Space Use by White-Headed Woodpeckers and Selection for Recent Forest Disturbances

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ABSTRACT White-headed woodpeckers (*Picoides albolarvatus*) are important cavity excavators that recently have become the focus of much research because of concerns over population declines. Past studies have focused on nest site selection and survival but information is needed on factors influencing their space use when away from the nest. We examined space use by white-headed woodpeckers during the nesting (May–Jul) and post-nesting (Jul–Oct) periods and compared the role of environmental factors (e.g., landcover) and socio-demographic factors (e.g., age, breeding success) in home range size and selection of location. Average size of 99% kernel home ranges was 125 ha (SD ± 59 ha; $n = 19$) in the nesting period and 137 ha (SD ± 70 ha; $n = 30$) in the post-nesting period. Minimum convex polygons were generally comparable to or smaller than ranges reported from previous radio-telemetry studies with this species. Although bird weight and age best explained variation in home range size compared to other factors, neither parameter estimate was significant in our models. Thus, even though weight and age were the most-supported factors in our analysis, home range size was largely influenced by factors that we did not measure. We found that most woodpeckers selected home ranges within forest patches that had undergone a recent disturbance; these areas included forests that had recently been burned with prescribed fire by the United States Forest Service (82%) or subject to disease (16%). Most burned patches in our study were small (approx. 4.8 ha) and occurred within otherwise live forest but had nearly complete mortality of adult trees. We suggest that recent forest disturbances, especially mixed-severity prescribed burns, may have been selected by white-headed woodpeckers because they created snags for nesting and future studies should explore this hypothesis. Because home range size was variable and not linked with productivity, it should not be used as an indication of habitat quality without more detailed studies on causal factors that affect space use in this species. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS burn, habitat selection, home range, mixed-severity prescribed fire, *Picoides albolarvatus*, *Pinus ponderosa*, ponderosa pine, resource selection, space use, white-headed woodpecker.

The white-headed woodpecker (*Picoides albolarvatus*) is a primary cavity excavator, whose cavities provide nest and shelter sites for a variety of small-bodied secondary cavity users (Tarbill et al. 2015). White-headed woodpeckers occupy dry pine forests in western North America, and in the northwestern United States they are considered a sensitive species associated with late-seral ponderosa pine (*Pinus ponderosa*) forests (Garrett et al. 1996). Large, old pines are considered important for providing reliable food and large-

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diameter snags for nesting (Raphael and White 1984, Dixon 1995*a*). Although quantitative data are lacking, it is therefore assumed that selective logging of large-diameter pines by European settlers in the 19th and 20th centuries contributed to wide-spread population declines (Dixon 1995*a*, Wisdom et al. 2000). Because of their association with mature pine stands (Dixon 1995*a,b*), white-headed woodpeckers also have been used as an indicator species for forest management practices aimed at restoring old-growth conditions in ponderosa pine forests in western North America (Altman 2000, Wisdom et al. 2000, Gaines et al. 2007).

Given their status as a sensitive indicator species, white-headed woodpeckers have become the focus of numerous research studies in recent years. Somewhat surprisingly, several of these studies have found white-headed woodpeckers in a variety of disturbed and managed habitats

including recent burns (Hanson and North 2008, Saab et al. 2009, Wightman et al. 2010, Tarbill et al. 2015), young (<75 yrs) forests used for timber production and livestock grazing (Lindstrand and Humes 2009, Kozma 2011), and salvage logged burns (Kozma 2012). In some of these areas, nest success and productivity rates were similar to rates in older stands of ponderosa pine (Kozma and Kroll 2012). Although comparisons across studies must be done with caution, these findings suggest that white-headed woodpeckers may be less restricted to old forests than originally thought. Unfortunately, past studies on white-headed woodpeckers in disturbed, young, or managed forests have been limited to observations at nest sites or detections during point count surveys. Thus, there is limited information on space use by white-headed woodpeckers in managed forests, such as characteristics of home ranges and habitat selection. Additionally, we found no studies that simultaneously related environmental factors (e.g., vegetation features, landscape composition, topography) and socio-demographic factors (e.g., productivity, population density, bird age, bird sex) to white-headed woodpecker space use. Past studies have considered only the effects of environmental factors (specifically, the proportion of old-growth forest within home ranges) on home range size (Dixon 1995a,b), even though socio-demographic factors such as population density and productivity affect ranging behavior in other woodpeckers (Hooper et al. 1982, Elchuk and Wiebe 2003, Leniowski and Wegrzyn 2013).

We designed a study to explore white-headed woodpecker space use in managed forest types to address some of these information gaps. We worked in forests subject to both historical (pre-1990) and recent (post-1990) timber harvest. We had 3 primary objectives. Our first objective was to obtain base-line information on white-headed woodpecker home range size in managed stands for comparison with other studies, because past studies have focused on their space use in forests with an old-growth component. Our second objective was to examine factors associated with variation in home range size. We were particularly interested in the degree to which socio-demographic factors such as bird age, population density, and nest productivity influenced space use compared to environmental factors such as stand age, tree size, and availability of old-growth forest. Lastly, we tested for selection of habitat features on the landscape for home ranges (second-order selection) during the nesting and post-nesting periods. Because old-growth forest was rare in our study areas, we were interested in determining features selected by white-headed woodpeckers in landscapes lacking large, old trees.

STUDY AREA

We selected 6 study sites on the east slopes of the Cascade Range in Yakima, Kittitas, and Chelan counties in Washington State (approximately 46° 45′ N, 120° 58′ W and 47° 30′ N, 120 ° 33′ W; Fig. 1). Study sites averaged 2,042 ha in size (SD ± 1,091 ha). Five sites were predominately on the Okanogan-Wenatchee National Forest. The 6th encompassed state and private lands.
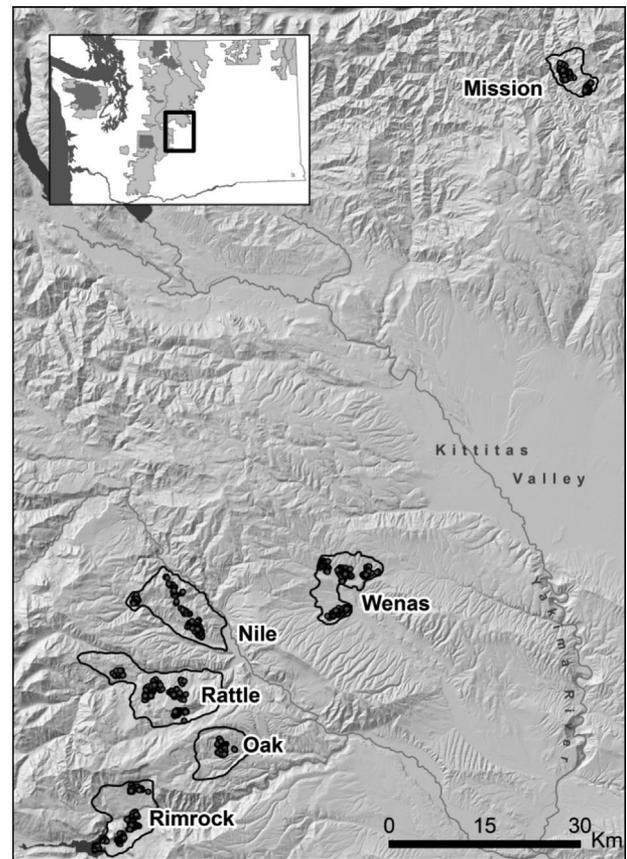

