The Influence of Fall Storms on Nest Densities of Geese and Eiders on the Yukon-Kuskokwim Delta of Alaska

Sarah T. Saalfeld,[1,2,]† Julian B. Fischer[2], Robert A. Stehn[2], Robert M. Platte[2], and Stephen C. Brown[1]

[1]Manomet Center for Conservation Sciences, P.O. Box 1770, Manomet, Massachusetts 02345, USA

[2]U.S. Fish and Wildlife Service, 1011 East Tudor Road, MS 201, Anchorage, Alaska 99503, USA

†E-mail:saalfeldst@gmail.com

Abstract. The Yukon-Kuskokwim Delta of Alaska is a globally important region for numerous avian species including millions of migrating and nesting waterbirds. Climate change effects such as sea level rise and increased storm frequency and intensity have the potential to impact waterbird populations and breeding habitat. In order to determine the potential impacts of these climate-mediated changes, we investigated both short-term and long-term impacts of storm surges to geese and eider species that commonly breed on the Yukon-Kuskokwim Delta. To determine short-term impacts, we compared nest densities of geese and eiders in relation to the magnitude of storms that occurred in the prior fall from 2000–2013. Additionally, we modeled geese and eider nest densities using random forests in relation to the time-integrated flood index (i.e., a storm-specific measure that accounts for both water depth and the amount of time the flooding occurred on the landscape) for four modeled storms (i.e., 2005, 2006, 2009, and 2011), as well as other environmental covariates. To determine long-term impacts, we modeled geese and eider nest densities using random forests in relation to the annual inundation index (i.e., a time-static storm footprint calculated based on the time-integrated flood index for seven modeled storms and their annual return rate), as well as other environmental covariates over a longer time frame (1985–2013). We failed to find any short-term or long-term impacts of storms on nesting geese and eiders, with storm magnitude, the time-integrated flood index, and the annual inundation index explaining little of the variation in geese and eider nest densities. Rather, other environmental variables such as distance to coast appeared to be more influential to both annual and long-term nest densities. The sampling design and the limited availability of inundation projections may have precluded us from finding a storm effect if one existed. For example, the monitoring design in which plots were surveyed once for waterbird nests then specifically not revisited the next five years precluded a more focused assessment comparing spatial distribution

of nest densities immediately before and after specific storms. Additionally, the temporal and spatial scale of the nest density and storm surge data may have been inadequate to detect trends if they existed. Future studies should implement more targeted sampling designs to determine if the apparent lack of an effect is real or simply reflects limitations of the sampling design, as well as investigate other demographic parameters (e.g., clutch size, nest success, fledgling success) that may be more impacted by storm surges.

Key words: Alaska; Arctic; breeding; eider; flooding; geese; nest density; predicted density surface; random forests; storm surge; waterbirds; waterfowl; Yukon-Kuskokwim Delta.

INTRODUCTION

The Yukon-Kuskokwim Delta of Alaska 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, King and Derksen 1986, Gill and Handel 1990). 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 (*Branta 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 of special conservation and management concern, including the threatened Spectacled Eider (*Somateria fischeri*), Common Eider (*S. mollissima*), Emperor Goose, and Black Brant. As such, these species may be particularly sensitive to habitat loss or alterations within this region.

Within the Yukon-Kuskokwim Delta, waterbird nest densities are greatest within coastal fringe habitats, with some species only occurring within these habitat types (Olsen 1951, Holmes and Black 1973, Mickelson 1975, Eisenhauer and Kirkpatrick 1977, Gill and Handel 1981, King and Dau 1981, Eldridge 2003, Platte and Stehn 2009). These habitats are especially influenced by coastal storms that frequently inundate low-lying areas up to 30–40 km inland (Dau et al. 2011, Terenzi et al. 2014). 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 at least three times in the last 50 years (Terenzi et al. 2014). Thus, long-term flooding within this region ultimately shapes the landforms and habitat on which nesting waterbirds in this region depend (Tande and Jennings 1986, Kincheloe and Stehn 1991, Babcock and Ely 1994, Sedinger and Newbury 1998, Jorgenson 2000, Jorgenson and Ely 2001, Jorgenson and Dissing 2010). However, annual storm surges can result in direct loss of breeding habitat (e.g., due to erosion, scouring, siltation, and displacement of nesting islands; Dau et al. 2011) and influence food availability (e.g., increased salinity altering plant and invertebrate communities) to adults and young over the short-term. These short-term impacts may result in distributional shifts of species to more suitable locations following major storm events. For example, the 1974 and 1978 November storm surges on the Yukon-Kuskokwim Delta covered portions of both coastal and inland areas with mud, silt, and pond detritus, preventing waterbird nesting in these locations the following spring (Dau et al. 2011). In addition, these storm surges displaced several island nesting sites, a preferred nesting location for many species of waterfowl (Dau et al. 2011). Both of these storms were major storm events, with the 1974 storm being the largest of the century with an estimated 100-year return period (Terenzi et al. 2014). However,

despite the potential for significant impacts, we are not aware of any study that has tried to assess both short-term (i.e., annual changes in breeding habitat due to specific storms) and long-term (i.e., cumulative changes in breeding habitat due to multiple storm surges over many years) impacts of fall storm surges to nesting waterbirds in this region.

As sea levels rise and storm surge frequency and intensity increases in this region as a result of global climate change, both short-term and long-term impacts to nesting waterbirds will also likely increase. For example, from 1961–2003, global sea levels have risen ~1.8 mm per year (IPCC 2007), with an additional 0.5–1.4 m projected to occur above the 1990 level by 2100 (Rahmstorf 2007). Rising sea levels should increase the frequency of tidal flooding on waterbird nesting habitats, permanently covering some habitats, increasing frequency of inundation in others, and exposing areas previously not impacted to periodic saltwater flooding. Jorgenson and Ely (2001) estimated that with a sea level rise of 49 cm, most brackish terrestrial ecotypes on the Yukon-Kuskokwim Delta would be inundated during high tide, while most non-saline lowland ecotypes would be inundated during storm surges. However, such predictions are complicated by the concurrent counteracting processes of natural levee formation, sediment deposition, organic matter accumulation, and permafrost aggradation (Jorgenson and Ely 2001). In addition, climate change models predict that future storms will increase in frequency and intensity, and the magnitude of storm-tide erosion will increase with reduction of permafrost or nearshore ice caused by warming temperatures (IPCC 2007). Therefore, for nesting waterbirds, the short-term impacts of annual storm surges on nest site availability the following spring will likely increase. Additionally, long-term changes in storm intensity and frequency will likely result in long-term habitat changes.

As a first step in evaluating the potential impacts of climate-mediated changes on waterbird species within the Yukon-Kuskokwim Delta, we identified important environmental variables related to waterbird nest densities and created and mapped predictive surfaces of waterbird nest densities on the Yukon-Kuskokwim Delta (Saalfeld et al., unpublished data). However, these models only included large-scale habitat features in predictions of nest densities and did not incorporate direct measures of short-term or long-term effects of storm surges. As a next step, this study aimed to determine historic responses of waterbirds to both short-term and long-term impacts of past storm surges while controlling for large-scale habitat selection patterns. Specifically, we determined short-term impacts by 1) comparing nest densities of geese and eiders in relation to magnitude of storms that occurred in the prior fall from 2000–2013 and 2) modeled geese and eider nest densities in relation to the time-integrated flood index (i.e., a storm-specific measure that accounts for both water depth and the amount of time the flooding occurred on the landscape) for four modeled storms (i.e., 2005, 2006, 2009, and 2011), as well as other environmental covariates. To determine long-term impacts we modeled geese and eider nest densities in relation to the annual inundation index (i.e., a time-static storm footprint calculated based on the time-integrated flood index from seven modeled storms and their annual return rate), as well as other environmental covariates over a longer time frame (1985–2013).

METHODS

Study area

The study area encompassed ~4650 km^2 of the central coastal zone of the Yukon-Kuskokwim Delta, between the Askinuk and Nelson Island mountains, and from the coast to ~50

km inland (Figure 1). Within this region, coastal processes shape vegetation along a gradient from coastal to inland areas (Tande and Jennings 1986, Thorsteinson et al. 1989, 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/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 1900's 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 regularly 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 ground surveys

Ground surveys were conducted during 29 years from 1985 to 2013 as part of the U. S. Fish and Wildlife Service's 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, various regions of the central coastal zone were sampled (i.e., extensive survey area; Figure 1) by randomly selecting plots within accessible areas (e.g., public lands). From 1994 to 1997, and since 2000, the survey focused within a smaller region of 716 km^2 (i.e., intensive area; Figure 1) corresponding to the area with the majority (~67%) of historic Spectacled Eider aerial observations, a priority species due to its threatened status. In all years, randomization was restricted so that plots did not overlap plots being surveyed in the same year or within the past five years. In most years (1988–1994 and 1997–2013), standardized plot sizes of 0.32 km^2 (402 x 805 m) were used; 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, plot boundaries were drawn on aerial photographs (1985–2007) or IKONOS satellite imagery (2008–2013) to facilitate orientation while in the field.

Each year, waterbird nests were surveyed using single-visit area searches during incubation (typically from early to mid-June). 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. All active and destroyed waterbird (i.e., waterfowl, crane, loon, gull, and tern) nests were recorded, as well as nests of other species as incidentally encountered. However, for these analyses, we focused only on geese and eiders, as these species occurred in the highest densities and had adequate spatial variability in nest densities among plots for modeling purposes. Once a nest was found, species were identified 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 as detection was high (average

annual nest detection rate > 75%) for geese and eider species and showed little variation among years or observers (Fischer and Stehn 2014).

Storm surge modeling

Time-integrated flood index. – Storm surges were modeled for four storms: 18-25 September 2005, 25-30 October 2006, 9-14 November 2009, and 7-12 November 2011 (Allen et al., unpublished data). These storms were selected as data were available for model assessment (e.g., water levels measured from USGS water level gages or time-stamped Synthetic Aperture Radar [SAR] imagery) and they varied in their intensity and return period, with the 2005 and 2011 storms identified as major storms with a 50-year return period, while the 2006 and 2009 storms were identified as minor storms with 5- and 1-year return periods, respectively (Terenzi et al. 2014). For each storm, a spatially-explicit time-integrated flood index layer was created, taking into account both water depth and the amount of time the flooding occurred on the landscape (i.e., time-integrated flood index = sum [water depth* time step], where each time step was ~15 minutes; Allen et al. unpublished data). These layers were available as point shapefiles, with points placed every ~ 0.15 km. From these points, we created rasters (cell size = 100 m) using natural neighbor interpolation (Sibson 1981), removing areas with no estimated flood index value (e.g., rivers, water bodies, coastline within the typical tidal range). For each surveyed plot we extracted the (spatial) mean time-integrated flood index from the modeled storm which occurred during the prior fall using Geospatial Modeling Environment (Beyer 2010).

Annual inundation index. – The time-integrated flood index was modeled for an additional six storms using the same modeling techniques as above. However, as model

assessment was not available for these additional storms, they were not included in the above analyses, but were necessary to include in the annual inundation index so that a complete storm history for the last decade could be accounted for in the calculations. Therefore, to calculate the annual inundation index, we used the time-integrated flood index level from seven storms identified as the largest storms (i.e., >5-year return period) since 1990: 3-10 October 1992, 28 October-4 November 1995, 26 October-2 November 1996, 13-20 November 1996, 16-23 October 2004, 18-25 September 2005, and 7-12 November 2011. All other storms within this time period were identified as minor storms (i.e., <5-year return period), and were therefore not included in the calculations. We defined the annual inundation index as the sum (time-integrated flood index / storm return period) / storm return period weight (Allen et al. unpublished data). The storm return period was defined as the expected return period of a storm (in years) with a given time-integrated flood index based on the maximum surge volume and assuming maximum volumes are well modelled by a Gumbel Distribution. The storm return period weight was defined as the sum (1 / storm return period). The annual inundation index was available as a point shapefile, with points placed every ~ 0.15 km. From these points, we created a raster (cell size = 100 m) using natural neighbor interpolation (Sibson 1981), removing areas with no estimated flood index value (e.g., rivers, water bodies, coastline within the typical tidal range) and adjusting negative values to zero (<3% of all points). For each surveyed plot we extracted the (spatial) mean annual inundation index using Geospatial Modeling Environment (Beyer 2010).

