

**HAIRY WOODPECKER WINTER ECOLOGY
FOLLOWING WILDFIRE: EFFECTS OF BURN
SEVERITY AND AGE**

By: Kristin A. Covert

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Approved:

Dr. William M. Block,
Ph.D., Co-chair

Dr. Tad Theimer, Ph.D., Co-chair

Dr. Russell Balda, Ph.D.

Dr. Steve Hempleman, Ph.D.

ABSTRACT

HAIRY WOODPECKER WINTER ECOLOGY FOLLOWING WILDFIRE: EFFECTS OF BURN SEVERITY AND AGE

Kristin A. Covert

Fire has been identified as one of the most important terrestrial disturbances that affect avian populations and the ecosystems in which they reside (Raphael et al. 1987, Hejl 1994, Hutto 1995, Brawn et al. 2001). Because fires change resources at multiple scales across space and time (Turner and Romme 1994), this disturbance mechanism has the potential to affect the hierarchical decision process a bird makes when selecting habitat. Woodpeckers may be especially affected by fire because they are intimately tied to vegetative and prey resources that are altered by fire including burn severity, vegetation structure, the distribution of dead and dying trees, bark-dwelling arthropods, and other factors. Hairy woodpeckers (*Picoides villosus*) were observed in ponderosa pine forests that had experienced wildfire in Northern Arizona during the winters of 2000-2003. Relative abundance, diurnal home range size, conspecific foraging rates, foraging habitat selection, and insect abundance were measured within high and moderate burn severities at four post-burn ages and in unburned controls. Hairy woodpecker relative abundance was greatest within high-severity burns relative to moderate-severity burns and unburned areas and decreased as burns aged. Diurnal home range size increased with post-burn age and selection of habitat variables varied by burn severity and burn age. Hairy woodpeckers selected trees and patches with greater tree-bole scorch within their home ranges than available. Conspecific foraging rates decreased with post-burn age and intersexual foraging behavior did not differ in the youngest post-burn age but did differ in older burns. Insect density decreased with post-burn age. All behavioral patterns suggested that prey resources and vegetative structure resulting from wildfire and subsequent changes as burns age, ultimately drives the selection of habitat by hairy woodpeckers at multiple scales. Understanding how wildfire affects this species is important for managing fire within ponderosa pine ecosystems of the southwest.

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TABLE OF CONTENTS

LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
PREFACE: THESIS ORGANIZATION.....	1
CHAPTER 1. INTRODUCTION	
Literature Review.....	3
<i>The Ecological Role Of Woodpeckers</i>	3
<i>Woodpeckers and Fire</i>	5
<i>Woodpeckers in Winter</i>	9
<i>Woodpecker Home Range and Estimation Methods Review</i>	11
<i>Hairy Woodpecker Foraging Ecology and Foraging Methods</i> <i>Review</i>	15
Conceptual Model.....	20
CHAPTER 2. MANUSCRIPT: Hairy woodpecker winter ecology following wildfire: effects of burn severity and age	
INTRODUCTION.....	23
METHODS.....	26
RESULTS.....	38
DISCUSSION.....	43
LITERATURE CITED.....	52
TABLES.....	71
FIGURES.....	77
APPENDIX.....	87

LIST OF TABLES

1. Methods used in 14 previous studies estimating woodpecker home range size.....	70
2. Methods used in 22 previous studies evaluating woodpecker foraging ecology.....	72
3. Summary of fires in which hairy woodpeckers were observed.....	75

LIST OF FIGURES

1. Conceptual model depicting intersexual foraging behavior resulting from changing resource availability and incurred competition. Male and female use of a niche dimension, for example tree size, overlaps completely when resources are super-abundant and competition is low, however, as resources decrease, competition increases, and the sexes segregate to partition resources to reduce competition.....76

2. Hairy woodpecker winter relative abundance ($\bar{X} + SD$) in two unburned areas (sites 1 and 2) and one site that burned in the Pumpkin fire (site 3), during the summer of 2000, Coconino National Forest, northern AZ, between 1997 and 2002.....77

3. Hairy woodpeckers relative abundance ($\bar{X} + SD$) in high and moderate burn severities in the Pumpkin (2 and 3 years post-burn) and Horseshoe/Hochderffer fire (6 and 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003. Unburned forests adjacent to the burned areas are shown for comparison..... 78

4. Hairy woodpecker home range size in two burned ponderosa pine forests following the Pumpkin Fire (2, 3 years post-burn) and the Horseshoe/Hochderffer Fire (6, 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003. Females are denoted as triangles and males as circles.....79

5. Change in percent observations where hairy woodpeckers were encountered foraging with a conspecific in two burn severities in the Rodeo/Chediski (1 year post-burn), Pumpkin (2 and 3 years post-burn), and Horseshoe/Hochderffer fires (6 and 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003.....80

6. Percentage observations where hairy woodpeckers were encountered foraging with a conspecific (observed) in comparison to expected encounter proportion, determined by Poisson probability modeling of relative abundance in two burn severities in the Pumpkin (2 and 3 years post-burn), and Horseshoe/Hochderffer fires (6 and 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003. Proportions for unburned provided for comparison.....	81
7. Selection of habitat components by hairy woodpeckers in two burn severities in the Pumpkin (2 and 3 years post-burn) and Horseshoe/Hochderffer fires (6 and 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003. Habitat components: (a) tree size (DBH in cm); (b) patch tree density; (c) patch average tree size (DBH cm); (d) tree bole scorch; and (e) patch bole scorch. Component $\bar{X} + SD$ selected by birds represented by solid lines and available component $\bar{X} + SD$ represented by dashed lines. Selection and available habitat components in unburned is shown for comparison, for first three habitat components.....	82
8. Intersexual selection of habitat components by hairy woodpeckers in the Pumpkin (2 and 3 years post-burn) and Horseshoe/Hochderffer fires (6 and 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003. Habitat components: (a) tree size; (b) foraging height; and (c) substrate selection of branch versus trunk (proportion of trunk use shown). Selection of habitat components in unburned areas shown for comparison.....	83
9. Mean insect density per 102cm ² bark samples taken from random ponderosa pine trees within two burn severities in the Rodeo/Chediski (1 year post-burn), Pumpkin (2, 3 years post-burn), and Horseshoe/Hochderffer fires (6, 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003.....	84

10. Change in a) density of snags within high severity and trees in moderate severity, and change in b) four size classes (DBH < 15cm, 15-30 cm, 30-45 cm, >45 cm) of snags within high severity and trees in moderate severity, in the Pumpkin (2 and 3 years post-burn) and Horseshoe/Hochderffer fires (6 and 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003.....85

PREFACE: THESIS ORGANIZATION

The organization of this thesis will not follow the traditional arrangement. Instead, I include an introduction, conceptual model, and extended manuscript. The purpose of these sections is to provide the reader with the foundations of the project while having the bulk of the thesis in publishable format.

The introduction presents the scientific foundation of the project. The introduction is divided into five sections with the following justifications for their review: (1) *The Ecological Role of Woodpeckers*, to identify the unique and important role woodpeckers play within the ecosystems in which they reside; (2) *Woodpeckers and Fire*, to explore how natural and human caused perturbations affect how woodpecker's select habitat variables at different scales; (3) *Woodpeckers in Winter*, to evaluate the critical time period affecting woodpeckers and justify the study period; (4) *Woodpecker Home Range and Estimation Methods Review*, to explore current knowledge of woodpecker home range size, its relationship to season and prey abundance, and to provide an evaluation of current methodology used to measure and estimate home range size; and (5) *Hairy Woodpecker Foraging Ecology and Foraging Methods Review*, to review current knowledge of hairy woodpecker foraging ecology, how hairy woodpecker foraging ecology is affected by fire, and to provide an evaluation of current methodology used to assess and evaluate woodpecker foraging behavior.

The second section is a presentation of a conceptual model that provides the basis for the development of this study's hypotheses and questions. Whereas I present this model at the beginning of the thesis, it was conceptualized after the collection of my first season's data. It is based on behavioral trends and patterns exhibited by hairy woodpeckers in winter following wildfire and differences detected in prey densities measured in this ponderosa pine system. The model expresses the relationship between resources and competition that drive changes in the foraging behavior of males and females.

The third chapter of the thesis is an extended manuscript. This will be an inclusive document with all traditional sections except for the abstract, which was presented at the beginning of this thesis, and the literature cited, which will include all citations for the entire

thesis and will follow the extended manuscript. It is my intention to get this document as close to publication format as possible.

CHAPTER 1: INTRODUCTION

Literature Review

The Ecological Role Of Woodpeckers

Woodpeckers perform multiple roles in forested and woodland ecosystems (Crockett and Hansley 1978, Torgersen et. al 1990, Conner et al. 1994, Mikusiński et al. 2001). They are the most common primary cavity-nesters, creating and maintaining cavities for a host of secondary cavity-nesting species (Shackelford and Conner 1997, Weikel and Hayes 1999). Secondary cavity-nesting species are often dependent on woodpecker excavations to serve as both nests (Shackelford and Conner 1997, Weikel and Hayes 1999) and as important roost sites for protection from predation and weather throughout the year (Dolby and Grubb 1999). Bull and Meslow (1977) found that 22 species of birds and 24 species of mammals utilize woodpecker-excavated cavities in the northeastern United States.

The hairy woodpecker (*Picoides villosus*) is one of the most abundant and conspicuous primary cavity-nesters in North America (Short 1982). In ponderosa pine forests of northern Arizona, it is also significantly more abundant than other primary cavity nesters such as the northern flicker (*Colaptes auratus*), downy woodpecker (*P. pubescens*), and three-toed woodpecker (*P. tridactylus*) (Block, unpublished point count data). As a result, this species probably makes most cavities used by secondary cavity-nesting species in our local ponderosa pine forest. Avian species that utilize cavities created by woodpeckers include violet-green swallow (*Tachycineta thalassina*), mountain chickadee (*Poecile gambeli*), white-breasted nuthatch (*Sitta carolinensis*) pygmy nuthatch (*Sitta pygmaea*), house wren (*Troglodytes aedon*), and the western bluebird (*Siala mexicana*). Mammals, such as the gray-collared chipmunk (*Tamias cinereicollis*), also use cavities created by these birds (personal observation). When considering the number of species for which the hairy woodpecker has positive and in some cases essential impacts (17% of the avian species present locally in the summer and 42% in the winter), management of forests to benefit hairy woodpeckers may likely have positive effects on many other species as well.

Woodpeckers are also important predators of bark-dwelling and wood-boring insects (Blackford 1955, Koplin 1969, Solomon 1969, Hay 1972, Kroll and Fleet 1979, Hanula and Franzreb 1998). These insects were estimated to cause up to \$120 million in annual loss of timber sales in the eastern United States (Donley and Worley 1976) with further damage resulting from large stands of bark beetle-killed trees that fuel high-intensity wildfires (Hadley and Veblen 1993, Lowell 1996). Woodpeckers were and are hypothesized to control bark beetle and woodborer arthropods at endemic levels, which likely prevent outbreaks or loss of timber (Hay 1972, Otvos 1965, Holmes 1990). Crockett and Hansley (1978) found a consistent negative impact of woodpeckers on bark beetles and woodborers, with predation rates reducing bark-dwelling arthropod populations as much as 98%. Woodpeckers in their study also heavily preyed upon secondary beetle and woodborer infestations. Massey and Wygant (1973) found up to 75% predation of spruce beetles by woodpeckers in Colorado. Several studies indicate that the greatest predation rates on woodboring insects occur during the winter (Solomon 1969, Hay 1972, Kroll and Fleet 1979, Nuorteva et al. 1981). In climates with freezing temperatures, insects are dormant or practically immobile and can therefore not avoid predation or replenish themselves (Conner, R.N. pers. com, Askins 1981). Woodpeckers easily capture larvae because they are accessible under the bark or just beneath the surface of the cambium (Short 1982). Because free-flying insects, fruits, nuts, and other food resources important to woodpeckers are not available in the winter, bark-dwelling arthropods become the major food items for woodpeckers at this time (Baldwin 1960, Askins 1981). Several authors have indicated that the hairy woodpecker is one of the major avian predators of these arthropods (Solomon 1975, Conner et al. 1994) and Otvos and Stark (1985) showed that 65-85% of the hairy woodpeckers diet consisted of bark- and wood-boring beetles in the summer.

Finally, woodpeckers in Europe are good indicators of forest bird diversity at three geographic scales (regional, landscape, and habitat) because they are often forest obligates and foraging specialists (Mikusiński et al. 2001). Virkkala et al. (1993) found that populations of white-backed woodpeckers declined because of a decrease in mature forests, suggesting these woodpeckers are sensitive to management practices. Species that were once considered common are also being found to be sensitive to management practices. Black woodpeckers that were

relatively common less than 50 year ago have experienced a long-term decline as forests decrease (Rolstad et al. 1998). Similarly, in the United States, the hairy woodpecker, a relatively ubiquitous species, has also experienced a steady decline as forests are converted to other land types. In 1975 and 1982, the hairy woodpecker was blue listed and subsequently listed as a species of special concern in 1986 (Tate 1986). More recently, CBC data indicated a decline of hairy woodpeckers in Arizona (CBC data 1987-1990, Sauer et al. 1996) and several studies suggest that this species was declining further in this and other Rocky Mountain areas because of fire suppression and logging management policies (Marshall 1988 and Hejl 1994).

Woodpeckers and Fire

Fires change the relative structure of forests and alter the availability of resources. Little is known about how the distribution of resources important to woodpeckers is affected by fire size, frequency, and severity. For example, high-intensity fires probably have greater impact on resources important to birds than moderate or low-intensity fires at both the spatial and temporal scale (Hejl 1994). In general large infrequent fire, termed wildfire here, is believed to affect resources that last not only through the breeding season but also into the winter and for years following (Turner and Romme 1994, Bebi et al. 2003, Turner et al. 2003).

Whether fire-induced changes in resources affect birds positively or negatively is under debate. However, fire changes many resources important to woodpeckers (Hejl 1994). Fire alters the distribution of seral stages of ponderosa pine (Fulé and Covington 1994), which diversifies habitat types that affect woodpecker presence and distribution (Hutto 1995). The abundance and distribution of dead trees and snags used by woodpeckers are also altered by fire (Balda 1975, Horton and Mannan 1988). Further, fire attracts wood-boring and bark-dwelling insects, which changes prey resource distribution (Blackford 1955, Koplín 1969, New and Hanula 1998). All of these components are important to woodpeckers because they could affect how woodpeckers select home ranges and use habitat within those home ranges.

In the southwestern United States, ponderosa pine forests and their associated avian communities have evolved with fire, which historically occurred every 2-12 years (Moir et al. 1997). Fire regimes in northern Arizona were altered drastically with the advent of fire

suppression, changing a once park-like open mature forest to one in which trees are dense and small diameter dog-hair thickets abundant (Covington and Moore 1994). Small diameter stands have increased in frequency across the landscape (Covington et al. 1997) and present abundant fuel for wildfires (Lowell 1996). These wildfires can burn so intensely that they kill large continuous swaths of trees, leaving high-severity burned areas ranging from a hundred hectares to 645 ha (as in the Rodeo Chediski Fire of 2002 located in the Apache-Sitgreaves National Forest, northern AZ, [Richardson 2002]). These fires drastically alter the larger landscape in comparison to historical fires, which typically burned approximately 1200 ha at lower severities (Fulé and Covington 1997).

Wildfires create a patchy, mosaic habitat in the form of differentially burned stands, and as time progresses, stands of different seral age (Bunnell 1995). High-severity habitat created by wildfire can have positive affects on woodpecker species at the population level. Hutto (1995) documented increased detection of 15 species in habitat after stand replacing fire, of which four were woodpecker species. Several species are restricted to, or limited by, high-severity post-fire habitat, including the black-backed and three-toed woodpecker (Murphy and Lehnhausen 1998, Saab et al 2002). Most studies that tested for differences in abundance of hairy woodpeckers in burned versus unburned forests found an increase in post-fire habitat (Brawn and Balda 1988, Raphael et al. 1987, Hobson and Shieck 1999). Koplín (1969) found a 50-fold increase in woodpeckers in a burn and attributed this response to the increase in arthropod infestation of fire-killed trees. When abundance data from Brawn and Balda (1988) were graphed according to years post-burn, hairy woodpecker density decreased with the age of the burn, suggesting that the benefit of post-fire habitat were temporally limited (Murphy and Lehnhausen 1998). This temporal decrease in habitat benefit could potentially result in larger home range size through time. Wiens et al. (1985) suggested that habitat quality should affect home range size because individuals in poorer habitats would require larger home ranges to sequester the same amount of resources as individuals in richer habitats.

Fire affects habitat at a finer scale by changing the distribution of snags and dying trees. This is important for woodpeckers because species likely select the composition of their home range based on the presence and abundance of these structural habitat components (Passinelli

2000a). Fire destroys and creates snags differentially according to burn severity and frequency. High-severity fires create snags over the short term (Conner 1981a, Hejl 1994, Raphael et al. 1987). Morrison and Raphael (1993) found that fire-killed trees fell more quickly than snags created by other mortality agents. However, of the fire created snags that stood longest, all were of large diameter (>38cm), which many authors consider important for woodpeckers as foraging, roost, and nest sites (Conner et al. 1994, Horton and Mannan 1988, Olsson et al. 1999). Additionally, Morrison and Raphael (1993) documented an overall increase in snags in burned plots because of small snag recruitment (13-38cm). While these snags might not be important for cavity sites, they are likely important for foraging (Murphy and Lehnhausen 1998) or as structural cover around nest trees as required by the black-backed woodpecker (Saab et al. 2002). In southeastern and southern forests, Conner (1981a) suggested that snags created by fire last longer than snags created by other mortality agents. Moderate-severity fires, however, appear to destroy more than make snags, at least in the short term. Randall-Parker and Miller (2002) showed that moderate-severity prescribed fires in northern Arizona ponderosa pine forests removed 20% of standing snags and created few new snags from old growth trees. Horton and Mannan (1988) showed that 50% of snags monitored were destroyed with destruction varying according to decay class and size. Information on trees that become snags after several years post-burn is lacking. This could be an important factor to woodpeckers, as several authors have suggested that fire-injured trees can take several years to senesce, and therefore become a snag years following the fire (Furniss 1965, Santoro et al. 2001).