Figure 1. Location of 6 study sites used to examine white-headed woodpecker space use in central Washington, USA, from 2011 to 2013. The polygons show the outline of each study site, and dots represent telemetry tracking locations from 35 radio-tagged woodpeckers.

White-headed woodpeckers are generally considered uncommon in Washington and so we initially relied on previously published information on white-headed woodpeckers to locate study areas. Thus, we selected Mission, Wenas, Nile, and Rimrock study sites (Fig. 1) because they contained known populations of woodpeckers from past research (Buchanan et al. 2003, Gaines et al. 2007, Kozma and Kroll 2012). We added Oak and Rattle as additional sites because reconnaissance surveys revealed breeding pairs of woodpeckers.

Within each of our 6 study sites, forest composition varied considerably based on aspect, slope, elevation, and longitudinal distance from the Cascade Crest. Generally, ponderosa pine was dominant or co-dominant with Douglas-fir (*Pseudotsuga menziesii*) or grand fir (*Abies grandis*). Other tree species included western larch (*Larix occidentalis*), quaking aspen (*Populus tremuloides*), and black cottonwood (*Populus trichocarpa*). We estimated that ≥92% of the area within study sites had been harvested for timber at least once since 1950 based on United States Forest Service Timber Harvest activity reports and Washington State Department of Natural Resources forest practice applications (FPAs). Most harvests were described as overstory removal cuts (removal of entire mature overstory) or partial removal cuts (removal of part of the overstory). Approximately, 10% of the

area within each study site had been burned with mixed severity prescribed fire and/or thinned by harvest within 10 years of the start of this study. Four sites were actively grazed by domestic livestock during summer: 2 by sheep (Nile and Rattle; Fig. 1) and 2 by cattle (Rimrock and Wenas).

METHODS

Field Data Collection
Rather than defining and searching in pre-defined forest types within the 6 study sites, we instead searched the entirety of each site from March through May, 2011–2013 for territorial, adult white-headed woodpeckers by broadcasting playback calls and drumming. Beginning in mid-May, we returned to these territories and searched for nests by following adults. We recorded the locations of all nest sites on portable global positioning system (GPS) units (location error ± 5–6 m). We randomly selected, without replacement, a subsample of woodpecker nest territories for radio-tracking each year. At these territories, we used several methods to capture woodpeckers. For males, we used their aggressive territorial behavior in spring to lure them to noose traps strung along branches near stuffed taxidermy mounts of white-headed woodpeckers. Males were lured into the vicinity of the taxidermy mount using playbacks broadcast from speakers (of drumming and calls). Typically, when males heard the playbacks and then sighted the taxidermy mount they moved in to attack whereupon their feet became entangled in nooses. We used this method only prior to the nesting season to avoid causing disturbance to nest sites. During the nesting season, we captured both male and female woodpecker at nest sites using mist-nests, noose traps, and hoop nets.

Whenever possible, we weighed woodpeckers although because of concerns over handling stress during the nesting season, 9 individuals were released without being weighed. We fit 1 adult from each territory with a 1.2-g very high frequency (VHF) transmitter (approx. 2% of body weight; Advanced Telemetry Systems, Islanti, MN) using an elastic leg-loop harness (Rappole and Tipton 1991) or by gluing transmitters to a central tail feather. We alternated the sex of the bird that was radiotagged between territories to ensure equal representation by both sexes in our sample and we radiotagged only 1 individual from each territory for independence among individuals.

We aged all captured woodpeckers using Pyle and Howell (1995) and grouped woodpeckers into first-year breeders (SY birds) and after-first-year breeders (ASY birds). All handling was in accordance with Institutional Animal Care and Use Committee guidelines (University of Idaho Protocol #2011-30) and in compliance with the Ornithological Council Guidelines for the Use of Wild Birds in Research (Fair et al. 2010).

We were interested in whether productivity influenced home range size. To estimate productivity, we checked nest contents using a hole saw (Ibarzabal and Tremblay 2006) or video inspection probe within 5 days of fledging and counted the number of nestlings. For successful nests, we confirmed fledging by radiotracking adults within 5 days of nest fledging and counting the number of young that were being tended (for failed nests, productivity = 0). We took several precautions to avoid affecting productivity and nest success of radio-tagged adults. First, adults were captured at nests only after incubation was underway to avoid nest abandonment. Second, we assumed that after capture adults would need several hours to grow accustomed to their transmitters and return to nest sites. Therefore, during incubation we captured woodpeckers at nest sites only on sunny, calm afternoons to minimize exposing eggs to cool temperatures. We also monitored nests for up to 250 minutes prior to trapping to ensure eggs were well attended. We waited to capture incubating adults only once we determined that the second adult was present nearby to take over incubation duties. We also avoided capturing males after approximately 1600 hours because males incubate and brood nestlings overnight. With these precautions in place, it is unlikely that we adversely affected productivity. We observed no cases of nest abandonment following radiotagging and across all years productivity of radio-tagged woodpeckers (mean fledglings = 2.17) did not differ from that of non radio-tagged woodpeckers (mean fledglings = 1.85) monitored in the same study areas ($t_{62} = 1.99$, $P = 0.370$).

We began tracking radio-tagged woodpeckers 1–4 days after trapping. We obtained point locations by homing to individuals until we saw or heard the bird or signal strength and direction indicated the tree that the bird was in, and recorded the locations visited by individuals using portable GPS units. We visited woodpeckers every 1–4 days and recorded point locations when birds changed their location. The duration of tracking sessions ranged from 1 to 120 minutes and we alternated the order in which birds were tracked each day, for approximately equal representation of morning (sunrise to noon) and afternoon (noon to sunset) observations for each individual.

