Hierarchical Den Selection of Canada Lynx in Western Montana

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ABSTRACT We studied den selection of Canada lynx (*Lynx canadensis*; hereafter lynx) at multiple ecological scales based on 57 dens from 19 females located in western Montana, USA, between 1999 and 2006. We considered 3 spatial scales in this analysis, including den site (11-m-radius circle surrounding dens), den area (100-m-radius circle), and den environ (1-km radius surrounding dens). Lynx denned in preexisting sheltered spaces created by downed logs (62%), root-wads from wind-thrown trees (19%), boulder fields (10%), slash piles (6%), and live trees (4%). Lynx preferentially selected den sites with northeasterly aspects that averaged 24°. Average distance between dens of 13 females monitored in consecutive years was 2,248 m, indicating low den site fidelity. Lynx exhibited habitat selection at all 3 spatial scales. Based on logistic regression, den sites differed from the surrounding den areas in having higher horizontal cover and log volume. Abundant woody debris from piled logs was the dominant habitat feature at den sites. Lynx generally denned in mature spruce–fir (*Picea–Abies*) forests with high horizontal cover and abundant coarse woody debris. Eighty percent of dens were in mature forest stands and 13% in mid-seral regenerating stands; young regenerating (5%) and thinned (either naturally sparse or mechanically thinned) stands with discontinuous canopies (2%) were seldom used. Female lynx selected den areas with greater spruce–fir tree basal area, higher horizontal cover, and larger-diameter trees compared to random locations within their home range. Lynx selected den environs in topographically concave or drainage-like areas, and farther from forest edges than random expectation. Maintaining mature and mid-seral regenerating spruce–fir forests with high horizontal cover and abundant woody debris would be most valuable for denning when located in drainages or in concave, drainage-like basins. Management actions that alter spruce–fir forests to a condition that is sparsely stocked (e.g., mechanically thinned) and with low canopy closure (<50%) would create forest conditions that are poorly suitable for lynx denning. (JOURNAL OF WILDLIFE MANAGEMENT 72(7):1497–1506; 2008)

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Habitat features associated with lynx dens may have important implications for population productivity, with den selection likely occurring at multiple spatial scales. Mowat et al. (2000) believed that lynx from northern populations selected den sites based on suitable den structures such as wind-felled trees, root-wads, or dense live vegetation, rather than on age or species composition of forest stands. The degree, however, that lynx from southern populations follow this pattern is poorly understood. Koehler (1990) described 4 dens from 2 females in Washington, USA, as being located in mature stands of Englemann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*), and Squires and Laurion (2000) described a natal and a maternal den from a single female in Wyoming, USA, that used similar forest types. Dens from both studies were located under downed logs in areas with high woody debris. Given the limited empirical data, Aubry et al. (2000) and Ruggiero (2000) stated that describing den habitat for southern populations is an important information need. This lack of information puts managers in an uncomfortable position of prescribing management for a threatened species under the Endangered Species Act with little empirical support (U.S. Fish and Wildlife Service 2000).

We studied den selection of lynx from 3 naturally occurring lynx populations in western Montana, USA. We predicted that resource selection of lynx is scale dependent and that dens may be selected in a hierarchical process that involves choosing among habitat features at multiple scales (Johnson 1980, Chamberlain et al. 2003, Apps et al. 2004). Our objective was to determine how habitat features affected den-site selection of female lynx at hierarchical scales. We were especially interested in evaluating the contention by Mowat et al. (2000) that lynx are unconstrained by specific stand types but rather choose habitat structure associated with the immediate den site.

STUDY AREA

We studied denning ecology of lynx at 3 study areas in western Montana (Fig. 1). The Seeley Lake study area was centered in the Clearwater River drainage, near the town of Seeley Lake, Montana, and extended east to west from the Swan Range to the Mission Mountains, and north to south from Lindbergh Lake to Salmon Lake. The Bob Marshall Wilderness complex and the Mission Mountain Wilderness Area flanked the east and west sides of the study area, respectively. The Garnet Range study area was south of

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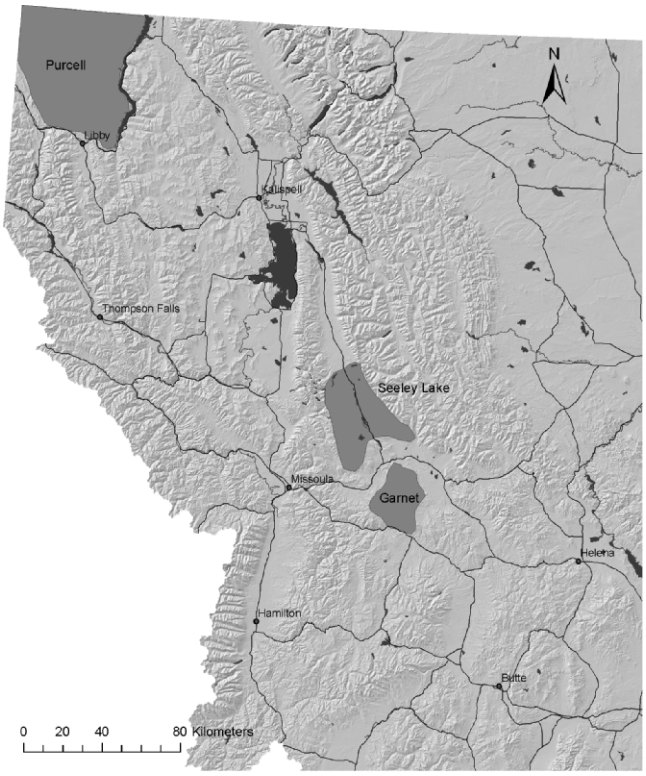

Figure 1. Location of Canada lynx study areas in western Montana, USA, 1999–2006.

Seeley Lake and east of Missoula, Montana. It was bounded to the north by the Blackfoot River and Highway 200 and to the south by the Clark Fork River and interstate highway I-90. The Purcell Mountains study area was in the northwest corner of Montana and was bounded to the north and east by Canada and Idaho, USA, and to the south and east by the Kootenai River and its reservoir, Lake Koocanusa.

Lands in Seeley Lake were primarily managed by the Lolo National Forest (48%) and Plum Creek Timber Company (37%), with smaller parcels of private, state, tribal, and Bureau of Land Management (BLM) holdings. Lands in the Garnet Range were a mix of state, BLM, and private ownership. The Purcell Mountains study area was almost entirely within the Kootenai National Forest. Forest management created an extensive road system and fragmented mosaic of forest species, ages, and densities across all study areas. The forest road (open and administratively closed) density averaged 3.2 km/km^2, 1.6 km/km^2, and 1.7 km/km^2 on the Seeley Lake, Garnet Range, and Purcell Mountains study areas, respectively.

