

Testing a Habitat Suitability Index Model for Boreal Owls in Western Newfoundland, Canada

Author: Munro, Kathrin J.

Source: Journal of Raptor Research, 50(4) : 325-337

Published By: Raptor Research Foundation

URL: <https://doi.org/10.3356/JRR-15-51.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

THE JOURNAL OF RAPTOR RESEARCH

A QUARTERLY PUBLICATION OF THE RAPTOR RESEARCH FOUNDATION, INC.

VOL. 50

DECEMBER 2016

No. 4

J. Raptor Res. 50(4):325–337

© 2016 The Raptor Research Foundation, Inc.

TESTING A HABITAT SUITABILITY INDEX MODEL FOR BOREAL OWLS IN WESTERN NEWFOUNDLAND, CANADA

KATHRIN J. MUNRO

*Environmental Science Graduate Program, Memorial University of Newfoundland,
St. John's, NL A1B 3X7, Canada,*

and

Biosystems and Biodiversity Graduate Program, University of Lethbridge, Lethbridge, AB T1K 3M4, Canada

IAN G. WARKENTIN¹

*Environmental Science Graduate Program, Memorial University of Newfoundland,
St. John's, NL A1B 3X7, Canada,*

and

Environmental Science Program, Memorial University of Newfoundland, Corner Brook, NL A2H 6P9, Canada

CHRISTINE M. DOUCET

*Environmental Science Program, Memorial University of Newfoundland, Corner Brook, NL A2H 6P9, Canada,
and*

*Wildlife Division, Newfoundland and Labrador Department of Environment and Conservation,
Corner Brook, NL A2H 7S1, Canada*

ABSTRACT.—Boreal Owls (*Aegolius funereus*) rely on mature forests and, consequently, are negatively affected by timber harvesting strategies that alter the composition and structure of these forests. We tested an existing Boreal Owl habitat suitability index (HSI) model created using data from across the species' North American breeding distribution, plus a modified Newfoundland version that incorporated local data. We assessed the applicability of these models to a population on the periphery of the species' North American range in Newfoundland, Canada. We also conducted habitat composition analyses and evaluated the Boreal Owl HSI model values associated with forest cover projections under three different forest harvesting scenarios. Overall output from both HSI models indicated low levels of suitability for locations across the study area. Long-term persistence in Newfoundland demonstrates that suitable habitat for Boreal Owls exists, but what constitutes suitable habitat for populations in other parts of North America may differ from that in our study area. Boreal Owls in Newfoundland occupied locations with a greater proportion of disturbed cover, and lesser proportions of deciduous and mixed coniferous and deciduous stands ≥ 60 yr old, compared to what was available in the surrounding region, as measured in randomly selected plots. Whereas Boreal Owl habitat use in Newfoundland was similar to that described for other populations, the limited use of deciduous and mixed stands was distinct. Forward projection modeling of forest cover indicated that there were no differences in the overall suitability of habitat available to Boreal Owls under the three harvesting scenarios. Our study highlights the importance of adjusting forest management strategies to account for differences in habitat use among populations.

KEY WORDS: *Boreal Owl*; *Aegolius funereus*; *breeding*; *habitat composition*; *Habitat Suitability Index*; *forest harvesting*.

¹ Email address: ian.warkentin@grenfell.mun.ca

EVALUACIÓN DEL MODELO DEL ÍNDICE DE ADECUACIÓN DEL HÁBITAT PARA *AEGOLIUS FUNEREUS* EN EL OESTE DE NEWFOUNDLAND, CANADÁ

RESUMEN.—*Aegolius funereus* depende de bosques maduros, por lo que es afectado negativamente por las estrategias de extracción forestal que alteran la composición y la estructura de estos bosques. Evaluamos un modelo existente del índice de adecuación del hábitat (IAH) creado con datos del rango de distribución reproductiva de la especie en América del Norte, y una versión modificada del modelo para Newfoundland que incluye datos locales. Evaluamos la aplicabilidad de estos modelos en una población periférica del área de distribución de esta especie para América del Norte en Newfoundland, Canadá. También realizamos análisis de composición del hábitat y evaluamos los valores del modelo del IAH para *A. funereus* asociados con proyecciones de la cobertura boscosa bajo tres escenarios diferentes de extracción forestal. El resultado general de ambos modelos de IAH indicó la presencia de sitios con niveles bajos de adecuación a lo largo del área de estudio. La persistencia de la especie a largo plazo en Newfoundland demuestra la existencia de hábitat adecuado, pero lo que constituye hábitat apto para poblaciones en otras partes de América del Norte puede diferir del hábitat apto de nuestra área de estudio. En Newfoundland, *A. funereus* ocupó lugares con una mayor proporción de cobertura boscosa perturbada y en menor proporción rodales de árboles caducifolios y rodales mixtos de coníferas y árboles caducifolios de ≥ 60 años, comparado con el hábitat disponible en la región circundante, evaluado a través de parcelas seleccionadas aleatoriamente. Mientras el uso de hábitat de *A. funereus* en Newfoundland fue similar al descrito para otras poblaciones, el uso limitado de los rodales de coníferas y árboles caducifolios fue diferente. La modelización de las proyecciones de la cobertura boscosa indicó que no hubo diferencias en la adecuación global de hábitat disponible para *A. funereus* bajo los tres escenarios de extracción. Nuestro estudio resalta la importancia de realizar ajustes en las estrategias de gestión de los bosques teniendo en cuenta las diferencias en el uso de hábitat entre las poblaciones.

[Traducción del equipo editorial]

Advances in harvesting techniques and technology during recent decades have both increased the rate of forest conversion to other land-cover types and decreased harvest rotation times, raising concerns over the effects of such landscape-level changes to forest structure on wildlife. Habitat loss and fragmentation, often associated with timber harvest, are widely regarded as major factors contributing to the decline of forest bird populations (Schmiegelow and Mönkkönen 2002, Betts et al. 2006, St-Laurent et al. 2009). Among the species most affected by such disturbances are those requiring large home ranges, patches of old-growth forest (i.e., >80 yr in Newfoundland; Bissonette et al. 1989, Thompson et al. 1999), and nest cavities in old and/or dead trees (Imbeau et al. 2001, Haskell et al. 2002, St-Laurent et al. 2009). Old-growth forests and species relying on them are of particular concern because these forests tend to be limited in landscapes managed with short harvest-rotation lengths designed to maximize timber yields (Thompson et al. 1999). Such harvest regimes typically reduce the amount of old-growth forest on the broader landscape and often lead to the elimination of trees capable of supporting nesting cavities (Wallin et al. 1996, Martin and Eadie 1999, Niemelä 1999). Therefore, understanding how old-growth boreal

forest specialists respond to landscape-level changes in forest composition and age-class structure is crucial when developing forest-management strategies (Bradshaw et al. 2009).