Because white-headed woodpeckers are sensitive to human disturbance at nest sites, we intentionally tracked woodpeckers only when they were at least 25 m from nest sites. When our presence obviously influenced adult behavior (e.g., incessant calls and refusal to leave the nest vicinity) we moved out-of-sight until the radio signal or vocalizations indicated that the woodpecker had resumed its normal activities. Most tracking did not likely disturb nesting birds because white-headed woodpeckers commonly travel out-of-sight of their nests while foraging (e.g., >50 m).

Following Elchuk and Wiebe (2003), we calculated nearest neighbor distances between nests for those in which we documented eggs or nestlings. Although it is possible that we missed some nests, this is unlikely for several reasons. First, in addition to searches for territorial white-headed woodpecker pairs, study areas were typically visited every 1–2 days for concurrent research on nesting, making it unlikely that pairs were missed or nests initiated in between visits. Second, white-headed woodpeckers are territorial during this period making them likely to respond to our call playbacks, which are a widespread and recommended tool for locating such

species (Dudley and Saab 2003). Third, white-headed woodpeckers generally are uncommon in this region and thus the probability of missing large numbers of breeders is low. Additionally, our average nearest neighbor distance of 878 m (range 106–2,723 m; $n = 19$ nests) is similar to an 8-year average from central Oregon with a robust sample of nests (mean $= 817$ m, range 126–2,424 m; $n = 127$ nests) corroborating our conclusion that few, if any, nests were missed.

Home Range Analysis

We estimated home ranges for 2 time intervals separately—the nesting and post-nesting periods. We defined the nest period as the interval between the start of nest excavation and the date of nest fledging. The post-nesting period extended from the date of nest fledging through either molt of the tail feathers or the first frost, whichever came first. Because individuals initiate nests and molt at different times, the start and end dates of each season varied by individual, although in general the nesting season extended from May through mid-July and the post-nesting season from mid-July through September.

To reduce potential issues with serially autocorrelated data in home range estimation, we removed point locations from moving birds that were <5 minutes apart. We assumed that this subsampling was sufficient to remove strongly autocorrelated data but provided enough observations from individual animals to maximize home range analyses (even at the expense of increasing autocorrelation) when systematic sampling is used (De Solla et al. 1999, Kernhonan et al. 2001, Fieberg 2007, Kie et al. 2010). Because of our sample scheme of visiting birds every 1–4 days, on average individual woodpeckers were visited on 13.8 different days (± 2.7 days) during the 5–6-week nesting period and 15.3 days (± 3.1 days) during the 8–10-week post-nesting period, equating to tracking on 36% and 24% of days for those periods, respectively.

For both periods, we delineated home ranges using the 99% contour interval of the fixed kernel distribution and plug-in bandwidth estimator in Geospatial Modeling Environment (version 0.7.1.0, www.spatialecology.com/gme, accessed 10 Apr 2014). Although 95% fixed kernels with least squares cross-validation (LSCV) are used more commonly than 99% fixed kernels, we observed that woodpeckers often foraged more than 500 m from nest sites during the nesting season (36% of foraging occurred >500 m from nests) and some of these observations were excluded from 95% kernels estimated with LSCV. Thus we used 99% kernels in our analyses, but we also report 95% fixed kernels and 100% minimum convex polygons for comparisons with other studies.

We constructed area observation curves (Odum and Kuenzler 1955) for 7 individuals and found that 99% kernels for both periods reached an asymptote between 25 and 30 point relocations. Therefore, we estimated home ranges only for individuals with at least 30 locations per period. We calculated the percent of home range overlap between nesting and post-nesting periods for the same individual following Kernohan et al. (2001). We also separately computed the area of home range overlap for all woodpeckers radiotracked in neighboring territories within a study area. We computed home range overlap only for individuals tracked in the same year and season and because territories were randomly selected (and thus it was rare to radiotrack individuals from adjoining territories) we were only able to compute overlap for a subset of telemetered birds. Similar to home range estimation, we computed areas of overlap only for comparison with other studies and did not use them in any analysis.

Land Cover in Home Ranges

To estimate land cover within home ranges, we used gradient nearest neighbor (GNN) models (Ohmann et al. 2011) derived from a combination of field plots, mapped environmental data, and Landsat Thematic Mapper (TM) satellite imagery from 2012. This dataset provided spatially explicit information on vegetation features at a 30-m resolution for all study sites. Based on a review of the literature, vegetation features that we considered important to woodpecker spacing behavior were mean basal area for ponderosa pine and Douglas-fir (Buchanan et al. 2003), percent canopy cover (Buchanan et al. 2003, Hollenbeck et al. 2011), proportion of late-successional old-growth forest (Dixon 1995a,b), proportion of the range with >40% canopy cover (Hollenbeck et al. 2011), variation in canopy cover (Hollenbeck et al. 2011), average quadratic mean diameter of trees (QMD; Hollenbeck et al. 2011), elevation, and average stand age (Dixon 1995a,b; Buchanan et al. 2003; Table 1). We derived mean slope within home ranges using a digital elevation model (DEM) because Buchanan et al. (2003) and Hollenbeck et al. (2011) suggested that white-headed woodpeckers select level ground for nesting.

Others have found that white-headed woodpeckers nest in recent burns (e.g., Wightman et al. 2010); therefore, we obtained data on forest disturbances from LandTrendr (Landsat-based detection of Trends in Disturbance and Recovery methods; Kennedy et al. 2010). LandTrendr uses multiple-year Landsat imagery to categorize forest disturbance based on magnitude and duration, and we considered recent (<10 year), short duration (<1 year), and high magnitude disturbance events from LandTrendr as representative of disturbances important in white-headed woodpecker space use. These data could not reliably distinguish between thinning, burning, and disease as short-term disturbance agents so we overlaid our Land-Trendr layer with the United States Department of Agriculture Forest Service Activity Tracking System (FACTS) database and FPAs to determine which disturbance events were caused by thinning, burning, combination of thinning and burning, or none of these, in which case we attributed the disturbance to disease. We then used ArcGIS 10 (Environmental Systems Research Institute, Inc., Redlands, CA) to extract these remotely sensed data for woodpecker home ranges in our study areas.

Availability of Habitat

For assessing second-order selection (Johnson 1980), we defined availability for white-headed woodpeckers based

Table 1. Description of parameters considered for examining variation in home range size and second-order selection by white-headed woodpeckers in central Washington, USA, 2011–2013.

