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ARTICLE

Multi-scale selection models predict breeding habitat for two Arctic-breeding raptor species

Philippe Galipeau, Alastair Franke, Mathieu Leblond, and Joel Bêty

Abstract: Raptors are important environmental indicators because they are apex predators and can be sensitive to disturbance. Few studies have addressed habitat preferences of tundra-nesting raptors, and those that exist have focused on fine-scale characteristics. With increasing economic development predicted to occur throughout the Canadian Arctic, the investigation of raptor breeding habitat at broad spatial scales is required. We modeled breeding habitat selection for two raptor species on north Baffin Island, NU, Canada. During aerial surveys conducted over six breeding seasons, we documented 172 peregrine falcon (*Falco peregrinus tundrius*) and 160 rough-legged hawk (*Buteo lagopus*) nesting sites. We used these locations in conjunction with remote sensing data to build habitat selection models at three spatial scales. Topography, distance to water, and normalized difference vegetation index explained selection at all scales; slope aspect was also important at the finest scale. To validate landscape scale models, we conducted a validation survey that resulted in the detection of 45 new nests (peregrine falcon $n = 21$, rough-legged hawk $n = 24$). We did not detect any new nests in areas where model-predicted occurrence was expected to be low. Conversely, we found more than half of previously undetected nests in areas where model-predicted occurrence was expected to be high.

Key words: Arctic, *Buteo lagopus*, *Falco peregrinus*, habitat selection, resource selection function.

Résumé : Les rapaces sont d'importants indicateurs environnementaux, car ils sont des prédateurs ultimes et qu'ils peuvent être sensibles à des perturbations. Peu d'études se sont penchées sur les préférences d'habitat des rapaces qui nichent dans la toundra, et celles qui existent se sont concentrées à des caractéristiques à petite échelle. Avec l'accroissement du développement économique qui devrait survenir à travers l'Arctique canadien selon les prédictions, des recherches sur les habitats de reproduction des rapaces à de larges échelles spatiales sont nécessaires. Les auteurs ont modélisé la sélection de l'habitat de reproduction de deux espèces de rapaces du nord de l'Île de Baffin, au Nunavut, Canada. Lors des inventaires aériens réalisés pendant six saisons de reproduction, ils ont répertorié 172 sites de nidification du faucon pèlerin (*Falco peregrinus tundrius*) et 160 sites de nidification de la buse pattue (*Buteo lagopus*). Ils ont utilisé ces localisations conjointement à des données de télédétection pour construire des modèles de sélection d'habitats à trois échelles spatiales. La topographie, la proximité de l'eau et l'indice différentiel normalisé

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de végétation expliquaient la sélection à toutes les échelles ; cet aspect était aussi important à l'échelle la plus fine. Afin de valider les modèles à l'échelle du paysage, les auteurs ont réalisé un inventaire de validation qui a donné lieu à la détection de 45 nouveaux nids (faucon pèlerin $n = 21$, buse pattue $n = 24$). Ils n'ont pas détecté de nouveaux nids dans les aires où l'on s'attendait que l'occurrence prédite par le modèle soit faible. Inversement, ils ont trouvé plus de la moitié des nids précédemment non détectés dans les aires où l'on s'attendait que l'occurrence prédite par le modèle soit élevée. [Traduit par la Rédaction]

Mots-clés : Arctique, *Buteo lagopus*, *Falco peregrinus*, sélection d'habitat, fonction de sélection de la ressource.

Introduction

Exploration and development of natural resources in the Arctic has increased in recent decades, and further increases are predicted, in part due to changes in climate (Harsem et al. 2011). Longer ice- and snow-free seasons are predicted to facilitate increased access, extraction, and transportation of natural resources (Prowse et al. 2009; Harsem et al. 2011). Environmental assessments associated with large-scale projects driven by economic development require collection of baseline data that can describe the distribution and abundance of plant and animal species of importance, or at risk. Pre-development data are often insufficient with regard to informing risk management, especially for species in remote areas such as the Arctic (Meltofte 2013), and few studies have estimated habitat use by Arctic wildlife in regions where large-scale industrial development projects are planned (Dickson and Smith 2013; Wilson et al. 2014). Models that describe habitat requirements of wildlife can be used for land-use planning and wildlife monitoring in the Arctic, particularly for those resource-rich regions where wildlife surveys are currently lacking.

Birds of prey are considered to be important environmental indicators for monitoring of terrestrial ecosystems because they are apex predators, and can be sensitive to environmental disturbance (Sergio et al. 2004). However, few studies have addressed habitat preferences of tundra-nesting raptors, and those that exist have focused on investigation of fine-scale nesting site characteristics (Poole and Bromley 1988*a*; Wightman and Fuller 2005; Coulton et al. 2013). With increasing economic development predicted to occur throughout the Canadian Arctic (Prowse et al. 2009), investigation of breeding habitat needs of raptors at broad spatial scales is of significant conservation and management value.

The Arctic peregrine falcon (*Falco peregrinus tundrius* C.M. White, 1968) is listed as "Special Concern" under the Canadian Species at Risk Act (SARA 2002, as amended), and is regarded as a valued component of Arctic ecosystems in environmental assessments. Arctic peregrine falcons are considered generalist predators, but the bulk of their diet consists of insectivorous birds (Passeriformes, Scolopacidae, and Charadriidae; Hunter et al. 1988; Rosenfield et al. 1995; Dawson et al. 2011; L'Hérault et al. 2013). Peregrine falcons typically nest on cliffs and rocky outcrops of varying height, but also use hill tops, river canyons, and rock screes. In the Canadian Arctic, some peregrine falcons nest directly on the ground, although rarely (Court et al. 1988).

The rough-legged hawk (*Buteo lagopus* (Pontoppidan, 1763)) is a widely-distributed cliff-nesting raptor for which small mammals are important prey (Poole and Bromley 1988*b*). It is listed as "Least Concern" (SARA 2002, as amended) in Canada. Declines have been reported in some regions of North America, however, and studies have suggested that the species is sensitive to human disturbance (Schmidt and Bock 2005; Pandolfino and Wells 2009). Furthermore, information on the breeding ecology of rough-legged hawks in North

America is limited, in part because they are not considered to be at risk, but also due to the challenges associated with accessing their remote breeding ranges.