One tool used to examine such wildlife-habitat interactions in the context of changing environmental conditions is the habitat suitability index (HSI) model (Van Horne and Wiens 1991). HSI models assign values ranging from 0 to 1 (unsuitable to highly suitable, respectively; Brooks 1997) that can be used to quantify wildlife-habitat interactions and predict sensitivity to disturbances by combining habitat attributes with species' life history and demographic information (U.S. Fish and Wildlife Service 1981, Brooks 1997, Strimbu and Innes 2012). An HSI model based on scientific literature and expert opinion was developed for Boreal Owls (*Aegolius funereus*) in western Newfoundland, Canada (Côté et al. 2004). This model was part of a suite of tools developed for the Western Newfoundland Model Forest (a consortium of industry, government, and nongovernment organizations) as the basis for recommending forest harvesting strategies that would sustain regional biodiversity (Dolter 2005). Boreal Owls were chosen as one focal species for this process because of their close association with mature conifer or mixed coniferous and

deciduous (hereafter mixedwood) forests and consequent perceived negative response to harvesting (Hayward 1994, 1997, Koopman et al. 2007). The HSI model created for Boreal Owls assessed both nesting and foraging requirements conjointly using spatially explicit relationships based on data from across the species' North American breeding distribution, rather than local data, due to limited knowledge of the species in Newfoundland (Côté et al. 2004). The limited point-count data available prior to our study suggested that Boreal Owls in western Newfoundland occur in naturally fragmented landscapes dominated by small-stature, slow-growing, balsam fir (*Abies balsamea*; Gosse and Montevecchi 2001), where stand senescence occurs before 100 yr and diameter at breast height (dbh, 1.3 m) is typically <30 cm (Moroni 2006). This forest configuration differs from that of forests used by Boreal Owls across the rest of their North American breeding distribution, where they occur in more contiguous, old-growth conifer forests for foraging and roosting, but conduct breeding activities in deciduous forests with a high proportion of potential nesting trees (e.g., >33 cm dbh; Bondrup-Nielsen 1978, Ryder et al. 1987, Hayward et al. 1993).

When using an HSI approach to assess habitat suitability, the model must first be tested for accuracy and reliability (Block et al. 1994, Brooks 1997). Given the lack of local data for Boreal Owls in Newfoundland, such testing is essential if the model is to be applied to the development of forest and species management strategies. Sensitivity analyses can identify parameters that most influence model performance or output, and highlight parameters of the model that need field-testing to improve predictive accuracy (Stoms et al. 1992). Preliminary analyses of this Boreal Owl HSI model determined that home-range size, foraging radius (i.e., distance moved by owls when foraging), and density of living and dead trees >30 cm dbh in nesting areas were the most sensitive parameters (X. Zhu unpubl. data). Estimates for these parameters were derived for the initial model based on studies conducted in Ontario, Alberta, and the northern United States (Côté et al. 2004). Using field data to validate an HSI model is generally accepted as a robust technique (Brooks 1997). Presence/absence or abundance data can be overlaid on a habitat suitability map to validate the accuracy of the model in a given area (Rickers et al. 1995), but a more powerful test is to combine sensitivity analyses and field data (Roloff and Kernohan 1999, Mitchell et al. 2002).

Our objectives were to examine habitat use by Boreal Owls in western Newfoundland and assess the effectiveness of an HSI model constructed on the basis of range-wide data (the Range-wide Model) versus one that incorporated existing locally collected data (the revised Newfoundland Model). To accomplish this, we compared the forest composition of locations in western Newfoundland where Boreal Owls occurred (i.e., Boreal Owl home ranges delineated using radiotelemetry and point counts with Boreal Owl detections) to that of random locations (surrogate home ranges where no Boreal Owls were detected) reflecting the overall availability of different forest cover types across the study area. To assess differences in Boreal Owl HSI model performance, we compared outputs from the Range-wide Model with those outputs generated using the Newfoundland Model. Finally, we used the Range-wide HSI Model to evaluate how three different forest harvesting scenarios would affect the amount of suitable Boreal Owl habitat available over the next 20, 40, and 60 yr.

METHODS

Study Area. Our study focused on Forest Management District 15 (Fig. 1), which encompasses approximately 560,000 ha of the Western Newfoundland ecoregion (Damman 1983) on the island of Newfoundland, Canada (48°95'N, 57°95'W). These forests are dominated by conifers, mainly self-regenerating stands of balsam fir with scattered patches of black spruce (*Picea mariana*); white spruce (*Picea glauca*), white birch (*Betula papyrifera*), white pine (*Pinus strobus*), red maple (*Acer rubrum*), and eastern larch (*Larix laricina*) also occur at low densities. Timber harvesting for paper production began in 1924, although small-scale harvesting has occurred for other purposes since the late 1800s; approximately 87,000 ha of the area is productive forest (Government of Newfoundland and Labrador 2014). The amount of old-growth forest (i.e., ≥80 yr) in Newfoundland has declined with a shift in forest management from harvest rotations up to 120 yr (S. Balsom pers. comm.) toward 60-yr rotations, which has reduced the amount of available suitable habitat for old-growth forest specialists (Thompson et al. 1999).

Point Counts and Related Statistical Analyses. We conducted surveys throughout the study area from mid-February through mid-April during 2006 and 2007 to determine the distribution and habitat associations of breeding Boreal Owls (Munro

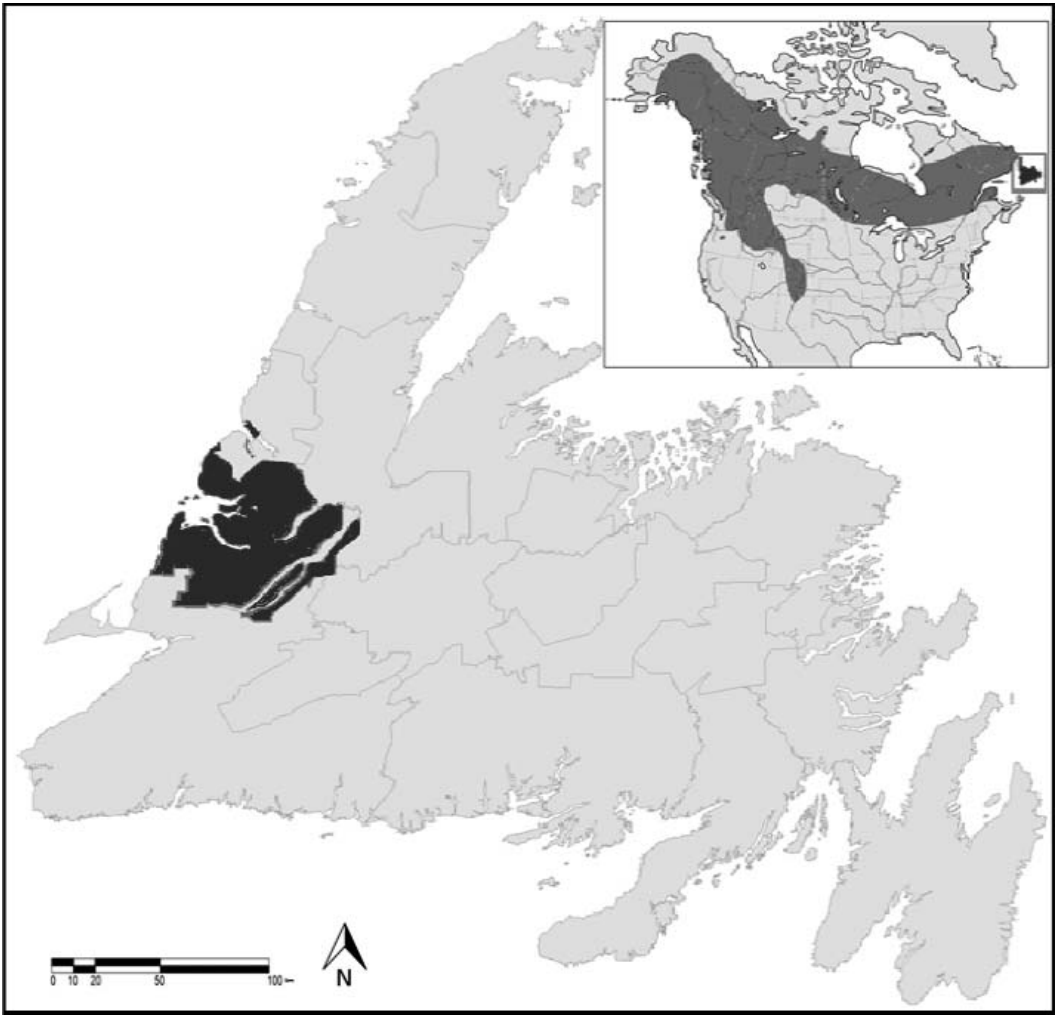


Figure 1. Forest Management District 15 (shaded) on the island of Newfoundland, which is located at the easternmost portion of the Boreal Owl distribution in North America (see inset with Boreal Owl breeding distribution in dark gray). Adapted from Hayward and Hayward (1993).

