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Predicting breeding shorebird distributions on the Arctic Coastal Plain of Alaska

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Abstract. The Arctic Coastal Plain (ACP) of Alaska is an important region for millions of migrating and nesting shorebirds. However, this region is threatened by climate change and increased human development (e.g., oil and gas production) that have the potential to greatly impact shorebird populations and breeding habitat in the near future. Because historic data on shorebird distributions in the ACP are very coarse and incomplete, we sought to develop detailed, contemporary distribution maps so that the potential impacts of climate-mediated changes and development could be ascertained. To do this, we developed and mapped habitat suitability indices for eight species of shorebirds (Black-bellied Plover [*Pluvialis squatarola*], American Golden-Plover [*Pluvialis dominica*], Semipalmated Sandpiper [*Calidris pusilla*], Pectoral Sandpiper [*Calidris melanotos*], Dunlin [*Calidris alpina*], Long-billed Dowitcher [*Limnodromus scolopaceus*], Red-necked Phalarope [*Phalaropus lobatus*], and Red Phalarope [*Phalaropus fulicarius*]) that commonly breed within the ACP of Alaska. These habitat suitability models were based on 767 plots surveyed during nine years between 1998 and 2008 (surveys were not conducted in 2003 and 2005), using single-visit rapid area searches during territory establishment and incubation (8 June–1 July). Species-specific habitat suitability indices were developed and mapped using presence-only modeling techniques (partitioned Mahalanobis distance) and landscape environmental variables. For most species, habitat suitability increased at lower elevations (i.e., near the coast and river deltas) and decreased within upland habitats. Accuracy of models was high for all species, ranging from 65–98%. Our models predicted that the largest fraction of suitable habitat for the majority of species occurred within the National Petroleum Reserve-Alaska, with highly suitable habitat also occurring within coastal areas of the Arctic National Wildlife Refuge west to Prudhoe Bay.

Key words: Alaska; Arctic; breeding; coastal plain; habitat suitability; niche model; North Slope; partitioned Mahalanobis distance; shorebirds.

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Introduction

The Arctic Coastal Plain (ACP) of Alaska encompasses several diverse landholdings including state and native corporation lands, the Arctic National Wildlife Refuge (ANWR), and the National Petroleum Reserve-Alaska (NPR-A), as well as the largest oil field in North America

(Prudhoe Bay Oil Field). This region provides important habitat for numerous avian species including millions of nesting and migrating shorebirds and waterfowl (Johnson et al. 2007, Bart et al. 2012). Shorebirds dominate, both in terms of abundance and diversity, the avian fauna of the ACP of Alaska (Johnson and Herter 1989, Bart et al. 2012), with many species exhibiting restricted breeding ranges solely within the Arctic (Poole 2005), making them ideal species to investigate potential impacts from development and climate change within this region. Moreover, numerous shorebird species, including those that nest within the ACP of Alaska have declined in recent years (Brown et al. 2001, Morrison et al. 2001, Morrison et al. 2006, Bart et al. 2007), with nine species considered species of high conservation concern or highly imperiled on a global or national scale (U.S. Shorebird Conservation Plan 2004). Additionally, due to their unique life history characteristics (e.g., specialized feeding, long-distance migrations, and diverse habitat associations), shorebirds have been identified as potential indicator species of environmental change (International Wader Study Group 2003, Piersma and Lindström 2004).

Two potential threats to shorebird breeding habitat in the ACP of Alaska are direct habitat loss and habitat modification due to climate change and development. Current projection models based on a moderate emissions scenario (scenario A1B) for the ACP of Alaska predict a 1.6°C increase in summer temperatures and 12% increase in summer precipitation by mid-century (i.e., 2051–2060) as compared to historic values (Martin et al. 2009). These climate changes are likely to have profound impacts on physical and ecological variables (e.g., surface water, vegetation community, and insect community), which will in turn affect both shorebird habitats and populations on the ACP of Alaska. For example, higher summer temperatures and a longer frost-free season are predicted to accelerate ice wedge degradation and thermokarst pond development (Shur et al. 2003), increase permafrost thawing (Arctic Climate Impact Assessment 2004) and evapotranspiration rates, lengthen the growing season (Myneni et al. 1997, Jia et al. 2003, Goetz et al. 2005, Bunn and Goetz 2006), and result in the northward expansion of shrubs (Sturm et al. 2001, Arctic Climate Impact Assessment 2004, Stow et al. 2004). Furthermore, loss of winter ocean ice, increasing tidal surges, and sea level rise are resulting in increased erosion rates, sedimentation, flooding, and salinization of low-lying habitats (Jorgenson and Ely 2001, Martin et al. 2009). Along with climate-mediated effects on shorebirds, increased human development could have a direct negative impact on shorebird populations and breeding habitat within the ACP of Alaska. For example, mineral, oil, and natural gas production in the ACP of Alaska has expanded in recent years (Gilders and Cronin 2000, National Research Council 2003, Bureau of Land Management 2011), and will likely continue to expand in the near future (National Research Council 2003). Potential negative effects of development on shorebird species include direct loss of habitat through the building of roads, drill pads, pipelines, landfills, gravel pits, and other infrastructure (Meehan 1986, McKendrick 2000, National Research Council 2003), as well as indirect effects such as increased risk from oil spills, increased levels of dust, altered hydrology, thawing of permafrost, altered vegetation communities, increased roadside snow accumulation (Auerbach et al. 1997, McKendrick 2000, National Research Council 2003), and increased habitat fragmentation (Meehan 1986). Furthermore, development may enhance predator populations by providing denning and nesting sites, perch sites, and supplemental food (e.g., human garbage; National Research Council 2003, Liebezeit et al. 2009).

The first step in evaluating the potential impacts of climate-mediated changes on habitat and development on shorebird species within the ACP of Alaska is to document the current distribution of shorebirds within this region. Unfortunately, the contemporary distribution of shorebirds is poorly known and only coarsely defined (e.g., distribution maps presented in the Birds of North America series; Poole 2005). Current distributions come from maps developed by The Nature Conservancy that use data acquired during aerial waterfowl surveys, which likely is a poor reflection of shorebird presence, or ground surveys representing only a small fraction of the entire ACP of Alaska (Johnson et al. 2007). Additionally, efforts to describe shorebird distributions using habitat associations come from small-scale studies based on only a few sites within the ACP of Alaska (Connors et al. 1979, Jones 1980, Myers and Pitelka 1980, Derksen et al. 1981, Martin 1983, Garner and Reynolds 1986, Cotter and Andres 2000). Few studies have attempted to use habitat classifications derived from satellite imagery to predict current shorebird habitat suitability across a large portion of their Arctic breeding range, although habitat associations have been used to estimate shorebird abundance within Canada (Gratto-Trevor 1996, Morrison 1997, Latour et al. 2005) and the ACP of Alaska (Bart et al. 2012). An understanding of contemporary distributions based on detailed, large-scale habitat associations will allow the identification of important areas as indicated by greater species richness and/or presence of imperiled or at risk shorebird species. Accordingly, our objectives for this study were to (1) identify the importance of physical and ecological variables to breeding shorebirds on the ACP of Alaska and (2) create and map habitat suitability indices that can be used to predict shorebird breeding distributions on the ACP of Alaska.

