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LIDAR-DERIVED CANOPY ARCHITECTURE PREDICTS BROWN CREEPER OCCUPANCY OF TWO WESTERN CONIFEROUS FORESTS

Jody C. Vogeler[1,4], Andrew T. Hudak[2], Lee A. Vierling[3], and Kerri T. Vierling[1]

[1]*Fish and Wildlife Resources Department, P.O. Box 441136, University of Idaho, Moscow, ID 83844-1136*
[2]*Rocky Mountain Research Station, 1221 South Main Street, Moscow, ID 83843*
[3]*Forest, Rangeland, and Fire Sciences Department, P.O. Box 441133, University of Idaho, Moscow, ID 83844-1133*

Abstract. In western conifer-dominated forests where the abundance of old-growth stands is decreasing, species such as the Brown Creeper (*Certhia americana*) may be useful as indicator species for monitoring the health of old-growth systems because they are strongly associated with habitat characteristics associated with old growth and are especially sensitive to forest management. Light detection and ranging (lidar) is useful for acquiring fine-resolution, three-dimensional data on vegetation structure across broad areas. We evaluated Brown Creeper occupancy of forested landscapes by using lidar-derived canopy metrics in two coniferous forests in Idaho. Density of the upper canopy was the most important variable for predicting Brown Creeper occupancy, although mean height and height variability were also included in the top models. The upper canopy was twice as dense and the mean height was almost 50% higher at occupied than at unoccupied sites. Previous studies have found indicators of canopy density to be important factors for Brown Creeper habitat; however, this represents the first time that lidar data have been used to examine this relationship empirically through the mapping of the upper canopy density that cannot be continuously quantified by field-based methods or passive remote sensing. Our model's performance was classified as "good" by multiple criteria. We were able to map probabilities of Brown Creeper occupancy in ~50 000 ha of forest, probabilities that can be used at the local, forest-stand, and landscape scales, and illustrate the potential utility of lidar-derived data for studies of avian distributions in forested landscapes.

Key words: Brown Creeper, Certhia americana*, forest, habitat, lidar, mapping, occupancy.*

La Arquitectura del Dosel Derivada de Lidar Predice la Ocupación de *Certhia americana* de Dos Bosques de Coníferas del Oeste

Resumen. En los bosques dominados por coníferas del oeste, donde está disminuyendo la abundancia de rodales maduros, las especies como *Certhia americana* pueden ser útiles como especies indicadoras para monitorear la salud de los sistemas maduros debido a que están fuertemente asociadas con las características del hábitat vinculadas con el bosque maduro y son especialmente sensibles al manejo del bosque. El sistema de detección y alcance de luz (denominado lidar, un acrónimo del inglés "light detection and ranging") es útil para adquirir datos tridimensionales de alta resolución de la estructura de la vegetación a través de grandes áreas. Evaluamos la ocupación de *C. americana* de paisajes boscosos usando métricas del dosel derivadas de lidar en dos bosques de coníferas en Idaho. La densidad del dosel alto fue la variable más importante para predecir la ocupación de *C. americana*, aunque la altura media y la variabilidad de la altura también fueron incluidas en los mejores modelos. El dosel alto fue dos veces más denso y la altura media fue casi 50% más alta en los sitios ocupados que en los sitios desocupados. Estudios previos han encontrado que los indicadores de densidad del dosel son factores importantes del hábitat de *C. americana*; sin embargo, esto representa la primera vez que datos de lidar han sido usados para examinar esta relación de modo empírico a través del mapeo de la densidad del dosel alto, de un modo continuo que no puede ser cuantificado por métodos basados en trabajo de campo o muestreo remoto pasivo. El desempeño de nuestro modelo fue clasificado como "bueno" por múltiples criterios. Fuimos capaces de mapear las probabilidades de ocupación de *C. americana* en ~50 000 ha de bosque, probabilidades que pueden ser usadas a las escalas local, de rodal de bosque y de paisaje, y que ilustran la utilidad potencial de los datos derivados de lidar para estudios de distribución de aves en paisajes boscosos.

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[4]Current address: Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331.
E-mail: jody.vogeler@oregonstate.edu

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INTRODUCTION

Wildlife-habitat models are important tools in understanding and depicting species' distributions for conservation and management purposes (Pearce and Ferrier 2000, Wintle et al. 2005). In particular, habitat models for species of concern can be used to identify areas of the landscape critical to conservation (Bradbury et al. 2005, Graf et al. 2009). For example, habitat-suitability models for the Western Capercaillie (*Tetrao urogallus*), an endangered forest grouse in the Swiss Alps, aided in conservation efforts by assisting in the identification and designation of a forest reserve of suitable habitat (Graf et al. 2004, 2009). Further studies were then able to refine the scale of habitat-suitability analyses to predict the Western Capercaillie's habitat use within the forest reserve to better guide management (Graf et al. 2009).