Parameter	Description	Considered for home range size model	Considered for second-order selection model
Productivity	Productivity, or number of nestlings that fledged	x	
Birdage	Whether individual was a first-year or after-first year bird	x	
Neighbor	Distance (m) to nearest neighbor's nest-site	x	
Weight	Adult weight (g) at time of capture	x	
Slope	Mean percent slope within home range	x	x
Elevation	Mean elevation (m) within home range	x[a]	x[a]
Oldgrowth	Proportion of home range composed of late-successional old-growth forest (i.e., >10% canopy cover and >50.8 QMD)	x[a]	x
Standage	Mean age of stands within home range (years)	x[a]	x[a]
SDcanopy	Standard deviation of percent canopy coverage within home range	x	x
Canopy	Mean percent canopy coverage within home range	x	x
PineBA	Mean basal area (m²/ha) of ponderosa pine within home range	x[a]	x
FirBA	Mean basal area (m²/ha) of Douglas-fir within home range	x[a]	x[a]
QMD	Mean quadratic mean diameter (cm) of trees within home range	x	x
Disturbed	Proportion of home range thinned, diseased, or burned within 10 years	x[a]	x
40canopy	Proportion of home range with >40% canopy cover	x[a]	x[a]

[a] Denotes variables that were considered for model but omitted because of correlations with other variables.

on juvenile dispersal distances because white-headed woodpeckers are considered non-migratory residents (Garrett et al. 1996) that likely select ranges during their first year or 2 of life. We used a hole saw to access nestling woodpeckers at nest sites and placed a unique combination of colored leg bands on each nestling. In subsequent years, we returned to study areas and used call playbacks to elicit responses from woodpeckers banded as nestlings. For each relocated juvenile, we estimated the straight-line distance between natal sites and site of farthest dispersal. Dispersal distances did not appear skewed and therefore we used the mean dispersal distance across all juveniles to define dispersal distance for our population. For each radio-tagged adult, we then placed a circular buffer around the home range centroid of equal radius to the mean juvenile dispersal distance. We considered this buffer as the area potentially available for each adult for second-order selection. Because, we likely missed many dispersing juveniles and were probably more likely to resight short-distance dispersers, these buffers should be considered conservative estimates of the area available to each adult. However, we documented 2 woodpeckers banded as nestlings that settled and attempted to breed within the area of mean dispersal distance (one of these woodpeckers successfully fledged young) and so we deemed that this buffer was a plausible, though potentially conservative definition of availability, given the information currently available on white-headed woodpecker home range selection in the literature.

Because white-headed woodpeckers are a territorial species that occur only in lowland forests in Washington, we further restricted availability to areas outside of known territories for other white-headed woodpeckers and to forests below 1,300 m in elevation, the approximate maximum elevation for a white-headed woodpecker nest in Washington. We then used a random sample tool in ArcGIS to generate 2 random circular areas within this buffer but outside of the actual home range for each individual. The size of each

circular available range was equal to the average range size for that season. Even though it is more common to compare a single random polygon to each used one, we generated 2 random polygons for comparison with each used home range because we were concerned that a single random polygon would not capture the variability in features within our study areas. We then determined the proportions of each of the aforementioned habitat variables within these available polygons for comparison with used home ranges.

Model Development

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate factors influencing home range size and second-order selection. We developed a set of a priori models based on published literature and our observations of woodpecker space use with the aforementioned habitat variables and 4 socio-demographic parameters important in space use for other woodpecker species (Hooper et al. 1982, Elchuk and Wiebe 2003, Leniowski and Wegrzyn 2013): distance to the nearest neighbor's nest, bird age, number of fledglings, and weight at time of capture. We considered weight at time of capture an indicator of body condition for the entire breeding and post-breeding period. Although we captured individuals over several weeks and body weight may change as the season progresses (but see Koenig et al. 2005), we found no significant correlation in mass by capture day for males ($t_{17} = -0.30$, $P = 0.767$) or females ($t_{17} = 0.99$, $P = 0.335$). We also found no significant correlation between date of capture and the ratio of weight to tarsus length ($t_{31} = -1.32$, $P = 0.196$) and therefore we considered a single measure of weight as representative of body condition regardless of day of capture.

To reduce problems caused by collinearity among predictor variables, prior to building our models we looked for correlations between all pairwise combinations of covariates and omitted covariates if their coefficient was >0.60 (Dormann et al 2013). For our analysis of home range

size, among our 10 potential habitat covariates, elevation, proportion of the home range with recent disturbance, and basal area of both ponderosa pine and Douglas-fir were all correlated with canopy cover, and therefore we included only canopy cover in our final models. Likewise, stand age, QMD, and proportion of late-successional old-growth forest were correlated. We consequently included only QMD in our models because QMD was implicated by Hollenbeck et al. (2011) as an influential variable for this species. For our analysis of home range size, we therefore included 8 covariates: QMD (cm), slope (%), canopy cover (%), standard deviation of canopy cover, nearest-neighbor distance (m), bird age class (SY or ASY), bird weight (g), and productivity (number of fledglings).

For assessing second-order selection, we omitted the 4 socio-demographic variables. We again assessed all pair-wise correlations and found the proportion of the home range that was thinned and burned was highly correlated and 78% of the area that had been burned had also been thinned. As a result, we lumped thinning, burning, and disease into a single variable, disturbance. We found no strong correlations between proportion of late-successional old-growth forest, QMD, and ponderosa pine basal areas and included all 3 covariates along with disturbance, slope, and canopy cover (Table 1). We then created between 8 and 10 models with combinations of these variables to test for the factors affecting home range size and selection by white-headed woodpeckers.

Analysis

We used t-tests and analysis of variance (ANOVA) to examine whether home range size differed by sex and study site. We previewed data before analyses using histograms, boxplots, and normal probability plots and found no violations of normality. We used linear mixed models to evaluate support for the aforementioned habitat and socio-demographic factors on white-headed woodpecker range size within the nesting and post-nesting season. We included a random factor for each individual to account for potential variation in error associated with tracking different wood-peckers. We log-transformed home range size prior to analyses to better meet assumptions of normality and equal variance among groups. To assess second-order selection for home ranges within our landscape, we used a case-control logistic model to compare habitats within used home ranges to randomly selected available ranges.