Environmental variables

We used the land cover map developed for the study area by Ducks Unlimited (Ducks Unlimited 2010) (based on 2000–2005 imagery; resolution = 30 m) to classify habitat, from which we identified six single or composite classifications as potentially important to nesting waterbirds (Table 1). We distinguished inland mudflats (i.e., located >1 km from the coastline) from the much larger coastal mudflats, as these river- or lake-edge mudflats often contain vegetated grazing lawn borders used by nesting waterfowl (Schmutz 2001, Lake et al. 2006). We obtained elevation values from a digital elevation model (DEM) developed for the study area (Allen et al., unpublished data). This DEM was developed using the Ducks Unlimited land cover map (Ducks Unlimited 2010) and previously identified elevation-ecotype relationships for this region (Macander et al. 2012). 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 (i.e., mean number of water bodies per km^2) using these data and ArcGIS 10 (Environmental Systems Research Institute, Redlands, CA) 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 both the land cover map and the hydrography datasets, we considered vegetated land areas as a measure of potential nesting habitat. Here, 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 2010) or water body or river according to the National Hydrography dataset (Simley and Carswell 2009).

For each surveyed plot or grid cell (see section “Long-term impacts of storms surges” below) we extracted mean elevation, density of water bodies, time-integrated flood index, and

annual inundation index; percent composition of each land cover class, potential nesting habitat, water body and riverine area; and total length per unit area of pond shoreline and riverine/tidal slough flow lines using Geospatial Modeling Environment (Beyer 2010). Within each surveyed plot or grid cell we also divided the total length of pond shoreline by the total 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 (see Table 1 for variable definitions).

Short-term impacts of storm surges

Annual changes in nest densities. – Nest densities (nests/km^2) within the study area were compared between years following large-magnitude storms verses other years without large storms using a linear regression, with the storm effect included as a categorical variable (i.e., years following a large-magnitude storm coded as 1 and without a large storm coded as 0). We restricted our analyses to surveys conducted from 2000–2013 to reduce the impacts of waterfowl population increases observed since the 1980s; however, as some species still experienced population increases in recent years, we also included year as a continuous variable to remove any potential confounding effects. During this time, three storms of large magnitude (i.e., 50-year return period) occurred (i.e., 16-23 October 2004, 18-25 September 2005, and 7-12 November 2011; Terenzi et al. 2014). However, it should be noted that smaller magnitude storms occurred within this time period as well, and more than one storm may have occurred within the same year; however, the three storms listed above were the only major storms that occurred within this time period (Terenzi et al. 2014).

Nest density models. –Nest densities (nests/km^2) for each species of geese and eider were modeled in relation to the time-integrated flood index from the modeled storm that occurred the previous fall, as well as time-static environmental variables (Table 1). Prior to analyses, we restricted our data to only years following modeled storms (i.e., 2006, 2007, 2010, and 2012). Thus, we determined the impact of fall storms on waterbirds the following spring/summer when they returned to nesting areas to breed and raise their young. Additionally, we removed seven plots (out of 297 plots sampled in 2006, 2007, 2010, and 2012) in which the time-integrated flood index was not estimated for >10% of the plot (e.g., plots overlapping large rivers or coastline within the typical tidal range). 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 four variables (percent upper coastal brackish meadow, percent sandbar/mudflat, percent area of riverine, and length of pond shoreline; see Table 1).

To model these short-term effects of storms we used random forests, an ensemble regression tree approach (Breiman 2001). In standard regression tree, 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. In order to achieve greater predictive accuracy, random forests combines predictions from many (e.g., 1,000 in this study) regression trees (Breiman 2001). Each regression tree is grown from a bootstrap sample of the data, with only a small number (e.g., 1/3 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. As 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. Partial dependence plots are used 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. All models were run using the "randomForest" package (Liaw and Wiener 2002) in program R (R Development Core Team 2011).

Long-term impacts of storm surges

Nest densities (nests/km^2) for each species of geese and eider were modeled in relation to the annual inundation index, as well as other time-static environmental variables (Table 1). Prior to analyses, we combined surveyed plots into 4 km^2 regular grid cells to reduce spatial redundancy and annual variability in nest densities. This spatial scale allowed us to combine several plots per regular grid cell while still maintaining a suitable sample size for all analyses. In order to reduce the survey data to regular grid cells, we first placed 2 x 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 per grid cell. With more than one plot per grid cell, we treated multiple surveys as replicates and calculated the average nest density per grid cell by dividing the total number of nests found for each species during all surveys within a grid cell by the total amount of area surveyed. Additionally, 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), as 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 four variables (percent upland, percent coastal dwarf shrub/pond mosaic, percent potential nesting habitat, and percent area of water bodies; see Table 1).

To model these long-term effects of storms we used random forests (similar to above) and 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.

RESULTS

Short-term impacts

Nest searches were conducted at 2,318 plots during 29 years between 1985 and 2013 (50–119 plots surveyed per year). We found that mean nest densities varied both spatially (i.e., high variability within years) and annually (i.e., high variability among years) from 2000–2013, but appeared to be unrelated to storm magnitude the prior fall for most species (Table 2). However, Spectacled Eider exhibited greater nest densities in years following large storms as

compared to years without large storms, a trend that remained apparent when accounting for increasing population densities through time (β = 1.299; Table 2), but opposite than expected if storms were having a direct negative impact. However, annual variability in nest densities may also be driven by numerous other factors not investigated in this study (e.g., predation rates, population size, weather, etc.).

The percentage of total variance in nest densities explained by the random forests models when the data were limited to only years following modeled storms (i.e., 2006, 2007, 2010, and 2012) varied among species, ranging from 19–44% (Greater White-fronted Goose = 43.5%, Emperor Goose = 27.5%, Cackling Goose = 25.0%, Spectacled Eider = 20.8%, Common Eider = 19.3%, and Brant = 18.8%). Variable importance plots suggested that the time-integrated flood index from modeled storms occurring during the previous fall did not improve estimates of spatial variation in geese and eider nest densities above that already explained by habitat (Figure 3). Other environmental variables such as percent lower coastal salt marsh, distance to coast, and percent potential habitat appeared to be more influential on nest densities (Figure 3). For example, distance to coast was a better explanatory variable for all species than the time-integrated flood index, with all species having greater nest densities closer to the coast, with the exception of Greater White-fronted Geese that showed greater nest densities further from the coast (Figures 4–9).

Long-term impacts

The percentage of total variance explained by the random forests models (including data from 1985–2013) varied among species, ranging from 14–68% (Greater White-fronted Goose = 68.3%, Cackling Goose = 53.7%, Spectacled Eider = 39.8%, Emperor Goose = 39.0%, Black

Brant = 17.8%, and Common Eider = 14.0%). Variable importance plots suggested that the annual inundation index did not improve estimates of spatial variation above that already explained by habitat in nest densities of geese and eiders (Figure 10). Other environmental variables such as year, distance to coast, and percent lower costal salt marsh appeared to be more influential on nest densities (Figure 10). For example, distance to coast was a better explanatory variable for all species than the annual inundation index, with all species having greater nest densities closer to the coast, with the exception of Greater White-fronted Geese that showed greater nest densities further from the coast (Figures 11–16). Among species, the annual inundation index was most important for Black Brant and Common Eider, ranked as the 2nd and 3rd most important variable explaining variation in nest densities, respectively (Figure 10). Both of these species exhibited a positive association between nest densities and the annual inundation index (Figures 13 and 16). However, these results are likely confounded by the fact that these two species nested within a narrow band close to the coast (see Figures 13 and 16), the area that is also most influenced by the annual inundation index (Figure 17). In fact, distance to coast explained much more of the variation than the annual inundation index did for these species (Figure 10).

DISCUSSION

This study failed to reveal any apparent short-term or long-term impacts of storms on waterbird nest densities. Rather, it appears individuals are selecting nest sites based on other habitat characteristics. A failure to find any short-term impacts of storms may be due to the high site fidelity exhibited by many of these species, with individuals returning to the same nesting areas despite annual changes due to fall flooding events. Instead, structural changes caused by

flooding (e.g., sediment deposition, scouring, island displacement) may result in individuals making small scale adjustments within previous territories, shifts that may not be at a large enough magnitude to be seen at the scale of this study (e.g., within 4km^2 grid cells). Alternatively, the modeled storms may not have been of large enough magnitude or occurred in such frequency to result in structural changes that would result in large scale distributional shifts by waterbirds. Therefore, smaller scale studies (i.e., based on smaller grid cells) may be needed to determine the role annual storm surges have on nesting habitat and habitat selection patterns of waterbirds in this region. Furthermore, waterbirds within this region have evolved with regular flooding, preferring to nest within habitats that rely on periodic flooding for long-term persistence. For example, waterbird nest densities are greatest within coastal fringe habitat types (Olsen 1951, Holmes and Black 1973, Mickelson 1975, Eisenhauer and Kirkpatrick 1977, Gill and Handel 1981, King and Dau 1981, Eldridge 2003, Platte and Stehn 2009) characterized by flat topography, where sedge/graminoid meadows are interspersed with numerous waterbodies (Tande and Jennings 1986, Kincheloe and Stehn 1991, Jorgenson 2000). Such areas have been shaped and are currently maintained by frequent flooding. Therefore, waterbird species nesting within these areas are likely adapted to annual or periodic flooding and therefore may not dramatically alter nest densities based on short-term flooding impacts that occur the prior fall. Conversely, these species appear to be selecting nest sites based on other, more persistent, habitat characteristics rather than recent inundation exposure. However, it should be noted that we only investigated the effects of flooding on nest densities (as these data were historically available for the study region) and not on other potentially important indices such as clutch size, nest success, and fledgling success (the latter two which have not been historically collected

across the entire study region). Thus, the effect of flooding on other demographic parameters remains unknown.

Because these species select habitats that are maintained by frequent flooding (e.g., low-lying areas close to the coast), it seems surprising that we were unable to detect any long-term impacts of storms on waterbird nest densities. However, despite the link between inundation rates and habitat type, the annual inundation index was not highly correlated with habitat features known to be influenced by (e.g., percentage of lower coastal salt marsh) or which influence the flooding rate (e.g., distance to coast, elevation), as measured within our study plots. Thus, the index of annual inundation may not be an accurate measure of what is driving long-term habitat patterns in this region. For example, the annual inundation index was based on only seven modeled storms from 1992–2011. As each storm has its own trajectory resulting in storm-specific inundation rates, more storms may be needed to accurately depict long-term impacts of storm surges to habitats within this region. Additionally, by excluding earlier storms, long-term impacts may be underestimated and the time scale may be incongruent with nest density data obtained prior to the 1990s. Impacts from smaller, but more frequent storms were also not taken into account, as storms with < 5-year return periods were excluded from the calculation of the annual inundation index, yet flooding from annual storms also likely shape habitat features.

Despite our inability to detect a direct association between the annual inundation index and waterbird nest densities, it is clear that changes in flooding regimes have the potential to dramatically impact nesting waterbirds within this region. For example, most species of geese and eiders selected low-lying habitats close to the coast that are directly impacted by flooding frequency and intensity. Thus, changes in these flooding regimes, as that predicted under future sea-level rise scenarios (see Figure 17), have the potential to dramatically alter waterbird nesting

habitat in this region. Thus, focusing research efforts on predicting long-term changes to waterbird habitats as a result of changes in flooding regimes may be more informative for developing climate change adaptation strategies and improving management of these species.

Our ability to infer the relationship between nest densities and short-term and long-term impacts of storms was limited by the sampling design, as well as the availability and scale of the avian data (e.g., nest density) and the inundation projections (i.e., only four modeled storms for the calculation of the time-integrated index and seven storms for the annual inundation index). For example, the nest density surveys were designed for a much different purpose (i.e., estimate population trends) than evaluating short-term and long-term effects of storms on waterbirds. The survey design in which plots were surveyed once then specifically not revisited the next five years precluded more focused assessments comparing spatial distribution of nest densities immediately before and after specific storms. If the objective of estimating direct impacts of storms is deemed a high priority information need, consideration should be given to modifying sampling design so that adequate spatial and temporal data are being collected to explicitly assess the impacts of storm surges. For example, resampling plots in consecutive years, before and after storm events would greatly enhance our ability to detect short-term impacts of storm surges on waterbird distributions.

Additionally, fine scale habitat data collected annually at the nest level would help elucidate small-scale habitat changes that birds may be using when making settlement decisions. However, we are currently limited by the scale of the storm surge models (e.g., 100 m resolution). While this scale would be adequate to detect large-scale changes, any small-scale shifts in relation to storm events would remain undetected. As many of these species are highly site faithful, individuals are likely making small scale adjustments in response to structural

changes caused by flooding; therefore, the scale of the study should be fine enough to capture these small shifts. However, due to the high site fidelity exhibited by these species, nest density may not be the appropriate metric to determine impacts of storm surges. Rather, other demographic metrics such as clutch size, nest success, or fledgling success may provide more useful information concerning impacts of storm surges on nesting waterbirds in this region. However, collection of these data, even on a small scale, is costly and requires a great deal of time and effort, especially within remote locations. Thus, future efforts should focus on implementing a sampling design specifically for the purpose of evaluating storm effects on waterbird demographics. By doing this, we will then be able to make more conclusive statements as to the impact of storms on waterbird nest densities, determine if the apparent lack of an effect is real or simply reflects limitations of the sampling design, and provide useful information that can directly feed into planning efforts to minimize the risk of future climate change scenarios to waterbirds in this region.

