Research Article

Predicting Waterbird Nest Distributions on the Yukon–Kuskokwim Delta of Alaska

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ABSTRACT The Yukon–Kuskokwim Delta of Alaska, USA is a globally important region for numerous avian species including millions of migrating and nesting waterbirds. However, data on the current spatial distribution of critical nesting areas and the importance of environmental variables in the selection of nest locations are generally lacking for waterbirds in this region. We modeled nest densities for 6 species of geese and eiders that commonly breed on the Yukon–Kuskokwim Delta, including cackling goose (*Branta hutchinsii minima*), emperor goose (*Chen canagica*), black brant (*B. bernicla nigricans*), greater white-fronted goose (*Anser albifrons frontalis*), spectacled eider (*Somateria fischeri*), and common eider (*S. mollissima*). The data used were from single-visit nest searches on 2,318 plots sampled during 29 years from 1985 to 2013. We modeled nest density for each species by combining data across years and using random forests methods and time-static landscape environmental variables. These models provide the first habitat-specific predictive distributions of nest density for these species breeding on the Yukon–Kuskokwim Delta of Alaska. Predictive performance of the random forests models varied among species, explaining 13–69% of the variance in nest density. For most species, nest density was greatest near the coast and within lowland habitats. Predicted nest densities mapped across the coastal zone of the Yukon–Kuskokwim Delta revealed areas of high and low nest densities that can be used to inform management and conservation decisions.

KEY WORDS Alaska, Arctic, eider, geese, nest density, predicted density surface, random forests, waterbirds, waterfowl, Yukon–Kuskokwim Delta.

The Yukon–Kuskokwim Delta of Alaska, USA is the largest intertidal wetland in North America (Thorsteinson et al. 1989), providing globally important habitat for numerous avian species including millions of nesting and migrating waterfowl and shorebirds (Gill and Handel 1981, 1990; King and Derksen 1986). The Yukon–Kuskokwim Delta supports almost the entire breeding populations of emperor geese (*Chen canagica*) and cackling geese (*Branta hutchinsii minima*) and the majority of the Pacific Flyway populations of black brant (*B. bernicla nigricans*) and greater white-fronted geese (*Anser albifrons frontalis*; King and Dau 1981, Schmutz 2001). In addition, several species that breed on the Yukon–Kuskokwim Delta are designated as special conservation and management concern, including the threatened spectacled eider (*Somateria fischeri*), common eider (*S. mollissima*), emperor goose, and black brant.

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Within the Yukon–Kuskokwim Delta, waterbird nest densities are greatest within coastal fringe habitats, with some species occurring only within these habitats (Holmes and Black 1973, King and Dau 1981, Platte and Stehn 2009). Coastal fringe habitats depend on coastal estuarine processes including tidal erosion, deposition of sediments, storm-tide flooding, and salt intrusion (Kincheloe and Stehn 1991, Jorgenson 2000, Jorgenson and Ely 2001). Currently, storm surges are relatively common on the Yukon–Kuskokwim Delta, especially in the fall (Wise et al. 1981, Mason et al. 1996, Terenzi et al. 2014), with small storms occurring nearly every year and larger storms (i.e., surges reaching heights >3.0 m above mean sea level) having occurred ≥3 times in the last 50 years (Terenzi et al. 2014). Such storm events can inundate low-lying areas up to 30–40 km inland (Dau et al. 2011, Terenzi et al. 2014). Thus, long-term flooding within this region ultimately shapes the landforms and vegetation communities on which nesting waterbirds in this region depend (Kincheloe and Stehn 1991, Jorgenson 2000, Jorgenson and Ely 2001). Because of the complex relationship between these terrestrial ecosystems and coastal estuarine processes and the global importance of migratory bird species, the Yukon–Kuskokwim Delta may be highly sensitive to climate-mediated changes (Jorgenson and Ely 2001, Jorgenson and Dissing 2010), with predicted changes related to climate (e.g., sea level rise, increased frequency and intensity of coastal storms, changes in seasonal patterns of storminess, reduction in permafrost; Intergovernmental Panel on Climate Change 2007) having the potential to dramatically alter waterbird nesting habitat in the near future.

A first step in understanding the relationship between habitat and nesting waterbirds on the Yukon–Kuskokwim Delta is to determine the current location of important nesting areas and understand how nest sites are selected in relation to environmental conditions. Although current breeding distributions of waterbirds on the Yukon–Kuskokwim Delta have been mapped based on United States Fish and Wildlife Service (USFWS) aerial waterbird survey observations (Eldridge 2003, Platte and Stehn 2009), the large-scale habitat selection patterns of these species in this region are largely unknown. Current efforts to describe habitat selection patterns are limited to observational studies (Olsen 1951, Spencer et al. 1951, Holmes and Black 1973, Mickelson 1975, King and Dau 1981) or small-scale habitat selection studies for only select species (Ely and Raveling 1984, Petersen 1990, Babcock and Ely 1994, Grand et al. 1997, Schmutz 2001). Identification and understanding of contemporary species distributions in relation to habitat availability, as revealed by large-scale habitat associations, will provide baseline data that are currently lacking for waterbirds within this region. Accordingly, our objectives for this study were to identify the important environmental variables related to geese and eider nest densities on the Yukon–Kuskokwim Delta and create and map predictive surfaces of geese and eider nest densities.

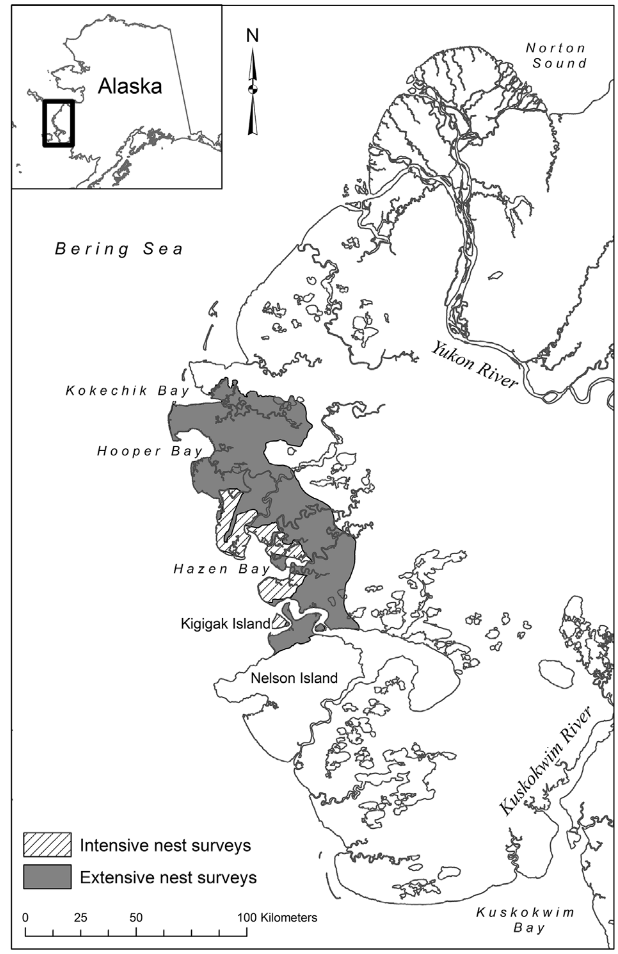

Figure 1. Location of study area, including areas of intensive and extensive waterbird nest surveys on the Yukon–Kuskokwim Delta of Alaska, USA, 1985–2013.