2012). We focused on this period for our analyses because of the heightened likelihood of response to broadcasted Boreal Owl songs associated with increased territoriality during the breeding season (Hayward and Hayward 1993). Surveys centered on rural portions of the study area that contained old-growth coniferous forests, mixedwood forests, regenerating forests, and clear-cuts (i.e., areas where most trees had been removed via harvest). We located point counts, separated by ≥ 1 km, along transects randomly allocated to existing secondary roads or trails that were accessible by truck, all-

terrain vehicle, or snowmobile. We conducted single-visit, 15-min point counts with alternating silent listening periods and broadcasts of a Boreal Owl primary (or staccato) song (see Bondrup-Nielsen 1984, Hayward et al. 1993) using a Nexxtech compact disc player (The Source [Bell] Electronics Inc., Barrie, Ontario, Canada; peak reported volume 112 dB). Broadcasts began with 3 min of silence followed by 2 min of broadcasting Boreal Owl songs; this sequence was repeated throughout the 15-min count period. Surveys began 1 hr after sunset and continued until 1 hr before sunrise on nights with

Table 1. Description of cover types used in Boreal Owl HSI models and extent (% of study area) in District 15, western Newfoundland, Canada.

COVER TYPE	DESCRIPTION	PERCENT OF STUDY AREA
Disturbed	Forest stands with wind or insect mortality; regenerating forest stands between 9–20 yr of age; regenerating forest stands subjected to silviculture treatment; forest stands subjected to silviculture treatments in the last 8 yr; stands harvested via clearcutting in the last 8 yr	15.2
Bog	Bogs/peatlands	11.5
Scrub	Forest land with >10% crown closure not capable of producing 30 m ³ /ha of wood at 60 yr	29.8
Deciduous	Pure deciduous stands >21 yr of age	0.9
Young mixedwood	Mixed deciduous/coniferous stands, 21–60 yr plus mixed-aged stands <60 yr	2
Mature-to-old-growth mixedwood	Mixed deciduous/coniferous stands 61 yr or older	8.9
Young coniferous	All coniferous stands between 21–60 yr of age	10.7
Mature-to-old-growth coniferous	All coniferous stands 61 yr of age or older	21.2

negligible rain or snow and winds <Beaufort 3 (12–19 km/hr). We used Kruskal-Wallis multiple comparison tests with a Bonferroni correction to compare the percent cover of selected cover types between occupied sites (point counts where we detected Boreal Owls and Boreal Owl home ranges identified with radiotelemetry) and apparently unoccupied sites (random surrogate home ranges; see description of surrogate home ranges below). We used a Tukey-type test for multiple comparisons among medians to isolate significant differences among groups (Zar 1999). Because our analyses indicated that many point count locations where we failed to detect a Boreal Owl could be considered as suitable (see Results), we did not include comparisons of cover types between occupied and unoccupied point counts.

Boreal Owl Habitat Suitability Index Model.
Habitat classification. We based our analyses on digitized forest inventory data developed for the provincial Forest Resources Division (Department of Natural Resources, Government of Newfoundland and Labrador, Corner Brook, Newfoundland and Labrador, Canada) from aerial photography for 2005 and updated with all forest management activity occurring in 2006 and 2007. We separated forested cover types into categories using the standardized classification scheme for the province, which assigns landscape elements to a variety of cover types (e.g., forest, bog, barrens, water) and further characterizes those landscape elements based on dominant species composition and esti-

mated 20-yr age classes. Non-forest cover included a variety of woody and nonwoody cover types (scrub and stand remnants, bogs and barrens; see Table 1 for definitions and overall percent cover for each type).

For our HSI modeling process, we considered stand age to be an important characteristic because it reflects stand structure (as assessed through interpretation of aerial photos) and hence suitability for nesting. In Newfoundland, stands are typically categorized as immature (0–20 and 21–40 yr), mature (41–60 and 61–80 yr), or overmature (old-growth; 81–100, 101–120, >120 yr) because of the very limited growth for most forests, with stands rarely reaching 100 yr old before senescence begins (Moroni 2006). As well, the forest harvest rotation in Newfoundland can be as short as 60 yr where productivity is high (Smith et al. 2008). Consequently, for Boreal Owl management in western Newfoundland, we believed it would be informative to examine forest stands ≥60 yr as distinguished from younger stands, given both their importance to Boreal Owls as “mature” forest and their potential value as a target for harvesting. Separating forest age classes into those <60 yr (young) and those ≥60 yr (mature-to-old-growth) was also necessary due to limitations on the number of parameters that could be successfully modeled with the sample sizes available. Thus, we identified all forest stands by general classification type and age class, creating eight categories for these analyses (disturbed, bog, scrub, deciduous, young mixedwood, mature-to-old-

growth mixedwood, young coniferous, mature-to-old-growth coniferous).

Model equations. Our Boreal Owl HSI development (both models) incorporated nesting and foraging habitats simultaneously using spatially explicit relationships (Côté et al. 2004). Focused on $25\text{ m} \times 25\text{ m}$ pixels as the base unit, the Range-wide Model assigned HSI values for each pixel in the study area by calculating the mean HSI pixel-value for individual parameters within a radius of 1784 m (i.e., sampling all pixels within a circle of 1000 ha for the Range-wide Model, see below for comparable input for the Newfoundland Model) corresponding to a “neighborhood window” surrounding a given point. These 1000-ha circles represent Boreal Owl breeding-season home-range area requirements in other parts of their North American distribution (Hayward et al. 1993). Thus, calculated HSI values for each pixel were:

$$\text{HSI} = \text{Window} (\text{HSI}_{\text{local}})_{1784\text{ m}}$$

where,

$$\text{HSI}_{\text{local}} = [\text{NESTING} * \text{FORAGING}]^{1/2},$$

where NESTING and FORAGING represented the suitability values for the nesting and the foraging components, respectively (Côté et al. 2004). For this study, “nesting” referred to resources conducive to courtship and breeding, assuming that the presence of a male Boreal Owl indicated adequate breeding resources during the survey period.

