

Hairy Woodpecker Winter Ecology in Ponderosa Pine Forests Representing Different Ages Since Wildfire

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Abstract

We investigated how changes in vegetation structure and prey resources following wildfire affected the winter ecology of hairy woodpeckers (*Picoides villosus*) in ponderosa pine (*Pinus ponderosa*) forests of northern Arizona, USA. Using point-counts, radiotelemetry, and focal bird observation, we assessed the relative abundance, home range size and composition, and habitat use by foraging hairy woodpeckers in 3 stands that had experienced wildfire in 1996, 2000, or 2002. Because we conducted the study over 2 years, we used the 1996 fire to represent 6 and 7 years after fire, while we used the 2000 fire to represent 2 and 3 years after fire in a space-for-time substitution chronosequence analysis. We also assessed bark beetle and woodborer density by x-raying bark samples collected from a subset of trees within burned areas. We detected significantly greater hairy woodpecker relative abundance in burned forests representing 1 and 2 years after fire, and bark beetle and woodborer density was highest in these stands as well. Woodpecker home range size increased across stands representing increasing time since fire. Within a burn, hairy woodpeckers used high-severity burned areas more than moderate-severity burned areas representing 2 and 3 years after fire, but not in areas representing 6 and 7 years after fire. Bark beetle and woodborer densities were also higher in high-severity burned stands representing 2 and 3 years after fire. Hairy woodpeckers used edges of high-severity burned areas more than the interior. We hypothesize that an initial increase in bark beetle and woodborer density following fire allowed for higher woodpecker abundance and smaller home ranges, but as burned forests aged, bark beetle and woodborer density within trees decreased, killed trees fell, and, in response, hairy woodpecker relative abundance decreased and home range size increased. These patterns suggest that high-severity burned areas provide important but ephemeral resources to this dominant primary cavity-nester. The higher bark beetle and woodborer densities and greater use of edges of high-severity burned areas by woodpeckers suggests that salvage logging of these areas could remove potential prey and preferred foraging areas for hairy woodpeckers, especially when trees are removed along severely burned edges. (JOURNAL OF WILDLIFE MANAGEMENT 70(5):1379–1392; 2006)

Key words

Arizona, foraging behavior, hairy woodpecker, home range, *Picoides villosus*, *Pinus ponderosa*, ponderosa pine, prey resources, wildfire, winter ecology.

Fire creates and maintains landscape heterogeneity that birds respond to across space and through time (Raphael et al. 1987, Hejl 1994, Hutto 1995, Brawn et al. 2001). Wildfire changes resources at multiple spatial and temporal scales (Turner and Romme 1994), resulting in a mosaic of intensely and moderately burned areas that may differ significantly both in resource levels and their trajectory of change over time (Hessburg et al. 2000, Turner et al. 2003). For example, large, infrequent wildfires create a mosaic of vegetative composition, structure, and ecosystem processes. This variation in fire-created habitat and the subsequent change through time could affect how birds distribute themselves across the landscape, establish home ranges, and use habitat (Hildén 1965, Hutto 1995). Additionally, high-severity fires may have greater impacts on resources important to birds than moderate- or low-severity fires (Hejl 1994).

In the southwestern United States, fire is the primary natural disturbance in ponderosa pine (*Pinus ponderosa*) forests (Covington et al. 1994). Historically, fire occurred every 2–12 years (Moir et al. 1997) at small scales (approx. 1,200 ha at low severities [Fulé and Covington 1997]) and every 6–9 years at larger spatial scales (tens of thousands of

hectares [Fulé et al. 2000, 2003]). In the last century, however, fire suppression, grazing, and logging have caused a significant increase in tree density (148 trees/ha increasing to 1,265 trees/ha; Fulé et al. 1997), particularly of small-diameter trees (<41 cm; Covington et al. 1997). The resulting closed canopy and increased ladder fuels caused increasingly larger wildfires (Lowell and Cahill 1996). Recent wildfires covered areas many-fold that of historical small-scale fires and contained large (up to several hundred hectares), continuous areas where tree mortality was >99%. While larger-scale fires existed historically (Fulé et al. 2000, 2003), they likely did not reach the intensity of modern-day fires. The difference between past and present fire regimes, and how best to reintroduce fire into systems in which it has been anthropogenically suppressed, presents a major challenge for land managers. Animal species that are dependent on resources directly related to fire may act as useful surrogates for understanding the ecological effects of differing fire sizes and intensities through time.

Many woodpeckers are intimately tied to resources altered by fire, such as the abundance and distribution of disturbed habitat (Shackelford and Conner 1997), dying trees and snags (Balda 1975, Horton and Mannan 1988, Morrison and Raphael 1993), and high densities of bark-dwelling arthropods (Blackford 1955, Koplin 1969, New and Hanula

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1998). For example, the distribution of black-backed (*Picoides arcticus*) and three-toed (*P. dorsalis*) woodpeckers is restricted to or limited by high-severity postfire habitat (Hutto 1995, Murphy and Lehnhausen 1998, Saab et al. 2002). While not all species are limited by postfire habitat, many are attracted to and likely benefit from burned areas because of higher abundances of bark and wood-dwelling arthropods in the families Scolytidae, Cerambycidae, and Buprestidae (Blackford 1955, Koplin 1969, Villard and Benninger 1993, Hutto 1995, Murphy and Lehnhausen 1998). Within burned areas, the amount of a tree that is burned is positively associated with the likelihood of bark beetle attack (Ryan and Reinhardt 1988, Bradley and Tuller 2001), suggesting that as burn severity increases so too might prey resources. Additionally, trees killed by high-severity burn are subsequently attacked by wood-boring beetles (Cerambycidae and Buprestidae) that bore initially into the heartwood and later return to the sapwood, cambium, and bark to feed within 2–3 years following attack (Murphy and Lehnhausen 1998). Woodpeckers could respond to fire-induced differences in prey abundance in several ways, including shifting patch choice (Lima 1983) or foraging behavior (Conner 1979, Morrison and With 1987) or altering home range size (Mikusiński 1997, Olsson et al. 2001).

In ponderosa pine forests of northern Arizona, USA, the hairy woodpecker is one of the most abundant primary cavity-nesters (Szarro and Balda 1979, Sauer et al. 1996, 2003; W. M. Block, United States Forest Service, unpublished data from this study area). Because of its abundance and tendency to make one to several new nest and roost holes each year (Kilham 1968, (Short 1982, Jackson et al. 2002), hairy woodpeckers likely provide the majority of cavities for secondary cavity-nesters and mammals in this system (Bednarz et al. 2004). Similar to other woodpecker species in western forests, hairy woodpecker population declines have been noted in Arizona (Sauer et al. 1996).

In burned pine forests, hairy woodpecker abundance is higher than in unburned forest (Brawn and Balda 1988, Raphael et al. 1987, Hobson and Shieck 1999) and abundance declines through time (Kreisel and Stein 1999). Most authors proposed that fire-created snags and the associated arthropods were likely the mechanism behind greater hairy woodpecker abundances in burned areas because a major portion of the hairy woodpecker's diet (65–95%) consists of bark-dwelling arthropods (Beal 1911, (Short 1982, (Otvos and Stark 1985). These relationships suggest that hairy woodpeckers may be selecting burned areas based on food availability and vegetative structure. During the winter, prey resources are likely critical for this resident bird because weather conditions are extreme and prey resources (e.g., free-flying insects and fruits) are either limited or dormant and non-replaceable (Askins 1981). Additionally, snow cover often limits available foraging substrates and prey resources to those in or on the bark of trees (Mannan et al. 1980, Bull 1987).