Methods

Study area

Our study area consisted of 85,000 km^2 of the ACP of Alaska, north of the Brooks Range to the Beaufort or Chukchi Sea, and between Icy Cape in western Alaska and the Aichilik River near the Canadian border. This area is characterized by flat topography underlain by thick permafrost, resulting in a treeless region dominated by herbaceous vegetation and numerous lakes and wetlands (Bliss et al. 1973, Gallant et al. 1995). Within this region, low-lying areas are typically characterized by flooded, moist patterned (e.g., high- and low-centered polygons), and non-patterned (e.g., meadows) wetlands, while upland sites consist mainly of drier tundra (e.g., tussocks; Walker et al. 1980, Jorgenson and Heiner 2003). Based on the land cover map by Jorgenson and Heiner (2003), dominant land cover classifications in our study area consisted of moist meadow (23%), upland tussock tundra (18%), wet meadow (17%), and water (13%). Summer temperatures on the ACP of Alaska usually range between 5–15°C (National Research Council 2003, Martin et al. 2009), with maximum summer temperatures averaging 8°C (Gallant et al. 1995). Winter temperatures are usually below −18°C and sometimes below −40°C (National Research Council 2003, Martin et al. 2009), with maximum winter temperatures averaging −21°C (Gallant et al. 1995). Annual precipitation averages 14 cm per year (Gallant et al. 1995), ranging from 12–20 cm in coastal and foothill regions (National Research Council 2003).

Ground surveys

During nine years between 1998 and 2008 (surveys not conducted in 2003 and 2005), we conducted ground surveys as part of the Program for Regional and International Shorebird Monitoring (PRISM; Skagen et al. 2003, Bart et al. 2005, Bart et al. 2012). As PRISM protocols were being developed over the course of this study, methods for plot selection varied among years. Detailed descriptions of plot selection methods for 1998–2004 can be found in Bart and Earnst (2002), Brown et al. (2007), Johnson et al. (2007), and Bart et al. (2012). Briefly, in early years (1998–2001), we randomly selected plots in the NPR-A within habitat strata (wetland and upland), where plot boundaries followed natural borders between wetlands and uplands (excluding unsuitable habitat [e.g., open water, mudflats]), resulting in variable plot sizes (2–342 ha) and shapes. In later years (2002–2008), plot sizes were restricted to 400 × 400 m^2 square plots (16 ha) and were primarily located randomly, with a few plots located nonrandomly. In 2002 and 2004, plots were located within the ANWR and west to the Colville River (eastern border of the NPR-A) independent of habitat type (in 2002) or based on stratified habitat types (in 2004; riparian, flooded, very wet, and upland developed from Jorgenson et al. [1994]). For logistical reasons, in 2001, 2002, and 2004, plots were located in two- and three-plot clusters, where second and third plots were selected randomly within 1–5 km from the initial plot.

In 2006, a portion of plots originally surveyed in 2001 within the NPR-A was surveyed again as part of a project to monitor avian influenza. Because we combined years in our analysis, each repeat sampled plot was only used once in the analysis. For these repeat sampled plots, we considered a species as present if it was detected during at least one survey. In 2007 and 2008, we randomly located plots within the Teshekpuk Lake Special Area (TLSA) of the NPR-A, with detailed description of plot selection methods found in Andres et al. (2012). Briefly, to ensure plots were surveyed throughout the entire region, we divided the TLSA into four geographic areas (NW, NE, SE, and SW) based on predominant land cover types defined for the NPR-A by Bureau of Land Management and Ducks Unlimited, Inc. (2002). Within each geographic area, we randomly selected a number of plots proportional to the relative area. We restricted plot locations in both 2007 and 2008 so as not to be the same as those sampled in 2001, and plot locations in 2008 so as not to be the same as plots sampled in 2007.

In all years, we surveyed shorebirds during pre- and early incubation periods (i.e., 7 June–1 July) when breeding shorebirds were most detectable. We conducted surveys using a single-visit, rapid area search technique, where one to two surveyors systematically traversed each plot and recorded the presence of all suspected breeding shorebirds within the plot boundary. We used an individual bird's behavior (e.g., territorial and courtship displays, attachment to the plot) to assess whether the pair was likely breeding in or very near the plot. Transient birds (e.g., flyovers) were not included in subsequent modeling.

Because of variability in plot selection and survey methods among years, we restricted plots used in subsequent modeling to ensure consistency and reduce potential bias. First, we excluded all plots that were located at elevations >350 m, as the majority of shorebirds breed below this elevation (Johnson and Herter 1989). Second, we excluded all plots that were >1 km^2 in size to decrease uncertainty in habitat use of an individual within a plot. Third, we reduced spatial clustering of occupied plots (as only occupied plots were included in the presence-only models) by (1) retaining only one randomly selected occupied plot for a given species within a sampling cluster in those years where two- and three-plot clusters were surveyed (2001, 2002, 2004, and 2006) and (2) excluding spatially redundant plots (i.e., <3 km between adjacent occupied plots for a given species). Finally, to maintain consistency in scale of habitat selection patterns, we centered all remaining plots within a 1-km^2 square plot (hereafter referred to as surveyed grid cell) within which environmental variables were assessed. This spatial scale was chosen to correspond with the largest plot size (1 km^2) included in the analysis. Environmental variables measured within the surveyed grid cell were highly correlated with those measured at the plot level.