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Table 1. Explanatory variables used to predict nest densities for geese and eider species breeding on the Yukon-Kuskokwim Delta of Alaska, USA, 1985–2013. Habitat descriptions taken directly from Ducks Unlimited (2010).

Variable	Abbreviation	Model[1]	Description/composition
Time-integrated flood index	Flood	Short-term	Integral of water depth over time (meter days)
Annual inundation index	AII	Long-term	Estimated annual inundation depth and duration (meter days/year)
Year	Year	Long-term	Mean year of surveyed plots
Mean elevation	Elev	Both	Mean elevation (m)
Percent coastal dwarf shrub	Cds	Both	25-100% shrub cover, shrubs <0.25 m most common, periodic tidal flooding. Common dwarf shrub species include *Empetrum nigrum*, *Salix ovalifolia*, and *Salix fuscescens*. Dominant graminoid is *Carex rariflora*, usually with a component of *Eriophorum* spp. Other graminoids include *Calamagrostis descampsioides*, *Deschampsia cespitosa*, and *Elymus arenarius*. Common forbs include *Sedum rosea*, *Chrysanthemum arcticum*, *Rubus chamaemorus*, *Ligusticum scothicum*, *Petasites* spp, and *Lathyrus* spp.
Percent coastal dwarf shrub/pond mosaic	Pm	Short-term	Same composition as coastal dwarf shrub, but in a mosaic with stable ponds
Percent lower coastal salt marsh	Lcsm	Both	≥40% herbaceous, <25% shrub cover, <50% of the herbaceous cover is bryoid, tidally flooded monthly or more frequently. Dominated by *Carex ramenskii* and/or *C. subspathacea*. *C. lynbyei* is found inland, on less saline sites along tidal sloughs
Percent upper coastal brackish meadow	Ucbm	Long-term	≥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 *Carex rariflora* most common. Other species include *Calamagrostis deschampsioides*, *Chrysanthemum arcticum*, *Salix ovalifolia*, *Eriophorum angustifolium*, and *Carex aquatilis*
Percent coastal graminoid	Cg	Both	≥40% herbaceous, <25% shrub cover, <50% bryoid, periodically tidally flooded, grass dominated. *Leymus mollis* is most common, but *Poa emimens*, *Calamagrostis deschampsoides*, *Potentilla egedii*, *Lathyrus* spp., and other forbs may be present
Percent sandbar/mudflat	Mud	Long-term	Percent sandbar or mudflat (non-vegetated soil)
Percent upland	Upld	Short-term	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/gravel, and snow/ice
Percent potential nesting habitat	Phbt	Short-term	Percent vegetated area that could be used for nest placement (areas not classified as water, sandbar/mudflat, or rock/gravel)
Mean density of water bodies	Dwtr	Both	Mean number of water bodies per km^2

Percent area of water bodies	Wtr	Short-term	Percentage of plot classified as water body
Percent area of riverine	Rvr	Long-term	Percentage of plot classified as riverine
Length of pond shoreline	Pshr	Long-term	Total length of pond shoreline divided by plot area (km/km^2)
Shoreline complexity	Cplx	Both	Total length of pond shoreline divided by the total area classified as water body within the plot (km/km^2)
Length of riverine and tidal sloughs	Flow	Both	Total length of riverine and tidal slough flow lines divided by plot area (km/km^2)
Distance to coast	Dcst	Both	Distance to coast (km)
Distance to inland mudflat	Dmdfl	Both	Distance to inland mudflat (km)

[1] Indicates if variable was included in models investigating short-term, long-term, or both short-term and long-term impacts of storm surges.

Table 2. Mean nest densities and linear regression results (i.e., parameter estimates, standard errors, and *P*-values for the effects of year and storm, as well as *F*- and *P*-values from the overall model) comparing nest densities of geese and eider species in years following large storms and without large storms on the Yukon-Kuskokwim Delta of Alaska, USA, 2000–2013.

	Mean (SE) nest density (nests/km^2)		Storm parameter[1]			Year parameter[2]			Overall model	
Species	Large storm	No large storms	β	SE	*P*	β	SE	*P*	$F_{(2,1090)}$	*P*
Cackling Goose	57.2 (3.1)	60.0 (1.8)	-5.778	3.776	0.126	1.820	0.391	<0.001	11.11	<0.001
Emperor Goose	13.9 (0.7)	13.1 (0.4)	0.211	0.861	0.806	0.348	0.089	<0.001	8.07	<0.001
Black Brant	9.9 (1.8)	14.2 (1.6)	-4.071	3.238	0.209	-0.169	0.335	0.614	1.06	0.347
Greater White-fronted Goose	26.6 (1.3)	24.7 (0.6)	-0.608	1.376	0.659	1.470	0.142	<0.001	54.19	<0.001
Spectacled Eider	5.1 (0.5)	3.5 (0.2)	1.299	0.451	0.004	0.191	0.047	<0.001	15.03	<0.001
Common Eider	1.8 (0.4)	1.4 (0.2)	0.351	0.385	0.363	0.039	0.040	0.327	1.084	0.339

[1]Categorical effect of storm with years without large storms the prior fall coded as 0, and with large storms coded as 1.
[2]Continuous effect of year to account for increasing population densities over time.

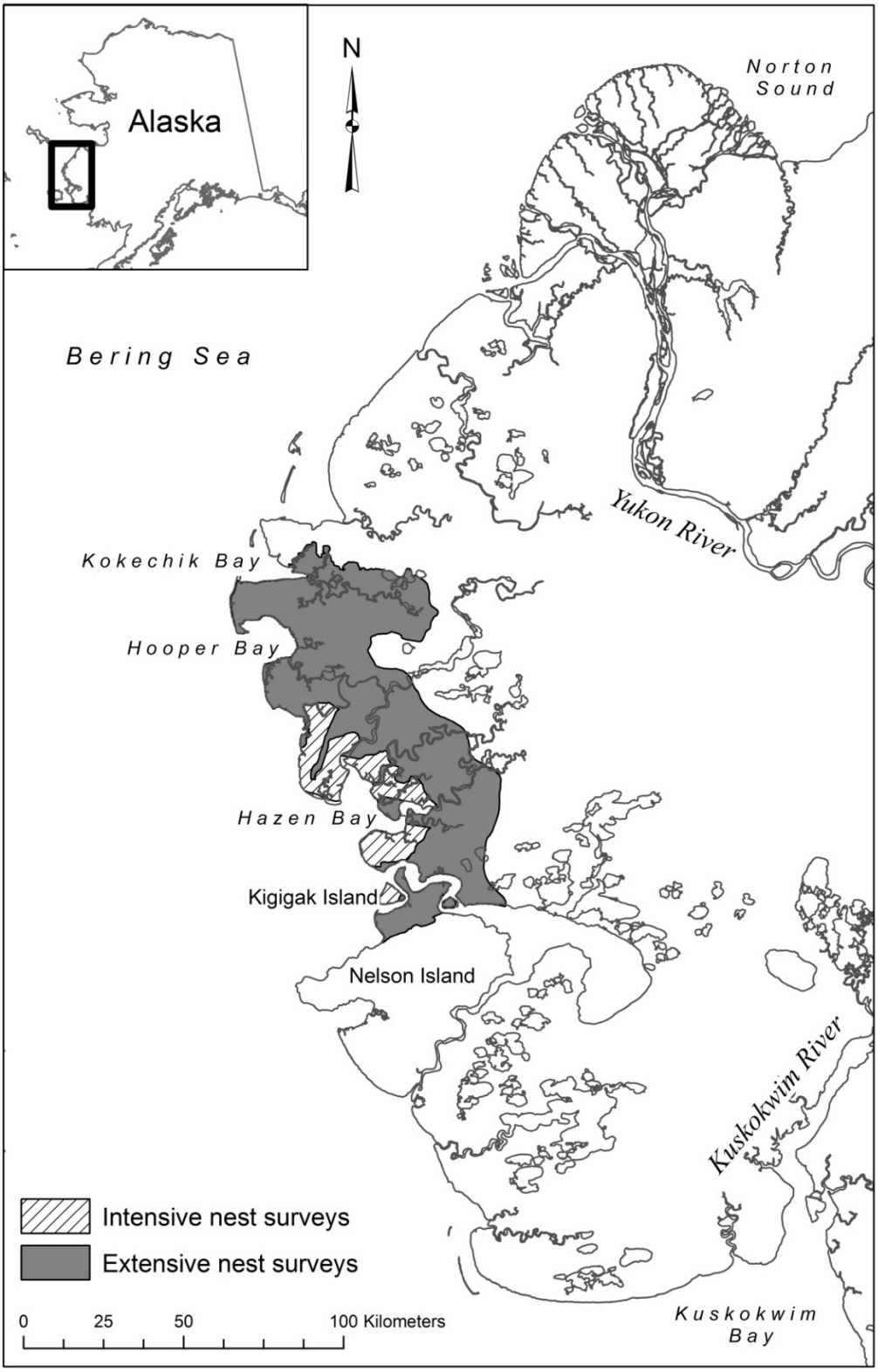

Figure 1. Location of study area, including areas of intensive and extensive waterbird nest surveys on the Yukon-Kuskokwim Delta of Alaska, USA, 1985–2013.

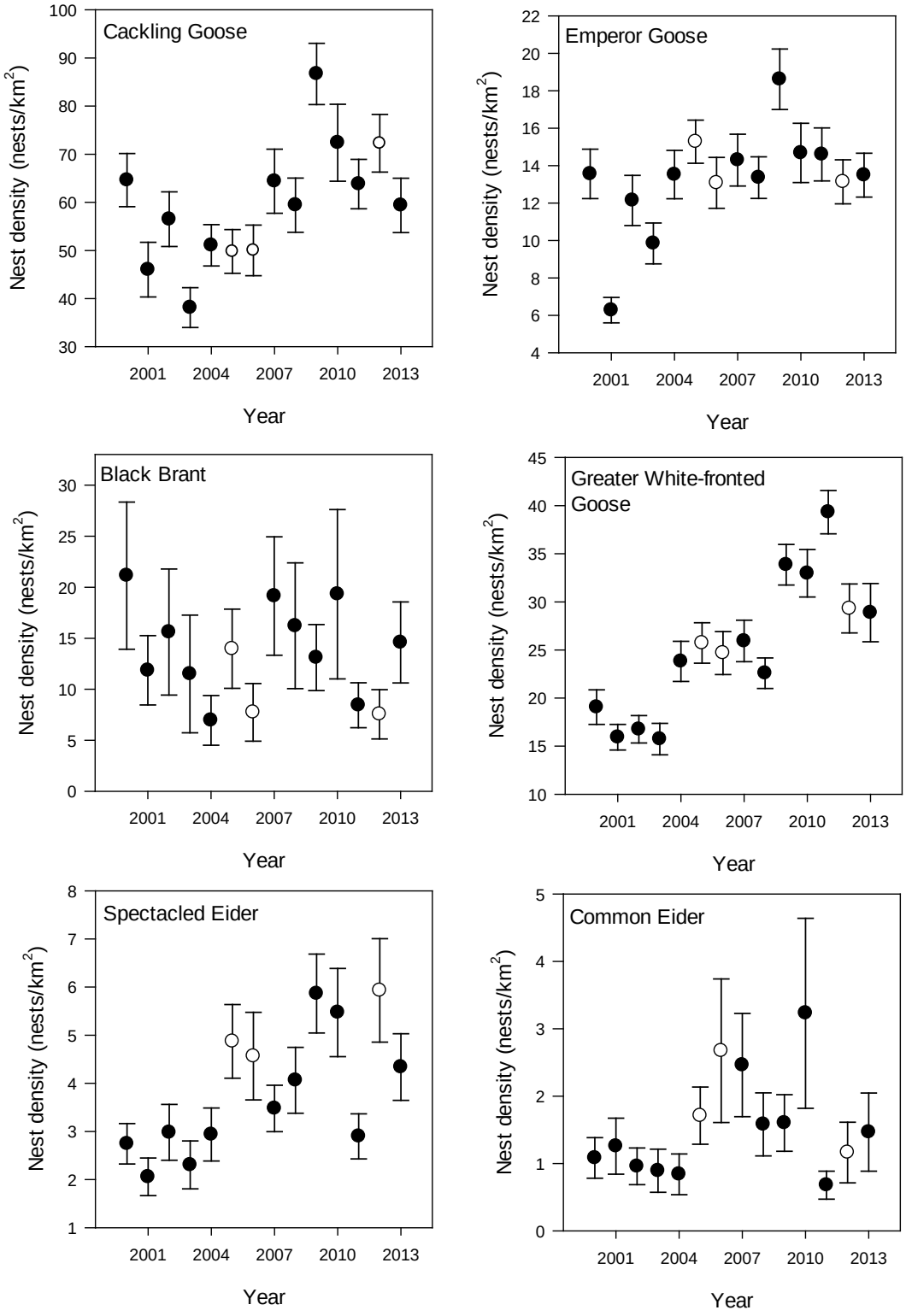

Figure 2. Annual nest densities (means ± SE) of geese and eider species on the Yukon-Kuskokwim Delta of Alaska, USA, 2000–2013. Years with open circles indicate breeding seasons following the largest (i.e., 50 year return period) storms recorded during this time period.

