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RESEARCH ARTICLE

Mapping and modeling the breeding habitat of the Western Atlantic Red Knot (*Calidris canutus rufa*) at local and regional scales

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ABSTRACT

The Western Atlantic population of Red Knot (*Calidris canutus rufa*) has undergone dramatic declines in recent decades and conservation biologists have sought to improve knowledge about the species' ecology in an effort to understand these declines. One major information gap has been the lack of a detailed understanding of range and habitat use during the breeding season, when the species is distributed sparsely across the Canadian Arctic. Airborne radio-telemetry surveys of Red Knots tagged in Delaware Bay, New Jersey, were conducted across the south and central Canadian Arctic, from Victoria Island in the west to Baffin Island in the east. Intensive field surveys were conducted on Southampton Island, Nunavut, over successive summer field seasons to locate nesting Red Knots and record characteristics of their nesting habitat. Maximum entropy modeling (Maxent) and geographic information system (GIS) data on environmental characteristics were used to predict Red Knot habitat suitability at 2 spatial scales: nesting site location suitability at the local scale across Southampton Island, and breeding habitat suitability (i.e. both nesting and foraging habitat) at a broader, regional scale across the south and central Canadian Arctic. Comparison of the local and regional scale models with independent validation data (i.e. occurrence data not used in the model calibration), showed both models to be useful predictors of habitat suitability. At both spatial scales, Red Knots were found to prefer sparsely vegetated tundra on sedimentary, primarily limestone, bedrock at elevations below 150 m. Our results suggest that it is highly unlikely that the availability of breeding habitat limits the population size of the subspecies. Regional scale mapping provides the basis for more precise geographic targeting of future survey efforts that will aid in the conservation and management of this threatened species.

Keywords: breeding habitat, Canadian Arctic, Maxent, nesting habitat, shorebird, Southampton Island, species distribution modeling

Mapeo y modelado del hábitat reproductivo de *Calidris canutus rufa* a escalas local y regional

RESUMEN

La población del Atlántico oeste de *Calidris canutus rufa* ha sufrido disminuciones dramáticas en las últimas décadas y los biólogos de la conservación han buscado mejorar el conocimiento sobre la ecología de esta especie en un intento por entender estas disminuciones. Un vacío principal de información ha sido la falta de un entendimiento detallado del rango y el uso del hábitat durante la estación reproductiva, cuando la especie se distribuye de modo muy esparcido a través del Ártico canadiense. Se realizaron censos aéreos con radio-telemetría de individuos de *C. c. rufa* marcados en la Bahía Delaware, Nueva Jersey a través del sur y el centro del Ártico canadiense, desde la Isla Victoria en el oeste hasta la Isla Baffin en el este. Se realizaron adicionalmente muestreos de campo intensivos en la Isla Southampton, Nunavut a lo largo de sucesivas estaciones de verano para localizar individuos anidando de *C. c. rufa* y registrar las características del hábitat de anidación. Se usaron modelos de máxima entropía (Maxent) y datos de características ambientales a partir de sistemas de información geográfica (GIS) para predecir la aptitud del hábitat para *C. c. rufa* a dos escalas espaciales: aptitud del sitio de ubicación del nido a escala local a través de la Isla Southampton, y aptitud del hábitat de anidación (i.e., hábitat de anidación y de forrajeo) a una escala regional más amplia a través del sur y del centro del Ártico canadiense. La comparación de los modelos a escalas local y regional con datos de validación independientes (i.e., datos de presencia no usados en la calibración del modelo) mostró que ambos modelos son útiles para predecir la aptitud del hábitat. A ambas escalas espaciales, se encontró que los individuos de *C. c. rufa* prefieren la vegetación diseminada de la tundra que crece en la roca madre sedimentaria, principalmente de tipo piedra caliza, a elevaciones menores a 150 m. Nuestros resultados sugieren que es altamente improbable que la disponibilidad del hábitat reproductivo limite el tamaño poblacional de la subespecie. El mapeo a escala regional brinda las bases para una ubicación geográfica mucho más precisa de los futuros esfuerzos de muestreo que ayudarán en la conservación y el manejo de esta especie amenazada.

Palabras clave: Ártico canadiense, ave playera, hábitat de anidación, hábitat reproductivo, Isla Southampton, Maxent, modelado de la distribución de la especie

INTRODUCTION

The Red Knot (*Calidris canutus*) is one of the Earth's longest distance migrants. The Western Atlantic Flyway's population of the Red Knot (*Calidris canutus rufa*; knot hereafter) winters in southern South America and then migrates north to the Canadian Arctic to breed—a one-way migration of over 15,000 km (Morrison and Harrington 1992, Baker et al. 2013). Other smaller, distinct groups of *rufa* winter in northern Brazil and in the southeast USA (USFWS 2014). Red Knots were once abundant but populations were decimated by market hunting in the late 1800s to early 1900s. Numbers had increased and stabilized throughout the 20th century, but have again declined precipitously in recent decades (Niles et al. 2008, USFWS 2014).

A large fraction of the knot population winters in Tierra del Fuego, South America. Counts there fell from 67,496 in 1986 (Morrison and Ross 1989) to as low as 9,850 in 2010–2011 (Morrison et al. 2004; Baker et al. 2013, and references therein). Similar decreases have been observed at the species' most important spring stopover location, Delaware Bay, where a major portion of the Atlantic Flyway's population stops on the US East Coast during the month of May (Niles et al. 2009). Feasting on horseshoe crab (*Limulus polyphemus*) eggs, the knots almost double their weight before flying on to the Canadian Arctic to nest and raise young. The ability of knots to achieve a threshold level of weight gain during this stopover has been linked to their subsequent survival (Baker et al. 2004, Duijns et al. 2017). Harvest of horseshoe crabs increased markedly during the 1990s, reducing the abundance of spawning individuals and the availability of their eggs (Walls et al. 2002, Smith et al. 2017). There is concern that this overharvest of horseshoe crabs has influenced the survival and abundance of Red Knots (Niles et al. 2009). These and other concerns prompted the state of New Jersey in 1999 to list the Red Knot as threatened and endangered in 2012 (New Jersey Department of Environmental Protection 2012).

More recently, the *rufa* population of Red Knots has been listed as Endangered in Canada (in 2012) under the Species at Risk Act and as Threatened under the United States Endangered Species Act (in 2014). The federal listing and recovery processes in both Canada and the United States have stringent requirements for information describing the distribution and habitats used by the species. For Red Knot, a species distributed across the length of the Western Hemisphere, an accurate description of distribution and overwintering, migratory stopover, and breeding habitat use is challenging (Niles et al. 2008). While there was a basic understanding of the geographic extent of the breeding grounds, many aspects of knot habitat use and spatial distribution during the breeding season in the Canadian Arctic were poorly understood (Morrison and Harrington 1992, ECCC 2016). Early ornithological expeditions across the Eastern Low Arctic occasionally reported observations of breeding pairs or young (e.g., Sutton 1932, Bray 1943, Parker and Ross 1973), but only a handful of knot nests have been documented. These difficulties in defining habitat use in the Arctic are now compounded by the species' small population size. In an attempt to address this knowledge gap, a concerted research effort was initiated in 1999.

Here we report radio-tagging, ground-based observation, and geographic information system (GIS)–based species distribution modeling to predict knot habitat suitability at 2 spatial scales: nesting site location suitability at the local scale across Southampton Island, and breeding habitat suitability (i.e. both nesting and foraging habitat) at a broader, regional scale across the eastern and central Canadian Arctic. We examine the relative influence of environmental characteristics, including elevation, geology, land cover, snow cover, distance to freshwater, and distance to wetlands on habitat suitability. We also consider bias inherent in such efforts for a sparsely distributed and difficult-to-study species. Finally, we assess implications of our models for conservation and future status assessments.