Here, we investigate the appropriate spatial scales for modelling breeding habitat selection of peregrine falcons and rough-legged hawks, and comment on how this impacts recommendations for management. More specifically, our objectives were to (1) quantify the relative importance of environmental factors typically cited as those associated with breeding habitat selection by peregrine falcons and rough-legged hawks in the Arctic; (2) map the breeding distribution of both species in the vicinity of an operating mining project that is considered to be important to the economic development of North Baffin Island, NU, Canada; and (3) evaluate the predictive capacity of our models using data independent from those used for model development.

In general, nesting sites of Arctic-breeding raptors are associated with rugged terrain (e.g., cliffs), in areas that provide suitable micro-climatic conditions, e.g., south-facing slopes (Poole and Bromley 1988*b*; Wightman and Fuller 2005; Brambilla et al. 2009; Peck et al. 2018) with abundant prey (McConnell et al. 2008; Booms et al. 2010). Thus, we predicted topography would be associated with breeding habitat selection at all scales (landscape, home range, and territory; see *Study design*), likely through breeding and roosting behaviors (Poole and Bromley 1988*a*; Brambilla et al. 2009). We expected that aspect would influence nesting habitat selection at the territory scale only, with selection for south-facing slopes that increase exposure to solar radiation and provide beneficial micro-climatic conditions in northern environments (Burton 2006, 2007*a*). We also predicted that areas with high primary productivity (generally found close to water) would provide areas of high prey abundance, and would be preferred by breeding raptors, especially in the Arctic, which is considered to have low primary productivity relative to more temperate regions (Gould et al. 2003). We tested our predictions of habitat preference by conducting a separate survey for previously unknown nesting sites in new areas.

Materials and methods

Study area

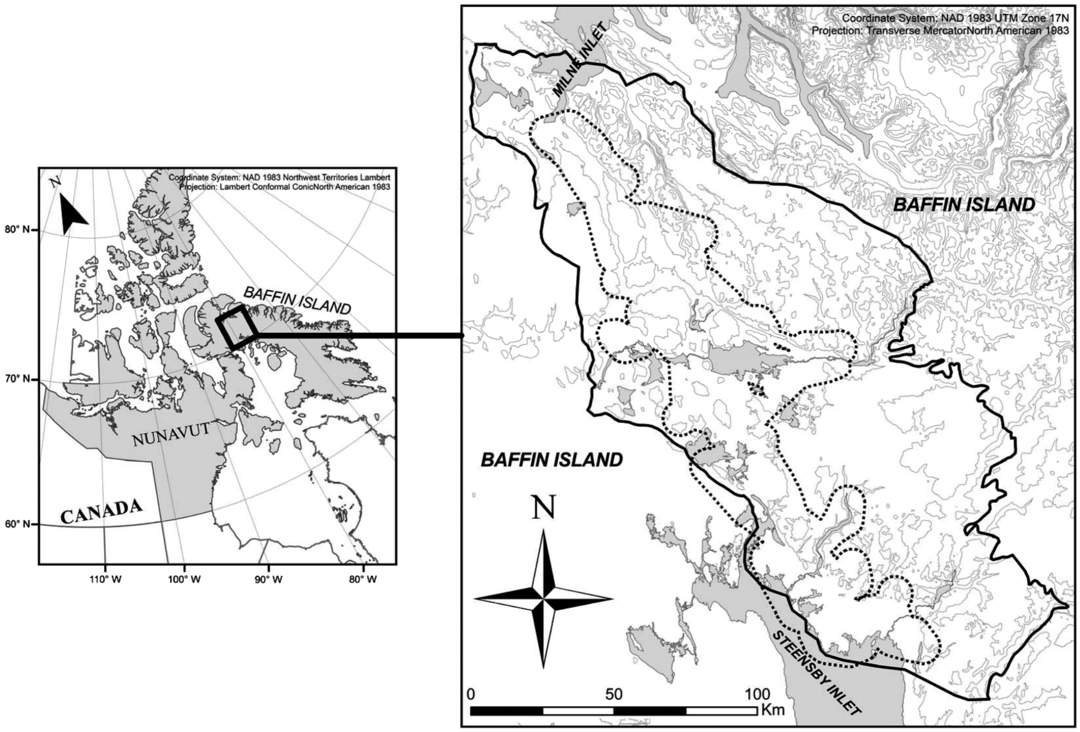
Our study area encompassed 21 000 km^2 of Baffin Island in the Canadian Arctic Archipelago, in NU, Canada (Fig. 1). Baffinland Iron Mines Corporation Mary River Mine site (71.326°, −79.374°) is one of the northern-most mines in the world, and is located approximately in the center of the study area. A 100 km road extends northward from the mine site to the Milne Inlet port (71.884°, −80.907°), and a proposed railway route extends southward from the mine site to Steensby Inlet, which has potential for development of a deep-water port (70.295°, −78.486°). Other than the mine site, permanent human settlement is minimal (0.02 inhabitants/km^2). We delineated the study area for environmental assessment baseline studies and project effects monitoring using the terrestrial ecozones and ecoregions classification for the Canadian Arctic (Ecological Stratification Working Group 1995), major topographic features, watersheds, and proposed or existing mining infrastructure (EDI 2017).

The landscape is generally rugged and elevation ranges from sea level to 950 m. High elevation plateaus interspersed with inlets and valleys on the northern coast give way to poorly drained plains and rolling tundra interspersed with rugged coastal cliffs, undulating bedrock, and exposed outcrops in the south. Dry or high elevation areas were sparsely vegetated, whereas wet areas were mainly covered by sedge (*Carex* spp. and *Eriophorum* spp.), saxifrage (*Saxifraga* spp. and *Dryas* spp.), shrub (*Salix arctica*), and moss (Ecological Stratification Working Group 1995).

Definitions

Terminology used to describe breeding habitat is summarized as follows.