The NESTING component of both HSI models reflected nest-site availability, which is primarily associated with the abundance of large stems capable of supporting nesting cavities (Bondrup-Nielsen 1978, Hayward et al. 1993, Kirk 1995). Côté et al. (2004) also developed an algorithm to estimate the density of live and dead stems with a dbh ≥ 30 cm (and a related HSI value) for each pixel based on data from permanent sample plots across the island and corrected for the species composition, site type, canopy cover, and stand age of a given location. Similarly, Côté et al. (2004) developed the FORAGING component to reflect the combination of open areas and their proximity to forest edges from which “sit-and-wait” hunting forays could be launched. Forest edges may be particularly important for Boreal Owls in Newfoundland due to the relative availability and vulnerability of small mammals in forest openings versus interiors (Hayward et al. 1993,

Whitman 2001) and the relatively limited small mammal prey base in Newfoundland (Thompson and Curran 1995). The FORAGING component of both models was determined using the sum of the “Adjusted Foraging Habitat Quality” (AFHQ) values for each pixel within a 500-m radius of a given point (Côté et al. 2004). The AFHQ parameter was a product of cover density categories (i.e., openings in the forest, three levels of forest cover, and water) that incorporated the distance between the center of the open foraging habitat and the nearest forest cover. Pixels in open habitat were assigned a value of 1 and water bodies had a value of 0; pixels in forested areas ranged from 0.25 (high stem density), to 0.5 (intermediate) and 0.75 (low stem density).

HSI Model Testing. Our analyses utilized an input shapefile created in ArcMap 9.2 (ESRI Redlands, CA, U.S.A.) to represent the digitized forest inventory data for the study area for 2006 and 2007. This resulted in two input shapefiles for 2006 and 2007. “Range-wide Model outputs” refer to outputs from 2006 and 2007 created with the Range-wide HSI Model based on expert opinion and literature review. “Newfoundland Model outputs” refer to outputs from model runs for both years using a smaller home-range radius of 1380 m (versus 1784 m in the Range-wide Model) based on average home-range sizes of eight radio-marked Boreal Owls in western Newfoundland (Munro 2012).

To represent the HSI values for home-range-sized areas available at random locations within the study area, we used the Animal Movement extension of ArcView 3.2 (ESRI 2008) to create 80 randomly placed surrogate home ranges, from which 40 were subsequently chosen at random. We excluded surrogate home ranges containing more area (i.e., $>12\%$) covered by water than found on average in the owl minimum convex polygon (MCP) home ranges (Munro 2012), and any that contained residential land cover. We created surrogate home ranges based on the largest reported home-range value in North America, 2386 ha (Hayward et al. 1993) to ensure adequate representation of cover types available in potential home ranges.

We compared the forest-cover composition among surrogate home ranges, point counts where Boreal Owls were present, and the estimated home ranges occupied by Boreal Owls as determined using telemetry (from Munro 2012). For each point count where we detected Boreal Owls, we calculated the proportion of each cover type within a 500-m area around the point, and the representative HSI value.

For home ranges estimated using radiotelemetry, we determined the proportional area of each cover type and respective HSI values based on MCP representations of the home range. We compared the HSI values for occupied point counts and estimated Boreal Owl home ranges relative to those determined for the 40 random surrogate home ranges using the log-ratio compositional analysis method (Aebischer et al. 1993; program Smith Ecology Compos Analysis 6.2 std., Smith 2008). We represented these data in 0.05- or 0.1-increment HSI value classes to demonstrate the relative distribution of HSI values assigned to locations used by or available to Boreal Owls in our study area, and in forward projection model outputs.

We tested chance correctness of the models using Cohen's MaxKappa statistic. We buffered point count locations (both with owls present, and where owls were not detected) with a 500-m exclusion zone so as to not overlap with adjacent points. Using the pixels within the 500-m exclusion zone, we extracted a weighted mean HSI value for each point. We used these mean values to analyze and assess each model's predictive capabilities based on the chance-corrected classification method of Titus and Mosher (1984). However, instead of determining Kappa, we used the threshold-independent method MaxKappa (Guisan et al. 1998) to lessen dependence on arbitrarily defining what was considered "suitable" (Hirzel et al. 2006). To determine whether distributions and means of HSI outputs differed between years, we performed Kolmogorov-Smirnov and Student's *t*-tests on HSI values calculated for points where owls were present and those where they were not detected, and for surrogate and estimated home ranges. There was no difference in HSI distributions between estimated home ranges and surrogate home ranges in 2006 and 2007; therefore, these data were pooled when testing each model's chance of correctness.

HSI Model Forward Projections. To assess how the amount of suitable habitat might change over time and under different harvest regimes, we examined the output from forward projection models developed for District 15 under three scenarios with varying distributions of harvest blocks and harvest levels across the landscape. The Business As Usual (BAU) scenario incorporated the current forest management practices in District 15. With BAU, the minimum industry harvest block size (i.e., areas to be cut on industry-controlled land) was 5 ha with a 200-m adjacency (i.e., all harvest clearings within 200

m of each other belong to the same harvest block). The minimum Crown Land harvest block (i.e., areas to be harvested on provincial-government-owned land under lease to industry) was 1 ha, with a 200-m adjacency, with no maximum block size or time delay in harvest to enable forest regeneration on recently cut nearby harvest blocks (R. Sutton pers. comm.). The Aggregated (AGR) scenario incorporated a pattern of large "aggregated" harvest blocks across the landscape. The minimum harvest block size for this scenario was 100 ha (industry and Crown), with a 200-m adjacency, a target harvest block size of 300 ha, and a maximum harvest block size of 800 ha (R. Sutton pers. comm.). The Fragmented (FRA) scenario incorporated a pattern of small harvest blocks across the landscape. The minimum harvest block size for this scenario was 10 ha (industry and Crown), with a 200-m adjacency, a maximum block size of 100 ha, and a 5-yr delay for forest regeneration within 200 m of any harvested block (R. Sutton pers. comm.).

We used Woodstock and Stanley (hereafter W-S) versions 3.00.0 and 4.5, respectively (Remsoft Inc. 2004), to develop a 60-yr harvest schedule for each of the three forest management scenarios. Once we completed a W-S run for a given scenario, we created an output for the forest structure (age and species composition) for 20-, 40- and 60-yr periods. We compared each forest management scenario over the three periods to assess differences in the distribution of HSI scores within 0.1 incremental HSI value classes using Friedman's two-way ANOVA tests. Similarly, we assessed 0.1 incremental HSI value class distributions across management scenarios for each projection period. We determined statistical significance based on using a Bonferroni corrected $\alpha = 0.05/6 = 0.008$ for these tests. We performed all statistical tests in Minitab v. 16.1.1 (2010), unless otherwise noted. Because of limited improvement in the Newfoundland HSI Model that included revised home-range estimates from Newfoundland, we only ran forward projections using the Range-wide HSI Model parameters.