METHODS

Field Surveys

Transmitter deployments and aerial surveys. We captured knots in May at Delaware Bay using small mesh (61-mm diagonal stretch) nets powered by 3 cannons using gunpowder charges (Lessels et al. n.d.). Birds were captured, processed, and released within 2 hr after net fire. Holohil Systems (Carp, Ontario, Canada) BD-2 radio-tags, weighing 1.8 g, were attached to knots with a body weight of at least 150 g (maximum of 3% of body mass). A small patch of feathers was clipped on the lower back, and transmitters were attached by gluing to the feather stubble of the synsacral area with surgical adhesive. Transmitters were expected to last at least 6 mo, but we expected them to be

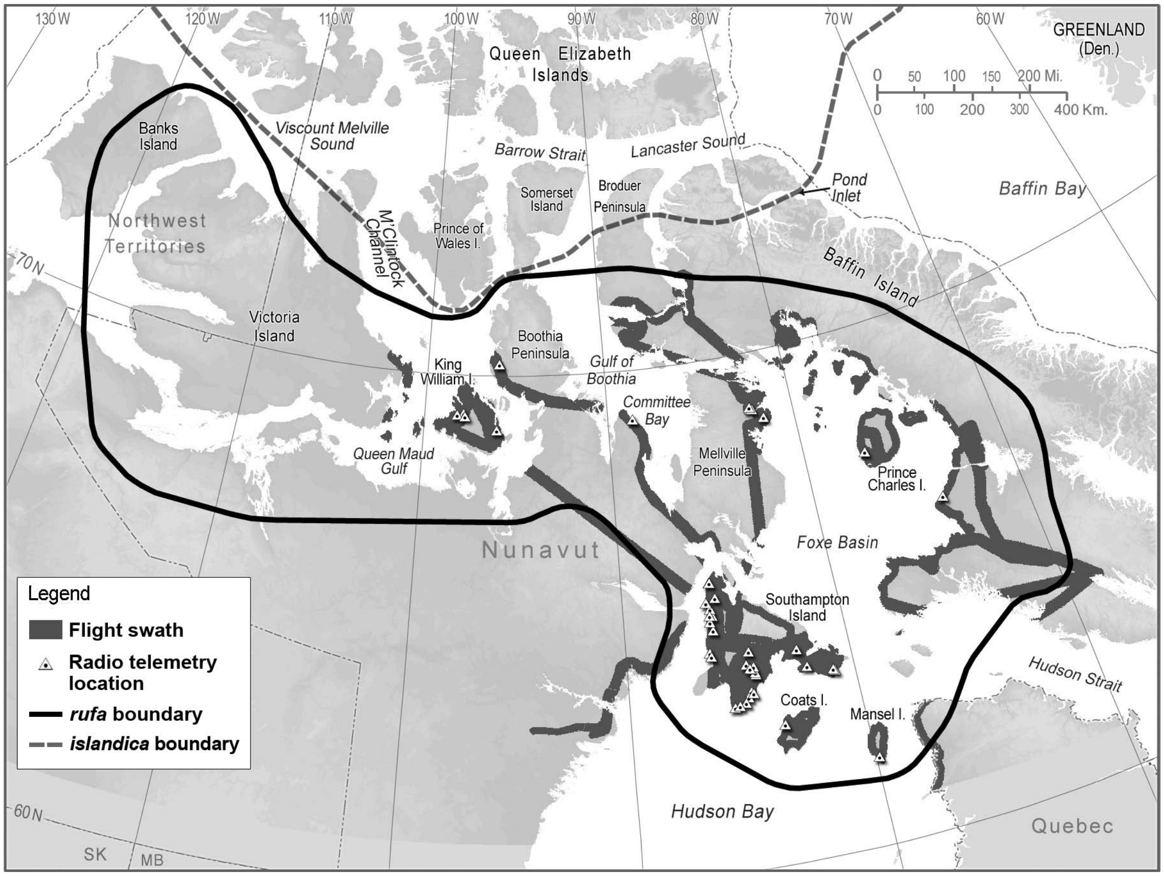

FIGURE 1. Map of central Canadian Arctic study region showing the *rufa* and southern extent of the *islandica* Red Knot range boundary (COSEWIC 2007), airborne radio-tag survey swaths, and location of radio-tag observations.

lost during molt in September–October. We outfitted 365 birds with radio transmitters (65 birds in 1999, 100 in 2000, 100 in 2001, 50 in 2003, 50 in 2006). We carried out aerial surveys (late June to mid-July) to detect them across much of the south and central Canadian Arctic, corresponding with what was known about knot breeding range (Figure 1). The study flights covered areas stretching from Victoria Island in the west to Baffin Island in the east, including Victoria, King William, Southampton, Coats, Mansel, Prince Charles, and Baffin Islands and the Boothia Peninsula (72°10′45″N to 60°36′32″N, 107°54′58″W to 67°50′25″W; Figure 1). Ground elevation within the flight paths spanned between 0 and 2,050 m above sea level (ASL). Flight routes were designed to survey primarily what we hypothesized as suitable knot breeding habitat, as determined by the available literature and an initial GIS model (land cover: barren to sparsely vegetated tundra; geology: sedimentary bedrock; elevation: snow-free areas <300 m ASL; distance to coast: <50 km). However, areas thought to be unsuitable were also deliberately surveyed in order to evaluate the validity of our species distribution modeling.

Aerial surveys were conducted using protocols outlined by Gilmer et al. (1981). Surveys were conducted within 2 mo of radio-tag attachment, so all tags should have been capable of transmitting during all aerial surveys. Yagi antennae were mounted, 45° off vertical, to each wing strut of a Cessna Caravan airplane. Flights were conducted at an altitude of approximately 300 m and speed of 130 kph. Prior to each flight, a decoy transmitter was placed on the ground and an effective detection range and point location accuracy was determined. The effective range was ∼13 km, giving a detection swath ∼26 km wide. During the radio-tag survey flights, once a radio signal was detected, the plane circled to pinpoint as accurately as possible the tagged bird's location, which we believe to be accurate to within ±100–200 m (based on our test flights). The geographic coordinates of these locations were recorded with a handheld global positioning system (GPS). The routing of the radio-tagging survey flights was similarly recorded by GPS. The detection swath of the surveys was mapped by buffering these GPS tracks by 13 km.