We evaluated how hairy woodpeckers used wildfire-created habitat during winter at multiple spatial scales through time and how that use varied with a measure of bark-dwelling prey density. Accordingly, we 1) compared the relative abundance of hairy woodpeckers in burned and unburned ponderosa pine forests and between high- and moderate-severity burned areas, 2) estimated home range size in fires representing 4 ages since wildfire, 3) documented foraging habitat selection within home ranges, and 4) examined whether variation in prey resources could explain hairy woodpecker selection and use of wildfire-created habitat through time by assessing the density of bark-dwelling arthropods within 2 burn severities in stands representing 5 postburn ages.

Study Area

We studied woodpeckers for 2 winters (2001–2002 and 2002–2003) in monotypic ponderosa pine forests of northern Arizona affected by 4 different wildfires. In May and June of 1996, the Horseshoe and Hochderffer fires burned 10,022 ha in the Coconino National Forest 48 km northwest of Flagstaff, Arizona (Fig. 1). Because these fires were adjacent to each other, we treated them as one site. The Pumpkin fire burned 5,973 ha in May 2000, in both the Coconino and Kaibab national forests adjacent to the earlier Horseshoe–Hochderffer fire (Fig. 1). This wildfire burned 1 10-point transect initially established to sample unburned forest adjacent to the Horseshoe–Hochderffer fire perimeter, resulting in a unique opportunity to collect pre- and postdisturbance relative abundance data. The Rodeo–Chediski fire burned 189,651 ha in June 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.

Other bark-foraging woodpecker species that we found in the study area throughout the winter, in decreasing relative abundance, included Williamson's sapsucker (*Sphyrapicus thyroideus*), three-toed woodpecker, and downy woodpecker (*P. pubescens*; W. M. Block, unpublished data). These species were relatively rare; the relative abundance of each species compared with that of the hairy woodpecker (with the hairy woodpecker as 1) was 0.048, 0.025, and 0.006, based on average detections per point-count station.

Methods

All fires burned with varying intensity, leaving a mosaic of high- and moderate-burn severities. We considered "high severity" as those areas where crown fire killed $\geq 99\%$ of all live ponderosa pine trees, whereas "moderate severity" were those areas where crown fire resulted in $< 10\%$ mortality of live trees > 2 m high (adapted from Dwyer and Block 2000). Analysis of first-year vegetation data indicated that total area of each severity was the same in the sampling areas of the Pumpkin and Horseshoe–Hochderffer fires. We considered each burn severity at a specific postfire age a treatment (e.g., moderate-severity at 2 years postfire). We also observed hairy woodpeckers within unburned areas

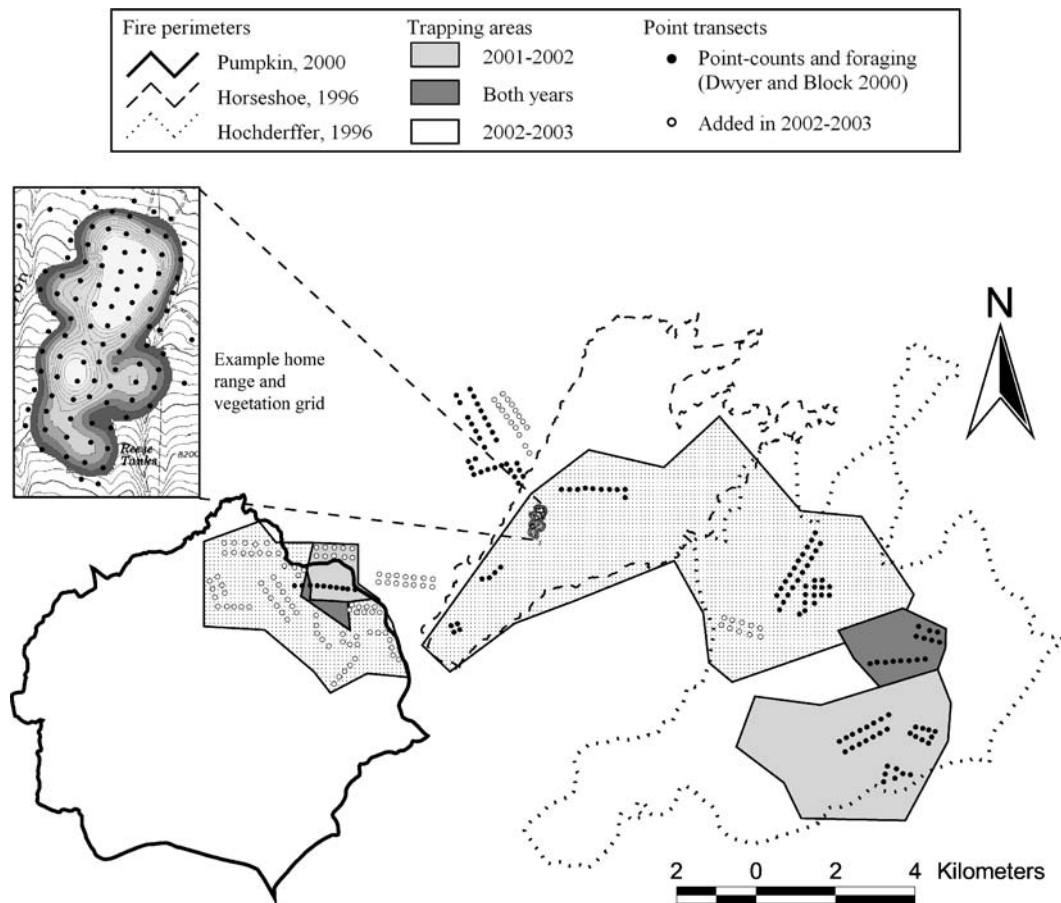


Figure 1. Study area and sites used for sampling hairy woodpeckers during the winters of 2001–2002 and 2002–2003, Coconino National Forest, Arizona, USA. Methods used in these areas included point-count surveys, home range assessment, foraging observations, and bark-dwelling arthropod sampling.

adjacent to or between, but >200 m from, fire perimeters (Fig. 1). We 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 density of small-diameter trees (Covington et al. 1997).

We employed a space-for-time substitution to create a chronosequence (Pickett 1989, Kotliar et al. 2002) of fires by their age (1, 2, 3, and 6, 7). To test the validity of the substitution and subsequent statistical methods applied to this design, we compared tree size distributions (mean diameter at breast height [dbh]) sampled at 2 years postburn in both the Pumpkin and Horseshoe–Hochderffer fires (using data in Dwyer and Block [2000]). Mean tree size within high- and moderate-severity burned areas differed by 2 and 5 cm, respectively, with substantial overlap in standard deviation, indicating that tree size distributions within each burn severity were comparable across sites (Table 1). Additionally, control sites adjacent to burned areas were similar (Underwood 1994) based on high overlap of means and standard deviations of live tree basal and snag basal areas while still representing the full spectrum of variability within unburned forests (Table 2). Secondly, we analyzed hairy woodpecker relative abundance at 2 and 3 years postburn in

high- and moderate-severity burned areas within the Horseshoe–Hochderffer and Pumpkin fires (winters 1998–1999 and 1999–2000, and 2001–2002 and 2002–2003, respectively) and found no difference between birds per point within the 2 fires using 3-way analysis of variance (ANOVA [Zar 1999:231]; $F_{1, 167} = 1.64$, $P = 0.2$). Thirdly, we analyzed the relative abundance of hairy woodpeckers in 3 unburned forests, one of which experienced wildfire. Within this test, we found no differences in hairy woodpecker relative abundance between the 3 unburned sites prior to fire or between the 2 unburned sites after fire. Overall, we felt that the similarity in tree size distribution and hairy woodpecker abundance, combined with the geographic proximity of the fires, justified the use of a time-for-space substitution. We used this substitution for all analyses with a temporal factor.

