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FACTORS RELATED TO NORTHERN GOSHAWK LANDSCAPE USE IN THE WESTERN GREAT LAKES REGION

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ABSTRACT.--Northern Goshawks (Accipiter gentilis) are a species of special conservation concern in the western Great Lakes bioregion and elsewhere in North America, and exhibit landscape-scale spatial use patterns. However, little information exists about Northern Goshawk habitat relations at broad spatial extents, as most existing published information comes from a few locations of relatively small spatial extent and, in some cases, short durations. We used an information-theoretic approach to evaluate competing hypotheses regarding factors (forest canopy cover, successional stage, and heights of the canopy top and base) related to odds of Northern Goshawk landscape use throughout the western Great Lakes bioregion based on an occupancy survey completed in 2008 (Bruggeman et al. 2011). We also combined these data with historical data of Northern Goshawk nest locations in the bioregion from 1979-2006 to evaluate the same competing hypotheses to elucidate long-term trends in use. The odds of Northern Goshawk use in 2008, and from 1979-2008, were positively correlated with average percent canopy cover. In the best-approximating models developed using 1979-2008 data, the odds of landscape use were positively correlated with the percentages of the landscape having canopy heights between 10 m and 25 m, and 25 m and 50 m, and the amount of variability in canopy base height. Also, the odds of landscape use were negatively correlated with the average height at the canopy base. Our results suggest multiple habitat factors were related to Northern Goshawk landscape-scale habitat use, similar to habitat use described at smaller spatial scales in the western Great Lakes bioregion and in western North America and Europe.

KEY WORDS: Northern Goshawk; Accipiter gentilis; habitat use, landscape, nest habitat; western Great Lakes bioregion.

FACTORES RELACIONADOS CON EL USO DEL PAISAJE POR *ACCIPITER GENTILIS* EN LA REGIÓN OESTE DE LOS GRANDES LAGOS

RESUMEN.—Accipiter gentilis es una especie de importancia especial de conservación en el oeste de la bioregión de los Grandes Lagos y en otros sitios de América del Norte y exhibe patrones de uso espacial a escala de paisaje. Sin embargo, existe poca información acerca de las relaciones de hábitat de *A. gentilis* en grandes extensiones espaciales, ya que la mayoría de la información publicada proviene de unos cuantos sitios de extensión espacial relativamente pequeña y, en algunos casos, de corta duración. Utilizamos un enfoque teórico-informativo para evaluar las hipótesis alternativas con respecto a factores (cobertura del dosel del bosque, estado sucesional y altura de la parte baja y alta del dosel) relacionados con las probabilidades de uso del paisaje de individuos de *A. gentilis* a lo largo de la bio-región de los Grandes Lagos, utilizando un censo de ocupación completado en 2008 (Bruggeman et al. 2011). También combinamos estos datos con datos históricos de localización de nidos de *A. gentilis* en la

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bio-región durante 1979–2006 para evaluar las mismas hipótesis alternativas para elucidar las tendencias de uso al largo plazo. Las probabilidades de uso por parte de *A. gentilis* en 2008, y de 1979 hasta 2008, estuvieron positivamente correlacionadas con el porcentaje promedio de cobertura del dosel. En los mejores modelos de aproximación desarrollados utilizando datos de 1979–2008, las probabilidades de uso del paisaje estuvieron positivamente correlacionadas con los porcentajes de paisaje que tenían alturas de dosel entre 10 m y 25 m y entre 25 m y 50 m, y con la cantidad de variabilidad en la altura de la base del dosel. Nuestros resultados sugieren que múltiples factores del hábitat estuvieron relacionados con el uso de hábitat a escala de paisaje por parte de *A. gentilis*, de modo similar al uso del hábitat descripto para escalas espaciales menores en la bio-región occidental de los Grandes Lagos y en el oeste de América del Norte y Europa.

[Traducción del equipo editorial]

Northern Goshawks (Accipiter gentilis) use habitat at a landscape scale, occur at relatively low breeding densities, and can be difficult to detect, complicating efforts to understand factors that influence abundance and habitat use at broad spatial scales (Andersen 2007). In the western Great Lakes region and elsewhere in North America, Northern Goshawks are a species of conservation concern, having been placed on state lists of species of special concern and petitioned for listing under the U.S. Federal Endangered Species Act (Andersen et al. 2005). Conservation efforts for Northern Goshawks have ranged from protection of individual nest sites (Wisconsin Department of Natural Resources 2012) to forest management plans based largely on Northern Goshawk habitat relations and providing suitable habitat for prey (Reynolds et al. 1992). However, in many portions of their range, Northern Goshawk habitat relations are not well described at broad spatial scales.