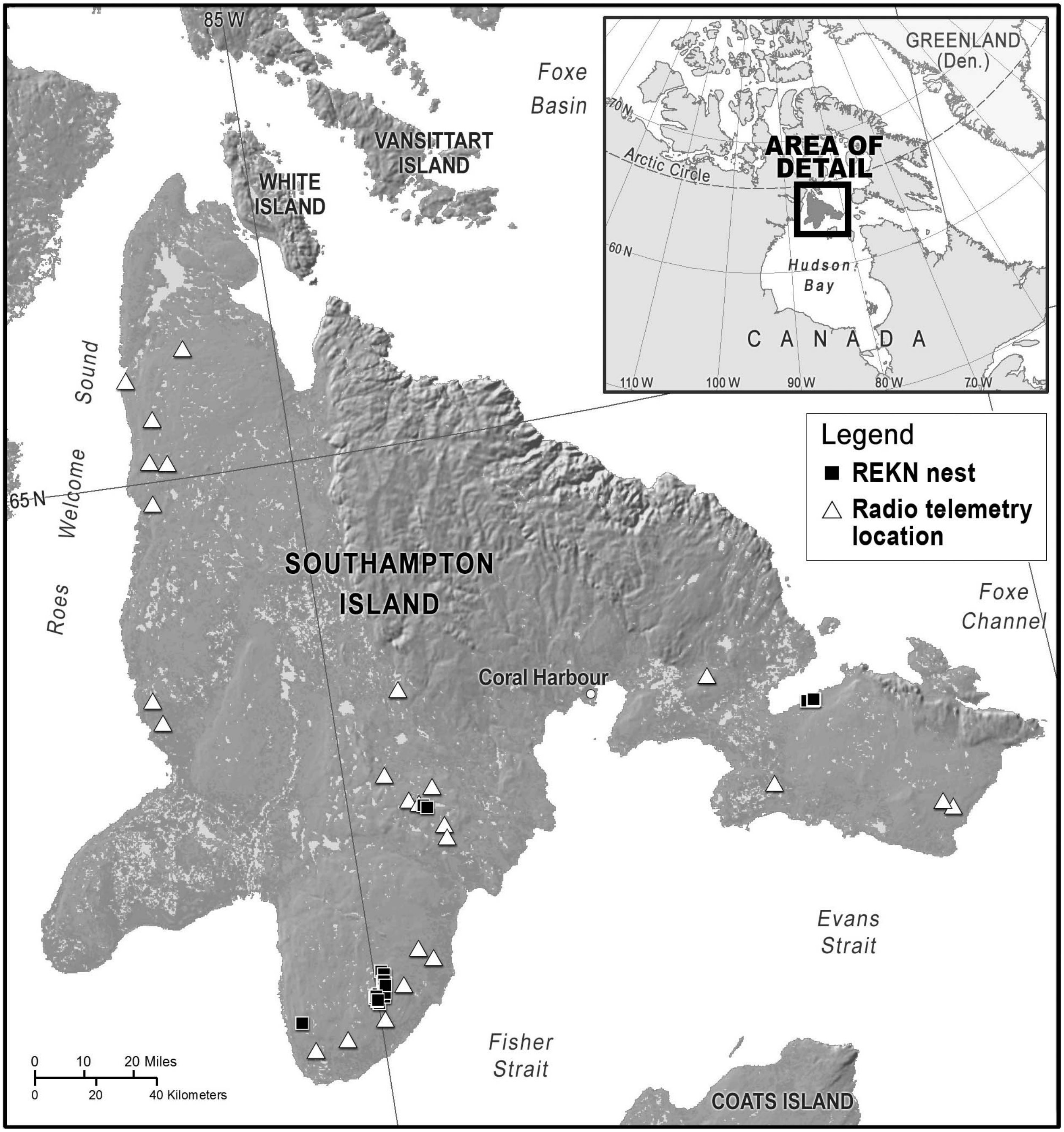

FIGURE 2. Map of Southampton Island study area showing locations of observed Red Knot (REKN) nests and radio-tag locations.

Southampton Island Intensive Study Area

Earlier work by Morrison and Harrington (1992) suggested that Southampton Island, Nunavut, Canada, was a "hotspot" for breeding knots, so this area was selected for subsequent intensive field surveys. Ground-based surveys for nesting knots were undertaken during the summers of 1999, 2000, 2001, 2003, and 2013 across southern Southampton Island and in 2000–2017 in the East Bay region (Figure 2). The surveys were conducted by 3–12 field observers who used a combination of area search and rope dragging to locate occupied nests. Nest location was recorded ±5 m with a handheld GPS and general habitat characteristics were noted, including type and extent of vegetation cover, surficial geology, position of nests with respect to topography, and proximity to wetlands.

Species Distribution Modeling

Developing a species distribution model (SDM) begins with observations of species occurrences, and incorporates environmental variables thought to influence habitat suitability and therefore species distribution (Guisan and Zimmerman 2000, Austin 2002, Elith and Leathwick 2009, Franklin 2010). The objective of the SDM is to show potential geographical distribution of the species in the form of a predictive map. While a number of authors have raised concerns about model parameterization, overfitting, sampling bias, and predicting distributions outside sampled areas (Elith et al. 2011, Warren and Seifert 2011, Radosavljevic and Anderson 2013, Kramer-Schadt et al. 2013, Merow et al. 2013, Convertino et al. 2014), when properly addressed, model-based predictions may provide the best available information for guiding management decisions where on-the-ground data are sparse or not available (Latif et al. 2013, Saalfeld et al. 2013).

We differentiated between 2 scales of habitat use: (1) localized nesting habitat with a focus on characterizing the environmental attributes associated with the nest site location; and (2) general breeding habitat, which incorporates both nesting and foraging habitat use for adult and juvenile birds. For the former, our modeling and mapping of nesting habitat is at a local scale (i.e. changing vegetation or land cover characteristics with a resolution [or grain size] ranging from 10s to 100s of meters over a spatial extent of over 40,000 km^2), while for the latter, our modeling of breeding habitat is at a coarser regional scale with a resolution of 250–400 m and a spatial extent of over 750,000 km^2. On Southampton Island we focused on mapping and modeling nesting habitat at a local scale. Our regional-scale modeling of breeding habitat covers much of the eastern and central Canadian Arctic. Finer, local-scale data are not available on a consistent basis across the broader region. At the coarser regional-scale resolution, we did not deem it feasible to spatially differentiate nesting habitat from foraging habitat, thus these were combined (hereafter referred to as "breeding habitat").

A key problem in the prediction of species' distributions is that species occurrence surveys are not exhaustive: absence of a detection does not necessarily equate to true absence. Newer machine-learning methods have been shown to be effective in working with presence-only data (Philips et al. 2006, Phillips and Dudik 2008, Elith et al. 2011) and are particularly well suited to noisy or sparse information (Elith et al. 2006). Maximum entropy modeling employs machine learning and maximum-likelihood methods to evaluate the significance of various input criteria individually and in combination based on maximum entropy criteria. One implementation of this approach, Maxent, has been used in a variety of contexts to model habitat suitability, on the basis of presence-only data, for a number of bird species (Stabach et al. 2009, Illera et al. 2010, Howell and Veloz 2011, Latif et al. 2013). Owing to its calibration using presence data only, Maxent results should be interpreted as a relative, rather than absolute, indicator of habitat suitability (Elith et al. 2006, 2011).

We used Maxent model version 3.3.3 (Philips et al. 2006). The Maxent model works by comparing the known locations of occurrence vs. a random sample of 10,000 background data points from the potentially available habitat area. To help address issues related to sampling selection and model overfitting, we employed a mask layer and cross-validation. For the local scale nesting habitat suitability model, we digitized a mask layer that represented the spatial extent of the training region (i.e. the geographic areas surveyed on the ground at each of the Southampton Island survey sites). For the regional scale model, the radio-telemetry survey detection swaths served as the training extent mask. For both models we employed leave-one-out cross-validation, where the occurrence data was randomly split into a number of 10 equal-size "folds," and models are created by leaving out each fold in turn. The final model is an average of the 10 individual models and the left-out folds were then used as test evaluation.

To evaluate the sensitivity (i.e. 1 − omission rate) vs. specificity (i.e. 1 − fractional predicted area) of the Maxent model, a receiver operator characteristic (ROC) curve was produced and the area under the curve (AUC) calculated. The test AUC (generated from the randomly selected test data withheld from the model construction) is generally thought not to suffer from the same overfitting problems that affect the training AUC (Warren and Seifert 2011) and we therefore gave it greater weight in evaluating the utility of the models. An optimal model has an AUC close to 1 while a model that predicts species occurrences at random has an AUC of 0.5. Elith et al. (2006) suggested a minimum threshold of AUC >0.75 for useful discrimination.

To evaluate which input variables are most important in the model, variable contributions were analyzed using several different metrics (see also Supplemental Material). Maxent uses the "gain" as a measure of the samples to be correctly predicted as present. The jackknife test shows the regularized training gain with all the variables included, with only the selected variable of interest and without the selected variable in the model. In an attempt to develop a robust model, we explored the relative importance of environmental variables by fitting a full model including all the variables and also reduced models, with only a subset of the variables. We modified the regularization multiplier from the default of 1 to a maximum of 4; higher regularization parameters help to reduce model overfitting, effectively "smoothing" the model outputs (Philips et al. 2006, Radosavljevic and Anderson 2013).