Changes in snag distribution have had different effects on woodpeckers in different areas and in different studies. Horton and Mannan (1988) showed that the initial loss of snags had a minimal negative impact on cavity nesters and the authors suggest that healthy trees stressed by fire could become susceptible to secondary mortality agents, thereby creating snags in the future. Raphael et al. (1987) found that fire removed snags and the decline was positively related to the abundance of bark-gleaning bird species. Balda (1975) showed that increased snag availability due to fire positively correlated with woodpecker densities. Kreisel and Stein (1999) also found an increase in woodpecker abundance following fire and suspected that it was due to increases in food availability in fire-created snags.

Fire also affects food availability within the habitat mosaic at both the stand and tree scale. Foresters have long known that burned areas attract high densities of bark-dwelling insects (Miller and Patterson 1927, Bradley and Tuller 2001), as well as the association of woodpeckers to bark-dwelling and wood-boring beetle infested trees (Beal 1911, Blackford 1955, Koplín 1969). Current literature on the relationship between fire and bark beetle attack suggests that at the level of the tree, burned trees are 24% more likely to be attacked by bark-beetles than unburned trees (Bradley and Tuller 2001), and that the level of scorch affects susceptibility to attack, with the relationship between the amount of scorch and probability of attack being positively related (Furniss 1975, Flanagan 1996). Blackford (1955) described woodpeckers as “drawn to” a burned section of forest infested by woodborers. Additionally, random searches for hairy woodpeckers resulted in no individuals found in unburned sections of the forest. This indicated that hairy woodpeckers immigrated into burned areas from unburned areas to forage, taking advantage of the increased food supply. Koplín (1969) and Massey and Wygant (1973) also found a positive response in woodpecker numbers to bark beetle increases following a burn. Conner et al. (1994) found that fire created snags used by woodpeckers had five times the dry arthropod biomass than those not used by woodpeckers, and Machmer (2002) found a 170% increase in insect densities trapped in burned study sites relative to unburned controls. Therefore, the attraction of insects to burned areas could affect how woodpeckers select habitat components at multiple scales. Rolstad and Rolstad (1995) found that woodpeckers selected home ranges with stands characteristics typical of those with maximum prey resources.

Because fire was a regularly occurring event in the ponderosa pine forests of northern Arizona (Covington et al. 1997), fire undoubtedly had significant effects on bark-dwelling arthropod distribution and density. Apfelbaum and Haney (1981) found that in the Great Lakes region, fire altered the types and distribution of food available. With the fire suppression policy of the last century, the occurrence, size, and frequency of wildfire has increased (Covington and Moore 1994). This change could alter arthropod infestation of fire-killed trees as well as increasing susceptibility of surrounding areas to outbreaks (Parker and Stipe 1993). Large swaths of fire-killed trees like those created by current large-scale fires (Richardson 2002)

provide attack sites for woodborers and bark beetles (Gibson et al. 1999, Santoro et al. 2001). Stand structure, such as dog hair thickets, resulting from fire suppression will also affect the likelihood of insect infestation. Obedzinski et al. (1999) showed that there is an increased susceptibility of ponderosa pine to mountain pine beetle (*Dendroctonus ponderosae*) in stands with dense, small diameter trees (<15cm). Both fire and fire suppression have major impacts on the distribution and abundance of insects, which influences woodpecker habitat selection, home range size and use, and foraging behavior.

Woodpeckers in Winter

Avian populations often experience their highest mortality rates during the non-breeding season (Newton 1998). For non-migratory, temperate zone birds such as woodpeckers, winter environments present extreme living conditions and populations often drop dramatically after harsh winters (Hejl et al. 1988, Baillie and Peach 1992, Greenwood et al. 1994). Graber and Graber (1983) found that population declines in most species following a severe winter were much greater than following a mild winter and that decline rates were negatively correlated to initial densities.

Winter affects the availability of resources by limiting the abundance of or accessibility to these resources. For example, snow could cover resources or habitat components important to woodpeckers. Mannan et al. (1980) suggested that during the winter, when downed logs were covered with snow and food items were limited, snags would be disproportionately used for foraging. Winter also changes the amount of time available for foraging. With decreasing light, birds need to allocate their time to maximize energy gain while minimizing predation (Lima 1986, Lima 1992, Rogers and Smith 1993). Ultimately, the time spent foraging must allow birds to accumulate enough fat reserves to survive the physiologically demanding requirements of a winter night (Houston et al. 1997). Houston and McNamara (1993), when modeling the most appropriate time schedule for small bird foraging in the winter, found that a bimodal foraging pattern, with increased feeding at dawn and dusk, was the optimal foraging pattern when resources were variable. When food resources were predictable, birds should forage later in the day to reduce predation exposure and acquire enough fat deposits needed for over-night

thermoregulation. Olsson et al. (2000) showed that in an area with relatively predictable resources, the lesser-spotted woodpecker (*Dendrocopus minor*) displayed a bimodal foraging pattern with the evening foraging period significantly greater than the morning period. Morrison and With (1987) found that hairy woodpeckers concentrated their foraging activities in the evening prior to roosting, suggesting this was a response to a “seemingly abundant food resource”. Changing climatic conditions such as wind and temperature, can affect where, how and for how long woodpeckers forage, further exacerbating the effects of diminishing daylight. Dolby and Grubb (1999) found that during times of high winds, bark-foraging birds were farther away from forest edges, and downy woodpeckers chose larger trees to forage on, possibly blocking wind from having negative impacts on their ability to thermoregulate. Grubb (1978) found that increasing wind and decreasing temperatures caused reductions in time spent foraging and distance traveled by downy woodpeckers.

Martin (1987) suggests that food availability during the non-breeding season is an important factor for reproductive success in birds. Olsson et al. (1999) found that woodpeckers that optimized their energy intake by foraging in areas with greater resources had greater fitness as measured by numbers of fledglings. Because fire changes the distribution of bark-dwelling arthropods spatially and temporally, and because these arthropods are the only food resource available to non-social woodpeckers in the winter due to climactic conditions limiting other food sources (Askins 1981), acquisition of food in burned areas could be critical to woodpeckers in the winter. As a result, woodpeckers should show a behavioral shift in foraging behavior (Conner 1981b) and location to deal with differing prey abundances resulting from fire and local climactic conditions. Martin and Karr (1990) suggest that behavioral shifts can indicate limited resources, such as food, under demanding environmental conditions. Conner, (1979, 1981b) studying hairy woodpeckers in Virginia, found moderate changes in foraging behavior after breeding with foraging breadth narrower during winter. Birds selected a narrower range of tree sizes, stem densities, and canopy heights. He hypothesized that the shift in hairy woodpecker behavior was in response to decreasing prey availability, which provided a mechanism for over-winter survival.

Woodpecker Home Range and Estimation Methods Review

Home range studies provide insight into habitat requirements (White and Garrott 1990, Aebischer et al. 1993), social organization (Elchuk and Wiebe 2003), foraging ecology (Dobrowolski et al. 1994), and aid in the development of management plans (Swihart and Slade 1985a). Studies of home range requirements for woodpeckers in North America were restricted primarily to endangered species or those of special concern (Bull and Meslow 1977, Sherrill and Case 1980, Hooper et al. 1982, Renken and Wiggers 1989, Doster and James 1998). The major goal of these studies was to provide enough information for managers to adequately provision species-specific habitat required for these species' conservation. Much of what we know about woodpecker home range characteristics beyond area and simple structural characteristics is based on woodpecker species in Scandinavia (Dobrowolski et al. 1994, Rolstad and Rolstad 1995, Mikusiński et al. 1997, Pasanelli 2000a, Rolstad and Rolstad 2000, Rolstad et al. 2000).

Home ranges size was shown to be larger in winter for several woodpecker species (red-cockaded woodpecker, *Picoides borealis*, [Hooper et al. 1982], three-toed and black-backed woodpeckers, *Picoides tridactylus* and *Picoides articus*, [Goggans et al. 1989], grey-headed woodpecker, *Picus canus*, [Rolstad and Rolstad 1995], middle spotted woodpecker, *Dendrocopos medius*, [Pasanelli 2000a]). Edenius et al. (1999) found that as winter progressed, home range size increased. Wiktander et al. (2001) found that out of four seasons, home range size was greatest in winter, approximately 17 times bigger than breeding home range size. Rolstad and Rolstad (1995) found a 100-fold increase in home range size from summer to winter. All authors suggested that home ranges were larger because of limitations imposed by winter, most likely the limitation of food.

Home range establishment and size is likely affected by food abundance (Weins et al. 1985, Szekely 1987). Studies on other bird species show that home range size decreases with increases in the availability of food (MacArthur and Pianka 1966, Eniksson and Nilsson 1983, van Riper 1984, Smallwood 1987 and 1988, Wiktander et al. 2001). Literature on woodpeckers suggests the same relationship but relatively few studies measured food. Goggans et al. (1989) suggested that as bark beetle densities decreased, home range size for black-backed and three-toed woodpeckers (*Picoides tridactylus* and *P. articus*) increased. Rolstad et al. (1995)

suggested that great-spotted woodpecker (*Dendrocopos major*) territories were established based on the availability of pine cones, their major food source during the winter. Rolstad and Rolstad (2000) found that black woodpecker (*Dryocopus martius*) home ranges were proportional to the area of land used for feeding. Additionally they noted that home ranges were often defined by area with bark beetle-killed trees. Mikusiński (1997) also found a correlation with prey abundance and home range size between ants and the black-backed woodpecker, in managed forests of Sweden. Thus, both time of year and prey distribution could affect home range size of woodpeckers.

Home range size for woodpecker species varied across studies in part due to differences in methods used by researchers to estimate home range size. Therefore, I reviewed methods researchers used in 14 publications that assessed home range size for non-communal woodpecker species (Table 1). I focused my review on the following factors: (1) field observation methods; (2) sample size used for estimation of average home range; (3) number of locations per individual to estimate home range; (4) whether location sampling independence per individual was addressed and if so how; and (5) statistical analysis used to estimate home range size.

Of the 14 papers reviewed, 10 were conducted in Scandinavian countries and none on the hairy woodpecker. Although studies on hairy woodpecker home range exist in the form of theses from the late 1940s and early 1950s (Allison 1947, Calef 1953, breeding, Staebler 1949, Dennis 1951, non-breeding), Jackson et al. (2002) cautioned against using these estimates because they lack adequate descriptions of season sampled and area of use, distinctions between territory versus home range, and have poor survey effort. I agree with Jackson that no methods or definition were given and effort was low, however, Staebler (1949) provides the only record on hairy woodpecker winter home range. While methods used are questionable under current scientific methods, Staebler (1949) does provide the relative differences between downy and hairy woodpecker home range size. He notes that hairy woodpeckers have home ranges approximately 10-times larger than the downy woodpecker. Obviously, home range size for *P. villosus* should be reevaluated under rigorous scientific study and current techniques, however, these studies do provide a good start.

Methods for locating and identifying birds included observation of individuals that were morphologically distinct (Hogstad 1970, Husak 2000), re-sighting color-banded birds (Hogstad 1970 and Mattyhysen et al. 1993), and radio telemetry (all others). Radio telemetry was by far the most common method as it reduced search time necessary to locate individuals and allowed detection and identification from a distance with a minimum of disturbance to the bird.

Accurately describing home ranges requires monitoring multiple individuals and obtaining sufficient locations for each of the individuals monitored (Worton 1987, Swihart and Slade 1985a). The number of birds monitored in these studies varied widely (2-40 individuals, \bar{X} 19.3 \pm 15.9) with more than half of the studies based on less than ten individuals. The number of points needed to estimate a home range accurately has been well examined (Kernohan et al. 1998). Several authors suggest 30-100 points be collected per individual (Worton 1987, White and Garrott 1990, Girard et al. 2002). Seaman et al. (1999) recommended 50 points per individual as an adequate goal for most study species based on a mathematical modeling of several data sets. In the papers reviewed, two did not report number of locations and six gave approximations of the number of locations per bird. I calculated the range of number of locations per individual and average number of locations taken for birds across all studies. I found the range to be 16-283 locations per individual and the average equal to 59.2 \pm 50.9. Out of 134 birds, 89, or 66%, had less than 50 points for estimation of home range. Only two papers addressed the number of points needed to accurately estimate home range size. Wiklander et al. (2001) and Edenius et al. (1999) described points necessary for home ranges across seasons interpreted from incremental area plot results. These plots express information accumulation (area estimated) as a function of increasing sampling effort (number of locations) that ultimately reaches an asymptote of no further information accumulation beyond some threshold of sampling effort.

The independence of successive location points (e.g. an animal's position at one time does not affect its position at another time) is an underlying assumption required to validate many home range estimators (Swihart and Slade 1985a, b; Weber et al. 2001). Multiple locations for the same individual can lead to underestimation of home ranges by a factor related to the covariance between successive points (Swihart and Slade 1985b). In general, the closer two

points are in time, the greater the covariance and dependence. In the papers I reviewed, the number of locations recorded for the same individual ranged from 1 to 17/day ($\bar{X} = 3.8 \pm 2.9$). Pasinelli (2000a) and Rolstad et al. (2000) did provide Pearson's correlation matrix analyses to assess the independence of location points, however this is not the recommended method for detecting time to independence between successive locations (Swihart and Slade 1985b, Weber et al. 2001). Swihart and Slade (1985b) suggested that 1-2 locations per 24-hour period are optimal to satisfy both independence and logistic requirements.

The most commonly reported home range estimator was the minimum convex polygon method, which estimates the home range area by connecting the outermost location points and calculating the area within. Because this is a non-parametric estimator and does not have any assumptions about the percentage of locations to be included, it is easily interpreted (Wiktander et al. 2001). However, this method is susceptible to poor estimation due to high correlation of locations, and non-independence of those locations (Worton 1987). In addition, minimum convex polygon overestimates home range size (Ford and Myers 1981).

My study addressed many of the concerns about home range size estimation in the following ways. First, to ensure accurate estimation of home range size, I located radio-tagged birds 30-50 times per individual (Seaman et al. 1999, Appendix A). On average, birds were tracked 42.75 ± 6.6 times. Area curves created using Monte Carlo randomization in the Animal Movement extension program (Hooge and Eichenlaub 1997) in ArcView 3x, indicated that approximately 32 locations were necessary to account for the area used within the sampling period and thereby accurately estimate home range. To ensure independence of locations, I attempted to track birds only once per day (Swihart and Slade 1985b). However, if I was not going to obtain 30 locations, or was close to 50 locations within the study period and prior to radio failure, I tracked birds 2 times per day, attempting to separate locations by 4-6 hours. Most birds (14 out of 16) were tracked more than once for at least 1 day. On average, the number of days birds had to be tracked twice was limited ($\bar{X} = 3 \pm 2.25$).

I chose to use the kernel method as suggested by Worton (1989) and Seaman and Powell (1996), to estimate home range area because it presents very little bias and is considered significantly better at estimating home range than the minimum convex polygon method.

Seaman et al. (1999) suggests that the 95% confidence interval represents area information of little biological importance to an organism as well as being mathematically biased because it is based on the least amount of data. These authors suggest that the 85% probability contour of location occurrence is a more appropriate measure and better for cross-study comparison. Therefore, I report this contour interval and not the 95% contour because it can be misleading as it likely represents locations that could result from a bird being stressed or pushed by an observer and might then fly beyond their normal activity area (personal observation).

Hairy Woodpecker Foraging Ecology and Foraging Methods Review

Much of what we know about the hairy woodpecker has come from the early anecdotal studies in the eastern United States (Bent 1939, Kilham 1965), in deciduous or mixed-coniferous forests (Connor 1979 and 1981b, Renken and Wiggers 1989, Mathyessen et al. 1993), or in conjunction with other species as a measure of niche or sexual differentiation (Morrison and With 1987, Petit and Grubb 1988, Weikel and Hayes 1999). While multiple studies conducted on woodpeckers have included the hairy woodpecker (Stallcup 1968, Morrison and With 1987, Weikel and Hayes 1999), Jackson et al. (2002) contends that this species still lacks detailed study and has been especially understudied in recent years. From the studies that do exist, however, we can generalize about the foraging behavior of the species. In contrast, sexual differences in foraging behavior were documented in only a few papers (Morrison and With 1987, Conner 1993, Murphy and Lehnhausen 1998) but information on this aspect of their foraging ecology is more limited and what information does exist is variable. It is important to keep in mind that behaviors, whether at the inter- or intraspecific level, have typically been observed in the presence of other species and therefore could be complicated by interspecific competition.

Early investigations noted differences in foraging behavior and attempted to describe general time-budgets of the hairy woodpecker. Kilham (1970) observed that foraging activity during the late winter only occurred for 75% of the day, with the rest being a time for leisurely activity including courtship, preening, and rest. Conner (1979, 1981b) found that hairy woodpeckers changed foraging methods in order to reach prey during the winter months when most arthropods are found on or within the bark of trees. Shackelford and Conner (1997) studied

a suite of woodpeckers in Texas and found hairy woodpeckers associated with lower hardwood basal area, opposite to what Conner (1981b) had found for individuals in Virginia where woodpeckers had no preference for any habitat component measured at this scale.

Hairy woodpecker foraging patterns in the western United States were also found to be variable, but slightly more consistent with regard to substrate selection than in the east. Stallcup (1968) studied hairy woodpeckers in Colorado's ponderosa pine, finding preferential use of dead trees, stumps, and logs and greater use of the trunk in comparison to other parts of the tree during winter. Weikel and Hayes (1999) studied cavity nesters in Oregon during the summer months and found that hairy woodpeckers selected larger and heavily decayed trees. Additionally, hairy woodpeckers favored the lower crown of deciduous trees for their foraging location. In a study on species niche overlap, Morrison and With (1987) found a concentration of foraging on trunks, preference for certain tree species, and a decrease in foraging overlap with sympatric species and between sexes during the winter. They suggested the mechanism behind the decrease in niche overlap and subsequent segregation of species during winter was indicative of resource limitation.