STUDY AREA

The study area encompassed approximately 4,650 km^2 of the central coastal zone of the Yukon–Kuskokwim Delta, between the Askinuk and Nelson Island mountains, and from the west coast to roughly 50 km inland (Fig. 1). Within this region, coastal processes shape vegetation along a gradient from coastal to inland areas (Kincheloe and Stehn 1991, Jorgenson 2000, Jorgenson and Ely 2001). Coastal areas are characterized by flat topography (e.g., ~1 m elevation change over 7.5 km on one toposequence from the coast; Jorgenson and Ely 2001), where sedge and graminoid meadows are interspersed with numerous tidal rivers and sloughs and irregularly shaped, shallow water bodies (Tande and Jennings 1986, Kincheloe and Stehn 1991, Jorgenson 2000). These areas are tidally influenced up to 39–55 km inland (Tande and Jennings 1986, Dau et al. 2011) by regularly occurring high tides and periodic flooding during extreme high tide events and storm surges. Storm surges occur most commonly in the fall, with the largest storms (i.e., minimum central surface pressures <1,000 mb) since the 1900s occurring from August to February (Terenzi et al. 2014). These storm surges can inundate areas up to 30–40 km inland (Dupré 1980, Dau et al. 2011, Terenzi et al. 2014). Conversely, upland areas, not historically prone to flooding, consist mainly of drier, salt-intolerant vegetation, dominated by dwarf shrubs, mosses, and lichens (Tande and Jennings 1986, Kincheloe and Stehn 1991, Jorgenson 2000). The Bering Sea moderates temperatures year round on the Yukon–Kuskokwim Delta, with mean monthly temperatures ranging from 10°C in the summer and −14°C in the winter (Thorsteinson et al. 1989). Annual rainfall averages 51 cm, with an additional 102–127 cm as snowfall (Thorsteinson et al. 1989). Avian species dominate the fauna of the Yukon–Kuskokwim Delta, with millions of waterbirds (i.e., ducks, geese, cranes, gulls, terns, shorebirds) nesting annually. Dominant nest predators include Arctic fox (*Vulpes lagopus*), glaucous gulls (*Larus hyperboreus*), mew gulls (*L. canus*), and parasitic jaegers (*Stercorarius parasiticus*). The study area is largely uninhabited with the exception of 2 villages along the northern border (Hooper Bay, population 1,180; Chevak, population 1,049) and 1 village along the southern border (Newtok, population 354). Inhabitants of these villages use the study area for subsistence hunting and fishing, accessing the area by motorboats.

METHODS

Nest Densities

The USFWS conducted ground surveys during 29 years from 1985 to 2013 as part of their annual waterbird monitoring program (Fischer and Stehn 2014). As information accumulated on the distribution of waterbirds over the years, protocols were updated and sampling design and effort varied. From 1985 to 1993 and in 1998 and 1999, USFWS sampled various regions of the central coastal zone (i.e., extensive survey area; Fig. 1) by randomly selecting accessible plots on public lands (~69% of the Yukon Delta National Wildlife Refuge; USFWS 2004). From 1994 to 1997, and since 2000, the survey focused within a smaller region of 716 km^2 (i.e., intensive area; Fig. 1) corresponding to the area with the majority (~67%) of historical aerial observations of spectacled eider, a priority species because of its threatened status. In all years, randomization was restricted so that plots did not overlap other plots being surveyed in the same year or within the past 5 years. In most years (1988–1994 and 1997–2013), the survey used standardized plot sizes of 0.32 km^2 (402 × 805 m); however, plot sizes varied from 1985 to 1987, ranging from 0.16–1.66 km^2, and standardized to 0.45 km^2 and 0.36 km^2 in 1995 and 1996, respectively. In all years,

Table 1. Explanatory variables used to predict nest densities of geese and eider species breeding on the Yukon–Kuskokwim Delta of Alaska, USA, 1985–2013. Habitat descriptions taken directly from Ducks Unlimited, Inc. (2011).

Variable	Abbreviation	Description and composition
% coastal dwarf shrub[a]	Cds	25–100% shrub cover, shrubs <0.25 m most common, periodic tidal flooding. Common dwarf shrub species include black crowberry (*Empetrum nigrum*), oval-leaf willow (*Salix ovalifolia*), and Alaska bog willow (*Salix fuscescens*). Dominant graminoid is looseflower alpine sedge (*Carex rariflora*), usually with a component of cottongrass (*Eriophorum* spp.). Other graminoids include circumpolar reedgrass (*Calamagrostis deschampsioides*), tufted hairgrass (*Deschampsia caespitosa*), and dunegrass (*Elymus arenarius*). Common forbs include roseroot (*Sedum rosea*), arctic daisy (*Chrysanthemum arcticum*), cloudberry (*Rubus chamaemorus*), Scots lovage (*Ligusticum scoticum*), coltsfoot (*Petasites* spp.), and peavine (*Lathyrus* spp.)
% coastal dwarf shrub-pond mosaic[a*]	Pm	Same composition as coastal dwarf shrub, but in a mosaic with stable ponds
% lower coastal salt marsh[a]	Lcsm	≥40% herbaceous, <25% shrub cover, <50% of the herbaceous cover is bryoid, tidally flooded monthly or more frequently. Dominated by Ramenski sedge (*Carex ramenskii*) and/or Hoppner sedge (*C. subspathacea*). Lyngbye sedge (*C. lyngbyaei*) is found inland, on less saline sites along tidal sloughs
% upper coastal brackish meadow[a]	Ucbm	≥40% herbaceous, <25% shrub cover, <50% of the herbaceous cover is bryoid, tidally flooded periodically during storm tides or extreme high tides. Sedge dominated, with looseflower alpine sedge most common. Other species include circumpolar reedgrass, arctic daisy, oval-leaf willow, common cottongrass (*Eriophorum angustifolium*), and water sedge (*Carex aquatilis*)
% coastal graminoid[a]	Cg	≥40% herbaceous, <25% shrub cover, <50% bryoid, periodically tidally flooded, grass dominated. American dunegrass (*Leymus mollis*) is most common, but coastal bluegrass (*Poa eminens*), circumpolar reedgrass, common silverweed (*Potentilla egedii*), peavine, and other forbs may be present
% sandbar or mudflat[a]	Mud	Sandbar or mudflat (non-vegetated soil)
% upland[a*]	Upld	Composite of the following land cover classifications: tall shrubs, low shrubs, alpine dwarf shrub lichen, crowberry heath, lowland dwarf shrub peatland, lowland dwarf shrub lichen, dwarf shrub-wet graminoid mosaic, moss-graminoid peatland, mesic-dry graminoid meadow, wet graminoid, emergent vegetation, sparse vegetation, rock or gravel, and snow or ice
% potential nesting habitat[b*]	Phabt	Vegetated area that could be used for nest placement (areas not classified as water, sandbar or mudflat, or rock or gravel)
$\bar{x}$ density of waterbodies[c]	Dwtr	$\bar{x}$ number of waterbodies per km^2
% area of waterbodies[c*]	Wtr	% area classified as waterbody
% area of riverine[c]	Rvr	% area classified as riverine
Length of pond shoreline[c]	Pshr	Length of pond shoreline (km)
Shoreline complexity[c]	Cplx	Length of pond shoreline divided by the total area classified as waterbody within grid cell (km/km^2)
Length of riverine and tidal sloughs[c]	Flow	Length of riverine and tidal slough flow lines (km)
Distance to coast[c]	Dcst	Distance to coast (km)
Distance to inland mudflat[a]	Dmdfl	Distance to inland mudflat (km)
Year	Year	$\bar{x}$ year of surveyed plots

[a] Obtained from the Ducks Unlimited land cover map (Ducks Unlimited, Inc. 2011).
[b] Developed based on both the Ducks Unlimited land cover map (Ducks Unlimited, Inc. 2011) and the National Hydrography Dataset (Simley and Carswell 2009).
[c] Obtained from the National Hydrography Dataset (Simley and Carswell 2009).
* Variable removed from analyses because of high correlation with other variables.

surveyors drew plot boundaries on aerial photographs (1985–2007) or IKONOS satellite imagery (2008–2013) to facilitate orientation while in the field.

Each year, the program surveyed waterbird nests using single-visit area searches during incubation (typically from early to mid-Jun). During surveys, 2–4 surveyors systematically searched each plot for nests. Search duration of 2–10 hours depended on the number of surveyors, available habitat, nest density, and surveyor experience. Surveyors recorded all active and destroyed waterbird (i.e., waterfowl, crane, loon, gull, and tern) nests and nests of other species as incidentally encountered. However, for these analyses, we focused only on geese and eiders because these species are of particular management concern and were the main focus of annual surveys; other species exhibited low nest densities throughout the study area (e.g., ducks), low variability in nest densities among plots (e.g., cranes, swans), or unreliable nest densities because many nests were likely missed (e.g., shorebirds, passerines). Once a surveyor found a nest, they identified species by either visual confirmation of an adult at the nest or by comparing down and contour feathers in the nest bowl with a photographic field guide (Bowman 2008). In all analyses, we did not correct for nest detection probabilities because detection was high ($\bar{x}$ annual nest detection rate >75%) for geese and eider species and showed little variation among years or observers (Fischer and Stehn 2014). Data collected during the course of this study followed consistent protocols with regards to animal welfare. Field procedures were observational in nature and were approved and permitted by the USFWS Region 7 Endangered Species Program.