Once a Maxent model was determined, the SDM results were projected across the entire Southampton Island or central Canadian Arctic study regions (ocean water was excluded). The resulting map of predicted species distribution was then masked by the spatial extent of the breeding range (Figure 1). To classify each pixel into one of two categories, "suitable" or "unsuitable" habitat, we selected a threshold of logistic probability such that the model sensitivity equaled specificity for the withheld test data. Sensitivity is defined as the percent of "true" presences correctly classified as present by the model, and specificity is the percent of "true" absences correctly classified as absent (Liu et al. 2005, Bean et al. 2012). Thus the sensitivity = specificity threshold treats "false" positives and "false" negatives as equally important. The thresholded mapped outputs were then compared with several independent bird survey datasets to evaluate the practical utility of the resulting habitat suitability maps. These validation data sets were spatially independent (i.e. not collected in the same geographic locations) and represent a broader range of environmental conditions. Truly independent evaluation data allow for more reliable estimates of model performance, generality, and transferability (Radosavljevic and Anderson 2013).

For the Southampton Island model, we used ground observed nest site locations ($n = 40$) to calibrate the Maxent model of nesting habitat suitability at the local level. Airborne radio-tagging observations ($n = 28$) were used for independent evaluation of the SDM model outputs. We recognize that the airborne radio-tagging data do not provide nesting site locations as a way of explicit comparison but the data do provide an indication of breeding season activity in the general vicinity (i.e. within several hundred meters). Owing to uncertainty assigning behavior at the time of observation (i.e. on the nest, in flight, foraging, or roosting), we buffered these locations by 0.5 km radius and extracted the maximum Maxent predicted likelihood value within that circle. This 1 km diameter circle is also supported by our field observations, which suggest that knots are solitary nesters that actively defend territories ~1 km in diameter, leading to well dispersed nest sites.

The regional scale model was developed using a total of 44 individual Red Knot locations recorded during the 5 airborne radio-tagging survey flights. Additional Red Knot sighting data were included from the Canadian Wildlife Service Northwest Territories and Nunavut Checklist survey (Canadian Wildlife Service 2013, retrieved March 2016) and the Arctic Program for Regional and International Shorebird Monitoring (PRISM) database (Canadian Wildlife Service 2017, retrieved March 2016). This combined PRISM and Checklist survey dataset includes 425 knot sightings at 200 distinct locations since 2000. These sightings were further winnowed to include only unique locations where evidence of active nesting was observed (i.e. nest with eggs or otherwise occupied nest, recently fledged young, or some type of distraction display or injury feigning). Only 3 Checklist and 7 PRISM observations ($n = 10$) within the Central Arctic study region met these criteria and were used as additional calibration data.

As means of validating the utility of the regional scale Maxent model's estimation of breeding habitat suitability, we compared the model's predictions with eBird occurrence data (eBird 2017). These eBird occurrence data points were not included in the Maxent model calibration and thus can be considered as independent validation. Only eBird records of knot sightings during the breeding period (June 10–July 25) were used. Due to the uncertainty in the exact spatial location of the survey points, a 1 km diameter circle centered on the observed coordinate location was used. From within this circle, we determined the maximum Maxent predicted likelihood value and used this to assess the validity of the model's predictions.

Geospatial Database of Environmental Data

Local scale: Southampton Island. A number of geospatial environmental data sets were acquired or developed to cover all of the Southampton Island study area at a grid cell resolution of 30 m, to support the development of a nesting habitat suitability model. The elevation data are based on the 1:50,000 scale Canadian Digital Elevation Data (Government of Canada 2000; Figure 3A). Bedrock and surficial geology were mapped by the Geological Survey of Canada and released in digital map form (Geological Survey of Canada 1999, 2001; Figure 3B). The land cover/habitat data set developed by Fontaine and Mallory (2011) was employed as the base map of habitat types (Figure 3C). These data were derived from Landsat Enhanced Thematic Mapper image data acquired in late July and early August 2000, classified and ground-truthed in 2001 and 2002 with a stated overall accuracy of 96%.

Knots arrive in the Arctic in late May or early June when the ground often remains largely covered in snow (Smith et al. 2010). We hypothesized that birds may preferentially select early snow-free areas as nest sites. Imagery from mid-June was acquired to capture the period of typical spring melt. At this time, ridge tops and other topographic features that tend to have lower snow depths or enhanced melting (e.g., south-facing slopes) were either completely or partially snow-free. Mid-June snow cover data were derived from Landsat 5 TM and 7 ETM+ imagery acquired over multiple years during the time period between June 9 to June 21 for the years between 2000 and 2011. A normalized snow index was computed for each image, cloud-free areas extracted, and selected index images mosaicked to produce a seamless composite (Figure 3D). The raw values were used to provide a relative index of snow cover; index values greater than 210 were interpreted to be complete snow cover. As our field observations suggested that Red Knot nests and territories were often associated with esker ridges (~10–15 m higher than the surrounding terrain), a landform shape index was calculated based on the digital elevation data as a measure of the landform topographic concavity or convexity (McNab 1993; not shown).

Our field observations revealed that adult knots generally nest in upland areas but forage in the neighboring marshes, wetland pools, or along lake edges. In many cases, knots from several nearby territories were seen foraging simultaneously in the same wetland complex. For each grid cell, we used the Euclidean distance tool of ArcGIS Spatial Analyst (ESRI, Redlands, California, USA) to calculate the distance to freshwater wetlands or lakes in the Southampton Island Land Cover map listed above (Fontaine and Mallory 2011; Figures 3E and 3F, respectively).

Regional scale: Central Canadian Arctic region. To support the SDM of breeding habitat at a regional scale, we developed a GIS database for the central Canadian Arctic study area (Figure 4A). Elevation data were from the Canada Digital Elevation Model (CDEM) mosaic data (400 m grid cell; Government of Canada 2014; Figure 4B). Land cover data were extracted from the North American Land Change Monitoring System (NALCMS 2005). The NALCMS land cover data are based on MODIS satellite imagery monthly composites from 2005 (spatial grid cell resolution of 250 m; Figure 4C). Bedrock geology data were from the Nunavut Bedrock Geology and Faults map produced by the Geological Survey of Canada (Geological Survey of Canada 1999). The scale of the source data is 1:5,000,000; the bedrock delineations in the mapped data that were utilized are the general rock categories of intrusive, metamorphic, sedimentary, and volcanic (Figure 4D). These delineations were rasterized at 250 m grid cells for the Arctic-wide modeling processes. Distance to water, both marine and inland (as mapped by the USGS NALCMS listed above), was calculated by using the Euclidean distance tool of ArcGIS Spatial Analyst (Figure 4E). Snow cover duration (SCD; in days) data for current conditions were from modeled data produced by Environment Canada (Derksen and Brown 2012). The SCD data have been re-projected and interpolated using an inverse distance weighted algorithm to create a continuous surface for incorporation into the Maxent model as an additional climate variable (Figure 4F). While the SCD data have been gridded at 250 m, the spatial resolution of the original data is significantly coarser at 24 km grid spacing.

The frequency distributions of calibration and validation observations as well as the percentage composition of the overall study and the training area by category/value for each of the 6 environmental parameters that were included in the Maxent model were computed. The resulting histograms were evaluated to determine how well the calibration (or validation) data represented the range of values across the study area and whether there were ranges of the environmental parameters that were not well sampled or surveyed (histograms for both the local and regional scale data are included in the Supplementary Material).

