



Avian Habitat Suitability Models for Puget Sound Estuary Birds

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Executive Summary

Extensive habitat loss and ecosystem degradation associated with human settlement in Puget Sound estuaries has resulted in an untold decrease in bird abundance and distribution. Protection and restoration actions associated with the [Puget Sound Action Agenda](#), the state plan that charts the course for recovery in Puget Sound, have the potential to benefit birds. However, meaningful recovery of estuary bird communities in Puget Sound requires that we have a clear understanding of species status and trends, where and when they occur, and the environmental conditions and human pressures that influence their occurrence.

In this report, we present bird-habitat suitability models for five “narrative” species that represent unique niches associated with Puget Sound estuaries: Brant, Dunlin, Greater Yellowlegs, Marsh Wren, and Northern Pintail. These species were selected to help inform and tell the story of the complexity of avian habitat use across tidal gradients and seasons in Puget Sound estuaries. Our study used avian monitoring data from tribal, state, federal and NGO partners, as well as community science data, to build separate habitat suitability models of occurrence and abundance by season for the five narrative species. Of the 21 environmental variables included in the models, the three that most strongly influenced probability of occurrence included proportions of estuarine emergent wetland, mudflat, and palustrine wetland cover. Where study species occurred, relative abundance was most strongly influenced by survey effort (survey distance and duration), followed by proportions of agriculture, estuarine emergent wetland, and mudflat cover.

This study provides valuable information about the environmental drivers of spatial patterns of bird distribution and abundance and identifies important

areas for birds around the Puget Sound. It also points to specific actions that land managers can take to ensure Puget Sound continues to serve as a vital link for Pacific Flyway birds. Our analytical approach can be replicated for other species, and the information can be used at a regional scale to identify priority areas for conservation. Similarly, the maps can be used to identify areas where birds are currently less abundant, but that are proximate to suitable habitat or marsh migration opportunities, suggesting that restoration may be beneficial. For example, we used our models to evaluate the potential benefit of estuarine wetland restoration for Northern Pintail and Greater Yellowlegs across the entire Puget Sound as well as a case study area in Port Susan Bay. Our identification of the environmental conditions that are most important to narrative species as well as the form of the relationship can also inform smaller scale habitat management.

An important theme that emerged from this exercise is that data quantity and quality are essential for a robust understanding of bird-habitat relationships and distributions in Puget Sound, which in turn informs habitat management and restoration actions. Model performance may be constrained for some species by insufficient monitoring data across relevant seasons, the concentration of monitoring data in certain well-studied estuaries, and differences in species detectability across habitat types. The development of a regional monitoring framework for estuarine birds that aligns bird survey and sampling methods is an ambitious but critical step that will dramatically improve our ability to develop predictive tools and generate adaptive feedback for natural resource managers in a time of rapid environmental change.

Introduction

The coastal ecosystems of Puget Sound have been severely altered since European settlement. Less than 25% of the region's historical estuarine wetlands remain, and shorelines have become shorter, straighter, and significantly more developed (Fresh et al. 2011). As a result, there is less coastal and estuarine habitat available to terrestrial and aquatic wildlife, and much of what remains is fragmented or otherwise degraded. Much attention has been paid to the impacts of coastal and wetland habitat loss and degradation on salmon populations and fisheries, but many other wildlife species are affected as well. Many bird species are reliant on coastal and estuarine habitat, yet relatively little is known about the specific impacts of habitat loss and degradation—or restoration on coastal birds in the Puget Sound region.

Bird Life of Puget Sound

Puget Sound and the greater Salish Sea provide a critical link in the annual life cycles of many marine and coastal bird species, supporting over 70 species of shorebirds, waterfowl, secretive marsh birds, and other marine bird species (Buchanan 2006). Avian use of coastal and marine habitats in the region varies by season, with migratory and overwintering species, especially waterfowl, outnumbering year-round residents (Johnson and O'Neil 2001). Dunlin (*Calidris alpina*) are the most common winter shorebird species, comprising 90-95% of the winter shorebird community, while Western Sandpiper (*Calidris mauri*) have the highest abundance during spring migration (Evenson and Buchanan 1997). The Salish Sea supports 38 species of waterfowl (Gaydos and Pearson 2011), including the largest wintering population of Pacific Flyway Black Brant (*Branta bernicla*) in the United States (Pacific Flyway Council 2002). Numerous landbirds, including raptors such as Northern Harriers and marshbirds such as Marsh Wren (*Cistothorus palustris*) and Virginia Rail (*Rallus limicola*) also use coastal wetland habitats (Gaydos and Pearson 2011). Three estuaries in the greater Salish Sea are recognized as sites of significant importance for migratory shorebirds by the Western Hemisphere Shorebird Reserve Network, including

the Greater Skagit and Stillaguamish Deltas. Dozens of Important Bird Areas have been designated within the Salish Sea, indicating where migratory waterfowl, shorebirds, and birds of prey congregate in globally, nationally, or regionally significant numbers (Figure 1).

Birds provide an array of ecological, cultural, and economic benefits to Puget Sound residents and communities. Access to coastal birds – whether for observation, hunting, photography, or simple enjoyment, brings economic and cultural benefits to coastal communities. Many Northwest Tribes rely on these birds for ceremonial and subsistence living purposes, and birds provide a connection to their traditional ecological knowledge systems and cultures. Numerous festivals occur throughout the region in celebration of birds, bringing additional tourist dollars and opportunities for new audiences to connect with nature. Birds also provide ecosystem services to river delta estuaries via dispersal of seeds and invertebrates, and as herbivores and predators (Green and Elmerg 2014).



Figure 1. Location of Western Hemisphere Shorebird Reserve Network (WHSRN) sites and Important Bird Areas in the Salish Sea.

Birds are indicators of marine and estuarine ecosystem health. They are culturally significant for tribal communities and beloved by millions of people. Birds also help generate funds to support conservation through the sale of duck stamps and recreational expenditures by birdwatchers and hunters.

Species and Habitats at Risk

There are no quantitative records available from which we might measure the extent of marine and coastal bird population declines associated with Euro-American settlement and the subsequent agricultural conversion of estuaries between the late 1800s and early 1900s (Petrie 2013). State-level inventories of marine and shorebird populations were initiated in the 1980s; these early efforts serve as a baseline for status and trend analyses today. The number of marine birds wintering in Puget Sound has declined significantly since the late 1970's (Bower 2009, [PSP Marine Bird Vital Signs](#)) and migratory, fish-eating birds appear to be at the greatest risk (Vilchis et al. 2014). Robust status and trend information on migratory shorebird abundance in our region is lacking. Shorebirds, seabirds, and marine waterfowl are experiencing global declines, and ecosystem changes associated with climate change further threaten food and habitat resources across their life cycle (e.g., Brown et al. 2001; Paleczny et al. 2015).

Hundreds of millions of dollars have been invested in Puget Sound recovery in recent decades, yet progress towards comprehensive ecosystem recovery targets remains slow. Many estuary restoration projects aim to restore habitat-forming processes in support of salmon, particularly the federally listed Chinook salmon (*Oncorhynchus tshawytscha*), and the ecosystem they rely on. Yet we know little about how these projects contribute to a variety of other ecosystem targets, including avian conservation objectives. Significant, dedicated restoration and monitoring

support and funding is uncommon in Puget Sound, particularly for birds (Koberstein et al. 2017).

Threats and Pressures

The Puget Sound region is home today to some 4.5 million people, with another 1.3 million expected by 2040 (PSP 2018). Habitat degradation continues to outpace restoration in our region, and projected population growth signals that we will continue to put significant pressure on our natural systems. The rapid pace of population growth in the region is exacerbating issues like storm water runoff and habitat conversion. Changes to ocean, freshwater, and terrestrial conditions associated with climate change further threaten species, habitats, livelihoods and Tribal treaty rights and cultural practices.

Local climate models for Puget Sound indicate that projected changes in sea level, sea surface temperature and ocean acidification may affect tidal wetlands and food sources in ways that will impact resident and migratory birds. For example, assuming landward migration is possible, sea level rise is projected to increase the area of some types of tidal wetlands (e.g., salt marsh, tidal flats) and reduce the area of others (e.g., estuarine beaches, brackish marsh) (Mauger et al. 2015). In addition, ocean acidification and projected increases in ocean temperatures are likely to affect aquatic vegetation and invertebrate and fish populations in ways that disrupt the marine food web, with unknown impacts on birds.

Problem Statement

The science foundation for bird management and conservation in Puget Sound is constrained by a lack of dedicated support and regional coordination among avian stakeholders. The use of disparate survey designs, protocols and objectives complicates our ability to interpret avian responses at local and regional scales—whether it be to local habitat management actions or large-scale environmental change (Koberstein et al. 2017).

Previous Puget Sound Ecosystem Monitoring Program (PSEMP) outreach efforts have determined that to recover and sustain bird populations in Puget Sound, estuary stakeholders and managers

need access to credible data at multiple spatial and temporal scales to understand and communicate the status of bird populations, understand the mechanisms driving their population trends, weigh the implications of different management actions, reduce human conflict, and invest strategically in conservation outcomes for birds and other species in a changing climate (Bayard et al. 2019).

Development of a regional monitoring framework for estuary birds is an ambitious but critical step that will dramatically improve our ability to develop predictive tools and deliver information for adaptive management in a time of rapid environmental change. As we work towards this goal, we are developing science products such as this report that inform estuary management and pinpoint data needs to be filled under a regional monitoring framework. Together, these actions will inform our efforts to conserve the estuarine habitats of the Puget Sound, and the birds and other species that rely on them.

Habitat Suitability Models

Development of bird-habitat relationship models is a foundational step in building a regional avian monitoring framework that supports avian conservation. These models provide valuable information about important areas for birds around the Puget Sound and the environmental drivers of spatial patterns of bird distribution and abundance. Additionally, the exercise enabled us to build and strengthen ties with partners, review the survey methods used, and identify regions with extensive monitoring as well as under-surveyed regions. The process of developing species-habitat models helped us better pinpoint gaps in current avian monitoring efforts and provide information and tools to inform habitat management.

Methods

Study Area

We defined the study area as the Puget Sound and southern Salish Sea region of Washington State (Figure 2). The study area is restricted to the marine

waters of Washington State east of Cape Flattery, and includes the U.S. portions of the Strait of Juan de Fuca, the southern Strait of Georgia, Hood Canal, Puget Sound proper and several other smaller basins. The study area contains portions of the ancestral lands of Tribes signatory to the Treaty of Point Elliot, Medicine Creek, and Point No Point. The study area boundary was derived from the Submerged Vegetation Monitoring Program (Christiaen et al. 2019) and expanded to include Lake Washington and the city of Seattle.

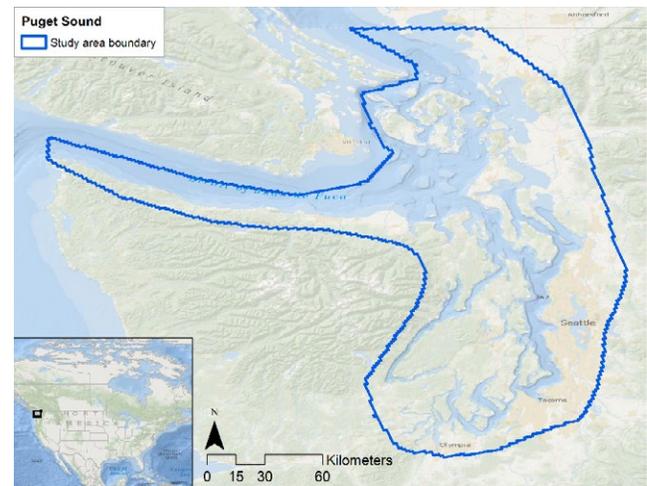


Figure 2. The study area includes Puget Sound and southern Salish Sea region of Washington State.

Narrative Species

We identified five narrative species for habitat suitability modeling (Table 1). We reviewed all species within each guild (waterfowl, shorebirds, landbirds) and selected species that represented unique niches (e.g., range of tidal gradients, diet, migratory patterns), that are common within the Puget Sound region in one or more stages of their annual cycle and are widely surveyed and easily identifiable by experienced observers. Together, these species provide examples for further outreach around avian use of Puget Sound, the potential value of avian predictive modeling tools for managers, and the benefits of a regional monitoring framework for management decision-making. Additional information on narrative species is included in Appendix A.

Table 1. Narrative species included in this analysis. Common and scientific names, number of birds observed, group size (median reported, range in parentheses), and number of grid cells (of 17,344 total) in which the species occurred in each season are reported.

Common Name	Scientific Name	Season	Number of Observations	Group Size	Number of Grid Cells
Brant	<i>Branta bernicla</i>	Winter	83,585	5 (1–1,500)	688
		Spring	77,626	29 (1–2,200)	158
		Fall	20	1 (1–6)	6
Dunlin	<i>Calidris alpina</i>	Winter	555,745	70 (1–15,000)	229
		Spring	109,161	15 (1–17,050)	138
		Fall	505	2 (1–141)	23
Greater Yellowlegs	<i>Tringa melanoleuca</i>	Winter	2,225	2 (1–44)	113
		Spring	3,458	2 (1–125)	199
		Fall	9,096	3 (1–92)	173
Marsh Wren	<i>Cistothorus palustris</i>	Winter	4,229	1 (1–60)	285
		Breeding	12,459	2 (1–40)	344
Northern Pintail	<i>Anas acuta</i>	Winter	224,699	10 (1–5,000)	609
		Spring	21,844	6 (1–500)	240

- Brant (*Branta bernicla*) are colonial waterfowl that feed on eelgrass and algae. The species consumes both native (*Zostera marina*) and invasive (*Z. japonica*) eelgrass, though the invasive species is smaller and an annual plant that is not widely available during the winter (Moore et al. 2004). Brant use coastal waters, especially lagoon systems behind barrier beaches, and are winter residents and passage migrants in the Puget Sound region (Lewis et al. 2020).
- Dunlin (*Calidris alpina*) are shorebirds that form large flocks in winter. This species forages for invertebrates on the edges of marshes, estuaries, coastal lagoons, and flooded farm fields. Dunlin are winter residents and passage migrants in the Puget Sound region (Warnock and Gill 2020).
- Greater Yellowlegs (*Tringa melanoleuca*) are shorebirds that are largely solitary. This species forages for aquatic invertebrates in fresh and brackish wetlands, mudflats, lake and pond edges, and flooded fields. Greater Yellowlegs are winter residents and passage migrants in the Puget Sound region (Elphick and Tibbitts 2020).
- Marsh Wren (*Cistothorus palustris*) are a passerine marshbird that forages for insects and spiders in wetlands, saltmarshes, brushy thickets, and agricultural canals. They are year-round residents of the Puget Sound region (Kroodsma and Verner 2020).
- Northern Pintail (*Anas acuta*) are a dabbling duck that gather in large flocks, particularly during the non-breeding seasons. They forage for insects, snails, seeds, and other plant material in estuaries, fresh and brackish wetlands, lakes, and flooded or dry agricultural fields. Northern Pintail are a winter resident and passage migrant in the Puget Sound region (Clark et al. 2020).

Avian Data

We compiled avian datasets collected across the Puget Sound region. We contacted PSEMP partners, habitat managers, and scientists known to have collected avian count data in the Puget Sound region and requested data for use in this analysis (e.g., Koberstein et al. 2017). In order to be included, the data needed to have been collected within our study area from 2010

onward, be associated with a location at a resolution no greater than 1 km, and include the survey date. We obtained 12 datasets from partners that met these criteria, including 6,236 surveys of one or more narrative species (Table 2). We defined surveys as counts conducted at a distinct location at a distinct date and time. For all field-based surveys (i.e., excluding the Midwinter Aerial Survey and telemetry data e.g., Fir Island), we created non-detection (i.e., absence) records for species that were not detected but occurred at that site.

Additionally, we extracted data from eBird (<https://www.ebird.org>) for the five narrative species. We filtered the data following standard procedures for modeling eBird data (Johnston et al. 2019) by

sub-setting checklists of ≤ 3 h duration and ≤ 1.1 km distance on which observers indicated all species were detected and recorded. We further subset checklists to include those using one of eight survey protocols relevant to our target species: Area, California Brown Pelican Survey, Coastal Shorebird Survey, eBird Pelagic Protocol, International Shorebird Survey, Random, Traveling, and Stationary. We retained all observations collected within the study area (Figure 2) between January 1, 2010 and February 29, 2020. Additionally, we extracted all checklists submitted within the study area that met the above criteria, and used these to create absence records for each narrative species for each checklist on which it was not detected.

Table 2. Avian data summary. The data owner, location or source of data, narrative species detected, years, and number of surveys conducted are reported for each partner dataset.

Data Owner	Location/Source	Species	Years	Number of Surveys
Olympic Peninsula Audubon Society	3 Crabs Beach	All	2014-2018	150
Skokomish Tribe	Anna's Bay	All	2010-2020	239
Cornell Lab of Ornithology & National Audubon Society	eBird	All	2010	166,421
Ecostudies Institute	Fir Island	Dunlin, Greater Yellowlegs, Marsh Wren, Northern Pintail	2016-2017	261
Washington Department of Fish & Wildlife	Greater Skagit and Stillaguamish Delta WHSRN	All	2010	38
Olympic Peninsula Audubon Society	Helen's Pond	All	2014-2018	6
Jamestown S'Klallam Tribe	Jimmycomelately Creek	All	2010-2011	156
Ecostudies Institute	Leque	Dunlin, Greater Yellowlegs, Marsh Wren, Northern Pintail	2016-2017	97
Washington Department of Fish & Wildlife	Midwinter Aerial Survey (PSAMP)	Brant, Greater Yellowlegs, Northern Pintail	2010-2017	3,921
U.S. Geological Survey	Nisqually Delta	All	2010-2015	688
Samish Indian Nation	Secret Harbor	Brant, Greater Yellowlegs, Marsh Wren	2011-2015	300
Ecostudies Institute	Wiley	Dunlin, Greater Yellowlegs, Marsh Wren, Northern Pintail	2016-2017	101
Stillaguamish Tribe	zis a ba	Dunlin, Greater Yellowlegs, Marsh Wren, Northern Pintail	2018-2020	279



We split the data into two to three seasonal datasets per species based on their timing of occurrence in the Puget Sound. Specifically, we focused on both stationary periods (breeding and winter) as well as spring and fall migratory periods when birds actively move through the area. For waterfowl (Brant, Northern Pintail) we produced three seasonal datasets: spring (March 1 – April 30), fall (August 1 – September 30), and winter (December 1 – February 28/29). For shorebirds (Dunlin, Greater Yellowlegs) we also produced three seasonal datasets: spring (April 1 – May 31), fall (August 1 – September 30), and winter (December 1 – February 28/29). For the sole year-round resident, Marsh Wren, we produced two seasonal datasets: breeding (April 1 – July 31) and winter (December 1 – February 28/29; non-breeding season). We assigned all records (presences and absences) to a fishnet grid spanning the study area that included 17,344 1-km² grid cells.