Environmental variables

We used the land cover map developed for the ACP of Alaska by Jorgenson and Heiner (2003) (resolution = 30 m) to classify habitat, from which we created seven composite classifications (see Table 1). We obtained elevation data from the National Elevation Dataset (Gesch 2007) (resolution = 2 arc second). We derived temperature data by averaging yearly June temperature maps (acquired from SNAP [Scenarios Network for Alaska Planning 2011]; resolution = 2 km) for the survey period from 1998 to 2008 (excluding 2003 and 2005) in ArcGIS 10 (Environmental Systems Research Institute, Redlands, CA). We derived density of water bodies using ArcGIS 10 (search radius = 10 km; output cell size = 1 km) and the National Hydrography Dataset (Simley and Carswell 2009), where each water body was represented by a point corresponding to the centroid of the water body. To characterize the entire study area, we created 85,083 regular 1 km^2 grid cells (hereafter referred to as unsurveyed grid cell) across the study area. For each surveyed and unsurveyed grid cell we extracted mean elevation, June temperature, and density of waterbodies using Geospatial Modeling Environment (Beyer 2010). For land cover classifications, we extracted percent composition for each surveyed and unsurveyed grid cell using Geospatial Modeling Environment (Beyer 2010). Finally, we estimated the distance from the nearest coastline edge to the centroid of each plot using ArcGIS 10.

Habitat suitability models

We developed habitat suitability models for shorebird species present in ≥25% of the survey plots. Because surveys were not conducted throughout the entire study area annually, we

Table 1. Environmental variables used to describe habitat suitability for eight shorebird species breeding in the Arctic Coastal Plain of Alaska, USA, 1998–2008.

Variable	Abbreviation	Description/composition
Elevation	Elev	Elevation (m)
Distance to coast	Dcst	Distance to coast (km)
Mean June temperature	Jtemp	Mean June temperatures averaged for 1998–2008, excluding 2003 and 2005 (°C)
Density of waterbodies	Dwtr	Number of waterbodies per km^2
Percent riverine	%rvr	Percent riverine barrens, riverine willow scrub tundra, riverine moist sedge-shrub tundra, riverine wet sedge tundra, and riverine waters
Percent water	%wtr	Percent coastal water and lake
Percent wet meadow	%wmd	Percent coastal wet sedge tundra and lowland wet sedge tundra
Percent moist meadow	%mmd	Percent coastal grass and DST and lowland moist sedge-shrub tundra
Percent upland tussock tundra	%utt	Percent upland tussock tundra
Percent upland shrubby tussock tundra	%ust	Percent upland shrubby tussock tundra
Percent upland scrub tundra	%usc	Percent upland dwarf dryas scrub tundra and upland shrub birch-willow tundra

combined years in our analysis. Because surveys were conducted rapidly with a variable amount of effort, the validity of true absences of a given species may be questionable, potentially resulting in considerable bias in presence/absence modeling results. Therefore, we used a modeling technique (partitioned Mahalanobis distance) that required only presence data to estimate and map habitat suitability for shorebird species. Mahalanobis D^2 is the standardized difference between the values for a set of environmental variables at any point in the landscape and the multivariate mean for the same environmental variables calculated at all locations where a species was detected (Clark et al. 1993, Dunn and Duncan 2000, Rotenberry et al. 2002, Browning et al. 2005, Rotenberry et al. 2006). The more similar environmental conditions are at a given point in the landscape to the species' mean, the smaller the D^2 value (Dunn and Duncan 2000, Rotenberry et al. 2002, Rotenberry et al. 2006). However, D^2 values range from zero to infinity, making interpretation difficult. Because D^2 follows a chi-square distribution (Clark et al. 1993), it can be rescaled to a Habitat Similarity or Suitability Index (HSI) ranging from 0 to 1, where 1 corresponds to areas with habitat variables identical to a species' mean and 0 correspond to highly dissimilar areas. Therefore, we define HSI as the capacity of a given location to support a specific species, where locations with higher HSI values are more likely to contain suitable habitat than areas with lower HSI values.

When applied to unsampled areas, the performance of D^2 can be improved by partitioning it into separate, additive components (*k*; Knick and Rotenberry 1998, Dunn and Duncan 2000, Duncan and Dunn 2001), where each component represents an independent relationship between a species' distribution and environmental variables (Dunn and Duncan 2000, Rotenberry et al. 2002, Rotenberry et al. 2006). These partitions are calculated from a principal component analysis, where the number of partitions (i.e., eigenvectors) is equal to the number of environmental variables entered into the model. These partitions can be sequentially summed, beginning with the partition associated with the single smallest eigenvalue (labeled with the highest partition number), followed by the sum of the two smallest values, and so on until all partitions are summed. The sum of all partitions is equal to the D^2 from the full model and labeled with the lowest partition number ($k = 1$). In this approach, emphasis is placed on smaller eigenvalues representing combinations of environmental variables that remain consistent (i.e., have the least variability) across a species' range, often indicating minimum habitat requirements for a given species (Dunn and Duncan 2000, Rotenberry et al. 2002, Rotenberry et al. 2006).

Prior to analysis, a validation dataset was created by setting aside 20% of the presence records following data restrictions (i.e., plot size, elevation, and spatial redundancy restrictions), independently for each species, with the remaining 80% used for model calibration. To ensure the validation dataset was representative of the entire survey area and sampling scheme, we selected validation plots within broad geographic regions (i.e., TLSA, remaining NPR-A, and the area east of NPR-A and including ANWR), based on a stratified random sampling technique. To model shorebird habitat suitability, we developed 28 a priori models using biologically relevant combinations of 11 variables (see Table 1) based on prior information on habitat use by Arctic-breeding shorebirds (e.g., Myers and Pitelka 1980).

For each species, we calculated partitioned Mahalanobis distances for each model using a principal component analysis (SAS Institute, Cary, NC) and the SAS code provided in Rotenberry et al. (2006). Similar to previous studies (Preston et al. 2008, Barrows et al. 2011, Hollenbeck et al. 2011), we determined the partition (k) to retain for each model by maximizing the median HSI value for the calibration dataset. Additionally, we assessed the performance of each model by examining the median HSI value for both the calibration and validation datasets at the selected partition, where the best performing model was selected by maximizing the median HSI value for the calibration dataset. We then used the best performing model for each species to create habitat suitability maps for the study area.

We evaluated the accuracy of the habitat suitability maps by selecting threshold values (i.e., cutoff value, above which HSI is indicative of suitable habitat and below which HSI is indicative of unsuitable habitat) so that we maximized predictive gain (Browning et al. 2005). This process maximized the number of calibration plots predicted as occupied while minimized the proportion of the landscape predicted as suitable (Browning et al. 2005). Similar to Griffin et al. (2010), we restrained threshold values so that at least 80% of the calibration dataset was accurately classified (this only influenced the American Golden-Plover threshold value). Finally, we assessed the accuracy of predictive maps by determining the proportion of validation plots accurately classified based on threshold values.