Elevations on the Seeley Lake, Garnet Range, and Purcell Mountains study areas ranged from 1,200 m to 2,500 m, 1,200 m to 2,400 m, and 800 m to 2,300 m, respectively. Average low and high temperatures for all study areas were between –2° C and 11° C, and annual precipitation averaged roughly 0.6 m/year in the Garnet Range and 1.0 m/year at Seeley Lake and the Purcell Mountains (Daly et al. 2002). As evidenced by annual precipitation and forest species composition, the Garnet Range was generally the driest area and the Purcell Mountains the wettest.

Forests on the Garnet Range ranged from drier ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*) stands at lower elevations to lodgepole pine, western larch (*Larix occidentalis*), subalpine fir, and Engelmann spruce at high-elevation sites. At Seeley Lake and the Purcell Mountains, tree species were similar, with subalpine stands dominated by subalpine fir and Engelmann spruce and containing lesser components of lodgepole pine and western larch. The Purcell Mountains supported more western red cedar (*Thuja plicata*) and mountain hemlock (*Tsuga mertensiana*). Subalpine forests were multistoried and multiaged, often with a dense shrub understory. Shrub communities in this zone were predominantly alder (*Alnus* spp.), huckleberry (*Vaccinium* spp.), and false huckleberry (*Menziesia ferruginea*). Forested riparian areas were primarily subalpine fir, Engelmann spruce, Douglas-fir, and black cottonwood (*Populus trichocarpa*).

METHODS

Trapping and Handling

We trapped lynx from December to April, 1998–2006, in activity areas identified using snow tracks. We initially captured lynx using Victor number 3 Softcatch™ traps (Oneida Victor Inc. Ltd., Euclid, OH) and Belisle® foot snares (Belisle, Labelle, PQ, Canada). We set foothold traps in temporary cubbies constructed of small-diameter pine boughs and brush that were easily knocked down without causing injury to the captured animal or in permanent cubbies that were sufficiently large to prevent trapped animals from striking or becoming entangled on the sides of the set. However, since 2000, we captured all lynx in box traps according to Kolbe et al. (2003). We baited all traps with beaver (*Castor canadensis*) carcasses and road-killed deer (*Odocoileus* spp.) scented with beaver-castor lure.

We chemically immobilized lynx with a syringe pole to administer a mixture of ketamine (8 mL/kg Ketaved® [Phoenix Scientific, Inc., St. Joseph, MO]; concentration 100 mg/mL) and xylazine (3 mL/kg; concentration 100 mg/mL). This capture dose produced predictable vital rates and immobilization periods. We fitted lynx with telemetry collars that weighed between 165 g and 200 g (Sirtrack Ltd™, Havelock North, New Zealand). After processing, we placed lynx in a hard-sided crate covered with a sleeping bag for insulation, and after approximately 75 minutes, we antagonized the xylazine with yohimbine (0.7–1 cm^3 Yobine® [Ben Venue Laboratories, Bedford, OH]; concentration 2 mg/mL). We kept captured lynx in the crate until they were fully recovered from drug effects (3–3.5 hr) before release.

Quantifying Habitat Characteristics at Dens

We located breeding-age (≥2-yr-old) females daily from 1 May to 15 June. We considered lynx located in the same place for 3 consecutive days during this period to have localized at a den site. We continued to remotely monitor females for the next 14 days, after which we visited dens to record their precise locations and determine litter size. We

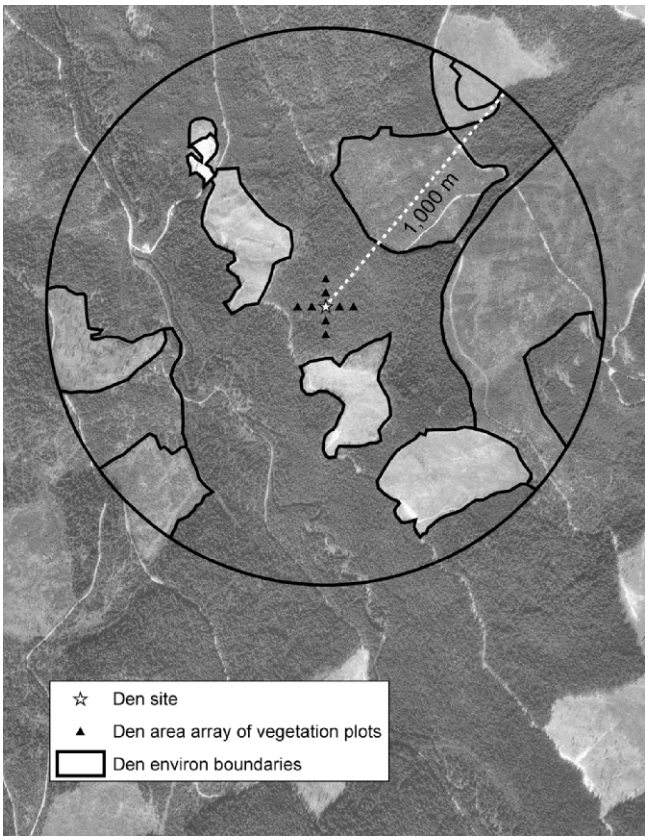

Figure 2. Sampling Canada lynx den selection at 3 hierarchical scales—den site, den area, and den environ—using a combination of field-based vegetation plots and Geographic Information System landscape analysis, western Montana, USA, 1999–2006.

limited time spent at the den to several minutes, and no lynx abandoned litters following our den visit or kitten handling.

Lynx often moved kittens to a nearby maternal den site within the 2 weeks following initial localization. We determined the site to be a natal den when evidence of sustained lynx use was found at the localization site (e.g., matted lynx hair in a cleared depression) and kitten ages confirmed that parturition was coincident with the initial localization. We returned to both maternal and natal den sites in August to quantify vegetation and stand characteristics after the family group had left the area.

To treat den selection as a hierarchical process (Johnson 1980), we assessed den selection at 3 spatial scales: 1) den sites (11.2-m-radius circle), 2) den areas (100-m-radius circle), and 3) den environs (1-km-radius circle) within female home ranges. We evaluated the microhabitat selection of den sites by comparing habitat characteristics at dens (use) to an array of 8 plots located within 100 m (availability; Fig. 2). For den areas selection, we compared the array of 8 vegetation plots surrounding dens (use) to a random plot placed within the respective female's home range (availability); we weighted use points so the sample size equaled the random data set. In cases where dens were adjacent to stand edges, these arrays included multiple stands within 100 m of the den. We then evaluated the habitat and topographic features of the den environ (1-km-radius circle) surrounding dens (use) to similar buffers randomly located within each female's home range (availability; Fig. 2).