With data accumulated over 29 years, there was a high degree of spatial overlap in surveyed plots, potentially resulting in pseudoreplication. In addition, there was large variation in the number of observed nests per plot among closely located plots. This was likely due to the size of each plot being too small to adequately represent the mosaic of interwoven wetland, lake, river, slough, and mudflat habitats, features nesting birds were likely using when making selection decisions. Therefore, we combined surveyed plots into 4-km^2 regular grid cells for all analyses. This spatial scale allowed us to combine several plots per regular grid cell while still maintaining a suitable sample size for all analyses. To reduce the survey data to regular grid cells, we first placed 2×2-km regular grid cells over the entire study area and then assigned survey plots to grid cells based on the location of the plot center. We removed grid cells from the model-fitting domain that had no surveyed plots within their boundaries. This resulted in 535 surveyed grid cells with 1–18 survey plots/grid cell. With >1 plot/grid cell, we treated multiple surveys as replicates and calculated the average nest density per grid cell by dividing the number of nests found for each species during all surveys within a grid cell by the amount of area surveyed.

Environmental Variables

We obtained 16 environmental variables to relate to geese and eider nest densities (Table 1). We used the land cover map developed for the study area by Ducks Unlimited, Inc. (based on imagery from 2000 to 2005; resolution = 30 m; Ducks Unlimited, Inc. 2011) to classify habitat, from which we identified 7 single or composite classifications as potentially important to nesting geese and eiders (i.e., percent coastal dwarf shrub, coastal dwarf shrub-pond mosaic, lower coastal salt marsh, upper coastal brackish meadow, coastal graminoid, sandbar-mudflat, upland). We distinguished inland mudflats (i.e., located >1 km from the coastline) from the much larger coastal mudflats because the former occur along edges of rivers or lakes and often contain vegetated grazing lawns used by nesting waterfowl (Schmutz 2001, Lake et al. 2006). We obtained locations and areas of water bodies, rivers, river and tidal slough flow lines, and the coastline from the National Hydrography Dataset (Simley and Carswell 2009) and derived density of water bodies using these data and ArcGIS 10 (Environmental Systems Research Institute, Redlands, CA, USA) where each water body was represented by a point corresponding to the centroid of the water body (search radius = 10 km; output cell size = 1 km). Using the land cover map and the hydrography datasets, we considered vegetated land areas as a measure of potential nesting habitat. We defined potential nesting habitat as all areas not classified as water, sandbar-mudflat, or rock-gravel according to the Ducks Unlimited land cover map (Ducks Unlimited, Inc. 2011) or water body or river according to the National Hydrography dataset (Simley and Carswell 2009).

For each surveyed grid cell, we extracted mean density of water bodies, percent composition of each land cover class and potential nesting habitat, percent composition of water body and riverine area, and total length of pond shoreline and riverine-tidal slough flow lines using Geospatial Modeling

Table 2. Summary statistics (i.e., number of nests found within surveyed plots and mean nest density within 4-km^2 survey grid cells) and percent variance explained from random forests models predicting nest density within 4-km^2 survey grid cells for geese and eider species (ordered by % variance explained) breeding on the Yukon–Kuskokwim Delta of Alaska, USA, 1985–2013.

		Nest density (nests/km^2)			
Species	No. nests found	$\bar{x}$	SE	Range	% variance explained
Greater white-fronted goose	12,119	10.1	0.5	0–69.5	68.7
Cackling goose	33,264	25.8	1.4	0–177.7	52.0
Emperor goose	9,328	9.0	0.4	0–57.8	40.2
Spectacled eider	2,254	1.7	0.1	0–18.5	37.8
Black brant	10,898	13.0	2.4	0–507.9	15.3
Common eider	835	0.8	0.1	0–33.9	13.0

Environment (Beyer 2012). Within each surveyed grid cell, we also divided the length of pond shoreline by the water body area as a measure of shoreline complexity. Finally, we estimated the distance from the nearest coastline edge or inland mudflat to the centroid of each plot using ArcGIS 10.

Although changes to habitat characteristics have occurred over time, we believe these changes are likely not at a large enough magnitude to bias large-scale habitat selection patterns based on nest density data collected over a long time scale (e.g., 1985–2013). For example, from 1980–2008, Jorgenson and Dissing (2010) reported that only approximately 8.3% of the investigated area on the Yukon–Kuskokwim Delta experienced changes in ecotype, with the greatest changes due to permafrost degradation, channel erosion, and channel deposition. Therefore, to relate mean geese and eider nest densities from 1985–2013 to environmental variables, we used static environmental variables developed from data within this same time period.

Nest Density Models

We modeled nest densities (nests/km^2) for each species of geese and eider in relation to the above environmental

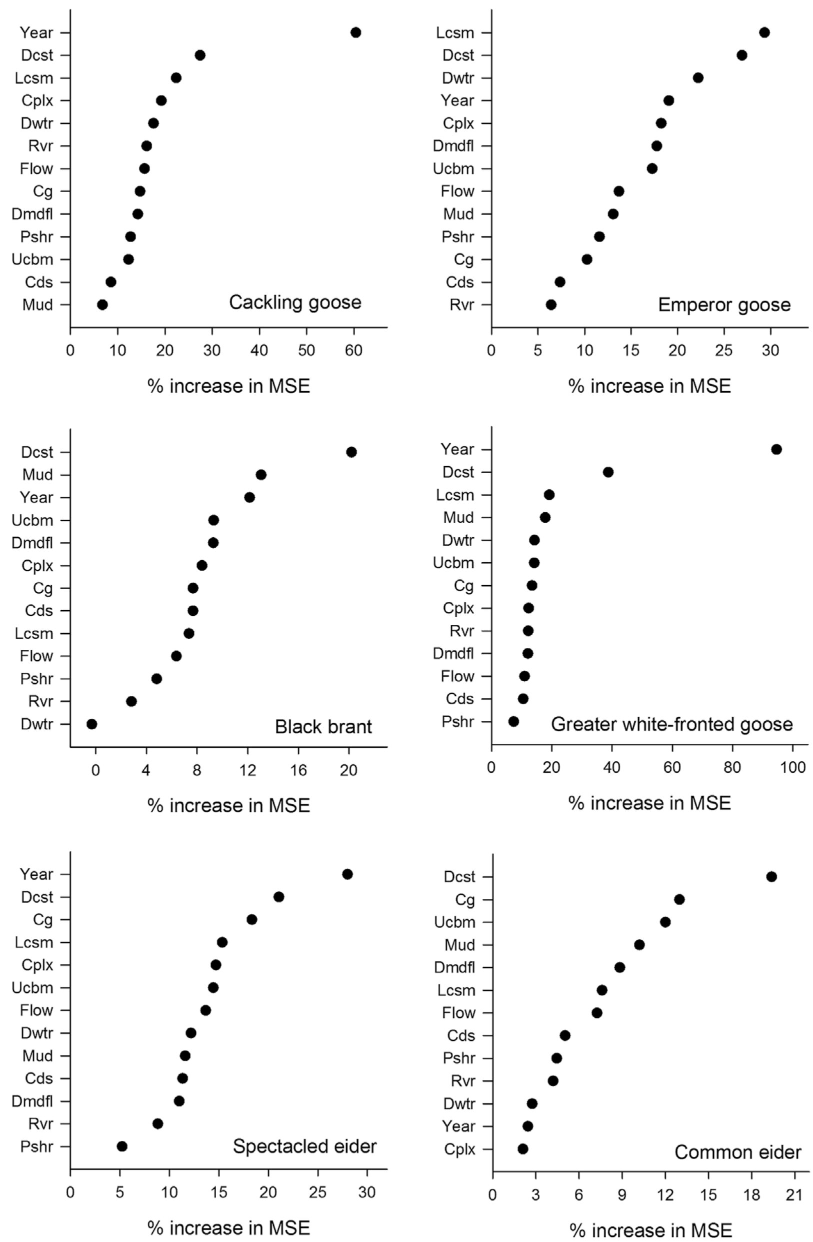

Figure 2. Variable importance plots from random forests models predicting geese and eider nest densities on the Yukon–Kuskokwim Delta of Alaska, USA, 1985–2013. Variable importance values indicate the percent increase in prediction error (MSE) after randomly permuting the values of the explanatory variable for the out-of-bag observations. Variables with higher values of percent increase in MSE indicate greater importance in predicting waterbird nest density. Cds = % coastal dwarf shrub, Lcsm = % lower coastal salt marsh, Ucbm = % upper coastal brackish meadow, Cg = % coastal graminoid, Mud = % sandbar or mudflat, Dwtr = $\bar{x}$ density of waterbodies, Rvr = % area of riverine, Pshr = length of pond shoreline, Cplx = shoreline complexity, Flow = length of riverine and tidal sloughs, Dcst = distance to coast, and Dmdfl = distance to inland mudflat.