Information on hairy woodpeckers foraging ecology in burned areas is scarce. Kreisel and Stein (1999) found that hairy woodpeckers, similar to other species present, selected dead trees 99% of the time, chose burned trees with brown needles more than expected from their availability, and selected western larch and ponderosa pine more than expected. Similarly, Murphy and Lehnhausen (1998) showed that hairy woodpeckers choose more heavily burned trees than black-backed and three-toed woodpeckers. Indirectly, Shakelford and Conner (1997) suggest that hairy woodpeckers are associated with disturbance in general, and it is plausible that fire satisfies their definition.

Sexual segregation is a mechanism by which males and females reduce competition by partitioning limited resources (Holmes 1986, Latta and Faaborg 2002). Intrasexual competition can be reduced by a variety of mechanisms ranging from short-term behavioral differences between sexes (Hogstad 1991) to long-term morphological differentiation (Selander 1966). Male and female woodpeckers are often strikingly dimorphic in plumage and because sympatric woodpeckers species regularly occupy the same areas, they are often subjects in studies

evaluating sexual differences that lead to coexistence (Morrison and With 1988). Miller et al. (1999) measured isolated populations of hairy woodpeckers in comparison to mainland races for differences in bill morphology and other sexually dimorphic traits but found none. This suggests that ecological factors have little influence on this characteristic and instead is a result of sexual dimorphic conservatism (Selander 1966). While bill morphology might not be plastic in response to short-term changes in ecosystems, behavioral selection of habitat types and components can be.

When selecting at the patch scale, Conner (1993) indicated that both male and female hairy woodpeckers selected habitat patches (11.3 m radius) with higher basal area. This could indicate that hairy woodpeckers do not use this level of selection to segregate. Behavioral segregation is based on the sexes' ability to monitor when resources are limited and to shift their behavior accordingly (Martin and Karr 1990). Lima (1983) found that a close congener of the hairy woodpecker, the downy woodpecker could monitor patch quality at a small patch level, four simulated trees, by food intake and energy gain. Because hairy woodpeckers were not found to use this level of habitat selection to partition resources, suggests that it is difficult for them to monitor resources at a scale this large.

Sexual differences at the level of the tree were noted but remain poorly described. Kisiel (1972) noted only subtle differences between the sexes, with females spending more time on live trees than males, but that both sexes foraged at the same height. Morrison and With (1987) observed that (1) females were more selective relative to tree species than males, (2) the sexes differed in foraging height and in height of trees selected in the winter but not in the summer, and (3) the sexes did not differ in selection based on tree size or foraging height to tree height ratio in either summer or winter. Overall, they found a decrease in niche overlap between the sexes in winter and attributed this to partitioning of limited resources. Conner (1993) found that males tended to be lower and on larger substrates while females tended to be higher and on smaller substrates, opposite of the previous authors. Kilham (1965 and 1970) described female foraging behavior as superficial, while males were excavators, while Conner (1993) found little difference in foraging method.

I know of only one paper that separated observations by male and female hairy woodpeckers in burned areas. Murphy and Lehnhausen (1998) investigated the foraging behavior of black-backed, three-toed, and hairy woodpeckers in one burned edge of a 3,500 ha fire in Alaska, at one and two-years post-burn which. Data from the two seasons were pooled. They found females selected spruce significantly less than males and pecked more than males, which excavated more. They found no differences in use of standing versus down trees (both sexes used standing trees), nor differences in use based on tree height, initial foraging height, foraging duration, or amount of the tree scorched by fire. However, sexual differences were likely undetected in the latter case due to small sample sizes. The major suggestion for the attraction of hairy woodpeckers to the burned area was the outbreak of bark dwelling arthropods. As a result, the lack of sexual segregation was likely due to increased food supply and low competition in the face of a non-limited resource. Super-abundant food resources probably account for lack of sexual segregation in diet and have been documented in other species. For example, diet composition of different warbler species completely overlapped during a spruce budworm outbreak (McMartin et al. 2002). Finally, Villard and Benninger (1993) also studied hairy woodpeckers in a burned area but females were rare in the area so their study focused only on males. This finding was similar to Murphy and Lehnhausen (1998), who also found few females in the burned area. Neither study addressed why females were in low numbers in the burned areas.

Foraging behavior can be interpreted in many ways depending on how it was observed and measured. Therefore, I reviewed the methods used in 22 publications that observed the foraging ecology of non-communal woodpeckers that either observed hairy woodpeckers within the community of species or were well-cited publications within the last 35 years (Table 2). I focused my review on the following questions: (1) how large was the study area sampled and how long was the study conducted, (2) what was the population size or how many birds were observed if population was not given; (3) what was the total observation sample size, number of observations per species, and number of observations per individual; and (4) what was the statistical experimental unit used in analyses?

Out of the 22 papers reviewed, the study area size ranged from 30-12,500 ha with a mean of 947.7 ± 2644.4 ha. Because woodpecker home ranges can be quite large (≈ 7 ha, three-toed and downy woodpeckers, Hogstad [1970] and Matthysen et al. [1993], 45.75 ha, great spotted woodpeckers, Rolstad et al. [1995], ≈ 100 ha, pileated and green woodpeckers, Renken and Wiggers [1989] and Rolstad et al. [2000], 449 and 226 ha, black woodpeckers Rolstad and Rolstad [2000], 742 ha, winter lesser spotted woodpeckers, Wiktander et al. [2001], 4950 ha, grey headed woodpecker, Rolstad and Rolstad [1995]), many of these studies could not have sampled sufficient numbers of individuals to use parametric tests (Zar 1999). Sample size, or in this case, number of individuals observed, is important for replication and randomization purposes. When using parametric evaluation, a minimum of 6 for detection at levels $p < 0.05$ is required (Aebischer et al. 1993), but also when using nonparametric descriptive tests, which must have the '5 per cell' rule satisfied to be valid (Agresti 1990). Suggestions for sample size begin at ten and are encouraged at 30 (Aebischer et al. 1993). With sources of variation occurring across years, seasons, sex, and age, it is difficult to capture, monitor, and collect enough observations, on the necessary number of individuals, to satisfy the above statistical requirements (Block 1990).

This logistical problem of studying birds that have large home ranges (being able to cover enough ground to encompass 10-30 individual home ranges to observe enough birds for adequate sample size) has probably been the major reason why most studies observe individual birds multiple times. Seventeen studies collected repeated observations on individuals and used each observation as the statistical experimental unit (e.u.). While this may not be statistical independence due to the same individual being observed multiple times, if enough time elapsed between observations each observation is independent because the behavior at time x would not effect the behavior at time $x + 1$. Timed observation and average time per foraging variable was also used as the statistical e.u., a subset of the above percentage. Only four studies used individual birds as the statistical e.u., while one corrected for multiple observations on an individual using statistical weighting of degrees of freedom (Imbeau and Desrochers 2003).

To address the issues outlined above in my own research, I sampled different areas in successive years (study sites overlapped less than 5%, Fig. 3) thereby minimizing the probability

that the same individuals were observed in successive years. For some birds, I recognized individuals based on unique combinations of color bands or radio frequencies. For other birds, I assumed that if I repeatedly encountered a bird of one sex within the same (400 x 400m) area, it was considered the same individual. This allowed me to evaluate how many individuals were observed in a relatively conservative manner. Based on this approach, no bird made up more than 20% of the data when testing within a burn severity for a particular year and the average contribution was $7 \pm 5 \%$. The mean number of observations/individual was 2.9 ± 1.3 . To maximize independence of repeated observations on the same individual, I restricted my analyses to those observations separated by the greatest length of time ($\bar{X} = 24.5 \pm 17.6$ days).

Conceptual Model

I developed a simple conceptual model to describe the potential relationship between the degree of sexual segregation and variation in resource abundance for species that do not show striking dimorphism in feeding structures. In stable environments, segregation is related to the amount of competition incurred by the current level of resources. If ecosystems were to remain constant, then behavioral patterns of resource partitioning should also remain constant. However, ecosystems are dynamic and their inherent variability will in turn affect resource availability. This model functions under several simplifying assumptions. First, the model system experiences a single pulse of resources great enough to reduce competition for those resources. This would be consistent with rapid increases in bark beetle and woodborer populations following a fire (Santoro et al. 2001). Second, following the initial pulse, resource abundance decreases at a constant rate. In real systems, the rate of decline may not be constant as further perturbations in the system could change the rate of decrease or increase. However, in winter, bark beetle and woodborer populations are not able to replace themselves, as insects are dormant during this period (Askins 1981). Further, other food sources that allow prey switching, such as flying insects, fruits and nuts, are not available. For the purpose of this model, I considered the removal rate of these insects by predators such as woodpeckers (Koplin 1969) to occur under a constant rate with no replacement and no alternative prey items to allow switching

by the predator. Third, I assume that the population of predators (woodpeckers) also remains stable through time. While studies have shown an initial increase in woodpeckers following a burn (Massey and Wygant 1973), for the purpose of the model, the population of woodpeckers following the initial increase remains constant.

Sexual segregation is the behavioral mechanism by which the sexes partition limited resources (Selander 1966, Holmes 1986). Partitioning of resources is observed in the field through shifts in male and female foraging behavior (Morrison and With 1987, Conner 1993). For example, when resources are abundant, males and females should forage on a broad distribution of tree sizes and the sexes would overlap completely in their use of this niche dimension (male and female hairy woodpeckers foraged on the same tree sizes in a young burn, [Murphy and Lehnhausen 1998]). However, when resources become limited and competition increases, the sexes might select different tree sizes on which to forage. The size of trees used by males is just one way that females and males could differ in their foraging behavior. They might also forage at different times of day, different heights, choose different tree species, or select different subsets of prey items within the overall resource base. Each different habitat component is considered a niche dimension, on the Y-axis, that is a dimensionless variable (Fig. 1). The X-axis of the model shows resources changing from super abundant to limited, following Murphy and Lenhausen (1998) and Martin and Karr (1990) respectively. A superabundant resource is one elevated to a level disproportionately higher than what would normally be found in an ecosystem on average (McMartin et al. 2002). Some examples of superabundant resources well documented in the literature include, hatchings of cicadas (Stephen et al. 1990), outbreaks of bark beetles (Schmid et al. 1995, Samman and Logan 2000), and population booms in rodents (Schmidt and Ostensfeld 2003). Most superabundant resources are not sustained and are therefore ephemeral. For example, on the Kaibab Plateau, AZ, bark beetle outbreaks lasted on average 3-7 years (Parker 1981). Because superabundant resources do not occur frequently within ecosystems, they represent a set point from which to monitor subsequent declines in resources and the associated behavioral responses by species affected by those resources.

As resources become limited, intraspecific competition between the sexes increases, and males and females will limit the amount of overlap in the use of a particular niche dimension. In the case of selected tree sizes, this is manifested by a decrease in the amount of overlap between the two tree size distributions used by males and females. This shift in behavior results in the partitioning of resources, which is termed sexual segregation. At moderate levels of resource limitation, sexual segregation is low, represented by the small double-sided arrow (Fig. 1), but at higher levels of resource limitation, sexual segregation is high, represented by the larger double-sided arrow. If this model holds for the hairy woodpecker-ponderosa pine system in winter, it makes the following predictions; (1) sexual segregation will be lowest immediately following a burn when arthropod abundances are at their peak and competition is low, and (2) sexual segregation should increase as arthropods decrease and competition for those resources increases. To test this prediction I observed hairy woodpecker foraging behavior in burns of four ages (2, 3, 6, and 7 years post-burn) and in comparison to a control (unburned). I specifically asked how males and females overlap in their use of tree size (DBH and height), foraging height, and substrate use (branch versus trunk). I used analysis of variance to test (Zar 1999) to assess differences in male and female use of each variable. I then discuss the change in male and female behavior across burn age. To test the underlying mechanism for competition, change in prey resources, I sampled insect densities in each burn age to evaluate if the pattern of insect abundance follows that predicted by the observed change in sexual segregation.

CHAPTER 2:

Hairy woodpecker winter ecology following wildfire: effects of burn severity and age

INTRODUCTION

Disturbance plays an essential role in creating and maintaining natural landscape heterogeneity that birds respond to in both space and time (Brawn et al. 2001). White and Pickett (1985) defined disturbance as “any discrete event that disrupts ecosystem, community, or population structure and changes resource, substrate availability, or the physical environment.” Fire is one of the most important terrestrial disturbances that affect avian populations and the ecosystems in which they reside (Raphael et al. 1987, Hejl 1994, Hutto 1995, Brawn et al. 2001). Because fire changes resources at multiple scales across both space and time (Turner and Romme 1994), where a burn is located, and its size and severity can affect how birds select habitat and function within it. The effects of large infrequent wildfires on resources persist immediately following the fire, and for years following, leaving an ecological legacy (Turner and Dale 1998, Turner et al. 2003, Bebi et al. 2003). Large, infrequent, high-intensity fires may have a greater impact on resources important to birds than moderate or low-intensity fires by altering resource spatial heterogeneity and complexity (Hejl 1994). These larger, infrequent fires may in fact overpower the effects of smaller, more frequent but less intense fires (Turner and Romme 1994, Romme et al. 1998).

By changing resource distribution, fire has the potential to affect multiple proximate cues (Hildén 1965) that birds use to discriminate among habitats for settling. Such cues can include vegetative composition and structure, presence and density of conspecifics and other species, and food (Block and Brennan 1993). Settling results from a hierarchical decision process that occurs through different orders of selection (*sensu* Johnson 1980). At each level of selection, birds discriminate between proximate cues organized at different spatial scales. For example, placement of the home range (second-order selection) may occur at a large spatial scale, while use of different habitat types within the home range (third-order selection) occurs at a smaller spatial scale. Because fire can alter the spatial distribution of proximate cues at multiple scales, it could affect a bird’s decisions at most levels of habitat selection.

Woodpeckers especially may be affected by fire because they are intimately tied to proximate cues that fire alters (Horton and Mannan 1988). Fire location may affect the selection of where a species establishes their home range (second-order selection). Several species of woodpeckers are restricted to or limited by the abundance of high-severity post-fire habitat, including the black-backed and three-toed woodpecker (Hutto 1995, Murphy and Lehnhausen 1998, Saab et al. 2002). Third-order selection, the selection of patches within the home range is also altered, as wildfire creates a complex mosaic of low and high severities as well as multiple vegetative successional stages (Turner and Romme 1994). The diversification of habitat types likely affects woodpecker distribution (Hutto 1995) and density as they choose to establish home ranges and concentrate activities in these different habitat types. Finally, fourth and fifth-order selection, selection of specific sites within the home range and the procurement of food from those sites, are also affected. Fire changes the density, abundance, and distribution of dead trees and snags (Balda 1975, Horton and Mannan 1988), and attracts high densities of wood-boring and bark-dwelling insects. This affects prey resource distributions (Blackford 1955, Koplín 1969, New and Hanula 1998) and ultimately how woodpeckers forage for them. Additionally there is a positive relationship between the amount of scorch, or the burned area of the trunk and needles, and the likelihood of bark beetle attack (Ryan and Reinhardt 1988, Bradley and Tuller 2001), suggesting that differences in burn severity may further affect the distribution of resources.

Following fire, proximate cues may change through time. Patches of different severity can succumb to other mortality agents (Horton and Mannan 1988) or recover, with each patch taking a different ecological trajectory (Hessburg et al. 2000). Vegetation structure can change as burns age. For example, density of fire created snags decreases through time due to wind-throw (Morrison and Raphael 1993). Lastly, food availability may change through time as the attraction of insects to differentially burned areas decreases (Veblen et al. 1994, Santoro et al. 2001). As resident species, woodpeckers only settle following dispersal and likely adjust their habitat selection as proximate cues change spatially over time. These adjustments should be reflected in their foraging behavior and home range behavior (Rolstad and Rolstad 1995, Olsson et al. 2000). Woodpeckers have been shown to monitor their food resources (Lima 1983),

change their foraging behavior in response to food limitation (Conner 1979, Morrison and With 1987), and to have home range sizes that correlate with vegetative features associated with greater food abundance (Mikusiński 1997, Olsson et al. 2001). Other behavioral responses exhibited by woodpeckers include changing interactions with conspecifics (Matthysen et al. 1993) and altered foraging behaviors between the sexes (Murphy and Lehnhausen 1989). Fire is the primary natural-disturbance force in the ponderosa pine forests of the southwestern United States (Covington et al. 1994). Woodpeckers in these ecosystems have evolved with fire, which occurred every 2-12 years at small scales (Moir et al. 1997) and every 9 years at larger spatial scales (thousands of hectares, [Fulé et al. 2003]). As a result of fire suppression, livestock grazing, and timber harvesting, forest structure changed from open, mature forests to extremely dense stands (148/ha increasing to 1265/ha, Fulé et al. 2003). These small diameter dog-hair thickets have become increasingly abundant (Covington and Moore 1994), providing abundant fuel for wildfires (Lowell 1996). While large-scale fires existed in southwestern forests prior to European settlement (Fulé et al. 2003), their intensity is unknown. Current wildfires cover areas 5-156 fold that of historical small-scale fires, which typically burned approximately 1,200 ha at low severities (Fulé and Covington 1997). Current wildfires also burn at such high intensities that large, continuous swaths of trees suffer greater than 99% mortality. These swaths can range in size from one to several hundred ha. For example, in the 189,000 ha Rodeo-Chediski Fire of 2002, the largest continuous swath of fire-killed trees was 645 ha (Richardson 2002). Effects of these large-scale wildfires on how birds select habitat is relatively unknown.

The hairy woodpecker (*Picoides villosus*) is the most abundant primary cavity-nester in ponderosa pine forests of northern Arizona (Block, unpublished data). Hairy woodpeckers have higher abundances in burned versus unburned forests (Brawn and Balda 1988, Raphael et al. 1987, Hobson and Shieck 1999), but abundances may decline as burns age (Kreisel and Stein 1999). Woodpeckers are apparently attracted to burned areas due to the high density of bark-dwelling arthropods (Koplin 1969, Villard and Benninger 1993, Hutto 1995, Murphy and Lehnhausen 1998). These arthropods compose 65-85% the hairy woodpecker diet during the summer (Otvos and Stark 1985). These relationships suggest that hairy woodpeckers may be

selecting burned areas based on vegetative structural cues as well as food availability. Additionally, the two types of cues may interact through time.