Hairy Woodpecker Relative Abundance

Field methods.—We estimated hairy woodpecker relative abundance by unlimited distance point-counts. We point-counted at stations located along transects established by Dwyer and Block (2000) within the Horseshoe–Hochderffer fire and adjacent unburned areas (Fig. 1). Transects were located within high-severity, moderate-severity, or unburned areas. Areas were large enough to

Table 1. Mean tree diameter at breast height (cm) for ponderosa pine trees present in high- and moderate-burn severity sites within the Horseshoe-Hochderffer and Pumpkin fires at 2 years postburn, 1998 and 2002, respectively, Coconino National Forest, Arizona, USA.

Fire severity	Horseshoe-Hochderffer					Pumpkin				
	<i>n</i>	$\bar{x}$	SD	SE	$\pm 95\%$ CI	<i>n</i>	$\bar{x}$	SD	SE	$\pm 95\%$ CI
High	44	23.9	3.6	0.5	1.1	42	22.2	7.1	1.1	2.2
Moderate	54	32.6	8.2	1.1	2.2	36	27.2	7.3	1.4	2.5

establish at least 3 point-count stations that averaged 200 m apart. Points were at least 100 m from the edge of adjacent burn severities on all sides. We point-counted at 49 points in high-severity, 50 points in moderate-severity burned areas, and 30 points within adjacent unburned areas. We subsampled all points 4 times each winter (1997–2003) with observers spread across treatments and points to minimize bias. Five observers recorded all birds seen or heard and their distance from the observer for an 8-minute period following a 1- to 2-minute waiting period.

Data analysis.—Because we only sampled 10 points in the Pumpkin fire, we randomly selected, with replacement, 5 sets of 10 points from the Horseshoe-Hochderffer fire to compare to the entire Horseshoe-Hochderffer data set. We did not detect any differences for birds per point for each year or severity between the 10-point and full data sets using 3-way ANOVAs. We maintained Type I error rates at $\alpha = 0.05$ for the group of 5 tests using the Bonferroni adjustment (Zar 1999:231, Neter et al. 1996:157). Therefore, we used the entire Horseshoe-Hochderffer data set for analysis because analysis of variance procedures were robust to differences in sample sizes. We used SPSS version 10.1 (SPSS, Inc. 2002) for this and all parametric analyses except when noted. For this and all subsequent analyses, we transformed non-normal data until assumptions of normality and homogeneity of variance were met (Zar 1999:275).

Because the Pumpkin fire burned 1 of 3 unburned transects, providing pre- and postdisturbance data, we compared the change in the relative abundance of hairy woodpeckers detected on this burned transect relative to the 2 transects that remained unburned. We applied a before-after, control-impact design (Morrison et al. 2001:121) to a negative binomial regression (White and Bennetts 1996).

Small sample sizes precluded our estimating detection functions and estimates of density for some times and locations (2002–2003 in the young burn; Buckland et al.

2001:299), but when sample sizes were sufficient we used Distance 3.5 (Thomas et al. 1998) to estimate detection probabilities. Because the difference in the probability of detecting an animal between high and moderate burn severities differed by <10% for each year, we assumed detection probabilities were sufficiently homogenous to use the index of birds per point as a satisfactory assessment of relative abundance.

We analyzed relative abundance in high and moderate burn severities across burn age with 2-way ANOVA and Tukey's honestly significant difference (HSD) test for multiple comparisons (Zar 1999:177, 210). We tested abundances in unburned areas for differences between years (2001–2002 and 2002–2003) using *t*-tests (Zar 1999:122). Because we did not find differences, we pooled these data and presented one overall value for these control plots for comparative purposes with the abundance data for burned sites. We did not perform any parametric tests on burn severity versus unburned abundances because postburn age does not equate to unburned year in a site-for-time analysis. Instead, we used 1-tailed Dunnett's control comparison test to compare the abundance means within each burned treatment to the unburned mean pooled across winters (Zar 1999:217), allowing for the comparison of relative abundance at multiple postdisturbance ages to one that is undisturbed (i.e., control). For this test we used JMP_{IN}, version 4.0.4 (SAS Institute 2001).

Diurnal Home Range

Field methods.—We studied hairy woodpecker diurnal home range size using a combination of radiotelemetry and color-band resighting. Between 18 October and 18 December, we mist-netted 13 individuals in 2001–2002 and 12 in 2002–2003, using tape playback (hairy woodpecker and northern pygmy-owl [*Glaucidium gnoma*] calls to induce territorial or mobbing behavior). Each year, we sampled birds in different areas of the study site to ensure

Table 2. Live tree diameter at breast height (dbh), live basal area, and snag basal area for ponderosa pine trees present in 3 unburned sites in 1997 adjacent to the Horseshoe-Hochderffer fire, Coconino National Forest, Arizona, USA, one of which (site 3) was burned in Jun 2000 by the Pumpkin fire.

Site	<i>n</i>	Vegetation characteristic								
		Live dbh (cm)			Live basal area (m ² /50 ha)			Snag basal area (m ² /50 ha)		
		$\bar{x}$	SE	$\pm 95\%$ CI	$\bar{x}$	SE	$\pm 95\%$ CI	$\bar{x}$	SE	$\pm 95\%$ CI
Site 1	15	32.2	2.4	5.1	108.0	18.9	40.5	0.7	0.7	1.4
Site 2	15	24.3	2.5	5.3	180.0	16.1	34.5	1.3	0.8	1.6
Site 3	10	21.0	3.1	7.3	238.0	43.4	98.1	0.5	0.5	1.1
All	40	26.6	1.6	3.3	167.5	16.1	32.5	0.9	0.4	0.8

independence of individuals from year to year (Fig. 1). We individually marked birds (United States Fish and Wildlife Service band, 2 color-bands) and fitted them with a BD-2 transmitter with a 14-week lifespan (Holohil Ltd., Carp, Ontario, Canada). Transmitter mass was approximately 3% of the bird's body mass. We attached transmitters to 1 or 2 central rectrices with an epoxy-based glue and secured with dental floss. Northern Arizona University's Institutional Animal Care and Use Committee (protocol 01-039) approved capture and observational methods used in our study.

We located radiomarked birds from 22 October to 14 March each winter between 0800 and 1600 hours. We tracked birds to within 10–15 m using radiotelemetry and determined their exact position by auditory or visual cues. When a transmitter failed, we obtained additional locations for a bird by surveying the area previously used and several hundred meters beyond using auditory cues, followed by color-band verification. We attempted to locate each bird 50 times during the study period (Seaman et al. 1999), with a minimum of 30 (Worton 1987). We located individuals once per day (Swihart and Slade 1985), except when we were unlikely to meet the goal of 50 locations. In this case, we located birds 2 times/day with successive locations separated by a minimum of 4 hours.

To assess the composition of burn severity within hairy woodpeckers' home ranges, we constructed 100-m² grids over home ranges designated by minimum convex polygons (MCP; "Convex hulls and Sample Points" ArcView script; Jenness 2003). We extended grids by at least one point in all directions beyond the MCP to ensure that the measured vegetation encompassed the full extent of the estimated kernel. We then classified each grid point by burn severity (high, moderate, unburned).

