SPACE USE AND FORAGING PATTERNS OF THE

WHITE-HEADED WOODPECKER IN

WESTERN IDAHO

by

Adam Roarke Kehoe

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

of

Master of Science

in

Fish and Wildlife Management

MONTANA STATE UNIVERSITY
Bozeman, Montana

January 2017

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

iv

LIST OF TABLES

v

LIST OF FIGURES

ABSTRACT

The white-headed woodpecker (*Picoides albolarvatus*) is a species of conservation concern that is strongly associated with ponderosa pine (*Pinus ponderosa*)-dominated forests in the Inland Northwest. More information on home range size and habitat selection patterns is needed to inform conservation of the white-headed woodpecker, a focal management species for dry-forest restoration treatments. We examined whether home range size was associated with food resources and if fine-scale habitat characteristics influenced selection of foraging sites. During the post-fledging periods of 2014 and 2015, we radio-tracked 11 white-headed woodpeckers in forests of west-central Idaho. These forests were historically managed for timber harvest, resulting in removal of large-diameter, cone-producing ponderosa pine trees. We hypothesized that ponderosa pine cones would be a highly-valued food resource providing seeds and arthropods. We expected smaller home ranges to be associated with a greater availability of cones for foraging and that cone foraging would be concentrated in core use areas. We used foraging behavior to test this hypothesis, specifically, the proportion of time foraging on cones as an index of cone availability. Home range sizes ranged from 24 to 169 ha (90% fixed-kernel estimates). Consistent with our hypothesis, individuals with relatively small home ranges spent a greater proportion of foraging time on cones (β_1[SE] = 2.48[1.32], *P* = 0.096; β_2[SE] = -5.00[1.61], *P* = 0.014). Cone foraging was also higher in core use areas compared to home range peripheries for individuals exhibiting at least moderate cone foraging. We also expected foraging woodpeckers to favor larger diameter pines in sites with moderate to high canopy closure. To test this hypothesis, we analyzed foraging-site selection by comparing habitat characteristics between foraging trees and available trees, which provided support for our foraging site prediction ($\beta_{TreeDiameter}$[SE] = 3.50[0.43], *P* <0.001; β_{Canopy}[SE] = 1.74[0.41], *P* <0.001; $\beta_{Species}$[SE] = 1.43[0.33], *P* <0.001). Our results suggest that large diameter pines provide important foraging resources, and that landscapes with more productive cone crops could support greater numbers of white-headed woodpeckers. We recommend restoration treatments that retain high-density patches of large diameter pines while promoting mosaics of open and closed canopies at larger spatial scales.

Introduction

The white-headed woodpecker (*Picoides albolarvatus*) is regionally endemic to dry-coniferous forests of western North America and strongly associated with ponderosa pine (*Pinus ponderosa*)-dominated forests in its northern range (Garrett et al. 1996). White-headed woodpeckers predominantly bark glean and peck for arthropods on live tree trunks (Morrison and With 1987, Dixon 1995*a*, *b*). Additionally, they may be dependent upon pine seeds for a portion of their diet, especially in cooler months (Ligon 1973, Garrett et al. 1996, Dixon 1995*a*). Large, mature pines are particularly important for this species as they provide reliable foraging opportunities and, as snags, provide nesting substrate (Raphael and White 1984, Dixon 1995*b*, Buchanan et al. 2003). The white-headed woodpecker is a species of conservation concern due to the loss and degradation of ponderosa pine-dominated forests from extensive logging, fire suppression, and climate change (Wisdom et al. 2000, Rich et al. 2004, National Audubon Society 2014).

The current structure of many western dry coniferous forests differs from conditions prior to Euro-American settlement (Schoennagel et al. 2004, Hessburg et al. 2005). These forests currently have fewer large, fire-resistant pines, are more homogeneous with increased stand densities, include more shade-tolerant species, and are more susceptible to large-scale, stand-replacing fire (Hessburg and Agee 2003, Schoennagel et al. 2004, Naficy et al. 2010). Historically, lower elevation dry-conifer forests of the Inland Northwest experienced mixed severity fires that promoted a mosaic of open- and closed-canopy forest dominated by larger diameter pines (Hessburg et al.

2005). These conditions are characteristic of breeding white-headed woodpecker habitat
(Buchanan et al. 2003, Wightman et al. 2010, Hollenbeck et al. 2011), although
successful breeding also occurs in managed areas where large, old pines are rare (Kozma
2011, Lorenz et al. 2015*a*).

Dry-forest restoration treatments have multiple objectives, including wildlife
habitat conservation and manipulating forest structure towards historical reference
conditions (Hessburg et al. 2005, Sánchez Meador et al. 2015). The white-headed
woodpecker is considered a focal species to inform management, because treatments are
aimed at restoring conditions associated with its preferred habitat (Altmann 2000, Gaines
et al. 2007). A wide variety of treatments exist, including timber harvest of varying tree
sizes and species, prescribed fire in the spring or the fall, and combinations of the two
(Brown et al. 2004). These treatments potentially have beneficial or negative impacts
upon woodpecker habitat quality.

Food availability is a major determinant of habitat quality that influences space
use patterns within populations (Olsson et al. 2001, Lyons 2005, Johnson 2007, Rota et
al. 2015). The home range (Burt 1943) is a fundamental unit of space use that contains
resources needed for an individual to survive and reproduce. The size of an individual's
home range represents an attempt to balance travel costs against resource acquisition
benefits (Ford 1983; Mitchell and Powell 2004, 2012). Larger home ranges can incur
greater energetic costs (Myers et al. 1979, Mace and Harvey 1983) and reduce fitness
(Rota et al. 2014, 2015). Animals often prefer areas where foraging substrate is spatially

clumped (i.e. maximum density) and most dependable (Ford 1983, Samuel et al. 1985, Mitchell and Powell 2004).

Tree size distributions, cone crop production, and canopy cover represent key factors potentially influencing space use patterns and foraging habitat quality for white-headed woodpeckers (cf. Red-cockaded woodpecker [*Picoides borealis*], Walters et al. 2002, McKellar et al. 2015). Large-diameter pines are an important food resource for providing large surface areas for foraging on bark- and canopy-dwelling arthropods and dependable cone crops for pine seeds and cone arthropods (Smith and Balda 1979, Raphael and White 1984, Dixon 1995*a*, Garrett et al. 1996). Cone crop productions vary annually (Keyes and González 2015) and large-diameter pines provide relatively frequent and abundant cone crops (Krannitz and Duralia 2004). Additionally, closed-canopy forests can provide attractive foraging habitat for other woodpeckers and pine seed-foragers (Latta et al. 2000, Vergara and Schlatter 2004), but high canopy closure could also negatively influence cone crop production (Krannitz and Duralia 2004).

Effective conservation and forest management strategies require detailed knowledge of foraging habitat selection and space use patterns, yet the few studies on white-headed woodpeckers do not provide consistent results. Lorenz et al. (2015*a*) examined foraging habitat selection and reported a lack of selection for areas of large pines, although the prevalence of large pines was quantified with coarse-resolution remotely-sensed data. In contrast, Dixon (1995*a*, *b*) suggested that large diameter pines were critically important for determining habitat quality for white-headed woodpeckers. Importantly, availability of tree sizes differed among these study areas as a result of

varying management activities. Additionally, past studies analyzing remotely-sensed, coarse-resolution landscape characteristics around nest sites suggest heterogeneity in canopy cover provides both foraging and nesting options (Wightman et al. 2010, Hollenbeck et al. 2011, Latif et al. 2015). Fine-scale, field-collected data with sufficient detail, however, are required to inform management prescriptions (Latif et al. 2015). Furthermore, foraging data are sparse, especially in western Idaho (Lorenz et al. 2016; e.g., Ligon 1973).

We examined foraging-site selection and home range size during the post-fledging period in west-central Idaho to improve knowledge of white-headed woodpecker habitat associations and to inform forest restoration activities. Our first objective was to estimate home range size. Secondly, we evaluated the relationship between home range size and cone availability as indexed by pine cone foraging, and whether cone foraging was higher in areas where space use was concentrated. Finally, we examined foraging-site selection at the tree-level, as a function of tree diameter, canopy closure, and tree species. Thus, we predicted: 1) home ranges would be smaller for individuals that exhibited a greater proportion of time foraging on cones; 2) cone foraging would be higher in areas of concentrated space use (i.e., core); and 3) woodpeckers would select larger diameter pines and sites of moderate to high canopy closure ($\geq$40%) for foraging.

Methods

Study Area

The study area was located in west-central Idaho on the Council (44˚44′ N, 116˚26′ W) and New Meadows (44˚58′ N, 116˚17′ W) ranger districts of the Payette National Forest (Figure 1). The study area was selected because it is part of a broader study evaluating occupancy rates, nest survival, and nest site selection in relation to restoration treatments (i.e., treatment effectiveness monitoring). This area has been historically managed for timber harvest and is undergoing extensive dry-forest restoration treatments. Vegetation structure and composition varied where ponderosa pine was either dominant or co-dominant with Douglas-fir (*Pseudotsuga menziesii*) or grand fir (*Abies grandis*). Other tree species included western larch (*Larix occidentalis*) and quaking aspen (*Populus tremuloides*). Elevation ranged from 1,100 to 1,900 m. Average annual precipitation was approximately 57 cm and average annual minimum and maximum temperatures were approximately -3.7° and 13.8° C, respectively (www.ndcd.noaa.gov, accessed 25 Oct 2016).
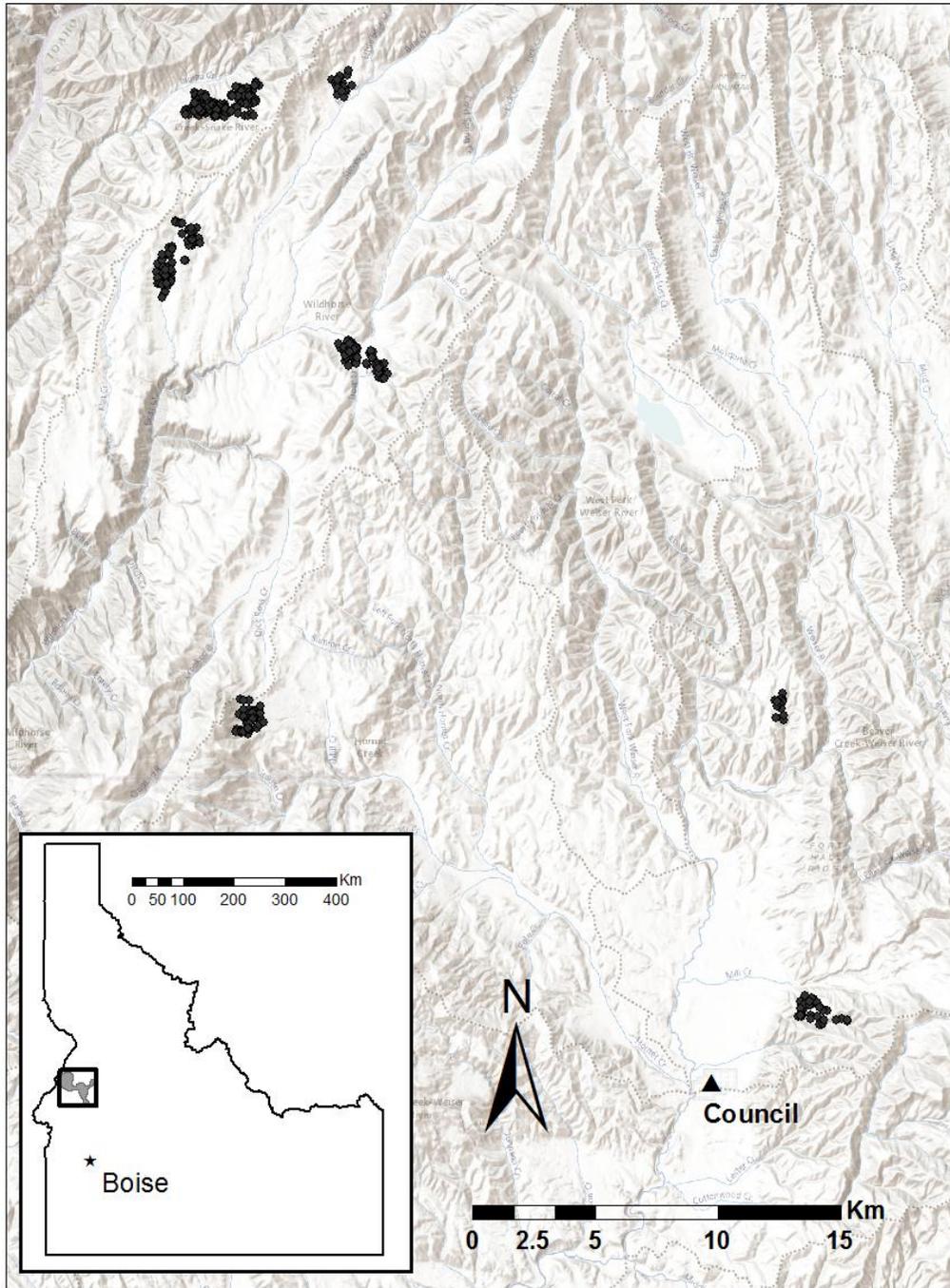
Figure 1. Study area location on the Council and New Meadows Ranger Districts, Payette, National Forest, Idaho. The dots represent telemetry locations from the 11 radio-tagged woodpeckers during the post-fledging periods of 2014−2015 (ESRI, Redlands, California).