Environmental Data

We used 21 environmental variables as well as three effort variables and one temporal variable in individual species models for each season to evaluate bird-habitat relationships (Table 3). Including the three effort variables in the same model is considered a best practice when working with data that were collected without a standard protocol (Johnston et al. 2019). Including effort predictors controls for the influence

of survey duration, distance, and area on observed count, while including it in the same model (rather than standardizing the counts beforehand) reduces the amount of error introduced through the modeling effort. The variables were determined based on expert opinion regarding the environmental conditions the narrative species were expected to respond to.

We sampled all variables for 17,344 1-km² grid cells, covering the study area and aligned with the avian density grid cells. Within each 1-km² grid cell, variables were calculated in one of several ways: as percent cover (e.g., aquaculture, open water), total length of linear features (e.g., manmade structures), mean value (e.g., tidal amplitude), or value at the grid centroid (e.g., latitude). For the three types of estuarine wetland (estuarine emergent wetland, estuarine forested wetland, and estuarine scrub/shrub wetland) we used the West Coast USA Estuarine Biotic Habitat layer (PMEP 2020a) to distinguish estuarine wetland habitat types. However, as this layer shows the historical wetland extent, we used the Indirect Assessment of West Coast USA Tidal Wetland Loss layer (PMEP 2020b) to mask out those areas where wetlands were lost, while keeping lost but restored wetlands. The merged palustrine wetland variable was created by merging the three types of palustrine wetlands in the C-CAP Regional Land Cover data: palustrine emergent wetland, palustrine forested wetland, and palustrine scrub/shrub wetland (NOAA 2018).

Table 3. Environmental, effort, and temporal variables used in habitat suitability models. Variables are grouped by type, and sources and citations are provided.

Type	Variable	Source
Anthropogenic	Aquaculture (shellfish, finfish, and other; %)	Office for Coastal Management (2020)
Anthropogenic	Distance to protected area (i.e., an area managed at least in part for conservation of biodiversity, including local, state, federal, or private parks, wildlife refuges, and conservation areas; m)	Protected Areas Database 2.0 (USGS Gap Analysis Project 2018)
Anthropogenic	Manmade structures (e.g., seawalls, riprap, dikes, docks, bulkheads, wharves, or boat ramps; linear m)	ShoreZone Inventory (WDNR 2019a)
Anthropogenic	Impervious surface (%)	National Land Cover Database 2016 (MRLC 2019)
Aquatic	Eelgrass (<i>Z. japonica</i> , %)	Puget Sound Seagrass Monitoring (WDNR 2019b)
Aquatic	Eelgrass (<i>Z. marina</i> , %)	Puget Sound Seagrass Monitoring (WDNR 2019b)
Aquatic	Open water (%)	C-CAP Regional Land Cover 2016 (NOAA 2018)
Effort	Area surveyed (ha)	Avian data
Effort	Distance surveyed (km)	Avian data
Effort	Duration of survey (min)	Avian data
Spatial	Distance to shore (m)	Coastline (Wessel & Smith 2017)
Spatial	Elevation / bathymetry (m)	WA Marine Bathymetry (WDFW 1999)
Spatial	Fetch	ShoreZone Inventory (WDNR 2019a)
Spatial	Latitude	Avian data, grid cell centroid
Spatial	Longitude	Avian data, grid cell centroid
Spatial	Tidal amplitude	NOAA (Mojfeld et al. 2002), SNDS (Vestbo et al. 2018)
Temporal	Year	Avian data
Terrestrial	Agriculture (%)	C-CAP Regional Land Cover 2016 (NOAA 2018)
Terrestrial	Grassland (%)	C-CAP Regional Land Cover 2016 (NOAA 2018)
Terrestrial	Sand/gravel beach (linear m)	ShoreZone Inventory (WDNR 2019a)
Wetland	Estuarine emergent wetland (%)	Estuarine Biotic Habitat & Wetland Loss (PMEP 2020a,b)
Wetland	Estuarine forested wetland (%)	Estuarine Biotic Habitat & Wetland Loss (PMEP 2020 a,b)
Wetland	Estuarine scrub/shrub wetland (%)	Estuarine Biotic Habitat & Wetland Loss (PMEP 2020 a,b)
Wetland	Intertidal mudflat (%)	Global Intertidal Change (Murray et al. 2019)
Wetland	Palustrine wetland (all types, %)	C-CAP Regional Land Cover 2016 (NOAA 2018)

Modeling Technique

We built separate habitat suitability models by species and season. Because the datasets we used did not include the extra information needed to correct for imperfect detection (e.g., distance or time to first detection) we were unable to estimate detection probabilities, and instead estimated occurrence probability and relative abundance (where species occurred). We modeled the relationship between bird observations (presence/absence and count) and the suite of environmental, effort, and temporal variables at the resolution of 1-km₂ grid cells using boosted regression trees (BRTs). BRTs are a machine learning approach that is ideal for modeling ecological relationships, which are often complex, curvilinear, and include multiple, often highly correlated, environmental variables (Elith et al. 2008). Prior to building BRT models we investigated correlations among predictor variables. All pairwise comparisons had Pearson's correlations $< |-0.85|$, below the threshold for spurious results (Elith et al. 2008).

Many species had skewed count (i.e., relative abundance) distributions with absences in many grid cells (i.e., zero inflation), which violates the Poisson model assumption that the mean equals the variance. Therefore, we implemented a hurdle model approach in which we separately modelled occurrence and relative abundance, then combined the models to estimate relative abundance only at grid cells that met a threshold occurrence level (per Michel et al. 2020). For the occurrence model, we used presence/absence as the response variable and for the relative abundance model we used count. For the relative abundance model, we used a Poisson distribution. If these models failed to converge, we log-transformed count to improve fit and used a Gaussian distribution.

Models were fit using packages *dismo* (Hijmans et al. 2015) and *gbm* (Ridgeway 2015) in R version 3.5.1 (R Core Team 2018). BRT models use three parameters—learning rate, bag fraction, and tree complexity—to shrink the number of terms in the final model and thus avoid overfitting. Learning rate shrinks the contribution of each tree in the boosted model, bag fraction specifies the proportion of data to be selected from the training set at each step, and tree

complexity determines the number of nodes and, consequently, level of interactions between predictors. We iteratively tuned these parameters to optimize model fit while ensuring a minimum of 1,000 trees using default parameter ranges recommended by Elith et al. (2008): learning rate 0.0001–0.1, bag fraction 0.55–0.75, and tree complexity 1–3. At each step we used 10-fold cross-validated area under the receiver operating characteristic curve (AUC), a measure of discriminatory capacity, and residual deviance to select the optimal parameter value. To reduce bias due to spatial autocorrelation, we used spatially stratified cross-validation by dividing the data set into 11 bins by latitude and longitude and withholding one latitudinal bin for testing at each fold (Roberts et al. 2017).

Ensemble Modeling Framework

Survey data were highly spatially unbalanced, with multiple repeated observations in some grid cells and few to no observations in others. In order to reduce spatial bias, we conducted geographic filtering in an ensemble modeling framework. Each species' seasonal model was run 11 times, and on each iteration a single observation was randomly selected for each month in each grid cell.

Model Performance

We estimated three model fit statistics for each model. For occurrence models, we calculated cross-validated AUC and deviance explained (i.e., proportion of variation in occurrence explained by the model). For relative abundance models, we calculated correlation between observed and predicted relative abundance and residual deviance. For both models, we also tested for residual spatial autocorrelation in the final model using Moran's I, calculated in package *ape* (Paradis et al. 2004). Higher values for AUC and deviance explained indicate better model fit, while Moran's I values < 0.3 indicate a lack of spatial autocorrelation. All model fit statistics were averaged across the ensemble of 11 models for each species in each season.

Effects of environmental variables on occurrence and relative abundance were evaluated in two ways. First, the relative importance of each land cover

predictor in the model was calculated, scaled so that all importance values sum to 100, and averaged across the 11 ensemble models. Second, the relationship between occurrence or relative abundance and the two predictor variables with highest relative importance was plotted as a marginal effect, meaning the mean estimated probabilities of occurrence (or relative abundance) was calculated across a range of values with all other variables held to their means. Mean relative importance was also calculated by averaging across all species in all seasons.

Two species (Brant, Dunlin) had insufficient data to produce either occurrence or relative abundance models in the fall. A third species, Northern Pintail, had sufficient data to produce occurrence models in the fall, but not relative abundance models. Therefore a total of 23 species-season habitat suitability models were produced (Table 4).

Model Predictions and Mapping

We used the occurrence and relative abundance models to generate predicted probability of occurrence and relative abundance across the entire Puget Sound study area. To do this, we extracted values for the 21 environmental variables for all 17,344 1-km² grid cells across the study area. In order to ensure the predicted values were standardized relative to effort, we generated all predictions using a hypothetical survey of 30 minutes duration, 0.5 km distance, and 0 ha area that occurred in the most recent full year (2019). Predictions were produced from each of the 11 ensemble models, then predicted values were averaged across the ensemble for each species and season. This produced a single mean probability of occurrence value and relative abundance value for each pixel. We then combined the probability of occurrence and relative abundance models to produce final estimates of relative abundance only for pixels that met a minimum probability of occurrence threshold. We calculated the minimum probability of occurrence threshold using maximum sensitivity

+ specificity in R package SDMTools (VanDerWal et al., 2014). We used this to mask median predicted relative abundance such that they were retained only at grid cells that surpassed the threshold hurdle. Maps for each species and season were produced in ArcGIS using the masked relative abundance rasters.

Restoration Scenario Modeling

We also evaluated the impacts of estuarine wetland restoration on occurrence and relative abundance of wetland birds across the entire study area, as well as a case study in Port Susan Bay. We simulated the complete restoration of estuarine wetland to its historic extent. Though impractical, this provides a ceiling on the potential increase in bird abundance in response to restoration efforts. We selected two species for this study based on their strong association (i.e., high relative importance) with emergent estuarine wetland: Greater Yellowlegs and Northern Pintail. We modelled Greater Yellowlegs in the winter and Northern Pintails in the spring because these seasons were when these species were most strongly associated with estuarine emergent wetland. We used the unmasked West Coast USA Estuarine Biotic Habitat layer (PMEP 2020a) to represent historical estuarine wetland extent. We recalculated the proportion cover of estuarine emergent, estuarine forested, and estuarine scrub/shrub wetlands in each grid cell using the historical extent layer. In order to avoid total land cover exceeding 100% within grid cells, we subtracted the difference between historical and current-day wetland extent from the proportion of agriculture in each cell. We then built new BRT occurrence and relative abundance models using the revised wetland and agriculture data. We used both the original models and the revised models to predict relative abundance in the entire study area and in Port Susan Bay, and calculated the difference as a measure of potential estuarine wetland restoration impacts on Greater Yellowlegs and Northern Pintail.



Results

We fit 12 habitat suitability models relating occurrence and/or relative abundance with environmental conditions for five species in 2-3 seasons each. Here we review the models and their predictions for each species and season in turn.

Table 4. Model performance statistics for the set of 23 habitat suitability models produced for five narrative species during 2-3 seasons across the Puget Sound. Mean cross-validated AUC, deviance explained, and Moran's *I* are reported for occurrence models. Mean cross-validated correlation, deviance explained, and Moran's *I* are reported for relative abundance models.

Species	Seasons	Occurrence			Relative Abundance		
		AUC	Deviance Explained	Moran's <i>I</i>	Correlation	Deviance Explained	Moran's <i>I</i>
Brant	Winter	0.97	0.83	0.02	0.41	0.57	0.01
	Spring	0.84	0.39	0.04	-0.02	0.03	0.00
Dunlin	Winter	0.80	0.89	0.02	0.09	0.35	0.03
	Spring	0.77	0.26	0.00	0.43	0.58	-0.01
Greater Yellowlegs	Winter	0.82	0.18	0.01	0.16	0.09	0.02
	Spring	0.79	0.22	0.00	0.63	0.20	-0.02
	Fall	0.75	0.20	0.02	0.27	0.47	-0.01
Marsh Wren	Winter	0.82	0.20	0.00	0.20	0.13	0.00
	Breeding	0.82	0.25	0.01	0.19	0.21	-0.01
Northern Pintail	Winter	0.89	0.53	0.01	0.11	0.45	0.02
	Spring	0.82	0.23	0.01	0.14	0.13	-0.02
	Fall	0.79	0.21	0.00	—	—	—

Brant - Winter

Brant occurrence and relative abundance models had excellent fit in winter (Table 4), due to the large number and spatial distribution (688 grid cells) of observations (Table 1). Brant were most abundant in the northeastern (e.g., Skagit and Padilla Bays) and southern (e.g., Budd and Totten Inlets) regions of the Puget Sound (Appendix B, Figure S1). Brant occurrence was overwhelmingly explained by survey duration (Figure 3A), due to the large number of observations (>3,900; Table 2) from the Midwinter Aerial Survey, which all had the same duration (i.e., 0 minute as

the observations were recorded independently). The two strongest environmental relationships with Brant occurrence included positive relationships with distance to shore (likely a proxy for location of eelgrass beds) and proportion of native eelgrass (Figure 3B). Where Brant occurred, relative abundance increased with proportion to agriculture (likely a proxy capturing an unmeasured relationship such as embayment size, which may in turn be linked to eelgrass cover, as Brant do not use agricultural fields) and length of sand/gravel beaches within the 1 km² grid cell (Figure 3C).

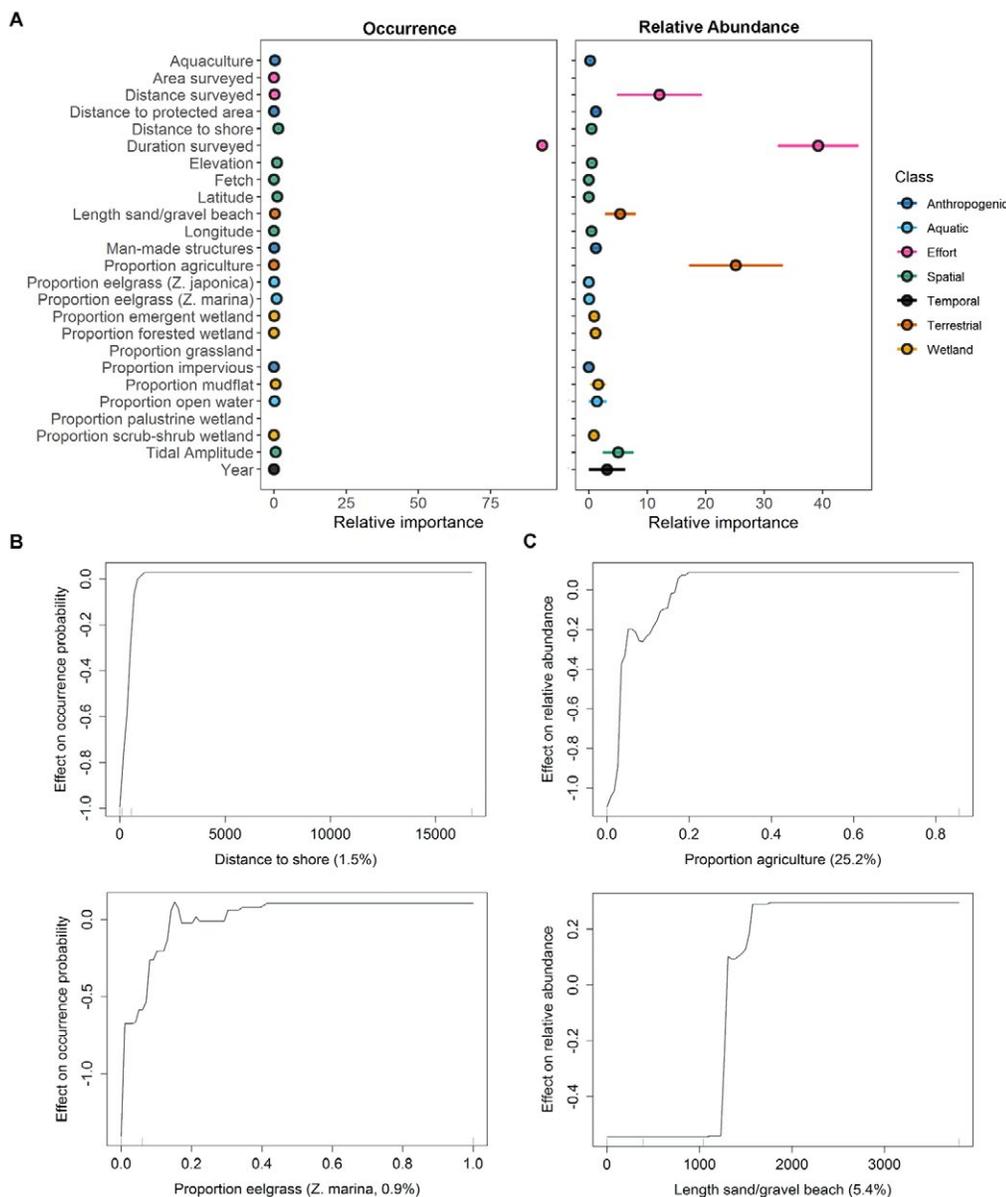


Figure 3. Habitat suitability modeling results for Brant in winter, including relative importance for all covariates in occurrence and relative abundance models (A), response plots for the two environmental variables with the highest relative importance in occurrence (B) and relative abundance (C) models. Emergent, forested, and scrub/shrub wetlands here are all estuarine, while palustrine wetlands refers to freshwater wetlands of all structural types.