Similar to previous studies (Browning et al. 2005, Griffin et al. 2010), we evaluated the uncertainty in the model selection procedure (i.e., confidence in the selection of the best performing model given a different random sample of the data), as well as the importance of environmental variables to species-specific habitat suitability indices, using 1,000 bootstrap samples that were obtained by randomly sampling with replacement both the calibration and validation datasets. Here, the sample size of each bootstrap sample equaled the sample size of the calibration dataset. For each bootstrap sample, we calculated and evaluated partitioned Mahalanobis distances for the same model set, where best performing models were selected by maximizing the median HSI value for the partition and the model. The proportion of times a given model was selected as the best performing model was recorded and used to evaluate the uncertainty in the model selection procedure and the importance of environmental variables. Additionally, bootstrap samples were used to evaluate the uncertainty in selecting a given partition (k) for the best performing model. For each bootstrap sample, the proportion of times a given partition was selected given the best performing model was recorded for each species.

We created final habitat suitability maps for each species by removing permanent water bodies from predictive HSI maps for the study area, as these areas are clearly unsuitable for nesting shorebirds, based on the National Hydrography Dataset (Simley and Carswell 2009). To locate areas containing suitable habitat for the most number of species, we mapped (1) predicted species richness (i.e., the predicted number of species exceeding selected threshold values) and (2) mean HSI values for the eight modeled species across the study area.

Results

Ground surveys

Surveys were conducted at 767 plots during nine years between 1998 and 2008 (24 in 1998, 136 in 1999, 80 in 2000, 107 in 2001, 118 in 2002, 141 in 2004, 50 in 2006 [of which 48 were repeat surveys], 40 in 2007, and 119 in 2008). Within these plots, 12,358 shorebirds were detected, representing 21 shorebird species (only the most recent count from repeat sampled plots was

Table 2. Number of shorebirds detected on 767 plots (only the most recent count from repeat sampled plots was included) surveyed as part of the Arctic PRISM (Program for Regional and International Shorebird Monitoring) in the Arctic Coastal Plain of Alaska, USA, 1998–2008.

Common name	Scientific name	TLSA (n = 264)	NPR-A (n = 198)	ANWR (n = 211)	Other (n = 94)
Black-bellied Plover†	*Pluvialis squatarola*	240	174	1	59
American Golden-Plover†	*Pluvialis dominica*	100	149	102	77
Semipalmated Plover	*Charadrius semipalmatus*	0	1	16	0
Lesser Yellowlegs	*Tringa flavipes*	0	1	0	0
Whimbrel	*Numenius phaeopus*	1	15	13	7
Bar-tailed Godwit	*Limosa lapponica*	11	51	0	53
Ruddy Turnstone	*Arenaria interpres*	29	17	13	0
Red Knot	*Calidris canutus*	2	0	0	0
Sanderling	*Calidris alba*	0	0	1	0
Semipalmated Sandpiper†	*Calidris pusilla*	972	934	188	463
Western Sandpiper	*Calidris mauri*	3	44	2	0
White-rumped Sandpiper	*Calidris fuscicollis*	4	0	1	0
Baird's Sandpiper	*Calidris bairdii*	6	2	8	3
Pectoral Sandpiper†	*Calidris melanotos*	1,045	724	263	333
Dunlin†	*Calidris alpina*	685	251	28	59
Stilt Sandpiper	*Calidris himantopus*	33	144	33	95
Buff-breasted Sandpiper	*Tryngites subruficollis*	13	14	34	13
Long-billed Dowitcher†	*Limnodromus scolopaceus*	404	552	39	110
Wilson's Snipe	*Gallinago delicata*	0	7	0	13
Red-necked Phalarope†	*Phalaropus lobatus*	530	549	231	249
Red Phalarope†	*Phalaropus fulicarius*	1,400	492	101	151
Total no. individuals		5,478	4,121	1,074	1,685

Notes: TLSA = Teshekpuk Lake Special Area, NPR-A = National Petroleum Reserve-Alaska, excluding Teshekpuk Lake Special Area, ANWR = Arctic National Wildlife Refuge, and Other = region between the National Petroleum Reserve-Alaska and the Arctic National Wildlife Refuge. A dagger (†) indicates species that had habitat suitability models developed. n = number of plots surveyed.

included; Table 2). Of the 21 species detected, only eight species (11,655 individuals) were present in $\geq$25% of plots and thus available for development of habitat suitability models. Although densities for these species vary across the ACP of Alaska (Johnson et al. 2007, Bart et al. 2012), breeding ranges for these species generally occur throughout the study area (Poole 2005). Following plot restrictions (i.e., plot size, elevation, and spatial redundancy), the number of plots used in the analysis was reduced by 76 to 268 (37–54%) depending on species, with survey effort ranging from 1.3–31.7 ha/hour ($\bar{x}$ = 12.5–12.9; SE = 0.17–0.30, depending on species).

Habitat suitability models

Of the 28 a priori models, the first partition (i.e., sum of all partitions) of the model containing elevation, percent upland tussock tundra, percent upland shrubby tussock tundra, and percent upland scrub was selected as the best performing model for Black-bellied Plover and Red-necked Phalarope (Table 3). Similarly, for Semipalmated Sandpiper, Pectoral Sandpiper, Dunlin, and Red Phalarope, the first partition of the model containing elevation, percent riverine, percent upland tussock tundra, percent upland shrubby tussock tundra, and percent upland scrub was selected as the best performing model (Table 3). For Long-billed Dowitcher, the second partition of the model containing percent upland tussock tundra, percent upland shrubby tussock tundra, and percent upland scrub was selected as the best performing model (Table 3). However, for American Golden-Plover, the sixth partition of the model containing percent riverine, percent water, percent wet meadow, percent moist meadow, percent upland tussock tundra, percent upland shrubby tussock tundra, and percent upland scrub was selected as the best performing model (Table 3). Median HSI values for both calibration and validation datasets were >0.80 for all species, >0.85 for seven species, and >0.90 for four species (Table 3), suggesting good predictive performance of the models for all species.

When compared to the entire landscape (i.e., study area), plots in which species were detected had lower mean estimates for percent upland tussock tundra and upland scrub for all species,

Table 3. Variables present and statistics from the five best performing models describing habitat suitability for eight shorebird species breeding in the Arctic Coastal Plain of Alaska, USA, 1998–2008.