Field Methods

Nest Surveys and Trapping: During the 2014−2015 nesting seasons, we systematically searched for nest cavities along 28 established transects while using broadcast calls to elicit responses from breeding woodpeckers and attempted to follow woodpeckers back to nest cavities (Dudley and Saab 2003). Survey transects were approximately 2700-m long and established based on recent forest treatments (15), areas with similar forest composition not receiving recent treatments (5), and areas with presumed highly-suitable white-headed woodpecker habitat (8). We searched primarily within 150 m of the transect centerline but also followed individual birds for up to 1 km away (Mellen-McLean et al. 2012). Additionally, we searched areas where nests were located in previous years and found nests opportunistically when travelling between transects within the study area.

We trapped adult woodpeckers at nest trees during the early nestling period. We placed a pole-mounted hoop net over the cavity (i.e., nest) entrance, after adults entered the cavity to feed nestlings, capturing the adult when it exited (Dudley and Saab 2007). We selected only one adult from each nesting pair and separate individuals from 2014 to 2015, to avoid pseudoreplication. We attempted to radio-tag males and females in equal numbers and to tag an equal number of birds in areas recently treated and those that were untreated with recent restoration prescriptions. However, birds commonly broke off antennas, which resulted in an unbalanced sample with respect to sex and forest treatment.

For each captured bird, we attached a 1.3 g transmitter (Advanced Telemetry Systems, model A1065) to the dorsal side of the two central rectrices using cyanoacrylate glue and braided fishing line (e.g., Stanton et al. 2014). Radio-transmitters were approximately 2% of the average mass of our birds ($\bar{x} = 58.5$ g, $n = 81$). We observed no negative effects or behavioral changes due to the radio transmitters. Transmitters shed during natural feather molt in late summer. We fit all birds with a unique combination of colored leg bands, including a numbered U.S. Fish and Wildlife Service aluminum leg band. All handling complied with Institutional Animal Care and Use Committee guidelines (Montana State University Protocol no. 2014-46), the state of Idaho (PERMIT 950228), and the USGS federal bird banding lab (PERMIT 22607).

Radio-telemetry and Foraging Observations: We radio-tracked 5 individuals from 09 July to 08 September 2014 and 6 individuals from 29 June to 10 September 2015. We radio-tracked birds to examine home range and foraging behavior during the post-fledging period, which is a discrete period critical to various fitness components (Chandler et al. 2012, Cox and Kesler 2012; cf. Gow and Wiebe 2014) and when space use is not centered upon nest sites. We tracked tagged individuals 2−3 times per week depending on functioning transmitters. To distribute sampling across birds, daylight hours, and the study period, we implemented a standardized tracking protocol with a randomly-selected order. Radio-tracking concluded when tail feathers were molted and transmitter shed or if mortality occurred.

We obtained telemetry locations (i.e. relocations) where we first observed the bird foraging (visual locations) or first pinpointed the bird's location without visual

observation (non-visual locations). Non-visual locations were used to avoid bias in home range estimation associated with factors (e.g., vegetation density, bird behavior) that could influence obtaining visual locations. We relocated birds with Telonics receivers (Model TR-4K, 164-166 MHz) and H-antennas (164-166 MHz). We relocated each scheduled individual once per tracking day, and obtained additional relocations as time allowed to obtain an adequate number of relocations representative of our study period. We recorded successive relocations per individual ≥20 minutes apart to avoid excessive temporal autocorrelation (Seaman et al 1999). This time spacing did not ensure statistical independence, but allowed birds to potentially traverse their home range, indicating biological independence (Barg et al. 2005; cf. Swihart and Slade 1997, Desolla et al. 1999, Cushman et al. 2005). When birds were visually located, we observed individuals continuously and recorded foraging substrate (cone/inflorescence, trunk, branch, or foliage), tree species, and length of time spent foraging on each. We identified seven substrate/species categories: ponderosa pine cone, fir cone (Douglas-fir and grand fir), live trunk/bole, live branch, foliage, dead stem (trunk and branch), and common mullein (*Verbascum thapsus*) flower heads. We also used Pearson's correlations to examine whether detectability (i.e., obtaining visual, foraging observations) was potentially influenced by number of young fledged, slope steepness, and overstory vegetation density.

Vegetation Measurements: We measured vegetation at foraging and paired available trees for analyzing foraging-site selection at the tree-level (i.e., 4th order selection [Johnson 1980]). This study design accounts for changing habitat availability

and does not require delineating home ranges (Arthur et al. 1996, Manley et al. 2002).
For each foraging tree, we identified a location at a random bearing (1−360°) and
distance (35−245 m away). We then identified an available tree as the live tree or
structurally-sound snag nearest to the random location, >30 m from the corresponding
paired foraging tree, and with a diameter at breast height (DBH; height at 1.37-m above
ground) of ≥7 cm (smallest foraging tree observed). We assumed random paired trees
were accessible and available to the specified woodpecker, but far enough away to
potentially be selected differently. We used handheld GPS units to obtain spatial
coordinates for all foraging and available trees (Universal Transverse Mercator Zone
11N, NAD 1983). We also recorded tree species, status (live or dead), DBH, height, and
canopy closure at the tree. We took two digital hemispherical photographs of the canopy
on opposite sides of each tree using a Nikon FC-E9 fish-eye lens mounted on a Nikon
CoolPix 8700 camera (Jonckheere et al. 2004). ImageJ (Fiji) editing software was used
to threshold and convert each photograph into a binary image (http://fiji.sc/Fiji). We
used CIMES software to estimate canopy closure (Gonsamo et al. 2010, 2011). The
required slope and aspect measurements were obtained from Landfire classified imagery
using ArcMap 10.3.1 (ESRI, Redlands, California). We used the mean of the two photos
per tree.

Data Analysis

Estimating Home Range Size

We estimated home range size (HRS) with the fixed-kernel method (Worton 1989) using the 90% probability contour and the plug-in smoothing parameter in Geospatial Modeling Environment (GME; Version 0.7.4.0, www.spatialecology.com/gme, accessed 15 March 2016). We used the fixed-kernel method because it performs better for relatively low relocation sample sizes than other methods (Seaman et al. 1999, Said et al. 2005, Borger et al. 2006, Lichti and Swihart 2011). Tested against other smoothing parameters, the plug-in smoothing parameter produced the most consistent home range contours across software packages and radioed individuals (Lawson et al. 1997, Hemson et al. 2005, Laver and Kelly 2008). We used the 90% contour, because the largest contours (>90%) are based on sparse data and potentially overestimate home range size (Borger et al. 2006). We estimated HRS for individuals with ≥30 relocations (following Seaman et al. 1999) and for which the area-observation curve (HRS plotted against relocation sample size) reached an asymptote (Odum and Kuenzler 1955, Laver and Kelly 2008). We also calculated Pearson's correlation coefficients relating sampling characteristics (number of days tracked, number of relocations, mean time interval between relocations, proportion of visual relocations, mean relocations per tracking day) with HRS to further verify sampling intensity did not substantially influence HRS estimation. We used Vander Wal and Rodgers (2012) criterion to identify the core area (i.e., area of concentrated use) for each home range. Based on this criterion, we identified the 40% contour as delineating core use areas. We primarily analyzed 90% and 40% kernels among individuals, but we

also report 100% minimum convex polygon size (MCP; Mohr 1947) for comparison with other studies. We used two-sample t-tests to examine if home range sizes were different between years and sex, respectively.

Home Range Size Variation and Cone Foraging

To test our prediction relating HRS and cone availability, we developed an index of pine cone availability from behavioral data. If pine cone resources were relatively available and a higher-quality food resource, we expected woodpeckers to spend more of their foraging time on cones relative to other substrates (Charnov 1976, Stephens and Krebs 2007; e.g., Lima 1984, Olsson et al. 1999, Vergara et al. 2016). Additionally, we did not expect overall foraging time to decline due to satiation or other fitness-enhancing behaviors (cf. Stephens et al. 2007), because past studies have consistently observed woodpeckers and nuthatches to spend most of their time foraging, especially during the post-fledging period (Short 1970, Dixon 1995*a*, Stanton et al. 2014,). Therefore, we used the proportion of time spent foraging on cones (i.e., minutes observed pine cone foraging divided by total minutes observed foraging) as an index of cone availability. This index was useful because it included information on both cone abundance and individual perception of cones as food (see Hutto 1990, Wolda 1990; e.g., Vander Wall 1988, Olsson et al. 1999).

We used an information theoretic framework to select models representing alternative hypotheses relating HRS with cone availability (Burnham and Anderson 2002). We log-transformed home range size (and core area size) before analysis to better meet normality and equal variance assumptions. We used linear regression models fitted

with the *lm* function in R version 3.1.3 (R Core Team, 2015) relating log-HRS with the

cone availability index (proportion of time foraging on cones). Scatterplots indicated the

potential for non-linear relationships, so we included linear and non-linear relationships

in our candidate model set. Specifically, we constructed models describing 4 different

relationships (e.g., Franklin et al. 2000): no relationship ([1] $ln.HRS \sim \beta_0$), a linear

relationship ([2] $ln.HRS \sim \beta_0 + \beta_1 * Prop.Cone$), a quadratic relationship ([3]

$ln.HRS \sim \beta_0 + \beta_1 * Prop.Cone + \beta_2 * Prop.Cone^2$), and a pseudo-threshold

relationship ([4] $ln.HRS \sim \beta_0 + \beta_1 * ln.Prop.Cone$). We selected the model ranked

highest by Akaike's Information Criterion corrected for small sample size (AIC_c) and

drew inference primarily from this model.

