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Source: Journal of Mammalogy, 92(3):561-567. 2011.

Published By: American Society of Mammalogists

DOI: <http://dx.doi.org/10.1644/10-MAMM-A-095.1>

URL: <http://www.bioone.org/doi/full/10.1644/10-MAMM-A-095.1>

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## Influence of stand and landscape features on snowshoe hare abundance in fragmented forests

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Habitat fragmentation often separates and reduces populations of vertebrates, but the relative effects of habitat attributes within remnant patches versus the matrix surrounding the patches are less clear. For snowshoe hares (*Lepus americanus*) lower densities and disrupted cycles in their southern range have been ascribed to habitat fragmentation, although relevant scales of landscape influence remain unknown. In a fragmented forest in north-central Washington we counted fecal pellets of snowshoe hares to examine the extent to which relative snowshoe hare densities within stands of suitable habitat changed with the composition of surrounding habitats. Pellet densities were associated primarily with density of large shrubs and saplings and medium trees within a stand. Pellet densities also were correlated positively with the amount of moist forest (dominated by Engelmann spruce [*Picea engelmannii*] and subalpine fir [*Abies lasiocarpa*]) and correlated negatively with the amount of open-structured habitat within 300 m of the stand perimeter. These results suggest that forest managers will have positive impacts on hare densities by managing both focal stands and the surrounding stands for the higher densities of large shrubs and saplings and medium trees that hares select.

Key words: fecal pellets, forest fragmentation, landscape, *Lepus americanus*, relative abundance, snowshoe hare, Washington

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DOI: 10.1644/10-MAMM-A-095.1

Habitat loss and fragmentation are dominant threats to biodiversity (Ewers and Didham 2006; Fahrig 2003). In forested ecosystems fire and management activities create mosaic landscapes of different stand ages and stem densities. Often these activities are additive to natural fragmentation arising from topography and other factors that influence forest habitat types. Although research has addressed the effects of patch size and isolation on the persistence of wildlife species, these metrics alone do not describe adequately or predict population persistence or extinction (Doak and Mills 1994; Prugh et al. 2008). The habitats in the matrix surrounding the remnant patches can be hostile, neutral, or beneficial to a population, and the attributes and spatial patterning of habitats within the matrix can affect population dynamics within habitat patches (Lindenmayer et al. 2008).

The composition of the matrix and movements of animals among habitat patches are presumed to drive population dynamics of snowshoe hares (*Lepus americanus*) in fragmented forests in southern parts of their range (Dolbeer and Clark

1975; Sievert and Keith 1985; Wolff 1980). Snowshoe hare densities, survival, and population growth are highest in densely forested stands where understory structure provides forage and protection from predators (Griffin and Mills 2009; Orr and Dodds 1982; Parker et al. 1983; Thompson et al. 1989; Wolff 1980). In the southern parts of snowshoe hare range patches of dense forest often are fragmented by natural and anthropogenic causes, resulting in a heterogeneous mix of habitat types that range from poor to high quality for hares. Hare densities vary widely in patches of dense forest with similar stand-scale attributes in fragmented forests in Montana and Wyoming (Griffin and Mills 2007; Hodges et al. 2009; Mills et al. 2005), suggesting that matrix habitats influence hare densities.



Understanding the processes that drive snowshoe hare dynamics is important for management of forests at southern latitudes, because hares are an important food source for many forest carnivores, including the federally threatened Canada lynx (*Lynx canadensis*). In the United States forest management strategies include guidelines for considering habitat for hares in areas where lynx occur (Ruediger et al. 2000). The effectiveness of these strategies could depend on the importance of matrix habitats for hare dynamics in fragmented forests at southern latitudes.

Most studies on densities of snowshoe hares have focused on relationships with stand attributes (Griffin and Mills 2007; Hodges 2000a, 2000b; Homyack et al. 2007). Open-structured stands, such as recent clear-cuts, natural meadows, and recently burned forests, support low densities of snowshoe hares (Ferron et al. 1998; Hik 1995; O'Donoghue 1983; Sievert and Keith 1985). Moderately dense stands can support moderate hare densities (Koehler 1990; Thompson et al. 1989). However, little is known about how densities of hares vary with the spatial structure of landscapes, where preferred habitat can be either abundant or scarce and set among a matrix of either poor- or intermediate-quality habitat types (but see Griffin and Mills 2009; St-Laurent et al. 2007, 2008).