Data analysis.—We used 30–50 locations to estimate diurnal home range size using nonparametric fixed kernel estimation to ensure reliable performance (Worton 1987, Seaman et al. 1999). We considered location points independent if taken 1–2 times per 24-hour period as recommended in Swihart and Slade (1985). We used incremental area curves to assess whether location points for each bird provided adequate sample size for home range estimation. All home range sample sizes reached asymptotes within the incremental plots and were included in our analyses. We estimated home range size using animal movement extension (Hooge and Eichenlaub 1997). We followed the recommendation of Seaman et al. (1999) to use the 85% contour interval because it was the most biologically meaningful and mathematically reliable estimate of home range size, which we reported here.

We log-transformed home range size based on the 85% kernel to account for increasing variability across burn age and regressed against burn age using linear regression (Neter et al. 1996:10). For our analysis, we pooled across sex because we did not have adequate samples of males and females within each burn age and because studies on other woodpecker species have detected no difference in home

range size between the sexes (e.g., the downy woodpecker; Matthysen et al. 1993).

To calculate the area of each burn severity within home ranges, we created polygons around the vegetation grid points using "Create Thiessen Polygons, v3.2" ArcView script (Ammon 2003). If polygons extended outside the 85% contour, we clipped them to the 85% contour interval before summing the area in each severity. We regressed the proportion of high and moderate-severity area against burn age using linear regression (Neter et al. 1996:10) to assess the pattern of change through time.

Foraging Behavior

Field methods.—We assessed habitat components used for foraging by hairy woodpeckers using focal animal observation (Altman 1974). We located birds by radiotelemetry or visually by systematically searching 300-m belt transects centered over point-count transects (Fig. 1; Morrison and With 1987, Murphy and Lehnhausen 1998). We added transects to those used by Dwyer and Block (2000) to increase the number of individuals sampled each year and covered a larger portion of the Pumpkin fire, which contained only one transect (Fig. 1). We searched transects 2–5 times per season with repeated sampling at different times of the day to account for temporal changes in foraging patterns. We attempted to collect 30 observations per treatment each winter (Morrison 1984).

Once we located a bird, we recorded 1) bird identity (transmitter frequency, color-band, or unbanded), sex, location (distance from nearest point-count station or Global Positioning System location), and burn severity within a 25-m radius, 2) bird foraging height, 3) foraging substrate (branch or trunk), and 4) selected tree dbh, height, and percent bole scorch. In addition, we measured small-scale patch characteristics around that tree using a point-center quarter method (Cottam and Curtis 1956) in which we recorded the distance from the tree selected by the bird to the 4 nearest trees in each cardinal quadrant. For each quadrant tree, we then recorded dbh and percent tree bole scorched. We considered observations on birds we encountered on the same day independent if the next bird was of the opposite sex or uniquely marked. Otherwise, we assumed sequential observations made at least 250 m apart from each other to be different individuals (Block 1991).

During 2002–2003, we recorded whether an edge between high- and moderate-severity burn occurred within the 25-m radius surrounding the bird. We added the edge assessment because observations in 2001–2002 suggested that birds were not using interior portions of high-severity burned areas as much as edges.

To compare vegetation components used by hairy woodpeckers for foraging to randomly selected sites, we used the 100-m² vegetation grids created for the home range analysis to measure the same habitat variables as those measured for foraging observations. We collected these data during the last month of each season. We collected data only in areas within home ranges to ensure comparison of selected to random habitat present within areas used by hairy wood-

peckers. Within belt transects, we measured vegetation at the 3 closest point-count stations relative to where we observed an individual.

Data analysis.—Because we searched transects multiple times, we sampled individual birds repeatedly ($\bar{x} = 2.9 \pm 0.16$ SE observations/bird/severity). However, we made most repeated observations after sufficient time ($\bar{x} = 24.5 \pm 1.7$ SE days) for us to consider each observation independent. As a result, the statistical experimental unit we used in analyses was observation. Within each analysis, an individual bird did not account for $>7 \pm 5\%$ of the total observations and therefore did not weight the analyses toward a single individual.

To determine whether radiotransmitters affected foraging behavior, we compared foraging observations taken on birds with radiotransmitters to unmarked birds during winter 2001–2002 for the following foraging variables: foraging height, foraging tree dbh, tree bole scorch, and patch dbh, density, and bole scorch. We found no significant differences with 2-sample *t*-tests with Bonferroni adjustments (Zar 1999:122, Neter et al. 1996:157); therefore, we pooled all observations for foraging behavior analysis.

To test the hypothesis that birds used the interior portions of high-severity burns less than the perimeters of those burns, we compared the number of bird locations in each to the distribution expected based on the relative area of interior and perimeter derived from the vegetation grids. We analyzed data for years 3 and 7 postburn with chi-square goodness-of-fit test (Zar 1999:462).

To compare habitat used for foraging by hairy woodpeckers to that present, we analyzed used versus random points for 5 habitat components at 3 spatial scales: 1) tree, 2) small-scale patch, and 3) postburn edge for year 3. Tree characteristics included foraging tree dbh and selected tree bole scorch (m^2). Patch characteristics that we calculated using the point-center quarter method were patch dbh (average of the 5 tree dbh measurements), density (average distance from the focal tree to each quadrant tree), and patch bole scorch (surface area of each tree multiplied by the percentage of bole scorched, then summed for all 5 trees). We transformed data to satisfy normality and equal variance concerns (Zar 1999:273), then tested data across severity and burn age using 3-way ANOVA with Bonferroni adjustments (Neter et al. 1996:989, 157). We used Tukey's HSD test for multiple comparisons to compare differences between years and treatments ($\alpha = 0.05$; Neter et al. 1996:725).

To compare habitat used for foraging by hairy woodpeckers to what was present in unburned areas, we analyzed used versus random points for the above habitat components except patch and tree bole-scorch. We first compared data from each winter using 2-way ANOVA with Bonferroni adjustment (Zar 1999:231, Neter et al. 1996:157). Because data were not significantly different by year for all 3 variables, we pooled and retested data for differences to those available using *t*-tests with Bonferroni adjustment (Zar 1999:122, Neter et al. 1996:157). We then applied

Dunnett's 1-tailed control comparison test to compare habitat component means chosen by hairy woodpeckers within each burned treatment to the unburned pooled mean (Zar 1999:217). We used this method to test patch dbh, density, and average tree size in each treatment to the unburned mean for that variable.

Arthropod Density

Field methods.—In winter 2001–2002, we collected bark samples from high-severity burned areas in the Pumpkin and Horseshoe–Hochderffer burns. At each high-severity point on the vegetation grid, we randomly selected 1 tree to sample from the 5 determined by point-center quarter. We removed similar numbers of bark samples from 4 size classes of trees (0–15, 15–30, 30–45, and >45 cm) for 40 samples per fire. We took samples from a random orientation of the vertical face of the trunk using a cordless handheld drill and hole-saw 2 m above ground because this height was within the range for several prominent bark-dwelling arthropod species in the study area (Amman et al. 1985). Because woodborers return to the surface to feed the winter prior or 2 years prior to their emergence (Murphy and Lehnhausen 1998), we were careful when removing the bark sample to collect all woodborers in the cambium, under the bark sample, in frass if present, and sticking out of the wood (partial emergence). We felt this was an appropriate sample of the prey available to hairy woodpeckers in our area because behavioral observations indicated that deeper excavations made up only 5% of all foraging observations over the course of the study in all postburn ages. Surface area of samples was 102 cm^2 of bark but varied in thickness due to differences in tree size. For each sample, we recorded 1) location, 2) sample tree percent bole scorch, and 3) dbh. Samples were then stored in zip-lock bags in a freezer until they were x-rayed.