After initial model selection, we conducted a post-hoc analysis to consider

additional factors that could also influence HRS and therefore potentially confound

estimates of its relationship with cone foraging (e.g., Tingley et al. 2014). We considered

4 potentially confounding factors (Table 1): 1) number of young fledged, 2) adult mass,

3) proportion canopy cover ≥40% within the home range, and 4) sex (cf. Elchuck and

Wiebe 2003, Lorenz et al. 2015*a*, Hooper et al. 1982, Vergara and Schlatter 2004,

Tingley et al. 2014). We were unable to assess whether recent treatments influenced

HRS, due to an unbalanced design between treatment types. To estimate the number of

fledged young, we used a pole-mounted camera (i.e., peeper) to view nest contents in

combination with nest observations (TreeTop II System, Sandpiper Technologies, Inc.,

Manteca, CA) within 5 days of the fledge date. We weighed birds at time of capture to

obtain adult mass. Seasonal timing of mass measurements varied by several weeks and

weak correlations were evident between mass and capture day ($r = -0.24$, $P = 0.03$, $n = 81$), however, we still considered this measure as representative of body condition (cf. Lorenz et al. 2015*a*). To obtain canopy cover we obtained classified Landsat imagery at the 30-m resolution with ArcMap 10.3.1 (ESRI, Redlands, California). We used plumage characteristics to sex individuals. None of the potential confounding variables except gender ($r = 0.68$) was substantially correlated with cone foraging ($r < 0.50$). We constructed 4 additional models with each one of our potentially confounding factors added separately to our top-ranked model. We compared parameter estimates for the cone foraging relationship from the 4 models with potentially confounding factors to those from the originally-selected model without additional covariates. We considered covariates to be potentially confounding and biologically supported if their addition changed the estimated relationship with cone foraging and that AIC_c indicated support for the model.

Table 1. Description of variables considered for examining variation in home range size (HRS) and foraging-site selection.

Parameter	Description	HRS Variation	Foraging-Site Selection
Prop.Cone	Proportion of time foraging on ponderosa pine cones	X	
CC40	Proportion of home range with >40% canopy cover [a]	X	
No.Flg	Number of young successfully fledged	X	
Mass	Mass of bird at time of capture	X	
Sex	Male or female	X	
DBH	Tree diameter at breast height (1.37 m)		X
CC	% canopy closure surrounding the tree		X
SPP	Tree species (ponderosa pine [*Pinus ponderosa*] or other[b])		X

[a] For core area analysis, we used proportion of core area with > 40% canopy cover
[b] Douglas fir (*Pseudostuga menziesii*), grand fir (*Abies grandis*), western larch (*Larix occidentalis*)

To test whether core use areas were centered in areas of high cone availability, we compared the proportion of time foraging on cones in the core versus periphery of home ranges. We only made this comparison for individuals that exhibited at least a moderate proportion of time foraging on cones (6 of 11 individuals with > 40% foraging time on cones), because we only expected cone availability to structure space use for individuals with at least moderate access to cones within their home ranges. For this analysis, we divided the time cone foraging in the core by total observed foraging in core, and we compared the resulting proportion to the equivalent for the periphery (foraging observations outside the core) using a bar graph. We expected proportion cone foraging to be higher in the core for the 6 individuals examined.

We also examined if there were differences between two key movement

properties associated with cone foraging versus non-cone foraging observations (cf. Van

Moorter et al. 2016). We used a two-sample t-test to assess if woodpeckers foraged for

different lengths of time per cone observations versus non-cone observations. We also

reported the number of foraging trees that were observed to be visited multiple times and

compared how many revisits were cone foraging trees versus non-cone substrates. We

expected cone foraging observations to be longer than non-cone foraging observations

(e.g., Vergara et al. 2016).

Foraging-Site Selection

We were interested in how tree diameter, tree species, and canopy closure

influenced the selection of forage trees. We analyzed foraging-site selection using

conditional logistic regression to compare habitat variables between pairs of foraging and

available trees. We fitted conditional logistic regression models using the COXME

package in R version 3.1.3 (R Core Team, 2015; Therneau 2012; e.g., Ewald et al. 2014).

We considered models representing all possible combinations of relationships with two

continuous variables (DBH and canopy closure[CC]) and one categorical variable (tree

species; ponderosa pine versus non-ponderosa pine]; Table 1). Scatterplots and past

literature indicated the potential for non-linear relationships, so we included linear and

non-linear relationships in our candidate model set (Hanula et al. 2000, Krannitz and

Duralia 2004, Latif et al. 2015, Lorenz et al. 2016). Specifically, for continuous

covariates we included three different forms: linear ([1] $\beta_1 * X$), quadratic ([2] $\beta_1 * X +$

$\beta_2 * X^2$), and pseudo-threshold ([3] $\beta_1 * ln. X$). We also initially considered interactive

relationships, but none were ranked higher than equivalent additive models, so we did not

include interactions in our final model set. All models included an individual-specific

random effect to account for different numbers of observations per individual (Gillies et

al. 2006, Duchesne et al 2010). We standardized ([observation - sample mean]/sample

standard deviation) both continuous variables (*DBH* and *CC)* prior to analysis (Schielzeth

2010), except the pseudo-threshold forms, which were log transformed (*ln.DBH* and

ln.CC). We ranked candidate models using AIC_c. We reported parameter estimates, odds

ratios, and 95% confidence intervals from our top-ranked model and derived inference

for foraging-site selection from this model.

We assessed goodness-of-fit for the top model, using k-fold cross validation

modified from Boyce et al. (2002; Bonnot et al. 2011). For each of 5,000 iterations, we

randomly withheld a fifth of use-availability pairs as test data, fitted the model to the

remaining training data, and assessed model performance as the percentage of use-

availability pairs withheld for testing whose members were correctly classified by the

model. Correct classification >50% suggested that our model predicted better than

random chance (Bonnot et al. 2011), however, classification success >65% was desired.

Results

Home Range Size Estimates

We obtained 46.5 $\pm$ 14.8 (mean $\pm$ SD; min = 30) relocations over 21.4 $\pm$ 6.2

days for each of 11 breeding adult white-headed woodpeckers (*n* = 5 females, 6 males),

totaling 511 relocations during the post-fledging periods of 2014 and 2015. Home range

size estimates varied substantially with an average 90% kernel estimate of 91 ± 43.9 ha (range $= 24.3-169.2$ ha), core area estimate of 18.9 ± 10.1 ha (range $= 3.1-35.7$ ha), and 100% MCP of 70.8 ± 26.5 ha (range $= 37.6-121.7$ ha). The 90% kernel estimates slightly differed between sex ($t_{11} = -1.514$, $P = 0.176$ [male $= 74.8 \pm 53.1$ ha; female $= 110.4 \pm 20.4$ ha]).

We found no evidence for sampling effects on HRS estimation. Area-observation curves showed home range size approximately leveling off before reaching maximum sample size for all 11 woodpeckers. Additionally, we only detected weak correlations between home range size and sampling characteristics (Table 2). The 90% kernel estimates were similar between years ($t_{11} = 0.509$, $P = 0.624$ [2014 $= 98.7 \pm 46.3$ ha; 2015 $= 84.6 \pm 45.0$ ha]).

Table 2. Pearson's correlation coefficients relating sampling characteristics with home range size estimates.

	Total Relocations	Total Days Tracked	Proportion Visual	Minutes Between Relocations	Relocations Per Day
90% Fixed Kernel	-0.18	-0.01	0.02	0.21	-0.22
40% Fixed Kernel	-0.07	0.10	-0.03	0.12	-0.22
100% MCP	-0.09	0.03	0.09	0.27	-0.17

* p-values indicated no evidence for correlations (all p-values were >0.42)

Foraging Behavior and Home Range Size

We observed 303.1 ± 169.3 min of foraging by each of 11 individuals for a total of 3,334 minutes (55.6 h). Averaged across woodpeckers, we observed similar lengths of time foraging on live trunks and on pine cones (Table 3), but cone and trunk foraging

were negatively correlated (r = -0.910, n = 11). Individuals spent most of their foraging

time on ponderosa pine (89.5 $\pm$ 10.5%). No significant correlations were detected

between observed foraging time and factors that could affect detection (number fledged,

[r = -0.196, P = 0.563]; mean home range slope, [r = 0.049, P = 0.887]; SD home range

slope, [r = -0.045, P = 0.896]; proportion of home range with canopy cover >70%, [r = -

0.006, P = 0.985]).

Table 3. Percent of time foraging on different substrates by 11 white-headed
woodpeckers in west-central Idaho, USA, 2014−2015.

	Trunk	Pine Cone[a]	Branch	Foliage	Mullein Flowers[b]	Dead Stem[c]	Fir Cone[d]
mean ±SD	44.4 ± 25.1	40.4 ± 28.2	6.7 ± 4.6	2.9 ± 4.4	2.3 ± 5.5	2.0 ± 3.7	1.2 ± 3.5
Range	15.7 − 96.0	0.2 − 79.5	0.8 − 16.4	0 − 14.9	0 − 17.1	0 − 12.6	0 − 11.6

[a] Ponderosa pine (*Pinus ponderosa*) seed cones
[b] Common mullein (*Verbascum thapsus*) flower heads (i.e., inflorescence)
[c] Trunk and branch from all dead tree species
[d] Douglas fir (*Pseudostuga menziesii*) and grand fir (*Abies grandis*) seed cones

Home range sizes remained fairly constant at low to intermediate time foraging on

cones, with a steep drop-off in home range sizes at higher levels of cone foraging (Figure

2). The best-supported model for home range and core area size included a quadratic

relationship with proportion of time foraging on cones, which explained substantially

more variation than other models (Table 4). There was also reasonable support for a

negative, linear relationship between core area size and cone foraging (Table 4). The

seven woodpeckers with proportion of time foraging on cones <0.50 had a mean 90%

kernel 2.5 times larger and core use areas 3 times larger than the four woodpeckers with

