

Resource Selection by Black-backed Woodpeckers (*Picoides arcticus*) and American Three-toed Woodpeckers (*P. dorsalis*) in South Dakota and Wyoming

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ABSTRACT Black-backed woodpeckers (*Picoides arcticus*, [BBWO]) and American three-toed woodpeckers (*P. dorsalis*, [ATTW]) are uncommon inhabitants of conifer forests and are sympatric in some areas, including the Black Hills. Both species exhibit genetic characteristics associated with isolated populations, are species of special management concern, and for which data are lacking concerning populations and habitats. We developed resource selection models of forest vegetation within 500 m radius plots (78.5 ha) for BBWOs and ATTWs to provide forest managers with stand-level information to estimate how forest management might affect habitat for these species in the Black Hills. Relative probability of selection by BBWOs increased with greater area of ponderosa pine (*Pinus ponderosa*) stands 41–70% overstory canopy cover up to approximately 20% (16 ha) of the surrounding area then declined when these stands comprised greater than 20% of the area. Relative probability of selection by ATTWs increased with greater area of white spruce (*Picea glauca*) up to a maximum of approximately 66% (50 ha) of the surrounding area and subsequently declined when white spruce comprised greater than 66% of the surrounding area. Increased area of aspen (*Populus tremuloides*) stands increased the relative probability of selection by ATTWs. During a period when the Black Hills lacked extensive disturbance from fire or insect infestation, BBWOs selected areas that were managed for moderate overstory canopy of ponderosa pine and ATTWs selected stands with large diameter spruce and aspen at the higher elevations that were not extensively harvested.

KEY WORDS American three-toed woodpeckers, Black-backed woodpeckers, forest management, resource selection.

Black-backed (*Picoides arcticus*, [BBWO]) and American three-toed (*P. dorsalis*, [ATTW]) woodpeckers are uncommon inhabitants of conifer forests (Bock and Bock 1974, Goggans et al. 1989, Steeger and Dulisse 1997) that depend on bark beetle (Family: *Curculionidae* and *Scolytinae*) and woodboring beetle larvae (Family: *Buprestidae* and *Cerambycidae*) in recently killed trees for food (Dixon and Saab 2000, Leonard 2001, Wiggins 2004). The range of ATTWs and BBWOs overlap in many areas, but BBWOs are absent from the central and southern Rocky Mountains (Dixon and Saab 2000, Leonard 2001). Black-backed woodpeckers are associated with a variety of conifers, while ATTWs usually occur in northern pine (*Pinus*) forests that include spruce (*Picea* spp.) and aspen (*Populus tremuloides* [Wesolowski and Tomialojc 1986, Loose and Anderson 1995, Villard 1994, Hill et al. 2001, Leonard 2001, Wiggins 2004, Ervin 2011]). Both species occur in the Black Hills and Bear Lodge Mountain of western South Dakota and eastern Wyoming. In the Black Hills, BBWOs are usually associated with pine forests (Bock and Bock 1974, Rota et al. 2014a) while ATTWs are associated with spruce (Ervin 2011), but also occur in burned ponderosa pine (*P. ponderosa*) forest (Giroir et al. 2007).

Both BBWOs and ATTWs are species of management emphasis and concern for the Black Hills National Forest (BHNF) and the state wildlife agencies of South Dakota and

Wyoming (Black Hills National Forest 1997, Black Hills National Forest 2005, South Dakota Department of Game Fish and Parks 2006, Wyoming Game and Fish Department 2010). North American populations of both species declined during the 20 years leading up to this study (Sauer et al. 2001, Leonard 2001) and recently the BBWO population in the Black Hills and Bear Lodge Mountains was petitioned for protection under the Endangered Species Act (Hanson et al. 2012) and both species show characteristics of genetic isolation (Pierson et al. 2010, Ervin 2011). Thus, there is increased attention to populations and habitats of these species in the Black Hills and Bear Lodge Mountains. To assist forest managers assessing the effects of forest management activities on these species, we evaluated stand-level habitat selection of BBWOs and ATTWs in the Black Hills of South Dakota and Wyoming using resource selection models.

STUDY AREA

Our study area included 543,591 ha of the central and northern Black Hills and Bear Lodge Mountains in southwest South Dakota and northeast Wyoming (Fig. 1). The Black Hills and Bear Lodge Mountains are a forest surrounded by prairies. Elevation ranged from approximately 1065 m to 2207 m (Hoffman and Alexander 1987) and climate varied