We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to assess the amount of support for different models. Based on Akaike weights, we considered models in the 90% confidence set of candidate models as the best approximating models given the data (Burnham and Anderson 2002). For variables in the 90% confidence set of models, we presented parameter estimates, their standard errors, and 95% confidence intervals (± 1.96 SE). When confidence intervals did not include 0, we concluded that the associated parameter had an effect on selection or range size. We used SAS version 9.3 statistical software (SAS Institute, Inc., Cary, NC) for all statistical analyses and we considered statistical results significant at $\alpha = 0.05$. We report means ($\pm$ SD) unless otherwise noted.

RESULTS

Home Range Characteristics

We obtained 3,994 locations on 39 breeding adult white-headed woodpeckers ($n = 19$ females, 20 males). We obtained at least 30 locations on 19 adults during the nesting season and 30 adults during the post-nesting season for an average of 116 points (± 37 points; range: 60–228) per individual. Home range size was not correlated with the number of tracking relocations for either the nesting ($R = 0.236$) or post-nesting seasons ($R = -0.008$). Mean 99% kernel home ranges were 125 ± 59.4 ha and 137 ± 69.5 ha for the nesting and post-nesting seasons, respectively (Table 2). Home range size varied among individuals by a factor of 5.5 during the nesting season and by a factor of 7.3 during the post-nesting season (Table 2). Home range size did not differ by sex for the nesting ($t_{17} = 1.09$, $P = 0.291$) or post-nesting ($t_{28} = 1.05$, $P = 0.301$) seasons (Table 2). Home range size also did not differ by study area for either nesting ($F_{4, 14} = 2.24$, $P = 0.117$) or post-nesting ($F_{5, 24} = 1.38$, $P = 0.268$) seasons.

For individuals that we tracked during both nesting and post-nesting seasons ($n = 14$), post-nesting home ranges overlapped nesting ranges on average by 55.8% (range 12.7–97.5%). We separately computed home range overlap for neighboring woodpeckers tracked in the same year and season. During the nesting season, home ranges for 11 neighbors overlapped on average by 22.6% (range 0.1–91.0%; Fig. 2). For the post-nesting season, home ranges for 15

Table 2. Mean, standard deviation, and range of home range size (ha) for 35 adult white-headed woodpeckers in central Washington, USA, 2011–2013. We provide the 99% kernel home ranges used for analysis as well as 95% kernel, 50% kernel, and 100% minimum convex polygon (MCP) home range estimates for comparison purposes.

|	99% kernel	95% kernel	50% kernel	100% MCP
Nesting (May–Jul)				
Females ($n = 9$)	109.3 ± 49.5 (51.6–193.8)	104.6 ± 48.5 (44.5–193.4)	20.1 ± 11.3 (8.9–39.3)	58.3 ± 34.7 (28.9–137.6)
Males ($n = 10$)	138.9 ± 66.5 (71.0–284.9)	137.9 ± 51.7 (64.3–231.1)	26.3 ± 14.2 (9.5–59.0)	68.9 ± 29.1 (39.9–130.5)
All birds ($n = 19$)	124.9 ± 59.4 (51.6–284.9)	124.9 ± 50.7 (44.5–231.1)	23.4 ± 13.0 (8.9–59.0)	63.9 ± 31.5 (28.9–137.6)
Post-nesting (Jul–Oct)				
Females ($n = 13$)	152.3 ± 94.4 (58.5–411.1)	144.9 ± 100.8 (54.4–427.2)	24.5 ± 12.8 (9.6–76.9)	80.6 ± 56.7 (23.7–238.4)
Males ($n = 17$)	125.3 ± 41.6 (56.7–199.3)	122.7 ± 45.1 (48.9–198.6)	27.1 ± 17.5 (9.6–76.9)	58.6 ± 30.5 (19.6–130.9)
All birds ($n = 30$)	137.0 ± 69.5 (56.7–411.1)	137.0 ± 72.9 (48.9–427.2)	22.5 ± 7.6 (10.3–38.2)	68.2 ± 44.4 (19.6–238.4)
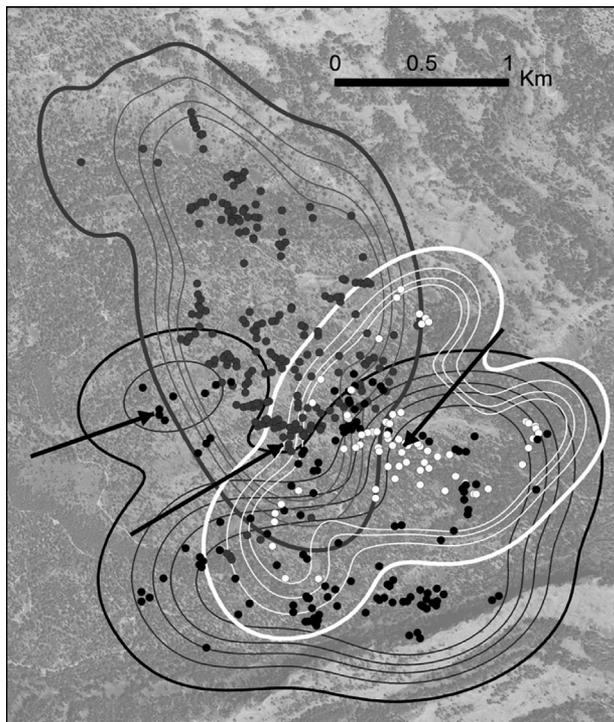
Figure 2. Overlap of home range kernels by 3 breeding adult white-headed woodpeckers in the Oak study site in Washington, USA, during the nesting season in 2013. Arrows point to nest sites for 3 individuals, and black, gray, and white dots and lines represent points and 99–75% contours for male #530, female #500, and female# 511, respectively.

neighboring woodpeckers overlapped 28.7% (range 7.3–56.5%).

On average home ranges contained more ponderosa pine than Douglas-fir (Table 3). Forests classified as late-successional old growth were uncommon in home ranges in both the nesting and post-nesting periods and the dominant forest layer in home ranges averaged approximately 100 years old (Table 3). Average slope within nesting and post-nesting home ranges was 12% (range 3–21% slope) and 13% (range 5–23%), respectively (Table 3), although some home ranges contained slopes as steep as 237% (equivalent to a slope of 67 degrees).

Factors Influencing Home Range Size

In both nesting and post-nesting seasons the best models predicting home range size included woodpecker weight and age (Table 4). Parameter estimates indicated that older, lighter woodpeckers occupied larger ranges although confidence intervals suggest that these parameter estimates were not significant (Table 5). Models that included the environmental predictors QMD, slope, and canopy cover were poorly supported compared to our top models, ranking lower than our null model (Table 4). Likewise, productivity and nearest neighbor distances were not influential in predicting white-headed woodpecker home range size in either season. Productivity was relatively high in our study ($\bar{x} = 2.2 \pm 1.2$ fledglings per nest; range 0–4) and 71% of individuals fledged at least 2 young. Nearest neighbor distances were highly variable, ranging from 106 m between nests in a small burned patch to 2,723 m for a nest offshore an isolated peninsula.