>0.55 proportion of time foraging on cones (Figure 2). Parameter estimates describing

the relationship between cone foraging and home range size changed minimally when

potential confounding factors were taken into account (Table 5). Additionally, AICc

indicated that the models with additional covariates were relatively unsupported by the

data (Table 6).
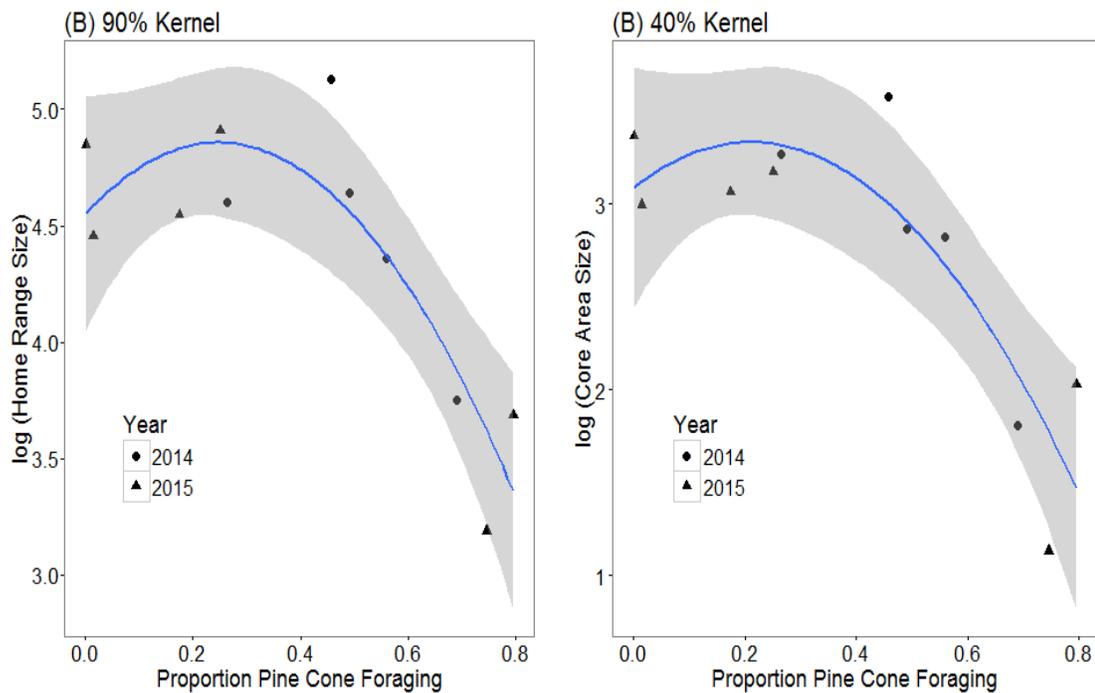
Figure 2. Relationship between proportion of time foraging on ponderosa pine cones (i.e., index of cone availability) and home range size (A, B) for 11 white-headed woodpeckers in west-central Idaho, USA, 2014−2015. Regression line and 95% confidence interval shown from the best-supported model (i.e., quadratic) explaining home-range variation as a function of pine cone foraging (see Table 3).

Table 4. Model selection results relating home range size with cone foraging for 11 white-headed woodpeckers in west-central Idaho, USA, 2014−2015.

Home-range estimator	Model	K	AIC_c	ΔAIC_c	w_i	R^2
90 % Fixed-Kernel	Prop.Cone (quadratic)	3	17.22	0	0.82	0.77
	Prop.Cone (linear)	2	20.73	3.51	0.14	0.49
	Intercept-only	1	24.14	6.92	0.03	0
	Prop.Cone (pseudo-threshold)	2	26.00	8.79	0.01	0.17
40% Fixed-Kernel	Prop.Cone (quadratic)	3	22.69	0	0.68	0.77
	Prop.Cone (linear)	2	24.45	1.76	0.28	0.56
	Intercept-only	1	29.50	6.81	0.02	0
	Prop.Cone (pseudo-threshold)	2	30.75	8.05	0.01	0.22

Table 5. Parameter estimates and standard errors for top-ranked model relating home range size with cone foraging. Also included are model results for additional covariates representing potentially confounding factors (remaining columns). The 90% kernel estimates for 11 white-headed woodpeckers in west-central Idaho, USA, 2014−2015, were analyzed here (40% kernel results were similar).

Models :	Selected	Selected + CC40	Selected + No.Flg	Selected + Mass	Selected + Sex
Parameter	Est. (SE)	Est. (SE)	Est. (SE)	Est. (SE)	Est. (SE)
Intercept	4.55 (0.22)	4.84 (0.26)	4.69 (0.27)	2.54 (2.32)	4.56 (0.24)
Prop.Cone	2.48 (1.32)	2.65 (1.18)	3.20 (1.54)	1.92 (1.49)	2.51 (1.43)
Prop.Cone^2	-5.00 (1.61)	-5.02 (1.44)	-6.09 (2.01)	-4.53 (1.72)	-5.00 (1.72)
CC40	NA	-0.87 (0.50)	NA	NA	NA
No.Flg	NA	NA	-0.12 (0.13)	NA	NA
Mass	NA	NA	NA	0.03 (0.04)	NA
Gender	NA	NA	NA	NA	-0.03 (0.28)

Table 6. Model selection results relating home range size with cone foraging, including models with potential confounding covariates singly added to the initial top-ranked model for 11 white-headed woodpeckers in west-central Idaho, USA, 2014-2015.

Home-range estimator	Model	K	AIC_c	ΔAIC_c	w_i	R^2
90% Fixed-Kernel	Prop.Cone (quadratic)	3	17.22	0	0.66	0.77
	Prop.Cone (quadratic) + CC40	4	20.65	3.43	0.12	0.84
	Prop.Cone (linear)	2	20.73	3.51	0.11	0.49
	Prop.Cone (quadratic) + No.Flg	4	23.32	6.1	0.03	0.79
	Prop.Cone (quadratic) + Mass	4	23.42	6.2	0.03	0.79
	Intercept-only	1	24.14	6.92	0.02	0
	Prop.Cone (quadratic) + Sex	4	24.54	7.32	0.02	0.77
	Prop.Cone (pseudo-threshold)	2	26.00	8.79	0.01	0.17
40% Fixed-Kernel	Prop.Cone (quadratic)	3	22.69	0	0.57	0.77
	Prop.Cone (linear)	2	24.45	1.76	0.24	0.56
	Prop.Cone (quadratic) + CC40	4	26.38	3.69	0.09	0.83
	Prop.Cone (quadratic) + No.Flg	4	28.42	5.72	0.03	0.80
	Prop.Cone (quadratic) + Mass	4	29.02	6.32	0.02	0.79
	Intercept-only	1	29.50	6.81	0.02	0
	Prop.Cone (quadratic) + Sex	4	29.97	7.28	0.02	0.77
	Prop.Cone (pseudo-threshold)	2	30.75	8.05	0.01	0.22

Six individuals in particular spent at least a moderate proportion of time foraging on cones (>0.40). All but one of these individuals exhibited more cone foraging in core use areas compared to the periphery of their home ranges (Figure 3). Cone foraging observations averaged 14.7 $\pm$ 13.8 min, while non-cone foraging observations were shorter, averaging 5.2 $\pm$ 6.2 min (t_{137} = -7.42, $P < 0.001$). We recorded 42 trees that were visited by woodpeckers multiple times, 32 trees were used for cone foraging and the 10 other trees for non-cone foraging.
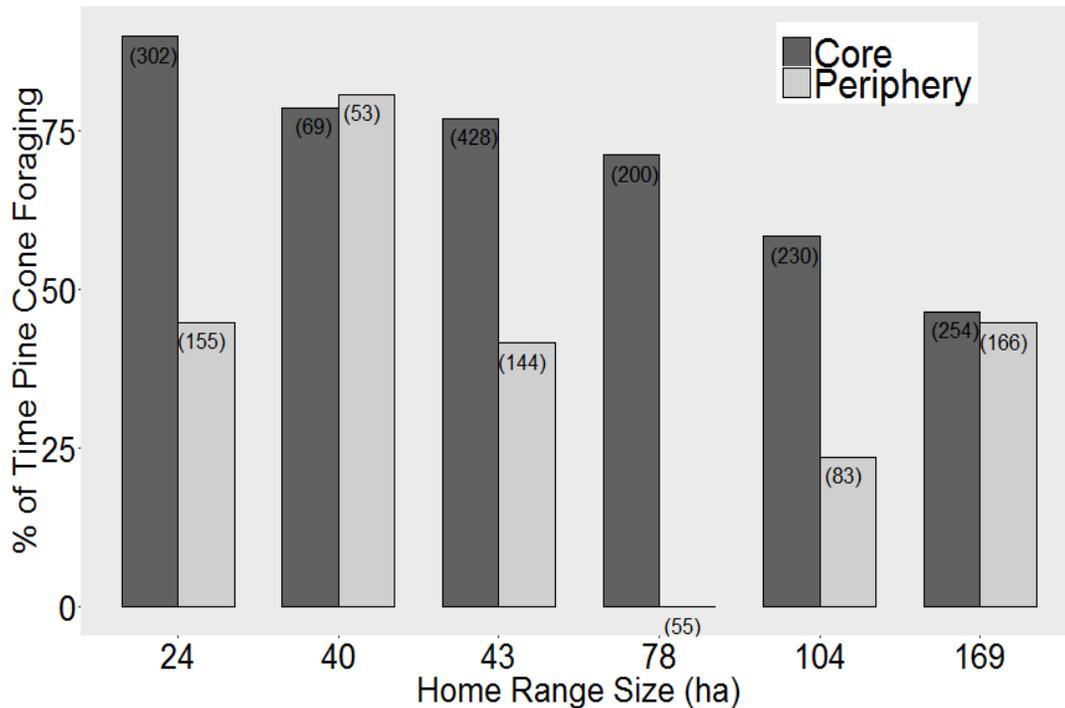
Figure 3. Bar graph illustrating percentage time pine cone foraging in the home range core versus home range periphery for the 6 white-headed woodpeckers that spent > 40% of their foraging time on pine cones. The numbers displayed within each bar show overall foraging time (mins) within core and periphery.

Foraging-Site Selection

We measured 34.4 ± 7.3 (range = 23−47) foraging locations over 20.0 ± 3.0 days and an equal number of paired available trees per individual woodpecker ($n = 4$ females, 6 males), totaling 344 use-availability observation pairs for modeling selection of foraging trees. This analysis included 1 less individual, because sample sizes of foraging observations (i.e., visual) were lower than total relocations (visual plus non-visual) used for home range estimation. Foraging woodpeckers favored relatively large diameter ponderosa pines at sites with moderate to high canopy closure (Table 7 and Figure 4). The best-supported model for foraging-site selection included tree species and pseudo-threshold relationships with DBH and canopy closure, respectively (Table 8). The small

variance of the individual specific random intercept indicated that selection of habitat characteristics was consistent across individuals ($\sigma^2 = 4e^{-04}$). Model selection results also indicated reasonable support for other relationships with canopy closure while DBH still had a pseudo-threshold relationship (Table 8). The 2nd-ranked model suggested selection for moderate canopy closure, while the 3rd-ranked model indicated selection for relatively higher canopy closure (Table 9). The odds of a woodpecker selecting a foraging tree were 6.60 (95% CI = 4.20−10.38) times greater for 60 cm versus 35-cm DBH tree and 3.12 (2.38−4.11) times greater for a 90 cm versus 65-cm DBH tree (Table 9). The odds of a woodpecker selecting a foraging tree were 2.78 (1.73−4.47) times greater for a site with 45% versus 25% canopy closure and 1.79 (1.37−2.35) times greater for a site with 70% versus 50% canopy closure (Table 9). The odds of a woodpecker selecting a ponderosa pine tree were 4.19 (3.53−4.85) times greater than a non-pine tree (Table 9). Model validation indicated that the top-ranked model performed well: 82.5 ± 4.4% of use-availability pairs from test data were correctly classified.

Table 7. Mean, standard deviation, and range of covariates describing foraging-site selection by 10 white-headed woodpeckers in west-central Idaho, USA, 2014−2015.