RESULTS

Local Scale: Southampton Island Nesting Habitat Suitability

The Southampton Island Maxent model had high explanatory power with an average test AUC for the replicate runs of 0.897. The omission on test samples closely approximates the predicted omission rate, as depicted in the plot of how testing omission varies with the choice of cumulative threshold (i.e. with suitable conditions predicted above the threshold and unsuitable below; see Supplemental Material for more detail). An overlay of the independent flyover radio-tag data (not used in the Maxent model calibration) with the map of Maxent model outputs (Figure 5) shows a high degree of spatial correspondence. Applying the sensitivity = specificity decision criteria for the default regularization of 1 (Maxent predicted likelihood threshold = 0.30), 96% of the radio-tag observations (not used in the Maxent model calibration) were within a 1 km neighborhood of habitat classified as suitable; 76% of the independent observations were within a 1 km neighborhood of Maxent values of greater than 0.60 (Figure 6). We experimented with increasing the regularization rate to assess the effect on model results. Increasing the regularization multiplier slightly lowered the average test AUC to 0.889, 0.870, and 0.860 for Regularization = 2, 3, and 4, respectively, and did not substantively improve the model accuracy (when compared to the independent validation data) over the default regularization. Given the high correspondence that we observed between the model outputs (for regularization multiplier of 1) and the independent validation data, we opted for this more restricted model. While the higher regularization multipliers produce "smoother" model outputs with potentially lower errors of omission, one might also expect higher errors of commission due to the greatly increased area classified as Suitable Habitat (grid cells above the sensitivity = specificity decision threshold). The percent of the Southampton Island classified as suitable nesting habitat increases from approximately 22% to 30% to 38% to over 45%, for regularization multipliers of 1, 2, 3, and 4, respectively.

Regional Scale: Central Canadian Arctic Breeding Habitat Suitability

Based on various model evaluation criteria, the regional scale Maxent model had an average test AUC for the

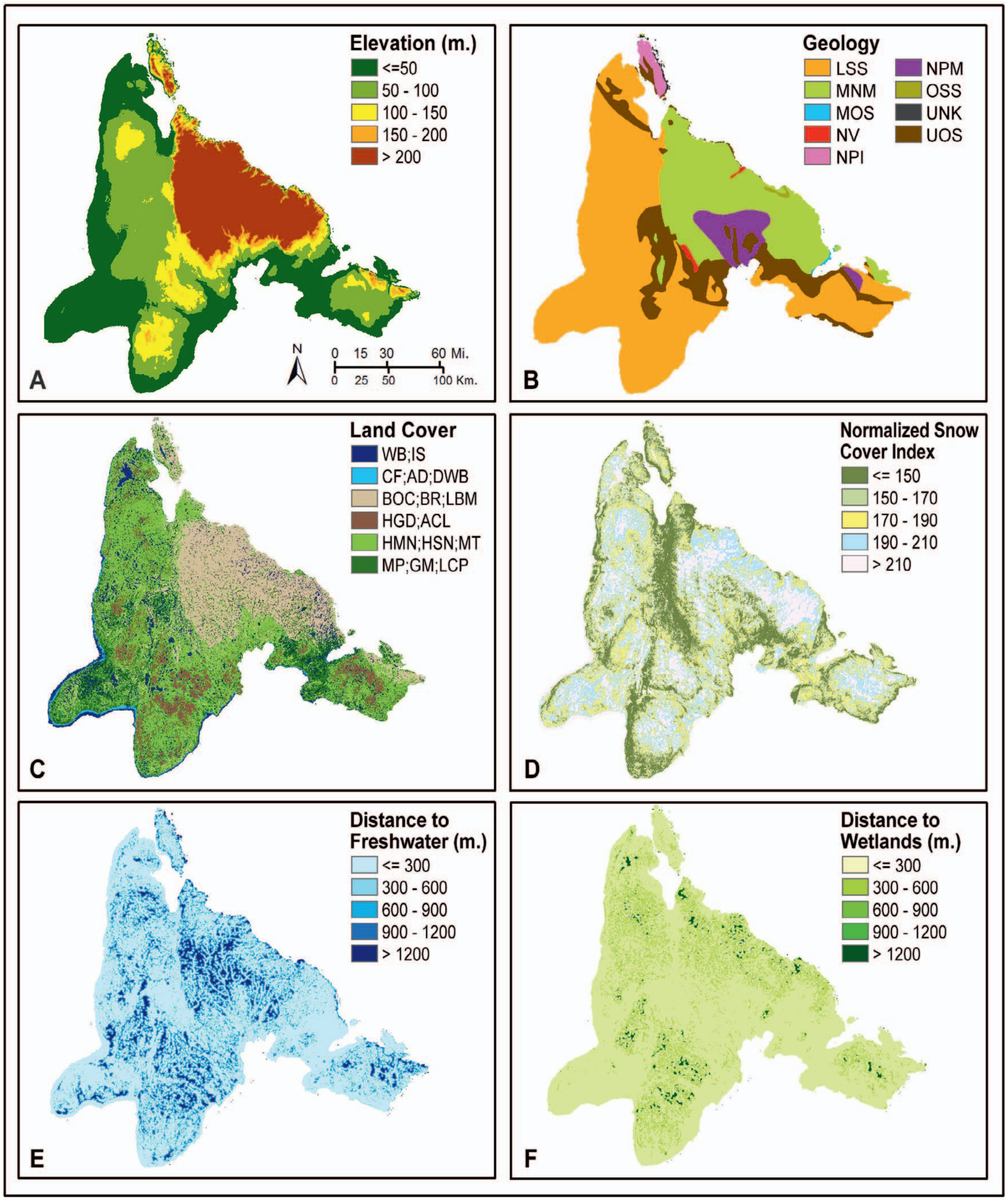

FIGURE 3. Map of environmental factors for Southampton Island study area and local scale species distribution model (SDM). Geology class categories are lower Silurian sedimentary offshore (LSS), Mesoarchean-Neo Metamorphic (MNM), Middle Ordovician sedimentary (MOS), Neoarchean volcanic (NV), Neoarchean-Paleo intrusive (NPI), Neoarchean-Paleo metamorphic (NPM), Ordovician-Silurian sedimentary (OSS), unknown (UNK), Upper Ordovician sedimentary (UOS). Land cover categories (from Fontaine and Mallory 2011) were simplified for visual display purposes: category WB:IS includes Classes 1.1–1.3 waterbodies and ice/snow ridges; CF:AD:DWB includes Classes 2.1–2.3 and 2.4 coastal flats, active deposits, and drained water bodies; BOC:BR:LBM includes Classes 3.1–3.4 bedrock outcrops, boulder ridges, and lichen-heath tundra; HGD:ACL includes Classes 4.1–4.3 gravel to hand size and larger fragment deposits and algae-covered lag; HMN:HSN:MT includes Classes 5.1–5.4 heath mats and nets, heavy heath shrub nets, and mixed tundra; MP:GN:LCP includes Classes 6.1–6.5 exposed peat, moss carpets, graminoid meadows, and low-center polygons.