This study was conducted to test the hypothesis that hairy woodpeckers respond to proximate cues within wildfire created habitat at multiple scales and that their response will change as a burn ages and proximate cues are altered. To test this hypothesis, I specifically asked: (1) what is the relative abundance of hairy woodpeckers in two burn severities, (moderate and high), in comparison to unburned ponderosa pine forests; (2) how does diurnal home range size change as a burn ages; and (3) how do hairy woodpeckers select habitat for foraging relative to what is available at the patch and tree level? Further, I investigated if male and female hairy woodpeckers altered their foraging behavior in response to spatial and temporal changes in post-fire habitat by asking: (1) how frequently do hairy woodpeckers forage with conspecifics in two burn severities at four post-burn ages; (2) do males and females select different foraging methods or habitat components for foraging at the level of the tree; and (3) if there are differences in male or female behavior, are those changes dependent on the presence of the opposite sex? Finally, I examined whether variation in prey resources could explain hairy woodpecker response to wildfire created habitat through time. Specifically I asked, what is the density of bark dwelling arthropods within two burn severities at four post-burn ages?

This study was conducted during the winter, a period critical for non-migratory, temperate zone birds because weather conditions are extreme and prey resources, such as free flying insects and fruits or berries, are either reduced, or are typically dormant and consequently non-replaceable (Askins 1981). Therefore, the acquisition of resources during winter should be of primary importance to hairy woodpeckers, which may affect home range size, social structure, and foraging behavior. This makes winter the ideal period to address these questions.

METHODS

STUDY AREA

Hairy woodpeckers (*Picoides villosus*) were observed for two winters beginning in October 2001 in four areas of ponderosa pine forest that had experienced high-severity wildfires. The study area was located 48 kilometers northwest of Flagstaff, AZ in the Coconino National

Forest and covered approximately 10,200 ha (N 39°27'-15', W 42°40'-00') between 2,100-2,600 m elevation. Northern Arizona's ponderosa pine forest is the largest contiguous stands of ponderosa pine (*Pinus ponderosa*) in the west (Burns and Honkalal 1990). Ponderosa pine is the dominant, climax, and seral species following disturbance (Cooper 1960). Other species encountered, typically only at life zone transitions between ponderosa pine and aspen, mixed conifer, and coniferous woodlands, included *Populus tremuloides*, *Abies concolor*, *Pinus edulis* and *Juniperus monosperma* (Dahms and Geils 1997). Based on climatological data taken in Flagstaff, AZ (Western Regional Climate Center 2003), weather patterns during the study period were within the 50-year average temperature range (\bar{X} = 1.67° C daily, -6.1° to 9.4°C min-max) but below average precipitation (70% and 30% less than 29.4 cm, 50-year average for October – March).

Sites were placed within four wildfire perimeters (Table 3). All wildfires occurred in the summer between the months of May and June. In 1996, the Horseshoe and Hochderffer fires burned within weeks of each other burning over 10,000 ha in the Coconino National Forest. Because these fires were adjacent to each other, they were considered one site. The Pumpkin fire burned approximately 6,000 ha in 2000, in both the Coconino and South Kaibab National Forests. This wildfire consumed one area initially established to sample within an unburned area adjacent to the Horseshoe-Hochderffer fire perimeters. As a result, this provided a site with both pre- and post-disturbance data. The Rodeo-Chediski fire was the largest fire sampled, burning over 189,000 ha in 2002. This fire was located in the Apache-Sitgreaves National Forest and Fort Apache Reservation approximately 200 km southeast of the Horseshoe-Hochderffer and Pumpkin fires. Sampling in this fire was limited to observations of conspecific foraging and insect density (see methods below). All fires burned with varying intensities, leaving a mosaic of high and moderate severities. Severity was defined as fire's effects on the system's organisms and ecosystem processes, while intensity was the temperature at which the fire burned (Turner and Dale 1998). High-severity burns were defined as those areas where fire reached the forest crown and killed 99% of ponderosa pine, whereas moderate-severity were those areas where low-intensity surface fires resulted in less than 10% mortality (adapted from Dwyer and Block 2000). Analysis of first year vegetation data indicated that high and moderate-severity burned

area was equal in both the Pumpkin and Horseshoe-Hochderffer fires. Within all fire perimeters, I sampled in both high and moderate-severity areas, being careful to maintain equal sampling effort and the relative size of each severity area. I sampled only in areas where ponderosa pine dominated. Two areas were sampled in the Pumpkin and Horseshoe-Hochderffer in successive winters, however, in each case, sites sampled in successive years overlapped by only 5%. This minimized overlap in the number of birds potentially resampled from one winter to the next. Hairy woodpeckers were also observed within unburned areas adjacent to or between fire perimeters. I consider unburned areas those portions of ponderosa pine forest that showed no visible scorch on the bark of trees and no visible tree mortality due to fire. These areas also had stand structure indicative of fire-suppressed areas, including high tree density and dog-hair thickets (Covington et al. 1997). Unburned forests have not burned for greater than 25 years, more than two times the hypothesized length of historical fire intervals (Moir et al. 1997). Other non-ground foraging woodpecker species found in the study area throughout the winter, in decreasing relative abundance, included Williamson's sapsucker (*Sphyrapicus thyroideus*), three-toed woodpecker (*P. tridactylus*), and downy woodpecker (*P. pubescens*) (Block, unpublished data). These species were rare in comparison to the hairy woodpecker as the relative abundance of each species versus the hairy woodpecker was 0.048, 0.025, and 0.006, respectively based on the average detections per point-count station.

I employed a space-for-time substitution to create a chronosequence (Pickett 1989) of fires by year post-burn (1, 2, 3, and 6, 7). I believe that the pre-stand structure across the different burned areas was similar based on each site's USFS stand structure classification. Tree size data (mean diameter at breast height) were taken two-years post burn in the Horseshoe-Hochderffer fire during a previous study on the same study sites (Dwyer and Block 2000). I compared the distribution of tree sizes at two-year post-burn from the Horseshoe-Hochderffer fire to data collected from this study within the Pumpkin fire and found substantial overlap for both the high-severity ($\bar{X} = 23.85 \text{ cm} \pm 3.6 \text{ SD}$ [n=44], Horseshoe-Hochderffer fire, $\bar{X} = 22.21 \text{ cm} \pm 7.1 \text{ SD}$ [n=42], Pumpkin fire) and the moderate-severity ($\bar{X} = 32.6 \text{ cm} \pm 8.2 \text{ SD}$ [n=54], Horseshoe-Hochderffer fire, $\bar{X} = 27.2 \text{ cm} \pm 8.2 \text{ SD}$ [n=36], Pumpkin fire). The similarity in means and considerable overlap in standard deviation suggest that mean tree size distributions

for each burn severity was comparable across sites. Additionally, I analyzed the relative abundance of hairy woodpeckers in unburned forests before and after fire, to test if basal population levels prior to wildfire were similar in two unburned areas and found no differences (see Relative Abundance below).

HAIRY WOODPECKER RELATIVE ABUNDANCE

Field Methods. Hairy woodpeckers relative abundance was estimated by point-counts. Points were located along transects established by J. Dwyer and W. Block (2000), within the Horseshoe-Hochderffer and Pumpkin burn areas. Transects were located within a swath of specific burn severity, high, moderate or unburned, large enough to encompass a transect with a minimum of three points. Points were separated by 200 m on average and had 100 m buffer zones between the transect and the swath edge. One hundred fifty points were evenly distributed across the two burn severities and unburned control. One ten-point transect line burned during summer 2000 by the Pumpkin fire (Table 3). All points were counted four times during each winter (1997-present). Five observers counted all birds seen or heard at all distances for an 8-min period following a 1-2 min waiting period.

Data Analysis. Because the Pumpkin burn only contained 10 points, I randomly selected 10 points from the Horseshoe-Hochderffer burn to use for analysis. I then compared relative abundance estimates from the randomly selected points to the entire data set and to five other randomly selected sets of 10 points. No difference was detected for birds/point for year or severity using 2-way ANOVA with Bonferroni adjustment, $\alpha = 0.05$ (Zar 1999, 231, Netter et al. 1996, 157). I therefore used the entire data set for analysis because analysis of variance procedures are robust to differences in sample sizes. To address likelihood of hairy woodpecker detection probabilities, I used Distance 3.5 (Thomas et al. 1998) to estimate detection probability functions for each severity within each year post-burn. This method allows for the standardization of variability due to detection differences caused by observer bias, environmental conditions, and the nature of the organism's state (Anderson 2001). Because most detection functions were between 90-100% of each other, I felt that birds in each treatment combination

had the same likelihood of detection. Therefore, I am confident that the abundance index of birds/point is a satisfactory assessment of abundance.

To determine the basal population of hairy woodpeckers at unburned sites in comparison to sites that experienced wildfire, I analyzed a greater dataset on hairy woodpecker abundance in unburned areas (Block, unpublished data). Data were collected using the same field methods described above. Data from three unburned sites were compared; two that did not experience wildfire and one that burned during the Pumpkin fire in 2000. Abundance indices at each unburned site were compared over six years using 2-way ANOVA and Tukey's HSD for multiple comparisons, (Zar 1999, 177, Netter et al. 1996, 725).

Abundance indices from burned points were analyzed with 2-way ANOVA and Tukey's HSD for multiple comparisons (Zar 1999, 177, Netter et al. 1996, 725). Abundances in unburned areas were tested for differences between season (2001-2 and 2002-3), using *t*-tests (Zar 1999, 122). Because no differences were found, these data were pooled and one overall value for these control plots is presented for comparative purposes with the abundance data for burned sites. No parametric tests were performed on burned versus unburned abundances as years were pooled for unburned sites but not for burned sites and because post-burn age does not equate to unburned season. Instead, Dunnett's control comparison test was used to compare burned abundance means to the unburned abundance mean (Zar 1999, 217). This test allows for the preservation of Type I error rates at $\alpha = 0.05$ when comparing a control (unburned) to multiple treatment means (severity by year). This allows for the comparison of abundance indices that have multiple post disturbance ages, to one that is "undisturbed" (unburned control). This provides the quantification of a reference condition to a disturbed condition in multiple states for discussion purposes.

DIURNAL HOME RANGE

Field Methods. Hairy woodpecker home range size was studied through radio telemetry. I mist-netted hairy woodpeckers between 18 October and 18 December each year (13 in 2001-2 and 12 in 2002-3). Unmarked birds were located by foot searches using auditory and visual cues and birds were attracted to nets with tape playback (hairy woodpecker and northern pygmy-owl

[*Glaucidium gnoma*] calls). Each bird was individually marked (USFWS band, 2 color bands) and fitted with a 1.8g BD-2 transmitter (Holohil Ltd., Canada). Transmitter weight was approximately 3% of the bird's body weight. Transmitters were attached to a single central tail feather (2001-2) or to both central tail feathers (2002-3) with an epoxy based glue and secured with dental floss. Transmitters lasted approximately 14 weeks.

I located birds from 22 October to 14 March in each winter between the hours of 0715 and 1815. Individuals were tracked to within 10-15 m using radio telemetry and then visually located by auditory or visual cues or to within 5 m if the bird was sensitive to the observer. Locations recorded for birds within 5 m of the observer were used for home range estimation. Locations during which the bird could be observed were used for both home range estimation and for foraging behavior analysis (see Foraging Behavior section). After a transmitter failed, observers would survey the known home range and beyond by several hundred meters to locate the bird using auditory cues. Searches continued until the bird was found. Once the individual was located, its identity was verified by its color band combination.

I attempted to locate each bird 50 times during the study period (Seaman et al. 1999) with a minimum of 30 (Worton 1987). Individuals were located once per day (Swihart and Slade 1985b) except when the goal of 50 locations was unlikely to be met. In this case, I located birds 2 times/day with successive locations being separated by a minimum of 4 hours (Appendix A). Once a bird was located, I recorded the following data: location as captured by a global positioning system (Trimble GeoExplorer 2 or Garmin 12), bird identity (transmitter frequency or color band), time, weather, burn severity within a 25 m radius (habitat type), and vegetation structure surrounding the bird (small-scale patch), the selected tree and four closest surrounding trees. The small-scale patch characteristics, tree density, patch diameter at breast height (average of all DBH values), and patch bole scorch was measured using point-center quarter method (Cottom and Curtis 1956). For this method, the distance from the tree selected by the bird to the four closest trees, one per cardinal quadrant, was measured and the following data were collected for all five trees: tree DBH and height (using a DBH tape and clinometer), whether the tree was topped (top section of the trunk felled), and percent tree bole scorch (percent of tree bole burned, unburned, and percent bark on tree bole missing). For cases in which birds could only be located

to within 5m of the observer, the tree closest to the estimated position of the bird was measured as the central tree for the point-center quarter measurements.

Data Analysis. Analysis of diurnal home range was limited to between 0800 and 1600 because night roost searches during the second winter showed a significant proportion of roosts were located outside the diurnal home range, and travel to and from roosts occurred outside of the above time period. Therefore, I only estimate the portion of the home range an individual used for foraging and other diurnal activities (Wilson 1975).

I used 30-50 locations to estimate diurnal home range size using non-parametric kernel estimation. Several authors have shown through mathematical modeling that 30-100 independent locations were needed for kernel methods of home range estimation to perform reliably (Worton 1987, Seaman et al. 1999). I considered location points to be independent if taken 1-2 times per 24-hour period as recommended in Swihart and Slade (1985b). I estimated the 85% home range using animal movement extension (Hooge and Eichenlaub 1997) in ArcView 3x. I agree with Seaman et al. (1999) that the 95% home range estimate is less biologically meaningful, and therefore report only the 85% contour interval. In this study, points where birds exhibited escape maneuvers from observers rather than normal foraging or other diurnal activities were most frequently in the 95% probability contour.

Home-range size based on the 85% kernel was log transformed to account for increasing variability across burn age and regressed against years post-burn using linear regression (Netter et al. 1996, 10). For this analysis, I pooled across sex because I did not have adequate samples of males and females within each burn age. Studies on other woodpecker species have detected no difference in home range size between the sexes (e.g. the downy woodpecker [*P. pubescens*] Matthysen et al. 1993).

CONSPECIFIC FORAGING.

Field methods. To assess the relative frequency that hairy woodpeckers foraged with conspecifics, each time a bird was located (radio telemetry or foraging observations), all conspecifics within 25 m were recorded, similar to methods in Hogstad (1991) and Matthysen et

al. (1993). The total number of birds, the sex of each bird, and the distance from each conspecific to the focal bird were approximated to within 1 m.

Data Analysis. I regressed the proportion of encounters in which birds foraged in groups of 2 or more hairy woodpeckers against years post-burn using linear regression (Netter et al. 1996, 10), in both the high and moderate severities, for the Rodeo/Chediski, Pumpkin, and Horseshoe/Hochderffer fires. Because encounter rates between conspecifics could be driven by differences in relative abundance alone, I modeled the expected rates of encountering 2 or more hairy woodpeckers foraging together given the relative abundance of birds within each treatment (severity by year post-burn). Expected encounter rates were calculated using the Poisson distribution (Zar 1999, 572, μ = relative abundance). I could not model encounter rates for the Rodeo-Chediski Fire (1 year post-burn) because woodpecker abundance was not estimated. Observed and expected numbers of observations in which hairy woodpeckers foraged alone or with conspecifics were compared using χ^2 contingency tables for each treatment combination (Zar 1999, 461). Aggregate significance within a burn severity was analyzed by combining all χ^2 values for each year post-burn (Fisher 1950, 99). Unburned conspecific and solo foraging rates were also compared between years using χ^2 (Zar 1999, 461) and against random Poisson distribution of rates expected by relative abundance in unburned forests for comparison.

To determine when conspecific encounter rates in a burned area were no different than those found in unburned forests, I compared the conspecific foraging rates and solo foraging rates found in unburned areas to those found in the moderate and high severities, for the oldest post-burn ages. Because relative abundance patterns suggested that encounter rates should approach that of the unburned severity only in the older burn (Horseshoe-Hochderffer Fire), I only tested rates from years 6 and 7 post-burn to unburned encounter rates using nominal logistic regression for severity and years post-burn (Netter et al. 1996, 608).

FORAGING BEHAVIOR

Field methods. Foraging behavior and selected habitat components for foraging by hairy woodpeckers was assessed using focal animal observation (Altman 1974). Radio-tagged and unbanded birds were located by radio telemetry or by area searches using auditory and visual

cues to locate individuals. Area searches were conducted by systematically searching 300 m belt-transects centered over point-count stations (Morrison and With 1987, Loose & Anderson 1995, Murphy and Lehnhausen 1998). Transects were searched 2-5 times per season with repeated sampling at different times of the day to account for temporal changes in foraging patterns. Prior to recording foraging data, I waited 10 sec to allow the bird to acclimate to the observer's presence and return to normal foraging behavior (Hejl and Verner 1990). If the bird expressed agitated behavior (e.g. cessation of foraging, climbing to the top of the tree, or becoming vigilant), I waited until the bird flew to another tree and observed at a greater distance. Once the bird left the area, the tree and patch used for foraging was measured. I recorded the following data for each bird: (1) transmitter frequency or color band (when possible), sex, age, and location (distance from nearest point-count station or GPS location), (2) foraging method (glean – removal of prey from the surface or crevices of the bark, peck/scale – prey is found through removal of bark, excavate – forceful removal of bark to get to prey in the sapwood), (3) substrate (branch or trunk), (4) substrate condition (burned, unburned, bark missing), (5) size of substrate (15 cm increments using the bird size as a reference), (6) foraging height of the bird (using a clinometer), (7) selected tree DBH and height (using a DBH tape and clinometer), if the tree was topped, and tree burn condition (percent of tree bole burned, unburned, and percent bark on tree bole missing), and (8, 9) habitat type and small-scale patch selection (see Diurnal Home Range field methods). Observations on sequentially encountered birds were considered independent if the next bird was of the opposite sex or uniquely marked. Otherwise, sequential observations made at least 250 m apart from each other were considered different individuals (Block 1991).