Fig. 1. Study area (solid boundary) encompassing 21 000 km^2 of Baffin Island in the Canadian Arctic Archipelago, Nunavut, Canada, extending from Milne Inlet in the north to Steensby Inlet in the south. The dotted boundary encompasses the spatial extent over which surveys were performed and breeding habitat selection models were developed (i.e., modelling extent) with data collected in 2006–2008 and 2011–2013 (EDI 2017).



Nest — The structure made or the place used by birds for laying their eggs and sheltering their young (Steenhof and Newton 2007) regardless of whether eggs are laid in the nest in a given year or in any year (Millsap et al. 2015; Franke et al. 2017). We considered nests to be used if one or more adult birds displayed territorial or reproductive behaviors (e.g., courtship, copulation, nest building, incubation, nest defense, or presence of eggs or nestlings), or by the presence of a breeding-aged pair (e.g., roosting). Used nests were paired with randomly generated “nests” (see *Study design*). We did not consider old, abandoned, or partially built nests as “used”.

Nesting site — The substrate that supports the nest or the specific location of the nest on the landscape (Millsap et al. 2015; Franke et al. 2017; Steenhof et al. 2017). We considered nesting sites used by the same species over multiple years that were located more than 50 m apart to be different nesting sites, and we assumed that habitat features within 50 m of nesting sites were homogeneous. We used a proxy for nesting site defined as a circle (radius = 50 m) centered on each nest, or randomly generated “nest”.

Nesting territory — An area that contains, or historically contained, one or more nests within the home range of a mated pair. A nesting territory is a confined locality where nests are found, usually in successive years, and where no more than one pair of birds is known to have bred simultaneously (Steenhof and Newton 2007; Franke et al. 2017). A nesting territory may or may not be defended (Postupalsky 1974), and probably does not include all of a pair’s foraging habitat (Steenhof and Newton 2007). We used a proxy for nesting territory defined as a circle (radius = 500 m) centered on each used, or randomly generated "nest".

Home range — The area traversed by an individual in its normal activities of food gathering, mating, and caring for the young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range (Burt 1943). We calculated the mean nearest neighbor distance among nesting sites for each species separately, and used these values to approximate a typical home range size. Given that values were similar for both species (4.5 km for peregrine falcons and 4.6 km for rough-legged hawks), we used a proxy for home range defined as a circle (radius = 5 km, area approximately 80 km^2) centered on each used, or randomly generated "nest".

Aerial surveys

We conducted aerial surveys by helicopter to search for peregrine falcon and rough-legged hawk nesting sites during six breeding seasons (2006–2008 and 2011–2013). We flew approximately 50 h per season, over 5–7 good-weather days between 15 June and 1 July, and between 3 and 20 August. We positioned one observer in the front seat on the left side of the aircraft, and a second observer in the rear on the right side of the aircraft. We recorded the location of all used nests with a handheld GPS unit (accuracy <10 m). To delineate the modeling extent, we bounded all used nests and survey routes by a minimum convex polygon (MCP) buffered by 2 km. Within the resulting MCP, we excluded areas that were not surveyed, resulting in a final modeling extent of approximately 7800 km^2 (Fig. 1). All surveys were approved under Government of Nunavut research permits and followed protocols approved by the Animal Care and Use Committee of the University of Alberta (AUP00000042, renewed annually).

Study design

We quantified breeding habitat selection for both species at three spatial scales (Johnson 1980), as follows: (1) home range selection within the landscape (i.e., hereafter the landscape scale); (2) nesting territory selection within the home range (i.e., home range scale); and (3) nesting site selection within the nesting territory (i.e., nesting territory scale) (Fig. 2). We assumed that the entire landscape (i.e., the modeling extent; see Fig. 1) was available to breeding pairs to establish a home range.

First, we generated as many random nests (i.e., random locations within the modeling extent) as there were used nests within the landscape. We then generated circular home ranges (radius = 5000 m) around them (Fig. 2). Although the location of each random nest was constrained to areas within the landscape boundary, we allowed portions of random home ranges to fall outside of the modeling extent. For nesting territory selection within the home range scale, we assigned one random nest to each used nest within the used home range, and generated circular nesting territories (radius = 500 m) around them (Fig. 2). Finally, for nesting site selection within the nesting territory scale, we assigned one random nest to each used nest within the used nesting territory and generated circular nesting sites (radius = 50 m) around them (Fig. 2). By constraining random nesting territories and nesting sites to the area within used home ranges and used nesting territories, respectively, we ensured that scale-specific breeding habitat was available to a given breeding pair.

Environmental variables

We measured seven environmental variables (Supplementary Table S1[1]) previously identified as important for nesting raptors (Wightman and Fuller 2005; Brambilla et al. 2009;

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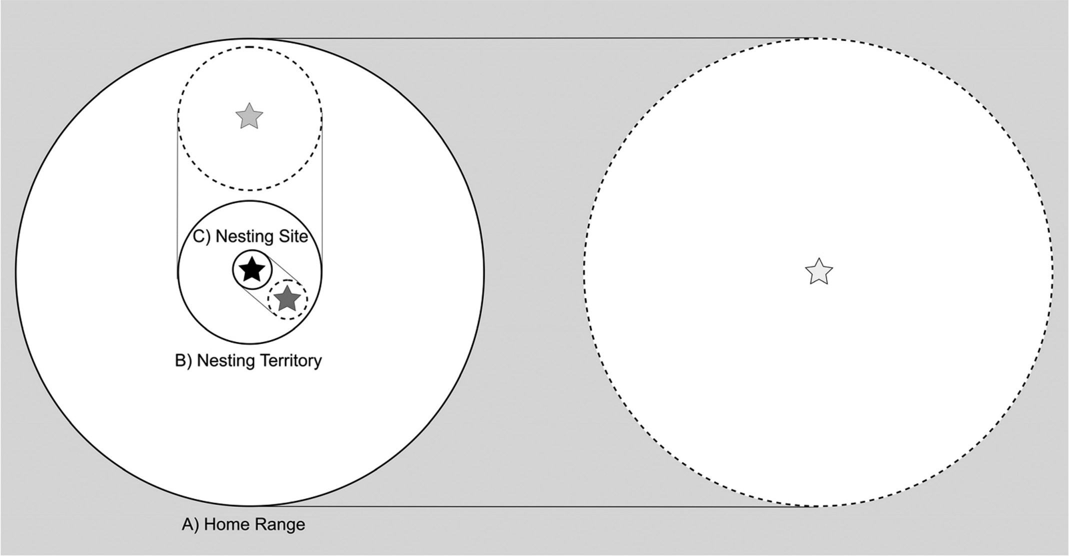
[1] Supplementary material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/as-2018-0026.