In forested settings, predictive models can help to assess a species' response to forestry practices and can be used to implement appropriate land-use plans (Mason et al. 2003, Hyde et al. 2005, Sallabanks et al. 2006). Poulin et al. (2008) modeled habitat selection by the Brown Creeper (*Certhia americana*) to identify thresholds of forest structure important to the species in order to determine if forest logged at low intensity provided suitable habitat. The reliance of the Brown Creeper on specific forest structures characteristic of mature forest suggests that low-intensity harvest does not provide suitable habitat and reserves of unharvested forest should be maintained for Brown Creeper conservation (Poulin et al. 2008).

Many wildlife-habitat models use a combination of field-based vegetation surveys and remote sensing. Field-based data often are expensive and labor intensive (Hyde et al. 2005, Clawges et al. 2008), but many techniques of remote sensing are unable to map the vertical and horizontal arrangement of vegetation, or canopy architecture, important to a wide range of wildlife (Vierling et al. 2008). An increasing number of wildlife studies have begun to use a newer form of remote sensing, light detection and ranging (lidar), which has emerged as a solution for acquiring accurate, three-dimensional data on vegetation structure data at a fine resolution with fewer limitations on spatial extent and intensity of sampling than field-based efforts have (Hyde et al. 2005, Vierling et al. 2008). The accuracy of derived lidar products has been tested and validated in forests on rugged terrain, in areas of disturbance, and in areas of varying canopy architecture; lidar is thus appropriate for measuring vegetation-structure data in montane forests (Hyde et al. 2005). Lidar is also becoming more available and accessible (Vierling et al. 2011) through efforts such as the Open Topography initiative (www.opentopography.org), facilitating the expansion of habitat types and geographic regions where researchers and managers may use lidar to explore wildlife–habitat relationships and guide forest management.

As human activities continue to change the natural structure and processes of habitats and their size, shape, and distribution in the landscape (Shinneman and Baker 1997, Morris 2003), it is likely that maps of lidar-derived forest structure may improve wildlife-habitat models because wildlife is often sensitive to vertical vegetation structure (Vierling et al. 2008, Martinuzzi et al. 2009). Management may alter the natural structure of the forest by reducing the size and abundance of standing live and dead trees and downed woody debris, changing understory distributions, and altering overall variance in attributes of vertical structure (Halpern et al. 1999, Siitonen et al. 2000, Kroll and Haufler 2006). Many of these forest characteristics can be modeled with lidar data (Lefsky et al. 2002, Martinuzzi et al. 2009).

Timber harvest, human development, and suppression of natural disturbance regimes have influenced western coniferous forests greatly. As a result, the abundance and distribution of various stages of forest succession have been altered, and the representation of some stages in the landscape (e.g., old-growth forests; Shinneman and Baker 1997) has been greatly reduced. In a larger sense, characteristics of old-growth forests such as large trees and snags are less abundant in the western landscape because of overly frequent logging, removal of hazardous snags during timber removal, and altered vertical distribution of biomass in the forest strata (Siitonen et al. 2000). Therefore, the potential of lidar to understand old-growth forest habitats is two-fold: it can be used both to identify the distribution of patches of old-growth forest across entire landscapes (Lefsky et al. 1999, Falkowski et al. 2009) and to quantify the specific architecture of individual stands of old-growth forest (Hyde et al. 2005, Martinuzzi et al. 2009, Falkowski et al. 2009).

In western coniferous forests where the abundance of old-growth stands is decreasing, animals strongly associated with old growth and especially sensitive to management may be useful as indicator species for monitoring the health of old growth (Lindenmayer et al. 2000, Poulin et al. 2008). The Brown Creeper is one such species that is strongly associated with structural attributes characteristic of mature and old-growth forests (Imbeau et al. 1999, Holmes et al. 2004, Sallabanks et al. 2006). The creeper's requirements for foraging are linked to forest structure requiring low levels of anthropogenic disturbance and longer intervals between logging (Holmes et al. 2004, Venier et al. 2007, Poulin et al. 2008). Brown Creepers forage primarily on invertebrates found on the boles of standing trees, both live and dead (Weikel and Hayes 1999). Larger trees with deep bark furrows, snags with diverse decaying surfaces, and vertical diversity of a forest stand are all attributes of old growth stands and drivers of arthropod abundance (Mariani and Manuwal 1990, Weikel and Hayes 1999, Halaj et al. 2009), therefore driving the prey base of the Brown Creeper.