In North America, Northern Goshawks occur as breeding birds across a wide range of landscapes (Squires and Reynolds 1997). They occur in landscapes dominated by deciduous and mixed deciduous-coniferous forests in the western Great Lakes bioregion (Boal et al. 2006), old-growth coniferous forests in the Pacific Northwest (Daw and DeStefano 2001) and Alaska (Titus et al. 1994, Iverson et al. 1996), conifer-dominated forests of the American Southwest (Reynolds et al. 1994), ecotones between forested and open cover types (Younk and Bechard 1994), and northern boreal forests (Doyle and Smith 1994). Northern Goshawk habitat relations have been assessed in a number of these landscapes, primarily at the spatial scales of nest sites, and postfledging areas (sensu post-fledging family area of Reynolds et al. [1992]), territories, or home ranges (but see Finn et al. [2002] for an evaluation of goshawk habitat relations at multiple spatial scales in a portion of the West Coast bioregion [Woodbridge and Hargis 2006]). Results of these assessments indicate that Northern Goshawks breed in forested landscapes and use relatively large trees with appropriate structure to support nests in relatively mature forest patches with relatively high canopy closure (summarized in Andersen et al. 2005). The species of trees used for nesting varies both within and among regions, as do forest type and the suite of primary prev (summarized in Andersen et al. 2005). At the scale of post-fledging areas, territories, or home ranges, the amount of relatively mature forest in the surrounding landscape often decreases as distance from the nest increases (McGrath et al. 2003), and breeding Northern Goshawks select relatively more mature forest patches within landscapes where they breed (summarized in Andersen et al. 2005).

At broader spatial scales, Northern Goshawk habitat relations are not as well understood. Within their breeding range, Northern Goshawks presumably select breeding areas or home ranges (second-order habitat selection sensu Johnson 1980) nonrandomly in locations with characteristics that enhance fitness. As with other raptors, Northern Goshawk population ecology is thought to be largely driven by prey availability and distribution and abundance of breeding locations (Newton 1979). Reynolds et al. (1992) based their management recommendations for Northern Goshawks in the southwestern United States on these relationships, with the objective of managing for landscapes that supported prey and forest structure that would provide nesting habitat. At broad spatial scales, it is difficult to directly assess prey availability, and distribution and abundance of mature forest has been proposed as a surrogate for assessing landscape-scale habitat suitability for Northern Goshawks (reviewed in Andersen et al. 2005). How well distribution and abundance of mature forest tracks Northern Goshawk habitat suitability is not clear (see Andersen et al. 2005) and factors related to

Northern Goshawk presence have not been evaluated at broad spatial scales (e.g., at the bioregional scale) in most landscapes where they occur. Recently, surveys (Beck et al. 2011, Bruggeman et al. 2011) based on protocols for assessing occupancy at bioregional scales (Hargis and Woodbridge 2006, Woodbridge and Hargis 2006) have been implemented as part of efforts to assess distribution and trends in occupancy of Northern Goshawks at broad spatial scales. Those protocols include classifying potential occupancy of Northern Goshawks based on vegetation characteristics associated with locations used in the recent past by Northern Goshawks, resulting in models of Northern Goshawk habitat relations at broad spatial scales. For most landscapes, knowledge of sites used recently by Northern Goshawks results from a mix of opportunistic encounters and, in some cases, systematic surveys. Developing models of habitat use based on these observations may introduce bias (Andersen 2007), but at least at the scale of characteristics of breeding areas, several studies (Daw et al. 1998, Rosenfield et al. 1998) suggest that any biases are small. Combining data resulting from more than one type of survey methodology and including data derived based on stratified random sampling also likely decreases the potential for bias. Herein, we evaluate factors associated with Northern Goshawk use at the scale of the western Great Lakes bioregion based on (1) historical data gathered between 1979 and 2006 from territory and nest monitoring, telemetry studies, and opportunistic sightings, and (2) results of a bioregional Northern Goshawk survey in 2008 (Bruggeman et al. 2011). We developed models based on Northern Goshawk locations from 1979 through 2008, and validated these models with a reserved subset of data. The resulting models provide insight into factors related to Northern Goshawk landscape use in the western Great Lakes bioregion.