Selection of Home Ranges

We banded 56 nestlings at 23 nest sites in 2011 and 2012. Five of these woodpeckers were resighted in subsequent years (1–2 years post-fledging) as adults and a female banded by an independent research group as a juvenile was resighted at a nest site in 2012 (3 years post-fledging). Average dispersal distance from natal sites for these 6 dispersers was 5.42 ± 1.21 km (range 4.1–7.4 km).

The best model explaining selection of where a home range was located in both seasons included recent (<10 year) forest disturbance (Table 6); woodpeckers selected for areas with a higher proportional area recently disturbed (nesting season relative risk ratio = 1.08, 95%CI = 1.03–1.13; post-nesting season relative risk ratio = 1.06, 95% CI = 1.03–1.09; Fig. 3). Thus in both seasons, the relative risk of a white-headed woodpecker selecting an area on the landscape for a home range increased by a factor of 1.1 for every 1% increase in the proportion of the area disturbed. On average, used home ranges contained 45.9 ha (± 28.4 ha) disturbed area compared to 7.0 ha (± 10.0 ha) for random ranges. Although our disturbance layer could not distinguish between the effects of recent thinning, burning, and disease, the FACTS database and FPAs

Table 3. Mean values for habitat features measured within used 99% kernel home ranges of white-headed woodpeckers versus available ranges in central Washington, USA, 2011–2013.

Habitat feature	Nesting season			Post-nesting season		
	Used ranges	Available ranges	P	Used ranges	Available ranges	P
Proportion >40% canopy cover	0.62 ± 0.24	0.47 ± 0.27	0.070	0.60 ± 0.32	0.57 ± 0.25	0.683
Proportion disturbed	0.45 ± 0.25	0.05 ± 0.07	<0.001	0.32 ± 0.21	0.08 ± 0.10	<0.001
Proportion old growth (LSOG)[a]	0.07 ± 0.12	0.07 ± 0.08	0.884	0.06 ± 0.09	0.05 ± 0.05	0.760
Slope (%)	12.18 ± 4.72	14.47 ± 4.96	0.091	12.58 ± 4.23	13.76 ± 5.89	0.404
QMD[b] (cm)	24.33 ± 4.34	26.17 ± 6.57	0.987	23.72 ± 5.37	23.82 ± 5.01	0.633
Douglas-fir basal area (m²/ha)	6.75 ± 2.32	7.52 ± 3.98	0.201	6.82 ± 2.84	7.97 ± 3.56	0.001
Ponderosa pine basal area (m²/ha)	8.08 ± 2.95	6.21 ± 2.64	0.018	8.39 ± 2.84	6.85 ± 2.80	0.002
Canopy cover (%)	42.86 ± 11.83	40.76 ± 18.00	0.863	42.08 ± 13.83	42.96 ± 14.98	0.060
Stand age (years)	99.82 ± 14.41	102.69 ± 21.34	0.589	94.27 ± 22.43	100.91 ± 22.29	0.060

[a] Proportion of home range composed of late-successional old-growth forest.
[b] Mean quadratic mean diameter (cm) of trees within home range.

Table 4. Support for models explaining variation in home range size by white-headed woodpeckers in central Washington, USA, 2011–2013.

Parameters[a]	AIC$_c$[b]	Δ_i[c]	w_i[d]
Nesting season			
Weight	26.76	0	0.48
Birdage + weight	27.05	0.29	0.41
Null (intercept only)	31.31	4.55	0.05
Birdage	33.05	5.23	0.03
Productivity	31.99	6.29	0.02
QMD	36.44	9.68	<0.01
Neighbor	46.21	19.45	<0.01
Canopy, QMD, SDcanopy, slope	47.2	20.44	<0.01
Birdage, canopy, neighbor, productivity, QMD, SDcanopy, slope, weight	52.47	37.01	<0.01
Post-nesting season			
Birdage, weight	30.98	0	0.80
Weight	33.82	2.84	0.19
Null (intercept only)	41.09	10.11	0.01
Birdage	41.20	10.22	<0.01
Productivity	44.12	13.14	<0.01
QMD	45.91	14.93	<0.01
Neighbor	57.86	26.88	<0.01
Canopy, QMD, SDcanopy, slope	64.72	33.74	<0.01
Birdage, canopy, neighbor, productivity, QMD, SDcanopy, slope, weight	71.50	41.44	<0.01

[a] Birdage = whether individual was a first-year or after-first year bird; canopy = mean percent canopy coverage within home range; neighbor = distance (m) to nearest neighbor's nest-site; productivity = number of fledglings; QMD = mean quadratic mean diameter (cm) of trees within home range; SDcanopy = standard deviation of percent canopy coverage within home range; slope = mean percent slope within home range; weight = adult weight (g) at time of capture.
[b] AIC$_c$ = Akaike's Information Criterion corrected for small sample sizes.
[c] Δ_i = Akaike's Information Criterion relative to the highest ranked model.
[d] w_i = Akaike weight.

indicated that 19% of selected disturbances had been burned with prescribed burns, 16% subject to recent disease, and 63% subject to a combination of thinning and prescribed burning. There was substantial variation in the estimated size of burned and diseased patches. Median patch size was 4.8 ha (± 5.3 ha) and ranged from 0.1 to 24.2 ha.

DISCUSSION

Selection of Home Ranges
Although earlier research emphasized the use of old-growth forest by white-headed woodpeckers (Dixon 1995*a,b*), numerous studies have now documented white-headed woodpeckers nesting in recently burned forest (e.g., Raphael and White 1984, Saab et al. 2004, Wightman et al. 2010, Tarbill et al. 2015), similar to our study. Whereas past studies in burns have focused on the selection of nest sites, this is the

first study to show that recent burns may also be selected for home ranges for 6 months of the year (May–Oct). Additionally, we documented white-headed woodpeckers using burns created by prescribed fire. All of the burns used by white-headed woodpeckers in this study had been created by mixed-severity prescribed fire that resulted in small patches (median 4.8 ha) of snags. These patches ranged in age from 1 to 10 years post-fire and were interspersed within a larger forest of live trees resulting in a mosaic of small burned and large unburned patches. White-headed woodpeckers also occurred less frequently in unburned forests in our study, and other research has likewise demonstrated that burns are not necessary for breeding (e.g., Hollenbeck et al. 2011). However, given the propensity or white-headed woodpeckers to use patchily distributed prescribed burns in our study, we suggest that mixed-severity prescribed fire may be an underappreciated mechanism for creating habitat for this species.