	DBH[a] use	DBH[a] avail	CC[b] use	CC[b] avail	PIPO[c] use	PIPO[c] avail
Mean ± SD	62.44 ± 9.58	41.15 ± 5.28	49.65 ± 7.00	43.77 ± 6.38	0.87 ± 0.11	0.68 ± 0.22
Range	50.29 − 74.68	35.19 − 51.28	40.19 − 62.78	32.75 − 52.87	0.66 − 1.00	0.37 − 0.96

[a] DBH = diameter (cm) at breast height (1.37 m)
[b] CC = % canopy closure
[c] PIPO = proportion of ponderosa pine (*Pinus ponderosa*) trees
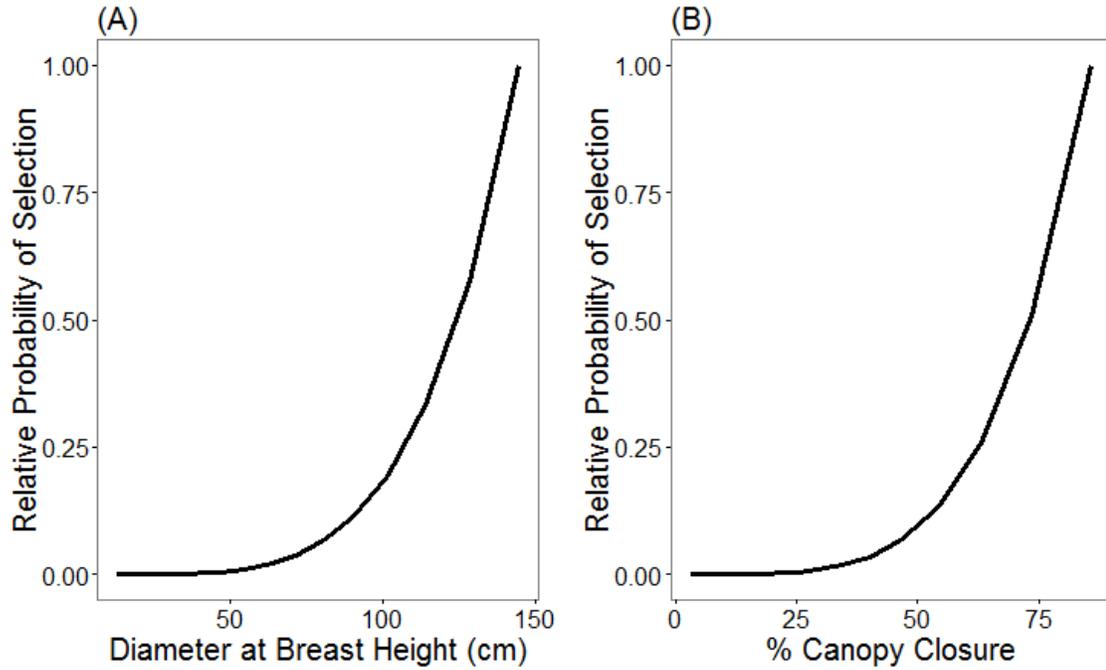
Figure 4. Relative probability of selection as a function of tree diameter at breast height (A) and % canopy closure (B) from the best-supported model for foraging-site selection from 10 white-headed woodpeckers in west-central Idaho, USA, 2014−2015. Relative probabilities in each panel were scaled to have a maximum value of 1. Habitat variables not plotted were held constant at their means.

Table 8. Model selection results (top 10 models) for tree-level, foraging-site selection by 10 white-headed woodpeckers in west-central Idaho, USA, 2014−2015.

Model	AIC_c	ΔAIC_c	K	w_i
1) ln.DBH + ln.CC + spp	243.72	0	3	0.47
2) ln.DBH + CC + CC^2 + spp	245.43	1.71	4	0.20
3) ln.DBH + CC + spp	245.79	2.07	3	0.17
4) DBH + DBH^2 + ln.CC + spp	247.03	3.31	4	0.09
5) DBH + DBH^2 + CC + CC^2 + spp	248.75	5.03	5	0.04
6) DBH + DBH^2 + CC + spp	249.13	5.42	4	0.03
7) DBH + ln.CC + spp	252.90	9.18	3	0
8) DBH + CC+ CC^2 + spp	255.02	11.30	4	0
9) DBH + CC + spp	255.26	11.54	3	0
10) ln.DBH + ln.CC	263.00	19.27	2	0

see table 1 for acronym descriptions

Table 9. Parameter estimates, standard errors, and odds ratios with 95% confidence intervals from the top-ranked, foraging-site selection model[a], for 10 white-headed woodpeckers in west-central Idaho, USA, 2014−2015.

Parameter	Est.	SE	Odds Ratio	95% CI	
				Lower	Upper
ln.DBH[b]	3.50	0.43	33.17	14.33	76.76
ln.CC[c]	1.74	0.41	5.69	2.54	12.75
spp[d]	1.43	0.33	4.19	2.17	8.08

[a] ln.DBH + ln.CC + spp
[b] pseudo-threshold form of foraging tree diameter at breast height (1.37 m)
[c] pseudo-threshold form of % canopy closure at foraging tree
[d] indicator variable for species: ponderosa pine (*Pinus ponderosa*) or other ([Douglas fir (*Pseudostuga menziesii*), grand fir (*Abies grandis*), western larch (*Larix occidentalis*)]

Discussion

This study provides new insight into white-headed woodpecker home range size and space use patterns. We found support for our hypothesis that home range size would decrease with increasing food availability. Specifically, home ranges were smaller for individuals that foraged more on cones (providing both seeds and arthropods), suggesting cone resources influenced home range size. Additionally, for individuals that exhibited at least moderate cone foraging, space use was concentrated in areas where cone resources were apparently more available (as indicated by foraging behavior). Foraging tree selection patterns were also consistent with our predictions; woodpeckers favored larger diameter, ponderosa pines in sites with moderate to high canopy closure.

Home Range Size and Space Use

Our results suggest pine cone resources influenced home range size and structured space use patterns. Pine cones (and seeds) are a pulsed resource often clumped in predictable locations, providing a temporally plentiful food source compared with bark-dwelling arthropods (cf. Charnov et al. 1976; Smith and Balda 1979, Koenig and Knops 2000, Ostfeld and Keesing 2000). Additionally, bark-dwelling arthropods are usually abundant during late summer and common in the white-headed woodpecker's diet (Otvos and Stark 1985, Morrison and With 1987, Garrett et al. 1996), suggesting food availability is probably highest during this time. With greater availability of pine cones, which promoted overall food availability, individuals secured adequate foraging resources in smaller areas. In contrast, individuals that foraged less on pine cones and more on tree trunks, apparently required larger home ranges to meet their foraging needs (e.g., Schoener 1971, Stephen and Krebs 1986, Stephens et al. 2007, Mitchell and Powell 2012). Our results appear to have consistencies with white-headed woodpeckers in Oregon, where median home range size was 62 ha with 58% trunk and 31% pine cone foraging (Dixon 1995*a*). During a low pine cone crop year on a different Oregon study site, median home range size was 302 ha with 69% trunk and 5% pine cone foraging (Dixon 1995*b*). This also suggests the possibility of climatic effects on space use because cone crop productions are influenced by temperature and precipitation during crucial cone development stages (Krannitz and Duralia 2004, Keyes and Gonzales 2015).

Pine cone resources enabled woodpeckers to minimize travel costs. We observed individual woodpeckers remaining on pine cones longer than non-cone substrates. Cone

foraging adults were likely obtaining food items relatively frequent, as indicated by

observed provisioning rates to fledglings. Whereas when non-cone foraging, individuals

were commonly moving within and between foraging substrates spending relatively more

time searching for food items (A. Kehoe, personal observation). Additionally,

woodpeckers revisited trees and patches, where they foraged on cones more frequently

than non-cone foraging. These observations further suggest the value of cones and their

potential to influence space use and allow smaller home ranges (cf. Charnov 1976, Van

Moorter et al. 2016, Vergara et al. 2016). Consistent with our predictions, woodpecker's

also concentrated their space use where food resources were dense and dependably

available (Ford 1983). Larger home ranges likely increased movement costs, which

could decrease time for foraging or parental care potentially incurring fitness costs

(Schoener 1983, Both and Visser 2000, Adams 2001; but see Hinam and Clair 2008).

Further research is needed to examine whether fitness benefits exist for individuals using

smaller home ranges with greater cone availability.

Variation in home range estimates across studies could be influenced by

differences in sampling design, sampling period (Dixon 1995*a, b*; Seaman et al. 1999,

Kernohan et al. 2001, Lorenz et al. 2015*a*), and habitat availability (Elchuck and Wiebe

2003, Ripper et al. 2007, Rota et al. 2014). Evidence for habitat effects on white-headed

woodpecker home range size varies among studies. In Oregon, more old-growth

ponderosa pine (>150-yrs old, mean tree DBH ≥53 cm; Hopkins et al. 1992) and less

fragmentation by silvicultural treatments were associated with smaller home ranges

(Dixon 1995*a*, *b*). In contrast, Lorenz et al. (2015*a*) suggested that home range size was

not related to old-growth pine and does not necessarily indicate habitat quality. We did

not measure old-growth; however, our results are more consistent with Dixon (1995*a*, *b*)

because older and larger-diameter pines produce more cones than younger and smaller-

diameter pines (Krannitz and Duralia 2004).

We used foraging behavior to index food availability for examining relationships

with space use (Hutto 1990, Olsson et al. 2001, Rota et al. 2015). Food availability is

difficult to measure directly (e.g., Robinson and Holmes 1982, Poulin and Lefebvre

1997). For example, cones with the same external appearance might vary in seed content

and quality. Seed-foraging birds often select higher quality cones (Vander Wall 1988,

Lindén et al. 2011). Arthropod-foraging woodpeckers can also recognize the type and

amount of food present in trees (Lima 1984, Olsson et al. 1999). Observing foraging

behavior led us to assess qualitative differences between closed, immature cones and

open, mature cones. Once cones opened, we observed woodpeckers shifting their

foraging time to the trunks of large diameter pines (A. Kehoe, personal observation),

suggesting a decrease in cone quality for foraging woodpeckers. The predominance of

closed-cone foraging perhaps is influenced by exploitative competition with red squirrels

(*Tamiasciurus hudsonicus*) and cone arthropods that exploit developing cones (Dale and

Schenk 1978, Smith and Balda 1979, Turgeon et al. 1994). Additionally, seeds shed and

most arthropod larvae die once the cone opens, decreasing the value for foraging

woodpeckers (Hedlin et al. 1980; e.g., Benkman 1987*a*, *b*).

Observing foraging behavior could be influenced by detectability, potentially

altering our cone availability index. For example, as numbers increase of fledglings

attended by an adult, visual observations are likely easier (McGowan and Woolfenden 1990). Additionally, visual detections of individual birds on relatively steep slopes and in areas with dense vegetation could be more difficult for observers. No correlation, however, was detected between observed foraging time and these factors (number fledglings attended, steep slopes, and dense vegetation) that potentially affect detection.

Sexual differences in foraging behavior exist for some woodpecker species, often attributed to sexual dimorphism (Morrison and With 1987, Aulen and Lundberg 1991, Chazarretta et al. 2012). Male white-headed woodpeckers might be more efficient at closed-cone foraging, because males have longer bills (8.8% longer in our study population; $t_{81} = 9.17$, P <0.001) and are generally stronger excavators than females (Ligon 1973, cf. Koch et al. 1970). We consistently observed males and females of the same breeding pair foraging on closed cones (see also Ligon 1973). Consequently, the positive correlation between males and cone foraging could have been an artifact of small sample size.