Methods

Study Area. The western Great Lakes bioregion encompasses northeast and north-central Minnesota, northern Wisconsin, and northern Michigan, U.S.A. (Hargis and Woodbridge 2006). Our study area within this bioregion encompassed parts of the presumed Northern Goshawk breeding range based on historical Northern Goshawk observations (Fig. 1). Bruggeman et al. (2011), due to limits on resources available for conducting an occupancy survey in 2008 across the entire bioregion, delineated a portion of the Northern Goshawk breeding range based on seven ecological sections (McNab et al. 2007) totaling 135 074 km² in area (Fig. 1) within the Laurentian Mixed Forest Province Ecoregion (Bailey 1995). The sections included in their occupancy survey were the Southern, Western, and Northern Superior Uplands, Northern Minnesota Drift and Lake Plains, Northern Highlands, and portions of the Eastern and Northern Upper Peninsula sections (McNab et al. 2007, Bruggeman et al. 2011). The western Great Lakes bioregion, including the seven ecological sections included in the survey of Bruggeman et al. (2011), is made up of a combination of private and public lands.

Our study area was characterized by deciduous hardwood, coniferous, mixed deciduous and coniferous, and boreal forests with elevations ranging between 200 m and 560 m (Lapinski 2000, Boal et al. 2005, 2006). Portions of the study area were interspersed with wooded wetlands, open wetlands, and swamps. The Western Superior Uplands were characterized by level and rolling glacial drift plains with forest vegetation of aspen (Populus spp.) and birch (Betula spp.), maple (Acer spp.) and birch, and spruce (Picea spp.) and balsam fir (Abies balsamea) cover types (McNab et al. 2007). The Northern Superior Uplands consisted of a glacially scoured plain with lakes, highlands, and uplands of low hills with forest vegetation consisting primarily of aspenbirch, spruce-fir, pine (Pinus spp.), and oak (Quercus spp.; McNab et al. 2007). The Southern Superior Uplands contained glacial landscapes with level lowlands and lacustrine plains with hilly uplands, and forests consisting mostly of maple, birch, and aspen (McNab et al. 2007). Level to gently rolling lowlands characterized by glacial features comprised the Northern Minnesota Drift and Lake Plains region, with forest cover consisting of aspen-birch, pine, and spruce-fir (McNab et al. 2007). The Northern Highlands were composed of a glacial plain with kettle lakes and moraines, and forest cover of spruce-fir, pine, maple, aspen, and birch (McNab et al. 2007). The Eastern Upper Peninsula section consisted of flat to gently rolling plains with aspenbirch, maple-birch, pine, and spruce-fir cover types, whereas the Northern Upper Peninsula section was comprised of level plains with exposed bedrock and forests of maple-birch and aspen-birch (McNab et al. 2007). Other tree species found throughout the ecological sections of the study area included basswood (Tilia americana), black ash (Fraxinus nigra), green ash (F. pennsylvanica), eastern hemlock (Tsuga

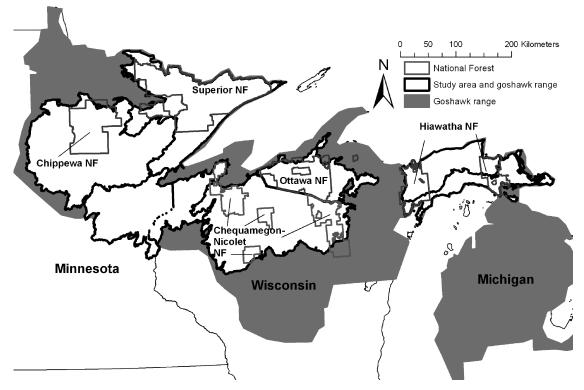


Figure 1. Northern Goshawk breeding range in the western Great Lakes bioregion, encompassing portions of Minnesota, Wisconsin, and Michigan, U.S.A. The 2008 occupancy survey of Bruggeman et al. (2011) occurred in the seven ecological sections within the Laurentian Mixed Forest Province Ecoregion. Historical Northern Goshawk locations were obtained between 1979–2006 in the shaded region.

canadensis), tamarack (Larix laricina), and northern white cedar (Thuja occidentalis).

Northern Goshawk Locations. We compiled historical records of Northern Goshawk nests from 1979-2006 in the western Great Lakes bioregion from the Michigan Natural Features Inventory, Michigan Department of Natural Resources (DNR), Minnesota DNR, U.S. Forest Service, and Wisconsin DNR. In addition to the historical information on Northern Goshawk locations from 1979-2006, we added locations where Northern Goshawks were detected during the bioregional occupancy survey of Bruggeman et al. (2011). Bruggeman et al. (2011) developed a stratified random sampling design to select areas to survey based on the protocol described by Hargis and Woodbridge (2006). That protocol consisted of dividing the western Great Lakes bioregion into 49146600-ha squares called Primary Sampling Units (PSUs, Hargis and Woodbridge 2006) and categorizing each of those PSUs based on habitat attributes, roads, and landownership into one of five categories: (1) primary habitat that was difficult to access, (2) primary habitat that was readily accessible, (3) secondary habitat that was difficult to access, (4) secondary habitat that was readily accessible, and (5) non-habitat (see Bruggeman et al. 2011 for details). Due to limitations of resources, the survey area of Bruggeman et al. (2011) was restricted to seven ecological sections (listed above) across northeastern and northcentral Minnesota, northern Wisconsin, and the Upper Peninsula of Michigan (Fig. 1) composed of 23 989 PSUs, which made up approximately 60% of the Northern Goshawk breeding range in the western Great Lakes bioregion. For this study, the nest locations and detection locations were both defined as "Northern Goshawk use sites."