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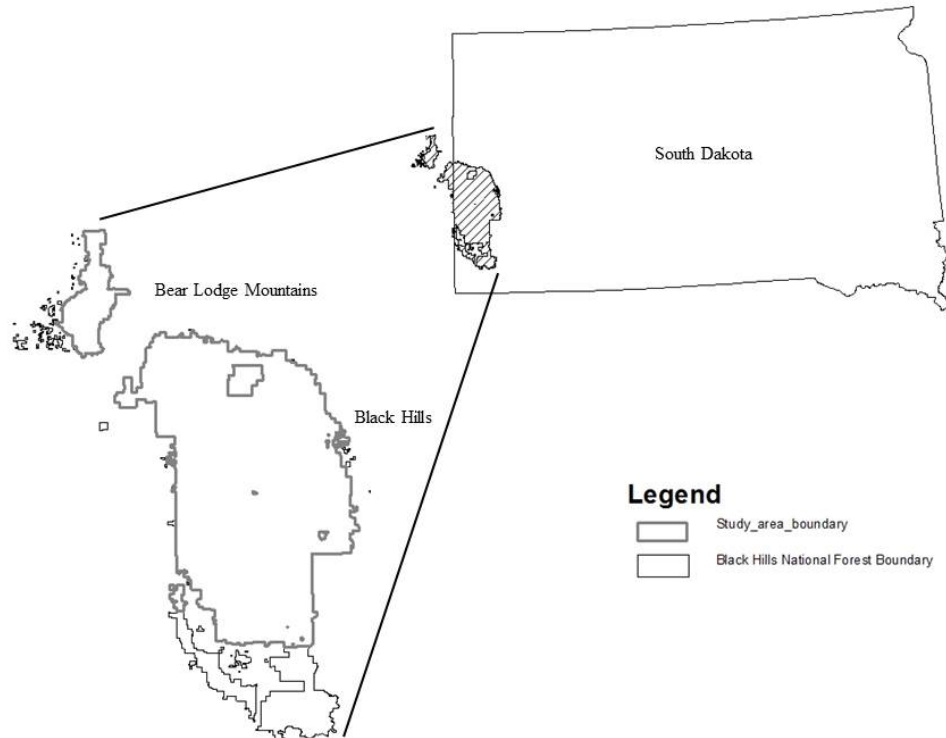


Figure 1. Study area for estimating resource selection of black-backed and American three-toed woodpeckers in the Black Hills and adjoining Bear Lodge Mountains of South Dakota and Wyoming, 2000–2001.

with latitude and elevation; northern portions tended to be colder and received more precipitation (Orr 1959). Ponderosa pine forest comprised approximately 85% of the BHNF with white spruce (*P. glauca*) and aspen being locally abundant, mostly in the northern portions of the Black Hills and on northerly aspects or drainages (Hoffman and Alexander 1987). Understory vegetation included species from the Rocky Mountains, northern boreal forest, eastern deciduous forest, and the northern Great Plains (Hoffman and Alexander 1987). Common shrubs included western snowberry (*Symphoricarpos occidentalis*), white coralberry (*S. albus*), kinnikinnick (*Arctostaphylos uva-ursi*), and common juniper (*Juniperus communis*; Severson and Thilenius 1976, Hoffman and Alexander 1987).

Historically, frequent low intensity fires at low elevations with large scale disturbance from fire and mountain pine beetle infestations primarily in the northern latitudes and higher elevations created the distinctive vegetation patterns found in the Black Hills (Brown and Sieg 1996, Parrish et al. 1996, Shinneman and Baker 1997, Brown and Sieg 1999). In the 90 years prior to our study, 84 wildfires occurred of which 6 were >4,000 ha (Black Hills National Forest 2008). Recent forest disturbance history included infrequent localized small

infestations of mountain pine beetles from 1984 to 1998 (K. Allen, R2 Entomologist, U.S. Forest Service, Rapid City, SD, personal communication) and 8 wildfires totaling 2,307 ha in the previous 4 years (Black Hills National Forest 2008). In late August-September 2000, a 33,809 ha fire occurred in the southern portion of the Black Hills. This burned area would not have been colonized by woodborers (Dickerson et al. 2015) and subsequently BBWOs or ATTWs until after our surveys in the summer 2001 (e.g. Vierling 2004).

Most of the Black Hills and Bear Lodge Mountains are managed by the BHNF. Management of forest structure occurs mostly through timber harvest in stands approximately 432 ha in size. Stands are delineated based on similar vegetation classified by dominant vegetation type, and if forested, stands are parsed into 3 age or diameter-at-breast height (DBH) classes (sapling/pole [2.522.9 cm], mature/sawtimber [22.935.6 cm], and old [>35.6 cm]). The sapling/pole and mature/sawtimber classes are further assigned overstory canopy cover classes of 0–40%, 41–70%, or >70% (Buttery and Gillam 1983). Hereafter these are referred to as vegetation structural stages. The digitized stand boundaries data are in a geographic information system (GIS) database with associated stand attributes and maintained by the BHNF.

METHODS

Field Surveys

We used a stratified random sampling approach to initially distribute 1-km transects throughout the BHNF. Stratifications included the U.S. Forest Service ranger districts (RD) and vegetation structure stages from the classification described above. Initially we included 20 vegetation structural stages that included each age/DBH class and overstory class for aspen, ponderosa pine and white spruce ($n = 18$), and the old age-class for ponderosa pine and white spruce. Each year, we randomly selected 5 stands from the GIS coverage for each of these vegetation structural stages, from each of 4 RDs in the BHNF. Some districts did not have 5 stands of each vegetation structural stage, so we selected additional stands for these vegetation structural stages from an adjacent RD. After selecting the stand from which each transect originated, we located a random point in the stand and initiated a transect of approximately 1.0 km in a random direction; transect length in the selected stand was maximized and passed through random points. Further, to improve efficiency of encountering uncommon species that are not randomly distributed, we incorporated an adaptive sampling strategy (Tompson and Seber 1996) that included additional transects perpendicular to the initial transect 800 m away. We surveyed 554 transects totaling 506.9 km; 111 transects on the Bear Lodge RD, 151 transects on the Hell Canyon RD, 164 transects on the Mystic RD, and 128 transects on the Northern Hills RD.