Brant - Spring

Brant occurrence models fit well in spring, while relative abundance models had poor fit (Table 4). Though there were still a large number of observations, they were dispersed among less than one-quarter as many grid cells (158) as in the winter (Table 1). Brant were most abundant in the northeastern region (e.g., Skagit, Samish, and Padilla Bays) of the Puget Sound (Appendix B, Figure S2). Brant occurrence was explained most strongly by native eelgrass and length of sand/gravel

beach; where Brant occurred, relative abundance was explained most strongly by distance surveyed, while the strongest environmental predictor was proportion of estuarine emergent wetland (Figure 4A). Brant occurrence probability increased with proportion of native eelgrass and length of sand/gravel beach (Figure 4B). Where Brant occurred, relative abundance increased with proportions of estuarine emergent wetland and mudflat within the 1 km² grid cell (Figure 4C).

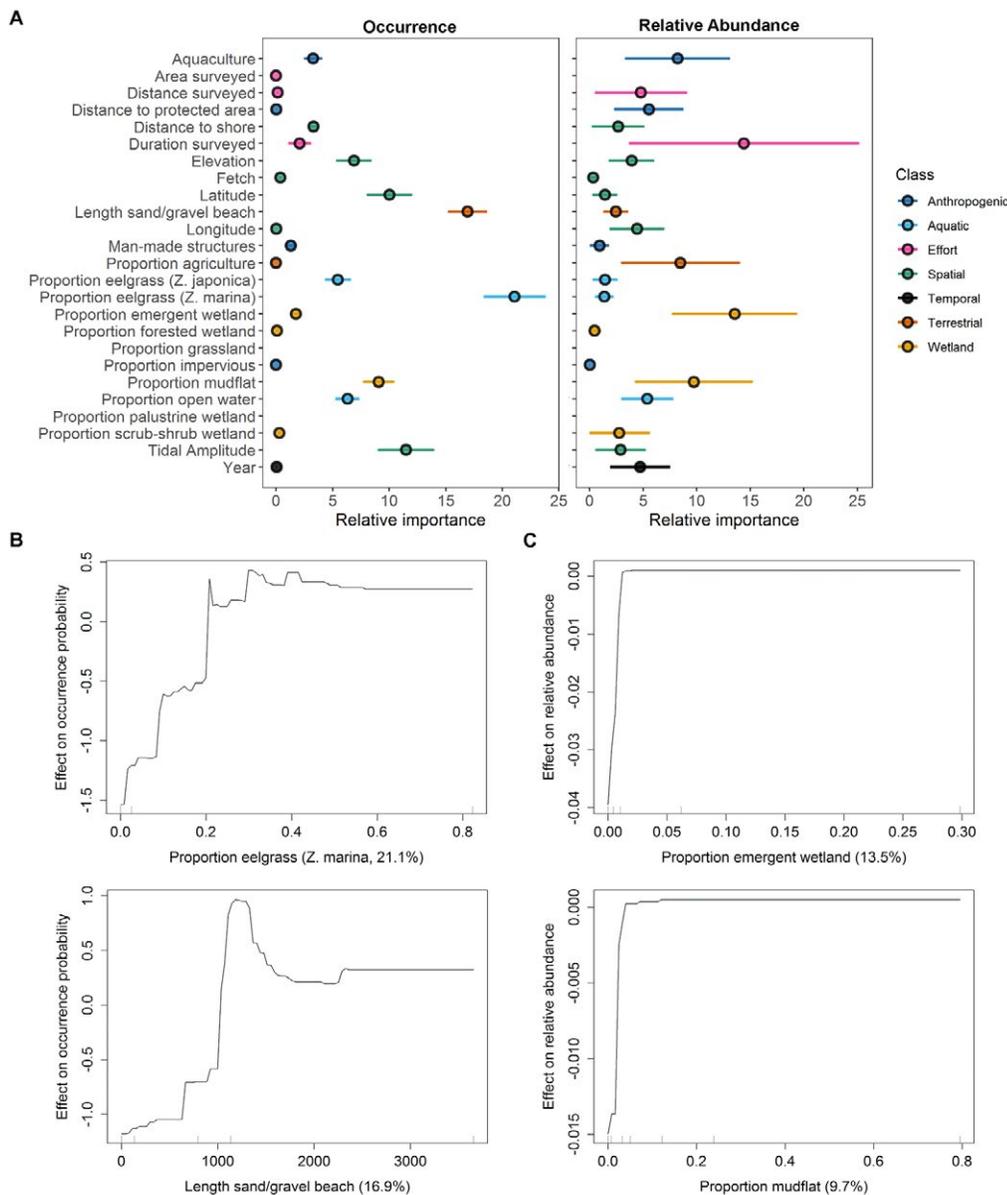


Figure 4. Habitat suitability modeling results for Brant in spring, including relative importance for all covariates in occurrence and relative abundance models (A), response plots for the two environmental variables with the highest relative importance in occurrence (B) and relative abundance (C) models. Emergent, forested, and scrub/shrub wetlands here are all estuarine, while palustrine wetlands refers to freshwater wetlands of all structural types.

Dunlin - Winter

Dunlin occurrence models had excellent fit (Table 4) due to the large number of observations (Table 1). The relative abundance models explained a good amount of variation in the winter, but did not fit as well as the occurrence models (Table 4). This is because Dunlin frequently gather in large aggregations in the winter and the wide range in group sizes makes fitting abundance models challenging. Dunlin were most abundant in the northeastern (e.g., Skagit, Samish, and Padilla Bays) and Snohomish regions of the

Puget Sound (Appendix B, Figure S3). Dunlin occurrence was explained most strongly by mudflat and estuarine emergent wetland; where Dunlin occurred, relative abundance was explained most strongly by agriculture and distance surveyed (Figure 5A). Dunlin occurrence probability increased with proportions of mudflat and estuarine emergent wetland (Figure 5B). Where Dunlin occurred, relative abundance increased with proportions of agriculture and estuarine emergent wetland within the 1 km² grid cell (Figure 5C).

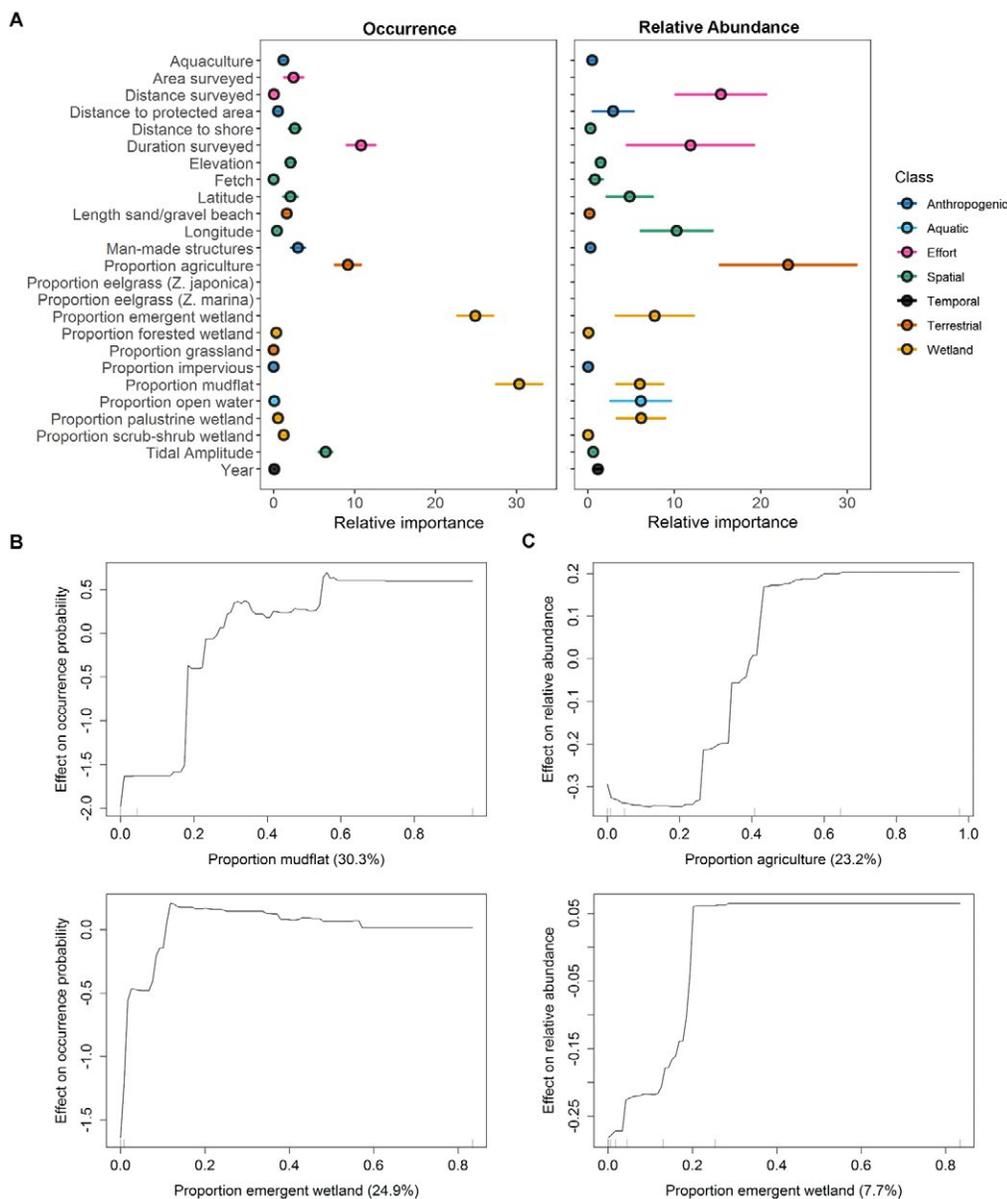


Figure 5. Habitat suitability modeling results for Dunlin in winter, including relative importance for all covariates in occurrence and relative abundance models (A), response plots for the two environmental variables with the highest relative importance in occurrence (B) and relative abundance (C) models. Emergent, forested, and scrub/shrub wetlands here are all estuarine, while palustrine wetlands refers to freshwater wetlands of all structural types.

Dunlin - Spring

Dunlin occurrence models in spring had reasonable fit, even though there were fewer and more sparsely distributed observations than in the winter (Table 1). However, relative abundance models had good fit because there were fewer large aggregations (i.e., >100 birds) in spring than winter (Table 4). Similar to the winter model, Dunlin were most abundant in the northeastern (e.g., Skagit, Samish, and Padilla Bays) and Snohomish regions of the Puget Sound (Appendix B, Figure S4). Dunlin occurrence was explained

most strongly by mudflat and estuarine emergent wetland; where Dunlin occurred, relative abundance was explained most strongly by effort variables (distance and duration; Figure 6A). Dunlin occurrence probability increased with proportions of mudflat and estuarine emergent wetland (Figure 6B). Where Dunlin occurred, relative abundance also increased with proportions of mudflat and estuarine emergent wetland within the 1-km² grid cell (Figure 6C).

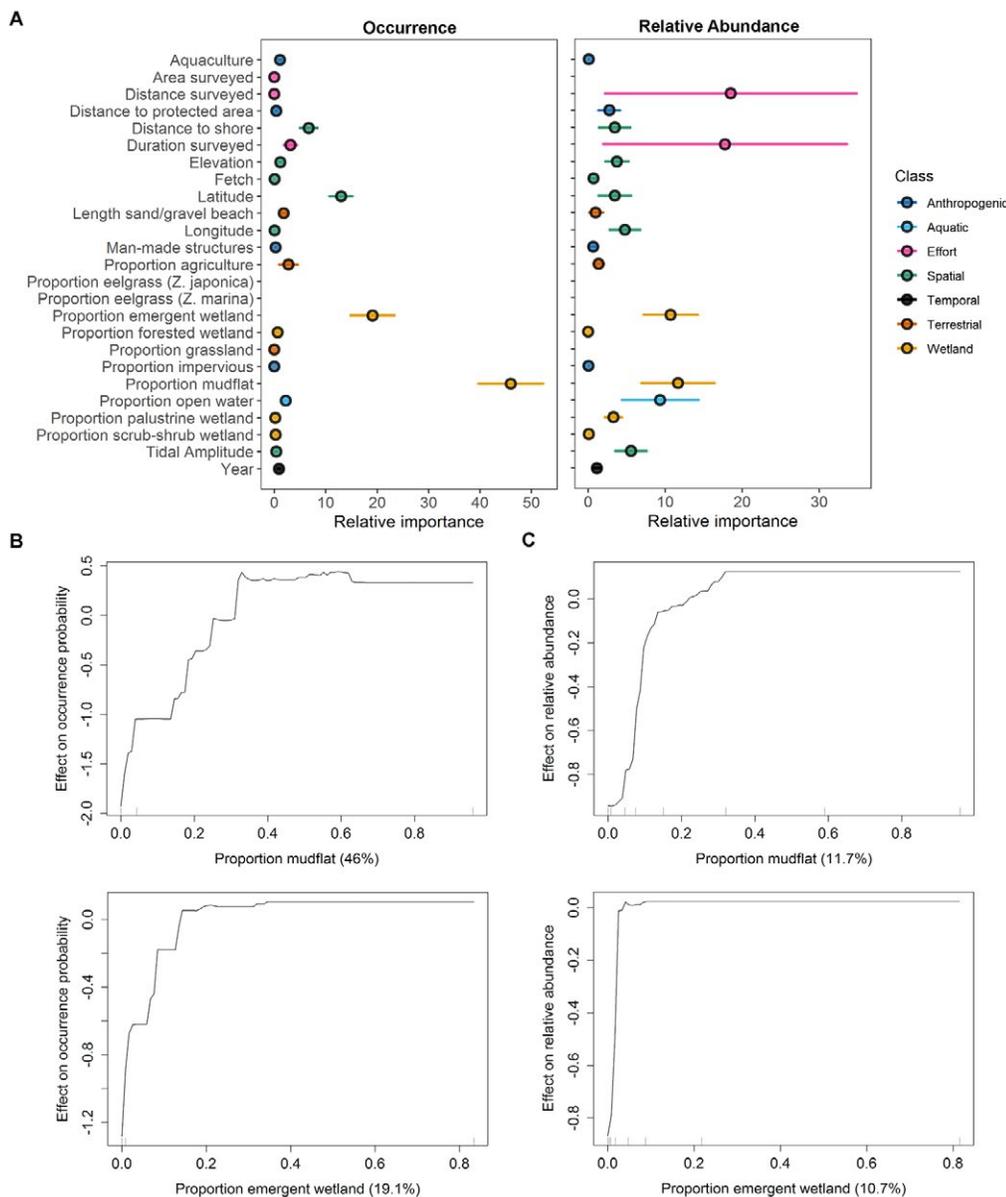


Figure 6. Habitat suitability modeling results for Dunlin in spring, including relative importance for all covariates in occurrence and relative abundance models (A), response plots for the two environmental variables with the highest relative importance in occurrence (B) and relative abundance (C) models. Emergent, forested, and scrub/shrub wetlands here are all estuarine, while palustrine wetlands refers to freshwater wetlands of all structural types.

Greater Yellowlegs - Winter

Greater Yellowlegs occurrence and relative abundance models had reasonable fit (Table 4) due to the moderate number and distribution of observations (Table 1). Greater Yellowlegs areas of highest abundance were scattered across the Puget Sound, including concentrations in the northeastern (e.g., Skagit and Padilla Bays and the Snohomish river mouth) and southern regions of the Puget Sound (Appendix B, Figure S5). Greater Yellowlegs occurrence was overwhelmingly

explained by estuarine emergent wetland; where Greater Yellowlegs occurred, relative abundance was explained most strongly by effort variables (distance and duration; Figure 7A). Greater Yellowlegs occurrence probability increased with proportions of estuarine emergent wetland and mudflat (Figure 7B). Where Greater Yellowlegs occurred, relative abundance increased with proportions of open water and palustrine wetland within the 1 km² grid cell (Figure 7C).