Northern Goshawk Habitat Relations Model Development. To identify factors related to Northern Goshawk use in the western Great Lakes bioregion

between 1979 and 2008, we conducted a habitat useavailability analysis. We developed a priori models (see below for description of model development) based on hypothesized effects of habitat covariates on the direction of the odds response. First, we hypothesized the odds of Northern Goshawk landscape use would be positively correlated with canopy cover within a PSU because increased canopy cover would afford better nesting habitat and potentially increased prey availability (Boal et al. 2005, Smithers et al. 2005). Second, we predicted the odds of Northern Goshawk use would be negatively correlated with variation in canopy cover because Northern Goshawks would likely avoid PSUs with a heterogeneous habitat mosaic of open meadows and/or clear cuts interspersed with forest owing to limited resource availability in open areas (Boal et al. 2005). Third, we hypothesized the odds of Northern Goshawk use would be positively correlated with higher proportions of mid-seral stage successional forest and moderate canopy heights, as these attributes are likely to afford increased prey availability and some trees with sufficient height and attributes for supporting nests (Boal et al. 2005). Likewise, we predicted that odds of Northern Goshawk use would be positively correlated with higher proportions of canopy with greater height because of the attributes that mature trees have (e.g., greater heights, larger diameters, more complex structure, and higher canopy closure) for supporting nests (Boal et al. 2005). Fourth, we expected odds of Northern Goshawk use to be positively correlated with average canopy base height within a PSU to provide adequate space between the canopy bottom and top of understory growth for Northern Goshawks to maneuver while foraging (Boal et al. 2005). Likewise, we predicted that odds of Northern Goshawk use would be negatively correlated with the variation of canopy base height.

We conducted separate use-availability analyses on two sets of data. For the first analysis, we included both historical use (i.e., nest) locations and use locations identified as part of the 2008 occupancy survey of Bruggeman et al. (2011). We conducted a second use-availability analysis with the same procedures but used only locations where Northern Goshawks were detected in the 2008 occupancy survey (Bruggeman et al. 2011) to evaluate whether the primary correlates of odds of landscape use were similar in an unbiased sample of Northern Goshawk locations. For both analyses, we denoted each PSU that had Northern Goshawk presence during the 2008 occupancy survey as "used" and assigned each a coded binary response variable of "1" (Hosmer and Lemeshow 2000, Manly et al. 2002). For the historical data from 1979–2006 we identified PSUs that contained a Northern Goshawk nest and also assigned each a "1." We denoted PSUs that were surveyed in 2008 and had no Northern Goshawk presence, along with the remainder of PSUs as "available" and assigned each a "0" as a response variable (Hosmer and Lemeshow 2000, Manly et al. 2002). We considered the PSUs that were surveyed and had no Northern Goshawk presence to be available because the survey methods used by Bruggeman et al. (2011) could not definitively determine absence.

In our analyses we created 120 random points within each PSU and used GIS data layers to determine habitat attribute covariates. We used a U.S. Geological Survey (USGS) forest canopy cover layer from the year 2000 with 30-m \times 30-m resolution (Huang et al. 2003) to determine the percent canopy cover at each random point and then calculated the average percent cover (COVER_{avg}) and standard deviation of percent cover (COVERsd) for each PSU. The forest canopy-cover layer provided a value of canopy cover in increments of one percent for each 30-m \times 30-m pixel. The forest canopy-cover layer, which has been assessed in other studies (Walton et al. 2008), was developed at a spatial resolution of 30 m based on empirical relationships between tree canopy density and Landsat 7 Enhanced Thematic Mapper Plus data from 2000, with 1-m digital orthophoto quadrangles from the late 1980s to mid-1990s used to derive reference tree canopy density data to calibrate relationships between canopy density and Landsat data (Huang et al. 2001, 2003).