The primary objective of this study was to determine whether snowshoe hare abundance within patches of good-quality habitat is influenced by single- and multiscale habitat factors. Because no previous work has identified landscape scales particularly relevant to snowshoe hares, we examined 3 landscape scales and stand-level attributes tied to different aspects of hare biology. Based on previous research on habitat relationships for hares (Hodges 2000a, 2000b), we expected a strong influence of stand-level understory structure on hare densities, but no existing literature suggests the magnitude or scale of any landscape-level impacts.

## MATERIALS AND METHODS

*Study area and vegetation classification.*—The field research was conducted during May–August of 2003 and 2004 in a 211-km<sup>2</sup> study area on the Okanogan National Forest in north-central Washington (48°N, 120°W) concurrent with research on lynx habitat in the same area (Koehler et al. 2008; Maletzke et al. 2008). Elevations ranged from 643 m to 2,134 m, and average snow depth was 315 cm at 655 m (Western Regional Climate Center; www.wrcc.dri.edu).

The study area contained a mosaic of habitats due to the varied topography and microclimates, natural and prescribed fires, and forest management activities such as roads, timber harvests, and timber thinning. The median stand size was 10 ha, and the mean was 21 ha ( $SE = 1.5$  ha); large patches of homogenous vegetation were rare, which reflects conditions typical of most lynx habitat in the state of Washington and throughout the mountainous western United States (Ruggiero et al. 2000).

We used geographic information system coverages developed by Maletzke (2004) to select sample sites and for spatial

analyses. Stand data included vegetation type, canopy cover, and understory cover. Stands were classified into 4 categories based on their dominant vegetation: moist forest, dry forest, recent burns, and natural openings. Moist forest stands were dominated by subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*), with subdominant Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), whitebark pine (*Pinus albicaulis*), or a combination of these. Shrub species that contributed substantially to understory cover included alder (*Alnus* spp.) and willow (*Salix* spp.). Moist forest stands covered 55% of the study area, mostly on north-facing slopes and steeper drainage bottoms. Dry forest stands were characterized by ponderosa pine (*Pinus ponderosa*) and Douglas fir, covered 37% of the area, and dominated lower elevations (<1,066 m), south-facing slopes at higher elevations, and broad drainage bottoms. Recent burns covered 6% of the study area, resulted from wildfires within the previous 10 years, and had sparse sapling regeneration (<10% understory cover from 0.5 to 2.0 m above ground). Natural openings, which included meadows and rocky slopes, covered 2% of the study area.

*Site selection.*—From the geographic information system layers we identified all stands ( $n = 356$ ) within the study area in which canopy cover was >40% or understory cover was >40%; that is, conditions that likely provided snowshoe hare habitat (Hodges 2000a, 2000b). From these 356 stands we randomly sampled 76 stands. Because we wanted to sample both stands that were surrounded by poorer-quality patch types and stands that had matrix habitats of similar quality to the focal stand, we selected 20 ha as our maximum stand size, even if the actual forest stand was larger. We chose 20 ha for this upper limit on our stand sampling because at least some hares could have their entire home range within the stand (hare home ranges typically do not exceed 10 ha—de Bellefeuille et al. 2001; Griffin 2003; Hodges 1999). For stands 3.4–20 ha we sampled the entire stand ( $n = 36$ ). For forest stands > 20 ha ( $n = 40$ , ranging from 21 to 190 ha) we delineated an arbitrary 20-ha stand boundary at the stand center within which we counted hare fecal pellets and recorded stand features. We used this boundary to calculate landscape metrics.

*Snowshoe hare relative abundance.*—Within each stand we counted fecal pellets in 50 randomly placed plots (3.05 m × 5.08 cm—Krebs et al. 2001), because this sample size has reasonable power for evaluating differences in relative abundances of snowshoe hares (Hodges and Mills 2008). The plots were not cleared previously and therefore integrate across an unknown time period, but uncleared plots are highly correlated with estimates from annually cleared plots (Hodges and Mills 2008). Although the density of snowshoe hares in any given forest stand is estimated best with mark–recapture approaches, Mills et al. (2005) and Murray et al. (2002) compared estimated hare densities to pellet counts in Montana and Idaho, respectively, and concluded that counts of pellets on uncleared plots are adequate for ranking relative hare abundance in many stands across large spatial scales. For

example, relative abundances of snowshoe hares from uncleared pellet plots have been used in Yellowstone National Park (Hodges et al. 2009) and in forestry-intensive landscapes in Labrador, Canada (Newbury and Simon 2005).