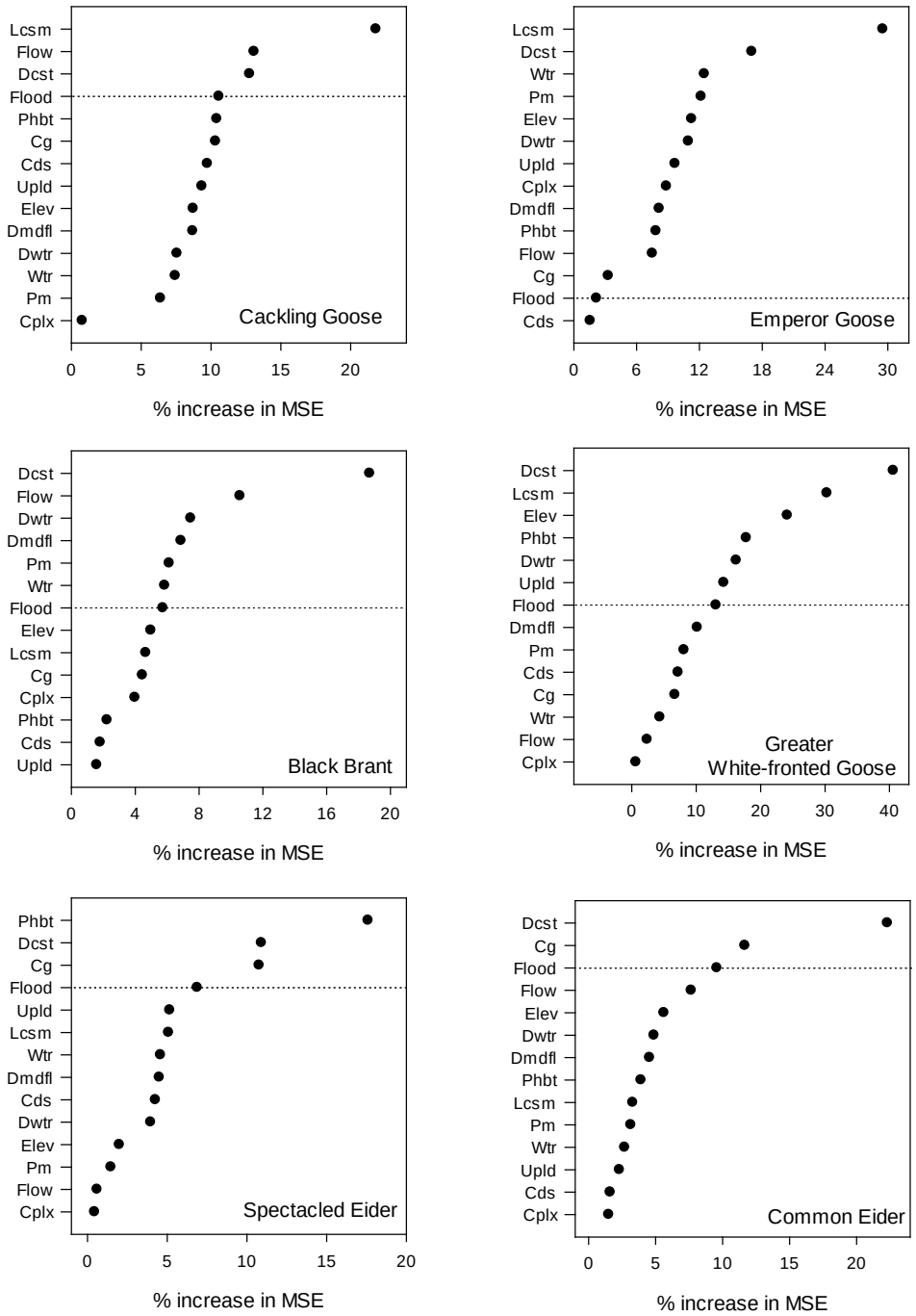

Figure 3. Variable importance plots from random forests models predicting geese and eider nest densities on the Yukon-Kuskokwim Delta of Alaska, USA in relation to short-term impacts of storm surges. Data restricted to 2006, 2007, 2010, and 2012 to correspond with years following modeled storm surges. Variable importance values indicate the percent increase in prediction error (MSE) for the out-of-bag observations after randomly permuting the values of the explanatory variable. Variables with higher values of % increase in MSE indicate greater importance in predicting geese and eider nest densities. Dashed lines mark the location of the variable 'Flood'. See Table 1 for explanatory variable abbreviations.

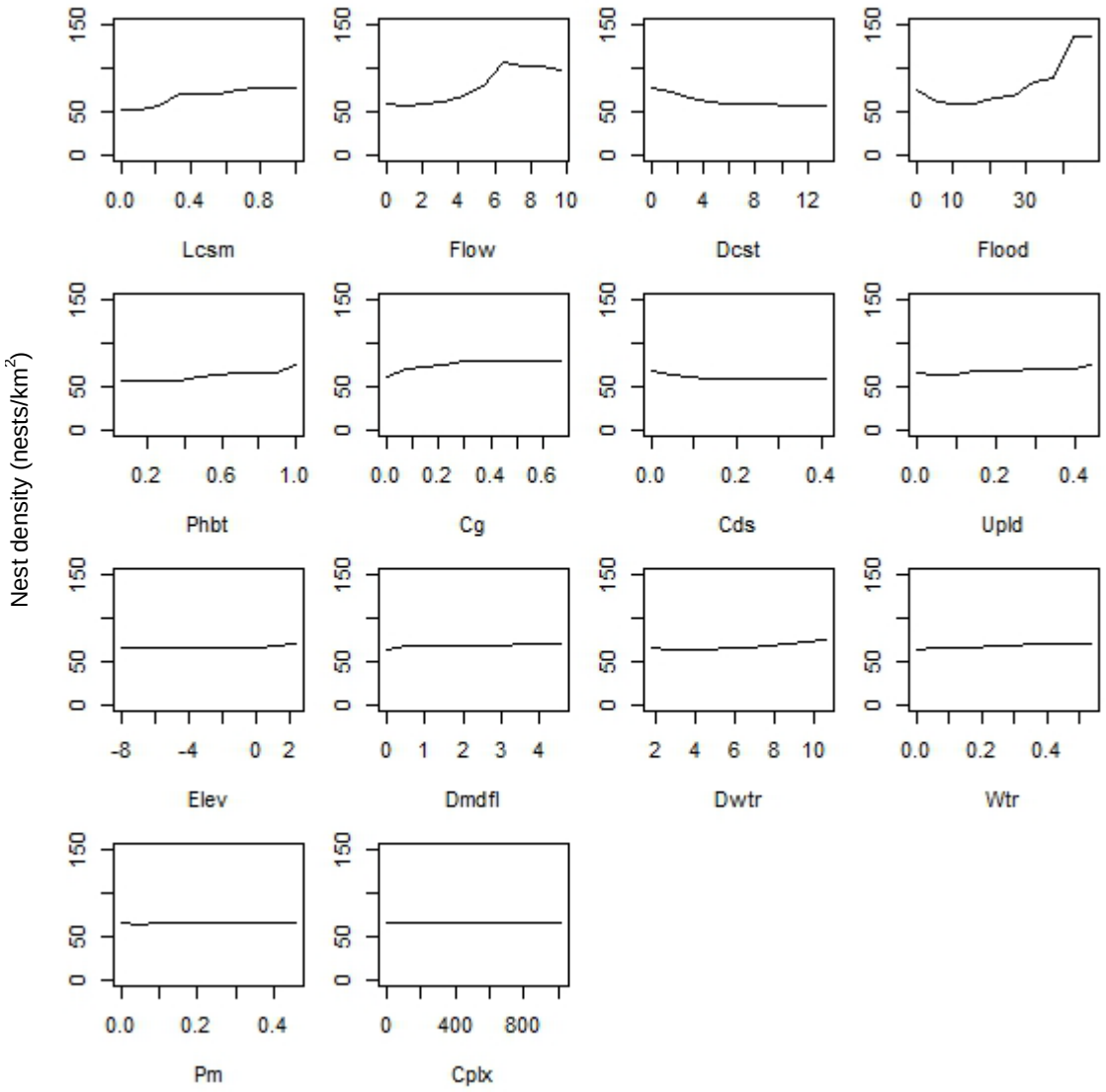

Figure 4. Partial dependence plots from random forests models predicting Cackling Goose nest density on the Yukon-Kuskokwim Delta of Alaska, USA in relation to short-term impacts of storm surges. Data restricted to 2006, 2007, 2010, and 2012 to correspond with years following modeled storm surges. Partial 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 (see Figure 3). See Table 1 for explanatory variable abbreviations and units.

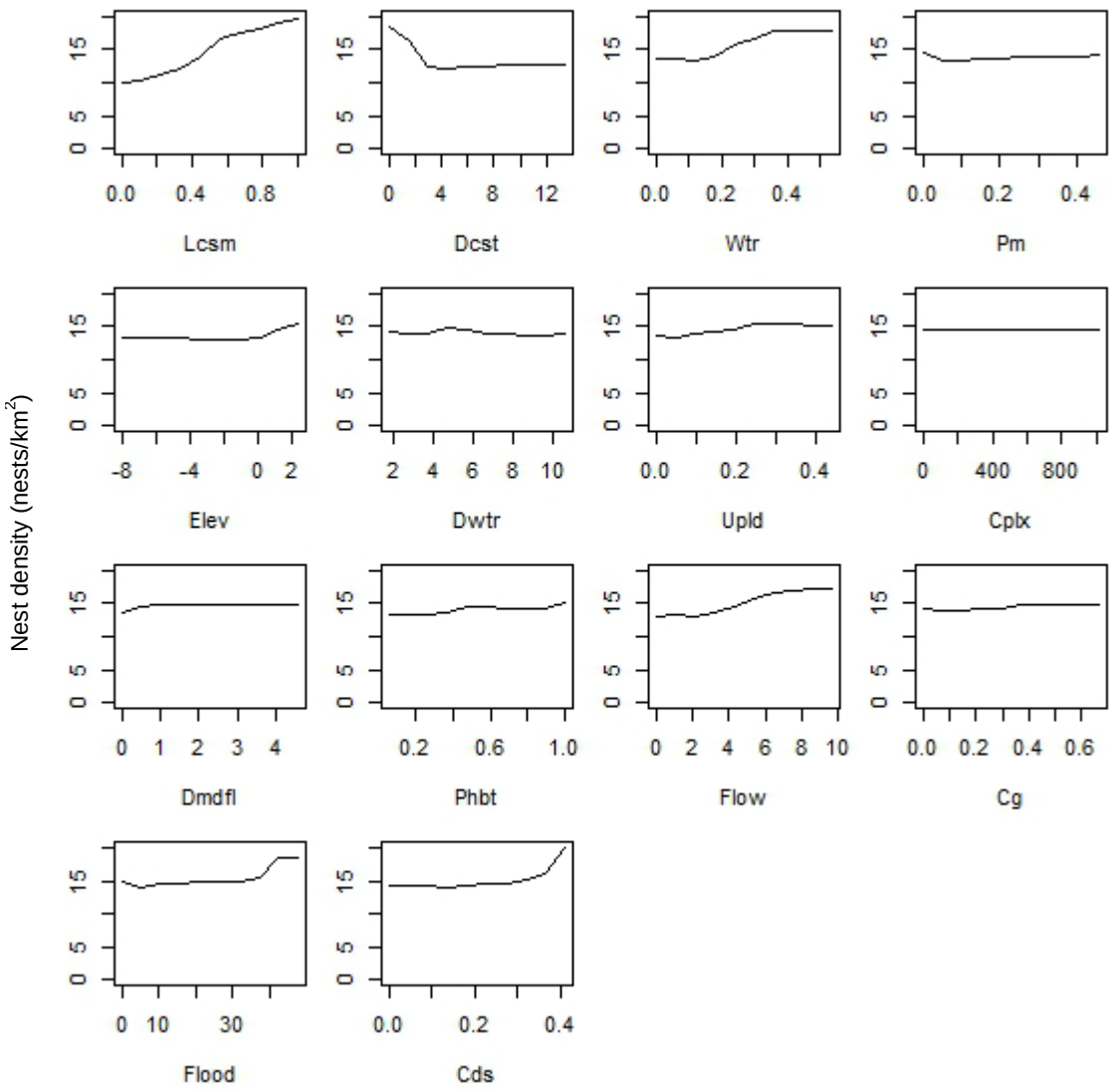

Figure 5. Partial dependence plots from random forests models predicting Emperor Goose nest density on the Yukon-Kuskokwim Delta of Alaska, USA in relation to short-term impacts of storm surges. Data restricted to 2006, 2007, 2010, and 2012 to correspond with years following modeled storm surges. Partial 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 (see Figure 3). See Table 1 for explanatory variable abbreviations and units.