The Brown Creeper's nesting habitat is also associated with mature and old-growth forests (Holmes et al. 2004, Venier et al. 2007, Poulin et al. 2008). Snags and large trees with decaying bark are important for the creeper, which builds a hammock-like nest under flaking bark of large standing trees, either live or dead (Poulin et al. 2008). As a result of its preferred habitat for both nesting and foraging, the Brown Creeper is often identified as a species of closed-canopy forest (Anderson and Crompton 2002, Sallabanks et al. 2006), preferring a high density of large trees that provide substrates for foraging and the recruitment of snags necessary for nesting (Poulin et al. 2008). Poulin et al. (2010) suggested that substrates for foraging may be a resource more limiting than are snags for nesting. The density of large-diameter trees important for the creeper's foraging is significantly lower even in forest logged selectively at low intensity (Poulin et al. 2010). The high sensitivity of the Brown Creeper to logging has raised concern about its population trends within the highly managed coniferous forests of the western U.S. (Hejl et al. 2002, Wiggins 2005).

Avian occupancy models that include lidar-based forest-structure data are relatively recent and limited (see Vierling et al. 2008 for review, Hinsley et al. 2008, Bellamy et al. 2009, Graf et al. 2009, Goetz et al. 2010). In particular, habitat-specific occupancy models using lidar data have not been devised for birds of mature/old-growth coniferous forests. Because lidar can map canopy architecture at broad spatial scales, it has a great potential to contribute toward modeling of wildlife habitat and mapping across landscapes. Lidar may also be able to provide new structural variables at the local scale that cannot be quantified through field-based methods or passive remote sensing (Vierling et al. 2008). One such metric is the density of the upper canopy, which is often represented by overall canopy cover independent of the forest strata in which the foliage cover occurs or as the density of large trees sampled in smaller plots and extrapolated to larger areas (Guénette and Villard 2005). These previous methods may overlook important relationships between organisms and specific forest strata at the local scale. Therefore, lidar may present new opportunities to examine the habitat preferences of wildlife. The purpose of our study was to evaluate the Brown Creeper's occupancy of forested landscapes by means of lidar-derived metrics. On the basis of literature specifying the Brown Creeper's preference for forest with a dense canopy and large trees (Hejl et al. 2002, Poulin et al. 2008), we hypothesized that the density of the upper canopy, as measured through lidar, should be the most important factor influencing Brown Creeper occupancy.

METHODS

STUDY AREAS

We surveyed two areas of north-central Idaho: Moscow Mountain and the drainage basin of Slate Creek. Moscow Mountain is located about 20 km northeast of the city of Moscow, Idaho (46° 49′ N, 116° 50′ W) and is an approximately 20 000-ha landscape of mixed conifer forest surrounded by agricultural lands. The majority of Moscow Mountain forests are managed for timber production by private industrial logging companies; the remainder is divided among a variety of owners including the University of Idaho Experimental Forest, the city of Troy, and private landowners. Forest trees include Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), western red cedar (*Thuja plicata*), ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), western hemlock (*Tsuga heterophylla*), Engelmann spruce (*Picea engelmannii*), western white pine (*Pinus monticola*), and subalpine fir (*Abies lasiocarpa*). The landscape contains many highly managed stands and therefore comprises a mosaic of successional stages ranging from recently logged to mature multi-story forest (Falkowski et al. 2009). Survey locations for this study ranged in elevation from 816 to 1242 m.

The Slate Creek study area is part of the Salmon River Ranger District of the Nez Perce National Forest (45° 39′ N, 116° 3′ W) and covers approximately 30 000 ha. Elevations of survey locations ranged from 1125 to 2250 m, the higher elevations in the Gospel Hump Wilderness. The diverse mixed conifer forest consists of an assemblage of conifers similar to that on Moscow Mountain, although varying in proportions. The full range of successional stages from recently logged to old growth was represented at the site. Slate Creek differs from Moscow Mountain in that it has steeper topography and is less intensively managed, with a greater proportion of older successional stages. Perhaps most importantly, Moscow Mountain is situated along the ecotone between forest and agriculture at the western extreme of the coniferous forest belt of north-central Idaho, while Slate Creek is set well within a larger forest matrix.