Throughout our analyses we used the mean number of pellets per plot per stand as the dependent variable. We also converted pellet counts into hare densities using the equation from Krebs et al. (2001) solely for easy comparison of hare densities in our study area to those in other studies, although our estimates are likely to be slightly high because we used uncleared plots, which do result in larger pellet counts than cleared plots (Hodges and Mills 2008). The Krebs equation, which was developed for another region, is a robust equation for other locations in the western United States (Mills et al. 2005).

*Stand-scale variables.*—Studies of snowshoe hare habitat conducted throughout their range have reported a variety of characteristics to explain hare densities or habitat use. The majority of these studies quantify characteristics of forest stands, such as vegetation density (stem counts or visual measures of cover), vegetation types, and patch characteristics such as size or aspect (Hodges 2000a, 2000b). Because no work had been done in our particular study area to determine which variables best explained hare densities within stands, we measured a suite of variables in an effort to discern which of the stand variables would be most appropriate for including in our a priori models.

We used geographic information system data to quantify stand size, perimeter length, and edge-to-area ratio of stands. To measure vegetation structure we randomly placed 10 circular plots with a 5-m radius in each stand. At each plot center we used a spherical convex densiometer to estimate canopy cover (Lemon 1957). To estimate understory cover we used a 0.5 × 2-m cover board viewed at 5 m from plot center and estimated the percentage of the board from 0 to 2 m that was obstructed by vegetation, recording the average horizontal cover at true north, 120°, and 240° to account for the high variation in understory cover. We counted the number of stems from all trees and shrubs > 1 m tall and > 2.5 cm diameter at breast height (DBH) within the circular plots and converted the counts to trees/ha. Tree size classes were: saplings (2.5–10.2 cm DBH), medium (10.3–27.9 cm DBH), or large (>27.9 cm DBH). Coniferous trees constituted approximately 90% of the sapling class of vegetation and 100% of the 2 larger classes; hereafter, we refer to the smallest class as saplings even though some shrubs were present in this class. We used the average of measures for canopy and understory cover readings, tree densities, slope, and aspect across the 10 plots to characterize each variable per stand.

*Landscape-scale variables.*—Because the appropriate landscape scale at which hares relate to their environment is unknown, we explored multiple scales (Fuhlendorff et al. 2002; Martin and McComb 2003; Naugle et al. 1999). We selected 3 hierarchical landscape scales likely to relate to snowshoe hare behavior and movement: perimeter, and distances of 300 m and 600 m from the perimeter. The perimeter scale examined the stands that directly border the

selected stand; for stands > 20 ha, in which we delineated an internal 20-ha patch to sample, some or even all of the perimeter would consist of the same stand type. Measures at the perimeter scale reflect the habitats immediately available to a hare should it decide to leave the focal patch. The 300-m and 600-m scales consider all stands within those distances of the focal stands, regardless of whether they directly touch the perimeter. The 300-m scale represented habitats available to hares on a daily basis, because it approximates the diameter of a hare's home range (de Bellefeuille et al. 2001; Griffin 2003; Hodges 1999) and is close to the maximum distance hares moved in an hour in this region (Walker 2005). The 600-m scale represented habitats available to a dispersing hare (Gillis and Krebs 1999; Griffin 2003).

We investigated 2 landscape-scale variables of high relevance to snowshoe hares and to forest management, the amount of moist forest and the amount of open-structured habitat. Open-structured habitat consisted of natural openings, recent burns, or timber harvest units where the canopy and understory were both ≤10%. These areas likely present barriers to interpatch movement by snowshoe hares (Griffin and Mills 2007, 2009; Hodges et al. 2009; Wirsing et al. 2002), because they provide little food or shelter, especially during winter. We calculated the percentage of the area adjacent to the stand perimeter or within a 300-m or 600-m buffer of the focal stand that was moist forest or open-structured habitat.