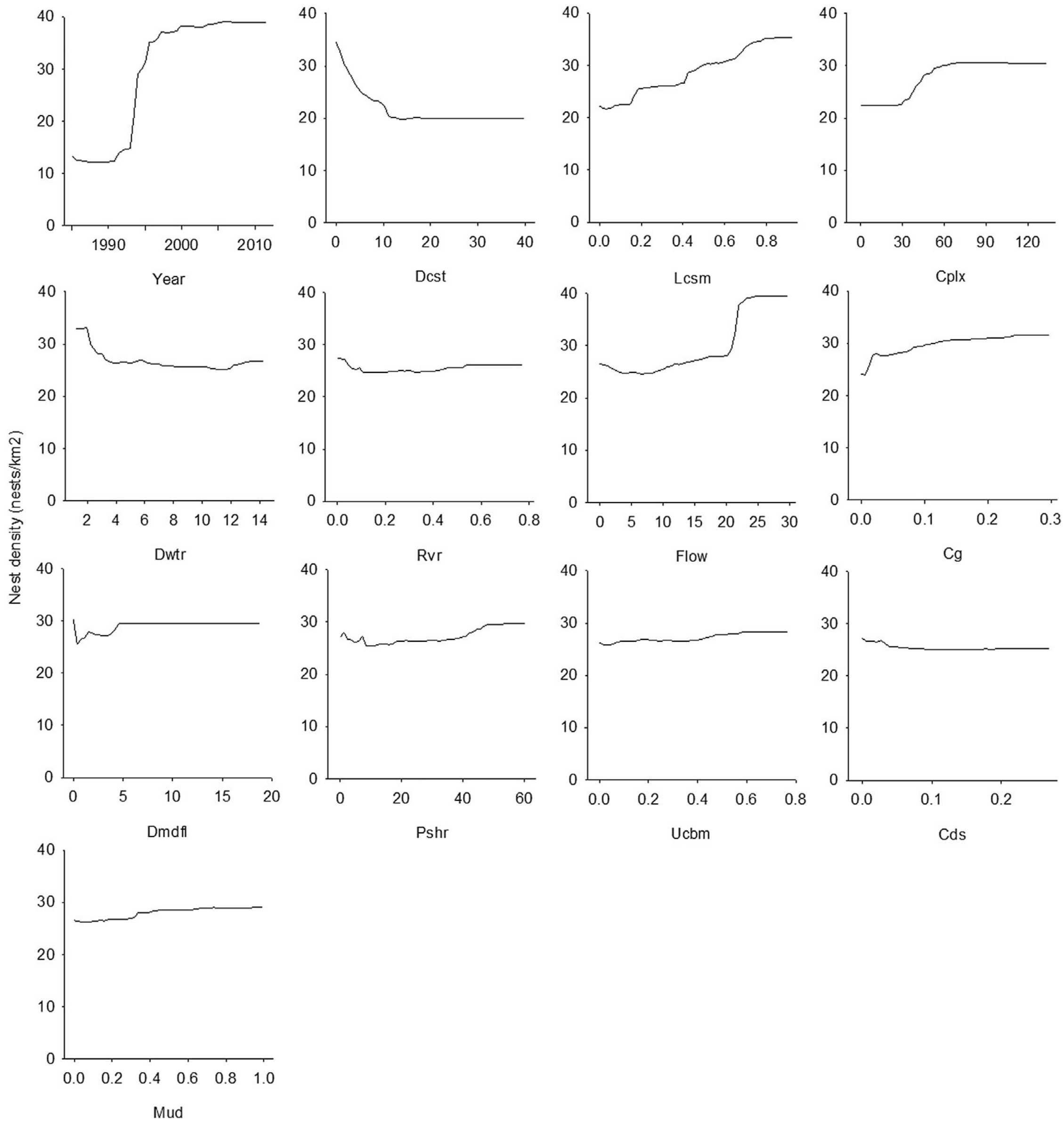

Figure 3. Partial dependence plots from random forests models predicting cackling goose nest density on the Yukon–Kuskokwim Delta of Alaska, USA, 1985–2013. Partial dependence plots represent the relationship between an explanatory variable and nest density while holding all other explanatory variables in the model at their mean. Explanatory variables are listed in order of importance. Cds = % coastal dwarf shrub, Lcsm = % lower coastal salt marsh, Ucbm = % upper coastal brackish meadow, Cg = % coastal graminoid, Mud = % sandbar or mudflat, Dwtr = $\bar{x}$ density of waterbodies, Rvr = % area of riverine, Pshr = length of pond shoreline, Cplx = shoreline complexity, Flow = length of riverine and tidal sloughs, Dcst = distance to coast, and Dmdfl = distance to inland mudflat.

variables and the mean of survey years from all plots within each grid cell to account for changing population densities through time (Table 1). Prior to analyses, we removed grid cells in which >10% of the land cover in the surveyed grid cell was unclassified (usually due to cloud cover along the coast) in the Ducks Unlimited land cover map ($n = 9$; Ducks Unlimited, Inc. 2011) because relationships between nest density and land cover would be unreliable. We also removed redundant variables using variance inflation factors (VIF), where we removed one variable from each highly correlated ($r > 0.60$) pair until remaining variables had a VIF ≤ 5.0. This resulted in the removal of 4 variables (% upland, % coastal dwarf shrub-pond mosaic, % potential nesting habitat, and % area of water bodies; Table 1) from all further analyses.

To model nest densities, we used random forests, an ensemble regression tree approach (Breiman 2001). In standard regression trees, the response variable is recursively partitioned into increasingly homogenous groups through binary splits of a single predictor variable at a time (Breiman et al. 1984). At each node, the threshold value and the predictor variable are selected from the entire suite of predictors, so that the difference between the resulting branches is maximized. To achieve greater predictive accuracy, random forests combines predictions from many (e.g., 1,000 in this study) regression