We sampled a single plot (11.2-m radius) centered on the den to describe the immediate area surrounding dens. We described den areas (100-m-radius circle) using an array of 8 plots located 50 m and 100 m in each of the 4 cardinal directions (Fig. 2). We also compared the den areas to a random point within the respective female's home range. On all plots (11.2-m radius), we recorded species and size (dbh) of trees ($\geq$7.6 cm), slope, aspect, and distance to water; we also estimated tree basal area using a 20-factor variable plot. We counted all conifer saplings $<$7.6 cm diameter at breast height and $\geq$0.5 m in height and all deciduous stems $\geq$1 cm diameter at breast height within a concentric 5.6-m-radius plot. We counted number of snowshoe hare (*Lepus americanus*) pellets within a 56-cm-radius circle established 5 m from plot center in a random direction as a non-calibrated index of hare abundance.

We generated a random azimuth and established a 22.4-m transect bisecting the plot center. Along this transect we measured and classified downed woody debris $\geq$7.6 cm in diameter and the amount of shrub cover by species that was $\geq$0.5 m but $<$2 m in height. We used a 0.5 $\times$ 2-m cover board (divided into 4 0.5-m^2 square blocks; Nudds 1977) to provide an ocular estimate of horizontal cover (visual obscurity). We took 4 horizontal cover readings at each plot: we took 2 board readings at the ends of the transect and 2 others at 11.2 m from plot center perpendicular to the transect. Finally, we used a vertical sighting tube (e.g., moosehorn densitometer) held at head height to assess presence–absence of canopy cover on a 11.2 $\times$ 11.2-m grid of 25 evenly spaced points centered on the plot. We then inverted the sight tube and used it to assess the presence–absence of grasses, forbs, shrubs, and conifer seedlings.

From these vegetation sampling data, we estimated a suite of habitat parameters for each vegetation plot: elevation (m), slope (%), aspect (transformed into a linear variable between southwest [215°] and northeast [35°]; Cushman and Wallin 2002), horizontal cover (%), log volume (m^3), hare pellets, canopy closure (%), shrub cover (%), seedling cover (%), grass cover (%), forb cover (%), sapling ($<$7.6 cm dbh) stem density, saplings (%) by species (including a combined spruce–fir category for Englemann spruce and subalpine fir), tree ($\geq$7.6 cm dbh) stem density, average tree size (cm dbh), trees (%) by size classes (dbh; 7.6–18 cm, 18–28 cm, 28–51 cm, and $>$51 cm), trees (%) by species (including a combined spruce–fir category for Englemann spruce and subalpine fir), total shrub cover (%), and shrubs (%) by species.

We compared habitat features within den environs (a 1-km-radius buffer surrounding each den site) to an equal-sized area located randomly within each female's home range. Within each 1,000-m circular buffer, we quantified variables relating to topography and forest composition and configuration using ArcGIS Desktop 9.0, ArcView 3.2a, and several spatial analysis extensions. To assess landscape

topography, we estimated elevation and topographic position of center points and roughness of the circular landscape using 30 × 30-m digital elevation models (DEMs; U.S. Geological Survey 2000). We defined surface roughness as the DEM-based ratio of 3-dimensional surface area to 2-dimensional surface area (Jenness 2004) and established landscape roughness with the Surface Areas and Ratios feature of the Elevation Grid v. 1.2 extension for ArcView 3.x. Topographic position refers to curvature of mountain slopes and the continuum between concavity (drainages) and convexity (ridges). The topographic position index (TPI) quantifies this continuum with negative values indicating concavity and positive values indicating convexity. We used the TPI extension (v. 1.3a; Jenness 2006) for ArcView 3.x to estimate TPI at scales of 500 m and 1,000 m. The 500-m distance tended to best delineate the scale of drainages in our study areas, whereas the 1,000-m scale matched the 1,000-m buffer size of our environ of interest. We also quantified the distance (m) of all dens and random center points from the nearest mapped stream or lake based on Census 2000 Topologically Integrated Geographic Encoding and Referencing system (TIGER) data (U.S. Bureau of the Census 2000).

Existing vegetation maps based on remote sensing did not have suitable spatial or classification accuracy to depict the forest composition surrounding dens. Thus, we developed a new map delineating forest stand types and boundaries using a combination of high-resolution aerial photos, 1-m digital orthophotos (United States Department of Agriculture, Farm Service Agency, Aerial Photography Field Office, National Agriculture Imagery Program, Salt Lake, UT) and United States Forest Service (USFS) Timber Stand Management Recording System paired with existing USFS digitized stand polygon layers. We classified stands into 5 simplified categories: 1) open—trees not present or at >50-m spacing, with ground cover primarily grass and shrub <0.5 m in height; 2) thin forest (naturally sparsely stocked or mechanically thinned)—forested stand with trees at <50-m spacing but having discontinuous canopy and visible forest floor; 3) young regenerating forest—regenerating trees generally <10 cm diameter at breast height, with continuous canopy or a dense deciduous shrub understory; 4) mid-seral regenerating forest—regenerating trees generally >10 cm diameter at breast height, with continuous canopy or a dense deciduous shrub understory with signs of management; and 5) mature forest—mature forest stand with large trees, continuous canopy, and no evidence of recent management activity. After digitizing and classifying all stands within den and random landscapes, we visited 187 random test locations (stand polygons) to visually assess classification accuracy. We stratified these test locations by study area and vegetation type and recorded field-based classifications of each location as ground-truth data with which to estimate the stand-class accuracy of our digitized vegetation maps. We classified 174 of 187 stands correctly, providing an overall estimated map accuracy of 93%.

We also used our digitized stand maps to estimate a suite of parameters describing habitat composition and configuration surrounding den and random locations. From each location, we measured distance (m) to the nearest edge, and area (m^2) of the patch surrounding dens within the 1,000-m buffer. For all den environs, we used Fragstats 3.3 (McGarigal et al. 2002) to quantify the area of each vegetation type (open [%], thin forest [%], young regenerating forest [%], mid-seral regenerating forest [%], and mature forest [%]), edge density (m/ha), mean patch area (ha), and the patch richness of the 1,000-m buffer.