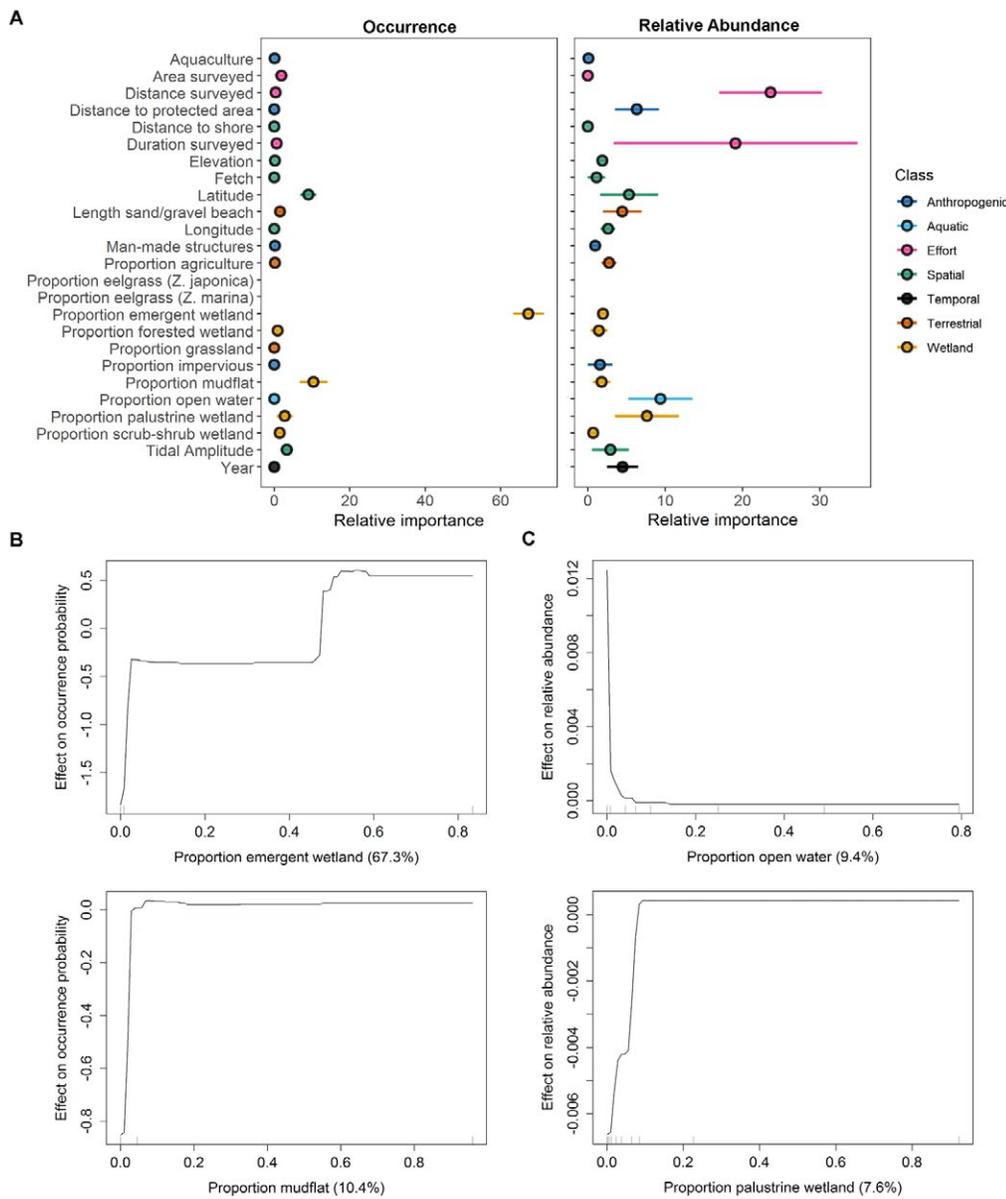


Figure 7. Habitat suitability modeling results for Greater Yellowlegs in winter, including relative importance for all covariates in occurrence and relative abundance models (A), response plots for the two environmental variables with the highest relative importance in occurrence (B) and relative abundance (C) models. Emergent, forested, and scrub/shrub wetlands here are all estuarine, while palustrine wetlands refers to freshwater wetlands of all structural types.

Greater Yellowlegs - Spring

Greater Yellowlegs occurrence models had reasonable fit while the relative abundance models fit better than the winter models (Table 4) due to the larger number and distribution of observations (Table 1). Greater Yellowlegs areas of highest abundance were scattered across the Puget Sound, including large concentrations in the northeastern region (e.g., Skagit and Padilla Bays) and scattered clusters in other regions of the Puget Sound (Appendix B, Figure S6). Greater Yellowlegs occurrence was overwhelmingly

explained by estuarine emergent wetland and mudflat; where Greater Yellowlegs occurred, relative abundance was explained most strongly by effort variables (distance and duration; Figure 8A). Greater Yellowlegs occurrence probability increased with proportions of estuarine emergent wetland and mudflat (Figure 8B). Where Greater Yellowlegs occurred, relative abundance increased with tidal amplitude and proportion of mudflat within the 1 km² grid cell (Figure 8C).

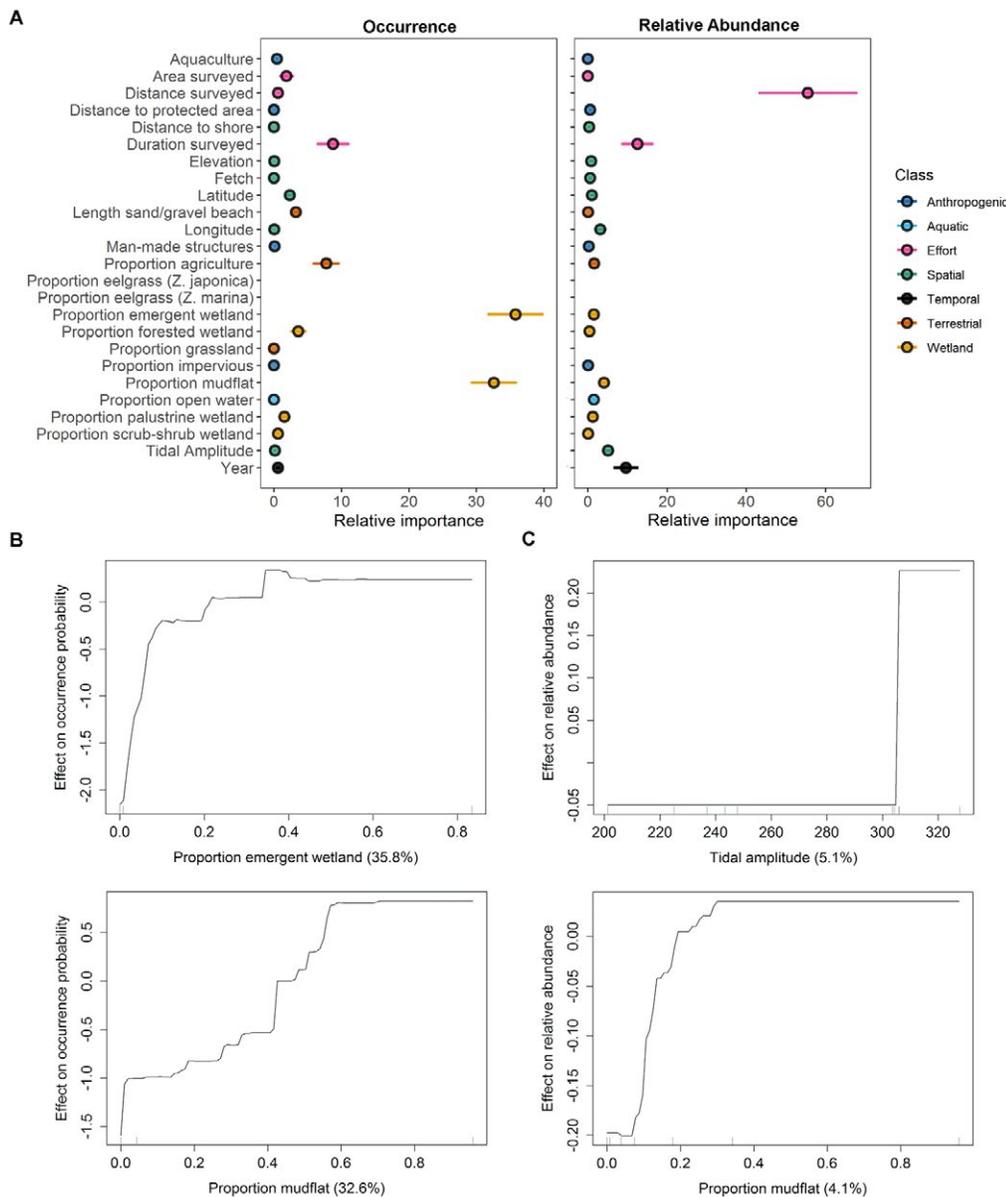


Figure 8. Habitat suitability modeling results for Greater Yellowlegs in spring, including relative importance for all covariates in occurrence and relative abundance models (A), response plots for the two environmental variables with the highest relative importance in occurrence (B) and relative abundance (C) models. Emergent, forested, and scrub/shrub wetlands here are all estuarine, while palustrine wetlands refers to freshwater wetlands of all structural types.

Greater Yellowlegs - Fall

Greater Yellowlegs occurrence models had reasonable fit while the relative abundance models explained more variation than the winter and spring models (Table 4) due to the larger number of observations (Table 1). Areas of highest abundance were more concentrated in the northeastern region (e.g., Skagit and Padilla Bays) as well as Whidbey Island and the southwestern region of the Puget Sound (Appendix B, Figure S7). Greater Yellowlegs occurrence was explained by estuarine emergent wetland and agri-

culture, whereas relative abundance, where they occurred, was explained most strongly by effort (distance), estuarine scrub/shrub wetland, and mudflat (Figure 9A). Greater Yellowlegs occurrence probability increased with proportions of estuarine emergent wetland and agriculture (Figure 9B). Where Greater Yellowlegs occurred, relative abundance increased with proportions of estuarine scrub/shrub wetland and mudflat within the 1 km² grid cell (Figure 9C).

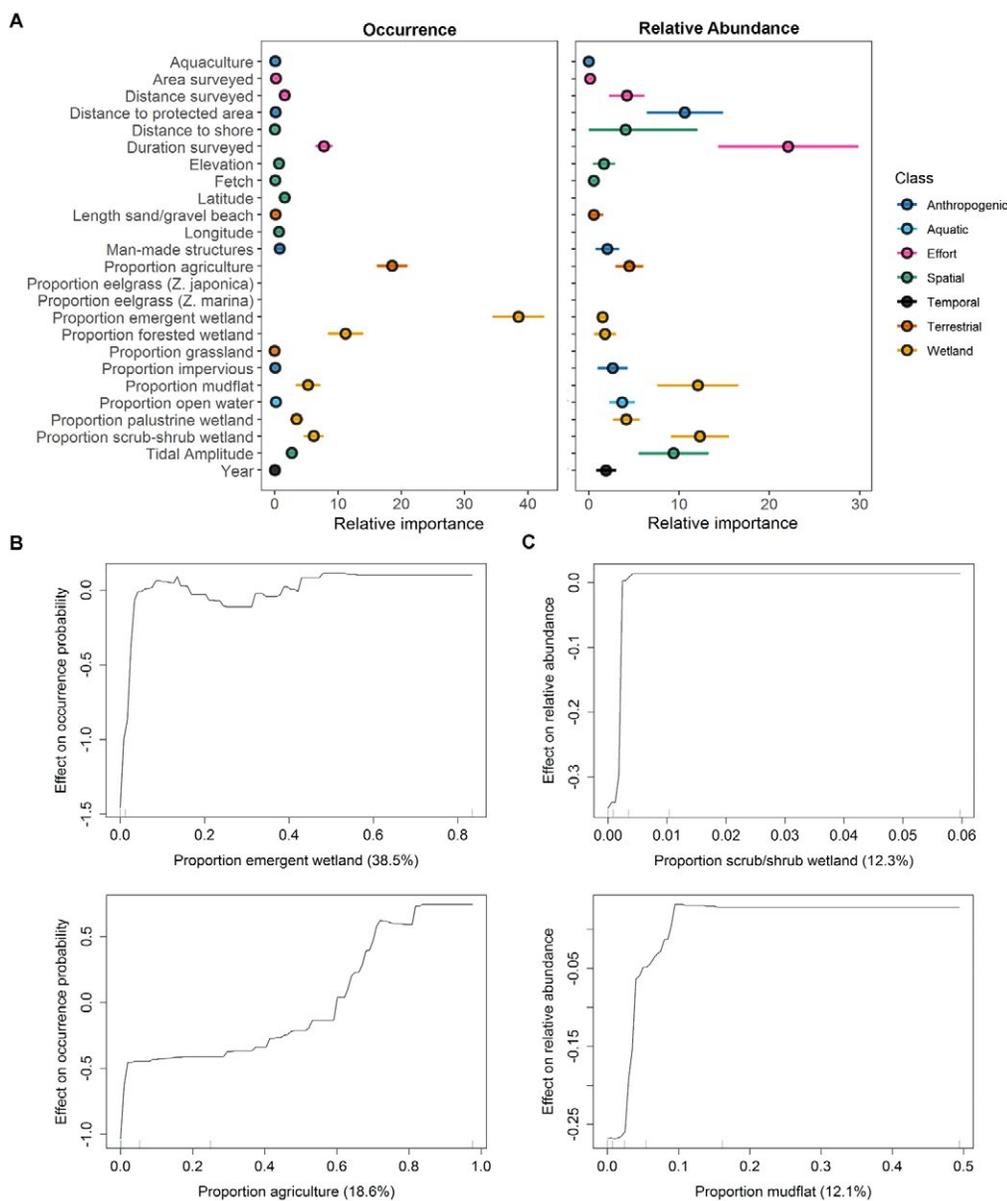


Figure 9. Habitat suitability modeling results for Greater Yellowlegs in fall, including relative importance for all covariates in occurrence and relative abundance models (A), response plots for the two environmental variables with the highest relative importance in occurrence (B) and relative abundance (C) models. Emergent, forested, and scrub/shrub wetlands here are all estuarine, while palustrine wetlands refers to freshwater wetlands of all structural types.

Marsh Wren - Winter

Marsh Wren occurrence and relative abundance models had reasonable fit (Table 4) due to the moderate number and distribution of observations (Table 1). Marsh Wren areas of highest abundance were scattered across the Puget Sound, with concentrations in the Snohomish delta, southern Whidbey Island, and Birch Bay (Appendix B, Figure S8). Marsh Wren occurrence was explained by palustrine wetland and estuarine emergent wetland; where Marsh Wren occurred,

relative abundance was explained most strongly by effort (distance), and palustrine wetland (Figure 10A). Marsh Wren occurrence probability increased with proportions of palustrine wetland and estuarine emergent wetland (Figure 10B). Where Marsh Wren occurred, relative abundance increased with proportion of palustrine wetland and decreased with tidal amplitude within the 1 km² grid cell (Figure 10C).

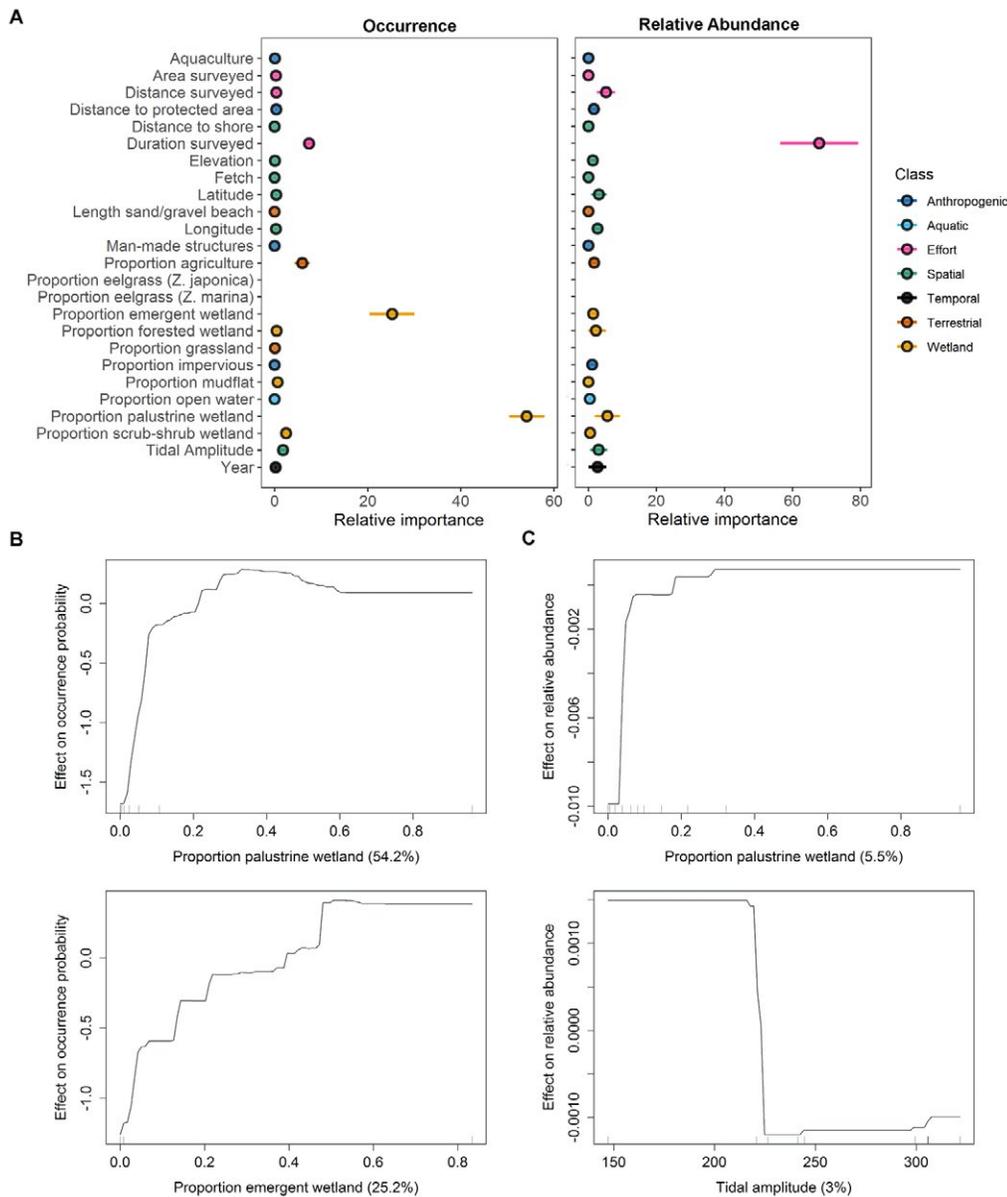


Figure 10. Habitat suitability modeling results for Marsh Wren in winter, including relative importance for all covariates in occurrence and relative abundance models (A), response plots for the two environmental variables with the highest relative importance in occurrence (B) and relative abundance (C) models. Emergent, forested, and scrub/shrub wetlands here are all estuarine, while palustrine wetlands refers to freshwater wetlands of all structural types.