Species	Variables included in model†												Bootstrap selection frequency
	Elev	Dcst	% rvr	% wtr	% wmd	% mmd	% utt	% ust	% usc	k‡	x̃ calib. HSI§	x̃ valid. HSI¶	
Black-bellied Plover													
	X						X	X	X	1	0.87	0.87	0.56
							X	X	X	1	0.84	0.89	0.04
	X	X					X	X	X	1	0.82	0.87	0.22
		X					X	X	X	1	0.81	0.88	0.00
			X	X	X	X	X	X	X	2	0.80	0.62	0.03
American Golden-Plover													
			X	X	X	X	X	X	X	6	0.93	0.81	0.04
	X						X	X	X	1	0.92	0.73	0.44
							X	X	X	1	0.91	0.76	0.41
	X		X	X	X	X	X	X	X	6	0.89	0.61	0.01
	X	X	X	X	X	X	X	X	X	7	0.89	0.62	0.00
Semipalmated Sandpiper													
	X		X				X	X	X	1	0.94	0.94	0.23
	X						X	X	X	1	0.94	0.93	0.24
	X	X					X	X	X	1	0.93	0.93	0.35
	X	X	X				X	X	X	1	0.92	0.95	0.04
			X				X	X	X	1	0.90	0.90	0.01
Pectoral Sandpiper													
	X		X				X	X	X	1	0.97	0.97	0.31
	X						X	X	X	1	0.96	0.97	0.11
	X	X	X				X	X	X	1	0.95	0.97	0.21
	X	X					X	X	X	1	0.95	0.96	0.28
			X				X	X	X	1	0.95	0.97	0.06
Dunlin													
	X		X				X	X	X	1	0.86	0.89	0.27
			X				X	X	X	1	0.86	0.86	0.04
	X	X	X				X	X	X	1	0.84	0.91	0.22
	X						X	X	X	2	0.84	0.90	0.12
							X	X	X	2	0.83	0.87	0.20
Long-billed Dowitcher													
							X	X	X	2	0.95	0.92	0.26
			X				X	X	X	1	0.95	0.95	0.23
	X	X					X	X	X	1	0.94	0.85	0.18
	X		X				X	X	X	1	0.94	0.90	0.07
	X						X	X	X	1	0.94	0.94	0.22
Red-necked Phalarope													
	X						X	X	X	1	0.96	0.96	0.68
	X		X				X	X	X	1	0.95	0.96	0.04
	X	X					X	X	X	1	0.94	0.95	0.23
			X				X	X	X	1	0.93	0.93	0.01
		X	X				X	X	X	1	0.93	0.87	0.00
Red Phalarope													
	X		X				X	X	X	1	0.88	0.87	0.23
	X	X					X	X	X	1	0.87	0.79	0.24
	X						X	X	X	1	0.85	0.85	0.21
							X	X	X	2	0.85	0.76	0.12
		X	X				X	X	X	1	0.85	0.81	0.07

Notes: The number of plots with detections following plot restrictions (combination of calibration and validation datasets) for Black-bellied Plover, American Golden-Plover, Semipalmated Sandpiper, Pectoral Sandpiper, Dunlin, Long-billed Dowitcher, Red-necked Phalarope, and Red Phalarope = 115, 130, 225, 228, 157, 177, 197, and 160, respectively.

† Variable abbreviations found in Table 1.

‡ Selected partition.

§ Median habitat suitability index for the calibration dataset.

¶ Median habitat suitability index for the validation dataset.

but similar percentage of upland shrubby tussock tundra (Table 4). For Black-bellied Plover, Semipalmated Sandpiper, Pectoral Sandpiper, Dunlin, Red-necked Phalarope, and Red Phalarope, plots in which species were detected had lower mean estimates for elevation than the landscape (Table 4). Plots in which American Golden-Plover, Semipalmated Sandpiper, Pectoral Sandpiper, Dunlin, or Red Phalarope were detected had larger mean estimates for percent

Table 4. Study area and calibration plot means of environmental variables used to describe habitat suitability for eight shorebird species breeding in the Arctic Coastal Plain of Alaska, USA, 1998–2008. Variable values indicate the mean value for each species and of the landscape (i.e., study area) for comparison.

		Surveyed plots							
Var.†	Study area	Black-belled Plover	Am. Golden-Plover	Semipalm. Sandpiper	Pectoral Sandpiper	Dunlin	Long-billed Dowitcher	Red-necked Phalarope	Red Phalarope
Elev	60.29	17.73*	40.09	21.95*	25.45*	10.71*	20.89	25.28*	12.00*
Dcst	54.83	29.42	28.21	23.85	23.36	18.55	25.54	23.58	19.10
Jtemp	7.04	6.24	5.83	5.63	5.50	5.41	5.80	5.50	5.35
Dwtr	1.60	4.02	2.75	3.24	3.03	3.73	3.51	3.10	3.37
%rvr	0.08	0.19	0.23*	0.14*	0.12*	0.11*	0.11	0.13	0.12*
%wtr	0.13	0.16	0.10*	0.17	0.15	0.19	0.16	0.16	0.16
%wmd	0.17	0.39	0.29*	0.33	0.34	0.36	0.38	0.35	0.37
%mmd	0.23	0.18	0.24*	0.25	0.27	0.25	0.25	0.24	0.27
%utt	0.18	0.04*	0.05*	0.05*	0.06*	0.03*	0.06*	0.05*	0.03*
%ust	<0.01	<0.01*	0.02*	<0.01*	<0.01*	0.00‡*	<0.01*	<0.01*	0.00‡*
%usc	0.08	0.02*	0.02*	0.03*	0.03*	0.02*	0.03*	0.03*	0.02*

Note: An asterisk indicates a variable selected in best performing partitioned Mahalanobis distance model for each species.
† Variable abbreviations found in Table 1.
‡ Variable constant within surveyed plots.

riverine than the landscape, but were still selected at low proportions (Table 4). Additionally, plots in which American Golden-Plover were detected had similar estimates for percent water and moist meadow, but greater percent wet meadow as compared to the landscape (Table 4).

Predicted HSI values were mapped across the study area for each species (see Fig. 1). Threshold values (above which HSI is indicative of suitable habitat and below which HSI is indicative of unsuitable habitat) were variable among species, ranging from 0.05–0.62 (Fig. 1). For all species, maximum predictive gain was achieved when 80–96% of calibration plots were accurately classified and 40–59% of the landscape was classified as suitable. Accuracy of predicted suitability for the validation dataset was relatively high for all species, ranging from 0.65–0.98 (Black-bellied Plover = 0.74 [17% increase over chance], American Golden-Plover = 0.65 [20% increase over chance], Semipalmated Sandpiper = 0.98 [56% increase over chance], Pectoral Sandpiper = 0.96 [55% increase over chance], Dunlin = 0.87 [27% increase over chance], Long-billed Dowitcher = 0.91 [50% increase over chance], Red-necked Phalarope = 0.85 [30% increase over chance], and Red Phalarope = 0.88 [31% increase over chance]).