We surveyed transects from 29 April to 25 June during 2000 and 2001 between 0600–1300 hrs. We did not conduct surveys on days with rain, or days with winds > 24 km/hr. We surveyed each transect 1 time for approximately 1 hr. We used a handheld global positioning system (GPS; Garmin International, Inc., Olathe, Kansas, USA) unit to navigate along each transect. The probability of detection for BBWOs and ATTWs is increased substantially when calls are used on surveys (Siegel et al. 2010, Ervin 2011). At the start, end, and at 200-m intervals along each transect, we broadcast a recorded ATTW drum followed by a BBWO drum 3 times. There is some evidence that BBWOs will occasionally move slightly toward the call (Mohren et al. 2014). When a response to the drum was heard, we approached the estimated location of the response and searched until we found the bird. All locations of BBWOs and ATTWs were visually confirmed, marked with flagging, and recorded in the GPS unit.

Habitat determinations

We assessed stand-level vegetation at used and 4 associated random sites using the GIS vegetation coverage obtained from the BHNF for 2000. We edited this vegetation coverage to identify and classify vegetation for private lands using aerial photographs and adjacent classified stands. Similarly, we updated the vegetation coverage to reflect the wildfire that

occurred in late Aug–Sep of 2000 to create a GIS vegetation coverage for 2001. We located random sites 1500 m from each used site in each of the 4 cardinal directions. Around each used and associated random site, we created a 500-m circular plot in ArcMap 10.1 (Environmental Systems Research Institute, Redlands, California, USA) and intersected these with the vegetation coverages for 2000 and 2001. These 78.5-ha circular plots represent approximately 25% of the average BBWO home range inhabiting forest with a mixture of mountain pine beetle affected stands (Rota et al. 2014a). We classified vegetation in the 500-m plots into vegetation structural stages (Buttery and Gillam 1983). We combined sapling/pole (2.5–22.9 cm DBH) and mature/saw timber (>22.9 –35.6 cm DBH) classes of ponderosa pine within overstory canopy cover classes and all structural stages of white spruce and aspen (Rumble and Anderson 1992). We dissolved boundaries from adjacent stands with the same classification and calculated the area of vegetation structural stages, length of edge, and number of patches in each plot. We excluded 2 random plots that extended beyond the boundaries of the GIS vegetation coverage and for which we did not have aerial photos.

Analyses

We developed resource selection models using conditional logistic models with Breslow approximation to the exact partial likelihood in PROC PHREG (SAS 9.4, SAS Institute Inc., Cary, North Carolina, USA). Prior to developing resource models, we evaluated each variable for linear, quadratic polynomial, or natural log form transformation (Franklin et al. 2000) and retained the linear form of variables unless the nonlinear form was $\geq 2 \Delta$ Akaike Information Criterion units for small samples (AIC_c , [Burnham and Anderson 2002]) less than the linear form. We ranked models based on AIC_c weights and models $< 2 \Delta AIC_c$ from the highest-ranked model were considered if the P -value of individual coefficients was ≤ 0.15 (e.g., Arnold 2010).

We evaluated the predictive capability of the supported resource selection models using AIC_{modavg} in Program R (R Version 3.0.1, 2012, www.R-project.org/, accessed 25 Apr 2012). We used a leave-one-out approach and predicted the used sites which were assigned to 1 of 5 equal size bins (determined by the 5 choices) based on relative probability conditioned on the associated random sites (Leblond et al. 2010). If models had good predictive capability, we expected a greater frequency of used sites to be assigned to the highest probability bins and a resulting high Spearman's rank correlation. We did not compute model averaged coefficients because interpretation of model coefficients with higher order polynomial terms may differ from their main effect interpretations among models and may be inappropriate (Burnham and Anderson 2002). We plotted response curves for the highest ranked models to provide visual aids for interpretation of resource selection models.

RESULTS

BBWO Resource Selection

Two resource models for BBWOs were considered within our criteria of $\leq 2 \Delta AIC_c$ units of the highest-ranked model. Both models included area of ponderosa pine stands with 41–70% overstory canopy cover in a quadratic polynomial form (Tables 1, 2). We discarded the second-ranked model because it offered no insight into resource selection as evidenced by

the nonsignificant coefficient ($\beta = -0.005$, $P = 0.69$) for area of ponderosa pine stands >70% overstory canopy cover. The relative probability of use by BBWOs in the highest-ranked model was maximized when approximately 20% of the surrounding plot (~16 ha) was comprised of 41–70% ponderosa pine overstory cover (Fig. 2). Cross-validation of the highest-ranked model indicated good fit of BBWO (Spearman's $r = 0.82$, $P \leq 0.05$); 59% of BBWO sites were included in the highest probability bin, which represented an improvement of 2.5 times over random selection.