Table 5. Parameter estimates for models in the 90% confidence set, unconditional standard errors, and 95% confidence intervals explaining variation in home range size by white-headed woodpeckers in central Washington, USA, 2011–2013.

Model[a]	Parameter	Estimate	SE	Lower CI	Upper CI
Nesting season					
Weight	Weight	−0.004	0.024	−0.052	0.043
Weight + birdage	Weight	−0.005	0.024	−0.053	0.043
	Birdage	−0.194	0.377	−0.932	0.545
Post-nesting season					
Weight + birdage	Weight	−0.005	0.016	−0.037	0.026
	Birdage	−0.187	0.225	−0.626	0.254
Weight	Weight	−0.004	0.016	−0.033	0.027

[a] Birdage = whether individual was a first-year or after-first year bird; weight = adult weight (g) at time of capture.

Table 6. Comparison of models explaining second-order selection by white-headed woodpeckers during the nesting and post-nesting seasons in central Washington, USA, 2011–2013.

Parameters[a]	AIC$_c$[b]	Δ_i[c]	w_i[d]
Nesting season			
Disturbed	69.10	0.00	0.99
Canopy, disturbed, oldgowth, pineBA, QMD, SDcanopy, slope	90.72	21.63	0.01
PineBA	94.48	25.38	<0.01
Null (intercept only)	94.66	25.57	<0.01
Canopy	96.90	27.80	<0.01
SDcanopy	97.12	28.03	<0.01
Canopy, pineBA	97.21	28.12	<0.01
Canopy, QMD, SDcanopy, slope	98.56	29.46	<0.01
Oldgrowth, QMD	99.21	30.11	<0.01
Canopy, oldgrowth, pineBA, QMD	102.40	33.30	<0.01
Post-nesting season			
Disturbed	127.09	0.00	0.98
Canopy, disturbed, oldgrowth, pineBA, QMD, SDcanopy, slope	140.64	13.55	0.01
PineBA	147.91	20.82	0.01
Null (intercept only)	149.24	22.15	<0.01
SDcanopy	149.87	22.79	<0.01
Canopy, pineBA	149.96	22.87	<0.01
Canopy	151.45	24.36	<0.01
Oldgrowth, QMD	153.96	26.88	<0.01
Canopy, QMD, SDcanopy, slope	154.09	27.00	<0.01
Canopy, oldgrowth, pineBA, QMD	154.19	27.11	<0.01

[a] Canopy = mean percent canopy coverage within home range; disturbed = proportion of home range thinned, burned, or diseased within 10 years; neighbor = distance (m) to nearest neighbor's nest-site; oldgrowth = proportion of home range composed of late-successional old-growth forest (i.e., >10% canopy cover and >50.8 QMD); pineBA = mean basal area (m^2/ha) of ponderosa pine within home range; QMD = mean quadratic mean diameter (cm) of trees within home range; SDcanopy = standard deviation of percent canopy coverage within home range; slope = mean percent slope within home range.
[b] AIC$_c$ = Akaike Information Criterion corrected for small sample sizes.
[c] Δ_i = Akaike's Information Criterion relative to the highest ranked model.
[d] w_i = Akaike weight.

Unlike species that forage on burned trees (e.g., black-backed woodpecker [*Picoides arcticus*]), the reasons that white-headed woodpeckers are attracted to burns are not well understood. White-headed woodpeckers are generally viewed as live-tree foragers (Raphael and White 1984, Morrison et al. 1987, Morrison and With 1987) and it seems counterintuitive that they would select burns for nesting. Wightman et al. (2010) hypothesized that white-headed woodpeckers selected burns because they contained fewer nest predators such as chipmunks (*Tamias* spp.), squirrels (*Tamiasciurus* spp.), and mice (*Peromyscus* spp.) compared to nearby unburned forest. However, Wightman et al. (2010) did not actually measure mammal abundance in burns and research studies have found that mammals do not always decrease following fire (Sullivan and Boateng 1996, Amacher et al. 2008, Maguire et al. 2008, Russell et al. 2010). In fact, multiple studies have reported that small mammal abundance can be higher in post-fire habitats compared to nearby unburned forests (Krefting and Ahlgren 1974; Converse et al. 2006; Zwolak and Foresman 2007, 2008) and Wiebe (2014) reported that depredation on northern flicker (*Colaptes auratus*) nests increased post-fire.

We suggest that recent burns are attractive because breeding white-headed woodpeckers are limited by nest site availability in some areas. In our study area, we estimated that 84–96% of the standing dead wood on the landscape was unsuitable for nesting because it was too hard to be excavated for a cavity (Lorenz et al. 2015). If this is the case, white-headed woodpeckers may be attracted to burns because they contain a higher number of snags and a correspondingly higher amount of softened wood for nesting. The use of burns for nesting has been documented in other woodpeckers that do not forage on dead wood like Lewis's woodpecker (*Melanerpes lewis*) and northern flicker (Linder and Anderson 1998, Vierling et al. 2008, Saab et al. 2009). Overall, white-headed woodpeckers may be less reliant on recent forest disturbances than species like the black-backed woodpecker but nevertheless attracted to recent disturbances if they provide opportunities for nesting not available in nearby, undisturbed forests. We suggest that future studies on white-headed woodpecker space use more fully examine the role of nest-site limitations in space use because it may be important for successful management of this species.