*Model selection and data analysis.*—We chose to use an information-theoretic approach to assess whether stand-scale variables, landscape-scale variables, or a combination of stand- and landscape-scale variables would best explain variations in pellet densities, and to assess which, if any, landscape scale was most appropriate. Because the snowshoe hare literature reports a variety of stand-scale variables as being the best predictors of hare density in different study areas, and the best predictor variables for hare habitat had not been explored in our study area, we 1st used Spearman rank correlations ( $r_s$ ) between pellet densities and each of the stand-scale variables to screen variables for inclusion in the models (SPSS, Inc., Somers, New York). We developed a suite of a priori linear regression models that examined pellet densities in relation to stand-scale variables only, landscape-scale variables only (at each of three different scales: perimeter, 300 m buffer, and 600 m buffer), and combinations of stand- and landscape-scale variables (Table 2). To avoid spatial autocorrelation of landscape variables we considered only 1 landscape scale at a time, except in the global model. We populated the models with the best stand-scale variables and with the landscape-scale variables described above, and used the log-transformed mean number of pellets per stand as the dependent variable (Krebs et al. 2001; Mills et al. 2005). For each candidate model we calculated the residual sum of squares using SPSS and used residual sum of squares to calculate Akaike information criterion corrected for small sample size (AIC<sub>c</sub>) values and Akaike weights (Burnham and Anderson 2002).

**TABLE 1.**—Spearman rank correlations ( $r_s$ ) between densities of snowshoe hare (*Lepus americanus*) pellets and vegetation variables measured in 76 forest stands in northern Washington during 2003–2004. Variables measured for each focal stand included length of the stand perimeter (m), stand area (ha), edge-to-area ratio (m:ha), slope (%), aspect ( $^\circ$ ), canopy cover (%), understory cover (%), and density (trees/ha) of saplings (<10.2 cm diameter at breast height [DBH]), medium-sized trees (10.3–27.9 cm DBH), and large-sized trees (>27.9 cm DBH).

	Perimeter	Area	Edge : area	Slope	Aspect	Canopy cover	Understory cover	Saplings	Medium trees	Large trees
Pellets	-0.15	-0.03	-0.12	-0.01	-0.09	0.15	0.34*	0.55*	0.54*	-0.09
Perimeter		0.72*	0.23	0.01	0.16	0.11	0.01	-0.01	-0.03	0.04
Area			-0.37*	0.07	0.14	0.09	-0.07	0.06	0.00	0.10
Edge : area				-0.07	-0.02	-0.04	0.05	-0.04	-0.11	-0.04
Slope					-0.09	-0.04	-0.20	-0.20	-0.08	0.15
Aspect						0.07	-0.13	0.02	-0.10	0.07
Canopy cover							0.29	0.14	0.33*	0.46*
Understory cover								0.39*	0.28	-0.03
Saplings									0.54*	-0.06
Medium trees										0.08

\*  $P < 0.05$  (with Bonferroni correction—Rice 1989).

*Modeling forest management scenarios.*—To explore the potential magnitude of effects on hare densities of making changes to either stand or landscape features within hare habitat, we used the best-fitting model to run a simple projection. We projected changes in pellet densities for 2 hypothetical stands with 4,000 saplings/ha and 500 medium trees/ha (similar to stands surveyed in the study area), but located in 2 different landscapes: within a high-quality matrix in which moist forest stands comprised 80% of the habitat within a 300-m buffer, or within a matrix of poor quality in which only 20% was moist forest stands and 80% was dry forest stands. In both projections we defined 20% of the surrounding matrix as open-structured habitat.

We examined 1 scenario in which the surrounding landscape was converted to 80% open-structured habitat (e.g., via timber harvest or fire); for a 20-ha stand this change would mean harvesting timber on about 48 ha within the 300-m buffer with a seed tree or similar prescription that would decrease the canopy and understory to <10%. We also examined the effect of thinning within the stand from 4,000 to 1,000 saplings/ha while leaving medium trees at 500 trees/ha. These alterations reflect strategies used by forest managers in harvesting timber and in thinning for fuels reduction or precommercial purposes. This analysis was designed as a heuristic example that simply illustrated the kind of possible effect rather than making specific inferences about these sample cases.

## RESULTS

The mean pellet density across 76 surveyed stands was 1.93 pellets plot<sup>-1</sup> stand<sup>-1</sup> ( $SE = 0.19$  pellets plot<sup>-1</sup> stand<sup>-1</sup>), with a range of 0.04–6.28 pellets plot<sup>-1</sup> stand<sup>-1</sup>. Converting mean pellets to hare density (Krebs et al. 2001) resulted in a range of 0.03–2.38 hares/ha, with a mean of 0.82 hares/ha ( $SE = 0.07$  hares/ha) and a median of 0.67 hares/ha.