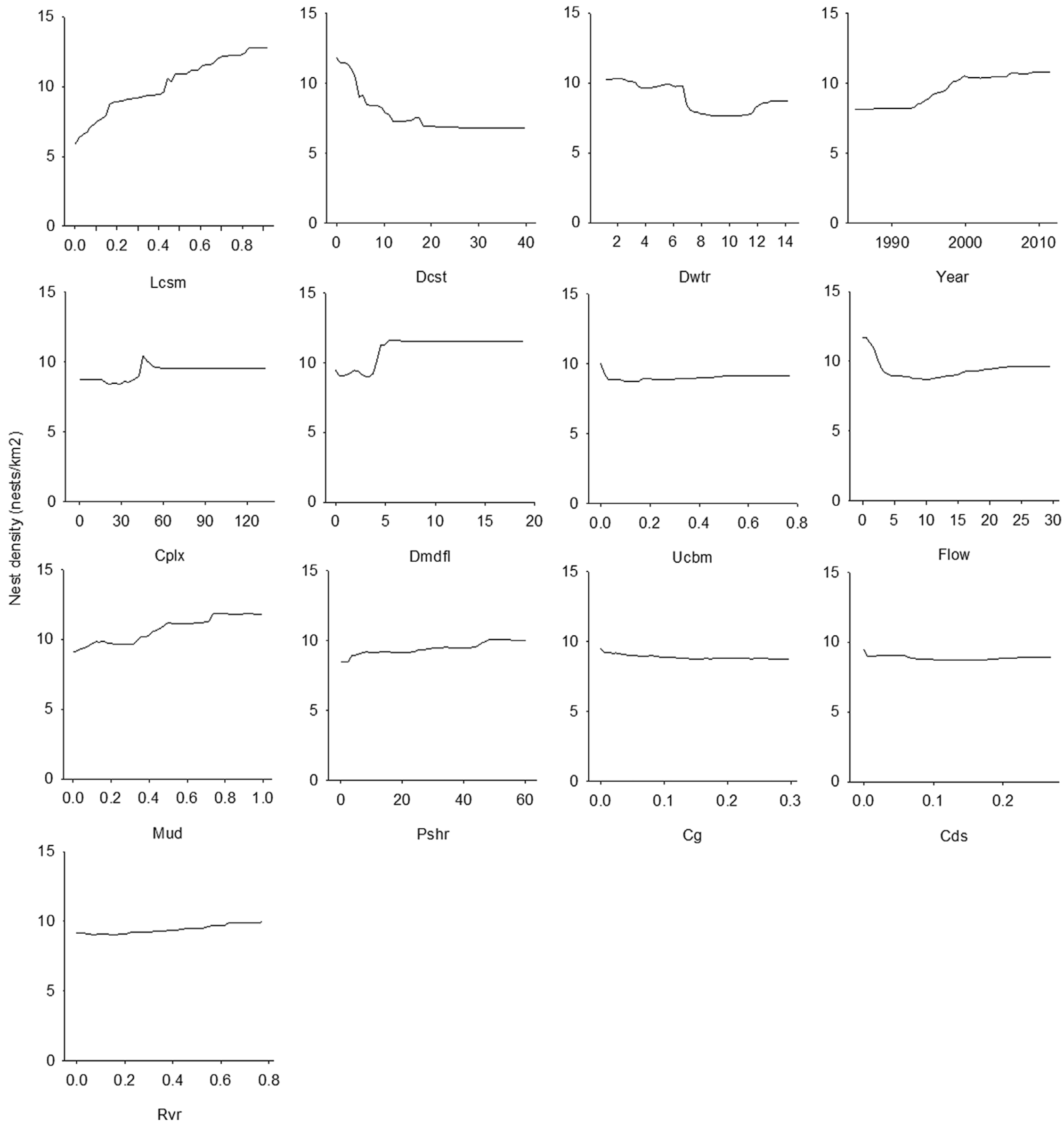

Figure 4. Partial dependence plots from random forests models predicting emperor goose nest density on the Yukon–Kuskokwim Delta of Alaska, USA, 1985–2013. Partial dependence plots represent the relationship between an explanatory variable and nest density while holding all other explanatory variables in the model at their mean. Explanatory variables are listed in order of importance. Cds = % coastal dwarf shrub, Lcsm = % lower coastal salt marsh, Ucbm = % upper coastal brackish meadow, Cg = % coastal graminoid, Mud = % sandbar or mudflat, Dwtr = $\bar{x}$ density of waterbodies, Rvr = % area of riverine, Pshr = length of pond shoreline, Cplx = shoreline complexity, Flow = length of riverine and tidal sloughs, Dcst = distance to coast, and Dmdfl = distance to inland mudflat.

trees (Breiman 2001). Each regression tree is grown from a bootstrap sample of the data, with only a small number (e.g., a third of all predictor variables in this study) of randomly selected variables available for partitioning at each node. Each fully grown tree is then used to predict the out-of-bag observations (i.e., observations not included in the bootstrap sample; ~37% of the observations) and estimate the percent variance explained by the model. Because the out-of-bag observations are not used to fit the model, these estimates are cross-validated accuracy assessments (Cutler et al. 2007). Out-of-bag observations can also be used to assess variable importance via the percent increase in prediction error (MSE) resulting from randomly permuting the values of an explanatory variable for the out-of-bag observations. We used partial dependence plots to characterize the relationships between explanatory variables and predicted nest densities (Cutler et al. 2007). These plots display the effect of one variable when all other predictor variables in the model are held at their mean values. For each species, we present the percent variance explained by the model, as well as variable importance values and partial dependence plots to estimate the relative effect of each environmental variable on nest densities. We ran all models using the randomForest package (Liaw and Wiener 2002) in program R (R Development Core Team 2011).

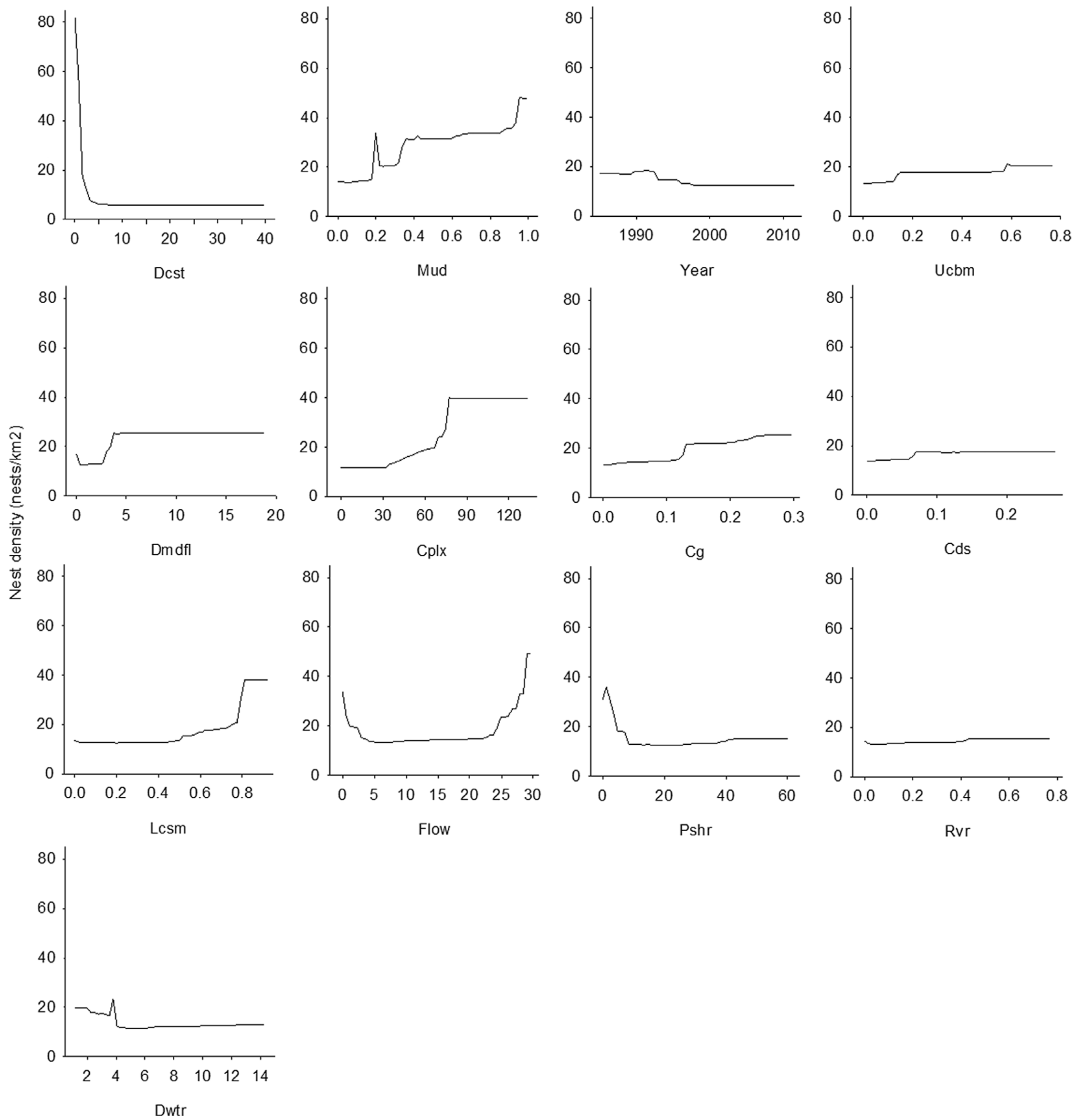

Figure 5. Partial dependence plots from random forests models predicting black brant nest density on the Yukon–Kuskokwim Delta of Alaska, USA, 1985–2013. Partial dependence plots represent the relationship between an explanatory variable and nest density while holding all other explanatory variables in the model at their mean. Explanatory variables are listed in order of importance. Cds = % coastal dwarf shrub, Lcsm = % lower coastal salt marsh, Ucbm = % upper coastal brackish meadow, Cg = % coastal graminoid, Mud = % sandbar or mudflat, Dwtr = $\bar{x}$ density of waterbodies, Rvr = % area of riverine, Pshr = length of pond shoreline, Cplx = shoreline complexity, Flow = length of riverine and tidal sloughs, Dcst = distance to coast, and Dmdfl = distance to inland mudflat.