BIRD SURVEYS

To ensure the range of forest structure was sampled, we first developed a lidar-derived map of canopy structure for both sites that encompassed both lidar-derived mean forest height and canopy density. We generated this nine-level map by combining three classes of mean forest height with three classes of canopy density. We randomly stratified count points across these nine canopy-structure classes to ensure the range of structure present at each study area was sampled in the proportion it occurred in the landscape.

We surveyed birds with point counts at Moscow Mountain in 2009 and at Slate Creek in 2010, during the breeding season from late May to early July. We visited each of the 151 points on Moscow Mountain and 164 at Slate Creek twice during the breeding season to increase the likelihood of detecting Brown Creepers if present. Under the forest canopy, the accuracy of hand-held GPS readers may be low, leading to errors in the georeferencing of point-count data with lidar-derived structure variables. Therefore, we located the points in the field with Garmin hand-held GPS units in conjunction with aerial photographs to minimize error in locating the points with the hand-held GPS only. Bird surveys began at sunrise and continued until 5 hr after sunrise to capture the period of active vocalization (Manuwal and Carey 1991). To minimize sampling bias associated with time of morning, we varied the times of the two visits to each point. We delayed point counts when heavy wind or rain inhibited the observer's ability to detect birds, and we also relocated or excluded points from loud stream noise to allow for the assumption of equal detectability among sites. Studies vary widely in their estimates of the size of a Brown Creeper's territory, but we chose to focus on the results of Davis (1978), who found a mean of 4.26 ha (±0.59), which translates to a mean radius of 232.9 m if the territory is round. Therefore, to minimize the chance of sampling the same bird at multiple points, we established a minimum distance of 250 m between points (Wintle et al. 2005), although in actuality our points were often farther apart than the minimum. A single observer (Vogeler) conducted the point counts at Moscow Mountain in 2009, while two observers (Vogeler plus one technician) conducted them at Slate Creek in 2010. For the 2010 survey with two observers, we trained intensively before the season to calibrate the observers' species identification and distance estimation. Each observer made one of the two counts at each point to further reduce detection bias due to multiple observers as well as provide complete replication.

OCCUPANCY DATA

Following the guidelines for maximum detection set forth by the Boreal Avian Modelling Project (2011), we attempted to minimize variability in the probability of detecting Brown Creepers by including only data from within a 75-m radius of the point. Differences in detectability are important considerations, and we attempted to minimize this potential error through using this smaller sampling scale and by eliminating survey locations with loud streams or surveys during inclement weather. Although these efforts may minimize errors associated with detectability, other sources of detection bias may still exist. We selected a random subset of "absent" survey locations from the total at which Brown Creepers were not detected by using the random-selection function in R (R Development Core Team 2005), to match the number of "present" survey locations at each site where creepers were detected (n = 31 for Moscow Mountain; n = 35 for Slate Creek). We compiled data on Brown Creeper occupancy from both Moscow Mountain and Slate Creek (n = 132) and added study area as a factor to the statistical models to test for site specificity in the Brown Creeper's habitat selection (Table 1).

LIDAR DATA

For all vegetation structure metrics, we used multiple-return discrete lidar data recorded from the air (Table 1) at Slate Creek in summer 2006 and at Moscow Mountain in summer 2009. Both lidar surveys were conducted by Watershed Sciences, Inc. (Corvallis, OR), with a Leica ALS50 system. We classified ground returns by the multiscale curvature classification algorithm (Evans and Hudak 2007), which were then subsequently interpolated into a 1-m digital terrain model. This model was subtracted from the all-return data for calculation of canopy heights, which were then binned into 20-m × 20-m grid cells for the calculation of height-based statistical metrics including the maximum, mean, and standard deviation. See Evans et al. (2009) for a complete list of canopy metrics that can be generated from height distributions recorded by lidar. To develop predictive models, we applied zonal statistics in ArcGIS to the 20-m output rasters to extract the mean and standard deviation of lidar-derived structure variables for the 75-m buffer surrounding bird survey points. Because the bird data and lidar data for the Slate Creek study area were recorded in different years, we relocated or eliminated count points that fell in recently disturbed stands.