We used a GIS layer of succession classifications with 30-m \times 30-m resolution (LANDFIRE 2013a) to assign a seral stage to each random point and then calculated the percent of mid-seral stage forest within each PSU (SUCCESSION_{mid}). Mid-seral stage forest comprised either closed forest with one or two upper canopy layer size classes, with standing dead and downed trees and litter/duff on the forest floor, or open forest with one size class in the upper canopy layer and scattered standing dead and downed trees. We used a GIS layer of average canopy height with 30-m \times 30-m resolution (LANDFIRE 2013b) to determine the estimated height at the top of the canopy at each random point, and then calculated the percent of forest within each PSU with a

canopy height between 10 m and 25 m (CANO-PY_{10to25}), and between 25 m and 50 m (CANO-PY_{25to50}). LANDFIRE (2013b) data classified tree heights as <5 m, >5 m to 10 m, >10 m to 25 m, >25 m to 50 m, and >50 m. We used two categories of height (>10 m to 25 m; >25 m to 50 m) because trees <10 m are least likely to provide adequate Northern Goshawk habitat and due to the paucity of trees >50 m in PSUs. We used a GIS layer of average canopy base height with 30-m \times 30-m resolution (LANDFIRE 2013c) to determine the estimated height at the bottom of the canopy at each random point, and then calculated the average canopy base height (BASE_{avg}) and standard deviation of canopy base height (BASE_{sd}) within each PSU. The LANDFIRE data used in our analyses were last updated in 2008.

We developed and compared *a priori* hypotheses, expressed as multiple logistic regression use-availability models (Hosmer and Lemeshow 2000), to estimate the relative contributions of forest canopy cover, successional stage, canopy height, and canopy base height on the odds of Northern Goshawk use. While forming the model list we calculated variance inflation factors (VIFs; Neter et al. 1996) to quantify multicollinearity between model predictors and excluded models containing covariates having a VIF > 10 (Neter et al. 1996). Based on multicollinearity, we included no interactions between covariates in our list of candidate models and examined our four *a priori* hypotheses using 64 candidate models.

We calibrated models based on 1979-2008 data using 75% of the data while reserving the remaining 25% for model validation (Pearce and Ferrier 2000). We used logistic regression in R (v2.8.1; R Development Core Team 2008) to fit models and estimate coefficients based on the calibration data set. We calculated an AIC value for each model and then ranked and selected the best-approximating models using Δ AIC values (Δ AIC < 2; Burnham and Anderson 2002). We then used the validation data set to evaluate the predictive capability of the best-approximating model. We used the Receiver Operating Characteristic (ROC) technique to generate a ROC curve by plotting model sensitivity against the false positive fraction for cutpoint values between zero and one (Fielding and Bell 1997, Hosmer and Lemeshow 2000, Pearce and Ferrier 2000). We calculated the area under the ROC curve (AUC) to assess the predictive capability of the model (Fielding and Bell 1997, Hosmer and Lemeshow 2000). We combined the calibration and validation data to provide final coefficient estimates with the complete data set and used logistic regression in R to fit models. We calculated an AIC value for each model based on the complete dataset, ranked and selected the best-approximating models using ΔAIC values, calculated Akaike weights (w) for each model to obtain a measure of model selection uncertainty, and calculated predictor weights (w_{+}) as a measure of covariate importance (Burnham and Anderson 2002). We assessed statistical significance of model parameters based on whether 95% confidence intervals (CIs) contained zero. For our analyses using only data from the 2008 survey of Bruggeman et al. (2011), we included all observations in a single data set, and evaluated whether any covariate(s) was related to odds of Northern Goshawk use.

RESULTS

We documented 304 Northern Goshawk nest locations obtained between 1979 and 2006 from historical data sources; these 304 nest locations occurred in 192 PSUs (i.e., multiple nest locations occurred within a single PSU). Bruggeman et al. (2011) recorded Northern Goshawk presence in 21 of 86 PSUs they surveyed. Therefore, we included 213 PSUs with Northern Goshawk presence and 23776 available PSUs in our analyses of data from 1979 through 2008. Of the 304 nest locations we considered, 263 (86.5%) were recorded from 1995-2006 and 158 (52.0%) were recorded from 2000-2006; close in time to 2000, when remotely sensed data from which canopy density estimates were derived and slightly earlier than the latest date (2008) that LANDFIRE data we used were updated. Our calibration data set (75% of the 1979-2008 data) consisted of 160 used and 17832 available PSUs. Our analysis of locations only where Northern Goshawks were detected in the 2008 survey of Bruggeman et al. (2011) included 21 use PSUs and 23968 available PSUs.

There were three models with $\Delta AIC < 2$ (Table 1) for our analysis of 1979–2008 data, with the best-approximating model having a w = 0.417 and relative likelihoods of 1.4 and 2.6 compared to the second- and third-best-approximating models, respectively. The best-approximating model included significant, positive COVER_{avg}, BASE_{sd}, CANOPY_{10to25}, and CANOPY_{25to50} covariates, and a significant, negative BASE_{avg} effect that each had coefficients with 95% confidence intervals that did not contain zero

Table 1. Best-approximating models relating habitat attributes to the odds of Northern Goshawk landscape use in the western Great Lakes region, U.S.A. from 1979–2008. The three best-approximating models (Δ AIC < 2) are listed along with the number of parameters (*K*), Δ AIC value, and Akaike weight (*w*). The response variable, *g*(x), is the logit and covariates are described in the text.