In winter 2002–2003, we took 40 samples from both high- and moderate-severity burned areas within the Rodeo–Chediski, Pumpkin, and Horseshoe–Hochderffer fires. Because analysis of first year samples indicated no difference in arthropod density by tree size, we took samples from trees ≥ 20 cm dbh because logistically it was the most efficient. We used the same methods from winter 2001–2002 to remove these samples.

We x-rayed bark samples because this method was shown to detect 95% of bark-dwelling arthropods in comparison to dissection (Fatzinger and Dixon 1965) and has been used for studying southern pine beetles (*Dendroctonus frontalis*; Conner 1979, Coulson et al. 1979). We used a Faxitron 2500, model 805400 (Faxitron X-ray Corp., Wheeling, Illinois) with the power set to 20 kVp and exposure time of 2–3 minutes with increasing sample thickness. We examined radiographs under a $5\times$ magnifying glass, and we identified all arthropod larvae and adults and classified them as bark beetle, woodborer, or other. To confirm classification to bark beetle and woodborer families, we dissected representative samples.

Data analysis.—We tested if the density for all bark beetle and woodborers combined varied across burn age and

between moderate- and high-severity burns using negative binomial regression (White and Bennetts 1996). We used and adjusted by hand maximum likelihood post hoc tests to maintain the Type I error rate at $\alpha = 0.05$.

Results

Hairy Woodpecker Relative Abundance

We detected hairy woodpeckers significantly more often in burned areas than in unburned sites of ponderosa pine forests ($\chi^2 = 80.30$, $P < 0.006$; Fig. 2) for 2 years following wildfire (Tukey's HSD P values < 0.05). The relative abundance of hairy woodpeckers 1 year after fire was 14 times greater compared with unburned areas and 18 times greater 2 years after fire. We did not detect a difference in relative abundance on unburned sites by year ($\chi^2 = 1.79$, $P = 0.181$).

For all years postburn, we detected greater relative abundance of hairy woodpeckers in high-severity burned areas than in moderate-severity burned areas ($F_{1, 207} = 10.7$, $P < 0.04$; Fig. 3). We recorded 1.2 times more detections in high-severity burned areas compared with moderate-severity burned areas 2 years after fire. Both abundance and the difference between the 2 severity types progressively decreased in stands of increasing burn age ($F_{7, 207} = 10.7$, $P < 0.001$). Abundances reached that of unburned areas by 7 years postburn for both burn severities (Dunnett's control test, $P > 0.05$).

Diurnal Home Range

Of the 25 hairy woodpeckers that we fitted with radio-transmitters and monitored, 16 retained transmitters long enough to accumulate the required number of locations to estimate home range size. Seven (2 F and 5 M) retained their transmitters during 2001–2002 and 9 (3 F and 6 M) during 2002–2003. Home range size increased with burn age ($R^2 = 0.72$, $F_{1, 14} = 35.6$, $P < 0.001$; Fig. 4a). 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. Within home ranges, the proportion of high-severity burn decreased significantly, on average 14% per year, with burn age ($R^2 = 0.37$, $F_{1, 14} = 8.21$, $P = 0.01$; Fig. 4b) and moderate-severity burn increased with burn age ($R^2 = 0.47$, $F_{1, 14} = 8.1$, $P = 0.02$; Fig. 4b). We did not detect unburned

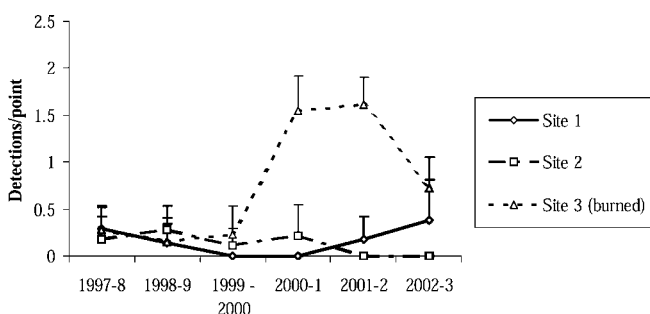


Figure 2. Hairy woodpecker winter relative abundance ($\pm$ SE) in 2 unburned areas (sites 1 and 2) and one site that burned in the Pumpkin fire (site 3) during the summer of 2000, Coconino National Forest, Arizona, USA, between 1997 and 2002.

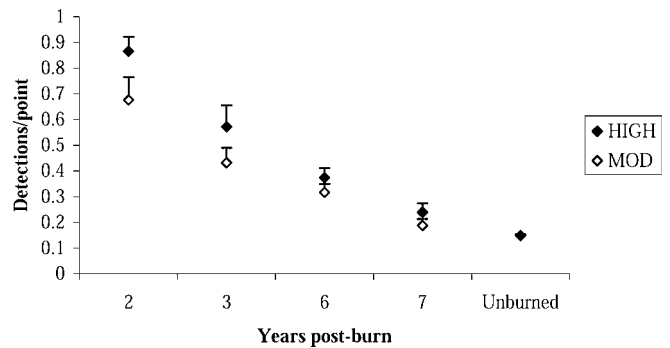


Figure 3. Hairy woodpecker relative abundance ($\pm$ SE) in high- and moderate-burn severities in the Pumpkin fire (2 and 3 yr postburn) and Horseshoe-Hochderffer fire (6 and 7 yr postburn), Coconino National Forest, Arizona, USA, during winters 2001–2003. Unburned forests adjacent to the burned areas are shown for comparison.

forest in home ranges until 6 years after fire, even though unburned habitat was available within and adjacent to the burn matrix.

Foraging Behavior

All of the foraging trees available to hairy woodpeckers in high-severity burns were standing dead trees; in moderate-severity burns, birds foraged on dead, dying, and living trees. In high-severity burns, we detected foraging hairy woodpeckers more often near (within 25 m) edges of moderate burn (70% of observations) than within the interior of high-severity burn patches (30%). This pattern was consistent for areas representing both 3 years postburn ($\chi^2 = 9.7$, $P = 0.002$) and 7 years postburn ($\chi^2 = 4.8$, $P = 0.034$).

At the patch level, observed hairy woodpeckers used patches with significantly greater mean tree diameter from that present in their home range when in high-severity burned areas but not in moderate-severity burned areas ($F_{1, 849} = 9.3$, $P = 0.01$; Fig. 5a). Hairy woodpeckers consistently foraged in patches with larger patch dbh in high-severity burns at all burn ages even though the patch dbh available increased through time ($F_{3, 849} = 2.5$, $P = 0.29$; Fig. 5a). Similarly, the patch dbh used by hairy woodpeckers in unburned areas was significantly larger than what was present (mean difference 7.8 ± 1.8 cm SE, $t_{64} = 3.72$, $P < 0.001$; Fig. 5a). Average patch dbh used in unburned areas was not, however, significantly different from that used within moderate-severity burned areas nor different from that used within the older high-severity burns (6 and 7 years postburn [Dunnett's test, $P > 0.05$]; Fig. 5a). Therefore, we only observed this difference in behavior within high-severity burns at 2 and 3 years postfire (Dunnett's test, $P < 0.05$).