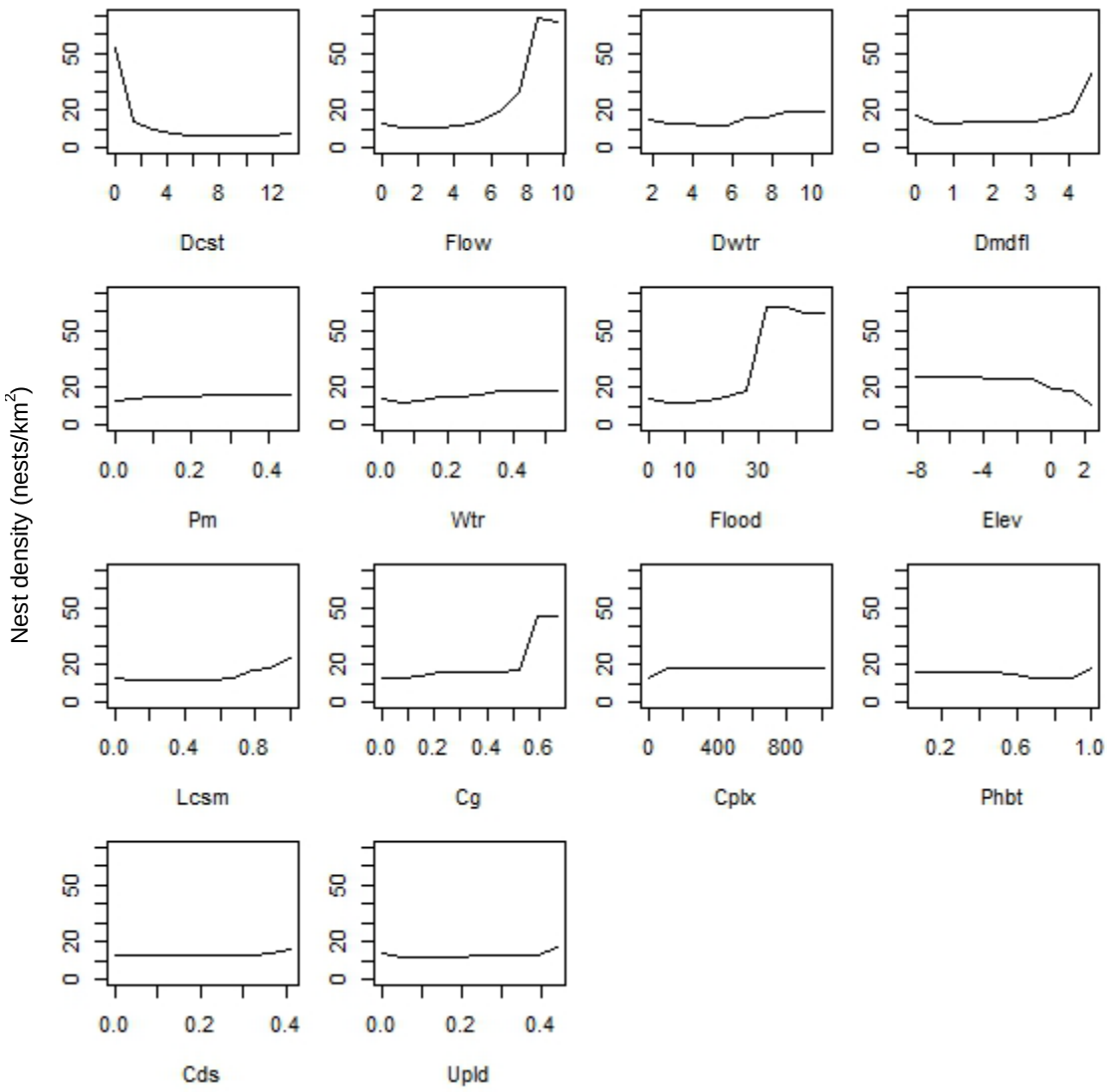

Figure 6. Partial dependence plots from random forests models predicting Black Brant nest density on the Yukon-Kuskokwim Delta of Alaska, USA in relation to short-term impacts of storm surges. Data restricted to 2006, 2007, 2010, and 2012 to correspond with years following modeled storm surges. Partial 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 (see Figure 3). See Table 1 for explanatory variable abbreviations and units.

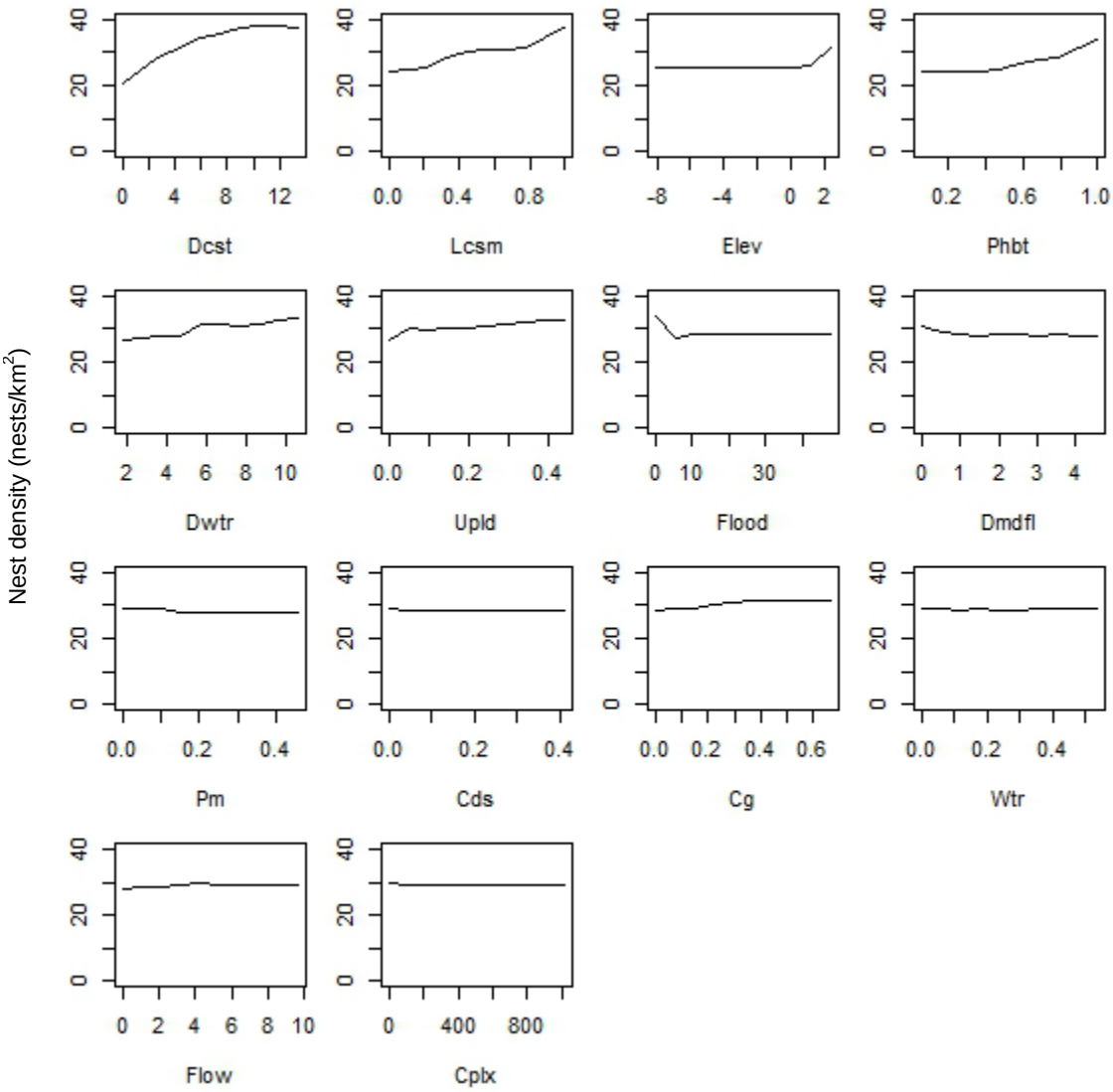

Figure 7. Partial dependence plots from random forests models predicting Greater White-fronted Goose nest density on the Yukon-Kuskokwim Delta of Alaska, USA in relation to short-term impacts of storm surges. Data restricted to 2006, 2007, 2010, and 2012 to correspond with years following modeled storm surges. 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 (see Figure 3). See Table 1 for explanatory variable abbreviations and units.

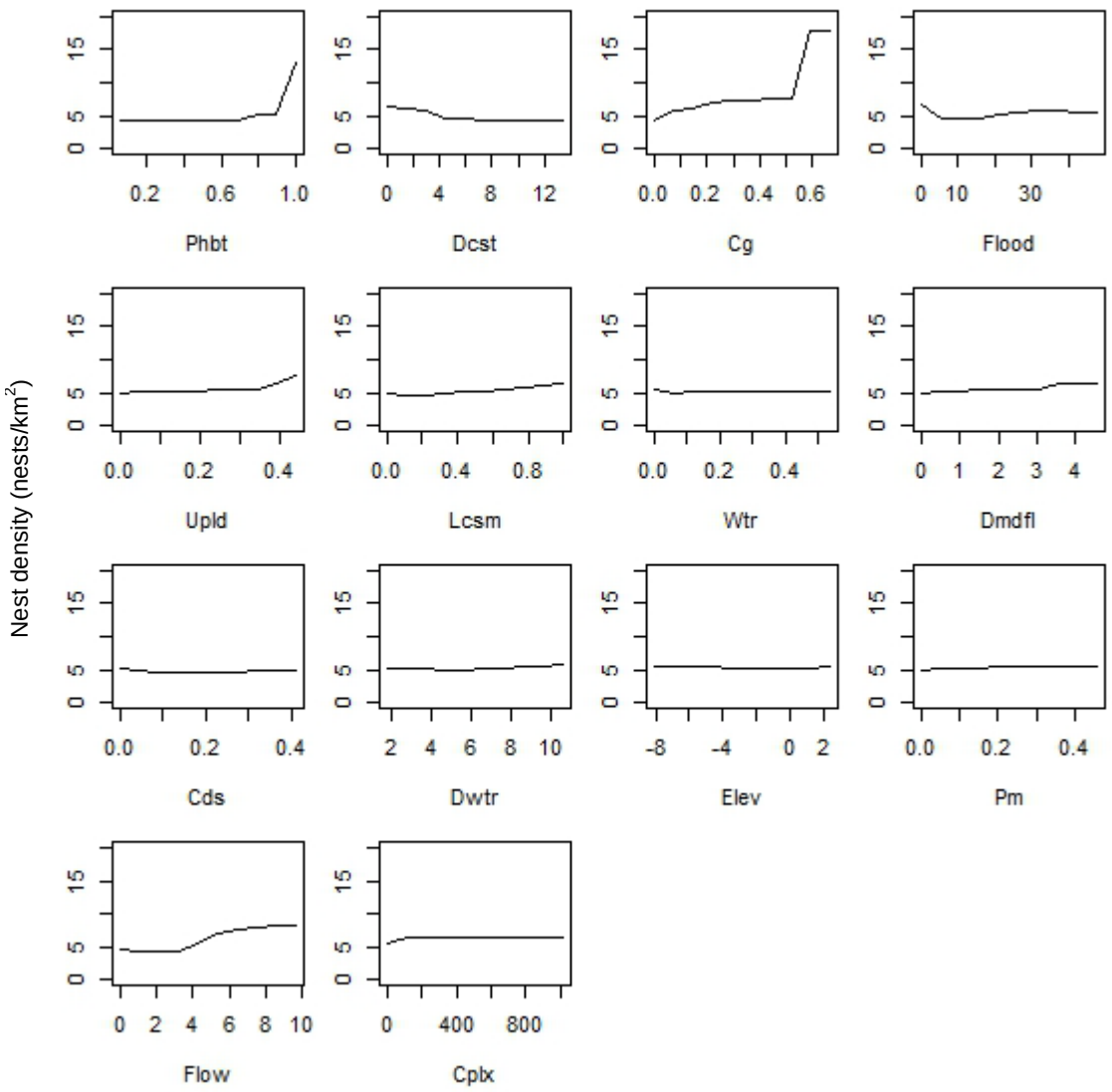

Figure 8. Partial dependence plots from random forests models predicting Spectacled Eider nest density on the Yukon-Kuskokwim Delta of Alaska, USA in relation to short-term impacts of storm surges. Data restricted to 2006, 2007, 2010, and 2012 to correspond with years following modeled storm surges. 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 (see Figure 3). See Table 1 for explanatory variable abbreviations and units.