To compare vegetation characteristics of locations where hairy woodpeckers were observed foraging to randomly selected sites, I constructed 100 m² grids within home range minimum convex polygons using a Jenness Enterprises script in ArcView ("Convex hulls and Sample Points", Jenness 2003). I then used point-center quarter at each grid intersection and measured the same variables as those taken for foraging observations. These data were collected during the last month of each season. Data were collected only in areas within home ranges to

ensure comparison of selected to random habitat within areas used by hairy woodpeckers. Within belt transects, vegetation was measured at the three closest point-count stations.

Data Analysis. Because transects were searched multiple times, I sampled individual birds repeatedly ($\bar{X} = 2.9 \pm 1.3$ observations/bird/severity). However, most repeated observations were made after sufficient time for me to consider each observation independent (24.5 ± 17.6 days). Further, within each analysis, any one individual did not account for more than $7 \pm 5\%$ of the total observations and therefore did not weight the analyses towards a single individual.

To determine whether radio-transmitters affected foraging behavior, we compared foraging observations of birds with radio-transmitters to unmarked birds during the 2001-2002 winter for all foraging variables. Two-sample *t*-tests with Bonferroni adjustments for multiple tests found no significant differences between groups (Zar 1999, 122, Netter et al. 1996, 157). Therefore, I pooled birds with radio-transmitters and unmarked birds for foraging behavior analysis.

To quantify habitat selected by hairy woodpeckers for foraging within their home ranges, I compared five selected habitat components to their respective mean present, three small-scale patch characteristics, and two tree characteristics. Patch characteristics were calculated using the point-center quarter method and included: patch DBH (average of all five trees), density (average distance from the focal tree to each quadrant tree), and patch bole scorch (surface area of each tree multiplied by the percent of bole scorched, then summed for all five trees). Tree characteristics compared included selected tree DBH and selected tree bole scorch (measured as surface area). Data were transformed to satisfy normality and equal variance concerns (Zar 1999, 273). The distribution of habitat components selected by hairy woodpeckers, were compared to the distribution of those components measured at random, across burn severity and burn age using 3-way ANOVA with Bonferroni adjustments for five multiple tests (Netter et al. 1996, 989, 157). Tukey's HSD test for multiple comparisons was used to compare differences among treatments (Netter et al. 1996, 725).

Comparing observations taken in burned and unburned ponderosa pine may provide insight into how long a burn may affect foraging behavior of hairy woodpeckers. I analyzed use

versus present habitat variables in unburned areas for each season (2001-2 and 2002-3), except those quantifying burn characteristics, using two-way ANOVA with Bonferroni adjustment for three multiple tests (Zar 1999, 231, Netter et al. 1996, 157). Because data were not different by year for all three variables, data were pooled and retested using *t*-tests with Bonferroni adjustment for three multiple tests (Zar 1999, 122, Netter et al. 1996, 157). These data are presented along with burned data in figures, but no parametric tests were performed on burned versus unburned as years were pooled and post-burn age does not equate to unburned season. Dunnett control comparison test was used for habitat components that did not summarize bole scorch characteristics (Zar 1999, 217). I tested the group of selected means for three habitat components, for each year post-burn, within both severities (eight means total), to the unburned mean.

I compared selection of tree and within tree habitat components by males and females to assess intrasexual behavioral differences. Foraging height, DBH, and substrate choice (branch versus trunk), were tested for differences in sex, burn severity, and burn age using 3-way ANOVA or log-linear analysis in the case of substrate choice with Bonferroni adjustment for three multiple tests (Zar 1999, p282, Netter et al. 1996, 608, 157). If no differences were found for severity, data were pooled and tested for difference in year post-burn using two-way ANOVA or χ^2 contingency analysis with Bonferroni adjustment for multiple tests (Zar 1999, 231, 461, Netter et al. 1996, 157). Tukey's HSD test for multiple comparisons was used to compare differences among treatments (Netter et al. 1996, 725). These analyses are termed selection by sex analyses below and are presented with unburned data for comparison and discussion.

Woodpeckers have been shown to alter their foraging behavior in the presence of the opposite sex (Austin 1976, Hogstad 1991). I therefore compared the foraging behavior within each sex when foraging alone or in the presence of the opposite sex. Tests were performed only when selection of tree or within-tree habitat component differed significantly by sex as indicated by the selection by sex analyses. If the selection by sex analyses resulted in non-significance for severity, data were pooled across this factor. Nominal logistic regression or two-way ANOVA

were used for categorical and continuous data analysis for sex by “alone versus with” by years post-burn (Netter et al. 1996, 608, Zar 1999, 231).

INSECT DENSITY

Field Methods. In winter 2001-2002, bark samples were collected from high-severity areas in the Pumpkin and Horseshoe-Hochderffer burns, across an area of 400 ha. At each high-severity point on the 100 m² vegetation grid (see Foraging Behavior) one tree was randomly selected for the sample. I attempted to remove an equal number of bark samples from four size classes of trees (as defined in Foraging Behavior). Samples were taken from the vertical face of the trunk, 2 m above ground, using a cordless hand held drill and hole-saw. Two meters above ground was thought to be an appropriate height as it is in the height range for several prominent bark dwelling arthropod species in the study area (Amman et al. 1985). Surface area of samples was 102 cm² of bark but varied in thickness due to differences in tree size.

In winter 2002-2003, samples were taken from the Rodeo-Chediski, Pumpkin, and Horseshoe-Hochderffer burns and from both the high and moderate-severity, across an area of approximately 700 ha. In the Rodeo-Chediski burn, samples were taken at four points, one per cardinal direction, 71 m from the location of each hairy woodpecker foraging observation creating a 100 m sampling grid, because home range and vegetation grids were not established at this site. In the Pumpkin and Horseshoe-Hochderffer burns, samples were removed from 80 randomly selected points from the 100 m² vegetation grid (40 samples/severity). Because analysis of first year samples indicated no difference in insect density by tree size, I took samples from trees ≥ 20 cm DBH because logistically it was the most efficient. If the sample did not peel from the trunk easily, I used a chisel and hammer to separate the bark from the cambium. If this process removed any cambium or wood, I dressed the tree wound with sealant. Samples were placed into zip lock bags and the following tree data was recorded: proximity to burn severity edge, surface area of bole scorch, and DBH. Samples were then stored in freezers until x-raying.

I used a Faxitron 2500, model 805400, to x-ray bark samples. X-raying bark was shown to detect 95% of the bark dwelling insects in comparison to dissection method by Fatzinger and

Dixon (1965) and has been used for studying southern pine beetles (Coulson et al. 1979, Conner 1979). The power setting was 20-kVp and exposure time increased from 2 to 3 minutes with increasing thickness. Radiographs were examined under a 5x magnifying glass and all insect larvae and adults counted. If larvae could be identified as either bark beetle or woodborer it was recorded as such, otherwise insects were recorded as large ($>0.5\text{cm}$) or small ($<0.5\text{cm}$).

Data Analysis. I tested if the density for all larvae varied across burn age and between moderate and high-severity using negative binomial regression (Zar 1999, 577). Post hoc tests were adjusted by hand to maintain type one error rate at $\alpha=0.05$.

For all parametric analyses, SPSS ver. 10.1 (SPSS, Inc. 2002) was used. Extreme outliers (Zar 1999, 86) were determined by SPSS explore function and removed if greater than three standard deviations from the mean. If data were non-normal, transformations were performed as suggested by SPSS or Zar (1999). For all non-parametric analyses, JMP_{IN} ver. 4.0.4 (SAS Institute 2001) was used. Type-one error rates were held at $\alpha = 0.05$ for all tests, unless indicated as adjusted by Bonferroni method. All means are given with \pm standard deviations in the text and only + standard deviations in the figures, with the exception of the insect analysis in which means are given with standard errors.

RESULTS

HAIRY WOODPECKER RELATIVE ABUNDANCE. Hairy woodpeckers were detected significantly more often in burned sites than unburned sites of ponderosa pine forests ($F_{10, 77}=15.25, p<0.001$, Figure 2). Relative abundance on unburned sites did not differ from each other by year (Tukey HSD all p -values >0.05). Relative abundance in burned sites differed from unburned sites for years 2000 and 2001 but not 2002 (Tukey HSD years 2000 and 2001 p -values <0.05 , year 2002 $p>0.05$).

Abundance estimates for hairy woodpeckers also differed by burn severity and age (Figure 3). Hairy woodpecker relative abundance decreased with burn age ($F_{7, 207}=10.7, p<0.001$), with abundances reaching that of unburned areas by 7 years post-burn for both burn

severities (Dunnett's control test, $p > 0.05$). At two and three years post-burn, relative abundance of hairy woodpeckers was greater in the high-severity burn than the moderate-severity burn (Tukey's HSD, all p -values < 0.05). Over time, however, hairy woodpecker abundance in the high-severity burn approached that of the moderate-severity and by six years post-burn, they were not significantly different (Tukey's HSD all p -values > 0.05).

DIURNAL HOME RANGE. Twenty-five hairy woodpeckers were fitted with radio-transmitters to assess how home range size changed across burn age. Of the 25 radio tagged birds, 16 birds retained working transmitters long enough to accumulate the required number of locations to estimate home range size (Appendix A). Of these 16 tagged and monitored birds, seven (2 females and 5 males) retained their transmitters during the first winter and nine (3 females and 6 males) during the second. Female (182) was radio-tagged in the Horseshoe-Hochderffer burn in 2002 and covered an abnormally large area. The 95% probability contour estimate of this female covered an area of 636.8 ha (3.7 times the average) and her 85% contour was 380.6 ha (3.8 times the average). I considered her nomadic and therefore eliminated her home range estimate from the analysis. Home-range size for all other hairy woodpeckers was estimated at the 85% contour and increased positively with years post-burn ($R^2 = 0.71$, $F_{1,13} = 32.1$, $p < 0.001$, Figure 4). Average home range size from youngest to oldest burn age was 7.85 ± 4.8 ha, 13.5 ± 16.4 ha, 65.3 ± 9.7 ha, and 146.4 ± 83.2 ha. While both males and females were caught within the same burn age only during the second winter (2002-2003), female home ranges were found to be both larger and smaller than male home ranges at the same site. Combined averages for females and males for that season were 69.9 ± 72.0 ha ($n=2$) for females and 69.7 ± 83.6 ha ($n=6$).

CONSPECIFIC FORAGING. The proportion of time hairy woodpeckers spent foraging with one or more conspecifics decreased significantly with burn age for both the high ($R^2 = 0.89$, $F_{1,4} = 33.2$, $p = 0.005$, Figure 5) and moderate severities ($R^2 = 0.85$, $F_{1,4} = 17.96$, $p = 0.024$). There was no difference between high and moderate severities in proportion of time that hairy woodpeckers spent foraging with conspecifics ($\chi^2 = 0.95$, $p = 1.0$). I found significantly higher

encounter rates in both the high ($\chi^2_4 = 226.2, p < 0.001$) and moderate-severity ($\chi^2_4 = 173.7, p < 0.001$) than expected when expected encounter rates were modeled from relative abundance alone. In all treatment combinations, the hairy woodpeckers were more commonly found with conspecifics than what would be expected at random (all p -values less than 0.001, Figure 6).

In unburned forests, encounter rates were also greater than what would be expected by random based on relative abundance for both years tested (2001-2: $\chi^2_1 = 42.6, p < 0.001$, 2002-3: $\chi^2_1 = 22364.3, p < 0.001$). There was, however, no difference between years in unburned forests ($\chi^2_1 = 0.476, p = 1.0$), suggesting hairy woodpecker conspecific foraging encounter rate remains constant in burned areas. Conspecific foraging rates were significantly different when tested between moderate-severity, high-severity, and unburned forests for year 6 and 7 ($\chi^2_5 = 32.5, p < 0.001$). While year was significant ($\chi^2_1 = 9.96, p = 0.0016$), severity and the interaction between severity and year were not ($p = 0.39, p = 0.74$). Therefore, conspecific foraging rates in unburned forests are significantly different than rates in either severity at 6 years post-burn but not 7 years post-burn.

FORAGING BEHAVIOR. *Habitat Selection* –All tree and patch habitat components selected by hairy woodpeckers differed significantly from that available within their home ranges with the exception of tree density (all corrected models, $p < 0.0001$, Figure 7a,c-e). The mean tree sizes (DBH) selected by hairy woodpeckers for foraging, across all burn severities, years post-burn, and in the unburned areas ranged from 30 ± 15.4 to 42 ± 15.1 cm (Figure 7a). Trees sizes selected as foraging sites were consistently larger than the mean DBH available ($F_{1, 852} = 32.7, p < 0.001$) within both severities, although differences in the moderate-severity were less pronounced ($F_{1, 852} = 8.27, p = 0.021$). DBH of available trees increased across burn age within high-severity burns but remained more constant within moderate- burn severities, although the interaction was not significant ($F_{3, 852} = 3.12, p = 0.13$). Regardless of burn age, mean tree size selected was consistently larger than that available ($F_{3, 852} = 1.35, p = 0.26$). One exception was found in the moderate burn at 3 years post-burn age (Tukey's $p > 0.05$, Figure 7b). Hairy woodpeckers also chose trees with greater DBH than the average available in unburned ponderosa pine ($t_{68} = 5.75, p < 0.001$). Mean DBH of selected trees in unburned forests did not

differ from those across all moderate post-burn ages nor high-severity burns 6 and 7 years post-burn (Dunnett's test, $p > 0.05$).

Hairy woodpeckers selected patches with a larger average tree size (patch DBH) than available at random points, but only in high-severity burns ($F_{1, 849} = 9.3$, $p = 0.01$, Figure 7c). Through time, selection of mean patch DBH was greater than available and both selected and available mean DBH increased as a function of burn age ($F_{3, 849} = 2.5$, $p = 0.29$). Average patch DBH selected by hairy woodpeckers in unburned areas was significantly greater than what was available ($t_{64} = 3.72$, $p < 0.001$) but selected patch DBH was not different from patch characteristics selected in the moderate-severity for any post-burn age. Selection of unburned patch DBH was different from patch DBH selected in the high-severity for years 2 and 3 post-burn but not 6 and 7 (Dunnett's test, $p < 0.05$).

Hairy woodpeckers did not select patches with tree densities different than that available ($F_{1, 857} = 5.34$, $p = 0.11$, Figure 7d). Available tree densities did differ by burn severity and age ($F_{3, 857} = 22.6$, $p < 0.001$). Tree density within the high-severity burn was greater than in the moderate-severity but approached that of moderate-severity by 6 years post-burn (Tukey's $p > 0.05$). In unburned portions of the forest, hairy woodpeckers selected patches with lower tree density than available ($t_{65} = -2.44$, $p = 0.017$). The selected tree density within unburned patches did not differ from those in the moderately burned severity for all burn ages, nor for 6 and 7 years post-burn in the high-severity burn (Dunnett's test, $p > 0.05$), but did differ from high-severity selection of tree density at 2 and 3 years post-burn.

Hairy woodpeckers selected trees with greater bole scorch than the available average in both burn severities ($F_{1, 885} = 2.1$, $p = 0.735$, Figure 7d). Within both high- and moderate-severity burns, the amount of bole scorch selected by hairy woodpeckers was greater than available for all burn ages except 7 years post-burn ($F_{3, 856} = 5.0$, $p = 0.01$, Tukey's HSD all p -values < 0.05 , except 7 years post-burn). Bole scorch within the high-severity on selected and available trees was consistently greater than bole scorch in the moderate-severity for both selected and available trees at all burn ages ($F_{3, 885} = 2.8$, $p = 0.2$).

Similar to selection of tree bole scorch, hairy woodpeckers consistently selected patches with greater total bole scorch in both the moderate and high-severity burns ($F_{1, 847} = 5.85$, $p = 0.08$,

Figure 7e). This pattern remained consistent at all years post-burn except in year 7, where in both severities selection of patch bole scorch was no different from what was available ($F_{3, 847}=10.2, p<0.001$, Tukey's HSD all $p<0.05$, except for 7 years post-burn).

Selection by Sex. The foraging methods used by hairy woodpeckers did not differ between the sexes for either severity or years post-burn ($\chi^2_3=3.63, p=0.3$). Both sexes used scaling significantly more than gleaning (77%, $W=15.7, p<0.001$). Additionally, males and females did not show a difference in their use of foraging methods within unburned portions of the study area ($\chi^2=2.4, p=0.12$) with both sexes scaling approximately 70% of the time. Woodpeckers were found excavating trees in only five percent of the observations (14 of 277), therefore this behavior was not included in these analyses. Males and females did not differ from each other in either foraging height ($F_{1, 598}=0.53, p=0.47$, Figure 8a) or selection of tree size (DBH) for foraging sites ($F_{1, 601}=0.48, p=0.48$, Figure 8b) for burn severity or burn age. Similarly, no intersexual differences were observed for these behaviors in unburned forests (foraging height: $t_{40}=-0.31, p=0.76$, tree DBH: $t_{41}=-0.14, p=0.88$). The sexes did differ, however, in their use of substrates through time but not by severity ($\chi^2_7=141.8, p<0.001$, Figure 8c). Males and females selected trunks similarly at 2 years post-burn (males = 89% and females 80%, $W = 0.355, p=0.551$). As the burn aged however, females switched to using branches significantly more ($\bar{X} = 65\%$ for all years, all p -values <0.001), while males maintained use of trunks ($\bar{X} = 85\%$, all p -values >0.24). The difference in use of branches and trunks in the unburned portions of the study area was also maintained ($\chi^2=11.3, p<0.001$). This behavior was not dependent on the presence of a member of the opposite sex, as there was no difference in substrate use between observations made when birds foraged alone and when they foraged with a member of the opposite sex ($\chi^2_5=6.97, p=0.22$).

INSECT DENSITY. Insect density varied through time ($\chi^2_4=22.94, p=0.001$, Figure 9) but not by severity ($\chi^2=1.72, p=0.19$). Insect density one-year post-burn (Rodeo-Chediski fire) was significantly different than that found in the two-year post-burn ($p=0.001$). Two-year post-burn (Pumpkin fire) insect density was also significantly different than 3 (Pumpkin fire), 6

(Horseshoe-Hochderffer), and 7 (Horseshoe-Hochderffer) years post-burn (all p values < 0.001). Multiple comparisons for all other years were not significantly different (all p -values > 0.77).

DISCUSSION

Temporal variability in the importance of burned versus unburned habitat.