Hairy woodpeckers used patches with greater total bole scorch in both the high- and moderate-severity burns ($F_{1, 847} = 529.75$, $P < 0.001$) until burned areas were 7 years old (Fig. 5b). Patches used by hairy woodpeckers in burns representing years 2, 3, and 6 in high-severity areas had on average 6.1 m^2 ($\text{SE} = \pm 1.9 \text{ m}$) more bole scorch and in the moderate-severity areas 4.1 m^2 ($\text{SE} = \pm 0.9 \text{ m}$) more bole scorch. By 7 years postburn, hairy woodpeckers foraging in

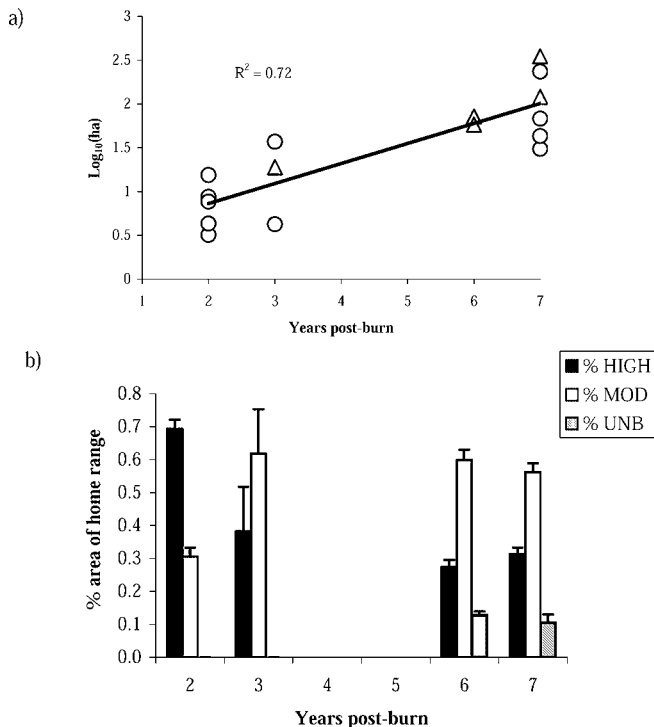


Figure 4. (a) Hairy woodpecker home range size in 2 burned ponderosa pine forests following the Pumpkin fire (2 and 3 yr postburn) and the Horseshoe–Hochderffer fire (6 and 7 yr postburn), and (b) proportion of high- and moderate-burn severities and unburned areas (+SE) within home ranges, Coconino National Forest, Arizona, USA, during winters 2001–2003. Females are denoted by open triangles and males by open circles.

both burn severities used patches with bole scorch similar to what was present ($F_{3, 847} = 10.2$, $P < 0.001$, Tukey's HSD all $P < 0.05$, except for 7 years postburn; Fig. 5b).

We did not observe hairy woodpeckers using patches with tree densities different from that present in their home ranges ($F_{1, 857} = 5.09$, $P = 0.12$; Fig. 5c). However, tree densities did differ by burn severity and changed through time ($F_{3, 857} = 22.6$, $P < 0.001$). In the high-severity burn, tree density was initially greater than in the moderate-severity burn but approached that of moderate-severity burn by 6 years postburn (Tukey's HSD, $P > 0.05$; Fig. 5c). Contrary to the behavior exhibited in burned forests, hairy woodpeckers in unburned areas foraged in patches 1.4 times less dense than that present ($t_{65} = -2.44$, $P = 0.017$; Fig. 5c). The tree density used in unburned forests was not different from that used in any burn severity at any age, except within the high-severity burn at young burn ages (2 and 3 yr postburn [Dunnnett's test, $P < 0.05$]; Fig. 5c).

Hairy woodpeckers chose trees larger than those present in their home ranges ($F_{1, 852} = 32.7$, $P < 0.001$; Fig. 5d) for both burn severities ($F_{1, 852} = 8.27$, $P = 0.02$). Average tree size used ranged from 30 ± 15.4 to 42 ± 15.1 cm for trees in both severities across all burn ages and in unburned areas (Fig. 5d). Diameter at breast height of trees present within home ranges increased across burn age within high-severity burns but remained more constant within moderate-severity burns, although the interaction was not significant ($F_{3, 852} =$

3.12 , $P = 0.13$; Fig. 5d). Foraging by hairy woodpeckers on trees with larger dbh than what was present was also exhibited in unburned ponderosa pine (mean difference 16.8 cm ± 1.8 cm SE, $t_{68} = 5.75$, $P < 0.001$; Fig. 5d). Mean dbh of trees used in unburned forests did not differ from those used in the moderate-severity across all postburn ages nor from those used in the high-severity burns 6 and 7 years postburn (Dunnnett's test, $P > 0.05$; Fig. 5d).

Hairy woodpeckers used trees with greater bole scorch than that available in both burn severities ($F_{1, 885} = 284.13$, $P < 0.001$; Fig. 5e). Hairy woodpeckers used trees with greater bole scorch than available on trees present within both high- and moderate-severity burns for all burn ages except 7 years postburn ($F_{3, 856} = 4.4$, $P = 0.02$, Tukey's HSD all P values < 0.05 , except 7 years postburn; Fig. 5e). Selected trees in the high-severity burn had on average 3.1 times the bole scorch than of those present, and those selected in the moderate-severity had on average 2.8 times the bole scorch than of those present.

Bark Beetle and Woodborer Density

Across all bark samples, we identified 97% of arthropods as bark beetle and woodborer larvae and adults. Total density of these varied through time ($\chi^2_4 = 22.94$, $P = 0.001$; Fig. 6a) but not by severity ($\chi^2 = 1.72$, $P = 0.19$). Density 1 year postburn (Rodeo–Chediski fire) was significantly less than that found 2 years postburn ($\chi^2 = 26.76$, $P = 0.001$; Fig. 6a), with insect density 1.4 times greater at 2 years postburn. Two-year postburn (Pumpkin fire) density was 2.5 times greater and significantly different than 3 (Pumpkin fire), 6 (Horseshoe–Hochderffer fire), and 7 (Horseshoe–Hochderffer fire) years postburn (all P values < 0.001). Multiple comparisons for all other years were not significantly different (all P values > 0.77).

Discussion

Response to Burn Age

Hairy woodpecker abundance and home range size differed among burned stands representing different times since fire, suggesting significant changes in the value of this habitat as time since fire increased. The initial increase in woodpecker abundance after fire that we documented was similar to that found in other short-term studies of woodpecker responses to fire (Raphael et al. 1987, Brawn and Balda 1988, Hobson and Shieck 1999, Kotliar et al. 2002). Likewise, the lower abundance in the older burned sites we studied and lack of difference between areas representing 7 years after wildfire and unburned forests was similar to that of woodpeckers in mixed-conifer forests of Washington, USA, where hairy woodpecker abundance returned to that of unburned sites 4 years after wildfire (Kreisel and Stein 1999). Hairy woodpecker home range size increased across areas representing burns of increasing time since fire, suggesting a reduction in habitat quality through time. While ours is the first study to our knowledge that documented change in home range over multiple winters, other studies found seasonal increases in home range size as resources became more limited (Wiklander et al. 2001) or correlated size differences with