Modeling Den Resource Selection

We first used descriptive statistics to describe habitat features used by lynx for denning, including circular statistics (Rayleigh's test) to quantify directionality of den sites (Batschelet 1981). We then used multiple logistic regression and the 3 scales of use–availability data to analyze selection at the scale of the den site, den area, and den environ. We began all analyses in GENMOD (SAS Institute, Cary, NC) to account for potential correlation associated with treating multiple records of an individual as independent. We also used GENMOD for the multivariate analyses of the den environ scale. However, we used PROC LOGISTIC (SAS Institute) to conduct den site and den area selection analyses because of the low correlation among observations within lynx and because the weighting function in this module allowed for balanced sample sizes between use and availability (Fielding and Bell 1997). Using logistic regression with use–availability data presents some problems; predicted values are not scaled between zero and one and may yield invalid resource-selection probabilities (Manly et al. 2002, Keating and Cherry 2004). However, logistic regression can provide a useful and unbiased method of assessing resource selection with use–availability data for ranking habitats rather than to generate specific probabilities (Keating and Cherry 2004, Johnson et al. 2006).

For each analysis, we used univariate logistic regression and the likelihood ratio chi-square test to screen variables for univariate significance before entering them in multivariate modeling (Hosmer and Lemeshow 2000). We considered all potentially important variables ($P < 0.25$) when building a multivariate model (Hosmer and Lemeshow 2000). We eliminated those variables that did not contribute to the multivariate model based on an examination of Wald statistics (z) for each variable, variation of parameter coefficients between univariate and multivariable models, and collinearity among variables as evident in inflated standard errors (Hosmer and Lemeshow 2000).

We used the area under the receiver operating characteristic (ROC) curve of models across spatial scales as an indicator of the ecological scale to which lynx most responded when selecting dens. Integrating area under the ROC curve provides an assessment of model performance and predictive power (Cumming 2000, Hosmer and Lemeshow 2000). We recognize that ROC scores for our data may be conservative because within the use–availability sampling framework, the dichotomous categories are not

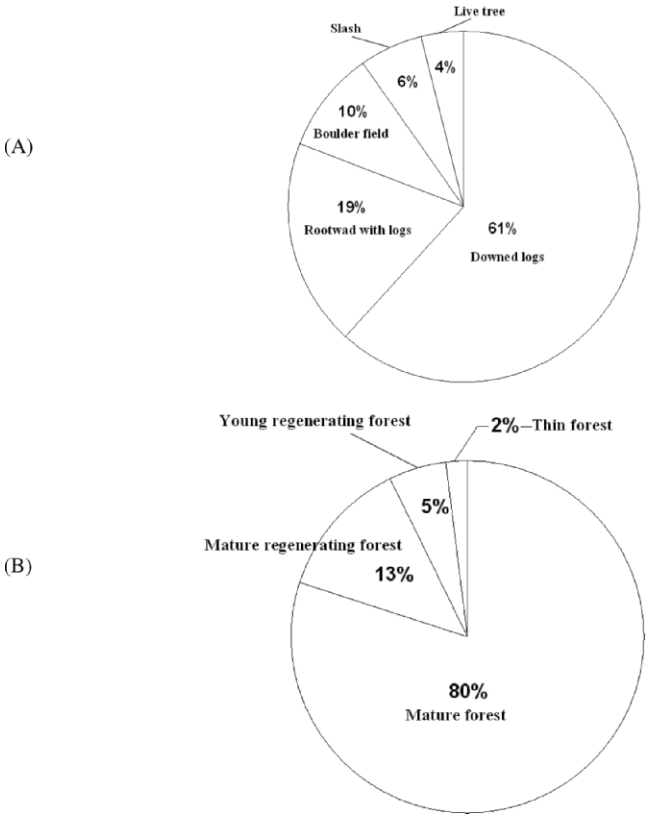

Figure 3. Canada lynx used a variety of (A) structures and (B) stand types for locating den sites, most often placing them under downed logs within mature forest stands, western Montana, USA, 1999–2006.

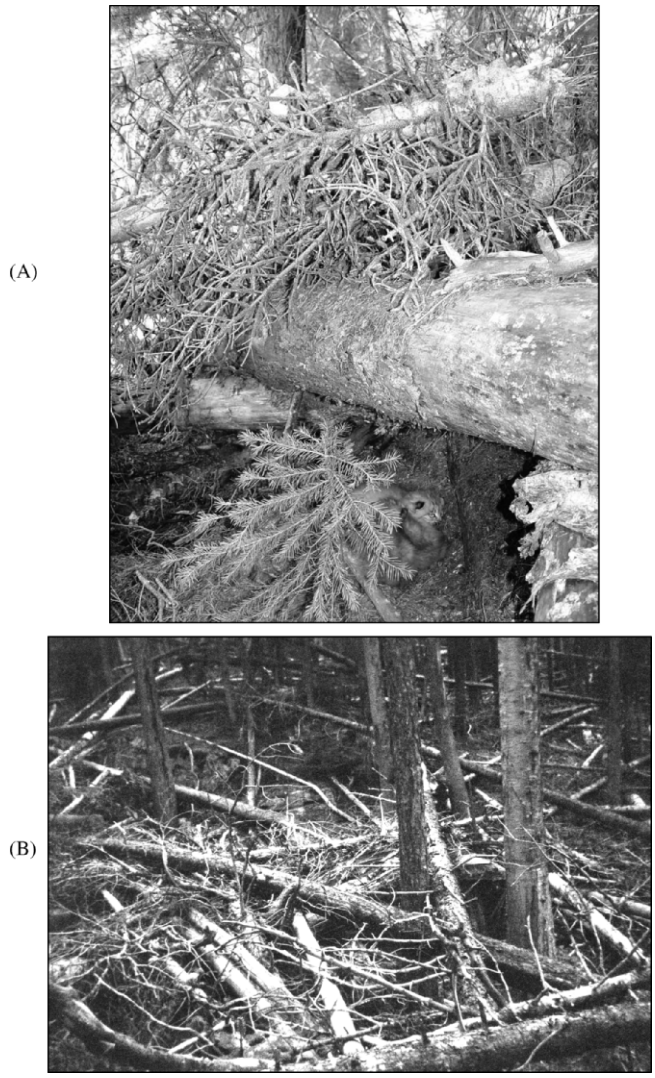

Figure 4. Canada lynx denned under (A) single large logs, as well as (B) crisscrossed piles of smaller logs, western Montana, USA, 1999–2006.

unique as is typical with logistic regression (Boyce et al. 2002, Keating and Cherry 2004). We used ROC scores as a relative ranking of the strength of the 3 logistic models that described the spatial scales (den site, den area, den environ) under consideration. We calculated ROC for each model with SAS PROC LOGISTIC. We assumed that stronger, more predictive models relate better to the ecological scale that is actually perceived by lynx when making habitat-use decisions compared to lesser models given our input variables and the limitations of observational data.