RESULTS

Habitat Selection. Boreal Owls were detected at 76 of the 310 point-count locations (25%) visited from mid-February to mid-April, during the breeding seasons of 2006 ($n = 43$) and 2007 ($n = 33$). The land cover associated with locations where we detected Boreal Owls (i.e., occupied point counts and estimated home ranges identified using radio-

Table 2. Comparison of percent cover type (median and range) among occupied sites (point counts where owls were detected, $n = 73$; and estimated Boreal Owl home ranges delineated using radiotelemetry, $n = 8$) and unoccupied sites (random surrogate home ranges, $n = 40$) during 2006–2007 in western Newfoundland, Canada. *P*-values in bold are significant based on a Kruskal–Wallis multiple comparison test ($\alpha = 0.05/8 = 0.00625$).^a

COVER TYPE	POINT COUNTS	ESTIMATED HOME RANGES	SURROGATE HOME RANGES	<i>P</i> -VALUE
Bog	4.8 (0–42.1)	4.0 (1.1–8.2)	4.0 (0–97.5)	0.769
Disturbed	28.4 (0–87.2) ^b	36.5 (14.0–66.8) ^a	8.2 (0–55.2) ^c	0.002
Scrub	10.4 (0–49.4)	8.1 (2.9–33.2)	16.2 (2.4–100)	0.035
Deciduous	0 (0–6.6) ^b	0 (0–0.1) ^b	0 (0–13.5) ^a	0.001
Young coniferous (<60 yr)	11.3 (0–81.4)	11.1 (0–69.8)	4.6 (0–67.5)	0.091
Mature-to-old-growth coniferous (>60 yr)	17.3 (0–67.6)	20.9 (3.5–50.8)	16.4 (0–73.3)	0.910
Young mixedwood (<60 yr)	0 (0–27.5)	0 (0–2.8)	0 (0–16.5)	0.211
Mature-to-old-growth mixedwood (>60 yr)	0 (0–21.6) ^b	0 (0–3.7) ^c	3.3 (0–67.2) ^a	<0.001

^a Values with different superscripted letters were significantly different from each other based on Tukey-type post-hoc comparisons.

telemetry; Munro 2012) differed from the land cover randomly available in the study area (i.e., on surrogate home ranges where no Boreal Owls were detected). Specifically, we found a greater proportion of the disturbed cover type among occupied sites (point counts and estimated home ranges) when compared to unoccupied (surrogate home range) sites (Kruskal–Wallis test; $H = 12.53$, $P = 0.002$) but lesser proportions of both deciduous ($H = 14.50$, $P = 0.001$) and mature-to-old-growth (≥ 60 yr) mixedwood ($H = 29.56$, $P < 0.001$) cover types (Table 2). The amount of disturbed cover was higher in estimated home ranges (Tukey-type post-hoc test; mean percentage \pm SD; $38.5 \pm 22.0\%$) than at occupied point counts ($31.2 \pm 23.7\%$) and also higher at occupied point counts than in surrogate home ranges ($16.0 \pm 19.0\%$; Table 2). Although frequently absent in the landscape, mature-to-old-growth mixedwood cover was significantly more abundant in surrogate home ranges ($9.2 \pm 13.8\%$) than at occupied point counts ($1.7 \pm 3.9\%$) and least common in estimated home ranges ($0.8 \pm 1.4\%$; Table 2). The amount of deciduous cover also was limited in extent overall, but we found statistically significantly higher amounts of deciduous cover in surrogate home ranges ($0.9 \pm 2.8\%$) than in either estimated Boreal Owl home ranges ($0.1 \pm 0.1\%$) or at occupied point counts ($0.2 \pm 1.0\%$; Table 2).

Assessing Habitat Suitability Models. Forests in District 15 of western Newfoundland had low but similar levels of suitability across the 2 yr of study and regardless of whether we used the Range-wide or Newfoundland versions of the HSI Model (Fig. 2). HSI values for the entire study area ranged from 0 to

0.60, whereas those for point counts ranged from 0.06 to 0.55 and those for home ranges extended from 0 to 0.35 (estimated) or 0 to 0.45 (surrogate). The HSI composition of point counts where Boreal Owls were present differed significantly from what was available at random in surrogate home ranges

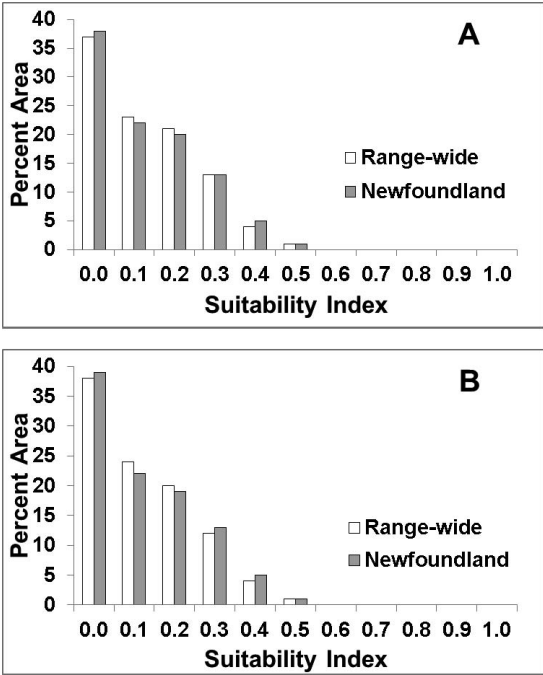


Figure 2. Percent of area in each 0.1-incremental habitat suitability index value class for the study area in western Newfoundland using both Range-wide and Newfoundland Boreal Owl HSI Model outputs in (A) 2006 and (B) 2007 (see Methods for model descriptions).

Table 3. Cohen’s MaxKappa analysis for the prediction of presence (detected) and absence (not detected) of Boreal Owls in western Newfoundland, Canada, by model type and year (percent in parentheses). The Range-wide HSI Model used literature values from across the North American distribution; the Newfoundland Model used estimates of home-range size from local field sampling.

	RANGE-WIDE MODEL PREDICTIONS				NEWFOUNDLAND MODEL PREDICTIONS			
	2006		2007		2006		2007	
	CORRECT	INCORRECT	CORRECT	INCORRECT	CORRECT	INCORRECT	CORRECT	INCORRECT
Owls detected	43 (100)	0 (0)	28 (85)	5 (15)	43 (100)	0 (0)	28 (85)	5 (15)
No owls detected	90 (96)	4 (4)	94 (67)	46 (33)	90 (96)	4 (4)	92 (66)	48 (34)
MaxKappa statistic	0.0271		0.0872		0.0271		0.0953	
P-value	0.9145		0.9750		0.9145		0.9839	

across the study area (log-ratio compositional analysis; Range-wide Model 2006: $\Delta = 0.0205$; $X^2 = 167.14$, $P < 0.001$; Range-wide Model 2007: $\Delta = 0.0699$; $X^2 = 87.83$, $P < 0.001$; Newfoundland Model 2006: $\Delta = 0.0279$; $X^2 = 153.88$, $P < 0.001$; Newfoundland Model 2007: $\Delta = 0.0454$; $X^2 = 102.01$, $P < 0.001$). Boreal Owls showed a preference for ≥ 0.41 and $0.36\text{--}0.40$ HSI classes and avoided $0\text{--}0.05$ and $0.06\text{--}0.10$ HSI classes. Similarly, HSI values for estimated male Boreal Owl home ranges differed significantly from what was available at random in both models (Range-wide Model: $\Delta = 0.0594$; $X^2 = 167.14$, $P < 0.01$; Newfoundland Model: $\Delta = 0.0311$; $X^2 = 27.77$, $P < 0.001$). In each comparison, Boreal Owls showed a preference for ≥ 0.36 and $0.31\text{--}0.35$ HSI classes and avoided $0.16\text{--}0.20$ and $0\text{--}0.05$ HSI classes.

Both HSI Models correctly predicted the presence of Boreal Owls with success ranging from $85\text{--}100\%$ between years and model types, with only 5 of 74 (7%) individuals present at locations where HSI models predicted owl absence (Table 3). All model runs indicated a large proportion of sites ($53\text{--}66\%$) where Boreal Owls were expected to be present but were not detected and only $3\text{--}31\%$ that were predicted to be unsuitable but had owls present. Assessments of chance correctness indicated, however, that overall accuracy was not greater than expected based on random chance (Table 3).