Our results are restricted to seasonal and regional patterns. The white-headed woodpecker exhibits plasticity in foraging behavior across seasons (Otvos and Stark 1985, Morrison and With 1987, Lorenz et al. 2016). Our results do not encompass important food resources during other seasons. For example, observations prior to the post-fledging period suggested that other foraging substrates were also important, including ponderosa pine pollen cones and dead wood during excavation and incubation periods, and fir foliage during the nestling period (A. Kehoe, personal observation). Habitat heterogeneity could benefit year-round food resource availability (c.f. Morrison

et al. 1987, Lorenz et al. 2016). Variation in foraging is expected when food availability differs due to variable tree size distributions and species composition, as affected by location-specific management activities (Porter and Labisky 1986, Lorenz et al. 2016). Consequently, our results are most applicable where ponderosa pine is dominant.

<u>Foraging-Site Selection</u>

Selection of larger diameter, ponderosa pine trees for foraging likely reflected the food resources available in those trees. This finding is consistent with other woodpecker and nuthatch species (Zwicker and Walters 1999, Weikel and Hayes 1999, Lyons et al. 2008, Pope et al. 2009, Farris et al. 2010). Larger diameter trees produce more abundant cone crops and provide more surface area and deeper furrows in the bark where arthropods can reside (Jackson 1979, Hanula et al. 2000, Krannitz and Duralia 2004). Other seed-foraging birds also prefer larger diameter pines, because they produce relatively more abundant and reliable cone crops (Latta et al. 2000, Krannitz and Duralia 2004, Thibault et al. 2006).

Selection of sites with moderate to high canopy closure observed here parallels patterns reported in other studies (Vergara and Schlatter 2004, McKellar et al. 2015). Sites with closed canopies probably provided more foraging resources and therefore required less movement between foraging substrates for resource acquisition. In Washington, white-headed woodpeckers foraged predominantly on live stem and pine foliage during late summer, resulting in selection for higher tree densities (Lorenz et al. 2016). Other seed-foraging birds also preferred foraging sites with higher canopy closure, due to a greater density of pine cones (Latta et al. 2000).

Our results fit into the larger context of white-headed woodpeckers selecting landscapes with heterogeneous canopy cover (Wightman et al. 2010, Hollenbeck et al. 2011, Latif et al. 2015). Habitat selection is a hierarchical, multi-scale behavioral process (Johnson 1980). White-headed woodpeckers select large-diameter snags in low canopy closure sites for nesting, and forage in nearby moderate to high canopy closure sites also with large diameter pines. To meet both these needs, white-headed woodpeckers tend to favor mosaics of relatively open and closed canopies for nesting habitat (Wightman et al. 2010, Hollenbeck et al. 2011, Latif et al. 2015).

Management Implications

Dry-forest restoration treatments in the Inland Northwest are increasingly common in forests occupied by the white-headed woodpecker. Large-scale forest restoration efforts aim to restore historic forest patterns since altered by anthropogenic activities. One key objective is to restore and preserve the large tree component of dry coniferous forests (Brown et al. 2004, Hessburg et al. 2005). Selection of the white-headed woodpecker as a focal species for dry-forest restoration objectives is supported by our results. Large, live ponderosa pines provided important foraging habitat in our study and were dominant features of pre-settlement landscapes (Arno et al. 1997, Youngblood et al. 2004). Additionally, our results are consistent with recent research, indicating the importance of large diameter snags and canopy mosaics across landscapes (Buchanan et al. 2003, Wightman et al. 2010, Hollenbeck et al. 2011, Lorenz et al. 2015*a*).

Our research suggests that landscapes with more productive cone crops could support greater numbers of breeding white-headed woodpeckers. Management activities that promote pine cone crops will benefit white-headed woodpeckers. In our study, average diameter of cone foraging trees was 65.2 ± 17.4 cm, while 98% of cone foraging observations were in trees >40 cm DBH (see also Fowells and Schubert 1956). Additionally, woodpeckers selected sites with relatively high canopy closure, which are presumed to have a greater density of foraging resources (e.g., Latta et al. 2000). Consequently, management treatments that retain large diameter pines and stands containing relatively high densities of large pines will be important for promoting cone crops and arthropods. Treatments that reduce stand densities while retaining larger pines can enhance cone crop production (Krannitz and Duralia 2004, Peters and Sala 2008), while decreasing the risk of tree mortality due to wildfires and beetle outbreaks (McDowell et al. 2003, Fajardo et al. 2007, Fettig et al. 2007, Zhang et al. 2008, Hayes et al. 2009). Treatments that create patchy, open canopy conditions can promote heterogeneity across landscapes (cf. Finney et al. 2001, Hessburg et al. 2007, Peterson et al. 2011). Treatments also have differential effects on large tree mortality rates (Swezy and Agee 1991, Ritchie et al. 2007,Youngblood et al. 2009, Prichard et al. 2010), cone crop production, and seed quality (Peters and Sala 2008, but see Keyes and Gonzales 2015). Additionally, retaining some smaller pines within a stand will be important for cross-pollinating with larger pines, contributing to more productive cone crops and increased seed quality (Krannitz and Duralia 2004).

Restoration treatments can have unintended consequences on woodpecker habitat (Metlen and Fiedler 2006, McIver et al. 2013). For example, white-headed woodpeckers could be limited by nest site availability (i.e., suitable snags; Lorenz et al. 2015*a*, *b*) and snag reductions per treatment entry are common (Gaines et al. 2007, Hessburg et al. 2010). This could have negative community-level effects as well, because white-headed woodpeckers create habitat for other cavity-dwelling vertebrate species (Tarbill et al. 2015).

Restoration treatments are expected to have tradeoffs that shift temporally (Lehmkuhl et al. 2007, McIver et al. 2013), resulting in variable influences on white-headed woodpecker habitat (Latif et al. 2015). For example, the desirable fire management outcome of reducing canopy bulk density could have an immediate, undesirable outcome of reducing woodpecker foraging resources. This direct negative effect is weighed against an indirect, lagged effect of potentially increasing foraging resources at future time periods (e.g., Ray et al. 2014). Treatment- and beetle-induced mortality of large, live pines reduces live-tree food resources (i.e., surface-bark dwelling and foliage arthropods, and cones) and increases dead wood resources (i.e., bark and wood-boring beetles, and future nesting substrates). Identifying context-dependent tradeoffs between the distribution of woodpecker foraging and nesting resources would advance management prescriptions to meet forest restoration goals. Consideration of management treatment tradeoffs and reserving the large, live and dead tree component of ponderosa pine forests will be essential for the future quality of white-headed woodpecker foraging and nesting habitat.

LITERATURE CITED

Adams, E.S. 2001. Approaches to the study of territory size and shape. Annual Review of Ecology and Systematics 32: 277–303.

Altmann, B. 2000. Conservation strategy for landbirds of the east-slope of the Cascade Mountains in Oregon and Washington. American Bird Conservancy, Corvallis, Oregon, USA. http://orwapif.org/sites/default/files/east_slope.pdf Accessed 09 Apr 2016.

Arno, S. F., H. Y. Smith, and M. A. Krebs. 1997. Old growth ponderosa pine and western larch stand structures: influences of pre-1900 fires and fire exclusion. No. 4; USDA, SD421 A7. US Department of Agriculture, Forest Service, Intermountain Research Station.

Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. Ecology 77:215–227.

Aulén, G., and A. Lundberg. 1991. Sexual dimorphism and patterns of territory use by the white-backed woodpecker *Dendrocopus leucotos*. Ornis Scandinavica (Scandinavian Journal of Ornithology) 22:60–64.

Barg, J. J., J. Jones, and R. J. Robertson. 2005. Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. Journal of Animal Ecology 74:139–149.

Benkman, C. W. 1987*a*. Crossbill foraging behavior, bill structure, and patterns of food profitability. The Wilson Bulletin 99:351–368.

Benkman, C. W. 1987*b*. Food profitability and the foraging ecology of crossbills. Ecological Monographs 57:251–267.

Bonnot, T. W., M. L. Wildhaber, J. J. Millspaugh, A. J. DeLonay, R. B. Jacobson, and J. L. Bryan. 2011. Discrete choice modeling of shovelnose sturgeon habitat selection in the lower Missouri River. Journal of Applied Ichthyology 27:291–300.

Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75:1393–1405.

Both, C., and M. E. Visser. 2000. Breeding territory size affects fitness: an experimental study on competition at the individual level. Journal of Animal Ecology 69:1021–1030.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Brown, R. T., J. K. Agee, and J. F. Franklin. 2004. Forest restoration and fire: principles in the context of place. Conservation Biology 18:903–912.

Buchanan, J. B., R. E. Rogers, D. J. Pierce, and J. E. Jacobson. 2003. Nest-site habitat use by white-headed woodpeckers in the eastern cascade mountains, Washington. Northwestern Naturalist 84:119–128.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Chandler, C. C., D. I. King, and R. B. Chandler. 2012. Do mature forest birds prefer early-successional habitat during the post-fledging period? Forest Ecology and Management 264:1–9.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129–136.

Charnov, E. L., G. H. Orians, K. Hyatt. 1976. Ecological implications of resource depression. The American Naturalist 110:247–259.

Chazarreta, L., V. Ojeda, and M. Lammertink. 2012. Morphological and foraging behavioral differences between sexes of the Magellanic woodpecker (*Campephilus magellanicus*). Ornitol Neotrop 23:529–544.

Cox, A. S., and D. C. Kesler. 2012. Reevaluating the cost of natal dispersal: post-fledging survival of red-bellied woodpeckers. The Condor 114:341–347.

Cushman, S. A., M. Chase, and C. Griffin. 2005. Elephants in space and time. Oikos 109:331–341.

Dale, J. W., and J. A. Schenk. 1978. Cone production and insect caused seed losses of ponderosa pine in Idaho and adjacent Washington and Montana. Bull Idaho For Wildl Range Exp Stn.

De Solla, S. R., R. Bonduriansky, and R. J. Brooks. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. Journal of Animal Ecology 68:221–234.

Dixon, R. 1995*a*. Ecology of white-headed woodpeckers in the central Oregon Cascades. Thesis, University of Idaho, Moscow, USA.

Dixon, R. D. 1995*b*. Density, nest-site, and roost-site characteristics, home range, habitat use, and behavior of white-headed woodpeckers: Deschutes and Winema National Forests, Oregon. Oregon Department of Fish and Wildlife Nongame Report No. 93-3-01, Portland, Oregon, USA.

Duchesne, T., D. Fortin, and N. Courbin. 2010. Mixed conditional logistic regression for habitat selection studies. Journal of Animal Ecology 79:548–555.

Dudley, J. G., and V. A. Saab. 2007. Home range size of black-backed woodpeckers in burned forests of southwestern Idaho. Western North American Naturalist 67:593–600.

Dudley, J. G., and V. A. Saab. 2003. A field protocol to monitor cavity-nesting birds. U.S. Forest Service. Report RMRS RP-44, Fort Collins, Colorado, USA. http://www.treesearch.fs.fed.us/pubs/6059 Accessed 14 Apr 2014.

Elchuk, C. L., and K. L. Wiebe. 2003. Home-range size of northern flickers (*Colaptes auratus*) in relation to habitat and parental attributes. Canadian Journal of Zoology 81:954–961.

Ewald, M., C. Dupke, M. Heurich, J. Müller, and B. Reineking. 2014. LiDAR remote sensing of forest structure and GPS telemetry data provide insights on winter habitat selection of European roe deer. Forests 5:1374–1390.