Table 1. Stand-level resource selection models with $\Delta AIC_c < 4$ for black-backed and American three-toed woodpeckers in the Black Hills of South Dakota and Bear Lodge Mountains of Wyoming, 2000–2001.

Model variables ¹	n	K	AIC _c	ΔAIC_c	W _i
Black-backed woodpecker (9 models were evaluated)					
Quadratic pine 41–70% OCC	215	2	130.35	0.00	0.43
Quadratic pine 41–70% OCC + Pine >70% OCC	215	3	132.25	1.90	0.18
Quadratic pine 41–70% OCC + Pine >70% OCC + Pine \leq 40% OCC	215	4	132.56	2.21	0.14
Quadratic pine 41–70% OCC + Pine >70% + Length of edge	215	4	133.47	3.11	0.09
Quadratic pine 41–70% OCC + Pine >70% + Number of patches	215	4	133.54	3.19	0.10
Quadratic pine 41–70% OCC + Pine >70% + Aspen	215	4	133.76	3.41	0.08
Three-toed woodpecker (18 models were evaluated)					
Quadratic spruce + Aspen	100	3	56.70	0.00	0.27
Quadratic spruce	100	2	57.37	0.67	0.20
Quadratic spruce + Pine 41–70% OCC + Aspen	100	4	58.52	1.87	0.11
Quadratic spruce + Length of edge	100	3	58.86	2.16	0.09
Quadratic spruce + Number of patches	100	3	58.87	2.17	0.09
Quadratic spruce + Pine 41–70% OCC	100	3	59.42	2.72	0.07
Pine 0–40% OCC + Pine 41–70% OCC + Pine .70% OCC	100	3	59.46	2.76	0.07

¹ Quadratic models are a polynomial including linear and quadratic terms as 2 variables.

Table 2. Model coefficients \pm SE from resource selection models for black-backed and American three-toed woodpeckers in the Black Hills and Bear Lodge Mountains of South Dakota and Wyoming, 2000–2001.

Model Rank	Variables in models							
	β	SE	β	SE	β	SE	β	SE
Black-backed woodpeckers models	Pine 41–70% overstory (linear)		Pine 41–70% overstory (quadratic)		Pine >70% overstory			
1	0.067	0.424	-0.002	0.001				
2	0.070	0.044	-0.002	0.001	-0.005	0.012		
Three-toed woodpecker models	White spruce (linear)		White spruce (quadratic)		Aspen		Pine 41–70% overstory	
1	0.204	0.073	-0.002	0.001	0.156	0.112		
2	0.198	0.073	-0.002	0.001				
3	0.195	0.073	-0.002	-0.001	0.169	0.117	0.011	0.178

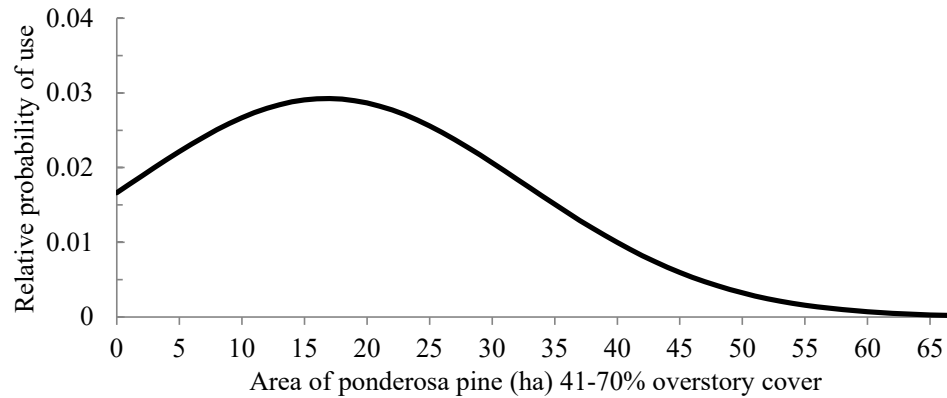


Figure 2. Response curve depicting relative probability of use for area of ponderosa pine 41–70% overstory from the highest-ranked conditional logistic regression model estimating stand-level resource selection by black-backed woodpeckers in the Black Hills and adjoining Bear Lodge Mountains of South Dakota and Wyoming in 2000–2001. Relative probabilities depend on the choice set which included 68 incremental increases of 1 ha within the range of values from our data.

ATTW Resource Selection

Three resource selection models were identified with <2 ΔAIC_c units of the highest-ranked model for ATTWs. Area of white spruce had a quadratic polynomial relationship to relative probability of selection by ATTWs and was included in all 3 models (Tables 1, 2). Area of aspen was included in the highest-ranked model and 41–70% ponderosa pine overstory canopy cover was included in the third-ranked model. The second-ranked model was a subset of the highest-ranked model, and the coefficient for 41–70% ponderosa pine overstory canopy cover in the third-ranked model was non-significant ($P = 0.55$) so this model was disregarded. Relative probability of use by ATTWs was greatest when approximately 66% (~50 ha) of the surrounding area was white spruce (Fig. 3). Aspen stands comprised a relatively low amount of the surrounding area at use sites and the relative probability of use by ATTWs increased consistently when aspen increased (Fig. 3). Cross-validation indicated good model fit (Spearman's $r = 0.90$, $P \leq 0.05$) and 60% used sites were included in the highest probability bin, also an improvement of 2.5 times over random selection.