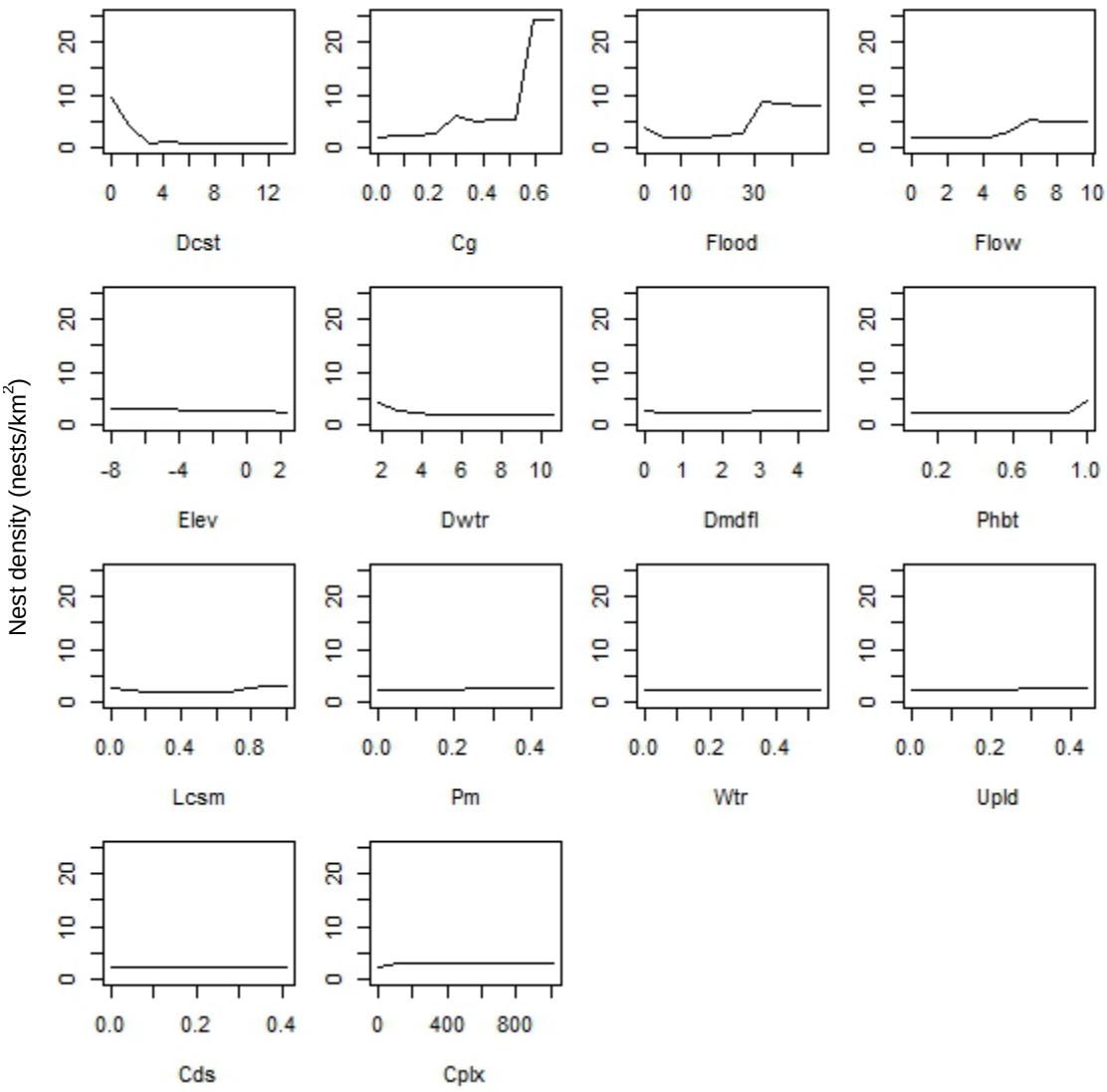

Figure 9. Partial dependence plots from random forests models predicting Common Eider nest density on the Yukon-Kuskokwim Delta of Alaska, USA in relation to short-term impacts of storm surges. Data restricted to 2006, 2007, 2010, and 2012 to correspond with years following modeled storm surges. Partial 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 (see Figure 3). See Table 1 for explanatory variable abbreviations and units.

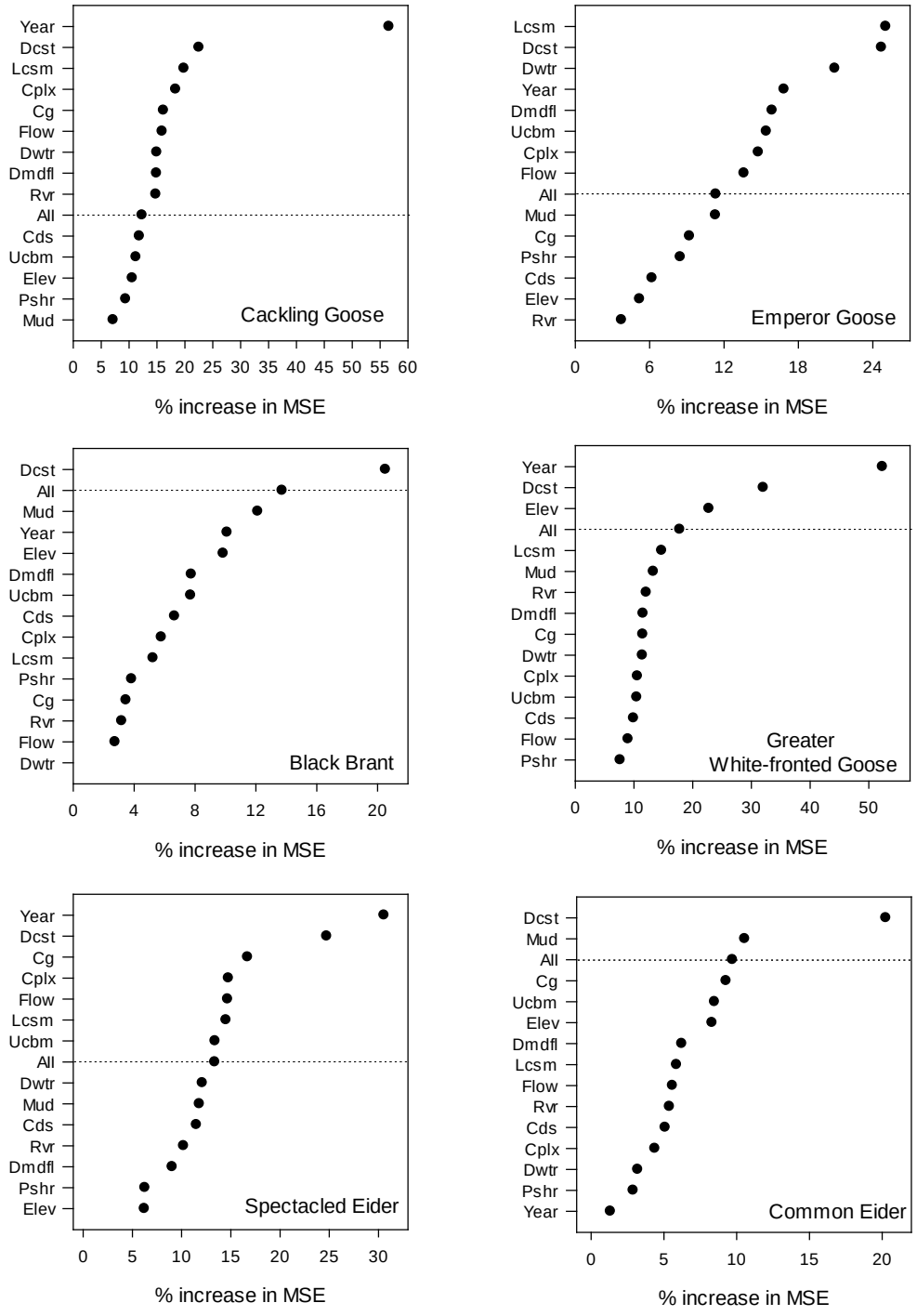

Figure 10. Variable importance plots from random forests models predicting geese and eider nest densities on the Yukon-Kuskokwim Delta of Alaska, USA, 1985–2013, in relation to long-term impacts of storm surges. Variable importance values indicate the percent increase in prediction error (MSE) for the out-of-bag observations after randomly permuting the values of the explanatory variable. Variables with higher values of % increase in MSE indicate greater importance in predicting geese and eider nest densities. Dashed lines mark the location of the variable 'AII'. See Table 1 for explanatory variable abbreviations.

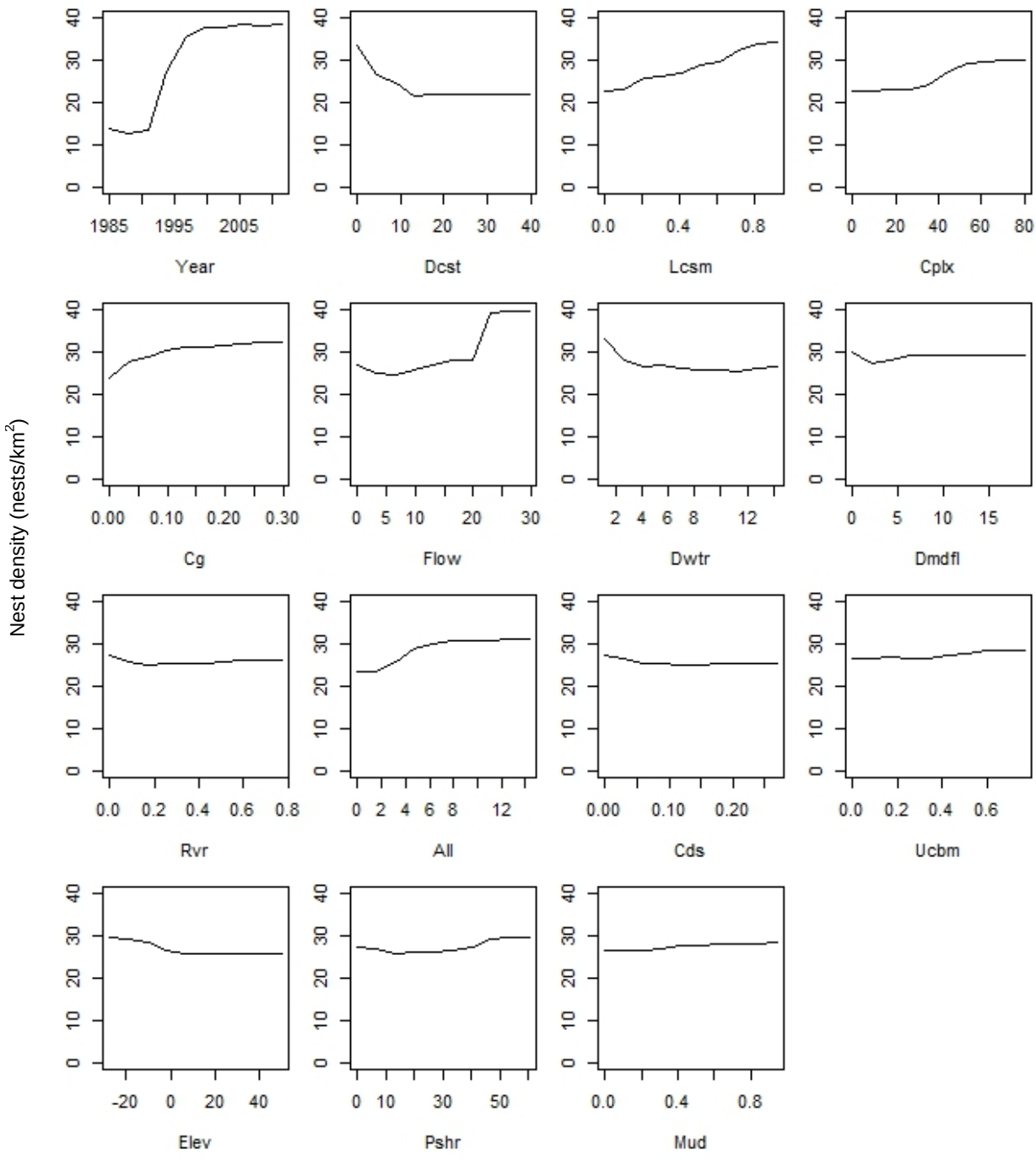

Figure 11. Partial dependence plots from random forests models predicting Cackling Goose nest density on the Yukon-Kuskokwim Delta of Alaska, USA, 1985–2013, in relation to long-term impacts of storm surges. Partial dependence plots represent the relationship between an explanatory variable and nest density while holding all other explanatory variables in the model at their mean. Explanatory variables are listed in order of importance (see Figure 10). See Table 1 for explanatory variable abbreviations and units.