Fajardo, A., J. M. Graham, J. M. Goodburn, and C. E. Fiedler. 2007. Ten-year responses of ponderosa pine growth, vigor, and recruitment to restoration treatments in the Bitterroot mountains, Montana, USA. Forest Ecology and Management 243:50–60.

Farris, K. L., S. Zack, A. J. Amacher, and J. C. Pierson. 2010. Microhabitat selection of bark-foraging birds in response to fire and fire surrogate treatments. Forest Science 56:100–111.

Fettig, C. J., K. D. Klepzig, R. F. Billings, A. S. Munson, T. E. Nebeker, J. F. Negrón, and J. T. Nowak. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. Forest Ecology and Management 238:24–53.

Finney, M. A. 2001. Design of regular landscape fuel treatment patterns for modifying fire growth and behavior. Forest Science 47:219–228.

Ford, R. G. 1983. Home range in a patchy environment: optimal foraging predictions. American Zoologist 23:315–326.

Fowells, H. A., and G. H. Schubert. 1956. Seed crops of forest trees in the pine region of California. U.S. Department of Agriculture, Technical Bulletin 1150, Government Print Office, Washington, DC.

Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat Quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539–590.

Gaines, W. L., M. Haggard, J. F. Lehmkuhl, A. L. Lyons, and R. J. Harrod. 2007. Short-term response of land birds to ponderosa pine restoration. Restoration Ecology 15:670–678.

Garrett, K. L., M. G. Raphael, and R. D. Dixon. 1996. White-headed woodpecker (*Picoides albolarvatus*). The Birds of North America Online. Cornell Lab of Ornithology. Issue 252. http://bna.birds.cornell.edu/bna/species/252/articles Accessed 06 Apr 2016.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Gonsamo, A., J.-M. N. Walter, and P. Pellikka. 2010. Sampling gap fraction and size for estimating leaf area and clumping indices from hemispherical photographs. Canadian Journal of Forest Research 40:1588–1603.

Gonsamo, A., J.-M. N. Walter, and P. Pellikka. 2011. CIMES: A package of programs for determining canopy geometry and solar radiation regimes through hemispherical photographs. Computers and Electronics in Agriculture 79:207–215.

Gow, E. A., and K. L. Wiebe. 2014. Determinants of parental care and offspring survival during the post-fledging period: males care more in a species with partially reversed sex roles. Oecologia 175:95–104.

Hanula, J. L., K. E. Franzreb, and W. D. Pepper. 2000. Longleaf pine characteristics associated with arthropods available for red-cockaded woodpeckers. The Journal of Wildlife Management 64:60–70.

Hayes, C. J., C. J. Fettig, and L. D. Merrill. 2009. Evaluation of multiple funnel traps and stand characteristics for estimating western pine beetle-caused tree mortality. Journal of Economic Entomology 102:2170–2182.

Hedlin, A. F., H. O. Yates, D. C. Tovar, B. H. Ebel, T. W. Koerber, and E. P. Merkel. 1980. Cone and seed insects of North American conifers. Environment Canada, Canadian Forest Service, Ottawa, Canada; USDA Forest Service, Washington, DC; Universidad Autonoma Chapingo, Chapingo, Mexico.

Hemson, G., P. Johnson, A. South, R. Kenward, R. Ripley, and D. MacDonald. 2005. Are kernels the mustard? Data from global positioning systems (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. Journal of Animal Ecology 74:455–463.

Hessburg, P. F., and J. K. Agee. 2003. An environmental narrative of Inland Northwest United States forests, 1800–2000. Forest Ecology and Management 178:23–59. The Effect of Wildland Fire on Aquatic Ecosystems in the Western USA.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management 211:117–139. Relative risk assessments for decision making related to uncharacteristic wildfire.

Hessburg, P. F., N. A. Povak, and R. B. Salter. 2010. Thinning and prescribed fire effects on snag abundance and spatial pattern in an eastern Cascade range dry forest, Washington, USA. Forest Science 56:74–87.

Hessburg, P. F., R. B. Salter, and K. M. James. 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. Landscape Ecology 22:5–24.

Hinam, H. L., and C. C. S. Clair. 2008. High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of northern saw-whet owls. Biological Conservation 141:524–535.

Hollenbeck, J. P., V. A. Saab, and R. W. Frenzel. 2011. Habitat suitability and nest survival of white-headed woodpeckers in unburned forests of Oregon. The Journal of Wildlife Management 75:1061–1071.

Hooper, R. G., L. J. Niles, R. F. Harlow, and G. W. Wood. 1982. Home ranges of red-cockaded woodpeckers in coastal South Carolina. The Auk 99:675–682.

Hopkins, W. E., S. Simon, M. Schaefer, and T. Lillybridge. 1992. Region 6 interim old growth definition for ponderosa pine series. U.S.D.A. Forest Service Deschutes N.F., Fremont N.F., and Wenatchee N.F.

Hutto, R. L. 1990. Measuring the availability of food resources. 13:20–28.

Jackson, J. A. 1979. Tree surfaces as foraging substrates for insectivorous birds. Pages 69–93 in J. G. Dickson, R. N. Connor, R. R. Fleet, J. A. Jackson, and J. C. Kroll, editors. The role of insectivorous birds in forest ecosystems. Academic Press, New York, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, M. D. 2007. Measuring habitat quality: a review. The Condor 109:489–504.

Jonckheere, I., S. Fleck, K. Nackaerts, B. Muys, P. Coppin, M. Weiss, and F. Baret. 2004. Review of methods for in situ leaf area index determination: part I. Theories, sensors and hemispherical photography. Agricultural and Forest Meteorology 121:19–35.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166. in Millspaugh, J. J. and J. M. Marzluff, editors. Radiotracking and animal populations. Academic. San Diego, California, USA.

Keyes, C. R., and R. M. González. 2015. Climate-influenced ponderosa pine (*Pinus ponderosa*) seed masting trends in western Montana, USA. Forest Systems 24:21–28.

Koch, R. F., A. E. Courchesne, and C. T. Collins. 1970. Sexual differences in foraging behavior of White-headed Woodpeckers. Bull. Southern California Acad. Sci. 69: 60–64.

Koenig, W. D., and J. M. H. Knops. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. American Naturalist 155:59–69.

Kozma, J. M. 2011. Composition of forest stands used by white-headed woodpeckers for nesting in Washington. Western North American Naturalist 71:1–9.

Krannitz, P. G., and T. E. Duralia. 2004. Cone and seed production in *Pinus ponderosa*: a review. Western North American Naturalist 64:208–218.

Latif, Q. S., V. A. Saab, K. Mellen-Mclean, and J. G. Dudley. 2015. Evaluating habitat suitability models for nesting white-headed woodpeckers in unburned forest. The Journal of Wildlife Management 79:263–273.

Latta, S. C., M. L. Sondreal, and C. R. Brown. 2000. A hierarchical analysis of nesting and foraging habitat for the conservation of the Hispaniolan white-winged crossbill (*Loxia leucoptera megaplaga*). Biological Conservation 96:139–150.

Laver, P. N., and M. J. Kelly. 2008. A critical review of home range studies. The Journal of Wildlife Management 72:290–298.

Lawson, E. J., J. Gallerani, and A. R. Rodgers. 1997. Differences in home-range size computed in commonly used software programs. Wildlife Society Bulletin 1997:721–729.

Lehmkuhl, J. F., M. Kennedy, E. D. Ford, P. H. Singleton, W. L. Gaines, and R. L. Lind. 2007. Seeing the forest for the fuel: integrating ecological values and fuels management. Forest Ecology and Management 246:73–80. Biodiversity management in Pacific Northwest Forests: strategies and opportunities. Selected papers from the conference on "Managing Biodiversity in Pacific Northwest Forests", Portland, Oregon, June 5–7, 2006.

Lichti, N. I., and R. K. Swihart. 2011. Estimating utilization distributions with kernel versus local convex hull methods. 75:413–422.

Ligon, J. D. 1973. Foraging behavior of the white-headed woodpecker in Idaho. The Auk 90:862–869.

Lima, S. L. 1984. Downy woodpecker foraging behavior: efficient sampling in simple stochastic environments 65:166–174.

Lindén, A., A. Lehikoinen, T. Hokkanen, and R. A. Väisänen. 2011. Modelling irruptions and population dynamics of the great spotted woodpecker – joint effects of density and cone crops. Oikos 120:1065–1075.

Lorenz, T. J., K. T. Vierling, J. M. Kozma, and J. E. Millard. 2016. Foraging plasticity by a keystone excavator, the white-headed woodpecker, in managed forests: Are there consequences for productivity? Forest Ecology and Management 363:110–119.

Lorenz, T. J., K. T. Vierling, J. M. Kozma, J. E. Millard, and M. G. Raphael. 2015*a*. Space use by white-headed woodpeckers and selection for recent forest disturbances. The Journal of Wildlife Management 79:1286–1297.

Lorenz, T. J., K. T. Vierling, T. R. Johnson, and P. C. Fischer. 2015*b*. The role of wood hardness in limiting nest site selection in avian cavity excavators. Ecological Applications 25:1016–1033.

Lyons, A. L., W. L. Gaines, J. F. Lehmkuhl, and R. J. Harrod. 2008. Short-term effects of fire and fire surrogate treatments on foraging tree selection by cavity-nesting birds in dry forests of central Washington. Forest Ecology and Management 255:3203–3211.

Lyons, J. E. 2005. Habitat-specific foraging of prothonotary warblers: deducing habitat quality. The Condor 107:41–49.

Mace, G. M., and P. H. Harvey. 1983. Energetic constraints on home-range size. The American Naturalist 121:120–132.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical analysis and design for field studies, 2nd ed. Kluwer, Boston.

Mcdowell, N., J. R. Brooks, S. A. Fitzgerald, and B. J. Bond. 2003. Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. Plant, Cell & Environment 26:631–644.

McGowan, K. J., and G. E. Woolfenden. 1990. Contributions to fledgling feeding in the Florida scrub jay. Journal of Animal Ecology 59:691–707.

McIver, J. D., S. L. Stephens, J. K. Agee, J. Barbour, R. E. J. Boerner, C. B. Edminster, K. L. Erickson, K. L. Farris, C. J. Fettig, C. E. Fiedler, S. Haase, S. C. Hart, J. E. Keeley, E. E. Knapp, J. F. Lehmkuhl, J. J. Moghaddas, W. Otrosina, K. W. Outcalt, D. W. Schwilk, C. N. Skinner, T. A. Waldrop, C. P. Weatherspoon, D. A. Yaussy, A. Youngblood, and S. Zack. 2013. Ecological effects of alternative fuel-reduction treatments: highlights of the National Fire and Fire Surrogate study (FFS). International Journal of Wildland Fire 22:63.

McKellar, A. E., D. C. Kesler, and J. R. Walters. 2015. Resource selection reflects fitness associations for an endangered bird in restored habitat. Animal Conservation 19:131-138.

Mellen-McLean, K., Saab, V., Bresson, B., Wales, B., Markus, A. and VanNorman, K., 2012. White-headed woodpecker monitoring strategy and protocols. USDA Forest Service. *Pacific Northwest Region, Portland, OR. Unpublished document*.

Metlen, K. L., and C. E. Fiedler. 2006. Restoration treatment effects on the understory of ponderosa pine/Douglas-fir forests in western Montana, USA. Forest Ecology and Management 222:355–369.

Mitchell, M. S., and R. A. Powell. 2004. A mechanistic home range model for optimal use of spatially distributed resources. Ecological Modelling 177:209–232.