Despite relatively high accuracy for habitat suitability models for all species, certainty in model selection procedure was lower and variable among species, with bootstrap selection frequencies for the best performing model ranging from 0.04–0.68 (Table 3). However, individual variables within the best performing model for each species had relatively high bootstrap selection frequencies. These results indicate high certainty that specific variables should be included in the best performing model; however, low certainty in the combination of variables found in the best performing model. For example, for all species, percent upland tussock tundra, percent upland shrubby tussock tundra, and percent upland scrub were always present in the best performing model for all bootstrapped samples, indicating the importance of these variables to habitat suitability for the eight species of shorebirds in this region. Similarly, for Black-bellied Plover, Semipalmated Sandpiper, Pectoral Sandpiper, Dunlin, Red-necked Phalarope, and Red Phalarope, elevation was selected in the best performing model >70% of the time. Selection of a specific partition, given the best performing model, had relatively high certainty with bootstrap selection frequencies >80% for most species (Black-bellied Plover = 0.88, American Golden-Plover = 0.30, Semipalmated Sandpiper = 1.00, Pectoral Sandpiper = 1.00, Dunlin = 0.97, Long-billed Dowitcher = 0.43, Red-necked Phalarope = 1.00 and Red Phalarope = 0.90).

Final HSI maps, with permanent water bodies removed, predicted that between 30% and 50% of

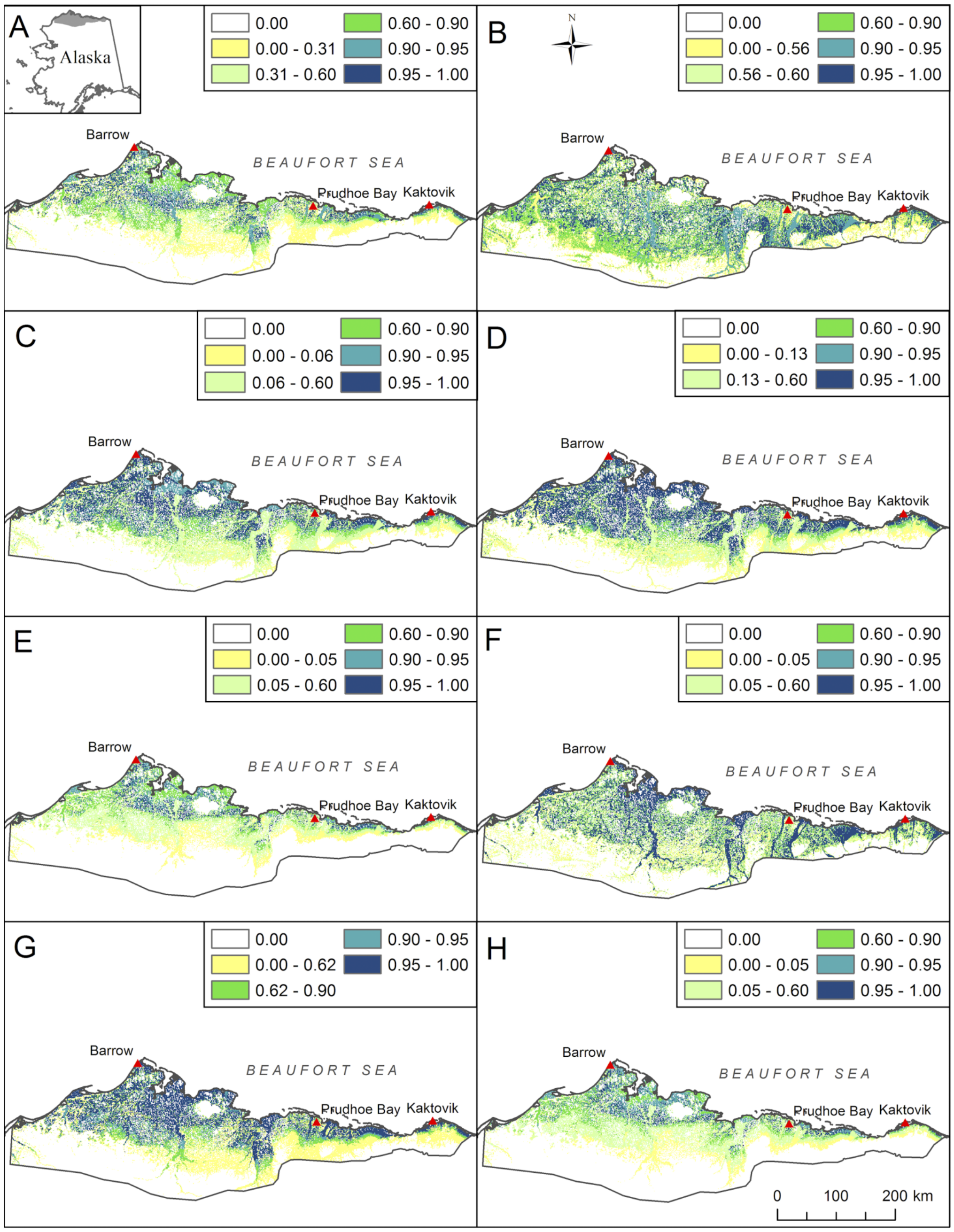

Fig. 1. Habitat suitability index for (A) Black-bellied Plover (*Pluvialis squatarola*; threshold = 0.31), (B) American Golden-Plover (*Pluvialis dominica*; threshold = 0.56), (C) Semipalmated Sandpiper (*Calidris pusilla*; threshold = 0.06), (D) Pectoral Sandpiper (*Calidris melanotos*; threshold = 0.13), (E) Dunlin (*Calidris alpina*; threshold = 0.05), (F) Long-billed Dowitcher (*Limnodromus scolopaceus*; threshold = 0.05), (G) Red-necked Phalarope (*Phalaropus lobatus*; threshold = 0.62), and (H) Red Phalarope (*Phalaropus fulicarius*; threshold = 0.05) breeding in the Arctic Coastal Plain of Alaska, USA, 1998–2008. Habitat suitability indices above threshold values indicate predicted suitable habitat for a species and below which indicate predicted unsuitable habitat for a species. Solid line indicates study area.