DISCUSSION

Forest management occurs at the stand level, and for the approximately 70% of the BHNF that is managed for timber production, ponderosa pine 41–70% overstory canopy cover is the desired long-term condition (Boldt and Van Duesen 1974, Dykstra et al. 1997). All observations of BBWOs occurred in stands of ponderosa pine. To achieve the desired conditions, management reduces overstory canopy cover to $<40\%$ at the time of harvest, which then increases as trees

grow (Boldt and Van Duesen 1974). Our models suggest that when then composition of ponderosa pine 41–70% overstory canopy cover exceeded about 20%, the probability of selection by BBWOs decreased. The risk for tree mortality from mountain pine beetles increases with greater tree density (Schmid et al 2007) and management for mature stands 41–70% overstory canopy cover reduces of risk of tree mortality. BBWOs depend on the bark beetle and woodborer beetle larvae in recently kill trees. Thus, it is likely that there were fewer food resources for BBWOs when extensive areas had 41–70% overstory canopy cover.

Woodboring and bark beetle larvae are important determinants in the resource selection by BBWOs in the Black Hills (Bonnot et al. 2009, Rota et al. 2015). Black-backed woodpeckers occur in late successional forests at low densities in the absence of large scale forest disturbance (Settingington et al. 2000) and establish home ranges that include open and dense forest if sufficient deadwood is present (Tremblay et al. 2009). Dykstra et al. (1997) reported greater abundance of BBWOs in harvested sapling/pole stands in the northern Black Hills than mature stands where they likely fed on woodborer larvae in the forest residue after harvest. Despite a period of relatively low levels of forest mortality by insects or fire, mountain pine beetles are endemic and the primary cause of tree mortality in the Black Hills. Risk of beetle infestations is greater in ponderosa pine stands $>40\%$ overstory canopy cover and increases with greater overstory canopy cover (Schmid et al. 2007, Negrón et al. 2008). Most observations of BBWOs in our study occurred in or near a small patch of recently killed trees (SRM, personal observation). Factors affecting food resources (woodboring and bark beetles) of BBWOs are more complex than simply stand structure. Suitability of recently killed forests for BBWOs de-

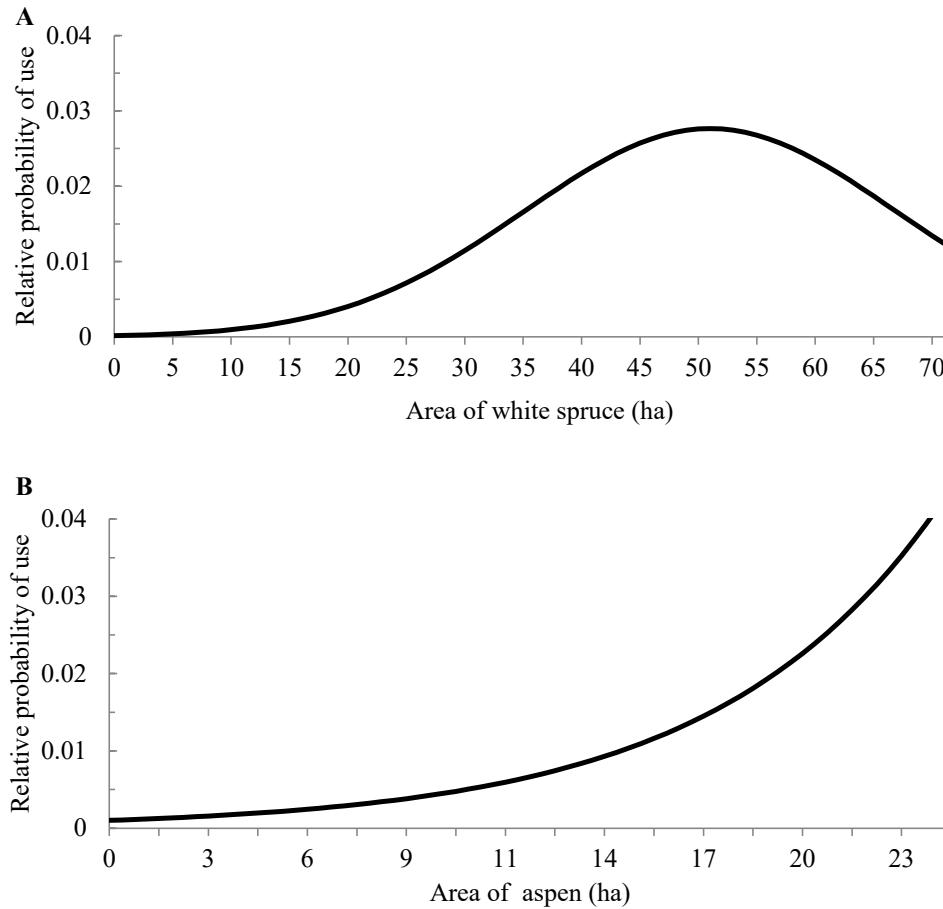


Figure 3. Response curves depicting relative probability of use for (A) hectares of white spruce and (B) hectares of aspen from the highest-ranked model conditional logistic regression model estimating stand-level resource selection by American three-toed woodpeckers in the Black Hills and adjoining Bear Lodge Mountains of South Dakota and Wyoming in 2000–2001. Relative probabilities depend on the choice set which included 72 incremental increases of 1 ha within the range of values in our data.

clines after about 2 years in the Black Hills (Rota et al. 2014 *a,b*; Rota et al. 2015). However, large wildfires or widespread insect outbreaks can negatively affect the local economies. Nonetheless, small patches of recently beetle-killed forests could be retained to provide habitat for BBWOs.