HSI Model Forward Projections. HSI values were similar among the three harvesting scenarios and across periods (Fig. 3). Average HSI values in District 15 under the AGR scenario at 40 yr were significantly lower than HSI values for both BAU and FRG scenarios at 40 yr ($S = 11.09$, $P < 0.008$). Otherwise, there were no significant differences within or between forest-harvesting scenarios across projected periods.

DISCUSSION

Boreal Owls in Newfoundland use mature, spruce-fir dominated forests interspersed with recently cleared areas, consistent with habitat preferences reported from North America (Bondrup-Nielsen 1978, Hayward et al. 1993) and Europe (Korpimäki 1981, Solheim 1983, Dejaifve et al. 1990). However, in Newfoundland, Boreal Owls occur in a landscape where mixedwood and deciduous stands are less prominent cover types than reported elsewhere (Korpimäki 1988, Hayward et al. 1993). In part, the absence of mixedwood and deciduous cover from the forests occupied by Boreal Owls in Newfoundland is simply a reflection of availability in this conifer-dominated system and confirms the earlier findings of Gosse and Montevocchi (2001), but these differences (and apparent avoidance of this deciduous component of the landscape) also may be linked to nest-site selection. In Ontario and the U.S.A., deciduous and mixedwood forests provide high numbers of nesting cavities (Bondrup-Nielsen 1978, Hayward et al. 1993, Lane 1997). By contrast, nesting cavities are potentially becoming rare across the Canadian boreal forest (Kirk 1995), particularly in areas where commercial logging has limited the presence of mature forest on the landscape (Imbeau et al. 2001). The scattered small patches of deciduous trees and mixedwood stands in Newfoundland may simply fail to provide sufficient suitable nest sites which, along with high prey density, are a key predictor of Boreal Owl occurrence (Hayward et al. 1993). Instead, Boreal Owls are attracted to stands characterized as “coniferous” by forest inventory assessments, but that frequently contain low densities of large-dbh deciduous trees and snags that are remnants of earlier successional stages or past forest cohorts in these otherwise even-aged stands. It is also

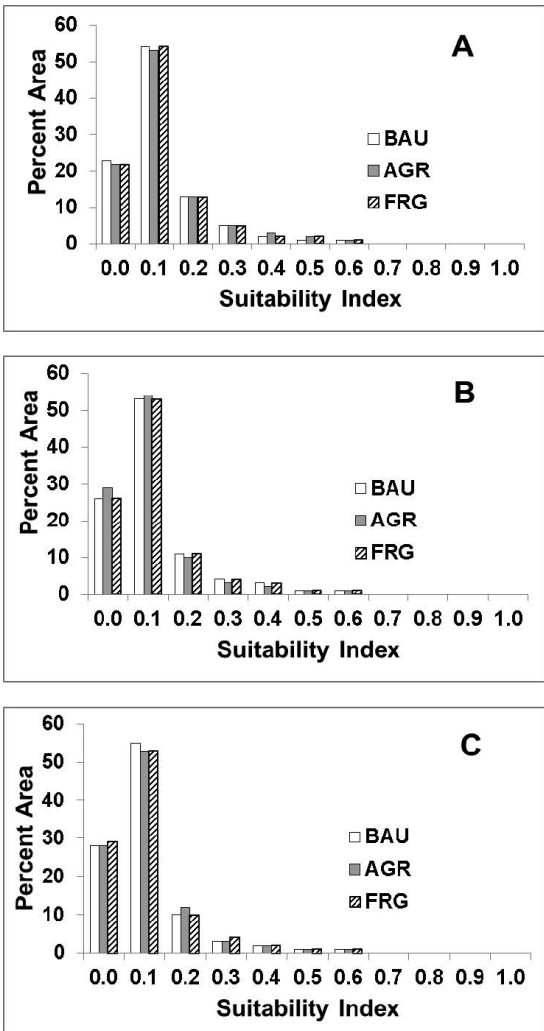


Figure 3. Projections for percent of area in each 0.1-incremental habitat suitability index value class at (A) 20, (B) 40, and (C) 60 yr into the future based on the Range-wide Boreal Owl HSI Model and using three forest management scenarios: Business As Usual (BAU), Aggregated (AGR), and Fragmented (FRG); see Methods for descriptions of management scenarios.

important to note that Northern Flickers (*Colaptes auratus*) are the sole providers of excavated cavities large enough for Boreal Owls in Newfoundland (Smith et al. 2008) and these excavators may also avoid deciduous and mixedwood stands for nesting in this region. The prominence of disturbed cover (characterized as recently cut or regenerating stands, etc.) in estimated home ranges and at

point-count locations where we detected Boreal Owls reflects foraging habitat that may be preferred by Boreal Owls in Newfoundland because snow melts faster and prey may be more accessible in these openings when compared to closed-canopy forest locations (Sonerud 1986).

Not surprisingly, Boreal Owls associated more often with sites (point counts where owls were detected and estimated home ranges) having higher HSI values than randomly available (as represented by surrogate home ranges). However, although an HSI model will typically assign higher scores to high quality habitat (i.e., 0.7–1.0) and lower scores to low quality habitat (i.e., 0.0–0.3), such results are not always obtained (Brooks 1997). The HSI values produced by both of our models were relatively low, ranging from 0.0–0.6, suggesting that our study area contains habitat that would be deemed less suitable in other portions of the Boreal Owl's breeding distribution in North America. HSI values remained low even after adjusting our model to incorporate home-range sizes derived from Boreal Owls in Newfoundland. This may indicate that the Range-wide HSI Model we used does not include all of the key parameters influencing Boreal Owls in Newfoundland. More extensive local data for sensitive model parameters (home-range size, foraging radius, and nest-site characteristics) would likely have enabled a more detailed assessment of our Range-wide versus Newfoundland Models. However, as Brooks (1997) also noted, uncalibrated HSI models (those developed without using local information to build the model) often generate scores with mid-range values, between 0.3 and 0.7, which may limit their capacity to assess differences in quality among sites. The long-term persistence of a Boreal Owl population in Newfoundland demonstrates that suitable habitat exists (given the limited likelihood of net immigration due to the isolation of this population), but what constitutes suitable habitat clearly differs among Boreal Owl populations across North America. Such circumstances are not completely unexpected. Populations at the periphery of a species' breeding distribution have been found to occupy what would be low-quality habitat for individuals in more central portions of distribution (Kawecki 2008, Romeo et al. 2010). Consequently, the nature of what constitutes suitable habitat can differ between populations at the core of the species' range and those at the edge. It would be valuable to test our Range-wide HSI Model in other parts of the

Boreal Owl breeding distribution to determine the broader applicability of this model.

The predictive capacity of our HSI models was no better than chance; however, almost all of the owls we detected were at locations with relatively high HSI values, and we detected few individuals in areas with low HSI values. The results of our modeling efforts may alternatively suggest that many suitable sites (i.e., sites with comparable HSI values to those where we detected Boreal Owls) are not currently occupied, indicating either our failure to detect Boreal Owls when they were present or that not all suitable habitat is occupied by Boreal Owls in our study area. We did not revisit points during the breeding season and were, therefore, not able to evaluate detection probability; future testing of HSI models could be improved through a better understanding of Boreal Owl detection probability in our study area.