Marsh Wren - Breeding

Marsh Wren occurrence and relative abundance models for the breeding season had reasonable fit (Table 4) due to the moderate number and distribution of observations (Table 1). Marsh Wren areas of highest abundance were scattered across the Puget Sound, with concentrations in the Snohomish delta, Skagit Bay, Birch Bay, and southern Hood Canal regions (Appendix B, Figure S9). Marsh Wren occurrence was explained overwhelmingly by palustrine wetland;

where Marsh Wren occurred, relative abundance was explained most strongly by effort (distance; Figure 11A). Marsh Wren occurrence probability increased with proportions of palustrine wetland and estuarine emergent wetland (Figure 11B). Where Marsh Wren occurred, relative abundance increased with proportion of palustrine wetland and estuarine emergent wetland within the 1 km² grid cell (Figure 11C).

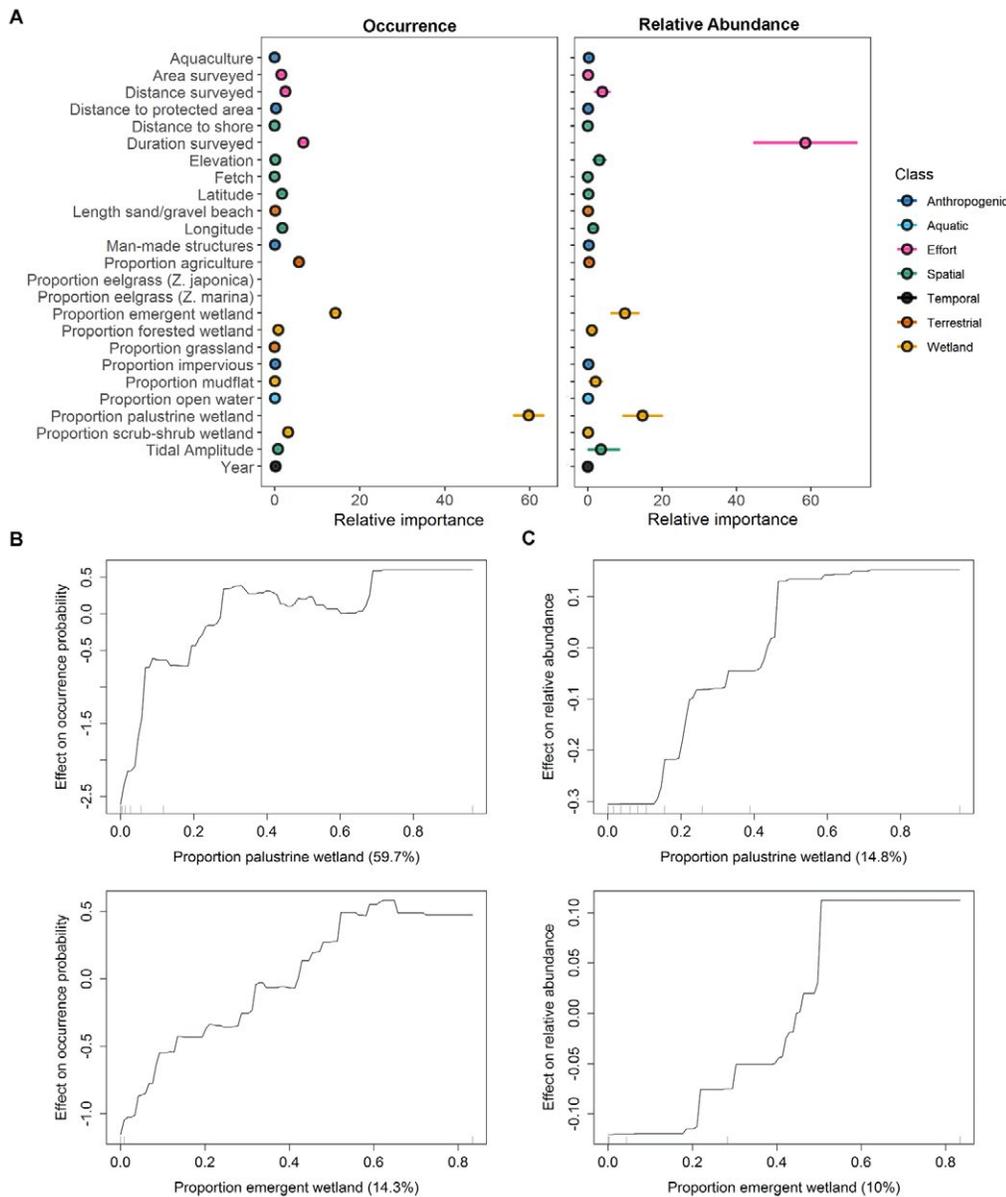


Figure 11. Habitat suitability modeling results for Marsh Wren in the breeding season, including relative importance for all covariates in occurrence and relative abundance models (A), response plots for the two environmental variables with the highest relative importance in occurrence (B) and relative abundance (C) models. Emergent, forested, and scrub/shrub wetlands here are all estuarine, while palustrine wetlands refers to freshwater wetlands of all structural types.

Northern Pintail - Winter

Northern Pintail occurrence and relative abundance models for winter had good fit (Table 4) due to the large number and wide distribution of observations (Table 1). Northern Pintail areas of highest abundance were scattered across the Puget Sound, with concentrations in the Snohomish region, Skagit Bay, and Birch Bay (Appendix B, Figure S10). Northern Pintail occurrence was explained overwhelmingly by survey duration, due the inclusion of >1,200 records from the Midwinter Aerial Survey. Where Northern

Pintail occurred, relative abundance was explained most strongly by man-made structures and longitude (Figure 12A). Northern Pintail occurrence probability increased with proportions of estuarine emergent wetland and mudflat (Figure 12B). Where Northern Pintail occurred, relative abundance increased with length of man-made structures (e.g., dikes, riprap, and docks) and proportion of palustrine wetland within the 1 km² grid cell (Figure 12C).

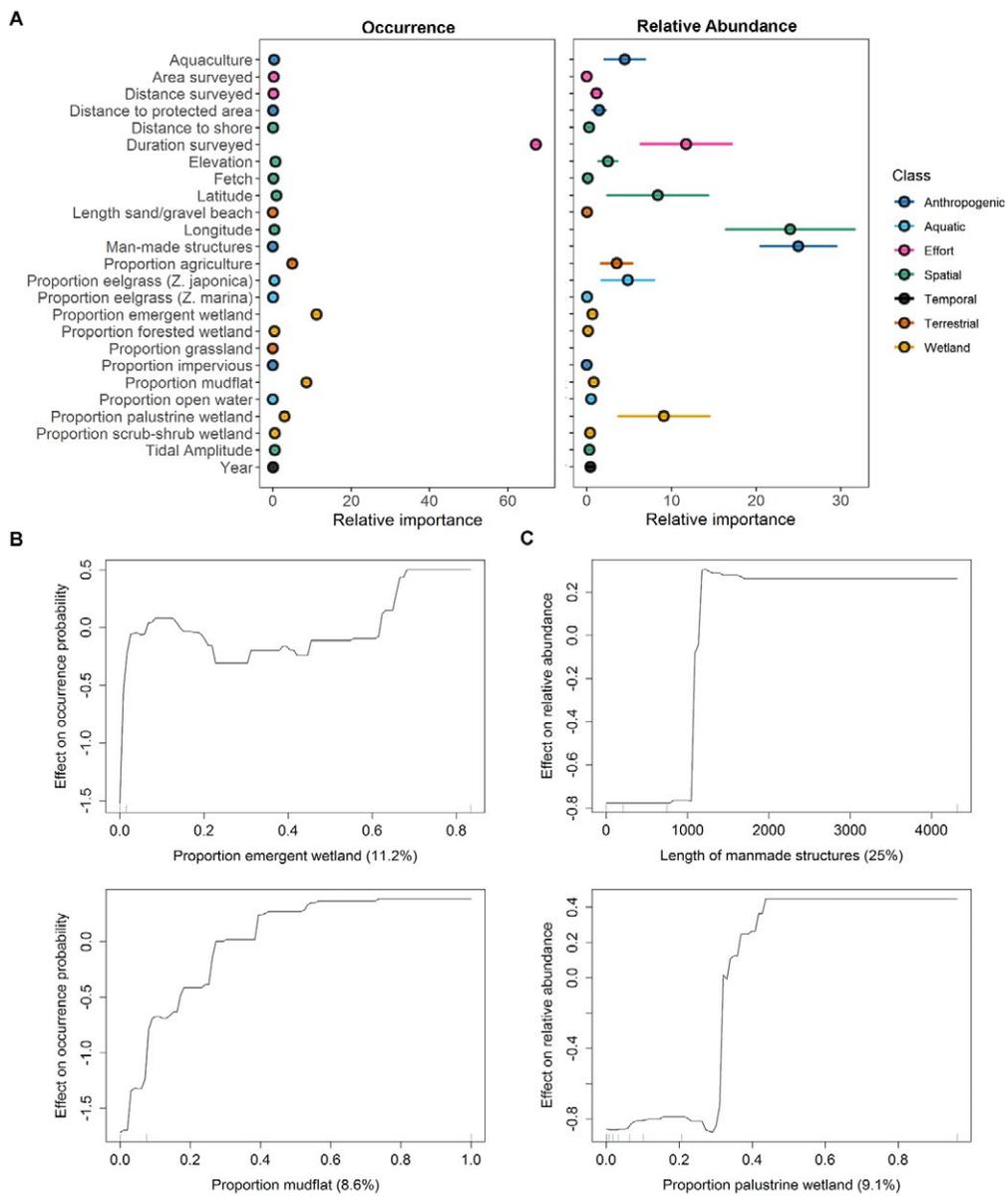


Figure 12. Habitat suitability modeling results for Northern Pintail in winter, including relative importance for all covariates in occurrence and relative abundance models (A), response plots for the two environmental variables with the highest relative importance in occurrence (B) and relative abundance (C) models. Emergent, forested, and scrub/shrub wetlands here are all estuarine, while palustrine wetlands refers to freshwater wetlands of all structural types.

Northern Pintail - Spring

Northern Pintail occurrence and relative abundance models for spring had reasonable fit (Table 4) due to the fewer and more sparsely distributed observations (Table 1). Northern Pintail were most abundant in the northeastern region of the Puget Sound (Appendix B, Figure S11). Northern Pintail occurrence was explained largely by estuarine emergent wetland and mudflat. Where Northern Pintail occurred, relative abundance

was explained most strongly by distance to protected area (Figure 13A). Northern Pintail occurrence probability increased with proportions of estuarine emergent wetland and mudflat (Figure 13B). Where Northern Pintail occurred, relative abundance decreased with distance to protected area and increased with proportion mudflat within the 1-km² grid cell (Figure 13C).

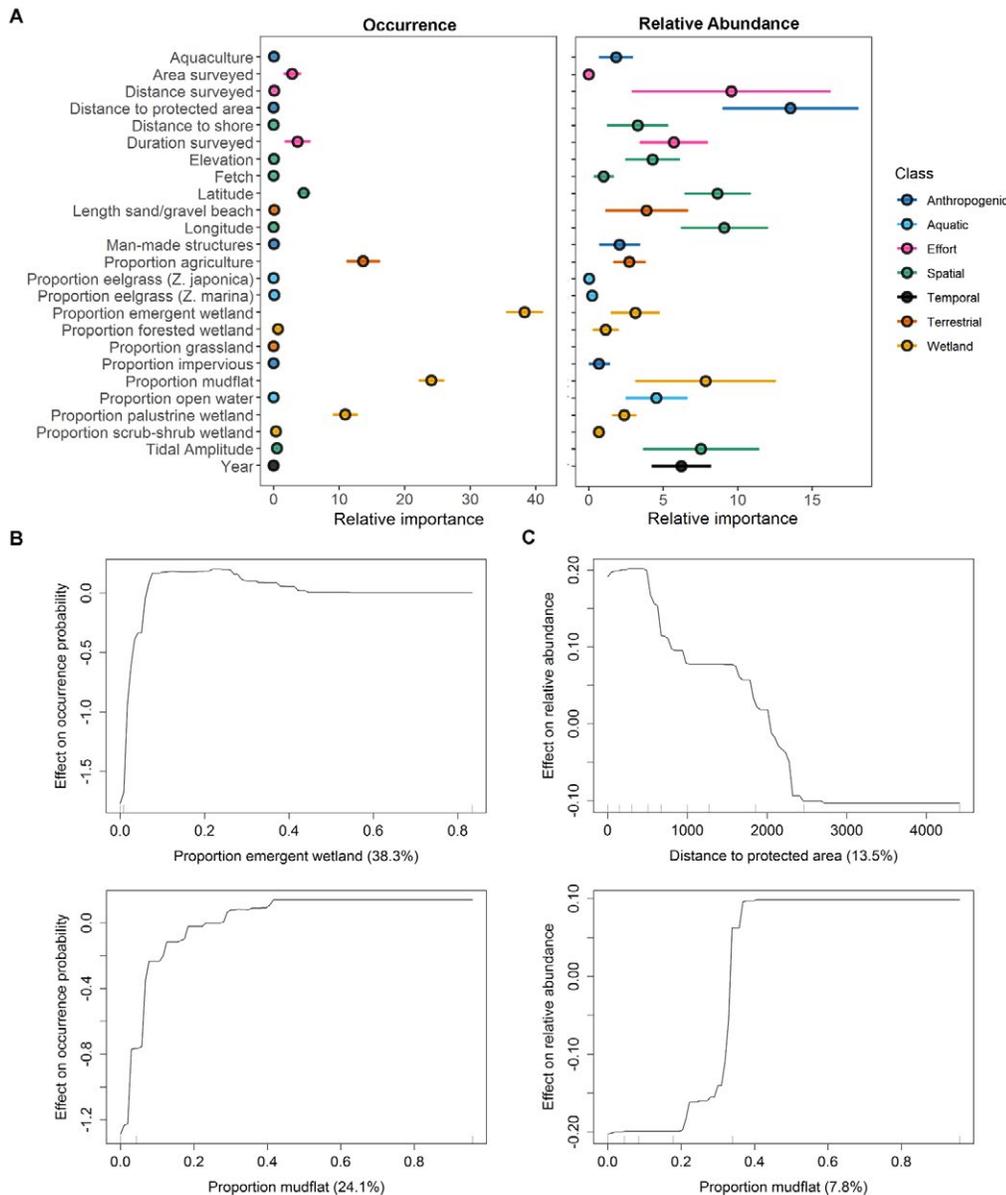


Figure 13. Habitat suitability modeling results for Northern Pintail in spring, including relative importance for all covariates in occurrence and relative abundance models (A), response plots for the two environmental variables with the highest relative importance in occurrence (B) and relative abundance (C) models. Emergent, forested, and scrub/shrub wetlands here are all estuarine, while palustrine wetlands refers to freshwater wetlands of all structural types.

Northern Pintail - Fall

Northern Pintail occurrence models for fall had moderate fit, but relative abundance models did not converge (Table 4) due to the fewer and more sparsely distributed observations (Table 1). Northern Pintail were most likely to occur in the northeastern region of the Puget Sound (Appendix B, Figure

S12). Northern Pintail occurrence was explained largely by estuarine emergent wetland (Figure 14A). Northern Pintail occurrence probability increased with proportions of estuarine emergent wetland and estuarine forested wetland (Figure 14B).

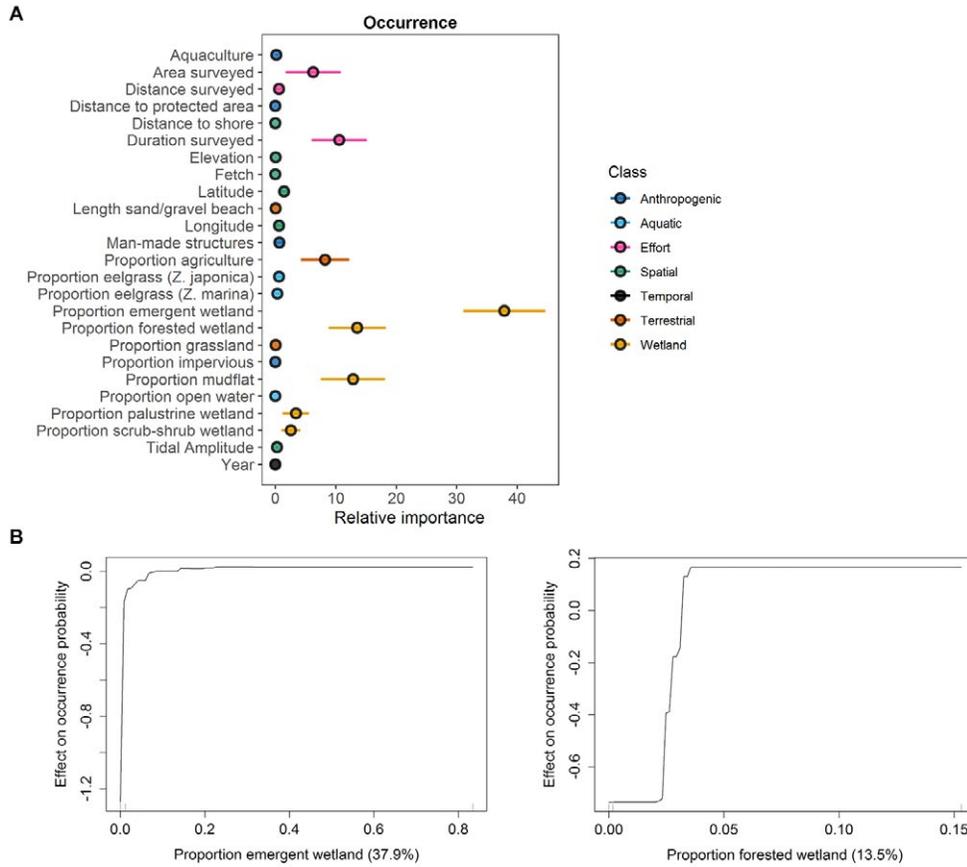


Figure 14. Habitat suitability modeling results for Northern Pintail in fall, including relative importance for all covariates in occurrence models (A), and response plots for the two environmental variables with the highest relative importance in occurrence models (B). Emergent, forested, and scrub/shrub wetlands here are all estuarine, while palustrine wetlands refers to freshwater wetlands of all structural types.