Previous studies in which vegetation was sampled in the field have identified the importance of tree size, forest age, and overall canopy density to Brown Creeper occurrence (Sallabanks et al. 2006, Poulin et al. 2008). Lidar is able to quantify aspects of canopy structure that are difficult or impossible to measure through field-based sampling, such as the density of the vegetation in multiple forest strata, metrics mapped continuously across the landscape as opposed to small field-sampled plots that are extrapolated to characterize the landscape, local and stand-level vertical and horizontal forest structure, and the closure of the upper canopy as seen from above (Dubayah and Drake 2000). We included the lidar-derived mean forest height (m), the variability of forest height, and the density of the upper canopy in our predictive models to test for relationships similar to those observed in previous field-based studies of Brown Creeper occupancy (Table 1). Tree height is highly and positively correlated with diameter at breast height (Bresnan et al. 1994). Therefore, forest height

TABLE 1. Descriptions of lidar-derived predictor variables used in models predicting Brown Creeper occupancy in two coniferous forests in Idaho.

Predictor variable[a]	Abbreviation	Metric description
Lidar-derived		
Mean canopy height (m)	Height	Mean canopy height
Variability in canopy height (m)	Heightσ	Standard deviation of canopy height
Density of upper canopy (%)	UpperC	Percent of lidar returns in stratum 5 (20–30 m)
Variability in density of upper canopy (%)	UpperCσ	Standard deviation of % returns from 20–30m
Study area	Site	Study area 1 (Moscow Mountain) or 2 (Slate Creek)

[a]Scale of radius 75 m.

is a robust indicator of tree diameter and, to a lesser extent depending on site conditions, tree age. The percent of returns of lidar data from the forest stratum between 20 and 30 m (lidar stratum 5), which correlates to the upper canopy at our study areas, was included in the model to represent the density of large trees included in the upper canopy, which is important to the Brown Creeper's habitat needs (Poulin et al. 2010).

STATISTICAL ANALYSES

From the total data set (n = 132), we used a random selection of 75% of the data in model creation (n = 100), withholding 25% for validation of the model (n = 32), with approximately half of both data sets coming from each study area. We used logistic regression (binomial error distribution and logit-link function) to evaluate the relationship between Brown Creeper occupancy and the lidar-derived variables predicting forest structure. We ensured that highly correlated variables were not included in the modeling process by using a threshold of 5 for the variance-inflation factor (Haan 2002). We calculated values of the Akaike (1973) information criterion (AIC) for a set of 20 candidate models including a null model (Table 2). We chose candidate models to test ecologically meaningful combinations of predictor variables as well as single-variable models in order to test our hypothesis that the density of the upper canopy should be the most important factor influencing Brown Creeper occupancy. We ranked AIC values to identify the model with the lowest AIC value and considered any model within 2 of the lowest value a competing model (Burnham and Anderson 2002). In addition to AIC model selection, we also compared the models' performance by calculating Akaike weights of each model and individual parameters for explaining the variance of the data (Johnson and Omland 2004).

We evaluated the performance of the models with competing AIC values by following the methods of Fielding and Bell (1997). Using weighted parameter estimates, we applied the top models to the training and validation data sets to calculate logit (P), with which we then estimated the probability of occurrence (see Fielding and Bell 1997 for details of the equation). We used receiver operating curves (ROC) to calculate the optimal probability of the occurrence threshold where sensitivity and specificity were balanced (Fielding and Bell 1997). This optimal probability was ≥0.5, from which we then created a 2 × 2 classification table of correct and incorrect predictions of presence and absence. Using the four values in the classification table (sites where the creeper was correctly and incorrectly predicted as present and absent), we calculated a set of model-performance statistics that included sensitivity, specificity, positive predictive power, negative predictive power, correct classification rate, and kappa (Fielding and Bell 1997). Sensitivity and specificity represent the ability of the model to correctly predict sites of presence and absence, respectively. The correct classification rate combines these measures to reflect the model's overall ability to predict sites of both presence and absence correctly. Positive and negative predictive power are the proportion of sites where the creeper was correctly classified as present or absent, respectively. Kappa (κ) expresses how well the model predicts the data set over what is expected by chance alone. Models with $\kappa < 0.4$ are considered "poor," those with $0.4 < \kappa < 0.75$ are classified as "good," and those with $\kappa \geq 0.75$ are "excellent" (Luck 2002).