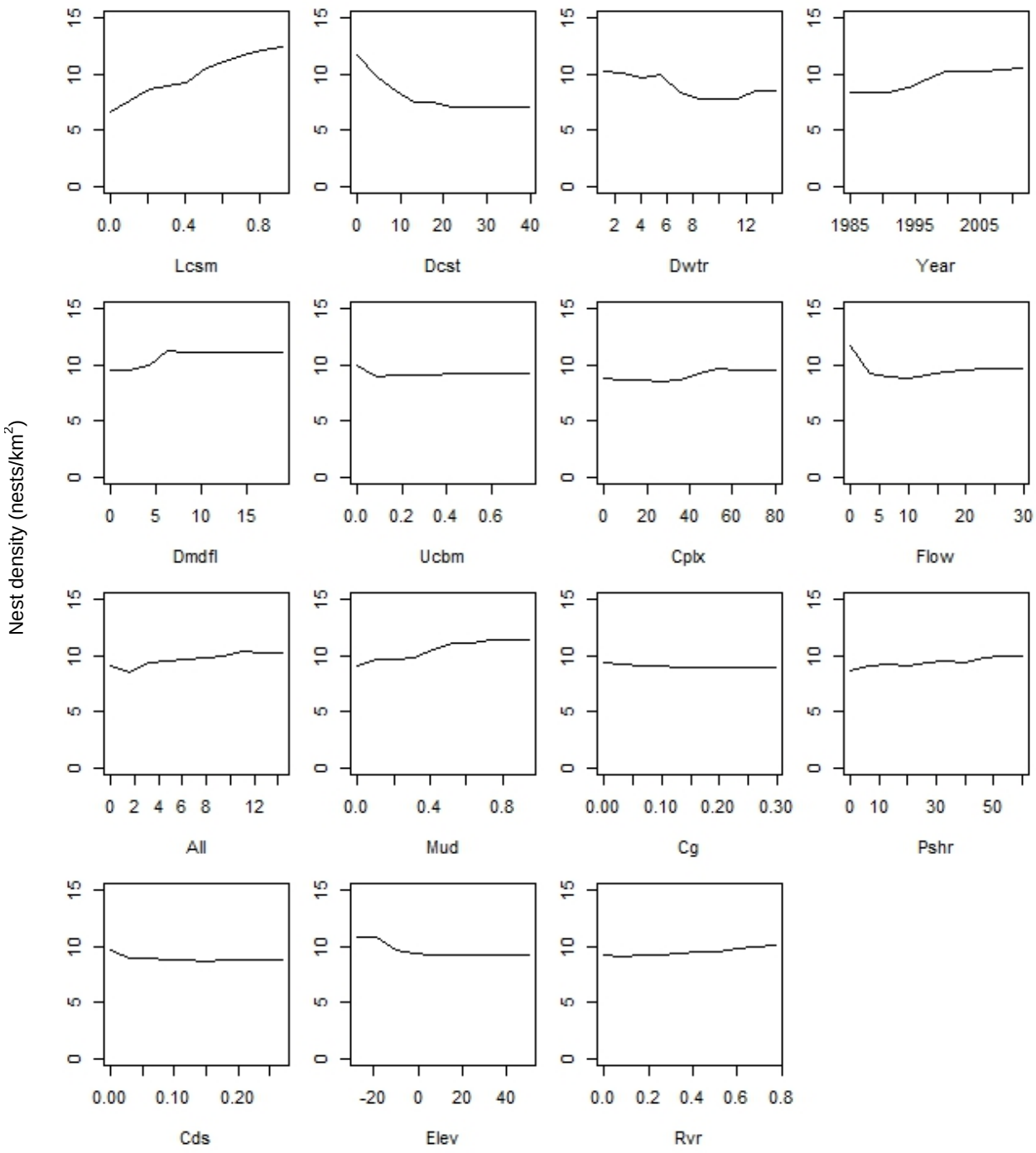

Figure 12. Partial dependence plots from random forests models predicting Emperor Goose nest density on the Yukon-Kuskokwim Delta of Alaska, USA, 1985–2013, in relation to long-term impacts of storm surges. Partial dependence plots represent the relationship between an explanatory variable and nest density while holding all other explanatory variables in the model at their mean. Explanatory variables are listed in order of importance (see Figure 10). See Table 1 for explanatory variable abbreviations and units.

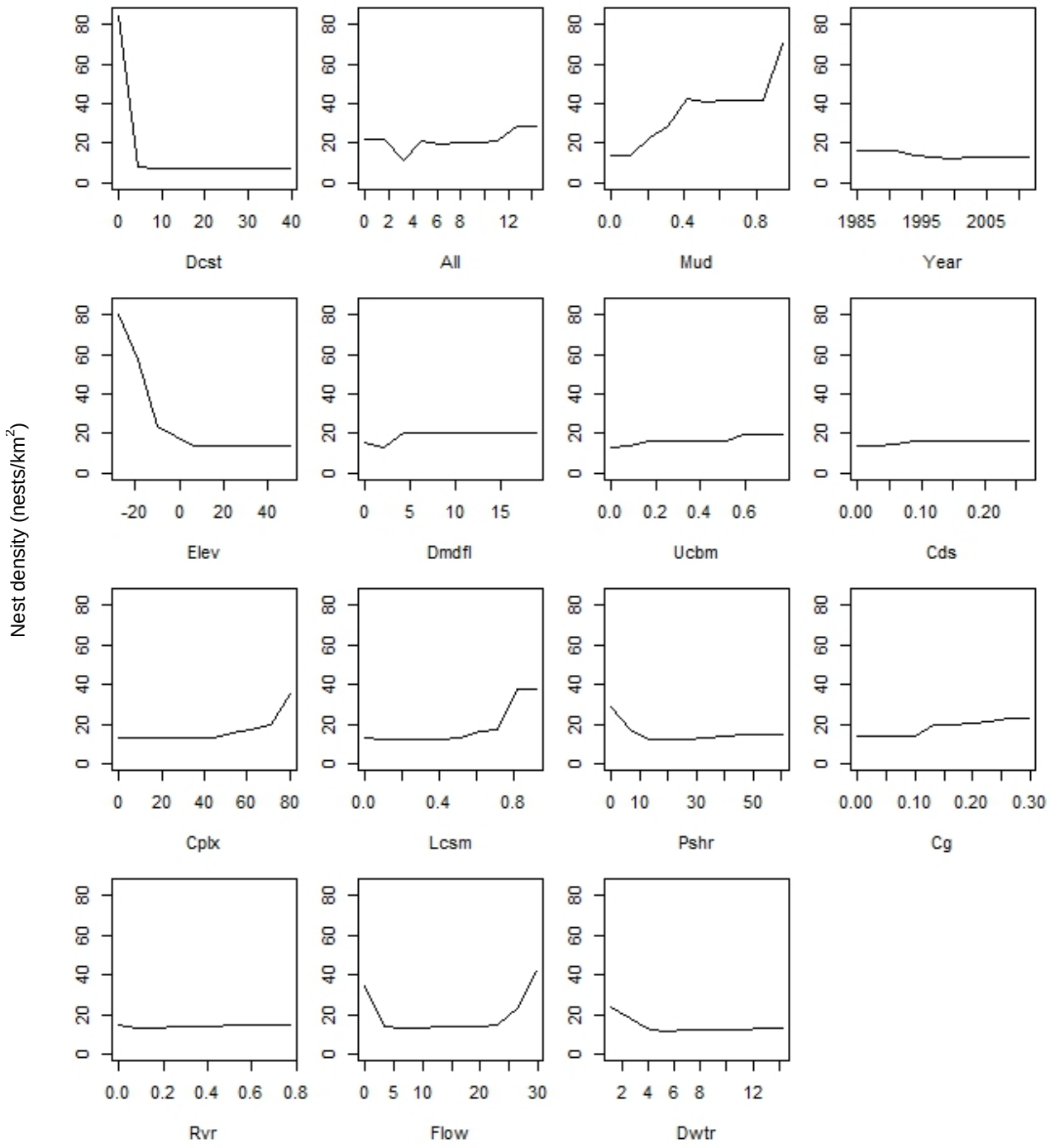

Figure 13. Partial dependence plots from random forests models predicting Black Brant nest density on the Yukon-Kuskokwim Delta of Alaska, USA, 1985–2013, in relation to long-term impacts of storm surges. Partial dependence plots represent the relationship between an explanatory variable and nest density while holding all other explanatory variables in the model at their mean. Explanatory variables are listed in order of importance (see Figure 10). See Table 1 for explanatory variable abbreviations and units.

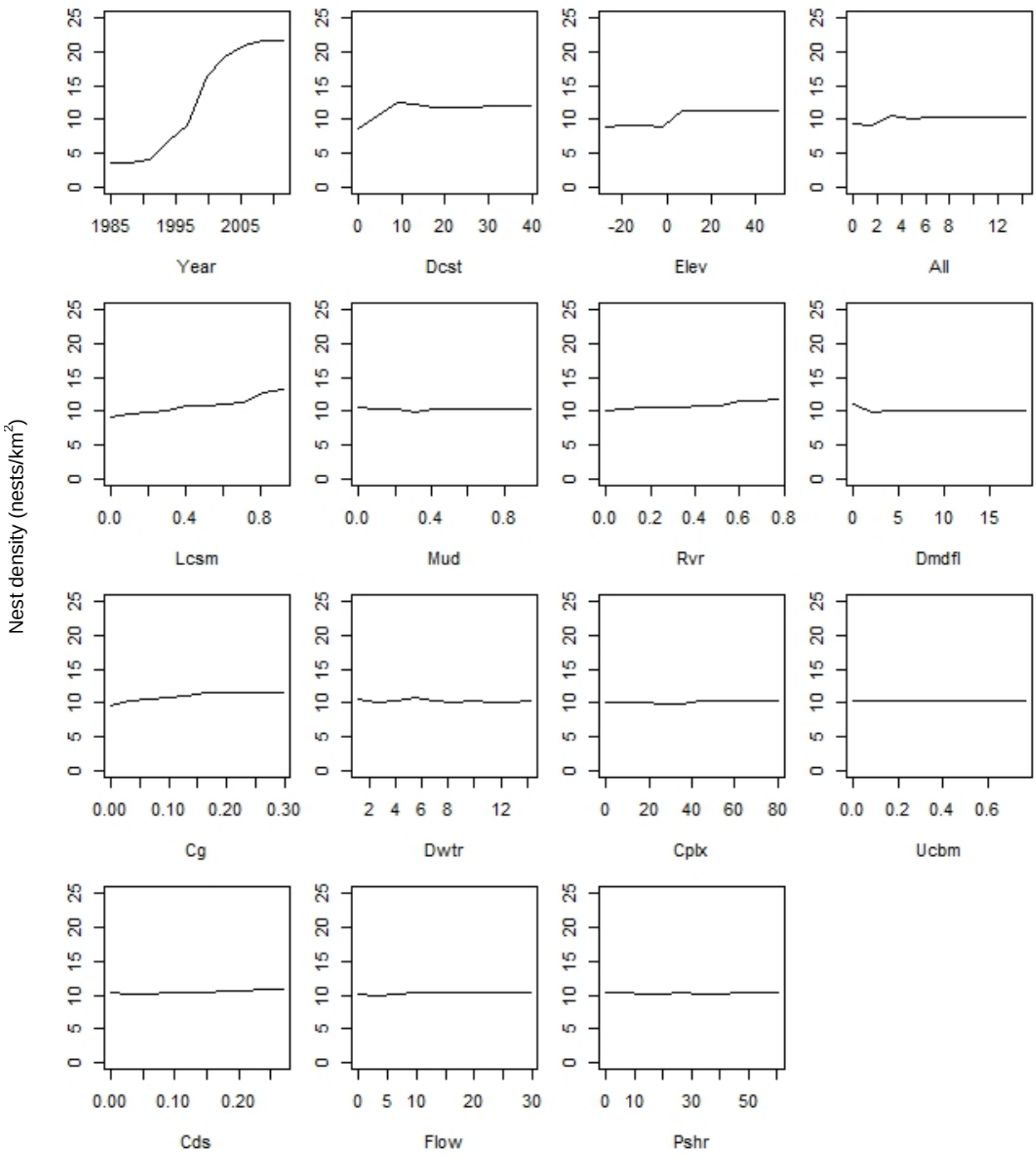

Figure 14. Partial dependence plots from random forests models predicting Greater White-fronted Goose nest density on the Yukon-Kuskokwim Delta of Alaska, USA, 1985–2013, in relation to long-term impacts of storm surges. Partial dependence plots represent the relationship between an explanatory variable and nest density while holding all other explanatory variables in the model at their mean. Explanatory variables are listed in order of importance (see Figure 10). See Table 1 for explanatory variable abbreviations and units.