We analyzed the proximity of dens to roads relative to paired random locations. We used a combination of Census 2000 TIGER–line data, USFS road data, and Plum Creek Timber Company road inventories to create a spatial layer of all roads on the study areas. We then measured the distance from den sites and random locations to all roads, as well as to only those roads open to traffic during the denning season. We used logistic regression (PROC LOGISTIC) to make these 2 comparisons.

Lynx give birth and initially raise kittens in a natal den. Soon after birth, females often move to one or a series of maternal dens until kittens are 6–8 weeks old and become mobile (Slough 1999, Squires and Laurion 2000). Few studies have empirically compared natal and maternal den features, although Slough (1999) noted no difference between these den classes. We used weighted univariate logistic regression in PROC LOGISTIC to compare natal and maternal dens relative to a suite of field-measured habitat features. In addition, we used generalized likelihood ratio tests to compare individual natal and maternal models to a single pooled model for all scales of resource selection modeling (Mood et al. 1974). A significant result from this test would suggest that separate natal and maternal models were warranted, whereas a nonsignificant result would justify pooling.

RESULTS

We located 57 dens from 19 female lynx across all study areas from 1999 to 2006. Of these dens, we located den cavities or sites at 52 dens and sampled fine-scale habitat structure at 51 dens; we sampled den stand and den environ-level features at 55 dens. Lynx denned in preexisting, usually sheltered spaces created by downed logs ($n = 32$ of 52 dens), root-wads from wind-thrown trees ($n = 10$), boulder fields ($n = 5$), slash piles ($n = 3$), and live trees ($n = 2$; Fig. 3A). Lynx denned under single large logs (>50 cm dbh), as well as piled logs of smaller (15–25 cm) diameter (Fig. 4). There

Table 1. Best multivariable logistic regression models of hierarchical selection of den sites, den areas, and den environs[a] by Canada lynx in western Montana, USA, 1999–2006.

Scale of selection	Variable	β	z	P
Den site[b]	Horizontal cover (%)	0.056	11.04	0.001
	Downed-log vol (m^3)	0.165	8.32	0.004
Den area[c]	Horizontal cover (%)	0.025	4.31	0.038
	Spruce–fir basal area (m^2/400 m^2)	1.189	3.71	0.054
	Average tree dbh (cm)	0.363	2.56	0.110
Den environ[d]	Topographic position index (500-m scale)	−0.004	−3.97	<0.001
	Distance to edge (m)	0.001	2.28	0.023

[a] $n = 51$ for den sites, and $n = 55$ for den area and environs.
[b] Global likelihood ratio test ($\chi^2 = 30.44$, df = 2, $P \leq 0.001$).
[c] Global likelihood ratio test ($\chi^2 = 15.74$, df = 3, $P = 0.001$).
[d] Global Wald ($\chi^2 = 11.10$, df = 2, $P = 0.004$).

were an average of 10.8 logs (>7.6 cm dbh) per transect at den plots, having an average diameter at breast height of 23.4 (SD = 8.6) cm. Spaces holding kittens within den structures were typically lined with forest litter and needles and averaged 80 (SD = 41) cm width × 71 (SD = 57) cm depth × 45 (SD = 16) cm height. Lynx preferentially selected den sites with northeasterly aspects, averaging 24° (Rayleigh's test, $r = 0.26$, $P = 0.04$). Atypical den sites included cases where females placed kittens next to a standing tree or in areas of dense, small-diameter stems (<7.6 cm dbh), such as in small (approx. 0.2-ha) pockets of alder or Pacific yew (*Taxus brevifolia*). We also documented 5 instances in which 3 females established dens under protected ledges found in boulder fields (individual boulders >1 m diam).

We commonly observed denning behavior of lynx for consecutive years ($\bar{x} = 3.0$ yr/lynx), including 2 females that denned on the study area for 6 and 7 consecutive years, respectively. Average distance between dens of the 13 of 19 females monitored for consecutive years was 2,248 m; distances ranged from one instance where a female reused the same den site for 2 consecutive years to a female whose 1999 and 2000 dens were 7,324 m apart.

We quantified vegetation characteristics at 40 natal and 11 maternal dens during 1999–2006. In 10 instances, we were able to locate natal and maternal dens for a single female in the same year. Natal and maternal dens were generally close together (median = 107 m), although one female moved her kittens 2,681 m to a maternal den. We did not detect differences between natal and maternal dens at the den site ($\chi^2_3 = 1.03$, $P = 0.794$), den area ($\chi^2_4 = 3.646$, $P = 0.456$), or den environ ($\chi^2_3 = 0.09$, $P = 0.993$) scales. Thus, all results are based on pooled data sets treating natal and maternal dens the same.

Resource Selection Analysis

Lynx selected den sites with higher horizontal cover and log volumes compared to the forests immediately surrounding dens (Table 1). Univariate results also indicated selection against grass cover and tree stem density (Table 2), which may have been a function of den structures like log piles or boulders dominating ground cover in the immediate den area.

Lynx established their dens in spruce–fir forests (average elevation 1,664 m, SD = 136 m) with high horizontal cover and abundant coarse woody debris. Dens ($n = 55$) were primarily within mature forest stands (80%) and mid-seral regenerating forests (13%), with less use of young regenerating stands (5%) and thinned stands (2%; Fig. 3B). Spruce and subalpine fir were the dominant (58%) combined tree species at den areas, but lodgepole pine (13%), snags (13%), Douglas-fir (8%), and western larch (7%) also were present. Tree density (≥7.6 cm dbh) in den areas was 653 (SD = 396) stems/ha; trees averaged 22.6 (SD = 7.1) cm diameter at breast height. Canopy coverage of the forests containing dens averaged 52% (95% CI = 50–54%). Den areas contained an average of 6.1 (SD = 4.9) logs and 3.0 (SD = 7.4) m^3 of coarse woody debris encountered per transect. Lynx avoided denning in high alpine areas above timberline and low-elevation dry forests that support park-like stands of ponderosa pine, lodgepole pine, and larch.

Compared to random locations within lynx home ranges, lynx denned in areas with a greater basal area of spruce–fir trees, higher horizontal cover, and larger tree diameters (Table 1). Univariate results also revealed higher volumes of downed logs, snag basal area, canopy closure, and shrub cover in stands where dens occurred (Table 2).