American three-toed woodpeckers are associated with spruce forests throughout their range (Bock and Bock 1974, Hoyt and Hannon 2002, Johnson 2011) and with white spruce forest in the Black Hills (Ervin 2011). White spruce stands comprised <2% of our study area and were limited to higher altitudes and northeast slopes of canyons of the Black Hills as pure stands. Additionally, ATTWs typically selected sites that included aspen and spruce, which supports previous associations of individuals with later seral stages of aspen (Hoffman and Alexander 1987). Moreover, our findings corroborate previous findings indicating that ATTWs frequently nest in

aspen and forage on large white spruce snags (Ervin 2011). Timber harvest and removal of dead wood may reduce ATTW habitat (Wesołowski et al. 2005, Stachura-Skierczyńska et al. 2009). However, timber harvest of white spruce comprises $\leq 1\%$ of round-wood harvesting in the Black Hills (Piva and Josten 2013).

Both BBWOs and ATTWs partition resources where they are sympatric (Short 1974, Murphy and Lehnhausen 1998, Hoyt and Hannon 2002) which also was evident in our study. In the Black Hills, BBWOs selected ponderosa pine stands whereas ATTWs selected areas with white spruce and aspen (Ervin 2011, our study). Nonetheless, ATTWs also occur in pine forests elsewhere (Goggans et al. 1989, Steeger and Dulisse 1997) and we (CPL and MAR) noted rare occurrences of ATTWs in recently burned ponderosa pine or mountain pine beetle invested stands in the Black Hills.

MANAGEMENT IMPLICATIONS

During periods of low forest disturbance from fire and mountain pine beetles, BBWOs selected areas where ponderosa pine in the desired management condition (41–70% overstory canopy cover) did not dominate the landscape. Although stands >70% overstory cover also should provide habitat in the absence of wildfire or widespread insect outbreaks, our models did not exhibit consistent trends for selection of these stands by BBWOs. Perhaps within stand heterogeneity of stand density provided resources for BBWOs. American three-toed woodpeckers were mostly restricted to white spruce and aspen which are not subjected to extensive forest management in the Black Hills (Piva and Josten 2013). Therefore, we would not expect forest management to affect ATTWs.

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LITERATURE CITED

- Arnold, T.W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *Journal of Wildlife Management* 74: 1175–1178.
- Black Hills National Forest. 1997. Land and Resource Management Plan: 1997 Revision. Record of Decision. U.S. Forest Service, Black Hills National Forest, Custer, South Dakota, USA.
- Black Hills National Forest. 2005. Black Hills National Forest Phase II Amendment. 1997 Land and Resource Management Plan, Amendment 6, Record of Decision. http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5112563.pdf. Accessed 2 July 2014.
- Black Hills National Forest. 2008. Bkf_firehis. <http://www.fs.usda.gov/detail/blackhills/landmanagement/gis/?cid=stelprdb5112497>. Accessed 4 December 2013.
- Bock, C. E., and J. H. Bock. 1974. On the geographical ecology and evolution of the three-toed woodpeckers, *Picoides tridactylus* and *P. arcticus*. *American Midland Naturalist* 92:397–405.
- Boldt, C. E., and J. L. Van Duesen. 1974. Silviculture of ponderosa pine in the Black Hills: status of our knowledge. Research paper RM124. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Bonnot, T. W., J. J. Millsbaugh, and M. A. Rumble. 2009. Multi-scale nest-site selection by black-backed woodpeckers in outbreaks of mountain pine beetles. *Forest Ecology and Management* 259:220–228.
- Brown, P. M., and C. H. Sieg. 1996. Fire history in interior ponderosa pine forests of the Black Hills, South Dakota, U.S.A. *International Journal of Wildland Fire* 6:97–105.
- Brown, P. M., and C. H., Sieg. 1999. Historical variability in fire at the ponderosa pine-Northern Great Plains prairie ecotone, southeastern Black Hills, South Dakota. *Ecoscience* 6:539–547.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical InformationTheoretic approach, second edition. SpringerVerlag. New York, New York, USA.
- Buttery, R. F., and B. C. Gillam. 1983. Ecosystem descriptions. Pages 42–71 in R.L. Hoover and D.L. Willis, editors. Managing forested lands for wildlife. Colorado Division of Wildlife in cooperation with the U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Denver, Colorado, USA.
- Dickerson, B., E., A. K. Ambourn, M. A. Rumble, K. K. Allen, and C. P. Lehman. 2015. Woodpecker forage availability in habitat disturbances of the Black Hills. *The Prairie Naturalist* 47:110–114.
- Dixon, R. D., and V. A. Saab. 2000. Black-backed Woodpecker (*Picoides arcticus*). Pages 1–19 in F. B. Gill and A. Poole, editors. *The Birds of North America* 509. The birds of North America, Inc., Philadelphia, Pennsylvania, USA.
- Dykstra, B. L., M. A. Rumble, and L. D. Flake. 1997. Effects of timber harvesting on birds in the Black Hills of South Dakota and Wyoming, USA. Pages 16–26 in J. E. Cook and B. P. Oswald, compilers. First biennial North American forest ecology workshop. Society of American Foresters, Raleigh, North Carolina, USA.
- Ervin, A. M. 2011. Habitat selection, nesting success and genetic structure of the American three-toed woodpecker (*Picoides dorsalis*) in the Black Hills of South Dakota. Dissertation. University of South Dakota, Vermillion, USA.
- 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 north western California. *Ecological Monographs* 70:539–590.
- Giroir, G., C. White, and R. Sparks. 2007. Monitoring the birds of the Black Hills, 2007 Field Season Report. Technical Report M-MBBH07-01. Rocky Mountain Bird Observatory, Brighton, Colorado, USA.
- Goggans, R., R. D. Dixon, and L. C. Seminara. 1989. Habitat use by three-toed and black-backed woodpeckers, Deschutes National Forest, Oregon. Technical Report 87302. Oregon Department of Fish and Wildlife, Salem, Oregon, USA.