Predictive Surfaces

To predict nest densities over the entire central coastal zone of the Yukon–Kuskokwim Delta, we used the 4-km^2 regular grid cells developed for the entire study area and the same environmental variables as the surveyed grid cells (Table 1). We then obtained predicted species-specific nest densities for each predictive grid cell using the random forests models developed above and 2013 as the survey year. We passed the environmental data from predicted grid cells down the regression trees, and obtained predicted nest densities by averaging model outputs from all trees. We then mapped predicted nest densities for the entire study area. Because slight differences in placement of grid cells could result in different predicted nest densities, we used a moving window approach, where we shifted predictive grid cells by 1 km in each orthogonal direction and then averaged cells to create final predictive surfaces. However, if >10% of the predictive grid cell was unclassified in the Ducks Unlimited land cover map (Ducks Unlimited, Inc. 2011), we removed these areas from final predictive surfaces.

RESULTS

Surveyors conducted nest searches at 2,318 plots during 29 years between 1985 and 2013 (50–119 plots surveyed/yr). Within these plots, the number of nests found and the mean nest density was greatest for greater white-fronted goose, cackling goose,

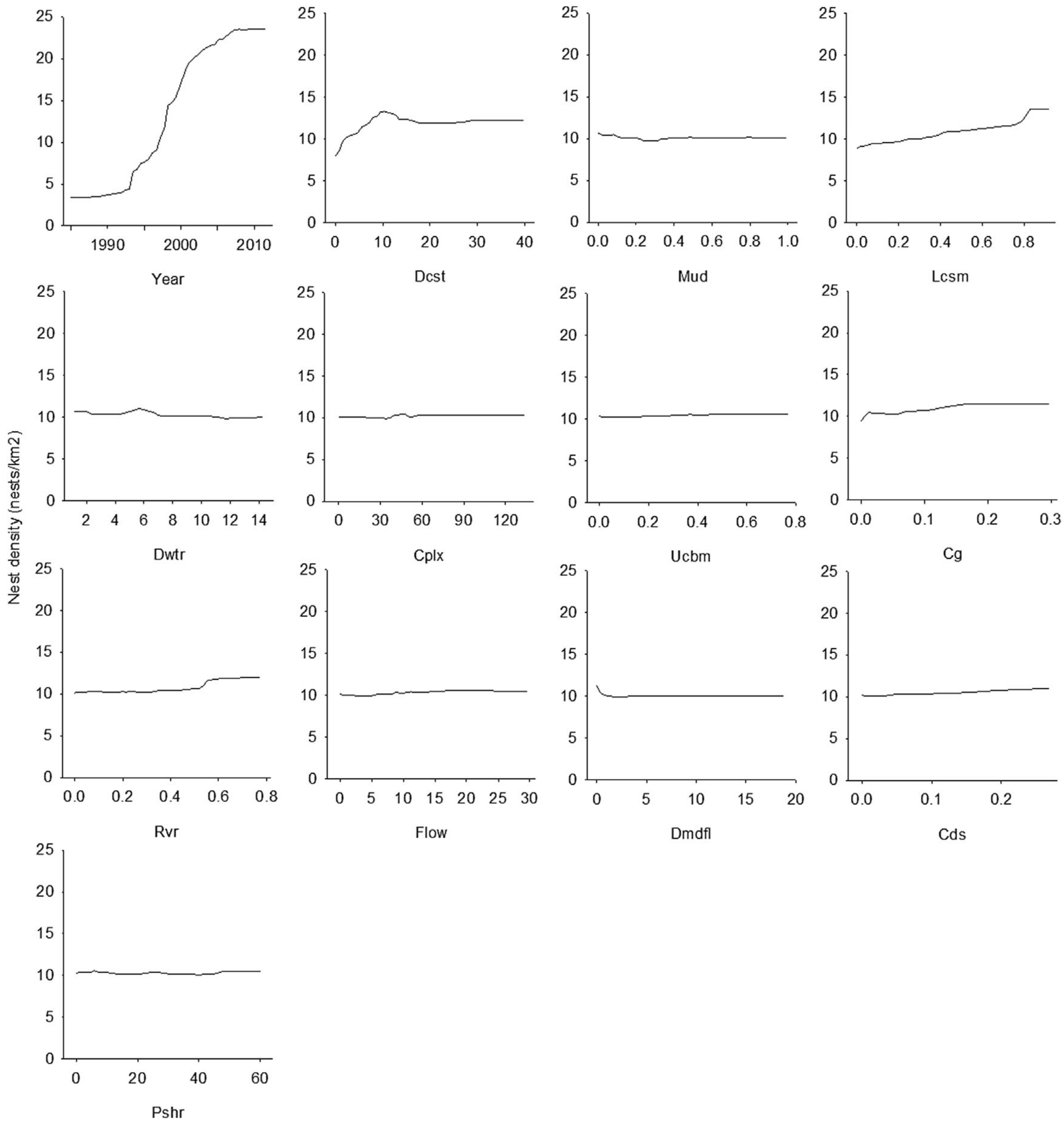

Figure 6. Partial dependence plots from random forests models predicting greater white-fronted goose nest density on the Yukon–Kuskokwim Delta of Alaska, USA, 1985–2013. Partial dependence plots represent the relationship between an explanatory variable and nest density while holding all other explanatory variables in the model at their mean. Explanatory variables are listed in order of importance. Cds = % coastal dwarf shrub, Lcsm = % lower coastal salt marsh, Ucbm = % upper coastal brackish meadow, Cg = % coastal graminoid, Mud = % sandbar or mudflat, Dwtr = $\bar{x}$ density of waterbodies, Rvr = % area of riverine, Pshr = length of pond shoreline, Cplx = shoreline complexity, Flow = length of riverine and tidal sloughs, Dcst = distance to coast, and Dmdfl = distance to inland mudflat.

emperor goose, and spectacled eider (Table 2). The percentage of variance explained by the random forests models varied among species, ranging from 13–69% (Table 2). Variable importance plots illustrated that distance to coast was an important explanatory variable for all geese and eider species (Fig. 2); black brant and common eider nest density declined sharply as distance to coast increased, whereas cackling goose, emperor goose, and spectacled eider exhibited more gradual declines (Figs. 3–8). Conversely, nest density of greater white-fronted goose was greatest at intermediate levels of distance to coast (Fig. 6). Most species also tended to select greater percentages of lowland habitats (Figs. 2–8). For example, greater nest densities of spectacled eider and common eider occurred when the percentage of coastal graminoid land cover class was greater, whereas the percentage of lower coastal salt marsh was positively related to nest densities of cackling goose, emperor goose, and greater white-fronted goose. Percentage of mudflats was also important for black brant, with greater nest densities occurring in areas with more coastal mudflats. In addition to environmental variables, mean survey year was important for cackling goose, black brant, greater white-fronted goose, and spectacled eider (Fig. 2), with all species except black brant exhibiting increases in nest densities in the mid-1990s (Figs. 3, 6, and 7). Black brant, on the other hand, exhibited relatively stable to slightly decreasing populations since 1985 (Fig. 5). Predicted nest densities mapped across the Yukon–Kuskokwim