Fig. 2. Schematic representation of the study design used to develop breeding habitat selection models for peregrine falcons and rough-legged hawks at three spatial scales: (A) home range selection within the landscape, (B) nesting territory selection within the home range, and (C) nesting site selection within the nesting territory. The grey rectangle represents the available landscape (modelling extent). The black star represents a used nest. The light grey star represents a randomly generated nest used to assess home range selection within the landscape. The medium grey star represents a randomly generated nest used to assess nesting territory selection within a home range. The dark grey star represents a randomly generated nest used to assess nesting site selection within a nesting territory.



Booms et al. 2010). We generated environmental variables using remote sensing data imported into a geographic information system (GIS) (ESRI 2010). We used a 30 m resolution digital elevation model (DEM) of Nunavut acquired from the Canadian Digital Elevation Data (Natural Resources Canada 2016) to estimate three topographical features: elevation (m), slope (degrees), and terrain ruggedness. We estimated the latter using vector ruggedness measure (VRM), which is known to be less correlated with slope than other topographical indices (Sappington et al. 2007). Low VRM values indicate flat or uniformly steep areas, whereas high VRM values identify irregular areas. We used the DEM to create two continuous aspect variables, northness and eastness (Poirazidis et al. 2004; Kneib et al. 2011). Northness values ranged from −1 (due south) to 1 (due north), and eastness values ranged from −1 (due west) to 1 (due east). We used digital maps of water bodies from CanVec+ (Natural Resources Canada 2014) to estimate the nearest Euclidian distance (truncated at 500 m) to any water source (i.e., lakes, rivers, and the Arctic Ocean). We used normalized difference vegetation index (NDVI, 30 m resolution) to quantify primary productivity, and assumed that areas within close proximity to water that were also associated with high NDVI values represented areas of high prey availability (Wightman and Fuller 2005; Booms et al. 2010; Coulton et al. 2013).

Statistical analyses

Model development

We imported our environmental data layers into R Statistical Environment version 3.1.1 (R Development Core Team 2017). For each species, we estimated the areal mean of each environmental variable for all used and random locations at each spatial scale.

Table 1. Candidate models used to assess peregrine falcon and rough-legged hawk breeding habitat selection at three spatial scales on north Baffin Island, NU, Canada, using survey data from 2006 to 2008 and 2011 to 2013.

Model #	Model structure	*k*
1	Null model (intercept only)	0
2	NDVI + Distance to water	2
3	Elevation + Slope + VRM	3
4	NDVI + Distance to water + Northness + Eastness	4
5	NDVI + Distance to water + Slope + Slope × NDVI	4
6	Elevation + Slope + VRM + NDVI + Distance to water	5
7	Elevation + Slope + VRM + Northness + Eastness	5
8	Elevation + Slope + VRM + NDVI + Slope × NDVI	5
9	NDVI + Distance to water + Northness + Eastness + Slope + Slope × NDVI	6
10	Elevation + Slope + VRM + NDVI + Distance to water + Slope × NDVI	6
11	Elevation + Slope + VRM + Northness + Eastness + NDVI + Distance to water	7
12	Elevation + Slope + VRM + Northness + Eastness + NDVI + Slope × NDVI	7
13	Elevation + Slope + VRM + Northness + Eastness + NDVI + Distance to water + Slope × NDVI	8

Note: The vector ruggedness measure (VRM) was correlated with slope at the landscape scale and was not included in any models at this scale. *k* = number of parameters. NDVI, normalized difference vegetation index.

To make variables numerically tractable for model fitting, we centered all variables on the mean and divided them by the standard deviation. Prior to model fitting, we assessed multi-collinearity among variables at each scale using the variance inflation factor (VIF). We subsequently excluded VRM from landscape scale analyses because it was highly correlated ($r > 0.7$, $p < 0.05$) with slope. All remaining covariates had VIF <4.0 and were retained.

We estimated resource selection functions (Boyce et al. 2002; Manly et al. 2002) for a set of 13 a priori candidate models (Table 1). We included an interaction between slope and NDVI in a subset of the candidate models because we wanted to test for the effect of slope given variation in primary productivity. At the landscape scale, we estimated resource selection functions (RSFs) using standard logistic regression in R (*glm*). At the home range and territory scales, we estimated selection coefficients using conditional logistic regression in R (i.e., clogit procedure implemented in the survival package; Therneau 2015), where we matched each used location to a random location in a matched case control design. We then used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to rank all candidate models (Burnham and Anderson 2002). To reduce the uncertainty that can result from a limited number of random locations (Barbet-Massin et al. 2012; Northrup et al. 2013), we replicated our models 100 times for each species at each scale, each time using a different pair of used and random locations, or, at the landscape scale, a different set of random home ranges for each replicate. We then recorded which of the 13 candidate models was ranked first (i.e., had the lowest AIC_c score) most frequently among the 100 iterations to determine the most parsimonious model. Then, for each species at each scale, we calculated the mean standardized coefficients ($\bar{\beta}$) of each covariate included in the most parsimonious model.