To create ROCs, we plotted cases of true and false positive predictions (sensitivity vs. [1 – specificity]) across a range of probability of occurrence thresholds against each other in R (R Development Core Team 2005). To assess model performance for the training and validation data sets, we calculated the area under the curve (AUC) for the ROCs by the methods of Luck et al. (2002). AUC values range from 0.5 (no model discrimination) to 1.0 (perfect model performance; Fielding and Bell 1997). Values between 0.5 and 0.7 denote poor discrimination, values between 0.7 and 0.9 reflect a model with reasonably good discrimination, and a model with excellent discrimination capabilities has AUC values >0.9 (Pearce and Ferrier 2000). In addition to examining model performance for the training and validation datasets, we also conducted a leave-one-out cross-validation (LOOCV) analysis on the undivided dataset in R (R Development Core Team 2005).

We mapped the variables selected by the predictive models at a 20-m × 20-m resolution across the full extent of the lidar surveys, then applied the models to generate predictive maps at the same resolution, using the AsciiGridPredict function in the yaImpute package of R. All data reported in the results are presented as means ± SE.

TABLE 2. List of the 20 candidate models used for predicting Brown Creeper occupancy in two western coniferous forests. All runs included the intercept.

Model	Variables
Intercept-only (null model)	Height, site
Height	UpperC, site
Heightσ	Height, heightσ, upperC
UpperC	Height, heightσ, site
UpperCσ	Height, upperC, site
Site	UpperC, upperCσ, site
Height, heightσ	Height, heightσ, upperC, upperCσ
UpperC, upperCσ	Height, heightσ, upperC, site
Height, upperC	Heightσ, upperC, upperCσ, site
Heightσ, upperC	Global

RESULTS

Lidar-derived metrics of canopy height and density were important predictors of Brown Creeper occupancy (Table 3). Density of the upper canopy was the most important structure variable for predicting Brown Creeper occupancy

TABLE 3. Top models predicting Brown Creeper presence/absence in two western coniferous forests, reduced from the original candidate set of 20 models. Models ranked by AIC values; models ΔAIC < 2 considered to be competing.

Confidence set of models	ΔAIC	w_i
UpperC, heightσ	0.00[a]	0.33
UpperC, height, heightσ	1.30	0.17
UpperC, upperCσ, height, heightσ	2.49	0.09
UpperC, height, height, site	2.78	0.08
UpperC, upperCσ, heightσ, site	3.00	0.07
UpperC, upperCσ	3.76	0.05
UpperC, height	4.00	0.04
Global	4.25	0.04
UpperC	4.35	0.04
UpperC, height, site	4.59	0.03

[a]Lowest value of AIC = 111.51.

at our study sites, although mean height and height variability were also included in the top models (Table 3). The upper canopy was twice as dense at occupied sites as at unoccupied sites, and mean height (m) was almost 50% greater at occupied sites than at unoccupied sites (Table 4). Study area was not a significant factor influencing occupancy (Table 5).

Multiple statistical measures found the two competitive models to have "good" predictive performance, although at the lower end of this range (Table 6). Both competing models had κ values specifying "good" performance for the sets of training data (Table 6). AUC values calculated from the ROCs classified both of the competing models performing well for both the training and validation data, although values for the validation data were slightly lower (Table 7). The two competing predictive models performed similarly, with equal AUC values of 0.83 and validation AUC values of 0.76 and 0.77 (Table 7). The bias for not using LOOCV in the predictive model was <0.001 and therefore negligible. The maps that we generated on the basis of the models' results (Fig. 1) identify

TABLE 4. Summary statistics of lidar-derived predictor variables for Brown Creeper presence and absence in two coniferous forests in Idaho. Metrics include the mean and standard deviation of canopy height (height and height σ) and the percent of lidar returns from stratum 5 (20–30 m), representing the density of the upper canopy (upperC and upperC σ). Means of variables are given with confidence intervals based on the standard error in parentheses.

	Mean (95% confidence interval)			
Occupancy	Height (m)	Height σ	UpperC (% density of lidar hits)	UpperC σ
Present	12.17 (11.05, 13.29)	3.79 (3.45, 4.13)	26.38 (23.82, 28.94)	10.53 (9.67, 11.39)
Absent	8.20 (7.01, 9.39)	3.05 (2.72, 3.38)	13.78 (11.08, 16.48)	7.93 (6.99, 8.87)

TABLE 5. Weighted parameter estimates and standard errors for modeled predictor variables. Akaike weights denote relative importance of variables.

	Parameter estimate	Standard error	95% confidence interval	w_i	*P*-value
Intercept	–3.19	0.91	(–4.99, –1.40)	–	<0.001
UpperC	0.09	0.02	(0.04, 0.14)	0.95	<0.01
UpperCσ	0.08	0.08	(–0.08, 0.24)	0.28	0.47
Height	0.05	0.06	(–0.06, 0.17)	0.46	0.39
Heightσ	0.38	0.18	(0.02, 0.75)	0.79	0.09
Site	–0.34	0.50	(–1.33, 0.64)	0.27	0.63

spatially explicit patterns of occupancy across the two study areas.