Of the suite of stand-scale variables considered, only 4 were highly correlated with pellet density (Table 1): vegetation type, understory cover, sapling density, and medium tree

density. Most variables were correlated with one another. To avoid overfitting by using autocorrelated variables we used only sapling and medium tree density as predictive stand-scale variables in the model, because they created understory cover, were more highly correlated with pellet density, and are the variables most directly targeted in forest management.

*Multiscale model evaluation.*—Models including only stand-scale variables better fit the data than models that included only landscape-scale variables. However, the model that best fit the data included stand- and landscape-scale (300-m) variables (Table 2), with an Akaike weight of 0.69 and >2.36 AIC<sub>c</sub> values separating it from the 2nd-best (global) model. The model showed positive relationships between pellet density and sapling and medium tree densities at the stand scale and moist forest at the 300-m scale and a negative correlation with open-structured habitat at 300 m:

$$\begin{aligned} \ln(\text{pellets}) = & -1.405 + 0.0003 (\text{saplings}) \\ & + 0.0007 (\text{medium trees}) \\ & + 0.0113 (\text{moist forest 300 m}) - 0.0021 \\ & (\text{open-structured habitat 300 m}). \end{aligned}$$

Projections based on field data indicated that matrix quality had a meaningful impact on hare densities. Patches of habitat with equal stand-scale attributes set within the moist forest matrix had approximately twice as many hares as did stands in the dry forest matrix—1.15 hares/ha versus 0.63 hares/ha, using the Krebs equation (Krebs et al. 2001) to convert pellet numbers to hare densities. In both types of landscape increasing the amount of open-structured habitat within 300 m of the focal stand decreased relative hare densities by approximately 11%. Reducing sapling density reduced hare density by approximately 55% in each landscape.

## DISCUSSION

Our study demonstrated that snowshoe hares are influenced by habitat at both stand and landscape scales. Pellet densities of snowshoe hares were explained best by stem density of

**TABLE 2.**—Models describing densities of snowshoe hare (*Lepus americanus*) pellets from 76 forest stands in northern Washington during 2003–2004. Values reported represent number of model parameters ( $K$ ), Akaike information criterion corrected for small sample size ( $AIC_c$ ) scores and differences ( $\Delta_i$ ), and Akaike weights ( $w_i$ ) for the 8 models. Stand-scale variables included the density of saplings (<10.2 cm diameter at breast height [DBH]) and medium trees (10.3–27.9 cm DBH) per hectare in the focal patch. Landscape variables were the amount of moist forest (dominated by Engelmann spruce and subalpine fir) and open-structured habitat (<10% understory and canopy cover) along the perimeter and within 300-m and 600-m buffers around the focal stand.

Model name	Model structure	$K$	$AIC_c$	$\Delta_i$	$w_i$	$R^2$
Stand + 300 m	Saplings + Medium Trees + Moist (300 m) + Open (300 m)	6	-5.25	0	0.69	0.40
Global	Saplings + Medium Trees + Moist (perim) + Moist (300 m) + Moist (600 m) + Open (perim) + Open (300 m) + Open (600 m)	10	-2.89	2.36	0.21	0.48
Stand	Saplings + Medium Trees	4	-0.76	4.49	0.07	0.32
Stand + 600 m	Saplings + Medium Trees + Moist (600 m) + Open (600 m)	6	1.14	6.39	0.03	0.35
Stand + Perimeter	Saplings + Medium Trees + Moist (perim) + Open (perim)	6	5.81	11.06	<0.01	0.32
300 m	Moist (300 m) + Open (300 m)	4	13.16	18.41	<0.01	0.19
600 m	Moist (600 m) + Open (600 m)	4	22.97	28.22	<0.01	0.09
Perimeter	Moist (perim) + Open (perim)	4	29.39	34.64	<0.01	0.01

trees within the stand and at the landscape scale within 300 m of the stand. Pellet densities were associated positively with the amount of moist forest and associated negatively with the amount of open-structured habitat within 300 m of a focal patch.