- Hanson, C. K., Coulter, J. Augustine, and D. Short. 2012. Petition to list the black-backed woodpecker (*Picoides arcticus*) as Threatened or Endangered under the federal Endangered Species Act. http://www.biologicaldiversity.org/species/birds/black-backed_woodpecker/pdfs/BBWO_FESA_Petition.pdf/. Accessed 10 May 2012.
- Hill, R. L., C. M. White, and J. T. Flinders. 2001. Three-toed woodpecker habitat selection in a managed Engelmann spruce forest on Monroe Mountain, Utah. Final Report. Utah Division of Wildlife Resources, Salt Lake City, USA.
- Hoffman, G. R., and R. R. Alexander. 1987. Forest vegetation of the Black Hills National Forest of South Dakota and Wyoming: a habitat classification. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station. Research Paper RM276, Fort Collins, Colorado, USA.
- Hoyt, J. S., and S. J. Hannon. 2002. Habitat associations of black-backed and three-toed woodpeckers in the boreal forest of Alberta. *Canadian Journal of Forest Research* 32:1881–1888.
- Johnson, D. K. 2011. Conservation assessment of the American three-toed woodpecker: emphasis on Dixie and Fishlake National Forests, Utah. https://cnr.usu.edu/files/uploads/Students/MNR/capstone_projects/Johnson_Devin_MNRCapstone.pdf. Accessed 27 August 2014.
- Leblond, M., C. Dussault, and J. P. Ouellet. 2010. What drives fine-scale movements of large herbivores? A case study using moose. *Ecography* 33:1102–1112.
- Leonard, D. L. Jr. 2001. American Three-toed Woodpecker (*Picoides dorsalis*). *The Birds of North America Online*. A. Poole, editor. Ithaca: Cornell Lab of Ornithology; Retrieved from the *Birds of North America Online*: <http://bna.birds.cornell.edu/bna/species/588>. Accessed 1 July 2014.
- Loose, S. and S. Anderson. 1995. Woodpecker Habitat Use in the Forests of Southeast Wyoming. *Journal of Field Ornithology* 66:503–514.
- Mohren, S. R., M. A. Rumble, and S. H. Anderson. 2014. Density and abundance of black-backed woodpeckers in a ponderosa pine ecosystem. *The Prairie Naturalist* 46:62–69.
- Murphy, E. C., and W. A. Lehnhausen. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. *Journal of Wildlife Management* 62:1359–1372.
- Negrón, J. F., K. Allen, B. Cook, and J. R. Withrow Jr. 2008. Susceptibility of ponderosa pine, *Pinus ponderosa* (Dougl. ex Laws.), to mountain pine beetle, *Dendroctonus ponderosae* Hopkins, attack in uneven-aged stands in the Black Hills of South Dakota and Wyoming USA. *Forest Ecology and Management* 254:327–334.
- Orr, H. K. 1959. Precipitation and streamflow in the Black Hills. Research Paper No. 44. U.S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Parrish, J. B., D. J. Herman, and D. J. Reyher. 1996. A century of change in Black Hills forest and riparian ecosystems. B 722. South Dakota State University, Agriculture Experiment Station, Brookings, South Dakota, USA.
- Pierson, J. C., F. W. Allendorf, V. Saab, P. Drapeau, and M. K. Swartz. 2010. Do male and female black-backed woodpeckers respond differently to gaps in habitat? *Evolutionary Applications* 3:263–278.
- Piva, R. J., and G. J. Josten. 2013. South Dakota timber industry: an assessment of timber product output and use 2009. Resource Bulletin NRS80. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newton Square, Pennsylvania, USA.
- Rota, C. T., M. A. Rumble, J. J. Millspaugh, C. P. Lehman, and D. C. Kesler. 2014a. 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.
- Rota, C. T., J. J. Millspaugh, M. A. Rumble, C.P. Lehman, and D. C. Kesler. 2014b. The role of wildfire, prescribed fire, and mountain pine beetle infestations on the population dynamics of black-backed woodpeckers in the Black Hills, South Dakota. *PLoS ONE* 9(4):e94700.
- Rota, C. T., M. A. Rumble, J. J. Millspaugh, C. P. Lehman, and D. C. Kesler. 2015. Apparent foraging success reflects habitat quality in an irruptive species, the Black-backed Woodpecker. *Condor* 117:178–191.
- Rumble, M. A., and S. H. Anderson. 1992. Stratification of habitats for identifying habitat selection by Merriam's turkeys. *Great Basin Naturalist* 52:139–144.
- Sauer, J. R., J. E. Hines, and J. Fallon. 2001. The North American Breeding Bird Survey, Results and Analysis 1966–2000. Version 2001.2, USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.
- Schmid, J. M., S. A. Mata, R. R. Kessler, and J. B. Popp. 2007. The influence of partial cutting on mountain pine beetle-caused tree mortality in Black Hills ponderosa pine stands. Research Paper RMRS-RP-68. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Fort Collins, Colorado, USA.
- Settingington, M. A., I. D. Thompson, and W. A. Montevecchi. 2000. Woodpecker Abundance and Habitat Use in Mature Balsam Fir Forests in Newfoundland. *Journal of Wildlife Management* 64:335–345.
- Severson, K. E., and J. F. Thilenius. 1976. Classification of quaking aspen stands in the Black Hills and Bear Lodge Mountains. U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, Research paper RM166. Fort Collins, Colorado, USA.