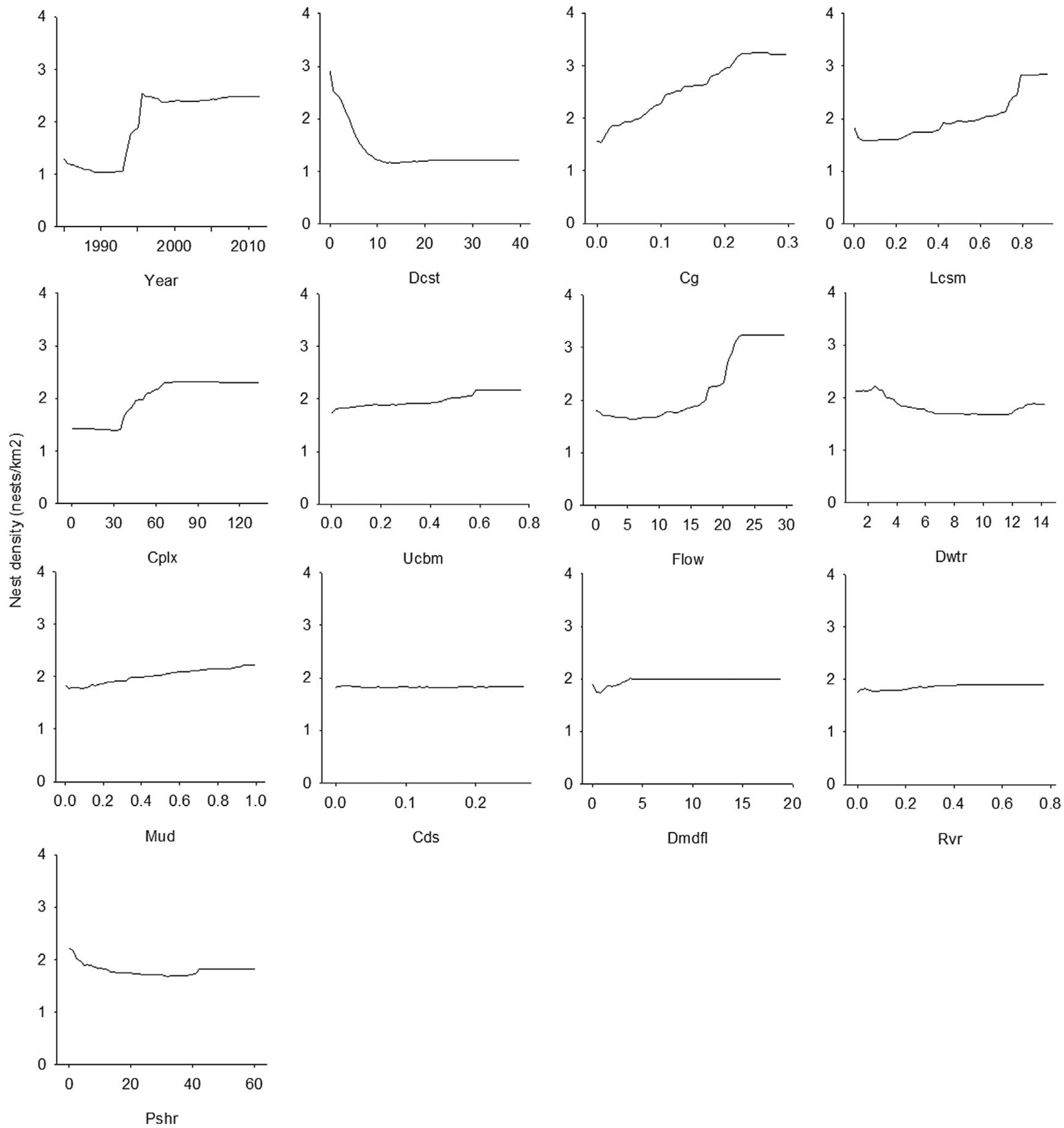

Figure 7. Partial dependence plots from random forests models predicting spectacled eider nest density on the Yukon–Kuskokwim Delta of Alaska, USA, 1985–2013. Partial dependence plots represent the relationship between an explanatory variable and nest density while holding all other explanatory variables in the model at their mean. Explanatory variables are listed in order of importance. Cds = % coastal dwarf shrub, Lcsm = % lower coastal salt marsh, Ucbm = % upper coastal brackish meadow, Cg = % coastal graminoid, Mud = % sandbar or mudflat, Dwtr = $\bar{x}$ density of waterbodies, Rvr = % area of riverine, Pshr = length of pond shoreline, Cplx = shoreline complexity, Flow = length of riverine and tidal sloughs, Dcst = distance to coast, and Dmdfl = distance to inland mudflat.

Delta coastal zone for each species revealed spatially explicit areas of high and low densities (Fig. 9).

DISCUSSION

This study provides the first habitat-specific predictive distributions of nest densities for the 6 species of geese and eiders breeding on the Yukon–Kuskokwim Delta of Alaska. These maps and the habitat associations for these species provide key baseline information that has thus far been lacking. For almost all species of geese and eiders investigated in this study, nest density increased closer to the coast and within lowland habitats (i.e., lower coastal salt marsh and coastal graminoid). These coarse habitat associations support previous studies, with several studies noting greater densities of waterbirds within these coastal fringe habitats (Holmes and Black 1973, King and Dau 1981, Platte and Stehn 2009). Selection of these habitats may be due to increased food availability or decreased predation pressure in these areas. For example, forage plants preferred by geese are more frequent in these coastal land cover types. In addition, because the numerous rivers, tidal sloughs, and lakes within the coastal fringe areas inhibit foraging movements and limit construction of subterranean dens by Arctic fox, selection of nests sites by geese and eiders within these areas may be a means by which individuals increase nest survival and reduce predation pressure (Olsen 1951, Spencer

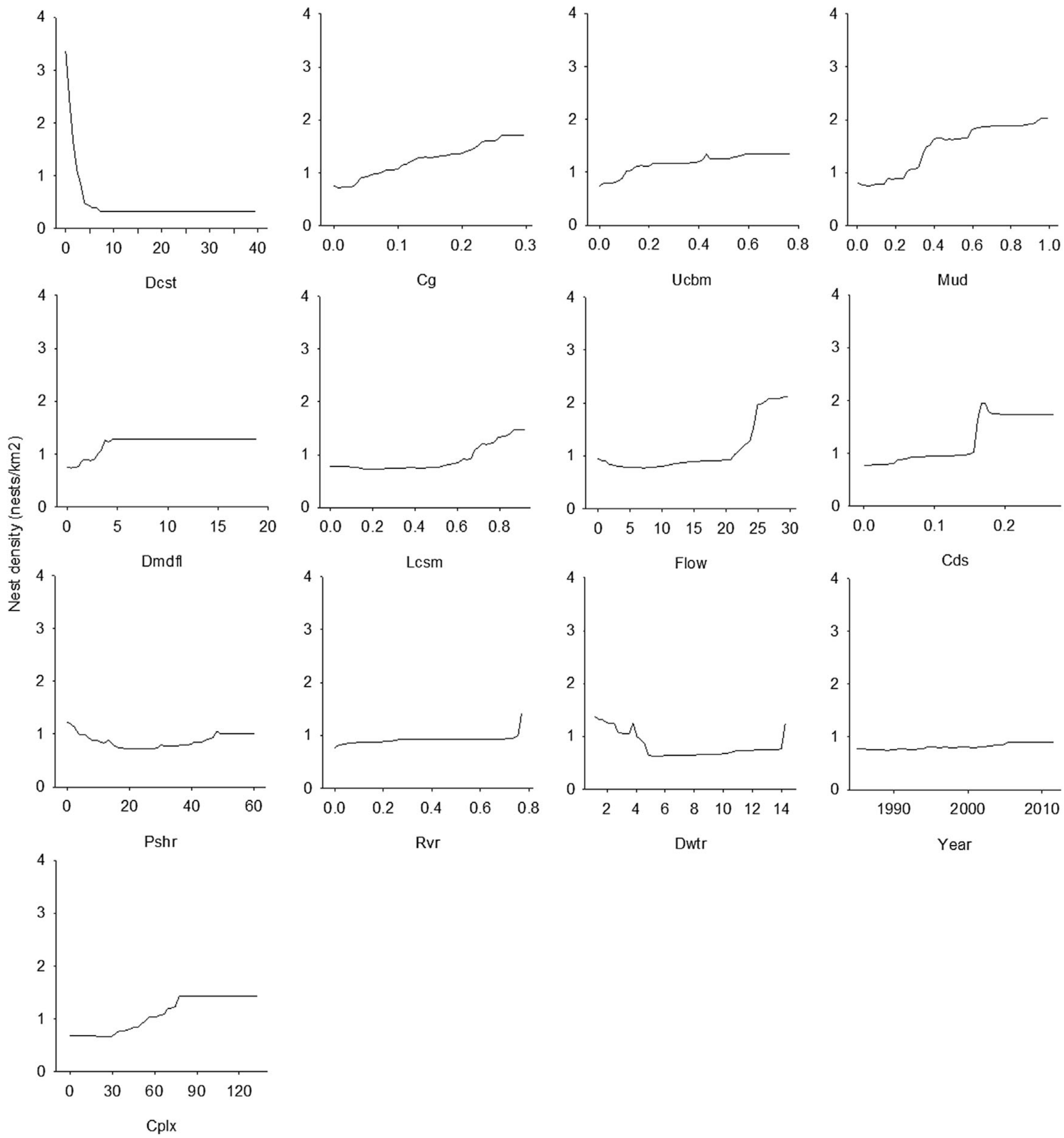

Figure 8. Partial dependence plots from random forests models predicting common eider nest density on the Yukon–Kuskokwim Delta of Alaska, USA, 1985–2013. Partial dependence plots represent the relationship between an explanatory variable and nest density while holding all other explanatory variables in the model at their mean. Explanatory variables are listed in order of importance. Cds = % coastal dwarf shrub, Lcsm = % lower coastal salt marsh, Ucbm = % upper coastal brackish meadow, Cg = % coastal graminoid, Mud = % sandbar or mudflat, Dwtr = $\bar{x}$ density of waterbodies, Rvr = % area of riverine, Pshr = length of pond shoreline, Cplx = shoreline complexity, Flow = length of riverine and tidal sloughs, Dcst = distance to coast, and Dmdfl = distance to inland mudflat.

et al. 1951, Grand et al. 1997). However, nesting within these areas is not without its risks because these areas are highly susceptible to flooding during high tide and storm events (Hansen 1961, King 1964, Jorgenson and Ely 2001); these risks are likely to increase with climate change as sea levels rise, storm intensity and frequency increase, and seasonal patterns of storminess change.