Landscape scale model predictions

RSFs are frequently used to generate spatially explicit maps that describe the relative probability of occurrence of wildlife (Johnson et al. 2006). For each of the 100 modelling iterations assessing home range selection at the landscape scale, we recorded the outputs of models <2 ΔAICc from the most parsimonious model, and averaged the standardized coefficients from these models (Supplementary Table S2[1]). We opted for an averaging approach because it is known to stabilize inference when prediction is the goal, and when several variables are present across all candidate models (Burnham and Anderson 2002). We then applied the mean standardized coefficients resulting from model averaging of our landscape-scale models to environmental data layers in a GIS. The output was a spatially-explicit prediction of the relative probability of nesting site occurrence (w) for each species on each 30 m cell of the study area. Then, using quantile breakpoints, we reclassified cells into five equally weighted probability classes (Boyce et al. 2002; Johnson et al. 2006) to generate a final predictive map for each species.

Landscape scale model evaluation

A common approach to model evaluation is to partition the data into training and testing data sets (Johnson et al. 2006). Alternately, model validation data collected independently of data used for model development is considered to be among the most rigorous approaches to model evaluation (Guisan and Zimmermann 2000; Araújo et al. 2005; Wiens et al. 2008). We therefore used our final predictive map to select areas that had not been surveyed as part of the model development phase, and conducted an additional aerial survey in 2014 specifically dedicated to the validation of the landscape-level models developed for each species.

We conducted the validation survey in seven distinct regions within the study area but outside of the modeling extent (only 6% overlap). We allocated 16 h of helicopter time to collection of field validation data, and ensured that survey effort among each of the five probability classes was approximately equal. We deviated from pre-determined transects only when breeding-aged birds or signs of breeding were detected (e.g., uric acid excreta or "whitewash", lichen *Xanthoria elegans*, and unused nests), or for short exploratory flights when topographical features (e.g., deep canyons, large cliffs, and wide inlets) obscured the view of observers.

We evaluated the predictive capacity of our species-specific landscape-scale RSFs following the approach proposed by Johnson et al. (2006). We calculated the utilization $U(x_i)$ value of each probability class as follows:

$$(1) \quad U(x_i) = w(x_i)A(x_i) / \sum_j w(x_j)A(x_j)$$

where $w(x_i)$ is the midpoint RSF score of class$_i$ and $A(x_i)$ is the area of class$_i$ for the set of classes$_j$. We then estimated the number of predicted nesting sites expected to be found within each probability class (N_i) using the formula:

$$(2) \quad (N_i) = N \times U(x_i)$$

where N is the total sample size of the validation data. We then regressed the proportion of observed nesting sites against the proportion of expected nesting sites in each probability class, and calculated the upper and lower 95% confidence intervals following the method recommended by Howlin et al. (2004). Following Johnson et al. (2006), we assessed whether the slope of the regression was significantly different from zero, which would indicate that breeding habitat selection was non-random. We also assessed whether the slope differed from 1.0 to evaluate whether or not our models were proportional to the probability of use of a resource unit. In addition, we assessed overall fit of the regression models using χ^2 goodness-of-fit and Spearman rank correlation tests.

Results

During the aerial surveys conducted from 2006 to 2008 and 2011 to 2013, we detected 172 peregrine falcon and 160 rough-legged hawk nesting sites. The most parsimonious model (i.e., the model which ranked first most often out of 100 iterations) explaining breeding

Table 2. Most parsimonious models explaining breeding habitat selection by peregrine falcons and rough-legged hawks at the landscape (5 km), home range (500 m), and territory (50 m) scales on Baffin Island, NU, Canada, in 2006–2008 and 2011–2013.

	Peregrine falcon				Rough-legged hawk			
Scale	Model No.	*k*	No. of times as first rank	No. of times present among highest-ranked models	Model No.	*k*	No. of times as first rank	Number of times present among highest-ranked models
Landscape	**10**	6	46	82 (0.35)	**10**	6	82	97 (0.57)
	13	8	35	67 (0.29)	13	7	14	36 (0.21)
	11	7	9	31 (0.13)	8	4	3	24 (0.14)
Home range	**6**	5	53	79 (0.29)	**6**	5	54	81 (0.31)
	11	7	23	55 (0.20)	10	6	19	80 (0.30)
	10	6	8	54 (0.20)	5	4	9	25 (0.09)
Territory	**11**	7	84	98 (0.41)	**11**	7	58	90 (0.31)
	12	7	10	48 (0.20)	12	7	17	61 (0.22)
	13	8	6	67 (0.28)	13	8	8	59 (0.20)

Note: For 100 iterations, models were ranked according to $\Delta\text{AIC}_\text{c}$. The retained model (in bold) at each scale ranked first most often over 100 iterations using different random locations for each iteration. For brevity, only the three highest-ranked models are presented. The number of parameters (*k*) and the number of times that each model was present among the highest-ranking models ($\Delta\text{AIC}_\text{c} < 2$) are also shown.

habitat selection varied among scales, but not between species (Table 2). At the landscape and home range scales, selection of breeding habitat by both species was best explained by models that included topography (elevation, slope, and VRM), NDVI, and distance to water. At the nesting territory scale, the most parsimonious models also included northness and eastness (Table 2). With the exception of VRM for peregrine falcons at the home range scale and eastness for rough-legged hawk at the territory scale, all variables included in the most parsimonious models were statistically significant (Table 3).

Both species demonstrated selection for steep and rugged terrain at low elevation and close to water (Table 3). Elevation and slope had the highest averaged coefficients ($\overline{\beta}$) among scaled variables. The relative importance of other environmental variables, however, differed between species and among scales. At the landscape scale, the effect of slope varied positively with NDVI, meaning that both species selected steep areas, but more so in areas of high primary productivity. At the home range scale, areas of low primary productivity (i.e., low NDVI) were likely to be occupied by peregrine falcons (NDVI $\overline{\beta} = -0.21$, SE = 0.02), whereas rough-legged hawks occupied nesting territories in areas with relatively high primary productivity (NDVI $\overline{\beta} = 0.08$, SE = 0.02). At the territory scale, both species selected nesting sites in areas associated with low NDVI values and moderately rugged terrain (Table 3). Peregrine falcons selected nesting sites with southwest facing slopes, whereas rough-legged hawks selected nesting sites with southeast facing slopes. The final predictive map (Fig. 3) illustrates that both species were most likely to select areas within productive river valleys and along shorelines, and avoided plateaus especially if they were sparsely vegetated.