MODEL STRUCTURE	Κ	ΔΑΙΟ	w
$g(\mathbf{x}) = \beta_0 + \beta_1 * \text{COVER}_{avg} + \beta_2 * \text{CANOPY}_{25to50} + \beta_3 * \text{BASE}_{avg} + \beta_4 * \text{BASE}_{sd} + \beta_5 * \text{CANOPY}_{10to25}$	6	0.00;	0.417
$g(\mathbf{x}) = \beta_0 + \beta_1 * \text{COVER}_{\text{avg}} + \beta_2 * \text{CANOPY}_{25\text{to}50} + \beta_3 * \text{BASE}_{\text{avg}} + \beta_4 * \text{BASE}_{\text{sd}} + \beta_5 * \text{SUCCESSION}_{\text{mid}} + \beta_6 * \text{CANOPY}_{10\text{to}25}$	7	0.60	0.309
$g(x) = \beta_0 + \beta_1 * \text{COVER}_{avg} + \beta_2 * \text{CANOPY}_{25to50} + \beta_3 * \text{BASE}_{avg} + \beta_4 * \text{COVER}_{sd} + \beta_5 * \text{BASE}_{sd} + \beta_6 * \text{CANOPY}_{10to25}$	7	1.94	0.158

‡ AIC value was 2313.732.

and high predictor weights (Table 2). The secondbest-approximating model had $\Delta AIC = 0.60$ (Table 1) and included the same five significant covariates as the best-approximating model, but also contained a positive SUCCESSION_{mid} effect that had coefficient confidence intervals containing zero (Table 2). The third-best-approximating model had $\Delta AIC = 1.94$ (Table 1), included the same five significant covariates as the other two best-approximating models, but also contained a COVER_{sd} effect that had confidence intervals that contained zero (Table 2). Therefore, both SUCCESSION_{mid} and COVER_{sd} had minimal influence among covariates and added little to the best-approximating model (Arnold 2010). The AUC value for the best-approximating model was 0.77, indicating the model had "acceptable discrimination capability" per the guidelines from Hosmer and Lemeshow (2000).

There were six models derived from 2008 occupancy survey data with $\Delta AIC < 2$ (Table 3),

with the best-approximating model having w = 0.117 and relative likelihood of 1.9 compared to the second best-approximating model. The bestapproximating model included a significant, positive COVER_{avg} covariate (coefficient estimate = 0.054; 95% CI = 0.019, 0.088) with $w_+ = 1.00$. The remaining five competing models all included a single additional covariate (Table 3), but coefficients for all other covariates had 95% CIs containing zero indicating they added little to the best-approximating model (Arnold 2010). Predictor weights for the other six covariates ranged from 0.271 to 0.354.

DISCUSSION

In our best-supported models of Northern Goshawk landscape use in the western Great Lakes region based on observations from 1979 through 2008, the odds of use were positively correlated with average percent canopy cover within a PSU. This result is consistent with results of studies of Northern Goshawk

Table 2. Coefficient estimates (β_i) and 95% confidence intervals (CI) for intercepts and covariates contained in the three best-approximating models, predictor weights (w_+) for each covariate, and model Δ AIC values for the analysis examining habitat attributes on the odds of Northern Goshawk landscape use in the western Great Lakes region, U.S.A. from 1979–2008. Covariates are defined in the text; "N/A" denotes the covariate was not included in the model.

COVARIATE	w_+	$\beta_i (95\% \text{ CI})$	$\beta_i~(95\%~CI)$	$\beta_i (95\% \text{ CI})$
ΔΑΙC		0.00	0.60	1.94
Intercept		-12.7 (-15.1 , -10.2)	-12.3 (-14.8 , -9.9)	-12.5 (-15.3 , -9.7)
COVERavg	1.00	0.030 (0.010, 0.050)	0.029 (0.009, 0.049)	0.029 (0.006, 0.051)
COVER _{sd}	0.273	N/A	N/A	-0.003 (-0.032 , 0.025)
CANOPY _{10to25}	0.999	0.073 (0.044, 0.103)	0.072 (0.042, 0.101)	0.073 (0.043, 0.103)
CANOPY _{25to50}	0.999	0.062 (0.032, 0.092)	0.060 (0.030, 0.090)	0.061 (0.031, 0.091)
BASE _{avg}	0.999	-0.328 (-0.453 , -0.203)	-0.354 (-0.484 , -0.224)	-0.326 (-0.452, -0.199)
BASE _{sd}	0.999	0.642 (0.352, 0.932)	0.597 (0.302, 0.892)	0.653 (0.350, 0.955)
$\mathrm{SUCCESSION}_{\mathrm{mid}}$	0.425	N/A	0.004 (-0.003, 0.012)	N/A