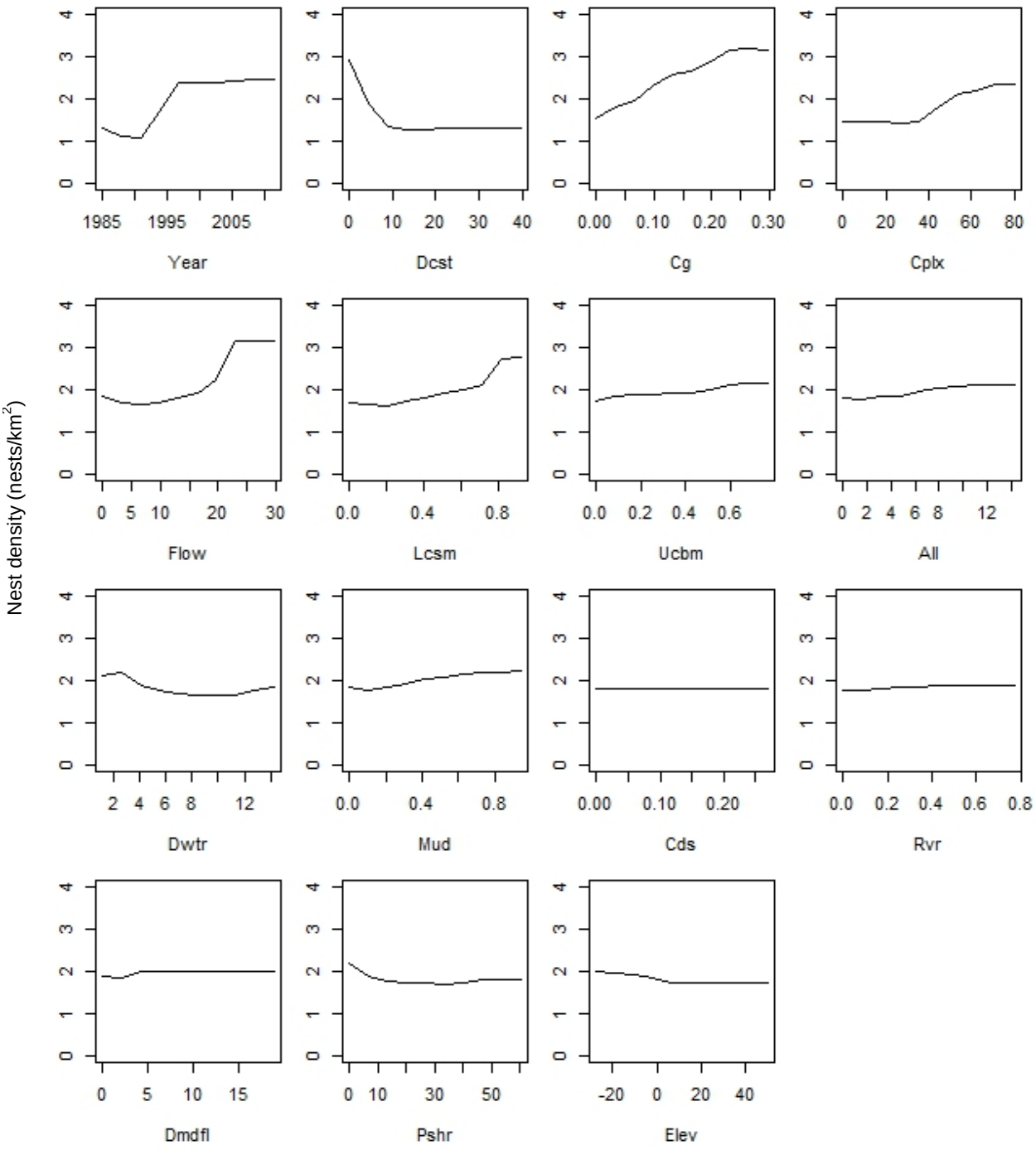

Figure 15. Partial dependence plots from random forests models predicting Spectacled Eider nest density on the Yukon-Kuskokwim Delta of Alaska, USA, 1985–2013, in relation to long-term impacts of storm surges. Partial dependence plots represent the relationship between an explanatory variable and nest density while holding all other explanatory variables in the model at their mean. Explanatory variables are listed in order of importance (see Figure 10). See Table 1 for explanatory variable abbreviations and units.

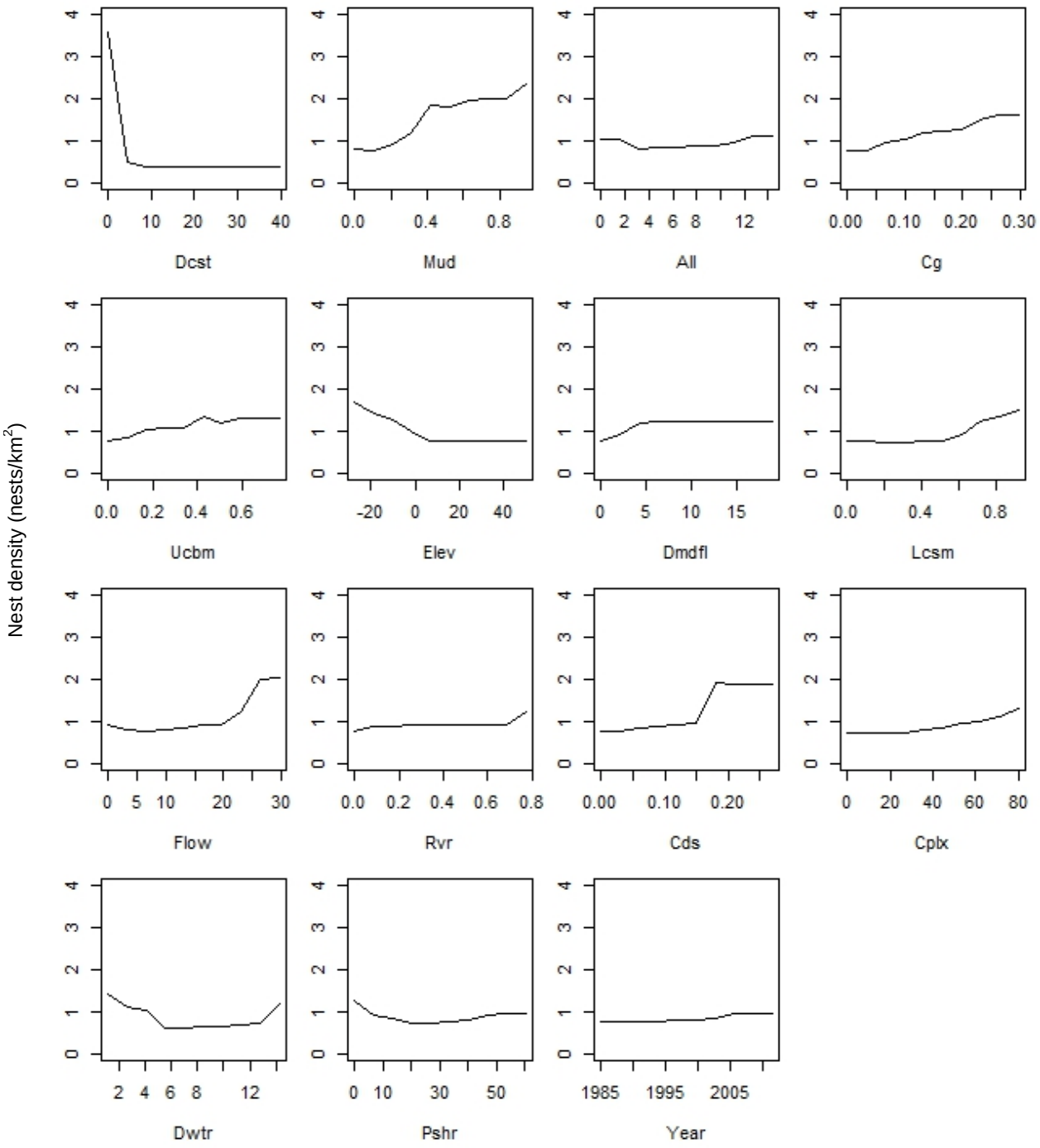

Figure 16. Partial dependence plots from random forests models predicting Common Eider nest density on the Yukon-Kuskokwim Delta of Alaska, USA, 1985–2013, in relation to long-term impacts of storm surges. Partial dependence plots represent the relationship between an explanatory variable and nest density while holding all other explanatory variables in the model at their mean. Explanatory variables are listed in order of importance (see Figure 10). See Table 1 for explanatory variable abbreviations and units.

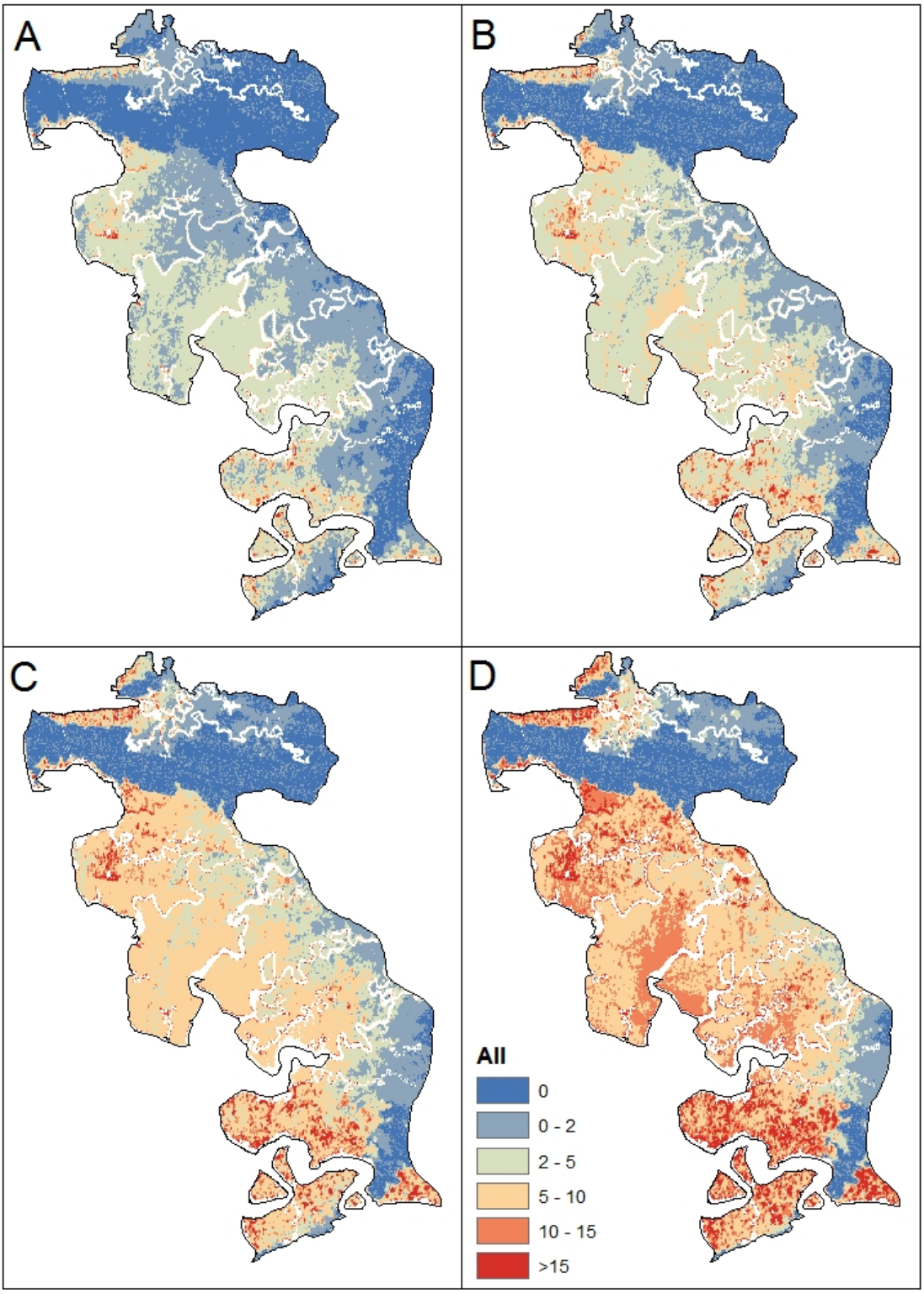

Figure 17. Annual inundation index (meter days/year; AII) under current (A) and future sea level rise scenarios of 40 cm (B), 80 m (C), and 120 cm (D) on the Yukon-Kuskokwim Delta of Alaska, USA.