All Species

Averaged across all species and seasons, the variables that most strongly influenced occurrence probability of our narrative species included proportions of estuarine emergent wetland, mudflat, and palustrine wetland (Figure 15). Where narrative

species occurred, relative abundance was most strongly influenced by survey effort (survey distance and duration), followed by proportions of agriculture, estuarine emergent wetland, and mudflat.

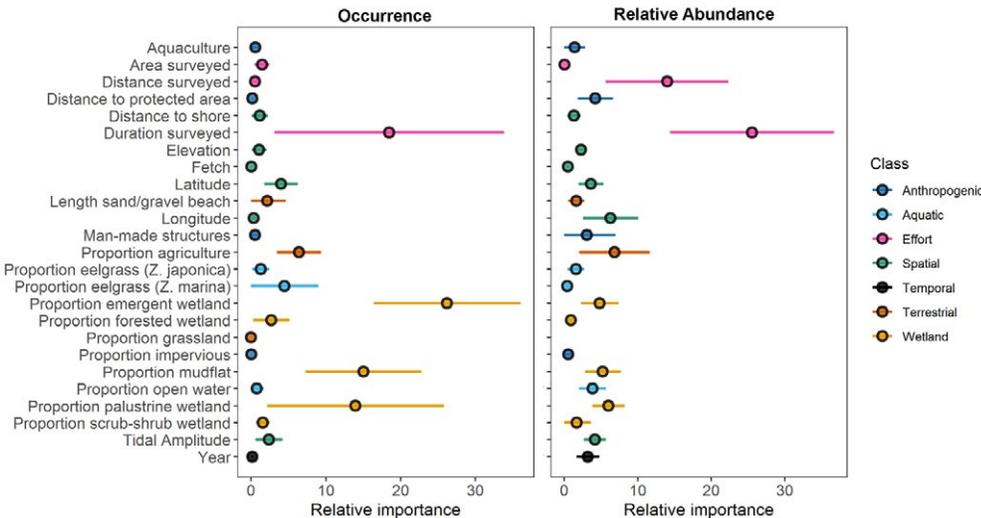


Figure 15. Relative importance for all covariates in occurrence (left) and abundance (right) habitat suitability models for all narrative species and seasons combined. Emergent, forested, and scrub/shrub wetlands here are all estuarine, while palustrine wetlands refers to freshwater wetlands of all structural types.

Restoration Scenario Modeling

The Puget Sound region historically supported 323.7 km² of estuarine wetland. Yet today just 77.3 km² remain, including 12.5 km² of restored wetland, indicating that 246.4 km² of historical estuarine wetlands have been lost. As an exercise to estimate the impacts of this wetland loss, we explored the potential increase in Greater Yellowlegs and Northern Pintail if estuarine wetlands were restored to their original extent across the entire Puget Sound study area and a smaller case study area of Port Susan and South Skagit Bays. We chose to use the Winter models for Greater Yellowlegs and the Spring models for Northern Pintail to conduct the scenario modeling, as these are the seasons when estuarine emergent wetland explained the most variation in occurrence and/or abundance of these species. We selected Port Susan and South Skagit Bays

as a case study because of ongoing progress in large scale restoration across the Stillaguamish River delta.

Model results indicated that, Greater Yellowlegs winter abundance was expected to increase by 20.7% if wetlands were restored to their original extent across the entire Puget Sound study area (Figure 16A, B). Northern Pintail spring abundance was expected to increase by 335.3% if wetlands were restored to their original extent across the Puget Sound (Figure 17A, B). Within the Port Susan Bay and South Skagit Bay case study area, Greater Yellowlegs winter abundance was expected to increase 1.7% from their previous numbers (Figure 16C, D), and Northern Pintail spring abundance 204.1% (Figure 17C, D) if wetlands in this region were restored to their original extent.

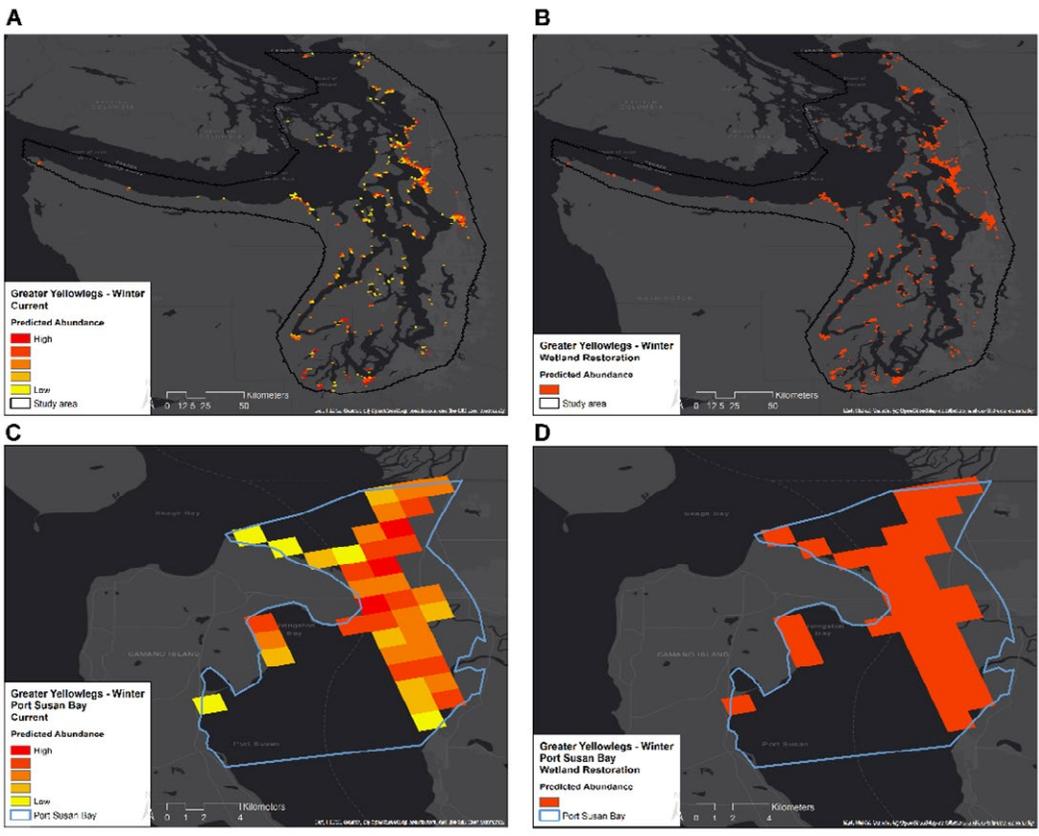


Figure 16. Relative abundance of Greater Yellowlegs in winter across the Puget Sound today (A) and assuming estuarine wetland restoration to their historic extent (B), as well as at Port Susan Bay today (C) and assuming estuarine wetland restoration (D).

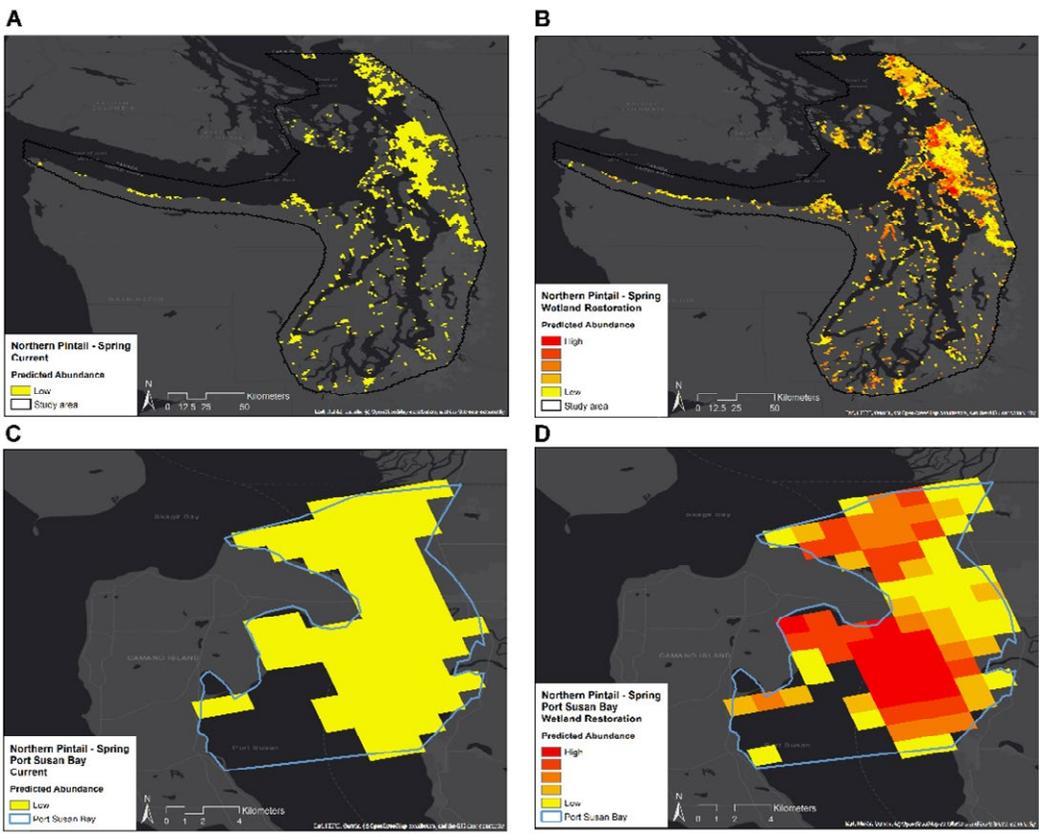


Figure 17. Relative abundance of Northern Pintail in winter across the Puget Sound today (A) and assuming estuarine wetland restoration to their historic extent (B), as well as at Port Susan Bay today (C) and assuming estuarine wetland restoration (D).

Discussion

While each species showed distinct habitat preferences that varied slightly among seasons, a common theme emerged: wetlands – particularly estuarine emergent wetlands – and mudflats were essential to support narrative species populations. Proportion of estuarine emergent wetland was the most important predictor of occurrence, and appeared as one of the top two predictors in one or both models for all species and seasons except for Brant in winter. Proportion of mudflat was the second most important predictor of occurrence, and appeared as one of the top two predictors in one or both models for most species and seasons, excluding Brant in winter, Marsh Wren in both seasons, and Northern Pintail in fall. Agriculture also emerged as an important predictor of species abundance for some species, though further examination is needed. In some cases, e.g., Brant, agriculture may act as a proxy capturing an unmeasured relationship. In other cases, species may use some agricultural fields (e.g., row or cover crop, fallow) for foraging and roosting, but berry production or greenhouses, for example, would be less suitable. Further exploration of species life history, modeling results, and management implications can be found in Table S1, Appendix A: Narrative Species Profiles, and Appendix B: Relative Abundance Maps.

Implications for Regional Monitoring Framework

An important theme that emerged from this exercise is that data quantity and quality are essential for a robust understanding of bird-habitat relationships and distributions around the Puget Sound. Model fit – particularly of relative abundance models that exclude non-detection records – varied widely depending on the number and distribution of surveys. Additionally, effort variables such as survey distance and duration had high relative importance in many relative abundance and some occurrence models. This is partly a reflection of the relationship between survey effort and the probability of detecting a species or the number of individuals detected. However, in some cases these effects resulted from the varied survey protocols used. Some survey data (e.g., the Midwinter

Aerial Survey and transmitter-based records) only reported detections, and because the detections weren't gathered as part of time-bound surveys at a fixed location, a duration of 0 was assigned to all records. When a dataset included a large number of detections with a common duration, this variable became an important predictor of probability of occurrence or relative abundance. The same is true for survey distance, which was not consistently recorded.

The habitat suitability modeling effort presented here highlights the need for a regional monitoring framework. Abundance and occurrence of the narrative species show clear relationships with large-scale environmental conditions across the extent of the Puget Sound. By developing a regional monitoring framework that collects consistent, standardized data across estuarine habitats we can understand the finer-scale processes affecting birds in the region and make informed management decisions that are applied consistently and broadly. If developed and implemented, managers can draw from lessons learned across the region to inform their management plans rather than having to conduct individual, site-specific monitoring efforts that often fail to yield robust results (Koberstein et al. 2017). A regional monitoring effort would also help reduce spatial and temporal data gaps and ensure consistent data collection, reducing the influence of the modeling issues discussed above. Consistent data collection would also allow the data to be entered into a common, region-wide database.

Implications for Management

The habitat suitability modeling effort can be used in a variety of ways to inform management. The maps can be used at a regional scale to identify priority areas for conservation that already support sizable populations of narrative species. Similarly, the maps can be used to identify areas that are proximate to suitable habitat, yet birds are less abundant, suggesting that restoration may be beneficial. At smaller scales, the variable importance figures and response plots convey the environmental conditions that are most important to narrative species as well as the form of the relationship. For example, landscapes with >20% palustrine wetland and >50% estuarine emergent wetland will support the most robust populations of breeding

Marsh Wrens; this information can be used to inform management and restoration plans for this species.

As a result of the species' reliance on estuarine wetland, wetland restoration holds potential to increase populations. Northern Pintail spring abundance could increase by up to 335% across the Puget Sound if all estuarine wetlands were hypothetically restored to their historic extent. Greater Yellowlegs occur in smaller aggregations than Northern Pintails so the simulated effects of wetland restoration were dampened, but the species' abundance could still increase by over 20%. It is important to note that these numbers represent the potential increase in carrying capacity of estuarine wetlands; many other factors beyond Puget Sound habitat availability limit populations of these species. Yet while restoring estuarine wetlands to their historic extent may not be possible and the effect is likely mixed across species, it is clear that estuarine restoration may play a key role in protecting our narrative species into the future, especially in the face of climate change.

Projected changes to Pacific Coast tidal wetlands due to sea level rise indicate that Puget Sound estuaries may become an increasingly important migratory stop-over and wintering habitat for Pacific Flyway birds. A recent assessment of coastal wetland resilience along the U.S. Pacific coast indicates that Washington's tidal wetlands are relatively resilient compared to those in Oregon and California. According to Thorne et al. (2018), 100% of the tidal wetlands evaluated in Oregon and California versus 68% of those in Washington are projected to be submerged under a high sea-level rise scenario by 2110. Local models of sea-level rise indicate that Puget Sound may see an expansion of salt marsh and mudflat habitat in the 21st Century, assuming that landward migration is not constrained (Mauger et al. 2015). Together, these studies make a pressing case for careful consideration of actions that promote marsh migration potential in our region.

Finally, the majority of restoration planning in the Puget Sound region has focused on salmon recovery. Habitat restoration efforts targeted for salmon focus on increasing estuarine emergent wetland and palustrine wetland, among other wetland types (Davis et al., 2019). This reduces agriculture and, in some cases, changes the availability of un-vegetat-

ed mudflats. Yet all three of these habitat types are important to most of our narrative species. Moreover, while an increase in estuarine emergent wetland may prove to be beneficial for our narrative species, the result is not universal throughout their life histories, as habitat use varies seasonally. Additionally, proximity to other land covers should be considered. For example, shorebirds may use mudflats during low or slack tides, but retreat to agricultural fields during high tides. Overall, our results suggest salmon-centric restoration alone may not be sufficient to increase habitat availability for our narrative species.

Recommendations for Restoration and Monitoring

Restoration

- Wetland restoration may greatly increase the carrying capacity of estuarine wetlands for wetland-dependent species, notably Northern Pintail.
- Where possible, target restoration to areas within the historical wetland extent with currently low numbers of birds, where the potential for bird abundance increases may be greatest, and where marsh migration potential is high.
- Involve avian specialists in restoration planning and design to maximize potential for achieving multi-species benefits.
- Coordinate avian habitat restoration efforts with tribes, land trusts, nonprofits and other entities interested in a resilient ecosystem approach to restoration.

Monitoring

- Additional monitoring is needed, especially for species and seasons with poor model fit, such as Greater Yellowlegs and Brant (spring, fall), Dunlin, Northern Pintail (fall). Monitoring commonly occurs during breeding and winter seasons, while most

waterfowl and shorebird species are migratory and use estuarine habitats throughout the year. In order to answer more complex questions about habitat associations monitoring during migration windows may also be warranted.

- Where possible, survey methods that are standardized and/or that include gathering of ancillary data needed to correct for imperfect detection (e.g., repeat surveys) would enable us to better understand species abundance, especially for comparisons across habitat types.
- Future monitoring efforts (e.g., regional avian monitoring framework) should consistently collect effort data such as survey distance and duration. Efforts to standardize monitoring efforts and house data in shared databases would greatly enhance our ability to understand habitat suitability and, ultimately, populations of birds in the Puget Sound region.
- Target additional monitoring to gap areas with little monitoring to date.
- Develop a better understanding of the impact of current ecosystem restoration practices have on a broader suite of estuarine-reliant species by working with agencies, non-profits, and tribes to incorporate avian monitoring into restoration activities.
- Coordinate avian monitoring with other biotic and abiotic monitoring efforts (e.g. salmon, vegetation, geomorphology) to develop predictive models that

can be applied to restoration planning and monitoring. Doing so would help elucidate data gaps and monitoring needs and improve social support for restoration, raising the profile of estuary birds in restoration planning.