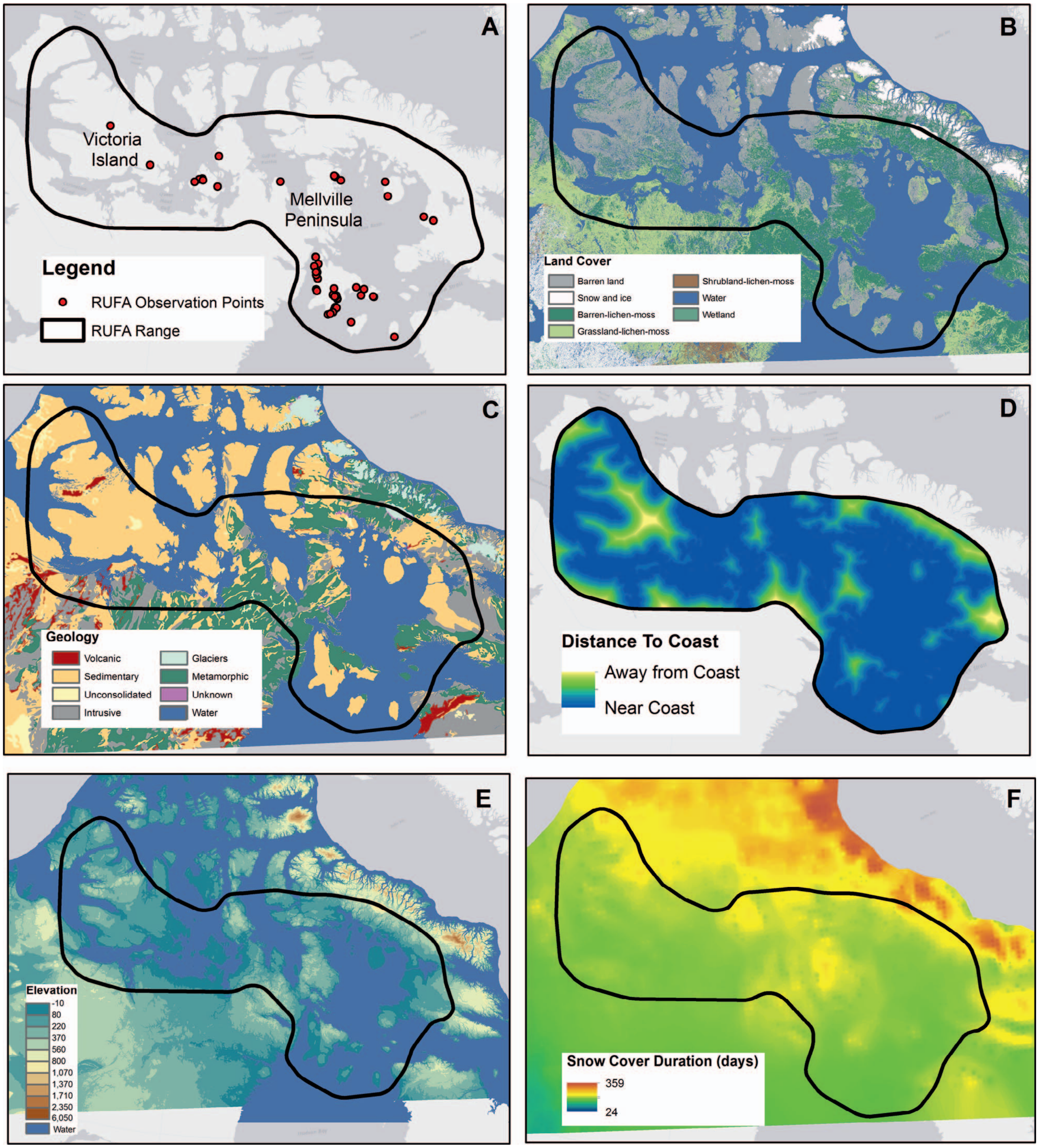

FIGURE 4. Map of environmental factors for Central Canadian Arctic regional scale species distribution model (SDM) showing *rufa* range boundary and locations of Red Knot (REKN) radio-tag observations and CWS Surveys.

replicate runs of 0.812 (see Supplemental Material for more details). Geology, followed by snow cover and land cover, were the most important input variables, both in highest gain in isolation or decrease in gain when omitted (Table S2). Using the sensitivity = specificity decision criteria, the Maxent predicted likelihood threshold is 0.42. An overlay of the independent eBird observation data (not used in the Maxent model calibration) with the map of Maxent model outputs (Figure 7) shows a high degree of spatial correspondence between the location of the 159 observation points and the zones of higher predicted breeding habitat suitability. Approximately two-thirds

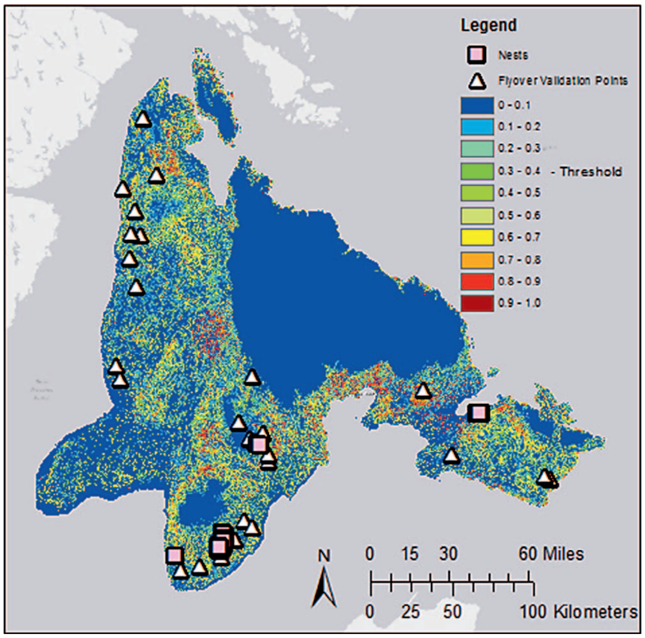

FIGURE 5. Maxent predicted nesting habitat suitability map for Southampton Island. Nest site model calibration locations shown as pink and black squares. Flyover validation locations shown as white and black triangles.

(66%) of the 159 eBird observations were correctly classified as suitable habitat (i.e. had maximum Maxent likelihood values within a 1 km neighborhood of greater than the threshold of 0.42; Figure 8).

DISCUSSION

Local Scale: Southampton Island Nesting Habitat Suitability

Using a combination of intensive nest surveys, local scale GIS of environmental characteristics, and maximum entropy (Maxent) modeling techniques, a spatial model of nesting habitat suitability for the Red Knot was developed for the Southampton Island study area at the local scale. Owing to the difficulty of access for field surveying, and the scarcity of knot nests, the SDM is based on a limited sample size of nest site locations from 3 intensively surveyed study areas collected over nearly 20 yr. As a result, this data set is likely subject to both sample selection bias and spatial clumping (Elith et al. 2011, Kramer-Schadt et al. 2013). Examination of the histograms (Supplementary Material) suggests several of the environmental parameters experienced sample selection bias (i.e. some landscape types were sampled more intensively than others) and thereby may potentially bias the resulting model predictions (i.e. lead to omission errors). For example, a number of land cover categories (e.g., 3.0 Bedrock and Boulders or 3.3 Lichen-Heath Tundra) or higher elevation ranges ($>$ 200 m) that cover significant portions of Southampton Island were not surveyed. Spatial clumping often results in spatial autocorrelation and can affect model quality by inflating model accuracy (Kramer-Schadt et al. 2013). However, efforts were made during the Maxent modeling process to reduce the impact of these problematic effects as well as model overfitting (e.g., exclusion of the Southampton nesting site data in the regional scale model, adjustment of the regularization parameter, and validation of the model results with independent data).

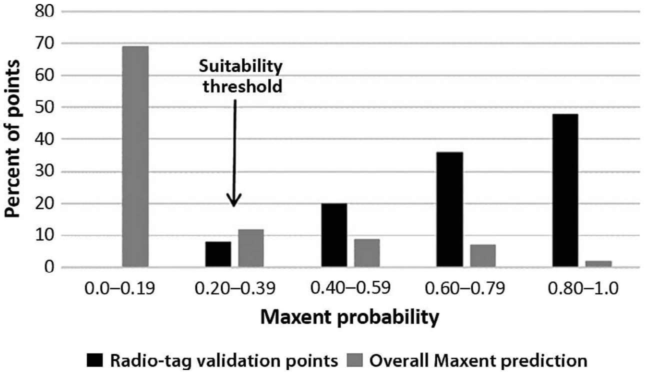

FIGURE 6. Percentage of Southampton Island Red Knot radio-tag observations classed by maximum Maxent predicted likelihood values for 1 km window centered on the radio-tag coordinate locations ($n = 28$). Sensitivity = Specificity habitat suitability threshold = 0.3043. Area distribution of Maxent predicted values included for comparison.

Comparison of the final mapped results with independent validation data (i.e. airborne survey radio-tag observations) suggest that the Southampton Island local-scale model is a useful predictor of nesting habitat suitability (Figure 5); 96% of the independent observations were within a 1 km neighborhood of grid cells classified as suitable nesting habitat while only 24% of Southampton Island so qualifies (i.e. Maxent model result greater than the sensitivity = specificity threshold). The Maxent modeling results coupled with an examination of the frequency distributions of the original field data (see Supplemental Material) point to the importance of specific environmental factors influencing Red Knot nesting habitat preferences.