Future study and HSI model development also will need to consider the changing prey base on Newfoundland. Meadow voles (*Microtus pennsylvanicus terraenovae*), the only indigenous prey species for Boreal Owls on Newfoundland, occur at low densities in both open (Folinsbee et al. 1973) and forested areas (Thompson and Curran 1995, Sturtevant and Bissonette 1997). Recent introduction of southern red-backed voles (*Clethrionomys gapperi*), the Boreal Owl's main prey species across much of its distribution (Korpimäki 1981, Hayward et al. 1993), has increased the potential prey base in forested areas (Hearn et al. 2006) and may influence habitat quality.

We failed to identify substantial changes in the amount of suitable habitat, identified based on HSI models, resulting from different forest harvest strategies. This finding suggests that natural fragmentation and anthropogenic fragmentation provide habitat of similar suitability for Boreal Owls, which was unexpected given the negative impact of anthropogenic landscape disturbance on this species elsewhere (Bondrup-Nielsen 1978, Korpimäki 1988, Hayward et al. 1993, Sleep 2005). Given that Boreal Owls in western Newfoundland appear to use habitat differently than individuals from mainland North American populations, effective management will require population-specific information.

ACKNOWLEDGMENTS

This work was supported by the Government of Newfoundland and Labrador's Wildlife Division and the

Institute for Biodiversity and Ecosystem Science, the Western Newfoundland Model Forest Biodiversity Assessment Program, Institut Québécois d'Aménagement de la Forêt Feuille, Corner Brook Pulp and Paper Ltd., the College of the North Atlantic's Geospatial Research Facility, Memorial University of Newfoundland, and the Natural Sciences and Engineering Research Council of Canada. Sharon Russell, Kevin Mitchell, Liz Moulton, Joe Brazil, and Bruce Rodriguez contributed to data collection; Soren Bondrup-Nielsen and Jim Duncan provided constructive comments. We conducted the associated fieldwork under federal permit 10475. The field protocol was approved by the Memorial University Institutional Animal Care Committee (07-09-IW).

LITERATURE CITED

- AEBISCHER, N.J., P.A. ROBERTSON, AND R.E. KENWARD. 1993. Compositional analysis of habitat use from radio-tracking data. *Ecology* 74:1313–1325.
- BETTS, M.G., G.J. FORBES, A.W. DIAMOND, AND P.D. TAYLOR. 2006. Independent effects of habitat amount and fragmentation on songbirds in a forest mosaic: an organism-based approach. *Ecological Applications* 16:1076–1089.
- BISSETTE, J.A., R.J. FREDERICKSON, AND B.J. TUCKER. 1989. American marten: a case for landscape-level management. *Transactions of the North American Wildlife and Natural Resources Conference* 54:89–101.
- BLOCK W.M., M.L. MORRISON, J. VERNER, AND P.N. MANLEY. 1994. Assessing wildlife-habitat-relationships models: a case study with California oak woodlands. *Wildlife Society Bulletin* 22:549–561.
- BONDURUP-NIELSEN, S. 1978. Vocalizations, nesting, and habitat preferences of the Boreal Owl (*Aegolius funereus*) in North America. M.S. thesis, Univ. of Toronto, Toronto, ON Canada.
- . 1984. Vocalizations of the Boreal Owl, *Aegolius funereus richardsoni*, in North America. *Canadian Field-Naturalist* 98:191–197.
- BRADSHAW, C.J.A., I.G. WARKENTIN, AND N.S. SODHI. 2009. Urgent preservation of boreal carbon stocks and biodiversity. *Trends in Ecology and Evolution* 24:541–548.
- BROOKS, R.P. 1997. Improving habitat suitability index models. *Wildlife Society Bulletin* 25:163–167.
- CÔTÉ, M., F. DOYON, AND N. BERGERON. 2004. Spatially explicit habitat suitability index model for the Boreal Owl (*Aegolius funereus*) in western Newfoundland, version 2. Institut Québécois d'Aménagement de la Forêt Feuille, Ripon, Québec, Canada.
- DAMMAN, A.W.H. 1983. An ecological subdivision of the Island of Newfoundland. Pages 163–206 in G.R. South [Ed.], *Biogeography and ecology of the Island of Newfoundland*. Dr. W. Junk Publishers, The Hague, Netherlands.
- DEJAIFVE, P.A., C.A. NOVA, AND R. PRODON. 1990. Habitat et densité de la chouette de Tengmalm (*Aegolius funereus*) à l'extrémité orientale des Pyrénées. *Alauda* 58:267–273.

- DOLTER, C.S. 2005. Using biodiversity indicators to assess the success of forecasting adaptive ecosystem management: the Newfoundland and Labrador experience. Pages 448–454 in C. Aguirre-Bravo, P.J. Pellicane, D.P. Burns, and S. Draggan [Eds.], *Monitoring science and technology symposium: unifying knowledge for sustainability in the western hemisphere*. Proceedings RMRS-P-42CD. U.S.D.A. Forest Service, Rocky Mountain Research Station, Fort Collins, CO U.S.A.
- ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE (ESRI). 2008. ArcView v. 3.2-Animal Movement Extension. ESRI: GSI and Mapping Software, Redlands, CA U.S.A.
- FOLINSBEE, J.D., R.R. RIEWE, W.O. PRUITT, AND P.R. GRANT. 1973. Ecological distribution of the meadow vole *Microtus pennsylvanicus terraenovae*, (Rodentia: Cricetidae), on the Main Island of Newfoundland. *Canadian Field-Naturalist* 87:1–4.
- GOSSE, J.W. AND W.A. MONTEVECCHI. 2001. Relative abundance of forest birds of prey in western Newfoundland, Canada. *Canadian Field-Naturalist* 115:57–63.
- GOVERNMENT OF NEWFOUNDLAND AND LABRADOR. 2014. Crown five-year operating plan: forest management districts 14 and 15, 2014–2018. Forestry and Agrifoods Agency. http://www.faa.gov.nl.ca/forestry/managing/pdf/fmd_14_15yr_plan_14_18.pdf (last accessed 2 January 2016).
- GUISAN, A., J.P. THEURILLAT, AND F. KIENAST. 1998. Predicting the potential distribution of plant species in an alpine environment. *Journal of Vegetation Science* 9:65–74.
- HASKELL, J.P., M.E. RITCHIE, AND H. OLFF. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature* 148:527–530.
- HAYWARD, G.D. 1994. [Ed.] *Flammulated, Boreal and Great Gray owls in the United States: a technical conservation assessment*. U.S.D.A. Forest Service Gen. Tech. Report RM-253. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO U.S.A.
- . 1997. Forest management and conservation of Boreal Owls in North America. *Journal of Raptor Research* 31:114–124.
- AND P.H. HAYWARD. 1993. Boreal Owl (*Aegolius funereus*). In A. Poole [Ed.], *The birds of North America* online, No. 063. Cornell Lab of Ornithology, Ithaca, NY U.S.A. <http://bna.birds.cornell.edu/bna/species/063> (last accessed 25 June 2016).
- , ———, AND E.O. GARTON. 1993. Ecology of Boreal Owls in the northern Rocky Mountains, USA. *Wildlife Monographs* 24:3–59.
- HEARN, B.J., J.T. NEVILLE, W.J. CURRAN, AND D.P. SNOW. 2006. First record of the southern red-backed vole, *Clethrionomys gapperi*, in Newfoundland: implications for the endangered Newfoundland marten, *Martes americana atrata*. *Canadian Field-Naturalist* 120:50–56.
- HIRZEL, A.H., G. LE LAY, V. HEFLER, C. RANDIN, AND A. GUISAN. 2006. Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 199:142–152.
- IMBEAU, L., M. MÖNKÖNEN, AND A. DESROCHERS. 2001. Long term impacts of forestry on birds of the eastern Canadian boreal spruce forests: what can we learn from the Fennoscandian experience? *Conservation Biology* 15:1151–1162.
- KAWECKI, T.J. 2008. Adaptation to marginal habitats. *Annual Review of Ecology, Evolution and Systematics* 39:321–342.
- KIRK, D.A. 1995. Status report of the Boreal Owl *Aegolius funereus* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, ON Canada.
- KOOPMAN, M.E., G.D. HAYWARD, AND D.B. McDONALD. 2007. High connectivity and minimal genetic structure among North American Boreal Owl (*Aegolius funereus*) populations, regardless of habitat matrix. *Auk* 124:690–704.
- KORPIMÄKI, E. 1981. On the ecology and biology of Tengmalm's Owl (*Aegolius funereus*) in southern Ostrobothnia and Suomenselka, western Finland. *Acta Universitatis Ouluensis A* 118 *Biology* 13:1–84.
- . 1988. Diet of breeding Tengmalm's Owl (*Aegolius funereus*): long-term changes and year-to-year variation under cyclic food conditions. *Ornis Fennica* 65:21–30.
- LANE, W.H. 1997. Distribution and ecology of Boreal Owls in northeastern Minnesota. M.S. thesis, Univ. Minnesota, St. Paul, MN U.S.A.
- MARTIN, K. AND J.M. EADIE. 1999. Nest webs: a community-wide approach to the management and conservation of cavity-nesting forest birds. *Forest Ecology and Management* 115:243–257.
- MINITAB, INC. 2010. Minitab 16.1.1 Statistical Software, State College, PA U.S.A.
- MITCHELL, M.S., J.W. ZIMMERMAN, AND R.A. POWELL. 2002. Test of a habitat suitability index for black bears in the southern Appalachians. *Wildlife Society Bulletin* 30:794–808.
- MORONI, M.T. 2006. Disturbance history affects woody debris dynamics of Newfoundland balsam fir (*Abies balsamea*) stands. *Canadian Journal of Forest Research* 36:3194–3208.
- MUNRO, K.J. 2012. Boreal Owls in western Newfoundland: using local field data to assess home range characteristics and test a habitat suitability index model. M.S. thesis, Memorial Univ., St. John's, NL Canada.
- NIEMELÄ, J. 1999. Management in relation to disturbance in the boreal forest. *Forest Ecology and Management* 115:127–134.
- REMSOFT INC. 2004. Forest and timberland management software. Fredericton, NB Canada.
- RICKERS, J.R., L.P. QUEEN, AND G.J. ARTHAUD. 1995. A proximity-based approach to assessing habitat. *Landscape Ecology* 10:309–321.
- ROLOFF, G.J. AND B.J. KERNOHAN. 1999. Evaluating reliability of habitat suitability index models. *Wildlife Society Bulletin* 27:973–985.