Table 3. Best-approximating models relating habitat attributes to the odds of Northern Goshawk landscape use in the western Great Lakes bioregion, U.S.A. based on locations with occupancy determined during a stratified random survey in 2008 (Bruggeman et al. 2011). The six best-approximating models are listed along with the number of parameters (K), Δ AIC value, and Akaike weight (w). The response variable, g(x), is the logit and covariates are defined in the text.

MODEL STRUCTURE	Κ	ΔAIC	w
$g(\mathbf{x}) = \beta_0 + \beta_1 * \text{COVER}_{avg}$	2	0.00	0.118
$g(\mathbf{x}) = \beta_0 + \beta_1 * \text{COVER}_{\text{avg}} + \beta_2 * \text{COVER}_{\text{sd}}$	3	1.23	0.064
$g(\mathbf{x}) = \beta_0 + \beta_1 * \text{COVER}_{\text{avg}}$	5	1.40	0.004
+ β_2 *CANOPY _{10to25}	3	1.48	0.056
$g(\mathbf{x}) = \beta_0 + \beta_1 * \text{COVER}_{\text{avg}} + \beta_2 * \text{CANOPY}_{25\text{to}50}$	3	1.88	0.046
$g(\mathbf{x}) = \beta_0 + \beta_1 * \text{COVER}_{\text{avg}}$	2	1.00	0.045
$+ \beta_2 * \text{SUCCESSION}_{\text{mid}}$ $g(\mathbf{x}) = \beta_0 + \beta_1 * \text{COVER}_{\text{avg}}$	3	1.93	0.045
+ β_2 *BASE _{sd}	3	1.95	0.044

prey and breeding areas at smaller spatial scales in the western Great Lakes region. Key Northern Goshawk prey in the western Great Lakes region include red squirrels (Tamiasciurus hudsonicus), eastern chipmunks (Tamias striatus), ruffed grouse (Bonasa umbellus), and snowshoe hares (Lepus americanus; Smithers et al. 2005, Woodford et al. 2008), and these species are primarily found in forested habitats, especially those with understory growth and woody debris (Litvaitis et al. 1985, Bayne and Hobson 2000). Additionally, Northern Goshawk nesting habitat consists of mature forest stands with high canopy closure in the western Great Lakes region (Boal et al. 2005) and elsewhere (e.g., Penteriani et al. 2001, Greenwald et al. 2005). Our results are consistent with numerous studies throughout North America and Europe that have documented associations between Northern Goshawks and mature, closed canopy forests (Daw and DeStefano 2001, Rutz et al. 2006, Squires and Kennedy 2006, Smith 2013).

Our best-supported models also indicated structural factors in forests beyond just high amounts of canopy cover may influence Northern Goshawks, as tree canopy height within stands was related to the odds of landscape use. Odds of use were positively correlated with the percentages of PSUs having canopy heights between 10 m and 25 m, and 25 m and 50 m, consistent with habitat-use patterns observed in the western Great Lakes region (Boal et al. 2006) and elsewhere throughout North America (Squires and Ruggiero 1996, Squires and Reynolds 1997) and Europe (Penteriani 2002), where Northern Goshawks tend to nest in the relatively tallest trees in relatively mature forest stands. In Wisconsin, Rosenfield et al. (1998) recorded attributes of trees supporting Northern Goshawk nests and found a mean tree height of 24.6 m and a mean nest height of 14.7 m. In addition to providing suitable locations for nesting, relatively taller trees and relatively mature forest patches may also be related to prey availability, in that late successional forests support a number of important Northern Goshawk prey (e.g., red squirrels).

Our best-approximating models of Northern Goshawk landscape use also included covariates related to the height of the base of the canopy. However, contrary to our prediction, average height at the base of the canopy within a PSU was negatively correlated with the odds of Northern Goshawk use. Also opposite our hypothesis, the amount of variability in canopy base height was positively correlated with odds of use. The height of the canopy at its base may influence Northern Goshawk landscape use in several ways. Higher canopy base heights may provide more space for maneuvering during flight between the canopy and understory, or canopy and shrub layers for forests with minimal understory growth (Penteriani 2002, Boal et al. 2005). Increased canopy volume, which is related to both taller canopy heights and shorter canopy base heights, may also result in more potential for nest sites resulting from higher stem densities and increased structural complexity for supporting nests (Penteriani et al. 2001, Squires and Kennedy 2006). In Minnesota, stands with Northern Goshawk nests had average canopy crown and base heights of 17 m and 9.5 m, respectively, along with high stem densities (Boal et al. 2005). Additionally, there were up to 4-m and 3.5-m layers in nest and foraging stands, respectively, between the canopy base and top of the understory that provided unobstructed flight paths (Boal et al. 2005). Because our GIS layers did not include information on the height of understory layers, it is difficult to fully evaluate the negative correlation between canopy base height and odds of Northern Goshawk use. There may be a trade-off between the attributes that canopies with high volumes provide for nests and the amount of space available for maneuvering during flight between the canopy base and the understory or