Abundances of hairy woodpeckers in unburned areas remained stable for six years. In contrast, relative abundance of hairy woodpeckers in my study area increased dramatically following wildfire (14-fold increase at one year post-burn and 18-fold increase at 2 years post-burn, relative to unburned). At three years post-burn, however, hairy woodpecker abundance declined until I observed no difference with unburned forest by seven years post-burn. The initial increase in woodpecker abundance documented here was similar to that found by Brawn and Balda (1988), Raphael et al. (1987), and Hobson and Shieck (1999). Similar to my study, Kreisel and Stein (1999) found that hairy woodpecker relative abundance returned to that of unburned sites four years following wildfire. The pattern of a large, dramatic increase in relative abundance followed by a decline to that of unburned areas suggests that wildfire provides an ephemeral benefit to hairy woodpeckers.

The proximate benefit of fire-disturbed areas is the increase in food abundance, primarily bark-dwelling insects (Miller and Patterson 1927, Bradley and Tuller 2001). Burned trees are 24% more likely to be attacked by bark-dwelling arthropods than unburned trees (Bradley and Tuller 2001). At a larger scale, Machmer (2002) found a 170% increase in insect densities in burned study sites relative to unburned controls. Because fire occurred regularly in the ponderosa pine forests of northern Arizona prior to European settlement (Covington et al. 1997), fire undoubtedly had significant effects on bark-dwelling arthropod distribution and density. Although I did not measure insect density in unburned forests, the pattern of insect density in post-burn ponderosa pine forests reflected that of hairy woodpecker abundance. My data show that insect densities increased in the high-severity burned areas before the onset of the first winter. During the first full summer post-burn, insect densities rose to their peak level, making them available for the second winter. At three years post-burn, however, insect densities leveled

off. Significant increases in bark-dwelling arthropods following fire were documented in other studies. For example, Santoro et al. (2001) found a doubling of *Ips pini* in burned plots. A similar temporal pattern in insect density was shown by the spruce beetle (*Dendroctonus rufipennis*) (McCambridge and Knight 1972). Additionally, in areas where bark beetles responded to low-intensity fire, irruptive population levels return to endemic levels by 3-5 years post-fire (Ryan and Reinhardt 1988, Weatherby et al. 1994, Gibson et al. 1999). Nappi et al. (2003) suggest that burns approximately 2 years old may have the highest insect densities because this is when woodborers surface into the bark to feed. The ephemeral benefit of wildfires in this area was likely insect densities, as hairy woodpecker abundance and insect density covaried.

Hairy woodpecker diurnal home range size increased with burn age, corresponding to the decreasing insect abundance from 2 through 3 years post-burn. Shifts in seasonal home range size have been documented for other woodpecker species. However, to my knowledge, this is the first study that has documented changes in winter home range size over multiple years. Because food is both less abundant and non-replacing during winter and extreme temperatures make the acquisition of food critical, home range size should increase during winter relative to summer. For example, lesser-spotted woodpeckers exhibited a 17-fold increase in home range size during the winter (Wiktander et al. 2001). While the relationship between food abundance and home range size has been shown for other species of birds empirically (MacArthur and Pianka 1966, Eniksson and Nilsson 1983, van Riper 1984), studies on woodpecker species have only suggested this relationship. Renken and Wiggers (1989) found that pileated woodpecker, (*Dryocopus pileatus*) home range size was inversely related to downed wood, the favored foraging substrate, and Rolstad and Rolstad (2000) found that black woodpecker (*Dryocopus martius*) home ranges were proportional to the area used for feeding. Neither study, however, measured prey abundance. In this study, home range size increased with burn age. The increase over the first few years was associated with a decrease in the abundance of wood-boring insects available in the trees I sampled. However, in the older burns, insect abundance per tree remained relatively stable while home range sizes continued to increase. Increased home range size was likely due to a continued decline in decreasing tree density (Figure 10a). The combination of an

initial decline in insect density and a continuous decline in tree abundance likely resulted in prey resources becoming increasingly dispersed across the landscape. In response, hairy woodpeckers may have compensated by increasing their home range.

Temporal changes in sexual segregation of foraging behavior

Because prey abundances in the burned areas decreased through time and across space, competition for those resources likely increased. The amount of direct interference an individual could withstand from its mate or other conspecifics should decrease as competition increases. In fact, the probability that hairy woodpeckers would be foraging in the vicinity of conspecifics did decline through time, consistent with the decline in insect and tree abundance. Although high foraging encounter rates could simply be the result of greater hairy woodpecker abundance in younger burns in comparison to older burns, when conspecific foraging rates were modeled on relative abundance estimates using the Poisson distribution, observed encounter rates were still higher than expected from the models for each year post-burn. At 7 years post-burn, conspecific foraging rates did not differ from those found in unburned areas. The need to maintain pair bonds throughout the winter may have resulted in the higher than expected conspecific foraging rates. If competition between the sexes increases through time, yet pair bonds still need to be maintained, the sexes may alter behavior in other ways to reduce intersexual competition. Selander (1966) suggested that when interspecific competition was low, intraspecific competition would increase because males and females would more fully exploit their available niches. In my study area, interspecific competition was probably negligible due to the relative rarity of other woodpecker species. Thus, intraspecific competition was expressed by a divergence in foraging behavior between the sexes, presumably in response to the decreased abundance of insects. This segregation was observed as a shift in female use of foraging substrates, from use of trunks in the young burns to primarily branches as the burns aged. In contrast to some studies (Kilham 1965, 1970; Murphy and Lehnhausen 1998) and consistent with others (Conner 1993), I detected no intersexual difference in foraging method. This may be due to the location of bark-dwelling insects within the tree. Black-backed woodpeckers fed primarily on woodborers that inhabit the sapwood of the tree and therefore required excavation (Murphy

and Lehnhausen 1998). In northern Arizona, most bark-dwelling insects were located within the bark or at the cambium (Amman et al. 1985, DeMars and Roettgering 1982), which could be acquired through scaling, the dominant foraging method used by both sexes at this study site.

Several authors have suggested that female woodpeckers changed their behavior due to the dominance of males (Williams 1980, Hogstad 1991, Pasinelli 2000b). However, I found that female foraging behavior remained consistent whether males were present or not. Females may be able to exploit branches more profitably because of subtle differences in bill morphology (Miller et al. 2003). Hanula and Franzeb (1998) found that dead branches did not differ from trunks in insect density, nor did I detect a difference in the first year of this study. Thus, at least with respect to insect density, females do not appear to be forced into a lower quality foraging niche.

Effects of burn severity on hairy woodpecker behavior

Within a burned area, fire creates a mosaic of burn severities because differences in pre-fire stand structure affect how fires burn across the landscape (Turner and Romme 1994). In southwestern ponderosa pine forests, high densities of small trees provide abundant fuel and create increased vertical continuity (Covington and Moore 1994). This stand structure supports crown fire and results in high-severity burned areas (Turner and Romme 1994). In contrast, areas with more open stand structures promote lower severity fires (Covington et al. 1997). Vegetation data from this study followed this pattern, with high-severity fire occurring in areas characterized by high densities of small trees and moderate-severity fire occurring where small trees were more rare and overall tree density lower (Figures 10a, b). Scorch levels differentially affect burned tree susceptibility to insect attack, with a positive relationship between the amount of scorch and probability of attack (Furniss 1965, Flanagan 1996). Thus, areas with intense fire and high-severity scorch should have had greater insect densities than moderate-severity areas. Large swaths of high-severity fire-killed trees, like those created by the three fires studied here, likely provided attack sites for woodborers and bark beetles (Gibson et al. 1999, Santoro et al. 2001). Although I detected no difference in insect density per tree between burn severities, the greater density of trees in high-severity burns likely resulted in greater insect densities at larger landscape scales. Additionally, as vegetation structure changed through time, with severe

intensity areas losing small stems at a greater rate, the relative difference between the two burn severities also decreased.

Within young burns, hairy woodpecker relative abundance was greater in the high-severity than in the moderate-severity burned areas. As the burns aged, however, woodpecker abundance in high-severity burn areas declined rapidly, approaching that of moderate burns by year 3, and with no difference at 6 years post-burn. This pattern suggests that high-severity areas, while initially more attractive, were more transient in nature in comparison to moderate-severity. The lower but more persistent attractiveness of moderate-severity burns may be due to the slower change in vegetative structure and prey resources in that burn severity (Figure 10b). Moderately burned trees have high susceptibility to secondary mortality agents such as insect attack or drought that remove them from the population over several years (Salaman 1934, Flanagan 1996, McHugh and Kolb 2003). Moderately burned areas likely provide more protection from both extreme weather conditions and predators because live trees provide foliage cover. Initially, greater insect densities in high-severity areas may outweigh the greater foraging costs due to predation and exposure to weather, but eventually these areas may lose their attractiveness as insect densities decline.

Hairy woodpeckers' selection of all habitat components reflected these severity-driven differences in residual stand structure. Hairy woodpeckers selected both larger trees and patches with greater than average DBH, suggesting an avoidance of the dense, dog-hair stand structure that characterized much of the unburned habitat. However, when stands were severely burned, hairy woodpeckers foraged in these high-density stands. Hairy woodpeckers have been shown to select trees of similar sizes in other studies of unburned forests (43-50 cm, Morrison and With 1987, 33.6 cm Conner 1981b). Several species of *Dendroctonus* beetles found in northern Arizona prefer trees of larger DBH (20-40 cm) as hosts in unburned forests (e.g. *D. ponderosae* [Amman and Pasek 1986], *D. brevicomis* [Kaufmann and Stevens 1984]). In burned areas at this study site, density of insects per bark sample did not differ among trees of differing size. Instead, larger trees may simply offer a larger surface area of bark and thereby represent a more profitable foraging patch than smaller trees. Murphy and Lehnhausen (1998) also found that hairy woodpeckers used larger tree sizes within the first and second year post-burn in Alaska.

While other woodpecker species were present in their study, interspecific competition did not exclude this species from smaller tree sizes as all species used trees of similar size (DBH = 36-42 cm). No comparisons can be made at the patch level, as information on hairy woodpecker foraging ecology in burned areas is limited. In unburned forests, no differences were found for this and several other *Picoides* species at the patch level (Conner 1981b). Hairy woodpeckers selected patches with larger than available average DBH in unburned areas, which was not different than selected patches within the moderate-severity burn or the older high-severity burn. Additionally, selection of patches with a greater average DBH may reflect the lower limit of average tree size that hairy woodpeckers are willing to investigate for prey resources.

Hairy woodpeckers selected trees with greater scorch at both the tree and patch level. Again, this was likely because greater bole scorch was found to increase the likelihood of bark-beetle attack (Furniss 1965, Ryan and Reinhardt 1988). This is similar to Murphy and Lehnhausen's (1998) findings that hairy woodpeckers used trees with heavy scorch in a young stand-replacing fire. Because trees that sustain moderate-severity scorch do not die immediately and have greater susceptibility to secondary mortality agents, monitoring these trees would allow hairy woodpeckers to maximize their energy gain by selecting trees with higher insect densities due to greater scorch while avoiding trees with low insect densities from low scorch. In both burn severities, hairy woodpecker selection of scorched trees did not differ from the average available once the burn reached 7 years post-burn. This suggested that the higher initial insect abundances in scorched trees likely declined to levels similar to those found in unburned trees.

While hairy woodpeckers often selected specific sub-sets of habitat from what was available, their foraging behaviors only differed in the high-severity at young ages in comparison to those exhibited in the unburned forests. In the moderately burned areas, no foraging behavior differed from those exhibited in the unburned forests except their selection of trees with greater scorch. This suggests that birds respond to the visual remnant of fire in the form of bole scorch. Because larger trees in groups with greater average DBH that have experienced higher than average scorch likely have the highest rate of insect attack, hairy woodpeckers are presumably selecting the optimal structure for resource acquisition. Additionally, because hairy woodpecker behaviors did change when foraging in the high-severity young burn it suggests that both scorch

and high insect densities were proximate cues that the birds responded to. Lima (1983) found that a close congener of the hairy woodpecker, the downy woodpecker, monitored habitat quality at the small patch scale (four simulated trees) by food intake and energy gain.

Conservation and Management Implications

For resident bird species that experience extreme climatic conditions and non-renewable resources, habitat quality may be more important for over-winter survival than breeding success (Kreisel and Stein 1999) as most mortality in resident species occurs during this critical time period (Lack 1967, Graber and Graber 1983, Newton 1998). Based on the limited number of banded birds at my sites, over-winter survival as indicated by return rates was apparently higher in younger than older burns (89%, n=11, versus 70%, n=14, Covert, unpublished data). As a result, higher over-winter survival in young burns may have resulted in more birds available for breeding in the young burns relative to older burns. Each data set supports the idea that habitat in young burns was of greater quality to hairy woodpeckers than old burns, and that high-severity habitat was of greater quality than moderate-severity habitat for foraging, however no data set alone is in itself conclusive. For example, while hairy woodpecker relative abundance was greatest in young, high-severity burns, birds may have suffered greater predation rates in this more open habitat type (Van Horne 1983). However, when considered together, the consistency of patterns found in all data sets suggested differential quality in habitat resulting from wildfire. In northern Arizona's ponderosa pine system, wildfires significantly increased habitat value for hairy woodpeckers for 2-3 years post-burn by increasing bark dwelling arthropod density. The initial increase in resources allowed for high woodpecker abundance, small home ranges, high conspecific foraging rates, and low sexual segregation. As burned areas aged, insect abundance within trees decreased, trees became less dense, and habitat quality decreased. In response, hairy woodpeckers adjusted their use of habitat components to maintain adequate acquisition of food resources, by increasing home range size, decreasing time spent with conspecifics foraging, and increasing sexual segregation. While reproductive success of hairy woodpeckers in burned in comparison to unburned areas has yet to be studied, several studies on other woodpecker species have shown higher reproductive success associated with burned forests. For example, the black-backed woodpecker (*Picoides articus*) had greater reproductive output in young burned forests in

Idaho (Dixon and Saab 2000) and Lewis' woodpeckers (*Melanerpes lewis*) had their highest reproductive output in 2 year post-burn areas (Saab and Vierling 2001).

Turner and Dale (1998) suggested that species adapted to disturbance evolved in response to the relationship between the frequency of disturbance and the organism's life span. Hairy woodpeckers can live up to 16 years (Clapp et al. 1983), and under historical fire regimes in the southwest, could experience 1-8 low intensity fires and one large-scale fire during an average lifespan (Fulé et al. 2000 and 2003). High-severity patches may have occurred within the broader matrix of low intensity fires, thereby providing rich food resources in smaller patch sizes but at higher densities than are currently present in northern Arizona's ponderosa pine systems. In Mexican ponderosa pine forests that have not experienced fire suppression but are otherwise similar in structure to those in northern Arizona, high-severity patches of fire-killed trees ranged in size from several trees to several ha of trees (Fulé and Covington 1997). Fulé (pers. com.) hypothesized that similar patches of fire-killed trees occurred within Northern Arizona's ponderosa pine forests during low-severity fires and ranged in size from several trees to 1.2 ha with the former being frequent within a fire perimeter. Additionally, Sánchez-Martínez and Wagner (2002) suggested that natural bark-beetle outbreaks also occurred over relatively small areas historically, which could have limited this resource to burned areas. As a result, hairy woodpeckers may have evolved in a system dominated by prey-rich, small-scale disturbances within a broader forest matrix that harbored lower prey densities. Observations that woodpeckers are often rare in the interior of large high-severity burned areas (Murphy and Lehnhausen 1998) and the fact that hairy woodpeckers in this study used edges between high-severity and moderate-severity patches significantly more than the interior portions ($\chi^2_3=31.35$, $p<0.001$, Covert unpublished data) are consistent with the hypothesis that these birds may have evolved with historical fire regimes that produced small, high-intensity patches occurring at a high spatial frequency.

In conclusion, I agree with many authors who argue that the major decline in forest dwelling birds, especially woodpeckers, results from fire suppression (Raphael et al. 1987, Hejl 1994, Hutto 1995, Hobson and Sheik 1999, Brawn et al. 2001). I further suggest that how wildfire is returned to fire-adapted ecosystems is important. Fire frequency, size, severity,

severity patch size, and patch distribution all determine the final landscape-level mosaic that wildfire creates. This mosaic in turn determines the presence, abundance and distribution of bark dwelling insects which themselves can affect the likelihood and structural impact of future fires. Furthermore, fire and bark-dwelling arthropods interact to alter hairy woodpecker abundance and behavior. Historical levels of fire and bark beetle disturbances provided many beneficial functions within forested ecosystems (Schowalter et al. 1981) creating a system of checks and balances (Veblen et al. 1994). The result was a shifting mosaic of spatial and temporal disturbances across the landscape that ultimately enhanced forest health and resilience to perturbation (Everett et al. 2000). Samman and Logan (2000) noted that the interplay of fire and bark beetle outbreaks was critical for beetles to maintain viable populations.

Current fire management practices usually strive to eliminate high-severity fire; a practice that reduces habitat clearly beneficial to hairy woodpeckers. Whether manager's use prescribed burns or let naturally ignited fires burn on their own accord, high-severity burned areas may be critical for resident bark-foraging birds as they provide high concentrations of over-winter prey resources. Although large-scale fires similar to those I studied may create far too much severe-burn in patches of excessive size, smaller patches, such as those expected from historical fire regimes, are likely an important resource for bark-foraging birds. Future research and management should consider the size, number, and distribution of high-severity burned patches needed to meet different management goals and how frequently such burns should occur. If managers wish to maintain healthy populations of fire-adapted species, they must incorporate the full range of fire behaviors in their land management plans.

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Table 1. Summary of methods used in 14 previous studies estimating woodpecker home range size.