Lynx selected den environs based on topographic position index (500-m scale) and distance to edge (Table 1). Lynx located their dens in generally concave or drainage-like topographies (Fig. 5) and farther from forest edges than randomly expected. As evidenced by univariate logistic regression results, lynx also selected environs for dens that contained larger forest patches containing higher proportions of mature forest and less open habitat compared to availability within home ranges, but these relationships did not strengthen the multivariate models (Table 2).

The ROC scores for the den area and den environ spatial scales had similar model strengths of 0.72 and 0.69, respectively. The ROC score for den sites was 0.82, indicating a stronger relationship compared with the other 2 spatial scales given our input variables.

Lynx denned farther from all forest roads ($\mu_{den} = 338$ m, $SD_{den} = 440$ m) compared to random locations within home ranges ($\mu_{random} = 165$ m, $SD_{random} = 211$ m, $P = 0.024$). Lynx, however, did not den further from the subset of forest

Table 2. Mean, standard deviation, and univariable logistic regression results for important ($P < 0.25$) variables that describe Canada lynx den selection at 3 hierarchical scales, western Montana, USA, 1999–2006. We considered only these variables in multivariate modeling procedures for each scale.

Variable	Use		Availability				
	$\bar{x}$	SD	$\bar{x}$	SD	β	z	P
Selection of den sites[a]							
Horizontal cover (%)	86.593	11.404	73.077	18.905	0.059	13.53	<0.001
Downed-log vol (m^3)	7.864	7.758	2.965	7.363	0.175	10.71	0.001
% grass cover	0.141	0.158	0.228	0.219	−2.452	−4.68	0.031
Shrub species: % huckleberry	0.126	0.194	0.248	0.304	−1.981	−4.54	0.033
Lodgepole pine basal area (m^2/400 m^2)	0.049	0.111	0.137	0.246	−2.922	−4.29	0.038
Tree species: % lodgepole pine	0.052	0.102	0.133	0.226	−3.092	−4.27	0.039
Tree stem density (stems/m^2)	0.053	0.023	0.065	0.040	−12.000	−3.13	0.077
Selection of den areas[a]							
Spruce–fir basal area (m^2/400 m^2)	0.589	0.513	0.282	0.329	1.813	9.73	0.002
Total tree basal area (m^2/400 m^2)	1.258	0.778	0.764	0.665	0.987	9.25	0.002
Horizontal cover (%)	73.077	18.905	61.224	22.761	0.027	6.90	0.009
Sapling species: % spruce–fir	0.640	0.344	0.463	0.362	1.393	5.50	0.019
Downed-log vol (m^3)	2.965	7.363	1.259	2.248	0.226	5.40	0.020
Canopy closure (%)	0.519	0.192	0.407	0.261	2.128	5.28	0.022
Snags basal area (m^2/400 m^2)	0.220	0.300	0.095	0.199	2.317	5.04	0.025
Shrub cover (%)	0.495	0.237	0.393	0.211	2.017	4.66	0.031
Tree diam (SD; cm)	4.459	2.146	3.470	2.034	0.604	4.56	0.033
Tree size class: % 28–51 cm	0.220	0.174	0.137	0.182	2.701	4.52	0.034
Shrub species: % fools' huckleberry	0.287	0.302	0.157	0.285	1.513	4.17	0.041
Trees: average dbh (cm)	8.888	2.794	7.679	2.902	0.390	3.82	0.051
Tree species: % spruce–fir	0.579	0.300	0.452	0.345	1.218	3.40	0.065
Tree size class: % 8–18 cm	0.470	0.249	0.556	0.272	−1.281	−2.43	0.119
Sapling species: % Douglas-fir	0.064	0.197	0.141	0.263	−1.518	−2.42	0.119
Shrubs: total length (m)	8.238	7.060	6.215	5.664	0.050	2.34	0.126
Slope (%)	34.431	16.525	29.286	19.501	0.016	1.93	0.164
Trees: % lodgepole pine	0.133	0.226	0.211	0.332	−1.003	−1.70	0.192
Saplings: % alder	0.162	0.275	0.098	0.208	1.104	1.61	0.204
Saplings: % lodgepole pine	0.041	0.142	0.085	0.207	−1.517	−1.41	0.235
Selection of den environs							
Topographic position index (500 m)	−13.49	30.87	3.02	27.37	−0.004	−3.8	<0.001
Topographic position index (1,000 m)	−21.88	57.67	6.53	51.16	−0.002	−2.7	0.007
Open habitats (%)	3.58	4.00	5.39	6.32	−0.010	−2.2	0.029
Den patch area (m^2)	1,599,442	897,015	1,187,969	828,679	0.000[b]	2.1	0.040
Distance to edge (m)	127.87	123.51	100.96	99.40	0.000[b]	2.0	0.048
Mature forests (%)	57.42	23.73	46.14	22.75	0.002	1.73	0.084
Surface topographic roughness	1.05	0.03	1.04	0.02	1.591	1.6	0.114
Mid-seral regenerating forests (%)	9.20	11.17	13.93	16.63	−0.003	−1.6	0.117
Distance to water (m)	360.97	291.37	432.05	274.85	−0.000[b]	−1.3	0.179
Edge density (m/ha)	52.78	17.64	57.37	14.91	−0.004	−1.2	0.221

[a] $n = 51$ for den sites, and $n = 55$ for den stands and environs.
[b] We present coeff. (β) <0.001 due to scaling of parameter units as 0.000 or −0.000 depending on direction of the effect.

roads that were open to vehicular traffic during denning season ($\mu_{den} = 705$ m, $\mu_{random} = 836$ m, $P = 0.346$). Thus, any disturbance from vehicular traffic on forest roads during den season apparently did not affect den site selection by lynx.

DISCUSSION

Our results support the conclusion of Mowat et al. (2000) that lynx select dens primarily based on habitat structure immediately surrounding den sites. Consistent with northern populations, lynx in western Montana preferentially denned in structures composed of woody debris from downed trees, and natal and maternal dens were similar (Slough 1999, Mowat et al. 2000). Den sites were usually sheltered by 1–2 large-diameter mature downed trees (>50 cm dbh) or by small-diameter piled logs (15–25 cm dbh) in areas with high horizontal cover. We assume dense horizontal and vertical cover found at den sites protects kittens from avian and mammalian predation and from inclement weather (Koehler 1990). The proclivity of lynx to den in coarse woody debris was also consistent with the few dens described for other southern populations, including 2 females from Washington and 1 female in Wyoming (Koehler 1990, Squires and Laurion 2000). It was interesting that 2 females found in the Garnet Range established dens under protected ledges in rock talus in 3 of 4 instances; in the fourth case the female also denned in rock talus, but in woody debris on top of a boulder. We do not know if these individuals were related or shared similar dens in talus as a parent or offspring.