DISCUSSION

Our results support our hypothesis that the density of the upper canopy should be the most important factor in predicting Brown Creeper occupancy in our study areas. Previous studies have found factors implying a dense upper canopy, such as overall canopy cover and density of large-diameter trees, to be factors important to Brown Creeper habitat (Anderson and Crompton 2002, Sallabanks et al. 2006), but ours is the first empirical examination of the relationship between Brown Creeper occupancy and the density of the upper canopy through the use of lidar data. Anderson and Crompton (2002) classified the Brown Creeper as a part of a

TABLE 6. Measures of predictive performance at a threshold for probability of occurrence of 0.5 for competing models applied to the training and validation datasets. Model 1 was the best model, and model 2 was within 2 ΔAIC of model 1. Sensitivity and specificity depict the ability of the model to correctly predict sites of presence and absence, respectively. The rate of correct classification reflects the model's overall ability to predict both presence and absence correctly. The proportion of sites correctly classified as "present" or "absent" are represented by positive and negative predictive power, respectively. Kappa (κ) is a model-performance statistic where performance at values <0.4 is considered poor, 0.4< κ <0.75 good, and κ ≥ 0.75 excellent.

	Model 1: heightσ, upperC		Model 2: height, heightσ, upperC	
	Training	Validation	Training	Validation
Sensitivity	0.74	0.75	0.88	0.81
Specificity	0.76	0.69	0.66	0.56
Correct classification rate	0.75	0.72	0.77	0.69
Positive predictive power	0.76	0.71	0.72	0.65
Negative predictive power	0.75	0.73	0.85	0.75
κ	0.50	0.44	0.54	0.38

TABLE 7. Area under the curve (AUC) results calculated from ROCs for competing models. AUC values range from 0.5 (no model discrimination) to 1.0 (perfect model performance), where values between 0.5 and 0.7 denote poor discrimination, those between 0.7 and 0.9 reflect reasonably good discrimination, and those >0.9 specify excellent discrimination.

Data set and model	AUC	*P*-value
Training		
UpperC, heightσ	0.83	<0.001
UpperC, height, heightσ	0.83	<0.001
Validation		
UpperC, heightσ	0.77	0.004
UpperC, height, heightσ	0.76	0.006

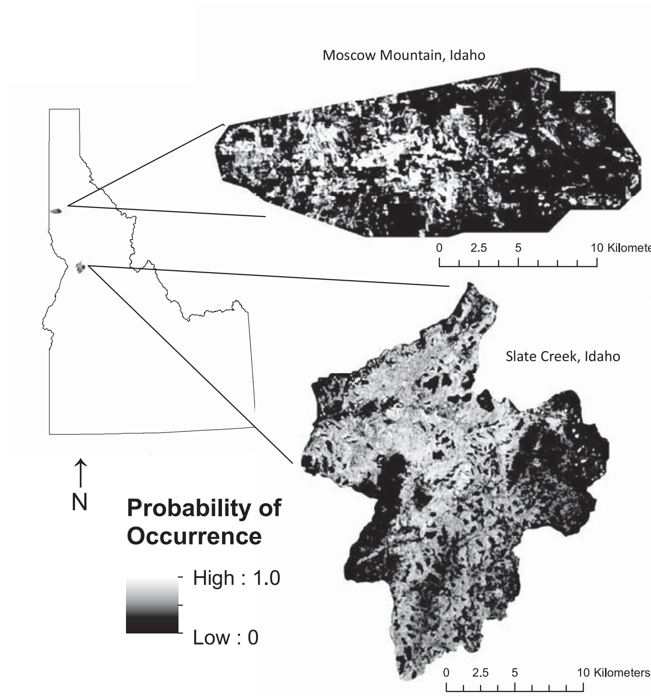

FIGURE 1. Maps depicting the probability of Brown Creeper occupancy on Moscow Mountain and in the drainage basin of Slate Creek, Idaho. The variables selected by the predictive models were mapped at a 20-m × 20-m resolution across the full extent of the lidar surveys. The AsciiGridPredict function in the yaImpute package of R was then applied to the models to generate predictive maps at the same resolution.