- ROMEO, C., L.A. WAUTERS, D. PREATONI, G. TOSI, AND A. MARTINOLI. 2010. Living on the edge: space use of Eurasian red squirrels in marginal high-elevation habitat. *Acta Oecologica* 36:604–610.
- RYDER, R.A., D.A. PALMER, AND J.J. RAWLINSKI. 1987. Distribution and status of the Boreal Owl in Colorado. Pages 169–174 in R.W. Nero, R.J. Clark, R.J. Knapton, and R.H. Hamre [EDS.], *Biology and conservation of northern forest owls*. U.S.D.A. Forest Service Gen. Tech. Rep. RM-142. Rocky Mountain Forest and Range Experimental Station, Fort Collins, CO U.S.A.
- SCHMIEGELOW, F.K.A. AND M. MÖNKÖNEN. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecological Applications* 12:375–389.
- SLEEP, D.J.H. 2005. Responses of boreal forest owls to landscape patterns originating from fire and timber harvest. Ph.D. dissertation, Univ. of Guelph, Guelph, ON Canada.
- SMITH, C.Y., I.G. WARKENTIN, AND M.T. MORONI. 2008. Snag availability for cavity nesters across a chronosequence of post-harvest landscapes in western Newfoundland. *Forest Ecology and Management* 256:641–647.
- SMITH, P.G. 2008. Smith Ecology Ltd. Compos Analysis Software, Wales, U.K.
- SOLHEIM, R. 1983. Breeding frequency of Tengmalm's Owl (*Aegolius funereus*) in three localities in 1974–1978. *Proceedings of the Nordic Ornithological Congress* 3:79–84.
- SONERUD, G.A. 1986. Effect of snow cover on seasonal changes in diet, habitat, and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia. *Holarctic Ecology* 9:33–47.
- ST-LAURENT, M-H., C. DUSSAULT, J. FERRON, AND R. GAGNON. 2009. Dissecting habitat loss and fragmentation effects following logging in boreal forest: conservation perspectives from landscape simulations. *Biological Conservation* 142:2240–2249.
- STOMS, D.M., W.F. DAVIS, AND C.B. COGAN. 1992. Sensitivity of wildlife habitat models to uncertainties in GIS data. *Photogrammetric Engineering and Remote Sensing* 58:843–850.
- STRIMBU, B.M. AND J.L. INNES. 2012. Framework for assessing the impact of human activities on the environment: the impact of forest harvesting and petroleum drilling on habitat of moose (*Alces alces*) and marten (*Martes americana*). *Biodiversity and Conservation* 21:933–955.
- STURTEVANT, B.R. AND J.A. BISSONETTE. 1997. Stand structure and microtine abundance in Newfoundland: implications for marten. Pages 182–198 in G. Proulx, H.N. Bryant, and P.M. Woodard [EDS.], *Martes: taxonomy, ecology, and management*. Provincial Museum of Alberta. Edmonton, AB Canada.
- THOMPSON, I.D. AND W.J. CURRAN. 1995. Habitat suitability for marten of second-growth balsam fir forests in Newfoundland. *Canadian Journal of Zoology* 73:2059–2064.
- , H.A. HOGAN, AND W.A. MONTEVECCHI. 1999. Avian communities of mature balsam fir forests in Newfoundland: age-dependence and implications for timber harvesting. *Condor* 101:311–323.
- TITUS, K. AND J.A. MOSHER. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. *American Midland Naturalist* 111:1–7.
- U.S. FISH AND WILDLIFE SERVICE. 1981. Standards for the development of suitability index models. Ecol. Serv. Man. 103. U.S.D.I. Fish and Wildlife Service, Division of Ecological Services. U.S. Gov. Print. Off., Washington, DC U.S.A.
- VAN HORNE, B. AND J.A. WIENS. 1991. Forest bird habitat suitability model and the development of general habitat models. Fish and Wildlife Resource Paper 8. U.S.D.I. Fish and Wildlife Service, Washington, DC U.S.A.
- WALLIN, D.O., F.J. SWANSON, B. MARKS, J.H. CISSEL, AND J. KERTIS. 1996. Comparison of managed and pre-settlement landscape dynamics in forests of the Pacific Northwest, USA. *Forest Ecology and Management* 85:291–309.
- WHITMAN, J.S. 2001. Diets of nesting Boreal Owls, *Aegolius funereus*, in western interior Alaska. *Canadian Field-Naturalist* 115:476–479.
- ZAR, J.H. 1999. Biostatistical analysis, Fourth Ed. Prentice Hall, Upper Saddle River, NJ U.S.A.

Received 5 August 2015; accepted 6 June 2016
Associate Editor: David E. Andersen