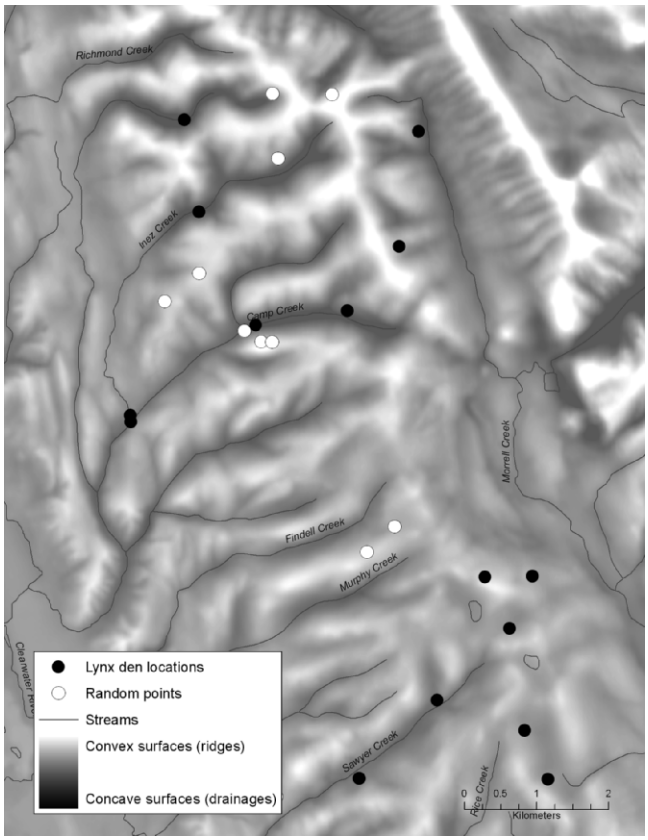

Figure 5. Canada lynx selected dens in generally more concave, or drainage-like, topography when compared to random within–home-range locations, western Montana, USA, 1999–2006.

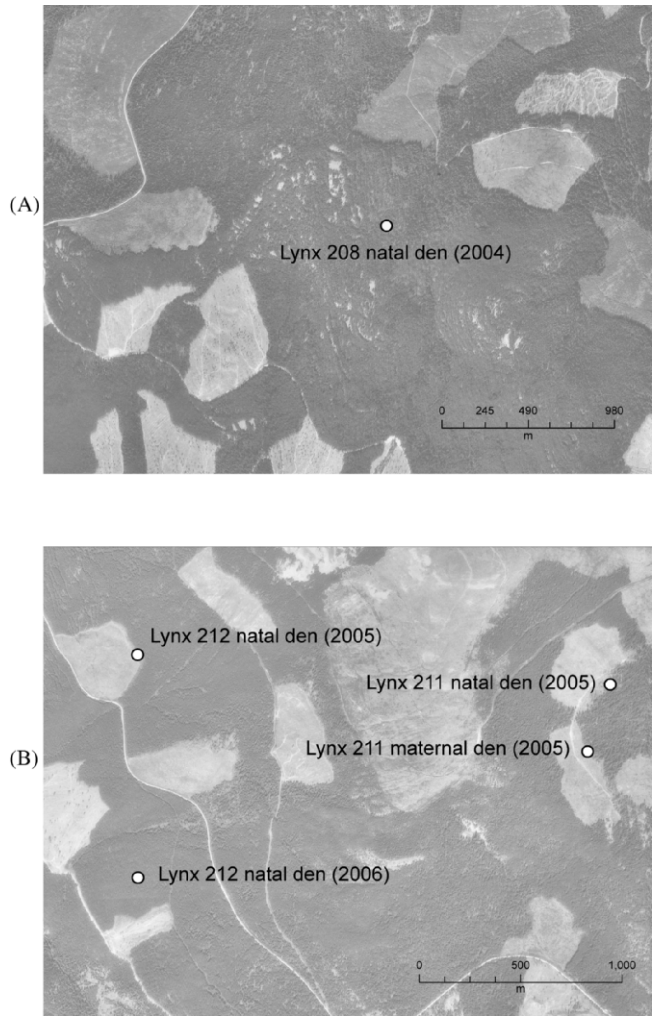

Figure 6. Although Canada lynx (A) overall denned farther from forest edges than random expectation, (B) some females showed a notable preference for blowdown log piles that are often along forest edges, western Montana, USA, 1998–2006.

Our results indicate that lynx also selected habitat characteristics at spatial scales beyond the immediate den site. For example, lynx denned in mature or mid-seral regenerating forest 93% (80% mature, 13% mid-seral regenerating stands) of the time. These mature and mid-seral regenerating forests were often multistoried and were composed of large-diameter trees with more continuous canopies compared to the other classes. Few (5% of dens in young regenerating clearcuts, 2% thin stands) dens were found in young (<30-yr-old) regenerating stands or in thin stands with discontinuous canopy. Females that denned in young stands used sites in piled woody debris from wind-thrown trees along the edges of the regenerating harvest units. The large-diameter, mature trees that dominated den areas were mostly spruce–fir that provided high horizontal cover; horizontal cover in these stands was also provided by dense shrub cover. This selection for mature forest types differs markedly from northern populations (Mowat et al. 2000). For example, in Yukon, Canada, only 3 of 39 dens were in mature forests, one was in riparian willow (*Salix* spp.), and 35 were located in a 40-year-old regenerating burn having abundant woody debris following a fire (Slough 1999). Our results were consistent, however, with 4 dens located in mature stands in Washington (Koehler 1990).

At a broader spatial scale, lynx preferentially selected den sites in concave or drainage-like topography and farther from forest edges than random expectation (Figs. 5, 6). Possibly, lynx denned in drainages to be closer to water, but we think this is unlikely given the abundance of water throughout the study area during early summer snowmelt. Lynx behavior regarding forest edges was highly variable. Some females repeatedly placed their dens along forest edges (Fig. 6B), possibly due to the abundance of wind-thrown, piled logs next to mature stands. Although we also found limited evidence that lynx denned in larger forest patches than were generally available within their home ranges, this landscape-level relationship was weak relative to the final multivariate model of den environs.