Despite the general association between nest densities and distance to coast, we also noted species-specific nest-site selection patterns such as the gradient of species from the coast to inland areas. Black brant and common eider were predicted to nest at greatest densities within a narrow band (i.e., <5 km) along the coastline, whereas cackling goose, emperor goose, and spectacled eider nested with greater densities farther inland (i.e., 10–15 km from the coast; Fig. 9). Greater white-fronted goose nested the farthest inland as compared to all other species. This gradient also likely reflects the relative vulnerability of these species to future climate change impacts. For example, those species with limited distributions closest to the coast (i.e., black brant, common eider) are likely to be at the greatest risk of habitat loss, habitat destruction, and losses of eggs and chicks during the nesting season as a result of rising sea levels and increased storm intensity and frequency. Moreover, a significant proportion of the entire population (e.g., emperor geese, cackling geese) or the Pacific Flyway population (e.g.,

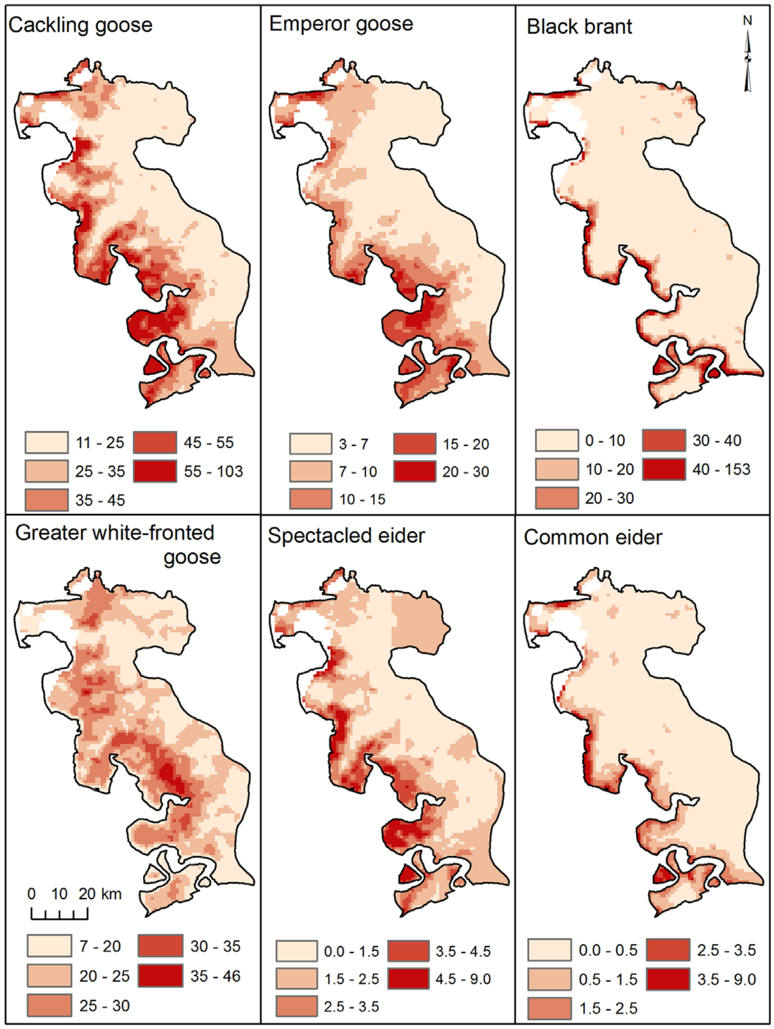

Figure 9. Predicted nest densities (i.e., no. nests/km^2) for cackling goose, emperor goose, black brant, greater white-fronted goose, spectacled eider, and common eider on the Yukon–Kuskokwim Delta of Alaska, USA, 1985–2013. Areas with no predictions (e.g., unclassified habitat was >10% in predictive grid cells) are in white.

black brant, greater white-fronted geese) of many of these species nest on the Yukon–Kuskokwim Delta (King and Dau 1981, Schmutz 2001), adding to the relative vulnerability of these species to climate-mediated changes within this region. However, the ability of individual species to adapt to increased flooding risks and habitat loss remains unknown.

The amount of variance explained by the predictive models developed in this study varied among species. Unexplained variance may have been due to several factors including explanatory variables important for individual species but not incorporated into the analyses, the accuracy and scale of environmental variables included in analyses, and annual variability in nest-site selection patterns. When conducting large-scale habitat assessments, potential explanatory variables are limited to those that can be mapped across a large spatial extent. However, waterbird nest densities may also vary as a result of factors such as social interactions (e.g., aggregation among colonial nesting birds such as black brant or inter- and intra-specific competition), predator densities, and fine-scale habitat features (e.g., vegetation height, water body depth and salinity, shoreline complexity, presence of islands and peninsulas) that are not currently (or unable to be) modeled at a large spatial scale. In addition, we suspect certain habitat features may also have been important that could not be incorporated because of a lack of current geographic information system (GIS) layers. For example, the amount and quality of grazing lawn habitat is especially important in brood-rearing areas for black brant and emperor geese (Schmutz 2001, Schmutz and Laing 2002). Specific variables for proximity to brood rearing habitat were not among our environmental variables and these could contribute to predicting the distribution of nest density for some species (Grand et al. 1997). Furthermore, predictive models depend on the scale and accuracy of the environmental variables used in these analyses. If there are classification errors in the GIS layers or if the scale at which these layers were developed are incongruent with the scale at which waterbirds select nesting habitat, then accuracy may decline. For example, better accuracy in environmental layers such as land cover classifications may increase the accuracy of models predicting waterbird nest densities within this region. Because we also combined many years of nest data in our analyses, our models were unable to account for any annual variability in nest-site selection patterns. Nest-site selection may vary annually in relation to annual changes in habitat conditions such as the amount and duration of snow cover (Ely and Raveling 1984, Petersen 1990) or deposition of sediment following fall storm surges (Dau et al. 2011). However, large annual movements among nesting locations detectable at the scale at which we conducted this study may be unlikely because most species of geese and eiders investigated in this study exhibit high natal and breeding site fidelity, with annual movements likely restricted to a local scale. These potential limitations must be considered when interpreting these results. Nevertheless, the predictive maps provide a baseline for geese and eider nest density distributions within this region, based on association of nest density with large-scale habitat features, and provide a fundamental advancement in predicting distributions of these species.

MANAGEMENT IMPLICATIONS

The predicted nest density maps developed in this study identify important regions for nesting geese and eiders that provide a basis for guiding future management and conservation decisions. For example, these maps can be used to assess the direct (i.e., habitat loss) and indirect (e.g., increased risk from oil spills, habitat alteration and fragmentation, increased disturbance, enhanced predator populations) effects of future development scenarios. Additionally, as models are developed to predict changes in environmental conditions (e.g., sea level rise, storm surge intensity, vegetation changes, changes to surface water hydrology) under various climate change scenarios, these predictive layers can be used in conjunction with waterbird nest density maps to develop species-specific vulnerability assessments and adaptation strategies based on waterbird breeding habitat refugia. Future monitoring efforts could also benefit from the predictive maps developed in this study by, for example, defining sampling strata based on expected nest densities. Future efforts should be made to validate and improve the current predictions presented here. For example, future efforts may benefit from implementing a standardized sampling design specifically for the purpose of habitat suitability modeling and including additional or more accurate environmental layers that were unavailable for this study.

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