closed-canopy-forest community, choosing the densest forest that included a dense middle stratum and abundant large trees (Anderson and Crompton 2002). These dense stands with abundant large live trees may provide important foraging substrates for the Brown Creeper. Larger trees often have deeper bark furrows, which support more bark-dwelling invertebrates, an important food source for the Brown Creeper (Mariani and Manuwal 1990, Weikel and Hayes 1999). A high density of large trees also ensures the recruitment of snags, the Brown Creeper's preferred nesting habitat (Poulin et al. 2008). The inclusion of the mean canopy height in one of the competing models we devised may also reflect this preference by the Brown Creeper for an abundance of large trees. Although the metric for mean height may reflect the presence of large trees in the study plot, the density of the upper canopy may better represent the abundance of this cohort of large trees, leading to a predictive strength for Brown Creeper occupancy greater than mean height alone.

The variability in canopy height also appeared in both of the competing models, although it was not quite significant at the 0.05 level, the 95% confidence interval estimated for this parameter included zero. Adams and Morrison (1993) found the Brown Creeper to prefer greater complexity of vertical structure. Variability in vertical forest structure may reflect the presence of a variety of forest strata and features that are important components of Brown Creeper habitat, such as an understory layer for arthropod production (Adams and Morrison 1993) and an abundance of large trees in the upper strata for foraging and nesting substrates (Poulin et al. 2010). Although multiple forest layers may be necessary to the Brown Creeper, our results suggest that the abundance of large trees creating a dense upper canopy may be the limiting resource for occupancy at our study sites.

The scale at which variables are quantified can affect a model's results significantly (Karl et al. 2000). The scale of our analysis, a radius of 75 m, identified the density of the upper canopy as an important predictor of Brown Creeper occupancy. Landscape-level variables not evaluated in our study also affect the suitability of habitat for the Brown Creeper; these include core stand size, distance to edge, and the stand's disturbance history (Poulin et al. 2008, 2010). To help inform forest management at the local and landscape levels, future research should explore the Brown Creeper's habitat relationships over a range of spatial scales, to identify thresholds or changes in drivers of occupancy, as well as examine the importance of lidar-derived landscape variables.

To address specific management and conservation goals, the threshold for probability of occurrence used in predictive mapping can be adjusted from the 0.5 optimal threshold we used. For conservation purposes where the intent is to concentrate efforts and resources on high-quality habitat, the threshold can be increased for a more conservative prediction of the Brown Creeper's occupancy. The more conservative prediction may be useful for the designation of conservation reserves or to concentrate habitat-restoration efforts. For research whose goal is to identify a range of areas where Brown Creepers may be present, so that field surveys for nesting or habitat-quality assessments may be prioritized, applying a lower probability of occurrence may be beneficial so that the survey area is widened across a gradient of habitat of "moderate" to "excellent" quality.

Many of the previous studies modeling avian habitat with lidar have examined relationships within a single study site (Graf et al. 2009, Goetz et al. 2010). The two areas of coniferous forest in which we modeled Brown Creeper occupancy, although both within Idaho, differ significantly in topographic gradient, land ownership and management goals such as intensity of timber harvest, proportion of late-seral stands, surrounding landscape (i.e., agricultural vs. forested), proximity to well-populated areas and high recreation pressures, and dissection by roads and thus accessibility. The inclusion of a study-area factor in our models did not disclose significant differences between the areas in the Brown Creeper's habitat preference. Habitat models that perform well across such gradients of landscape characteristics and land use should be more robust than those tested in one study area. Future studies should test for similar occupancy relationships across other parts of the Brown Creeper's range. We acknowledge that occupancy data, while informative, does not truly reflect habitat quality. Therefore, future studies might address relationships between lidar-derived canopy architecture and the Brown Creeper's density and demographic variables.

Our results add to the growing number of studies showing an association between the Brown Creeper and forest-structure attributes that are characteristic of mature and old-growth forest. Importantly, we were able to use lidar-derived metrics in our analysis and map probability of occupancy across ~50 000 ha of forest, representing, to our knowledge, the first time that spatially explicit maps of Brown Creeper occupancy have been published. The fine-scale metrics of vegetation height and density that can be mapped with lidar provide data for habitat models at the local, stand, and forest-wide scales. Forest-structure metrics that can be mapped over a landscape with remote sensing and that predict wildlife needs may be important for conservation and management. As timber harvest continues to reduce large tracts of older forest stands in western North America, monitoring of species such as the Brown Creeper, strongly associated with structural attributes of these older seral stages and sensitive to habitat disturbance, may become of increasing importance in management and conservation.

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