Author, Journal	Species	Study Length and Seasons	Study Area	Locating Method	# Birds Estimated	Total Locations/Bird	Locations per Day	Analysis Method
Hogstad, 1970	Three-toed	1 Winter	UNK†	Bird observation, 1 of 4 banded	4 ♂	83	1	MCP
Renken & Wiggers 1989	Pileated	3 Breeding	1567 ha	Radio telemetry	13, sexes UNK	≈ 25‡	1-6	MCP, HM
Matthysen et al. 1993	Downy	2 Winters	29.9 ha	Colored leg streamers	21 ♀ 12 ♂	≈ 36	1-2	MCP
Dobrowolski et al. 1994	Great Spotted	2 Winters 2 Breeding	1350 ha	Single individual*	12 ♀ 16 ♂	UNK	UNK	MCP
Rolstad & Rolstad 1995	Grey-headed	1 Winter 1 Breeding	15000 ha	Radio telemetry	1 ♀ 2 ♂	≈ 50	< 10% of total	MCP
Rolstad et al. 1995	Great Spotted	1 Breeding	15000 ha	Radio telemetry	2 ♀ 2 ♂	20-42 $\bar{X} = 30.5$	UNK	MCP
Mikusiński 1997	Black	1 Winter	20000 ha	Radio telemetry	2, sexes UNK	34, 50 $\bar{X} = 42$	UNK	MCP
Edenius et al. 1999	Grey-headed	1 Winter	18250 ha	Radio telemetry	3 ♀ 2 ♂	22-121 $\bar{X} = 64.6$	2-3	MCP
Husak 2000	Golden-fronted	1 Years Continuous	410 ha	Bird observation, banded or morphologically identifiable birds	20 pair 9 summer 11 winter	≥ 150	UNK	MCP
Pasanelli 2000a	Middle spotted	5 Winters	800 ha	Radio telemetry	9 ♀ 17 ♂	≈ 27	5, max	MCP
Rolstad & Rolstad 2000	Black	1 Winter	15000 ha	Radio telemetry	8 ♀ 15 ♂	≥ 20	UNK	MCP
Rolstad et al. 2000	Green	3 Years Continuous	30000 ha	Radio telemetry	5 ♀ 4 ♂	16-41 $\bar{X} = 28.5$	UNK	MCP
Wiklander et al. 2001	Lesser spotted	6 Years Continuous	85000 ha	Radio telemetry	12 ♀ 16 ♂	24-283 $\bar{X} = 153.5$	4-17 $\bar{X} = 8.3$	MCP

Table 1. Continued...

Author, Journal	Species	Study Length and Seasons	Study Area	Locating Method	# Birds Estimated	Total Locations/Bird	Locations per Day	Analysis Method
Elhuck & Wiebe 2003	Northern Flicker	2 Breeding	20000 ha	Radio telemetry	27 ♀ 25 ♂	UNK	1 location / 30 min	MCP
Covert	Hairy	2 Winters	10000 ha	Radio telemetry	5 ♀ 11 ♂	33-56 $\bar{X} = 42.75$	1-2	AK

† UNK = Unknown

‡ Jaremovic and Croft 1987

? = Assumed, logical interpretation

* Odum and Kuenzler 1955, Blank and Asch 1955

AK = Adaptive Kernel

HM = Harmonic Mean

MCP = Minimum Convex Polygon

Table 2. Summary of methods used in 22 previous studies evaluating woodpecker foraging ecology.

Authors, Journal	Study Length and Seasons	Study Area Size	Population Estimate or # Birds Observed	Observations <i>Total, #species, #bird</i>	Statistical e.u.
Stallcup 1968	2 Years	30.3 ha	0.025 bird/ha	142 winter, 74 summer HAWO obs*	Observation (average time/category)
Jackson 1970	3 Winters	24 ha	35 bird (min)	372 obs 10.6 obs/bird	Observation (initial contact)
Kiesel 1972	1 Winter	UNK	UNK†	128 obs HAWO 243 obs DOWO	Observation
Williams 1980	2 Winters	18.9 ha	8 birds	730 obs 91-12 obs/bird	Observation
Conner 1981b	3 Breeding 3 Post-breed 3 Winters	2020 ha	UNK	411 macro, 133, micro, 121, forage method observations for HAWO	Observation (initial contact)
Sullivan 1984	2 Winters	12 woodlots, area UNK	20 DOWO, 4-6 birds/test 2 HAWO	48-212 obs/test 9.6-17 obs/bird	Observation (time/category)
Morrison et al. 1987	3 Breeding	420 ha, 1 st two seasons 210 ha, last season	Ranked abundance of spp. 89 HAWO	89 observations 1 obs/bird	Bird (yr. pooled)
Morrison & With 1987	3 Breeding 2 Winters	420 ha, 1 st two seasons 210 ha, last season 100 ha, winter	0.19 birds/count winter 0.13 birds/count summer	UNK	Observation [?] Careful when interpreting data at p<0.05
Block 1991	3 Breeding 2 Winters	6800 ha	≈ 54 NUWO	426 obs 3 obs/bird.	Observation (yr. or sex pooled when appropriate)
Hogstad 1991	17 Winters	10 km ²	1-4 birds	229 obs 3-11 obs/bird $\bar{X} = 6.2$	Observation (yr. pooled)
Villard & Beninger 1993	1 Winter	54 ha	UNK	≈8 hr - BBWO ≈7 hr - HAWO	Observation (average time/category)
Conner et al. 1994	2 Years	1038 ha	UNK	> 100 n for sp to be included	Observation [?]
Villard 1994	1 Summer	600 ha	31 birds	7.4 hr TTWO 4.6 hr BBWO	Observation (average time/category)

Table 2. Continued

Authors, Journal	Study Length and Seasons	Study Area Size	Population Estimate or # Birds Observed	Observations	Statistical e.u.
Loose & Anderson 1995	2 Breeding	6-8 2.54 km ² w/ clear cuts	UNK	56 obs HAWO 31 obs TTWO 9, 7, 4 obs YBSA, NOFL, WISA	Observation
Osiejuk 1998	4 Winters	30 ac.	8-12 individuals	UNK.	Observation
Kreisel & Stein 1999	4 Winters	160+ ha burn 80 ha unburn	0.41 HAWO/pt. – burn 0.056 HAWO/pt. – unburn	55 obs HAWO 42 obs BBWO 26 obs DOWO 12 obs TTWO	Observation [?] (yr. pooled)
Murphy & Lehnhausen 1998	2.5 Years Continuous	67 ha	0.2 birds / ha 8-13 birds	41, 13 obs on ♂ and ♀ HAWO, 4.2-6.8 obs/bird, \bar{X} = 5.1 81, 12 obs on ♂ and ♀ TTWO 134, 14 obs on ♂ and ♀ BBWO	Observation
Weikel & Hayes 1999	2 Breeding	12 stands, ≈ 420 ha	29 HAWO	85 obs 2.9 obs/bird	Observation
Olsson et al. 2000	6 Winters	125 km ²	85 birds	85 obs on LSWO 35 samples for foraging substrate	Bird (proportion of time in one activity)
Passinelli 2000a	3 Seasons Jan.-June	1300 ha	26 birds	Instantaneous Sampling (obs taken every 15s) ⁺ 10 obs or more/bird 21 min/bird	Bird (average value/category, yr. pooled)
Imbeau & Desrochers 2003	2 Breeding 1 Winter	4,000 ha	33 TTWO over 2 summers 22 TTWO over 1 winter	98% obs on 12 birds ≈ 21 hr - summer ≈ 18 hr - winter	Foraging analysis – Bird (average time/category) Tree selection analysis - Observation (weighted bird to 1 d.f. ^{***})

Table 2. Continued

Authors, Journal	Study Length and Seasons	Study Area Size	Population Estimate or # Birds Observed	Observations <i>Total, #species, #/bird</i>	Statistical e.u.
Nappi et al. 2003	1 Month	100 ha	30 BBWO	119 snags 1-19 snags / bird	Observation - snag
Covert	2 Winters	10000 ha	186 HAWO	500 obs ≤ 6/bird per burn severity $\bar{X} = 2.9$	Observation (average/category, 24.5 average # days between obs)

* obs = Observations
 ALAP = As long as possible
 † UNK = Unknown
 ** Degree of freedom
 ‡ Martin and Bateson 1993
 ? = Assumed, logical interpretation

Table 3. Summary of fires in which hairy woodpeckers were observed.

Burn	Burn Start Date	Area Burned	Year Surveyed	Age post burn at sampling	Approximate Area Surveyed
Rodeo-Chediski	June 2002	189,651 ha	2002-03	1	200 ha
Pumpkin	May 2000	5,973 ha	2001-02 2002-03	2 3	3,000 ha
Horseshoe-Hochderffer	May 1996/June 1996	10,022 ha	2001-02 2002-03	6 7	7,000 ha

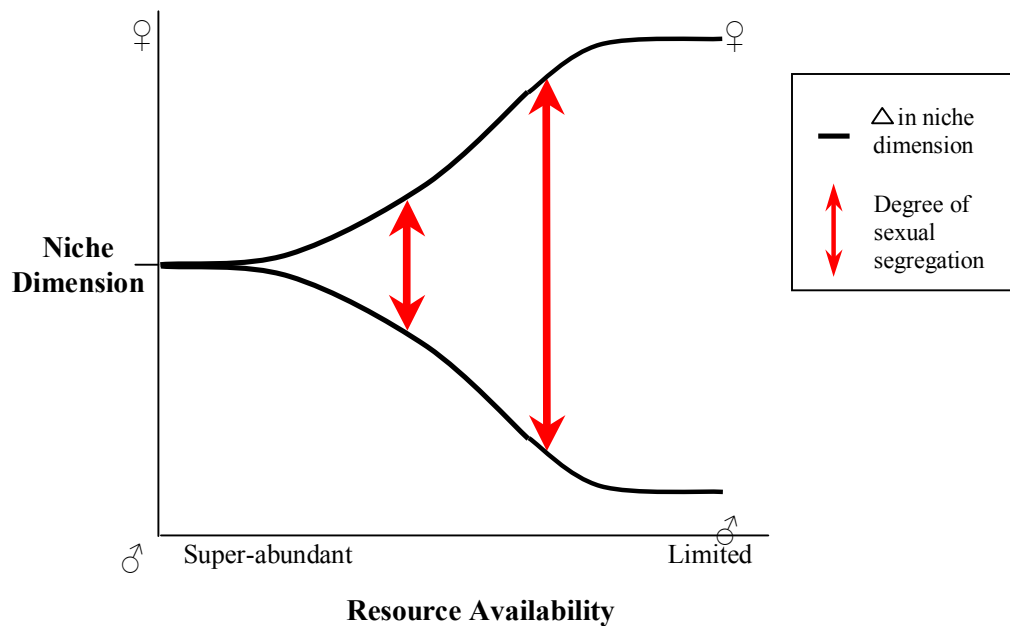


Figure 1. Conceptual model depicting intersexual foraging behavior resulting from changing resource availability and incurred competition. Male and female use of a niche dimension, for example tree size, overlaps completely when resources are super-abundant and competition is low, however, as resources decrease, competition increases, and the sexes segregate to partition resources to reduce competition.

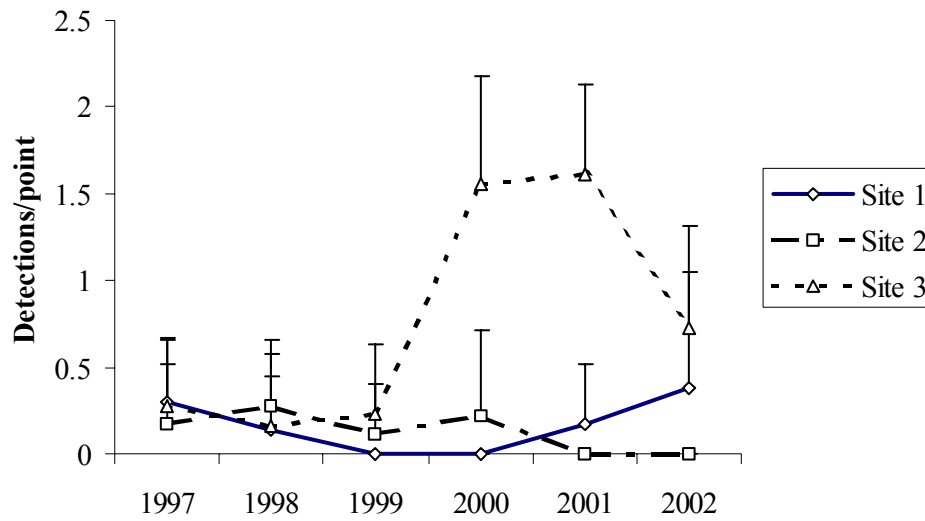


Figure 2. Hairy woodpecker winter relative abundance ($\bar{X} + SD$) in two unburned areas (sites 1 and 2) and one site that burned in the Pumpkin fire (site 3), during the summer of 2000, Coconino National Forest, northern AZ, between 1997 and 2002.

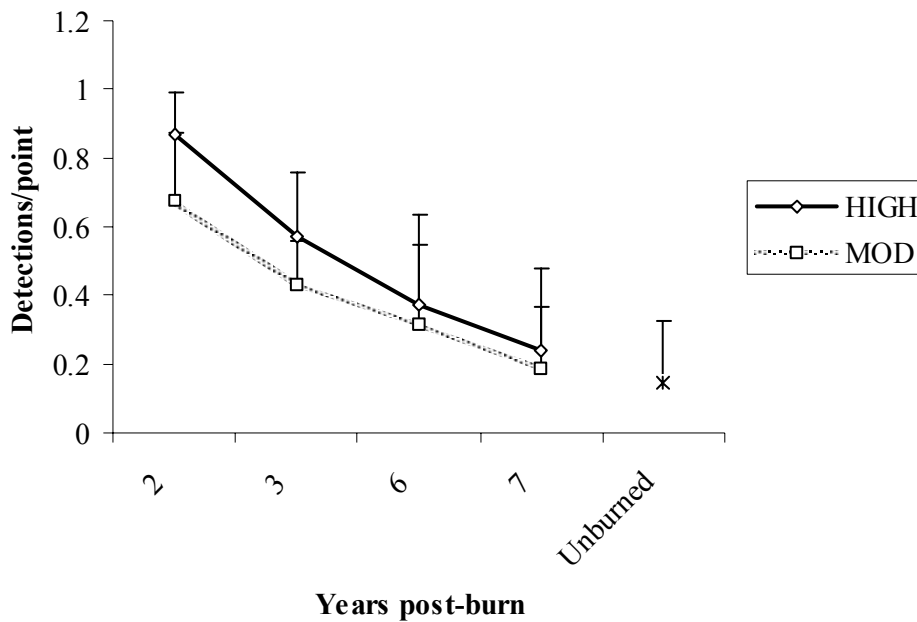


Figure 3. Hairy woodpeckers relative abundance ($\bar{X} + SD$) in high and moderate severities in the Pumpkin (2 and 3 years post-burn) and Horseshoe/Hochderffer fire (6 and 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003. Unburned forests adjacent to the burned areas are shown for comparison.

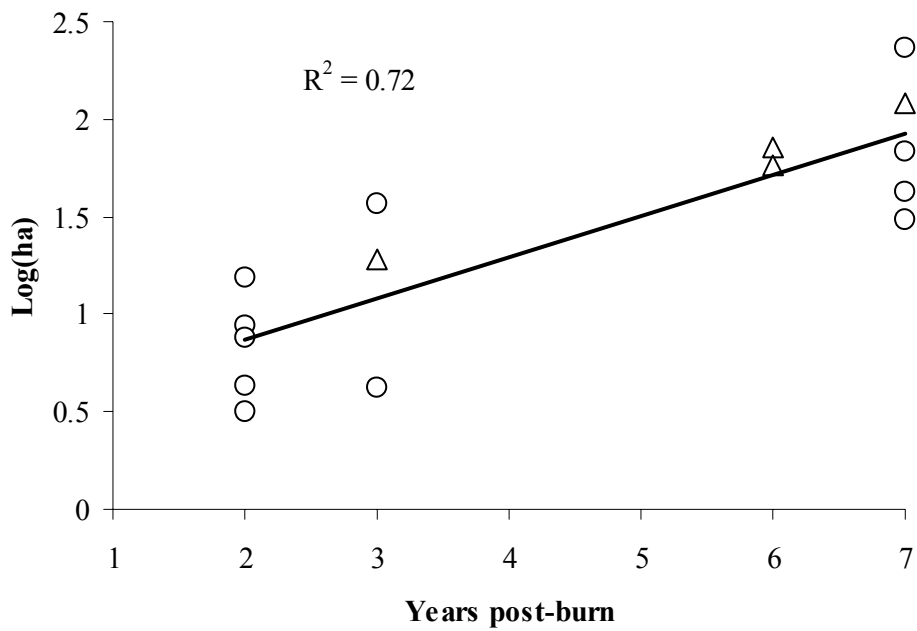


Figure 4. Hairy woodpecker home range size in two burned ponderosa pine forests following the Pumpkin Fire (2, 3 years post-burn) and the Horseshoe/Hochderffer Fire (6, 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003. Females are denoted as triangles and males as circles.

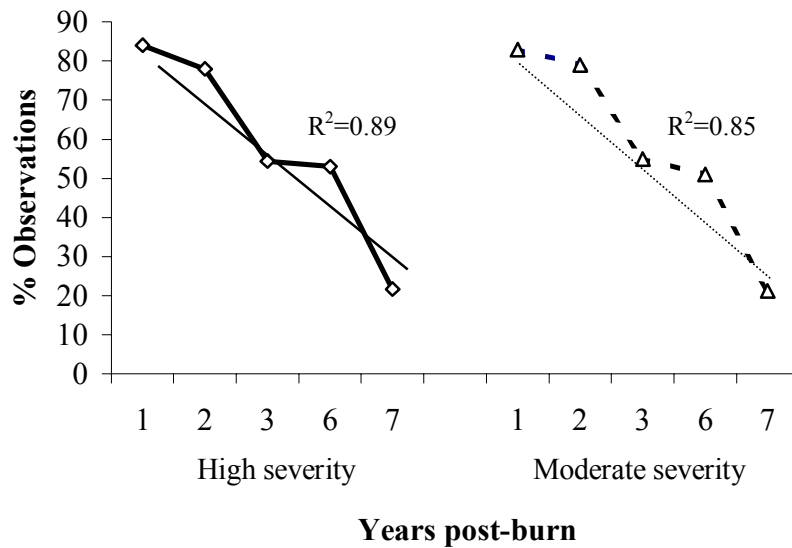


Figure 5. Change in percent observations where hairy woodpeckers were encountered foraging with a conspecific in two burn severities in the Rodeo/Chediski (1 year post-burn), Pumpkin (2 and 3 years post-burn), and Horseshoe/Hochderffer fires (6 and 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003.