- Shinneman, D. J., and W. L. Baker. 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. *Conservation Biology* 11:1276–1288.
- Short, L. L. 1974. Habitat interactions of North American three-toed woodpeckers (*Picoides arcticus* and *Picoides tridactylus*). *American Museum Novitates* 2547:1–42.
- Siegel, R. B., J. F. Saracco, and R. L. Wilkerson. 2010. Management Indicator Species (MIS) Surveys on Sierra Nevada National Forests: Black-backed Woodpecker. 2009 Annual Report. The Institute for Bird Populations, Sierra-Nevada Observatory, Point Reyes Station, California, USA.
- Stachura-Skierczyńska, K., T. Tumił, and M. Skierczyński. 2009. Habitat prediction model for three-toed woodpecker and its implications for the conservation of biologically valuable forests. *Forest Ecology and Management* 258:697–703.
- Steeger, C., and J. Dulisse. 1997. Ecological interrelationships of three-toed woodpeckers with bark beetles and pine trees. Nelson Forest Region Forest, Sciences Extension Note RS035. Ministry of Forests, Lands, and Natural Resource Operations, Kamloops, British Columbia, Canada.
- South Dakota Department of Game, Fish and Parks. 2006. South Dakota Comprehensive Wildlife Conservation Plan. South Dakota Department of Game, Fish and Parks, Wildlife Division Report 2006-08. Pierre, South Dakota, USA.
- Tompson, S.K., and G.A.F. Seber. 1996. Adaptive Sampling. John Wiley and Sons, Inc. New York, NY, USA.
- Tremblay, J. A., J. Ibarzabal, C. Dussault, and J.-P. L. Savard. 2009. Habitat requirements of breeding Black-backed Woodpeckers (*Picoides arcticus*) in managed, unburned boreal forest. *Avian Conservation and Ecology - Écologie et conservation des oiseaux* 4:2. <http://www.ace-eco.org/vol4/iss1/art2/>
- Vierling, K. T. 2004. Report on woodpecker breeding in the Jasper fire, Black Hills National Forest, Custer, South Dakota, USA.
- Villard, P. 1994. Foraging behavior of black-backed and three-toed woodpeckers during spring and summer in a Canadian boreal forest. *Canadian Journal of Zoology* 72:1957–1959.
- Wesołowski, T., and L. Tomiałojc. 1986. The breeding ecology of woodpeckers in a temperate primeval forest—preliminary data. *Acta Ornithologica* 22:1–21.
- Wesołowski, T., D. Czeszczewik, and P. Rowiński. 2005. Effects of forest management on three-toed woodpecker *Picoides tridactylus* distribution in the Białowieża Forest (NE Poland): conservation implications. *Acta Ornithologica* 40:53–60.
- Wiggins, D. 2004. American three-toed woodpecker (*Picoides dorsalis*): a technical conservation assessment. U.S. Forest Service, Rocky Mountain Region, Species Conservation Project. <http://www.fs.fed.us/r2/projects/scp/assessments/americanthree-toedwoodpecker.pdf>. Accessed 2 July 2014.
- Wyoming Game and Fish Department. 2010. State Wildlife Action Plan. http://wgfd.wyo.gov/web2011/Departments/Wildlife/pdfs/SWAP_2010_FULL_OCT0003090.pdf. Accessed 29 April 2014.

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