Mitchell, M. S., and R. A. Powell. 2012. Foraging optimally for home ranges. Journal of Mammalogy 93:917–928.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:233–249.

Morrison, M. L., and K. A. With. 1987. Interseasonal and intersexual resource partitioning in hairy and white-headed woodpeckers. The Auk 104:225–233.

Morrison, M. L., K. A. With, I. C. Timossi, W. M. Block, and K. A. Milne. 1987. Foraging behavior of bark-foraging birds in the Sierra Nevada. The Condor 89:201–204.

Myers, J. P., P. G. Connors, and F. A. Pitelka. 1979. Territory size in wintering sanderlings: the effects of prey abundance and intruder density. The Auk 96:551–561.

Naficy, C., A. Sala, E. G. Keeling, J. Graham, and T. H. DeLuca. 2010. Interactive effects of historical logging and fire exclusion on ponderosa pine forest structure in the northern Rockies. Ecological Applications 20:1851–1864.

National Audubon Society. 2014. Audubon's birds and climate change report: a primer for practitioners. National Audubon Society, New York. Contributors: Langham, G. , J. Schuetz, C. Soykan, C. Wilsey, T. Auer, G. LeBaron, C. Sanchez, and T. Distler. Version 1.2. http://climate.audubon.org/sites/default/files/Audubon-Birds-Climate-Report-v1.2.pdf Accessed 06 Apr 2016.

Odum, E. P., and E. J. Kuenzler. 1955. Measurement of territory and home range size in birds. The Auk 72:128–137.

Olsson, O., U. Wiktander, A. Malmqvist, and S. G. Nilsson. 2001. Variability of patch type preferences in relation to resource availability and breeding success in a bird. Oecologia 127:435–443.

Olsson, O., U. Wiktander, N. M. A. Holmgren, and S. G. Nilsson. 2001. Gaining ecological information about bayesian foragers through their behaviour. II. A field test with woodpeckers. Oikos 87:264–276.

Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution 15:232–237.

Otvos, I. S., and R. W. Stark. 1985. Arthropod food of some forest-inhabiting birds. The Canadian Entomologist 117:971–990.

Peters, G., and A. Sala. 2008. Reproductive output of ponderosa pine in response to thinning and prescribed burning in western Montana. Canadian Journal of Forest Research 38:844–850.

Peterson, D. L., J. E. Halofsky, and M. C. Johnson. 2011. Managing and adapting to changing fire regimes in a warmer climate. Pages 249–267 *in* D. McKenzie, C. Miller, and D. A. Falk, editors. The landscape ecology of fire. Ecological Studies, Springer Netherlands. http://link.springer.com/chapter/10.1007/978-94-007-0301-8_10 Accessed 25 Oct 2016.

Pope, T. L., W. M. Block, and P. Beier. 2009. Prescribed fire effects on wintering, bark-foraging birds in northern Arizona. The Journal of Wildlife Management 73:695–700.

Porter, M. L., and R. F. Labisky. 1986. Home range and foraging habitat of red-cockaded woodpeckers in northern Florida. The Journal of Wildlife Management 50:239–247.

Poulin, B., and G. Lefebvre. 1997. Estimation of arthropods available to birds: effect of trapping technique, prey distribution, and bird diet. Journal of Field Ornithology 68:426–442.

Prichard, S. J., D. L. Peterson, and K. Jacobson. 2010. Fuel treatments reduce the severity of wildfire effects in dry mixed conifer forest, Washington, USA. Canadian Journal of Forest Research 40:1615–1626.

Raphael, M. G., and M. White. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs 3–66.

Ray, C. T., B. G. Dickson, T. D. Sisk, and S. E. Sesnie. 2014. Spatial application of a predictive wildlife occurrence model to assess alternative forest management scenarios in northern Arizona. Forest Ecology and Management 322:117–126.

Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher , M. S. W. Bradstreet, G. S. Butcher, D. W. Demarest, E. H. Dunn, W. C. Hunter, E. E. Inigo-Elias, J. A. Kennedy, A. M. Martell, A. O. Panjabi, D. N. Pashley, K. V. Rosenberg, C. M. Rustay, J. S. Wendt, and T. C. Will. 2004. Partners in flight North American landbird conservation plan. Cornell Laboratory of Ornithology, Ithaca, New York, USA. http://www.partnersinflight.org/cont_plan/PIF2_Part1WEB.pdf Accessed 06 Apr 2016.

Ripper, D., J. C. Bednarz, and D. E. Varland. 2007. Landscape use by hairy woodpeckers in managed forests of northwestern Washington. The Journal of Wildlife Management 71:2612–2623.

Ritchie, M. W., C. N. Skinner, and T. A. Hamilton. 2007. Probability of tree survival after wildfire in an interior pine forest of northern California: effects of thinning and prescribed fire. Forest Ecology and Management 247:200–208.

Robinson, S. K., and R. T. Holmes. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology 63:1918–1931.

Rota, C. T., M. A. Rumble, C. P. Lehman, D. C. Kesler, and J. J. Millspaugh. 2015. Apparent foraging success reflects habitat quality in an irruptive species, the black-backed woodpecker. The Condor 117:178–191.

Rota, C. T., M. A. Rumble, J. J. Millspaugh, C. P. Lehman, and D. C. Kesler. 2014. Space-use and habitat associations of black-backed woodpeckers (*Picoides arcticus*) occupying recently disturbed forests in the Black Hills, South Dakota. Forest Ecology and Management 313:161–168.

Said, S., J. M. Gaillard, P. Duncan, N. Guillion, S. Servanty, M. Pellerin, K. Lefeuvre, C. Martin, and G. Van Laere. 2005. Ecological correlates of home-range size in spring-summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. Journal of Zoology 267:301–308.

Samuel, M. D., D. J. Pierce, and E. O. Garton. 1985. Identifying areas of concentrated use within the home range. Journal of Animal Ecology 54:711–719.

Sánchez Meador, A. J., K. M. Waring, and E. L. Kalies. 2015. Implications of diameter caps on multiple forest resource responses in the context of the four forests restoration initiative: results from the forest vegetation simulator. Journal of Forestry 113:219–230.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103–113.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369–404.

Schoener, T. W. 1983. Simple models of optimal feeding-territory size: a reconciliation. The American Naturalist 121:608–629.

Schoennagel, T., T. T. Veblen, and W. H. Romme. 2004. The interaction of fire, fuels, and climate across Rocky Mountain Forests. BioScience 54:661–676.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. The Journal of Wildlife Management 63:739–747.

Short, L. L. 1970. The habits and relationships of the Magellanic woodpecker. 82:115–129.

Smith, C. C., and R. P. Balda. 1979. Competition among insects, birds and mammals for conifer seeds. American Zoologist 19:1065–1083.

Stanton, R. A., D. C. Kesler, and F. R. Thompson. 2014. Resource configuration and abundance affect space use of a cooperatively breeding resident bird. The Auk 131:407–420.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press.

Stephens, D. W., J. S. Brown, and R. C. Ydenberg. 2007. Foraging: behavior and ecology. University of Chicago Press.

Swezy, D. M., and J. K. Agee. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Canadian Journal of Forest Research 21:626–634.

Swihart, R. K., and N. A. Slade. 1997. On testing for independence of animal movements. Journal of Agricultural, Biological, and Environmental Statistics 2:48–63.

Tarbill, G. L., P. N. Manley, and A. M. White. 2015. Drill, baby, drill: the influence of woodpeckers on post-fire vertebrate communities through cavity excavation. Journal of Zoology 296:95–103.

Therneau, T. 2012. Coxme: mixed effects cox models. R package version 2.2-3.

Thibault, J.-C., R. Prodon, P. Villard, and J.-F. Seguin. 2006. Habitat requirements and foraging behaviour of the Corsican nuthatch *Sitta whiteheadi*. Journal of Avian Biology 37:477–486.

Tingley, M. W., R. L. Wilkerson, M. L. Bond, C. A. Howell, and R. B. Siegel. 2014. Variation in home-range size of black-backed woodpeckers. The Condor 116:325–340.

Turgeon, J. J., A. Roques, and P. Groot. 1994. Insect fauna of coniferous seed cones: diversity, host plant interactions, and management. Annual Review of Entomology 39:179–212.

Van Moorter, B., C. M. Rolandsen, M. Basille, and J.-M. Gaillard. 2016. Movement is the glue connecting home ranges and habitat selection. Journal of Animal Ecology 85:21–31.

Vander Wal, E., and A. R. Rodgers. 2012. An individual-based quantitative approach for delineating core areas of animal space use. Ecological Modelling 224:48–53.

Vander Wall, S. B. 1988. Foraging of Clark's nutcrackers on rapidly changing pine seed resources. The Condor 90:621–631.

Vergara, P. M., G. E. Soto, D. Moreira-Arce, A. D. Rodewald, O. L. Meneses, and C. G. Perez-Hernandez . 2016. Foraging behaviour in Magellanic woodpeckers is consistent with a multi-scale assessment of tree quality. PLoS ONE 11(7):e0159096.

Vergara, P. M., and R. P. Schlatter. 2004. Magellanic woodpecker (*Campephilus magellanicus*) abundance and foraging in Tierra del Fuego, Chile. Journal of Ornithology 145:343–351.

Walters, J. R., S. J. Daniels, J. H. Carter, and P. D. Doerr. 2002. Defining quality of red-cockaded woodpecker foraging habitat based on habitat use and fitness. The Journal of Wildlife Management 66:1064–1082.

Weikel, J. M., and J. P. Hayes. 1999. The foraging ecology of cavity-nesting birds in young forests of the northern coast range of Oregon. The Condor 101:58–66.

Wightman, C. S., V. A. Saab, C. Forristal, K. Mellen-Mclean, and A. Markus. 2010. White-headed woodpecker nesting ecology after wildfire. The Journal of Wildlife Management 74:1098–1106.

Wisdom, M. J., R. S. Holthausen, B. C. Wales, C. D. Hargis, V. A. Saab, D. C. Lee, W. J. Hann, T. D. Rich, M. M. Rowland, W. J. Murphy, and M. R. Eames. 2000. Source habitats for terrestrial vertebrates of focus in the interior Columbia basin: broad-scale trends and management implications. Volume 2 -group level results. General Technical Report - Pacific Northwest Research Station, USDA Forest Service: 157-434.

Wolda, H. 1990. Food availability for an insectivore and how to measure it. Pages 38–43 *In* M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr. editors. Avian foraging: theory, methodology, and applications. Stud. Avian Biology No. 13, Cooper Ornithological Society, California.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Youngblood, A., J. B. Grace, and J. D. McIver. 2009. Delayed conifer mortality after fuel reduction treatments: interactive effects of fuel, fire intensity, and bark beetles. Ecological Applications 19:321–337.

Youngblood, A., T. Max, and K. Coe. 2004. Stand structure in eastside old-growth ponderosa pine forests of Oregon and northern California. Forest Ecology and Management 199:191–217.

Zhang, J., M. W. Ritchie, and W. W. Oliver. 2008. Vegetation responses to stand structure and prescribed fire in an interior ponderosa pine ecosystem. Special forum on ecological studies in interior ponderosa pine — First findings from blacks mountain interdisciplinary research. Canadian Journal of Forest Research 38:909–918.

Zwicker, S. M., and J. R. Walters. 1999. Selection of pines for foraging by red-cockaded woodpeckers. The Journal of Wildlife Management 63:843–852.