Table 5. Amount and percentage of area predicted as suitable (i.e., habitat suitability index above selected threshold) for eight shorebird species breeding in three administrative units in the Arctic Coastal Plain of Alaska, USA, 1998–2008.

	TLSA ($6,854\ km^2$)		NPR-A ($55,457\ km^2$)		ANWR ($6,213\ km^2$)		Study area ($85,108\ km^2$)	
Species	km^2	%	km^2	%	km^2	%	km^2	%
Black-bellied Plover	3,909	57%	16,670	30%	1,376	22%	27,753	33%
American Golden-Plover	3,570	52%	27,524	50%	1,955	31%	42,491	50%
Semipalmated Sandpiper	4,398	64%	23,008	41%	2,278	37%	39,297	46%
Pectoral Sandpiper	4,437	65%	23,469	42%	2,244	36%	39,462	46%
Dunlin	3,739	55%	15,891	29%	1,176	19%	25,877	30%
Long-billed Dowitcher	4,339	63%	22,745	41%	3,086	50%	40,461	48%
Red-necked Phalarope	4,038	59%	17,289	31%	1,456	23%	29,027	34%
Red Phalarope	3,990	58%	17,064	31%	1,313	21%	28,124	33%
Mean for all species	4,053	59%	20,458	37%	1,861	30%	34,062	40%

Notes: TLSA = Teshekpuk Lake Special Area, NPR-A = National Petroleum Reserve-Alaska, excluding Teshekpuk Lake Special Area, and ANWR = Arctic National Wildlife Refuge.

the entire study area was suitable (i.e., HSI above selected threshold) habitat for the eight modeled species (Table 5). A comparison of the major ecogeographic regions of the ACP indicated that the NPR-A had the greatest amount of suitable habitat for the most number of species followed by the ANWR (Table 5, Fig. 2).

Discussion

For the first time, this study provides habitat suitability maps that illustrate predicted distributions for eight species of shorebirds breeding within the ACP of Alaska. These maps and the habitat associations for these species provide key information that has thus far been lacking, but are important for management decisions in light of future development and climate change scenarios. In this study, habitat suitability increased at lower elevations for most species and decreased (approaching zero) in upland habitat, suggesting that the shorebird species examined here preferred lowland habitats (i.e., water, wet meadow, and moist meadow), but had no preference among specific lowland habitat types. However, lack of detection among lowland habitat types may be a result of accuracy or scale of land cover maps used in the analysis. These coarse habitat associations are comparable to previous studies, with several studies noting greater shorebird numbers (measured as either abundance or density) in lower, wetter areas during nesting and brood rearing (Myers and Pitelka 1980, Garner and Reynolds 1986, Cotter and Andres 2000, Latour et al. 2005, Liebezeit et al. 2011). Unlike the majority of species, however, elevation was not an important variable for American Golden-Plover and Long-billed Dowitcher, with predicted ranges for these species extending further south into the foothill region. Johnson and Herter (1989) describe similar distribution trends for American Golden-Plover and Long-billed Dowitcher within this region, with both species nesting in coastal and inland sites, but with Long-billed Dowitcher more common inland than near the coast. In this study, American Golden-Plover also tended to select lowland areas with lower proportion of water in relation to wet meadow and moist meadow habitats, indicating their preference for drier landscapes, as shown in other studies (Jones 1980, Martin 1983, Garner and Reynolds 1986, Morrison 1997, Latour et al. 2005).

Our models predicted that the study area contained the most amount of suitable habitat for American Golden-Plover (50%), Long-billed Dowitcher (48%), Pectoral Sandpiper (46%), and Semipalmated Sandpiper (46%); and lower amounts for Red-necked Phalarope (34%), Red Phalarope (33%), Black-bellied Plover (33%), and Dunlin (30%; Table 5). These results are consistent with current distribution and habitat selection patterns for these species. For example, both American Golden-Plover and Long-billed Dowitcher were not restricted by elevation; therefore, predicted ranges for these species were much greater, extending into the foothill region. A large percentage of the study area also was predicted