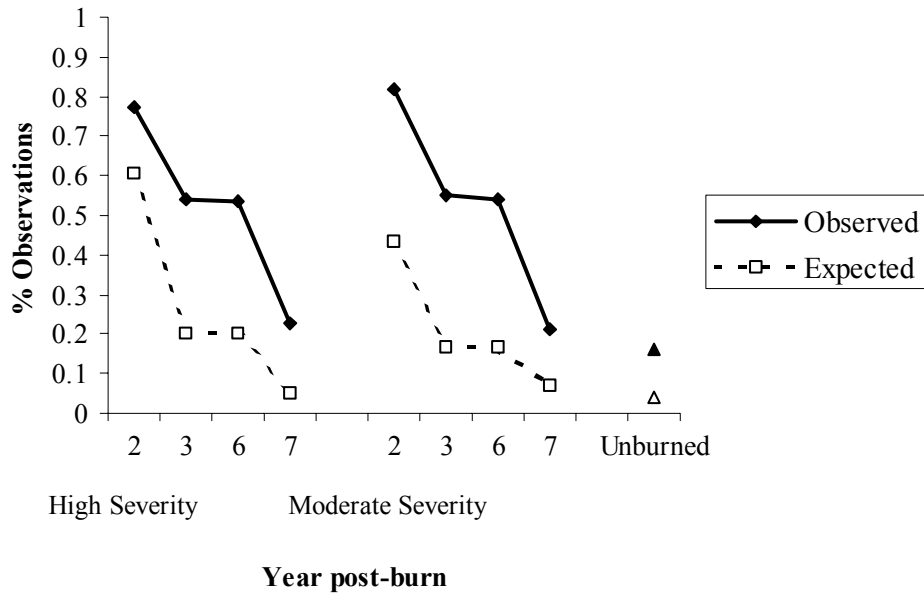


Figure 6. Percentage observations where hairy woodpeckers were encountered foraging with a conspecific (observed) in comparison to expected encounter proportion, determined by Poisson probability modeling of relative abundance in two burn severities in the Pumpkin (2 and 3 years post-burn), and Horseshoe/Hochderffer fires (6 and 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003. Proportions for unburned provided for comparison.

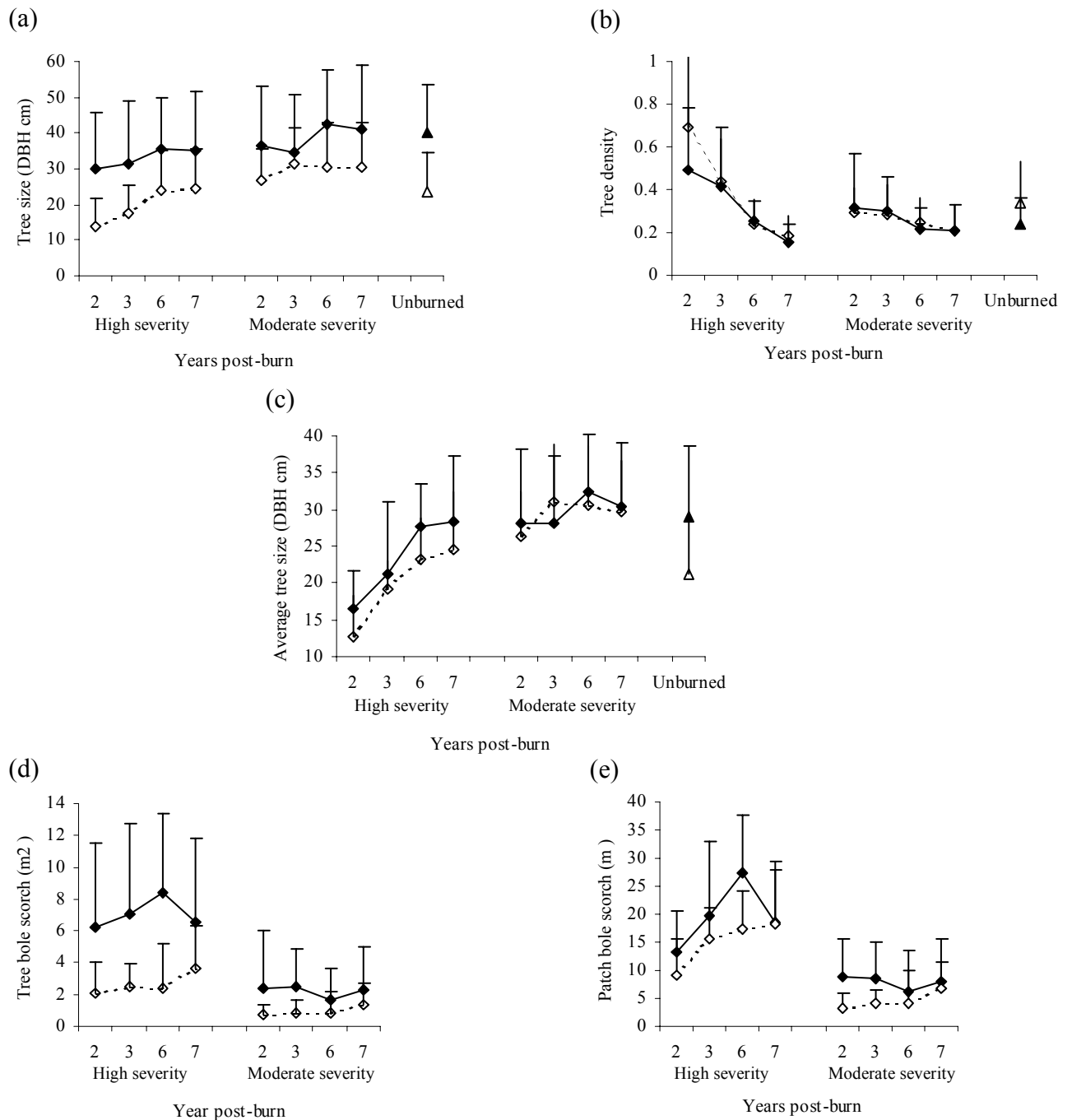


Figure 7. Selection of habitat components by hairy woodpeckers in two burn severities in the Pumpkin (2 and 3 years post-burn) and Horseshoe/Hochderffer fires (6 and 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003. Habitat components: (a) tree size (DBH in cm); (b) patch tree density; (c) patch average tree size (DBH cm); (d) tree bole scorch; and (e) patch bole scorch. Component $\bar{X} + SD$ selected by birds represented by solid lines and available component $\bar{X} + SD$ represented by dashed lines. Selection and available habitat components in unburned is shown for comparison, for first three habitat components.

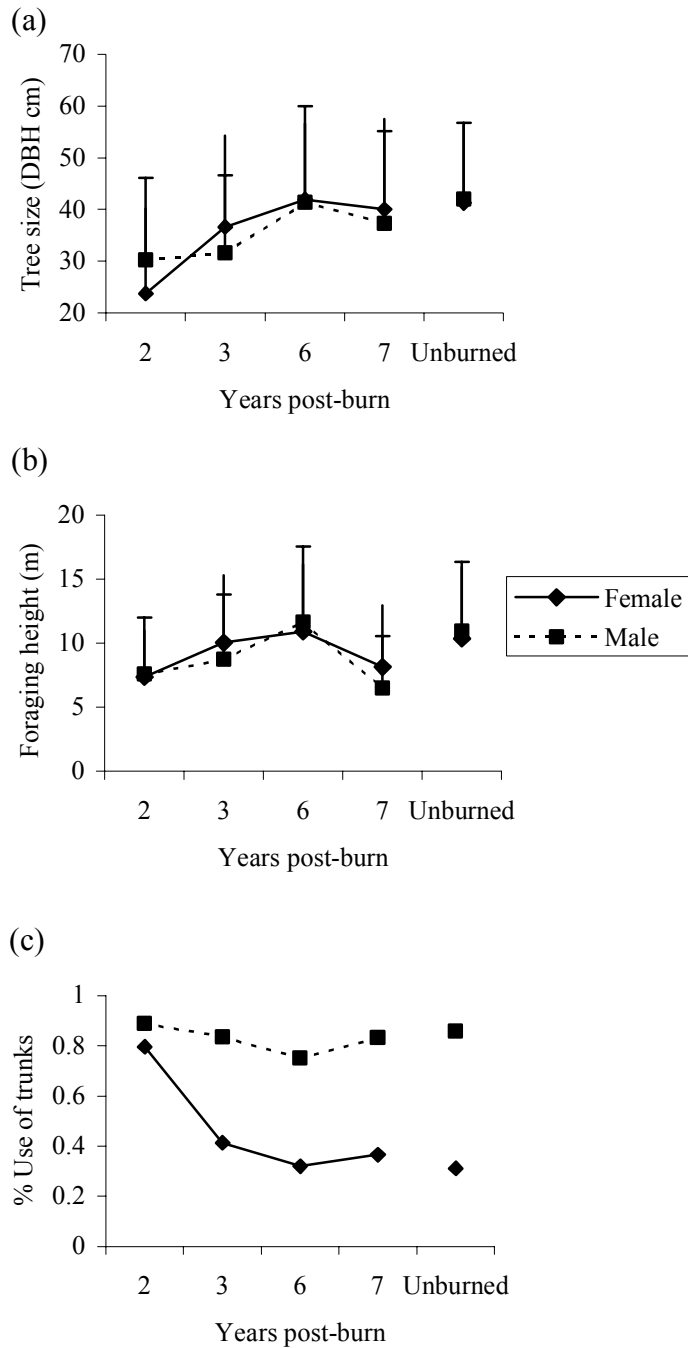


Figure 8. Intersexual selection of habitat components by hairy woodpeckers in the Pumpkin (2 and 3 years post-burn) and Horseshoe/Hochderffer fires (6 and 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003. Habitat components: (a) tree size; (b) foraging height; and (c) substrate selection of branch versus trunk (proportion of trunk use shown). Selection of habitat components in unburned areas shown for comparison.

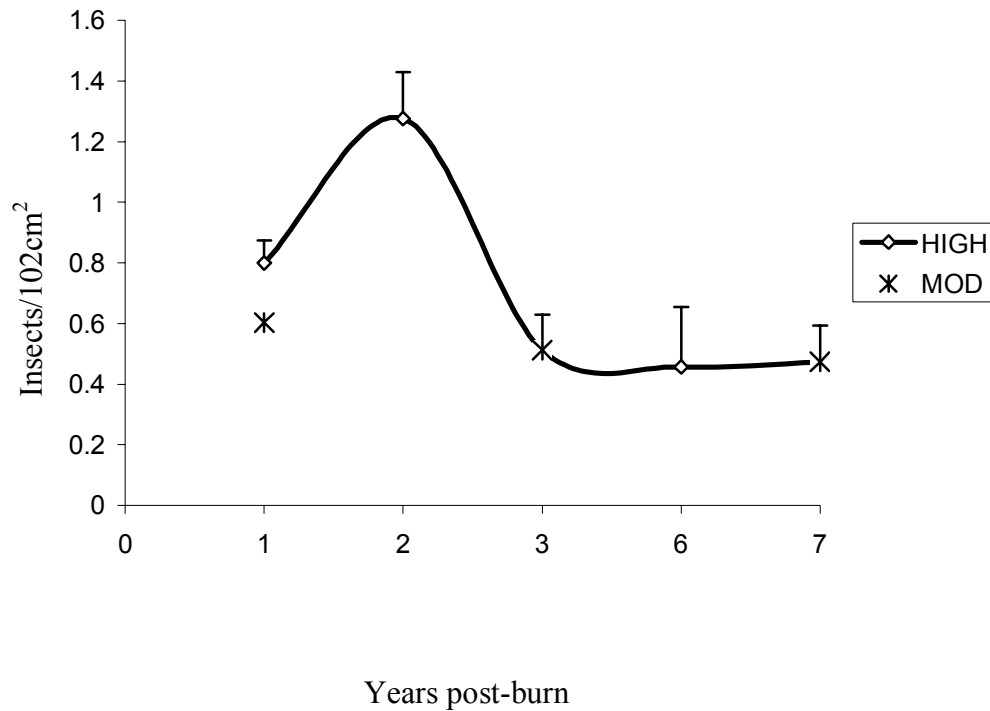


Figure 9. Mean insect density per 102 cm² bark samples taken from random ponderosa pine trees within two burn severities in the Rodeo/Chediski (1 year post-burn), Pumpkin (2, 3 years post-burn), and Horseshoe/Hochderffer fires (6, 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003.

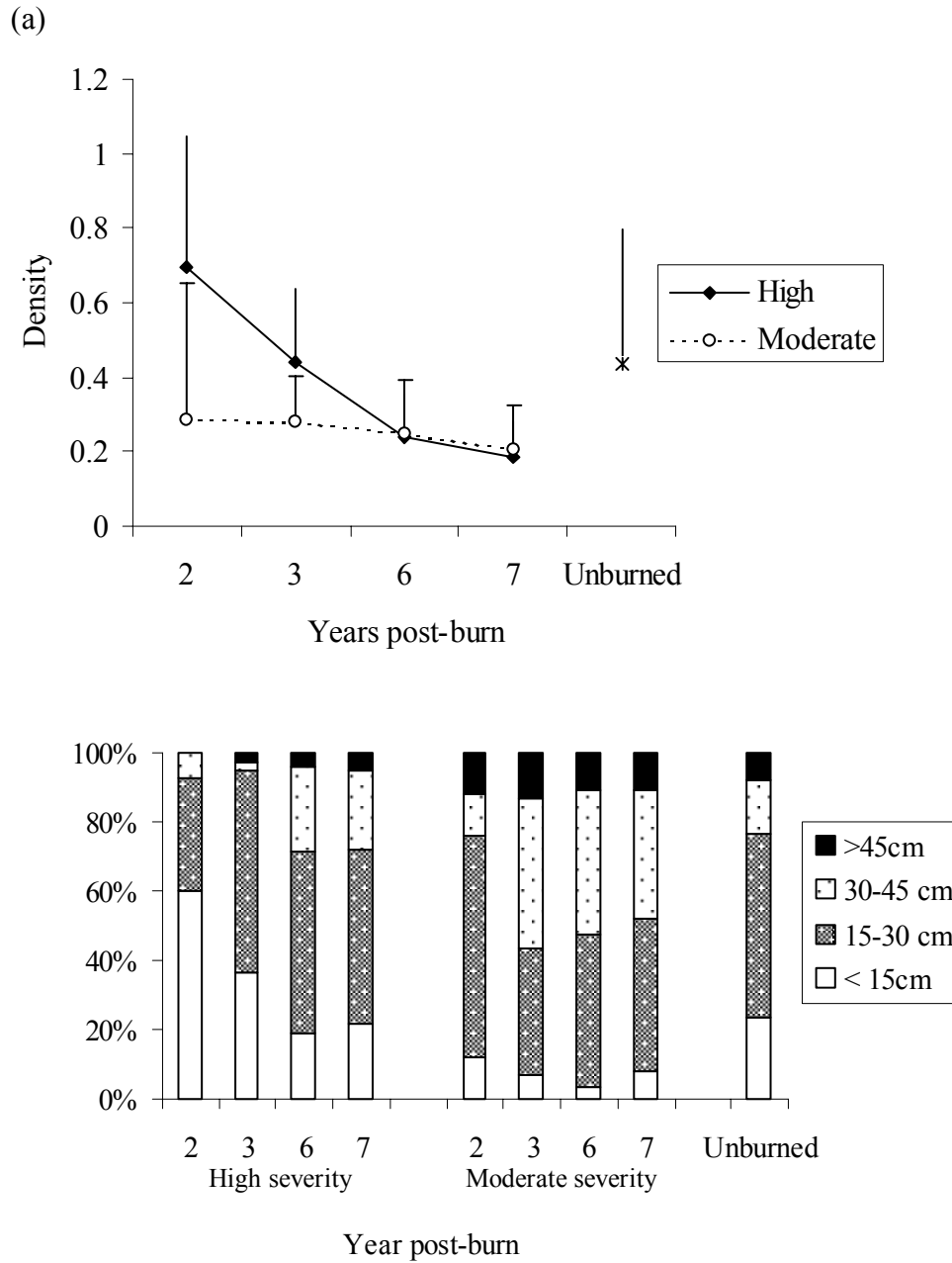


Figure 10. Change in a) density of snags within high severity and trees in moderate severity, and change in b) four size classes (DBH < 15cm, 15-30 cm, 30-45 cm, >45 cm) of snags within high severity and trees in moderate severity, in the Pumpkin (2 and 3 years post-burn) and Horseshoe/Hochderffer fires (6 and 7 years post-burn), Coconino National Forest, northern AZ, during winters 2001-2003.

Appendix A. Telemetry summary statistics for birds radio-tracked during winter 2001-2 and 2002-3 in the Pumpkin Fire (2, 3 years post burn) and Horseshoe/Hochderffer Fire (6, 7 years post burn).

Burn Age	Sex-frequency i.d.	Date Range	# Locations	# Days Tracked	# days w/2 locations	95% kernel HR size
2	M-473	11/9 - 2/15	50	48	2	6.17
2	M-556	11/08 - 2/15	56	55	1	8.18
2	M-599	11/06 - 2/15	50	48	2	13.13
2	M-653	11/06 - 2/22	52	48	4	10.89
2	M-344	12/20 - 2/22	40	32	8	34.43
3	F-894	11/13 - 2/27	38	38	0	31.26
3	M-100	12/9 - 2/21	51	46	5	6.9
3	M-951	12/6 - 2/27	48	42	6	71.3
6	F-713	10/26 - 1/30	49	46	3	90.84
6	F-360	12/11 - 2/28	48	37	1	105.9
7	F-182	12/5 - 2/28	38	34	4	6368.4-nomadic
7	F-990	11/25 - 2/14	41	41	0	189.19
7	M-209	12/16 - 2/26	51	48	3	61.69
7	M-293	12/2 - 2/27	50	45	5	104.48
7	M-835	11/25 - 3/3	33	32	1	97.94
7	M-910	11/25 - 3/8	47	44	3	396.1