Our data suggest that lynx select den sites through a hierarchical process that includes ≥3 spatial scales (den site, den area, den environ). The ROC curve statistics of multivariate models indicate that selection was evident at all 3 scales, with selection strongest for habitat features (e.g., woody debris) at the den site. However, lynx selecting dens in mature forests also may be important in providing protection from predators and in meeting thermoregulatory needs. The Purcell and Seeley Lake study areas provided a

mosaic of young and regenerating stands that contained many residual slash piles and much residual woody debris. Yet, females rarely selected these habitats, suggesting that factors in addition to woody debris are necessary to explain lynx use of mature forests. We assume the observed selection patterns for lynx was reflective of habitat quality and affected demographic fitness, but we were unable to relate kitten survival or recruitment to habitat quality (Van Horne 1983); this would be a valuable topic for future research.

We doubt that females were constrained by a lack of suitable den sites, even in intensively managed landscapes. Females from southern populations have large home ranges that include many potential den sites, given the abundance of coarse, woody debris in mature and regenerating forests (Koehler 1990, Koehler and Aubry 1994, Aubry et al. 2000). Lynx den sites averaged >2 km from their previous years' location, and we observed only one female using the same den site in a subsequent year. Low den site fidelity may suggest that many suitable sites are present throughout female home ranges. We acknowledge, however, that lynx may select dens based on habitat features that we did not sample (e.g., odor, predation risk, prey abundance, or thermoregulatory considerations).

Lynx denned farther from all roads compared to random expectation, but we do not think this was due to active avoidance of human disturbance. Lynx first occupied dens in early May when most forest roads were impassible to wheeled traffic due to lingering snow drifts and muddy conditions; snowmobile use of the road system mostly ends by early denning. In addition, lynx did not avoid the subset of roads open to vehicular traffic. Thus, the observed avoidance of roads that we documented was likely a function of how roads correlated to landscape pattern (e.g., fewer roads in mature forests where lynx mostly denned, higher road density along forest edges and managed stands that lynx avoided) rather than a response to human disturbance.

MANAGEMENT IMPLICATIONS

Forest management in mature or mid-seral regenerating spruce–fir forests with high horizontal cover and abundant woody debris has the greatest potential impact on lynx den habitat, especially when conducted in concave or drainage-like basins. Lynx avoided forests with thin canopy coverage (<50% canopy closure), either naturally sparsely stocked or mechanically thinned. Management actions that maintain coarse woody debris in areas occupied by lynx, such as leaving large-diameter logs in piled configurations or by retaining patches of dense burned forests that will wind-throw over time, may provide future den sites as managed or burned stands regenerate. Although we believe that few lynx populations are limited by a lack of immediate den sites given their large home ranges and low den site fidelity, we showed that forest area and environ-level habitat features are also important in defining lynx denning habitat.

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LITERATURE CITED

Apps, C. D., B. N. McLellan, J. G. Woods, and M. F. Proctor. 2004. Estimating grizzly bear distribution and abundance relative to habitat and human influence. Journal of Wildlife Management 68:138–152.

Aubry, K. B., L. F. Ruggiero, J. R. Squires, K. S. McKelvey, G. M. Koehler, S. W. Buskirk, and C. J. Krebs. 2000. Conservation of lynx in the United States: a systematic approach to closing critical knowledge gaps. Pages 455–470 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

Batschelet, E. 1981. Circular statistics in biology. Academic Press, London, United Kingdom.

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

Chamberlain, M. J., L. M. Conner, B. D. Leopold, and K. M. Hodges. 2003. Space use and multi-scale habitat selection of adult raccoons in central Mississippi. Journal of Wildlife Management 67:334–340.

Cumming, G. S. 2000. Using between-model comparisons to fine-tune linear models of species ranges. Journal of Biogeography 27:441–455.

Cushman, S. A., and D. O. Wallin. 2002. Separating the effects of environmental, spatial and disturbance factors on forest community structure in the Russian Far East. Forest Ecology and Management 168: 201–215.

Daly, C., W. P. Gibson, G. H. Taylor, G. L. Johnson, and P. Pasteris. 2002. A knowledge-based approach to the statistical mapping of climate. Climate Research 22:99–113.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Jenness, J. S. 2004. Calculating landscape surface area from digital elevation models. Wildlife Society Bulletin 34:829–839.

Jenness, J. S. 2006. Topographic Position Index (tpi_jen.avx) extension for ArcView 3.x. Version 1.3a. Jenness Enterprises, Flagstaff, Arizona, USA. <http://www.jennessent.com/arcview/tpi.htm>. Accessed 2 Feb 2007.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use–availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.

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

Keating, K. A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. Journal of Wildlife Management 68:774–789.

Koehler, G. M. 1990. Population and habitat characteristics of lynx and snowshoe hares in north central Washington. Canadian Journal of Zoology 68:845–851.

Koehler, G. M., and K. B. Aubry. 1994. Lynx. Pages 74–98 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, technical editors. The scientific basis for conserving forest carnivores American marten, fisher, lynx, and wolverine in the western United States. U.S. Department of Agriculture Forest Service General Technical Report RM-254, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Kolbe, J. A., J. R. Squires, and T. W. Parker. 2003. An effective box trap for capturing lynx. Wildlife Society Bulletin 31:980–985.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, D. L. McDonald, and W.

P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, Dordrecht, The Netherlands.

McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst, USA. <www.umass.edu/landeco/research/fragstats/fragstats.html>. Accessed 4 Jun 2006.

Mood, A. M., F. A. Graybill, and D. C. Boes. 1974. Introduction to the theory of statistics. Third edition. McGraw-Hill, New York, New York, USA.

Mowat, G., K. G. Poole, and M. O'Donoghue. 2000. Ecology of lynx in northern Canada and Alaska. Pages 265–306 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. Wildlife Society Bulletin 5:113–117.

Ruggiero, L. F., K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires. 2000. The scientific basis for lynx conservation: qualified insights. Pages 443–454 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

Slough, B. G. 1999. Characteristics of Canada lynx, *Lynx canadensis*, maternal dens and denning habitat. Canadian Field-Naturalist 113:605–608.

Squires, J. R., and T. Laurion. 2000. Lynx home range and movements in Montana and Wyoming: preliminary results. Pages 337–349 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the United States. University Press of Colorado, Boulder, USA.

U.S. Bureau of the Census. 2000. Census 2000 TIGER® data. U.S. Census Bureau, Geography Division, Cartographic Operations Branch, Washington, D.C., USA. <http://www.esri.com/data/download/census2000_tigerline/description.html>. Accessed 9 Apr 2007.

U.S. Fish and Wildlife Service. 2000. Endangered and threatened wildlife and plants; determination of threatened status for the contiguous U.S. distinct population segment of the Canada lynx and related rule. Federal Register 65:16051–16086.

U.S. Geological Survey. 2000. National elevation dataset. Earth Resources Observation and Science Data Center, Sioux Falls, South Dakota, USA.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

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