Land cover type. On Southampton Island, knots appear to strongly prefer sparsely vegetated areas for nesting. While our field observations suggest that the general area surrounding nest sites was predominantly unvegetated, the actual nests were located in small patches (0.25–1 m^2) of either prostrate shrub (primarily Arctic dryad [*Dryas integrifolia*]) or sedge (Figure 9).

Bedrock geology. Nests were universally found in areas where sedimentary bedrock predominates. Sedimentary bedrock appears to facilitate the sparsely vegetated habitat

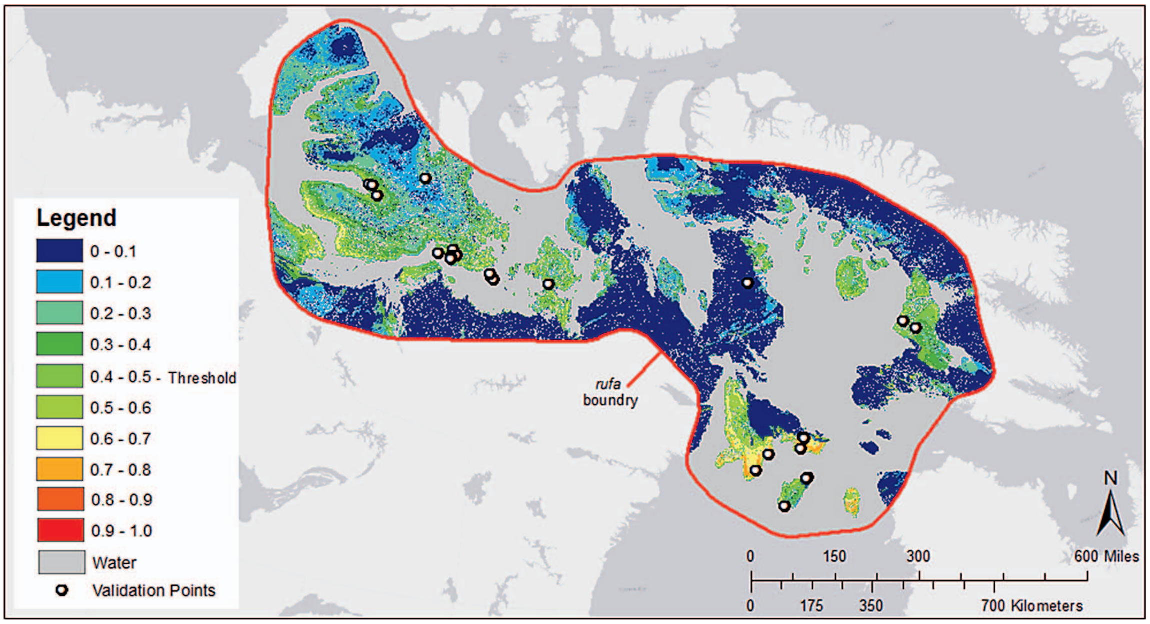

FIGURE 7. Map of Maxent model outputs for the Central Canadian Arctic study region (*rufa* range included as red line) with eBird survey Red Knot observation points ("validation points": white circles). Note knot observations on both Southampton and Coats Islands.

that knots prefer. Sedimentary bedrock, in particular limestone, is especially prone to freeze–thaw cracking and the development of frost boils that limit the development of thick vegetation cover. Field observations from nest site surveys also show that knots will nest on coarse-textured, unconsolidated glacial deposits such as esker ridges, moraines, and kames. In our study area, there is a high correlation between the sparsely vegetated land cover types (categories 4.1, 4.2, and 5.1 from Fontaine and Mallory 2011) and Silurian age sedimentary bedrock geology. In western Alaska, *roselaari* knots appear to prefer nesting on *Dryas*/sedge found on dry alkaline soils (i.e. derived from limestone) amid lichen-covered granitic rock fields (Johnson et al. 2011).

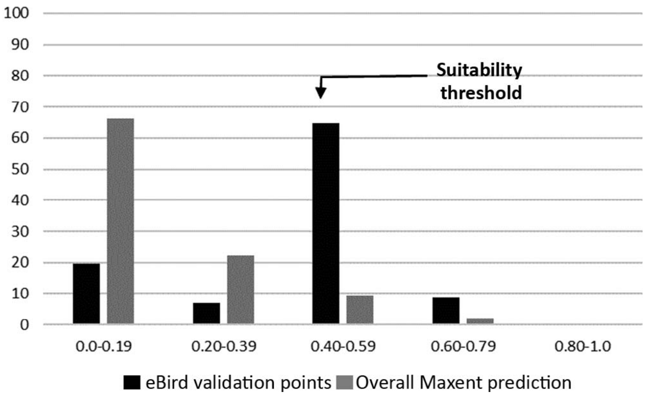

FIGURE 8. Percent of Central Canadian Arctic Red Knot eBird occurrence points classed by maximum Maxent predicted likelihood values for 1 km window centered on the eBird coordinate locations ($n = 159$). Sensitivity = Specificity habitat suitability threshold = 0.42. Area distribution of Maxent predicted values included for comparison.

Elevation. Nearly 100% of nests in southern Southampton Island were at elevations of 90–130 m ASL. In the East Bay area of Southampton Island, knots nested below 15 m ASL.

Foraging habitat. Vast tracts of Southampton Island are barren, while other areas are a mosaic of barren or sparsely vegetated tundra interspersed with areas of emergent herbaceous wetlands and inland water (i.e. ponds and lakes). Knots appear to show a preference for areas near freshwater wetlands or freshwater lakes or rivers but not directly adjacent to these features. Our field observations of nesting knots revealed that they travel to these neighboring marshes and wetland pools to forage. This behavior of foraging at some distance from the nesting territory is not uncommon for shorebirds. For example, Western Sandpipers (*Calidris mauri*) defend small nesting territories in heath tundra but travel to nearby wetlands and pond margins to forage; it has been suggested that this separation of breeding and foraging allows for selection of nest sites that minimize predation irrespective of food abundance (Holmes 1971). Whether knots travel from inland nesting sites to coastal wetlands to forage, especially early in the season when freshwater inland sites might still be frozen, is still an open question.

Comparison of nest locations with the radio-tagging data suggests that radio-tagged birds were observed at

FIGURE 9. Red Knot on nest in *Dryas integrifolia* patch amidst limestone gravel. Photo credit: Mark Peck

lower elevations and in closer proximity to wetlands and/or freshwater lakes and rivers than the Maxent modeling results might suggest (see Supplemental Material). Thus one possible interpretation is that these individuals were not on the nest but rather foraging either in close proximity to nesting areas or not. This suggestion is supported by field observations at a long-term study site at East Bay Southampton Island. Work at this site is carried out in low-lying wetlands, 0–4 km from the coast. Knots are observed regularly at this site throughout the breeding season, but in 18 yr of study and with over 1,500 shorebird nests found, only 6 knot nests have been located, suggesting they only forage at this coastal site (P. Smith personal observation).

Regional Scale: Central Canadian Arctic Breeding Habitat Suitability

Using a combination of airborne radio-tagging surveys, regional scale GIS of environmental characteristics, and Maxent modeling techniques, a spatial model of breeding habitat (i.e. both nesting and foraging habitat) suitability for the Red Knot was developed for the Central Canadian Arctic regional study area. Examination of the frequency distributions for the environmental parameters (in the Supplementary Material) suggests that due to the broader area covered by the airborne telemetry surveys there was less sample selection bias. Based on the various metrics of model fit, this model was deemed a useful predictor of potential nesting habitat. Comparison of the final mapped results with independent validation data (i.e. eBird observations) suggest that the regional scale model is a useful predictor of nesting habitat suitability; 66% of the independent observations were within a 1 km neighborhood of grid cells classified as suitable nesting habitat while approximately 10% of the knot range area so qualifies (i.e. Maxent model result greater than the sensitivity = specificity threshold). The lower "accuracy" of the regional scale model, as compared to the local model, may be a function of the quality of the eBird observations in that they are "volunteered" data and only constrained by the date of observation, not the behavior of the observed bird (i.e. whether they were nesting or defending a territory, etc.) or the experience of the observer.