Acknowledgments

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Supplemental Material

Table S1. Top two environmental variables in each species-season model that explain the greatest variation in occurrence and relative abundance. The form of the relationship between occurrence / relative abundance and the environmental variable is indicated in parentheses (positive: +, negative: -).

Species	Seasons	Occurrence		Relative Abundance	
		Variable 1	Variable 2	Variable 1	Variable 2
Brant	Winter	Distance to shore (+)	Proportion eelgrass (+)	Proportion agriculture (+)	Length sand/gravel beach (+)
	Spring	Proportion eelgrass (+)	Length sand/gravel beach (+)	Proportion estuarine emergent wetland (+)	Proportion mudflat (+)
Dunlin	Winter	Proportion mudflat (+)	Proportion estuarine emergent wetland (+)	Proportion agriculture (+)	Proportion estuarine emergent wetland (+)
	Spring	Proportion mudflat (+)	Proportion estuarine emergent wetland (+)	Proportion mudflat (+)	Proportion estuarine emergent wetland (+)
Greater Yellowlegs	Winter	Proportion estuarine emergent wetland (+)	Proportion mudflat (+)	Proportion open water (-)	Proportion palustrine wetland (+)
	Spring	Proportion estuarine emergent wetland (+)	Proportion mudflat (+)	Tidal amplitude (+)	Proportion mudflat (+)
	Fall	Proportion estuarine emergent wetland (+)	Proportion agriculture (+)	Proportion estuarine scrub/shrub wetland (+)	Proportion mudflat (+)
Marsh Wren	Winter	Proportion palustrine wetland (+)	Proportion estuarine emergent wetland (+)	Proportion palustrine wetland (+)	Tidal amplitude (-)
	Breeding	Proportion palustrine wetland (+)	Proportion estuarine emergent wetland (+)	Proportion palustrine wetland (+)	Proportion estuarine emergent wetland (+)
Northern Pintail	Winter	Proportion estuarine emergent wetland (+)	Proportion mudflat (+)	Length of man-made structures (+)	Proportion palustrine wetland (+)
	Spring	Proportion estuarine emergent wetland (+)	Proportion mudflat (+)	Distance to protected area (-)	Proportion mudflat (+)
	Fall	Proportion estuarine emergent wetland (+)	Proportion forested wetland (+)	—	—

Appendix A: Narrative Species Profiles

Pacific Brant (*Branta bernicla*)

General Description, Habitat, and Range

Brant are a small, darkly colored goose. Brant breed primarily in arctic regions of Alaska, Canada and eastern Russia, with the largest concentrations found on the Yukon-Kuskokwim Delta, Alaska. Brant winter range is along the Pacific Coast, primarily in bays from the Alaska Peninsula to the Baja California Peninsula in Mexico. Brant are considered a 'sea goose' and 'seagrass-obligate' meaning they are highly dependent upon eelgrass estuaries as well as low disturbance sandbars to ingest grit, small rock and sand fragments.

Conservation Status

Range wide (IUCN): Least Concern

North America (NABCI): Moderate Concern

The population status of Brant is stable. However, long-term declines in regional breeding and wintering sites have been documented, and both regions are vulnerable to threats such as sea-level rise impacts to nest sites and eelgrass conditions across the Pacific Coast.

Occurrence in Puget Sound

Rare during fall migration, common during winter, and increasing numbers and distribution during spring migration

During winter they are most abundant in Padilla, Samish, Lummi, and Dungeness bays accounting for 10,000 – 20,000 individuals. During spring, other regions of the Puget Sound, like the Nisqually Reach, provide additional suitable habitat as the relationship between tide and eelgrass beds become more favorable to access food.

Integrating Model Results with Life History

Habitat suitability model results re-enforced this species' unique environmental constraints, while highlighting the need to better describe these relationships, especially the need for spring survey data. Sand/gravel beach was a strong environmental predictor of occurrence during spring and winter abundance. This habitat type is not well mapped in Puget Sound, though is likely limited in abundance, or constrained by activities not conducive to Brant (e.g. recreation activities), across the landscape.

Implications for Management

Harvest management objectives are based on winter status, though status during spring may be more important to regional planning, as food quality has been linked to future nesting success. Spring models emphasized the difference between native (*Zostera marina*) and non-native (*Z. japonica*) eelgrass. Understanding future conditions and the interaction between these two types could be significant in understanding site suitability and anticipated shifts or declines in occurrence, under sea-level rise scenarios.



Brants. Photo: Hillary Eggers

Dunlin (*Calidrus alpina*)

General Description, Habitat, and Range

Dunlin are a small, chunky shorebird with a distinctly drooped bill. Dunlin breed in arctic and subarctic regions around the world. In North America, Dunlin breed in Alaska and Canada and winter along the coastlines and. The Pacific Flyway population (*C. a. pacifica*) winters along the Pacific Coast from SW British Columbia to northern Mexico. During migration and the nonbreeding season they are often found in large aggregations (>5,000), primarily using coastal mudflats. Other coastal and non-tidal habitats, including adjacent agricultural lands, are also used when mudflats are inaccessible.

Conservation Status

Range wide (IUCN): Least Concern

North America (NABCI): Moderate Concern

There is no range-wide program to estimate population size and trends for the Pacific Flyway population, although there is anecdotal evidence that populations have declined in recent decades. In North America breeding and non-breeding habitat conditions are vulnerable to future threats, such as sea level rise.

Occurrence in Puget Sound

Common during spring and fall migration and winter

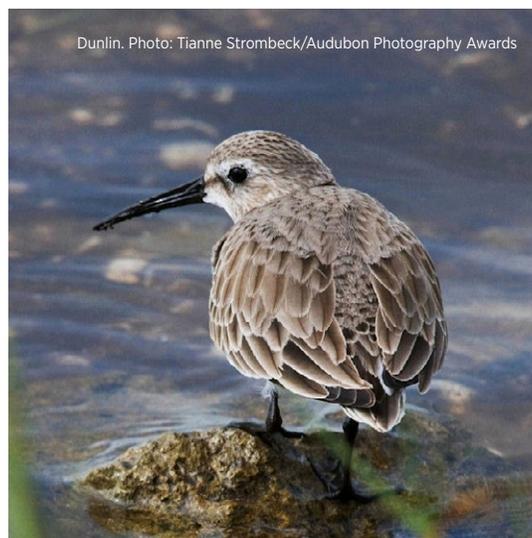
During winter, Dunlin are the most abundant shorebird species in Puget Sound, with the largest numbers of individuals occurring in the bays of North Puget Sound (Evenson and Buchanan 1997). Padilla, Skagit, and Port Susan Bays all have counts of >30,000, likely due to extensive areas of both estuarine emergent wetlands and adjacent agricultural lands. Throughout the rest of Puget Sound, they are found in smaller numbers (<1, 000) and are patchily distributed.

Integrating Model Results with Life History

The habitat suitability models for Dunlin during wintering and spring migration periods correctly predicted the center of abundance in North Puget Sound estuaries and bays. In both periods, models showed a strong association with estuarine emergent wetlands and mudflats. In the winter, Dunlin occupancy was associated with agricultural lands, a habitat they often use for high-tide roosts.

Implications for Management

Climate change threats are a significant concern for Dunlin populations. Sea level rise may decrease the amount of available mudflat habitat and may affect the estuarine food web. Estuarine restoration is likely to benefit Dunlin in the face of climate change by allowing habitat migration and increasing resilience of its preferred habitat. The consequence of continued human development in agricultural landscapes is unclear on Dunlin populations.



Greater Yellowlegs (*Tringa melanoleuca*)

General Description, Habitat, and Range

The Greater Yellowlegs is a relatively large migratory North American shorebird with long legs, neck, and bill. The species breeds in the boreal forest region of Canada and Alaska. In migration and winter, they use a wide variety of fresh- and saltwater wetland habitats (flooded tidal flats and agricultural fields, emergent wetlands, lake and river margins, sewage ponds) throughout North America. These birds forage in shallow water, where they eat insects, other invertebrates, and small fish.

Conservation Status

Range wide (IUCN): Least Concern

North America (NABC): Moderate Concern

There is no range-wide program to estimate population size and trends for the Pacific Flyway population of Greater Yellowlegs.

Occurrence in Puget Sound

Common during spring and fall migration, uncommon during winter

Greater Yellowlegs is one of the most ubiquitous shorebirds in the region. In coastal estuaries, they commonly use low-stature estuarine emergent wetland habitats, including channels, as well as the ecotone between mudflat and marsh. However, they can also be found during spring and fall migration using many freshwater habitats, including rivers.

Integrating Model Results with Life History

Results from the habitat suitability model predicted the broad distribution of Greater Yellowlegs across Puget Sound and their use of both estuarine and inland habitats. Across all season, models affirmed their strong positive association with estuarine emergent wetland and mudflat habitats, but also highlighted their plasticity in habitat use as agriculture, estuarine scrub-shrub wetlands, and palustrine wetlands were all associated with either abundance or occurrence.

Implications for Management

With its strong positive relationship to estuarine emergent wetland habitat and mudflats, this species has likely been severely impacted by the loss of estuarine habitat throughout Puget Sound. Indeed, the restoration scenario modeling analysis indicated yellowleg abundance would increase by ~20% if wetlands were restored to their original extent in Puget Sound. Estuarine restoration would increase habitat availability for this species.



Northern Pintail (*Anas acuta*)

General Description, Habitat, and Range

Northern Pintail are a dabbling duck with a long slender neck. They are strongly associated with shallow-water emergent wetland habitats where they seek seeds, plant material, and small invertebrates by skimming the water surface, sifting through sediment, or tipping to reach underwater. They breed in Alaska and regions of Alberta, Canada. During migration and winter months, they can be found in coastal and inland marshes between Alaska and Mexico.

Conservation Status

Range wide (IUCN): Least Concern

North America (NABCI): Moderate Concern

The North American population of Northern Pintail are considered below population objective, with long-term counts from aerial breeding surveys conducted since 1955 consistently below long-term averages. Due to this status, Northern Pintail are the most restricted dabbling duck in annual waterfowl regulations and pose a management challenge and conservation priority.



Occurrence in Puget Sound

Common during spring and fall migration, and winter

During winter, the largest concentrations are found in the North Puget Lowlands, but Northern Pintail can be found anywhere that shallow water provides opportunities to find food. The proximity of estuarine wetlands and mudflats to inland freshwater wetlands determines how long Northern Pintail are able to forage in a given area, and how many individuals the area can support. During spring, Northern Pintail passing through from southern wintering areas are highly associated with the Alaska breeding segment, and require more energy-rich prey than other seasons to fuel their migration and breed successfully.

Integrating Model Results with Life History

Results from the habitat suitability model predicted persistent concentrations in the North Puget Lowlands with smaller scattered concentrations in other areas. Models during all periods affirmed their strong positive association with estuarine emergent wetlands, with other wetland types shifting in importance across seasons, e.g., mudflats in winter and spring, and estuarine forested wetlands in the fall. These shifts are likely due to seasonal changes in diet requirements and shallow water availability across the landscape. Information on the seasonal occurrence of water and proximity between the network of estuarine and palustrine wetlands would likely improve model predictions, emphasizing the need for repeated assessments of habitat and Northern Pintail abundance, particularly during spring months.

Implications for Management

With its strong positive relationship to emergent wetland (both estuarine and palustrine) Northern Pintail has likely been severely impacted by the loss of a diverse wetland complex. Estuarine restoration may increase habitat for this species at certain times of the year, but this relationship is likely dependent upon the surrounding landscape. They would benefit from a comprehensive approach to wetland restoration. Understanding the linkage between Northern Pintail and seasonally-influenced habitat attributes would be significant in understanding site suitability under anticipated changes in precipitation and runoff during spring. Additionally, insights into sites providing resting versus feeding habitat are important to differentiate. In particular, adequate feeding habitat during spring would have direct implications for female body condition and reproduction.

Marsh Wren (*Cistothorus palustris*)

General Description, Habitat, and Range

The Marsh Wren is a small, round-bodied member of the wren family that is ubiquitous throughout North American marshes, both fresh- and saltwater. It breeds in dense patches of cattails, bulrushes, and other marsh vegetation; typically 1-3 feet over water.

Conservation Status

Range wide (IUCN): Least Concern

North America (NABC): Low Concern

Although this species has undoubtedly declined due to the loss coastal and freshwater marshes, it is considered widespread and common. Breeding Bird Survey results indicate Marsh Wrens with stable to increasing trends across North America since 1966.

Occurrence in Puget Sound

Year round resident

Marsh Wrens use coastal areas, particularly marshes higher in the tidal gradient where tall cattails and bulrushes occur. A variety of shrubby habitats, especially along unmaintained dikes adjacent to estuaries and freshwater wetlands further inland, are also used.

Integrating Model Results with Life History

The habitat suitability model highlighted the Marsh Wren generalist habitat needs. It was strongly associated with estuarine emergent wetland and palustrine wetlands, which included a diverse array of wetland types including emergent, forested, and scrub/shrub wetland

Implications for Management

With its strong positive relationship to emergent and non-tidal wetlands, this species has likely been severely impacted by the loss of all wetland types throughout the region. Although estuarine restoration will increase habitat availability for this species, it would also benefit from a more comprehensive approach to wetland restoration including palustrine wetlands that may or may not be connected to river floodplains.



Appendix B: Relative Abundance Maps from Habitat Suitability Models

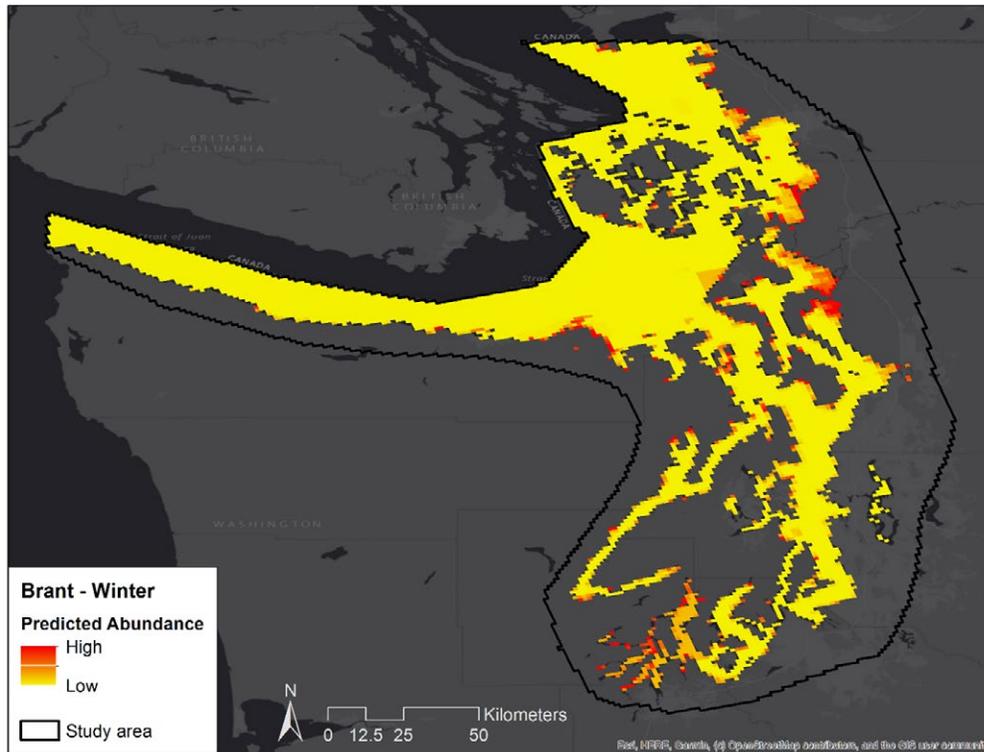


Figure S1. Relative abundance map of Brant in winter across the Puget Sound study area from habitat suitability models.

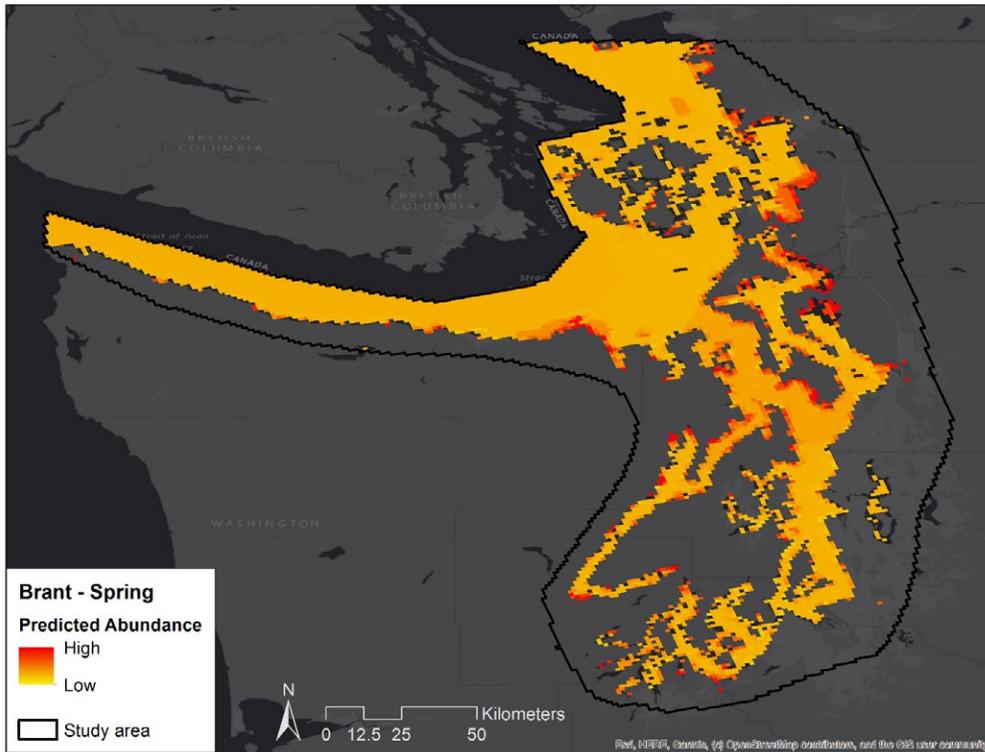


Figure S2. Relative abundance map of Brant in spring across the Puget Sound study area from habitat suitability models.