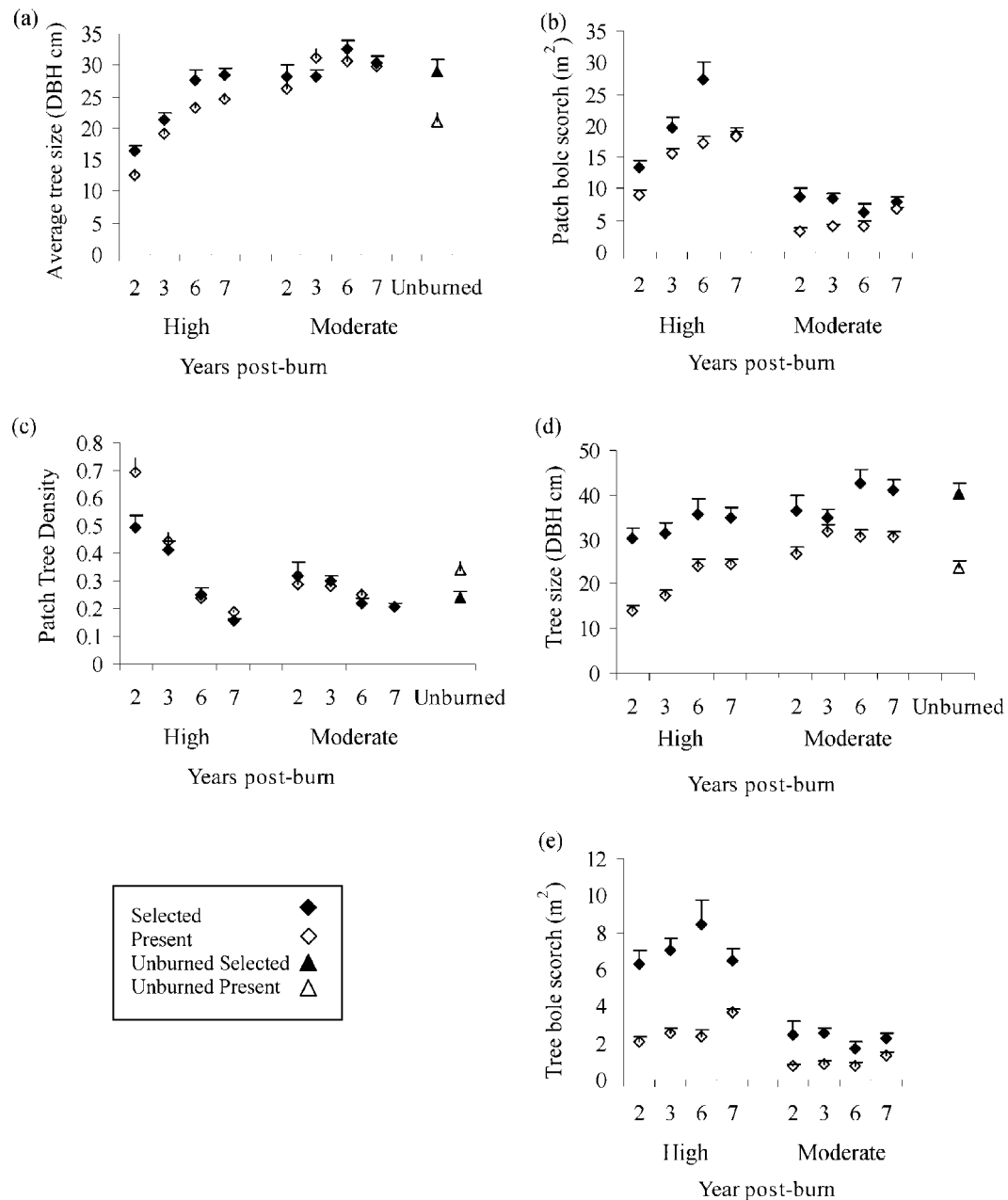


Figure 5. Selection of tree and small-scale patch habitat components ($\pm$ SE) by hairy woodpeckers in high- and moderate-burn severity areas in the Pumpkin fire (2 and 3 yr postburn) and Horseshoe-Hochderffer fire (6 and 7 yr postburn), Coconino National Forest, Arizona, USA, during winters 2001–2003. Habitat components: (a) average tree size, (b) patch bole scorch, (c) patch tree density, (d) tree size, and (e) tree bole scorch. Selection and available habitat components in unburned areas are shown for comparison.

resource indices (Renken and Wiggers 1989, Rolstad and Rolstad 2000).

The increase in relative abundance of hairy woodpeckers in burned areas in the years following fire is consistent with the hypothesis that fire causes a temporary increase in bark-dwelling arthropod prey (Miller and Patterson 1927, Hutto 1995, Murphy and Lehnhausen 1998, Bradley and Tueller 2001). Burned trees are 24% more likely to be attacked by bark beetles than unburned trees (Bradley and Tueller 2001), and densities of both bark beetle (*Ips pini*; Santoro et al. 2001) and spruce beetle (*Dendroctonus rufipennis*) have been shown to double in burned areas (McCambridge and

Knight 1972). Likewise, wood-boring beetle larvae that initially excavate galleries bored into the heartwood return to the bark to feed 2–3 years after oviposition (Rose 1957, Hanks 1999). In areas where bark beetle populations irrupted following low-intensity fire, populations returned to endemic levels by 3–5 years postfire (Ryan and Reinhardt 1988, Weatherby et al. 1994, Gibson et al. 1999). Our arthropod sampling showed this predicted pattern of initial increase followed by decline, with arthropod densities within the trees we sampled slightly higher in the stand representing the first winter after fire (Rodeo-Chedeski fire) and markedly higher in the stand representing 2 years after

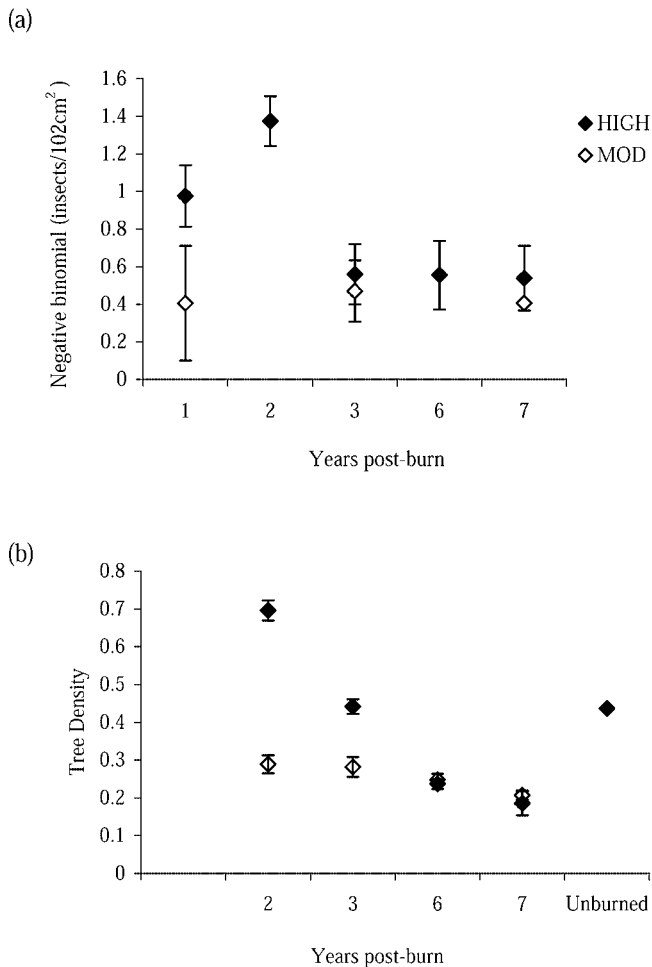


Figure 6. (a) Bark-dwelling insect density per 102-cm² bark samples (+SE) taken from random ponderosa pine trees within high- and moderate-burn severities in the Rodeo-Chedeski (1 yr postburn), Pumpkin (2 and 3 yr postburn), and Horseshoe-Hochderffer fires (6 and 7 yr postburn), and (b) change in density of snags within high-burn severity and trees in moderate-burn severity within the Pumpkin and Horseshoe-Hochderffer fires, Coconino National Forest, Arizona, USA, during winters 2001–2003.

fire (Pumpkin fire 2001) compared to sites representing 3 (Pumpkin fire 2002), 6, and 7 years after fire (Horseshoe-Hochderffer fire). Although our experimental design used different sites to represent different times since wildfire, and therefore could potentially confound site and time effects, we observed the biggest change in both arthropod density and hairy woodpecker abundance (from 2-yr-old to 3-yr-old fires) at the site (Pumpkin) we sampled in succeeding years.