The following characteristics appear to be important factors in determining the suitability of an area as Red Knot breeding habitat.

Land cover type. As with the local scale study, knots appear to strongly prefer areas that are sparsely vegetated (i.e. barren) at a regional scale, with over 80% of the sightings in such land cover types.

Bedrock geology. Similar to the local scale study, knots were nearly always found in areas where sedimentary bedrock predominates.

Elevation. The majority of the knot airborne radio-tag sightings (over 95%) were found below 100 m ASL. This elevation range is lower than that observed for the local scale study, where birds were found up to 150 m ASL. Knots have been found to nest up to 200 m ASL in the vicinity of Cambridge Bay (Parmelee et al. 1967), and *C. c. roselaari* have been observed nesting between 100 and 700 m ASL in Alaska (Johnson et al. 2011).

Foraging habitat. Knots appear to show a slight preference for areas near but not directly adjacent to the coast. Nearly 60% of sightings were within 5–15 km of the coast. As noted above, field observations suggest the possibility that Red Knots might travel from inland nesting sites to coastal wetlands to forage, especially early in the season when freshwater inland sites are still frozen.

Snow cover. Knots appeared to prefer areas with a moderate snow cover duration of approximately 205 days. The full SCD data set displayed a range between 190 and 265 days across the knot breeding range.

Conservation Implications

As elucidated by Elith et al. (2006, 2011), species distribution models based on presence-only data (as is the case here) may not always accurately predict absolute probability of presence for a species. Even so, these models are useful in their ability to rank sites for relative suitability. As Saalfeld et al. (2013) have shown for the Arctic Coastal Plain of Alaska, the resulting habitat suitability maps identify important regions for nesting shorebird species and are useful for setting conservation

TABLE 1. Area of Maxent-predicted *local* scale nesting and *regional* scale breeding habitat suitability likelihoods. Suitable habitat was defined by applying the sensitivity = specificity decision criteria; the Maxent predicted likelihood threshold for *local* scale model = 0.30 and for *regional* scale model = 0.42. Note that the Central Arctic region includes only the area within the *rufa* range excluding ocean water.

Maxent likelihood	Area of local scale model: Southampton Island		Area of regional scale model: Southampton Island		Area of regional scale model: Central Arctic	
	(km^2)	(%)	(km^2)	(%)	(km^2)	(%)
0.0–0.19	28,124	69.1	13,598	35.6	493,234	66.2
0.2–0.39	5,222	12.8	3,224	8.4	166,241	22.3
0.4–0.59	3,597	8.8	10,746	28.1	69,682	9.4
0.6–0.79	2,929	7.2	10,608	27.8	15,707	2.1
0.8–0.1.0	850	1.9	0	0.0	0	0.0
Suitable habitat	9,638	23.7	20,752	54.4	74,302	10.0

priorities. Climatically suitable breeding conditions for Arctic shorebirds, including knots, are predicted to shift and decline in coming decades (Wauchope et al. 2016), and an understanding of species–habitat relationships could allow for a more precise understanding of the future impacts of changing climate and shifting habitats.

Approximately 9,638 km^2 (or 23.7%) was classed as suitable nesting habitat at the local scale (Table 1). Comparison of the Maxent model results for the local scale vs. regional scale model for the Southampton Island area reveals that the regional scale estimate of suitable breeding habitat is over 2 times larger (20,752 km^2 vs. 9,638 km^2; Table 1). This is not unexpected; the coarser regional scale data do not resolve finer-scale landscape features (e.g., most emergent wetlands) but may merge these areas in with the dominant matrix of barren uplands. Thus while the local scale mapping delineates areas suitable for placement of nests, the coarser regional scale habitat mapping better delineates breeding territories that include both nesting and adjacent foraging habitat.

Across the entire Central Arctic breeding range, our results suggest that there is 74,302 km^2 of suitable breeding habitat, which represents approximately 10% of total extent of the published knot range (Table 1). Assuming a territory size of approximately 1 km^2 and our regional scale results, the Central Arctic could support at least 74,000 breeding pairs. These results suggest that it is highly unlikely that availability of breeding habitat currently limits the population (~42,000 individuals; Andres et al. 2012), although the estimated 50,000–75,000 pairs in the 1980s (Morrison and Harrington 1992) would have been closer to the limit of breeding habitat.

Our Maxent model suggests that Southampton Island has extensive areas of suitable nesting habitat (20,752 km^2 or nearly 28% of the total 74,302 km^2), and our finding that 28/47 (60%) of airborne radio-tag observations occurred here despite significant aerial survey efforts throughout the eastern Arctic confirms Southampton Island as a hotspot for knot breeding. Importantly, our predictions also suggest areas of habitat suitability where few if any intensive ground surveys for knots have occurred. Ornithological expeditions frequently focus on coastal wetlands; without a dedicated effort to locate breeding Red Knots away from coasts, they might easily be missed. Among other areas, the Brodeur Peninsula, Foxe Basin between Igloolik and Steensby Inlet, King William Island, the areas north and west of Kugaaruk, and eastern Victoria Island are predicted to contain significant amounts of suitable breeding habitat (Figure 7) but to our knowledge have not been surveyed extensively for breeding knots. The area from King William Island, through Somerset Island and east to the Brodeur Peninsula, merits attention. This latitude (~71°N) represents the presumed boundary between the *rufa* and *islandica* subspecies (COSEWIC 2007). Knots breed in northern Baffin Island and neighboring Bylot Island (300 km west of the Brodeur Peninsula at 72.5°N; Renaud et al. 1981), and a photograph of a radio-tagged individual in Pond Inlet, Nunavut, suggests that *rufa* may occur in this region. Further studies in these areas may help to resolve the northern extent of the breeding range of the *rufa* population and whether *rufa* and *islandica* are sympatric breeders in a portion of the range. Refining knowledge of breeding habitat preferences for *rufa*, as we have done here, and defining the northern limit of the breeding distribution are both identified as critical research needs in the species' proposed Canadian recovery strategy (ECCC 2016).

Our work suggests that *rufa* knots strongly prefer tundra environments that are sparsely vegetated to almost barren of vegetation as nesting habitat. Where it occurs, the dominant vegetation is a patchy cover of *Dryas*, sometimes mixed with sedges. Selection of these sparsely vegetated nest site locations may be a mechanism for knots to reduce nest predation and nest site competition (see Martin 1993) with other breeding shorebirds or songbird species that use the more heavily vegetated sedge wetlands or willow shrublands. Densities of birds are extremely low in sparse vegetation, perhaps making it unprofitable for nest predators.

Models calibrated by ground observations and aerial surveys of birds with radio-tags provide a useful tool in understanding the distribution of Arctic-nesting shorebirds. This is particularly true for species occurring in low numbers or low densities, which are often the most in need of broad-scale status assessment. Because of their low density, knots may be one of the most difficult species to survey in the vast expanses of the Canadian Arctic. Johnson et al. (2007) encountered similar difficulties when surveying for knots on the Arctic Coastal Plain of Alaska. Bart et al. (2012) had difficulty developing a population estimate of knots after a 10-year survey that covered much of the same area we determined to be knot habitat. This difficulty was partly a consequence of knots using barren habitat that was not a good target for multi-species surveys. A further complicating factor is that knots' low density and secretive nest behavior thwarted the efforts of surveyors with limited time to spend in each survey location. The same challenges are encountered for other low-density species, such as Sanderling (*Calidris alba*) and Ruddy Turnstone (*Arenaria interpres*), which are also declining and in need of a similar broad-scale status assessment (Andres et al. 2012). Our habitat modelling approach, particularly with more data, could yield more reliable estimates of carrying capacity as well as provide the basis for more precise geographic targeting of survey efforts. This information could play an important role in the design of more efficient and effective surveys for shorebirds in the Arctic, and in the conservation and management of their declining populations.

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