	0	0	0	1	0
Warm Lake 4	594120	4941250	2009	0	0	0	0	0	0	0	0	0
Warm Lake 5	595109	4942028	2009	0	0	0	0	0	0	0	0	0
Warm Lake 6	596727	4942934	2009	0	0	0	0	0	1	1	0	0
Warm Lake 7	603042	4945839	2009	0	0	0	0	1	1	0	0	0
Warm Lake 8	604279	4946699	2009	0	0	1	0	0	1	0	0	0

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* Other owls detected included Barred Owls at Beaver Creek 1, Centerville 2, and Warm Lake 1, a Long-eared Owl at Rabbit Creek 2, a Northern Pygmy-Owl at Centerville 1, and a Western Screech-Owl at Centerville 2 and Deadwood River 1.

**Other woodpeckers detected included a Downy Woodpecker and White-headed Woodpecker at Featherville Road 1 and Williamson's Sapsuckers Sunset Peak 1 and 2.