During the validation survey conducted in 2014, we detected a total of 45 new nesting sites (21 peregrine falcons and 24 rough-legged hawks) in an area totaling 3775 km^2 (Fig. 4). Consistent with our predictions, detection rate in the lowest probability class ("unsuitable") was low ($n = 0$ nesting sites detected), and >50% of new nesting sites ($n = 24/45$) were detected in the highest probability class ("highly suitable"), with equal search effort among classes. Species-specific linear regression estimating the relationship between the proportion of expected vs. observed nesting sites within each probability class indicated that our models were valid (rough-legged hawk $R^2 = 0.87$; peregrine falcon

Table 3. Model averaged coefficients ($\overline{\beta}$), standard error (SE), and 95% confidence limits obtained using 100 iterations of the most parsimonious models explaining breeding habitat selection by peregrine falcons and rough-legged hawks at the landscape (5 km), home range (500 m), and territory (50 m) scales on north Baffin Island, NU, Canada.

		Peregrine falcon				Rough-legged hawk			
Scale	Variable	$\overline{\beta}$	SE	Lower CI	Upper CI	$\overline{\beta}$	SE	Lower CI	Upper CI
Landscape (Model No. 10)	Intercept	0.131	0.005	0.121	0.141	0.188	0.006	0.176	0.200
	Elevation	−0.859	0.013	−0.884	−0.834	−0.674	0.013	−0.649	−0.699
	Slope	0.802	0.014	0.775	0.829	0.875	0.015	0.846	0.904
	Distance to water	−0.321	0.008	−0.337	−0.305	−0.305	0.008	−0.321	−0.289
	NDVI	0.158	0.009	0.140	0.176	0.303	0.011	0.281	0.325
	Slope × NDVI	0.348	0.011	0.326	0.370	0.505	0.011	0.483	0.527
Home range (Model No. 6)	Elevation	−1.806	0.046	−1.896	−1.716	−1.307	0.047	−1.399	−1.215
	Slope	1.961	0.046	1.871	2.051	1.849	0.044	1.763	1.935
	VRM	0.083	0.049	−0.013	0.179	0.170	0.044	0.084	0.256
	Distance to water	−0.360	0.014	−0.387	−0.333	−0.514	0.016	−0.545	−0.483
	NDVI	−0.208	0.016	−0.239	−0.177	0.076	0.016	0.045	0.107
Territory (Model No. 11)	Elevation	−1.915	0.063	−2.038	−1.792	−1.588	0.079	−1.743	−1.433
	Slope	1.154	0.027	1.101	1.207	0.925	0.023	0.880	0.970
	VRM	0.504	0.036	0.433	0.575	0.571	0.037	0.498	0.644
	Northness	−0.381	0.018	−0.416	−0.346	−0.363	0.018	−0.398	−0.328
	Eastness	−0.138	0.017	−0.171	−0.105	0.011	0.017	−0.022	0.044
	Distance to water	−0.389	0.019	−0.426	−0.352	−0.351	0.022	−0.394	−0.308
	NDVI	−0.222	0.014	−0.249	−0.475	−0.052	0.016	−0.083	−0.147

Note: CI, confidence interval; NDVI, normalized difference vegetation index; VRM, vector ruggedness measure.

Fig. 3. Predictive map showing the locations of used nesting sites (black circles) and predicted probability of occurrence of (A) peregrine falcon and (B) rough-legged hawk nesting sites within five probability classes across the study area on north Baffin Island, NU, Canada. We developed the models using 172 peregrine falcon and 160 rough-legged hawk nesting sites located within the modeling extent (dashed boundary) identified during six surveys performed in 2006–2008 and 2011–2013 (Natural Resources Canada 2014, 2016).

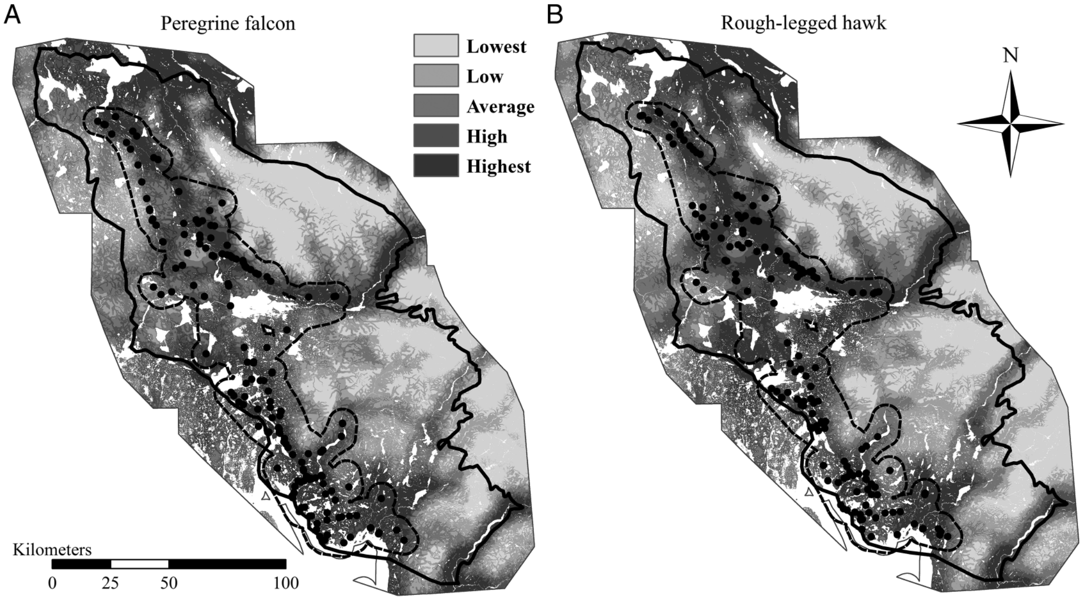


Fig. 4. Aerial survey routes (black lines) and nesting sites (white dots) of (A) peregrine falcons ($n = 21$) and (B) rough-legged hawks ($n = 24$) detected during the validation survey on Baffin Island, NU, Canada, in 2014 (EDI 2017).