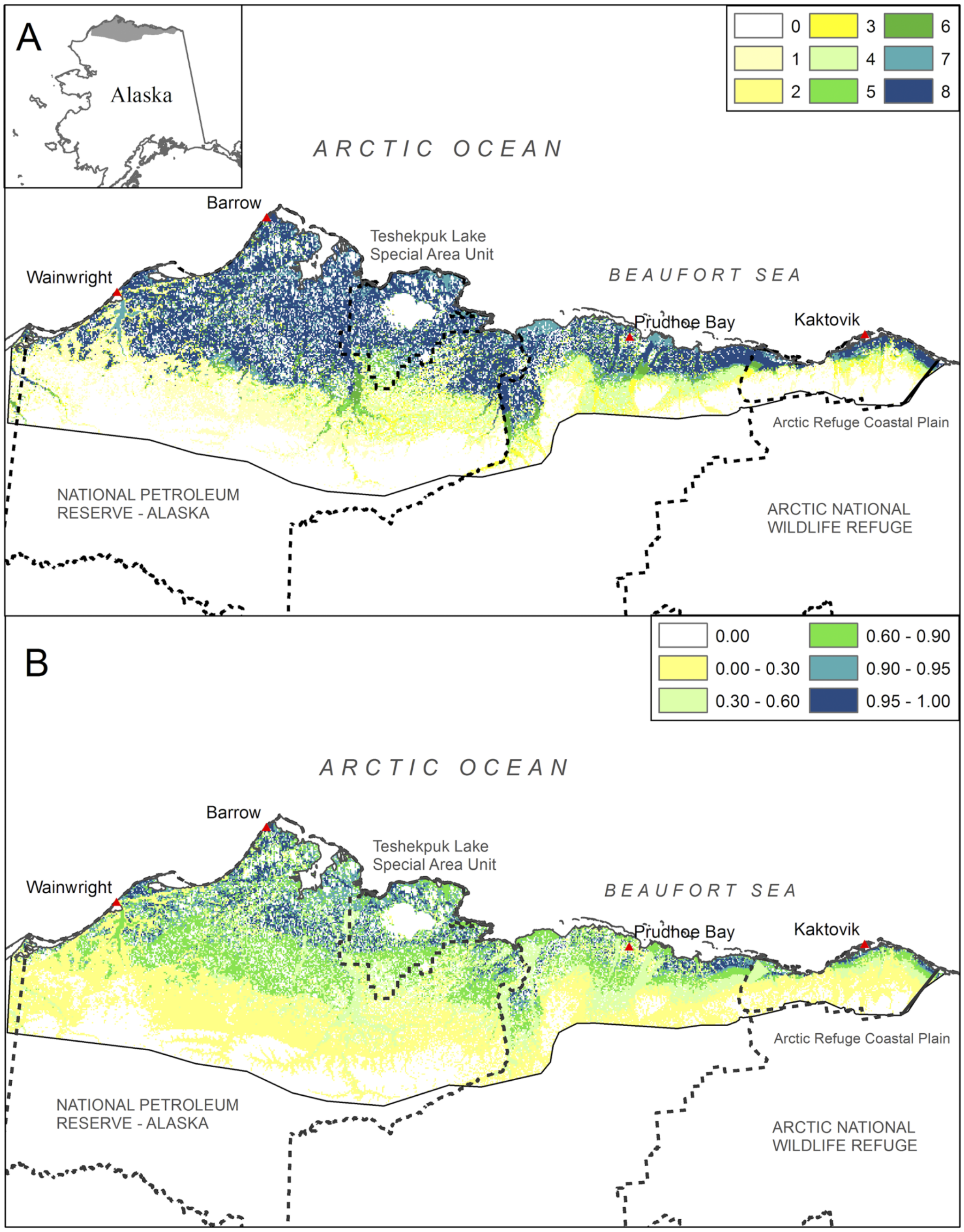

Fig. 2. (A) predicted species richness (i.e., number of shorebird species exceeding selected threshold values) and (B) mean habitat suitability index for eight shorebird species (i.e., Black-bellied Plover [*Pluvialis squatarola*], American Golden-Plover [*Pluvialis dominica*], Semipalmated Sandpiper [*Calidris pusilla*], Pectoral Sandpiper [*Calidris melanotos*], Dunlin [*Calidris alpina*], Long-billed Dowitcher [*Limnodromus scolopaceus*], Red-necked Phalarope [*Phalaropus lobatus*], and Red Phalarope [*Phalaropus fulicarius*]) in relation to administrative boundaries (dashed lines) and study area (solid line) in the Arctic Coastal Plain of Alaska, USA, 1998–2008.

as suitable for Pectoral and Semipalmated Sandpiper. Although preferring lower regions, Pectoral and Semipalmated Sandpipers were the most detected species within our study, and have been described as common and abundant breeders throughout the ACP of Alaska (Derksen et al. 1981, Garner and Reynolds 1986, Johnson and Herter 1989, Cotter and Andres 2000), with several studies indicating wider habitat preferences by these species (Garner and Reynolds 1986, Liebezeit et al. 2011). Conversely, Red-necked Phalarope, Red Phalarope, Black-bellied Plover, and Dunlin had more restricted distributions within the study area. These species have been described to be more common within coastal regions, with Black-bellied Plover, Dunlin, and Red-necked Phalarope more common in the western portion of the ACP of Alaska (Johnson and Herter 1989). These descriptions are consistent with our predicted distributions.

Latitudinal and longitudinal gradients of shorebird distributions have often been observed within the ACP of Alaska. Within this study, we noted greater habitat suitability for all species occurring closer to the coast and within the western portion of the study area. Several studies have noted shorebird density and species richness decreasing further from the coast (Pitelka 1974, Derksen et al. 1981, Johnson and Herter 1989, Boyd and Madsen 1997, Morrison 1997), with mean shorebird population estimates 16–19 times greater in coastal portions of the NPR-A as compared to southern portions (King 1979). However, within the ANWR, Brown et al. (2007) suggested that the coastal gradient was an artifact of the wetland habitat being close to the coast and river deltas that bisect the coast. Thus, coastal gradients may be based on habitat selection patterns rather than an affinity to coastal regions (Boyd and Madsen 1997). We found that distance to coast was not an important variable in the top performing model for all species, suggesting that distribution patterns are more influenced by elevation and habitat (i.e., upland verses lowland) than distance to coast. Johnson and Herter (1989) described Black-bellied Plover, Dunlin, and Red-necked Phalarope as more common in the western portion of the ACP of Alaska. As the eastern portion of the ACP of Alaska is very narrow (with the foothills of the Brooks Range extending nearly to the coast) and characterized by few wetlands (except river deltas), while the western portion has a broad coastal plain with numerous wetlands and large lakes (Pitelka 1974, Meehan 1986), longitudinal gradients are also likely the result of spatial distributions of selected habitats (Boyd and Madsen 1997).

A comparison of the percentage of habitat suitable for breeding shorebirds across the predominant ecogeographical regions of the ACP of Alaska indicated that the most suitable habitat was present in the NPR-A, followed by the ANWR. Within the NPR-A, the TLSA has been recognized as an important region for molting waterfowl (King and Hodges 1979), a calving ground for the Teshekpuk Lake caribou herd (Carroll et al. 2005), and most recently, for the high density of shorebirds (Andres et al. 2012). Our results also indicate the importance of this region for nesting shorebirds, with 52–65% (depending on species) of the TLSA predicted as suitable nesting habitat for eight shorebird species. These results are consistent with previous studies where high species richness and shorebird abundance and densities were observed within the NPR-A (King 1979, Johnson et al. 2007, Bart et al. 2012), especially around Teshekpuk Lake (King 1979, Johnson et al. 2007, Liebezeit et al. 2011, Andres et al. 2012).

The habitat suitability maps developed in this study identify important regions for nesting shorebird species that may be used when establishing conservation priorities. For example, as models are developed to predict changes in environmental conditions (e.g., habitat, surface water hydrology, permafrost) under various climate change scenarios, these predictive layers can be used in conjunction with shorebird habitat suitability maps to locate shorebird breeding habitat refugia, as well as areas at risk under various climate change scenarios. Additionally, current shorebird distribution maps can now be used to understand and compare the potential impacts of specific development scenarios on nesting shorebirds. For example, our results illustrate the importance of specific administrative units, specifically the NPR-A and the TLSA within the NPR-A, to nesting shorebirds within this region. Although the prospects of oil and gas within the NPR-A may be lower than previously estimated (Houseknecht et al. 2010), lease sales have increased within this region and exploration continues (Bureau of Land Management 2011). As pressure to develop within this region continues to increase, these findings may be useful in management deliberations involving shorebird nesting habitat. Additionally, interest in potential reserves within the ANWR may be revaluated in the near future. As highly suitable habitat was predicted to occur along coastal regions within the ANWR, offshore and onshore development within this region have the potential to impact suitable nesting shorebird habitat. Because habitat suitability maps depict areas with minimum habitat requirements for a given species, ground surveys should be conducted prior to establishing final recommendations for future development to verify the utilization of an area by nesting shorebirds.

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