Our results suggest that landscapes in which hare habitat is more contiguous, or where good patches of hare habitat are surrounded by other patches of similar habitat quality, support more hares than landscapes that are more fragmented or include matrix habitats that are poorer quality. The importance of matrix quality for snowshoe hares is supported by Walker's (2005) observation of significantly higher averages and lower variation in pellet densities across stands in a nearby area where similarly dense forest was less fragmented—2.8 pellets/plot in the "Meadows" area described by Koehler et al. (2008) compared to the 1.9 pellets/plot described here.

Although our results demonstrated that matrix composition influenced pellet densities, the models reiterated the importance of vegetative density within forest patches, because all of the top models contained stand-scale variables. The model containing only stand-scale variables explained 32% of the variation in pellet densities; including variables at the 300-m landscape scale explained another 8% of the variation. Similarly, our projection scenarios showed that decreasing sapling density in a stand might decrease hare densities by >50%, a finding supported by experimental studies of forest thinning (Ausband and Baty 2004; Bull et al. 2005; Griffin and Mills 2007; Homyack et al. 2007). Although this level of effect emphasizes the importance of managing stand-scale characteristics, activities that increase the amount of open-structured habitat in the matrix can reduce hare densities by  $\geq 10\%$ .

Our conclusions are based on using pellet counts from uncleared plots as an index of snowshoe hare density. Although this index is adequate for evaluating coarse patterns in hare density or relative use of different habitats (Hodges and Mills 2008; Krebs et al. 2001; McCann et al. 2008; Mills et al. 2005; Murray et al. 2002), pellet counts are not as reliable as mark-recapture models for estimating hare density in the individual focal stands. Although this choice of index

could have reduced our overall model fit (our best-fit model explained only 40% of the variation and the global model 48%), we suspect that unexplained variance also arose from factors that we did not model explicitly, including stand and landscape factors such as availability of specific food plants and locations of predators.

The relative influence of landscape characteristics on hares might reflect the degree to which the matrix is used. Although the majority of a hare's activities take place at the stand-level scale (Ferron and Ouellet 1992; Griffin 2003; Hodges 1999; Walker 2005), dispersal and mate-seeking behaviors occur at larger scales (up to thousands of meters—Gillis and Krebs 1999) and necessitate that hares also use matrix habitats. Low-quality matrix habitat could decrease survival for hares, because predators might have higher hunting success or be more numerous in the matrix habitats (Griffin and Mills 2009). Conversely, a high-quality matrix could provide alternative or supplemental resources (Dunning et al. 1992; Norton et al. 2000), thus supporting higher densities of hares in the focal stand. Further exploration of hare densities in relation to larger landscape scales could add insight as to whether hare densities are further influenced by wide-ranging predators or rare long-distance dispersal of hares.

When managing for snowshoe hares, managers should consider the potential effects of changing the landscape matrix and also within-stand alterations. Specifically, good stands for hares in poor matrix landscapes could benefit from changes made in the matrix, whereas if the best stands in a landscape are only mediocre for hares, the best strategy might involve focusing 1st on improving stand-level attributes. Although our results showed that stand-level vegetative structure had roughly 5 times the influence that landscape-level vegetation did on hare density, we do not know how robust this result is across different landscapes. Because vegetation, soil, and weather conditions vary throughout the range of snowshoe hares, research is needed on the influences of landscape-scale characteristics on snowshoe hare numbers in different regions. Information on movements, diets, and behavior of hares in fragmented landscapes would help determine the mechanisms by which stand and landscape habitats affect hare densities.

## ACKNOWLEDGMENTS

Funding for this project came from the Washington Department of Fish and Wildlife through United States Fish and Wildlife Service State Wildlife Grants, Okanogan–Wenatchee National Forest, the University of Montana, and the National Science Foundation (DEB-9870654 to LSM). D. Naugle and K. Foresman improved earlier versions of this work. E. Crone provided statistical assistance. S. Blum helped with the geographic information system. K. Aubry helped initiate, design, and fund the research. B. Maletzke, J. Rohrer, and R. Naney provided logistical support and knowledge of the study area. We thank our field technicians: J. Barrett, B. Fritz, S. Harmon, C. Kim, D. Knowles, M. Moses, K. Nagel, and N. Stone.

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*Submitted 9 February 2010. Accepted 27 November 2010.*

*Associate Editor was Janet L. Rachlow.*