Although the increase in home range size from 2 to 3 years postfire could be attributed solely to the decreasing density of bark-dwelling arthropods available in the trees we sampled, in burned areas representing 6 and 7 years after fire we did not detect a difference in arthropod density per tree between years even though woodpecker home range size continued to increase. We hypothesize that changes in home range size between years 6 and 7 were due to a decrease in tree density as dead, standing snags created by high-severity fire continued to fall. Tree density across the stands we studied was consistent with this hypothesis (Fig. 6b),

although our lack of prefire data precluded our ruling out the possibility that these differences were due to stand differences in initial tree density rather than to tree fall through time. We hypothesize that this combination of an initial decline in arthropod density per tree and continuous decline in tree abundance resulted in prey resources becoming increasingly dispersed across the landscape, causing hairy woodpeckers to compensate by increasing their home range.

Response to Burn Severity

Both hairy woodpecker abundance in each burn severity and the relative amount of each burn severity within home ranges varied across stands representing increasing time since fire, indicating that burn age and burn severity interacted to affect woodpecker response. Hairy woodpecker relative abundance was greater in high-severity versus moderate-severity burned areas in stands representing 2 and 3 years after wildfire, but it was not different between these burn severities in stands representing 6 and 7 years postfire. Similarly, while hairy woodpeckers always maintained high-severity areas within their home ranges, the proportion of high-severity areas decreased across stands representing increasing times since fire, with moderate-severity composing the majority of home ranges in the stands representing 6 and 7 years after fire. Scorch levels of individual trees have been positively associated with probability of arthropod attack (Furniss 1965, Flanagan 1996) suggesting that areas experiencing intense fire and severe scorch should have greater arthropod densities than moderate-severity burned areas. Unfortunately, we did not sample arthropod density in moderately burned areas in the Pumpkin fire in 2001, the year with the greatest arthropod density. However, our samples from the 1-year-old fire (Rodeo-Chedeski) suggest that arthropod densities may have been higher in severely burned areas. Even if no difference in arthropod densities within trees exist between severities, because high-severity burns have greater tree density, arthropod densities at the landscape scale would be greater initially at younger burn ages before trees fall. We would therefore expect both greater abundance of hairy woodpeckers within high-severity burns and larger proportions of high-severity burn within home ranges at young burn ages with a decrease in both through time. 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 (Fig. 6b). Moderately burned trees have high susceptibility to secondary mortality agents such as arthropod attack or drought that remove them from the population more slowly after the initial wildfire event than severely burned trees that are removed by toppling in high winds (Salaman 1934, Flanagan 1996, McHugh and Kolb 2003).

When foraging in high-severity portions of their home range, hairy woodpeckers used edges adjacent to moderately burned areas rather than interior portions of the high-severity burn more than expected based on the relative area of each available in their home range. Moderately burned

areas likely provided more protection from both extreme weather conditions and predators because live and dying trees provided foliage cover. Higher arthropod densities in high-severity burned areas may partially compensate for these greater energetic costs and predation risks, but using edges likely ensures quick retreat to the denser cover afforded by moderate-severity burns. This is consistent with observations that woodpeckers are often rare in the interior of large high-severity burned areas (Murphy and Lehnhausen 1998). These results indicate that any benefit hairy woodpeckers gain from high-severity burned areas decreases after patches reach a size that does not allow birds to access trees near the edge of moderately burned areas.

Response to Tree Size and Stand Structure

Hairy woodpeckers selected both larger trees and patches with greater than average dbh, suggesting an avoidance of dense, dog-hair stand structure that characterized much of the unburned habitat. Hairy woodpeckers have been shown to select trees of similar or slightly smaller sizes in other studies of unburned forests (33.6 cm [Conner 1981]; 43–50 cm [Morrison and With 1987]). Several species of *Dendroctonus* beetles found in northern Arizona prefer host trees of this dbh (20–40 cm) in unburned forests (e.g., *D. ponderosae* [Amman and Pasek 1986], *D. brevicornis* [Kaufmann and Stevens 1984]). In burned areas at our study site, density of arthropods per bark sample did not differ among trees of differing size. Therefore, 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 during the first and second years following wildfire in Alaska, USA. If larger trees have more arthropods overall than smaller trees, then patches of larger trees would further increase foraging profitability. In our study, hairy woodpeckers selected patches with larger average dbh than available in all burn severities and unburned areas. This pattern is similar to that found for this species in unburned longleaf pine (*Pinus palustris*) systems in Texas, USA, where birds exhibited preference for patches with greater basal area and sapling snags (Shackelford and Conner 1997).

Hairy woodpeckers selected trees with greater scorch at both the tree and patch level in the years following fire. Again, this was likely because greater bole scorch increased 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 but have greater susceptibility to secondary mortality agents, monitoring these trees would allow hairy woodpeckers to maximize their energy gain by selecting trees with a greater likelihood of arthropod attack through time. Lima (1983) found that a congener of the hairy woodpecker, the downy woodpecker, monitored habitat quality at the small patch scale (4 simulated trees) by food intake and energy gain. In burned areas representing 7 years since wildfire,

hairy woodpecker selection of scorched trees did not differ from the average present in both burn severities, indicating that by this time scorched trees no longer represented a higher-value resource.

How important burned areas are to the maintenance of hairy woodpecker populations through time remains unknown. However, prey availability over winter, when mortality rates are often greatest for resident birds, has often been argued to be an important factor in population regulation (Lack 1967, Graber and Graber 1983, Newton 1998). Likewise, many authors have argued that the major decline in forest-dwelling birds, especially woodpeckers, has resulted from fire suppression (Raphael et al. 1987, Hejl 1994, Hutto 1995, Hobson and Shieck 1999, Brawn et al. 2001). Samman and Logan (2000) noted that fire was critical for bark beetles to maintain viable populations, and Sánchez-Martínez and Wagner (2002) reported that during the past 100 years of fire suppression in northern Arizona's ponderosa pine forests, bark beetle pockets were small and infrequent and outbreaks were rare (one known case) and smaller than reported in other ponderosa pine forests. Overall, our data suggest a dynamic interplay between time and fire severity, with hairy woodpecker abundance, home range size, and foraging behavior changing in response to a pulse of arthropods in the years immediately after fire overlaid on different dynamics of resource availability due to burn severity.

Management Implications

We suggest that forest managers retain small stands of small-diameter trees that could support high-severity fires within the greater forest matrix. Allowing wildfire to create small patches of high-severity burn may be consistent with patterns of historical fire regimes that likely supported the presence of patches up to 9 ha (Fulé and Covington 1997, Fulé et al. 2004). Many current forest thinning and restoration plans for ponderosa pine forests in the southwestern United States advocate the use of low-intensity prescribed fire and the removal of small-diameter trees (<41 cm dbh; Covington et al. 1997) that fuel high-intensity fires. Because this definition of "small-diameter trees" includes the majority of the tree sizes used by hairy woodpeckers for foraging in our study, silvicultural treatments that retain small patches of high-density, small-diameter trees within a broader matrix of thinned stands should produce the highest-quality habitat for hairy woodpeckers. Additionally, if salvage logging is undertaken in large high-severity burned areas, dead trees along the perimeter of these areas should be retained.

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