Variation in Home Range Size
Despite relatively clear selection for recent disturbances, home range size was highly variable in our study and not associated with any measured habitat characteristics. Even for individuals of the same sex and tracked within the same year and study area, home range size ranged between approximately 80 ha and 400 ha. Large intraspecific variation in home range size has been noted in all major taxa, including mammals (e.g., moose [*Alces alces*]; van Beest et al. 2011), birds (e.g., Swainson's warblers [*Limnothlypis swainsonii*]; Anich et al. 2010), bald eagles [*Haliaeetus leucocephalus*]; Garrett et al. 1993), reptiles (e.g., milk snakes [*Lampropeltis triangulum*]; Row and Blouin-Demers 2006), and amphibians (e.g., gold-spotted frog [*Rana chosenica*]; Ra et al. 2008).
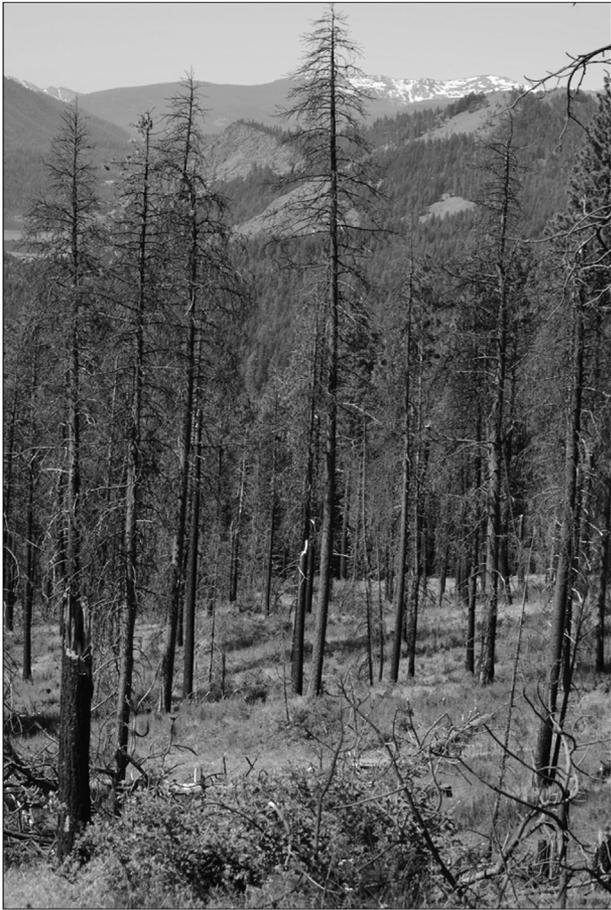
Figure 3. Example of a disturbed, burned patch used by white-headed woodpeckers for nesting in the Rimrock study area in central Washington, USA, 2011–2013.

In woodpeckers, numerous studies have likewise reported large variation in home range size among individuals. Elchuk and Wiebe (2003) reported northern flicker (*Colaptes auratus*) home range size varied from 5 to 109 ha, whereas Rota et al. (2014) reported that black-backed woodpecker home range size varied from 20 to 1,248 ha.

Variation in woodpecker home range size in other studies has been attributed to habitat (Tremblay et al. 2009, Rota et al. 2014, Tingley et al. 2014), dependent young (Mellen et al. 1992), nearest-neighbor distance (Elchuk and Wiebe 2003), and a combination of factors (e.g., habitat and population density; Hooper et al. 1982). For white-headed woodpeckers specifically, Dixon (1995*a,b*) linked home range size variation to habitat fragmentation, where large ranges occurred in sites where old-growth ponderosa pine was fragmented by younger forest types. However, in our study we observed variation in home range size even though younger, second-growth stands dominated our landscape, suggesting that other factors were responsible for this variation in home range size. Also, despite occurring in young forest types, white-headed woodpeckers in our study had home ranges that were comparable to or smaller than those reported by Dixon (1995*a,b*) in areas with old-growth. For example, Dixon (1995*a,b*) reported median minimum convex polygons of 104–342 ha, compared to our

median of 79 ha. The largest range reported by Dixon (1995*b*) of 704 ha is also nearly 3 times larger than our largest range of 238 ha. If range size is negatively correlated with the amount of old-growth, as suggested by in these early studies, then our ranges should have been larger than those reported by Dixon (1995*a,b*), not smaller. Although some of these differences may be due to differences in sample size, effort, and timing, it is important to consider that we based our sample scheme on Dixon (1995*a,b*). The primary difference between our study and Dixon (1995*a,b*) is that we differentiated between nesting (May–Jul) and post-nesting (Jul–Oct) space use, whereas Dixon only considered space use post-nesting (Jul–Dec). However, even when comparing only individuals tracked from July to October in both studies, the same pattern holds: our median range size from July to October was 67 ha, compared to 65 ha for Dixon (1995*a*) and 212 ha for Dixon (1995*b*). Collectively, these observations highlight 3 key findings. First, white-headed woodpecker home range size can vary considerably both within and across regions; second, white-headed woodpeckers occur and successfully breed in areas with essentially no remaining old-growth; and third, variation in home range size is not primarily a function of the availability of old-growth, at least in our study area.

Our study builds on past research on home range size by Dixon (1995*a,b*) by considering demographic consequences of ranging behavior. We found that home range size was not correlated with number of fledglings, which is an important measure of habitat quality. Moreover, the association between home range size and adult age was positive, indicating that older woodpeckers with higher survival and presumably more experience occupied larger ranges than younger, less experienced birds. This was contrary to our expectations from Dixon (1995*a,b*) who indicated that large home ranges should occur in poor-quality habitat, where one would expect corresponding low productivity and young birds. Our seemingly contrary findings may be due to many reasons. For example, productivity may be more influenced by factors such as nest site characteristics, weather, predator density or predator motivation, such that the ranging behavior of 1 parent has little relative effect. Additionally, wide-ranging behavior may not be maladaptive for this species. It is possible that the large ranges observed by older birds in our study resulted from exploratory behaviors, which can have long-term fitness benefits. Wandering individuals may gain information on food, shelter, and future mates or rivals that is not gained by more sedentary individuals and thereby enhance their long-term reproductive success (Inglis and Ferguson 1986, Forkman 1991, MacLean et al. 2005). Overall, the assumption that large ranges signify bad habitat may be overly simplistic for this species and we feel that additional, more rigorous studies are needed to understand factors that affect space use, productivity, and survival in white-headed woodpeckers.

MANAGEMENT IMPLICATIONS

Our findings add to the growing body of literature that white-headed woodpeckers occur and successfully breed in forests with both historical and recent timber harvest activity.

However, in conjunction with other research, our observations that woodpeckers select for recently (<10 year) disturbed forest indicate that the availability of snags for nesting may be important for maintaining this species within managed forests. Most (63%) of the disturbed patches used by woodpeckers in our study had been created using a combination of thinning and mixed-severity prescribed fire by the United States Forest Service, or prescribed fire alone (19%). This indicates that mixed severity prescribed fire may be an important tool for creating white-headed woodpecker breeding habitat. We suggest that managers interested in increasing numbers of breeding white-headed woodpeckers consider creating a landscape mosaic of burned and unburned forest patches. In our study, woodpeckers used burned patches that were approximately 4.8 ha in size and these patches typically had substantial mortality of trees. Meanwhile, protecting standing snags through policies that prohibit the felling of snags may be important to maintain nest site availability within these disturbed patches.

ACKNOWLEDGMENTS

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