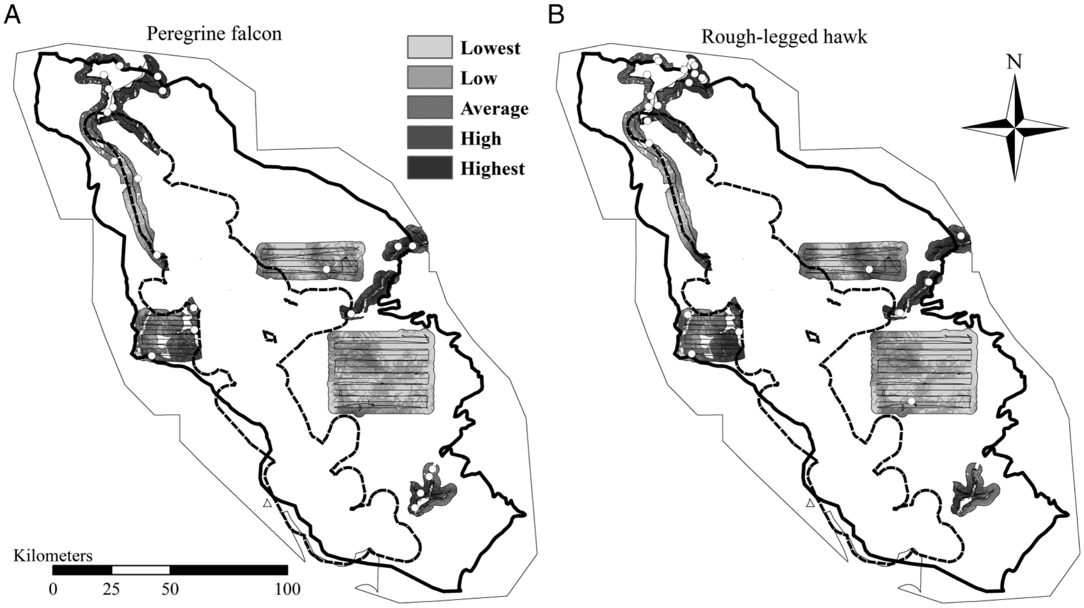
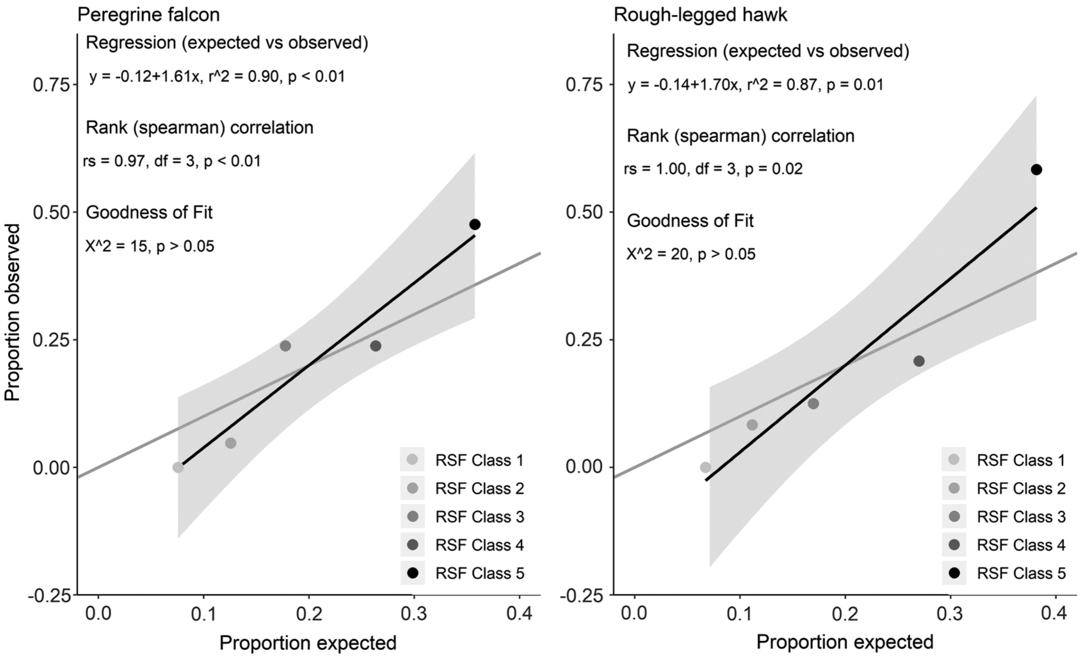


Fig. 5. Peregrine falcon (left) and rough-legged hawk (right) linear regression models with 95% CI for observed vs. expected proportions of nesting sites detected during the validation survey in 2014, separated by probability classes. Results are based on the validation of breeding habitat selection models for peregrine falcons and rough-legged hawks on Baffin Island, NU, Canada, developed from surveys conducted in 2006–2008 and 2011–2013. The grey line represents a slope of 1.0 and intercept of zero (i.e., where observed = expected). Greyscale points represent the number of nesting sites observed against the number expected for each resource selection function (RSF) class. R^2, Spearman rank correlation and χ^2 goodness-of-fit are reported as evidence of overall model fit and predictive capacity.



$R^2 = 0.90$; Fig. 5). Slopes were significantly different from zero for both species (rough-legged hawk = 1.70, $p = 0.01$; peregrine falcon = 1.62, $p = 0.01$; Fig. 5), indicating that species-specific RSFs were non-random. Furthermore, 95% confidence intervals overlapped 1.0 for both species (0.75–2.48 for peregrine falcons; 0.67–2.73 for rough-legged hawks), indicating that models were proportional to the probability of use, and intercepts were not significantly different from zero (peregrine falcon = −0.12, $p = 0.13$; rough-legged hawk = −0.14, $p = 0.16$). Using criteria recommended by Howlin et al. (2004), the predictive capacity of each species-specific RSF as determined by the slope and 95% confidence intervals was considered "good". In addition, for each RSF class, goodness-of-fit χ^2 tests indicated that the proportion of observed nesting sites was not different from the proportion of expected nesting sites (i.e., $p > 0.05$). Spearman rank correlation tests also indicated that the proportion of new nesting sites detected was significantly correlated with the proportion of expected nesting sites within each class ($r_s \geq 0.98$, $p = 0.02$).