shrub layer. The positive correlation between variability in canopy base height and odds of Northern Goshawk use we observed suggests that stands providing a combination of trees with high canopy volume and adequate space for maneuvering during flight beneath the canopy may have the best combination of resources for both nesting and foraging. Our results are in general agreement with previous research that suggests a combination of habitat structure and prey availability is an important consideration for Northern Goshawks (Beier and Drennan 1997). Prey availability is also an important factor related to Northern Goshawk occupancy (summarized in Andersen et al. 2005), and some potentially important prey species in the western Great Lakes region (e.g., Ruffed Grouse and snowshoe hares) are associated with regenerating forest cover. We were unable to assess whether odds of Northern Goshawk occupancy were related to prey availability because there were no prey data available at the scale of PSUs for the bioregion. However, we speculate that prey availability during both the breeding and winter periods likely influences Northern Goshawk occupancy in the western Great Lakes region, as has been hypothesized elsewhere (e.g., Boal et al. 2006).

Except for the 2008 locations that were collected based on a stratified random sampling design (Bruggeman et al. 2011), the historical Northern Goshawk nest locations from 1979-2006 were obtained by assorted methods including many opportunistic sightings near roads or searching what was considered high quality Northern Goshawk habitat. Whether locations obtained opportunistically introduce a bias with respect to significant habitat covariates in our best-supported models is unknown. However, some previous studies on Northern Goshawk habitat use have evaluated the bias associated with opportunistically compared to systematically obtained nest locations. In Oregon, Daw et al. (1998) found similar levels of canopy closure and densities of large trees around nests that were found using opportunistic and systematic search methods. Rosenfield et al. (1998) also documented no statistical difference between 23 habitat features recorded at nests in Wisconsin found by unbiased compared to potentially biased means. Our ability to compare modeling results using 2008 survey data and historical location data was hindered by the small sample size of 2008 locations. Only COVER_{avg} was significant in the best-approximating models in both modeling exercises and had the highest predictor weight of any covariate, but undoubtedly Northern Goshawk nest use in 2008 was related to additional factors beyond just the amount of canopy cover.

In addition to limitations of small sample size for our analysis of the 2008 data, we should note the potential drawbacks of the GIS layers we used. First, our historical database consisted of 29 yr of Northern Goshawk locations and we were limited to using GIS layers of forest canopy cover and attributes that were produced based on satellite and other data primarily from 2000 and later. The majority of PSUs occupied by goshawks in our historical database was coincident with our remotely sensed vegetation data, but we were unable to account for forest management practices and natural disturbances that occurred prior to 2000 that may have affected Northern Goshawk landscape use during that period. In Oregon, Desimone and DeStefano (2005) reported that change in land cover surrounding Northern Goshawk nests was related to occupancy, and we suspect that a similar relationship exists for Northern Goshawks in the western Great Lakes region. Second, the resolution of GIS layers we used was limited to 30-m pixels, which may fail to capture microscale features of nest sites that make them attractive and suitable to Northern Goshawks.

The odds of Northern Goshawk landscape use in the western Great Lakes bioregion were greater in areas with higher canopy cover, higher percentage of tall trees, lower canopy base heights, and high amounts of variability in canopy base height, based on our 1979-2008 data. Our results suggest, at the bioregional scale, managing for relatively extensive forested landscapes that can provide a combination of: (1) mature and closed canopy forest to support prey populations and an abundance of suitable nest sites; (2) stands with high canopy volume and structure for supporting nests, and (3) variability in the height at the bottom of the canopy to provide space for maneuvering during flight beneath the canopy and foraging. These factors are in general agreement with those from the few studies conducted at smaller spatial scales (i.e., nests, breeding areas, and foraging locations) in the western Great Lakes region (Rosenfield et al. 1998, Boal et al. 2005, 2006) and the more extensive literature from research in the western United States and Europe (e.g., Hayward and Escano 1989, Bright-Smith and Mannan 1994, Beier and Drennan 1997, Penteriani 2002, Andersen et al. 2005).

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