Discussion

Insights into the breeding habitat requirements of Arctic-nesting raptors is especially relevant because of the potential for economic development in the Arctic in the context of climate change. This study details the breeding habitat selection at multiple scales by peregrine falcons and rough-legged hawks in the Canadian Arctic, and is particularly relevant given its geographic overlap with a large-scale development project. In general, our findings are consistent with our predictions and with previous studies (Gainzarain et al. 2000; Wightman and Fuller 2005), indicating that both peregrine falcons and rough-legged hawks select steep areas in rugged terrain that are relatively close to water and associated with relatively high primary productivity. Steep and rugged terrain associated with panoramic views of the surrounding landscape has been cited as important for increased hunting efficiency (Wightman and Fuller 2005), protection against predators (Gainzarain et al. 2000), and shelter from inclement weather (Anctil et al. 2014; Bruggeman et al. 2015). Annual variation in food supply is known to play a key role in limiting abundance and distribution of breeding raptors (Mearns and Newton 1988). In our study, slope and terrain ruggedness dominated selection of breeding habitat at all three scales. This finding implies that availability of steep and rugged terrain contributes to the establishment of peregrine falcon and rough-legged hawk breeding pairs on Baffin Island (see also Peck et al. 2018). However, we caution against arguing that availability of rugged terrain is a limiting factor per se.

As predicted, both species preferred south-facing slopes (specifically, southwest for peregrine falcons and southeast for rough-legged hawks). In the northern hemisphere, south-facing slopes receive more solar radiation compared to north-facing slopes (McCutchan and Fox 1986), which influences microhabitat characteristics including light intensity, soil and air temperature, humidity, and soil moisture (Bolstad et al. 1998). Birds breeding at high latitudes in North America generally prefer east- or south-facing slopes to build their nests (Burton 2007*b*; Landler et al. 2014). This behavior is likely related to the avoidance of environmental conditions that can result in brood failure and, subsequently, reduced reproductive success (Burton 2006). Exposure of eggs and nestlings to cold temperatures, wind, and rain has been shown to reduce breeding success in Arctic-nesting peregrine falcons (Bradley et al. 1997; Anctil et al. 2014). Furthermore, exposure to solar radiation on south-facing slopes likely increases availability of snow-free ledges used by mated pairs for nesting.

The selection of productive areas in close proximity to water by peregrine falcons and rough-legged hawks was likely linked to the availability of accessible prey (Wightman and Fuller 2005; Booms et al. 2010; Coulton et al. 2013). Arctic-breeding passerines and shorebirds are more abundant in well-vegetated lowlands and wetlands than in sparsely vegetated areas (Robinson et al. 2014), and are a key food source for breeding peregrine falcons (Court et al. 1988; L'Hérault et al. 2013; Robinson et al. 2017). Furthermore, the abundance and distribution of Arctic grazers such as lemmings, which are important prey for peregrine falcons (Bradley and Oliphant 1991; L'Hérault et al. 2013; Robinson et al. 2017) and rough-legged hawks (Potapov 1997; Bechard and Swem 2002) are also correlated with tundra productivity during summer (Rodgers and Lewis 1986; Olofsson et al. 2012). Nesting site selection was associated with low NDVI, which likely indicates that habitat within 50 m of nesting sites was bare rock typical of cliff faces, slot canyons, and rock outcrops on which breeding pairs were detected. This finding highlights the importance of studying habitat selection at multiple scales, as fine- and broader-scale selection may be driven by different factors, in this case microhabitat topography vs. food availability.

The validation data set collected in 2014 (i.e., after model development) clearly demonstrated that our breeding habitat selection models could predict nesting site locations outside of the spatial extent over which the models were estimated. Although we are confident that our models can identify breeding habitat throughout the north Baffin Island region, we caution against generalizing to far-removed regions of the Arctic without considering other covariates that may be location-specific (e.g., differing climate regimes or ecozones). We also advocate that independent evaluation procedures should be an integral part of resource selection analyses undertaken as part of environmental assessments in the future.

Investigation of habitat selection per se is of considerable value for large-scale landscape planning in under-studied or remote areas, in part due to the role of landscape-scale patterns in species persistence, but also due to the expansion and intensification of anthropogenic land use (Fedy et al. 2014). This is particularly true for the conservation and management of wildlife in the Arctic, where increased exploration and development are predicted (Harsem et al. 2011). Successful mitigation of disturbance of raptor nesting sites usually involves easy-to-follow guidelines that involve adherence to minimum setback distances (e.g., no-stopping zones for vehicular traffic and prohibited zones for pedestrians), and respect of milestones associated with breeding phenology (e.g., completing work-related disturbance prior to the arrival of birds on the breeding grounds). A key finding derived directly from our results was evidence for habitat selection at multiple scales and, in particular, emphasizes the value of managing for disturbance at scales broader than the nesting site, which is often used in environmental assessments.

For both species, it is likely that very fine scale (within a few meters) habitat selection is critically important to placement of nests, which almost certainly impinges on reproductive outcome in any given breeding season. Although our study is not informative at very fine scales (i.e., the nest), it provides valuable information at scales relevant to landscape planning that are germane to industry-related projects, particularly those associated with economic development in remote northern regions where cliff-nesting raptors are identified as valuable ecosystem components. Further, breeding habitat selection was similar for both species, and implies that managing land-use (e.g., road placement) for one species confers habitat protection for both species, including management at scales important to prey species (e.g., dust management). Based on the results presented here, we argue that fine-scale habitat features important to nesting site selection are not limiting. We further suggest that broader scale attributes (e.g., foraging habitat), and factors not directly related to selection of breeding habitat (e.g., annual variation in rainfall or microtine abundance) strongly influence whether breeding pairs occupy nesting sites each breeding season, and whether they are successful reproductively.

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