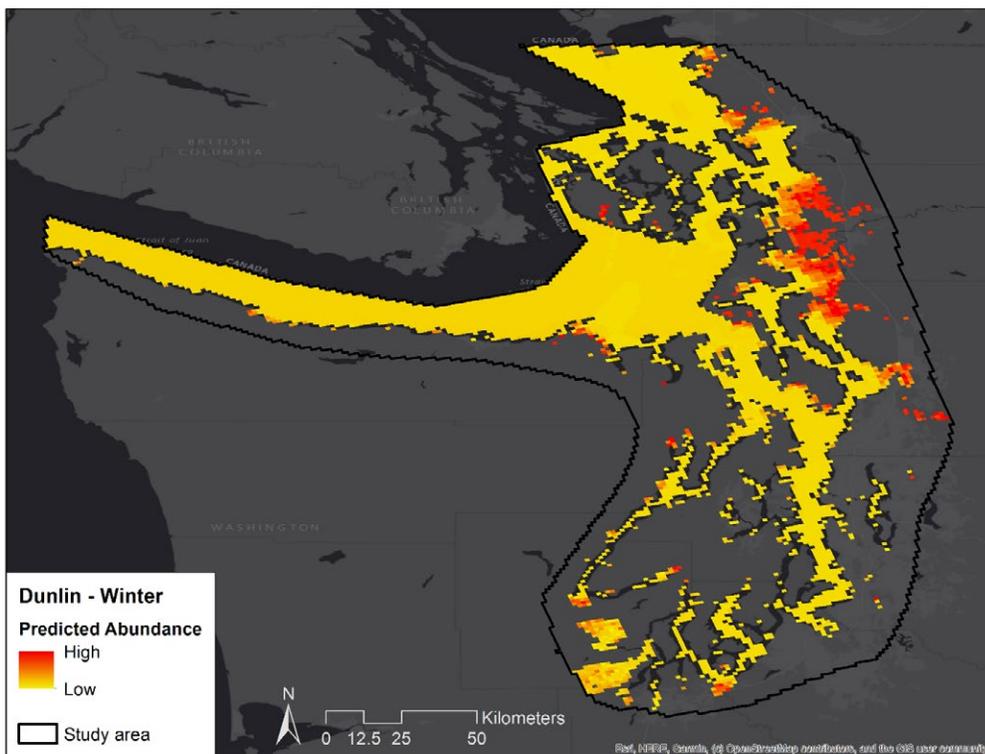


Figure S3. Relative abundance map of Dunlin in winter across the Puget Sound study area from habitat suitability models.

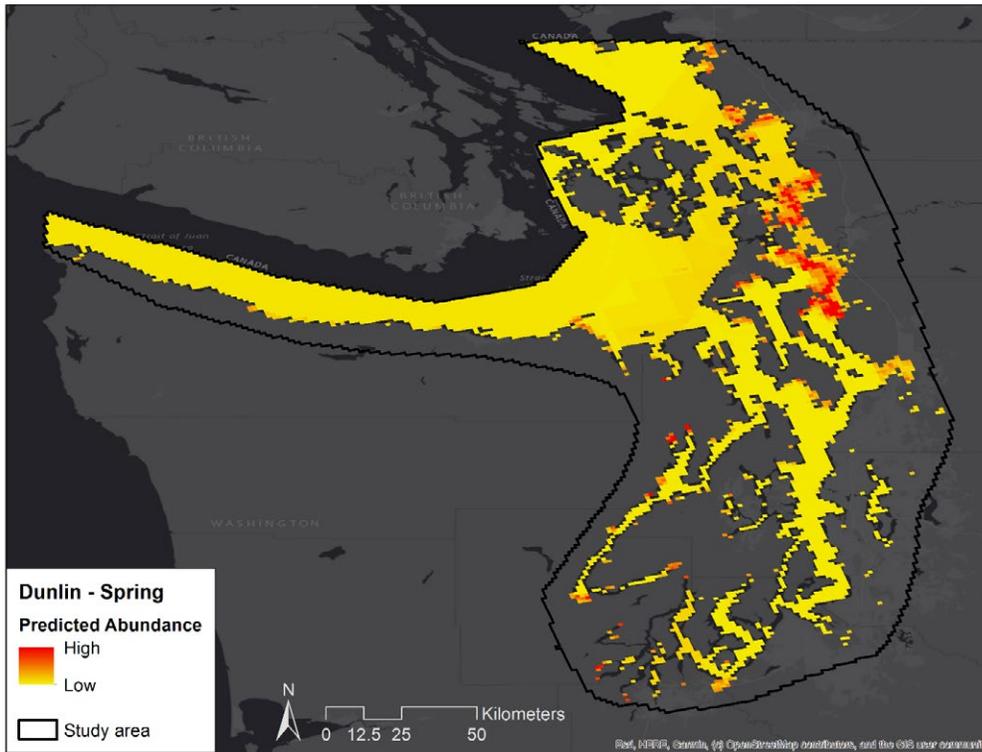


Figure S4. Relative abundance map of Dunlin in spring across the Puget Sound study area from habitat suitability models.

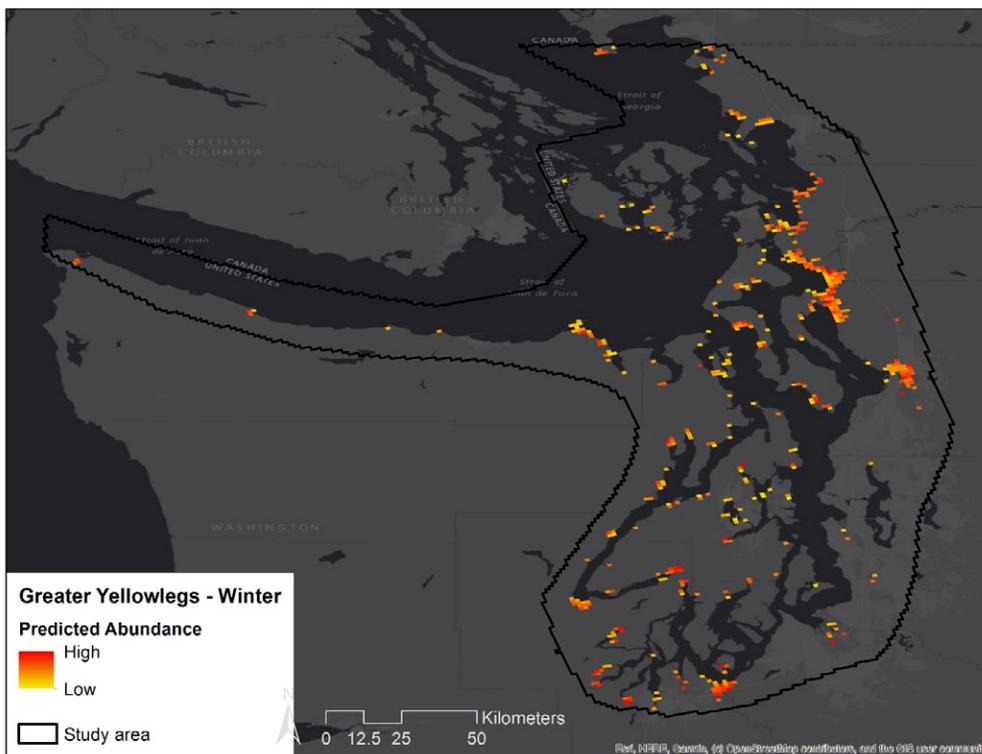


Figure S5. Relative abundance map of Greater Yellowlegs in winter across the Puget Sound study area from habitat suitability models.

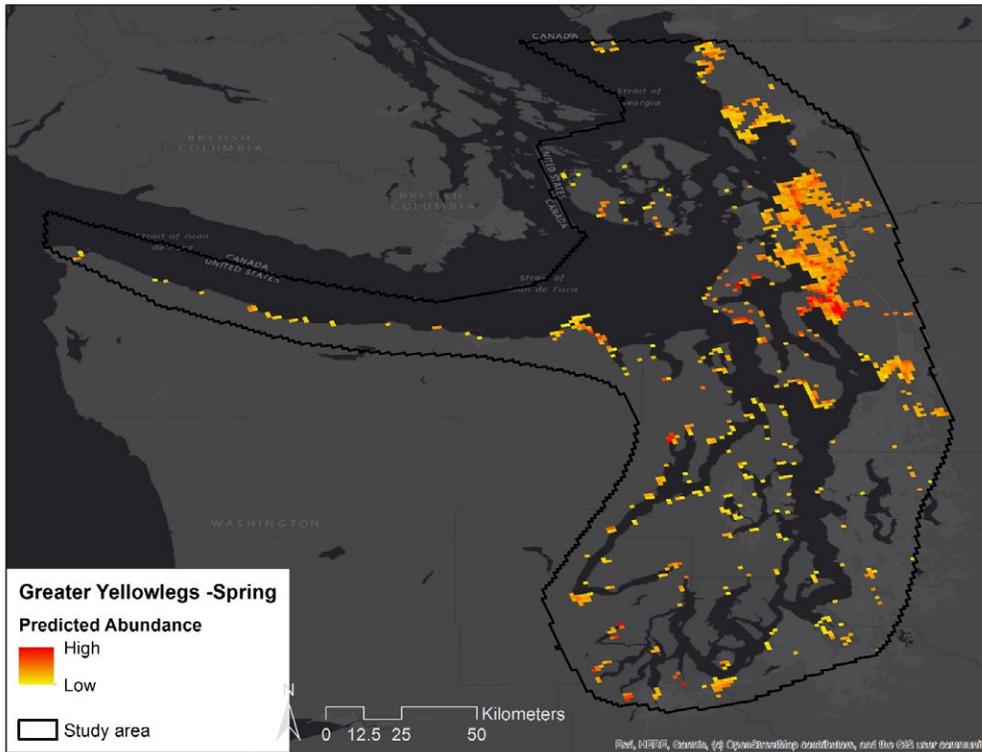


Figure S6. Relative abundance map of Greater Yellowlegs in spring across the Puget Sound study area from habitat suitability models.

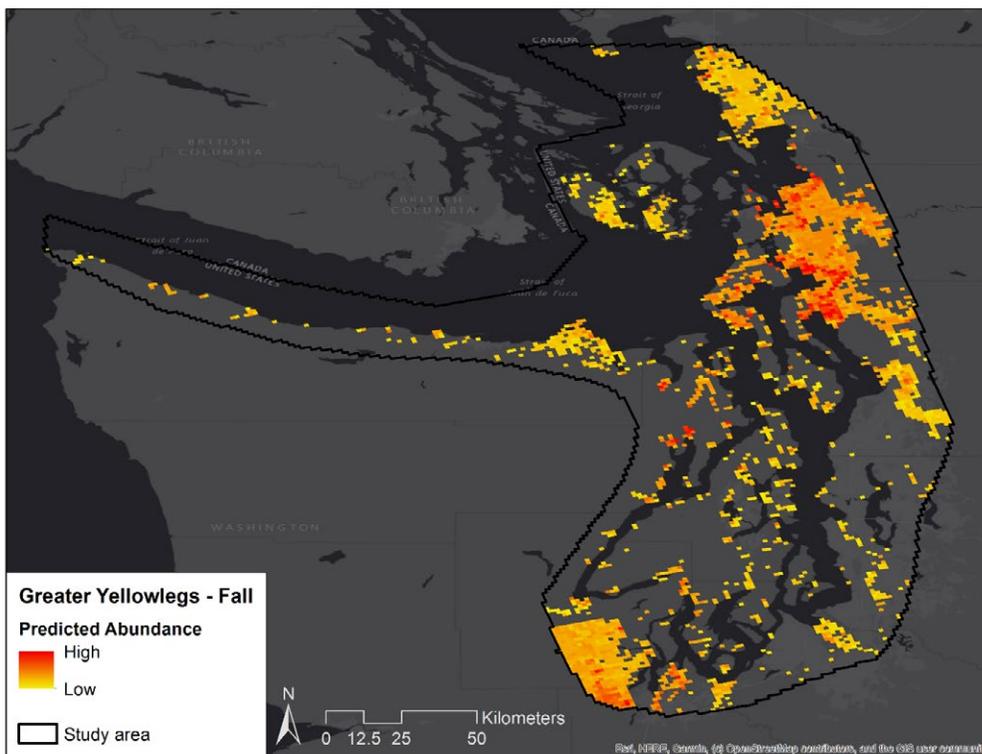


Figure S7. Relative abundance map of Greater Yellowlegs in fall across the Puget Sound study area from habitat suitability models.

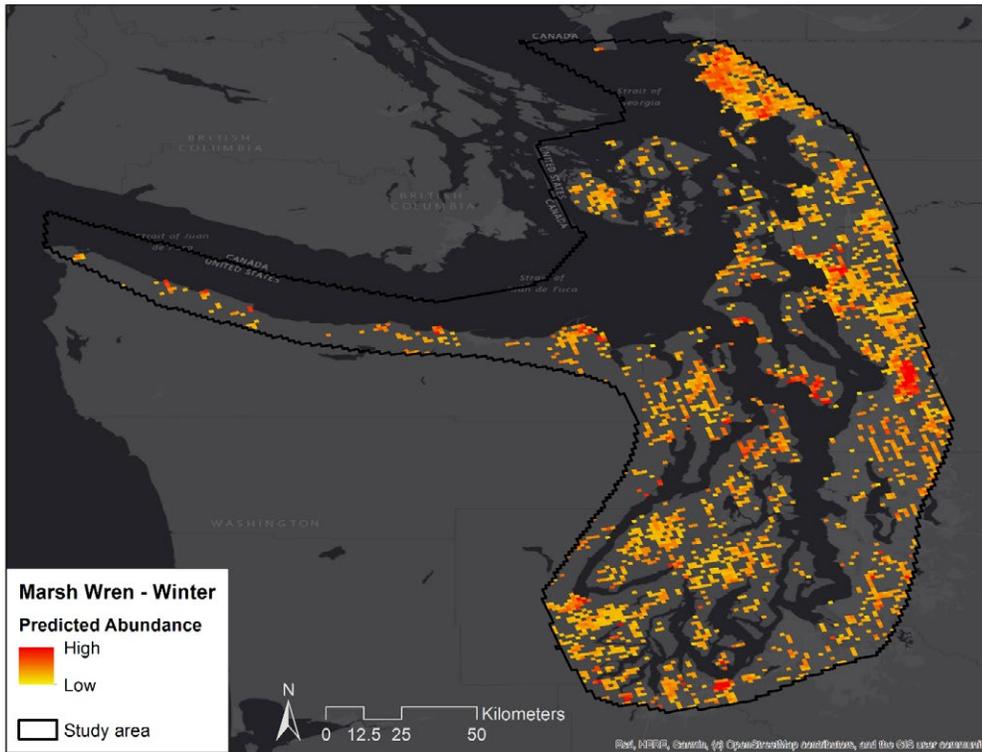


Figure S8. Relative abundance map of Marsh Wren in winter across the Puget Sound study area from habitat suitability models.

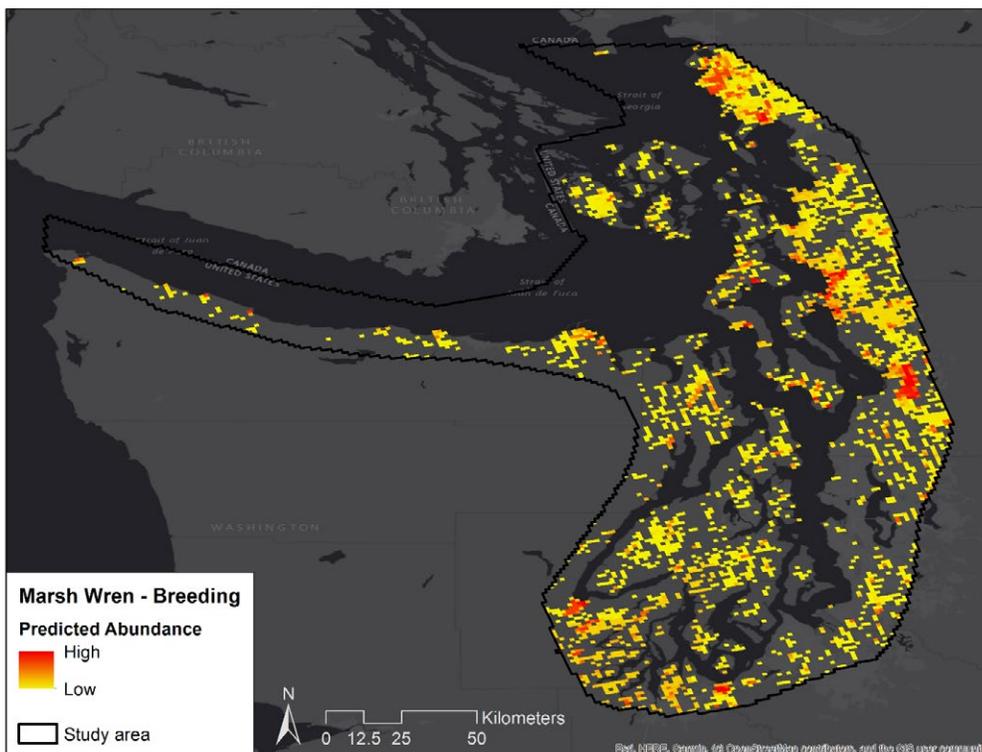


Figure S9. Relative abundance map of Marsh Wren in the breeding season across the Puget Sound study area from habitat suitability models.

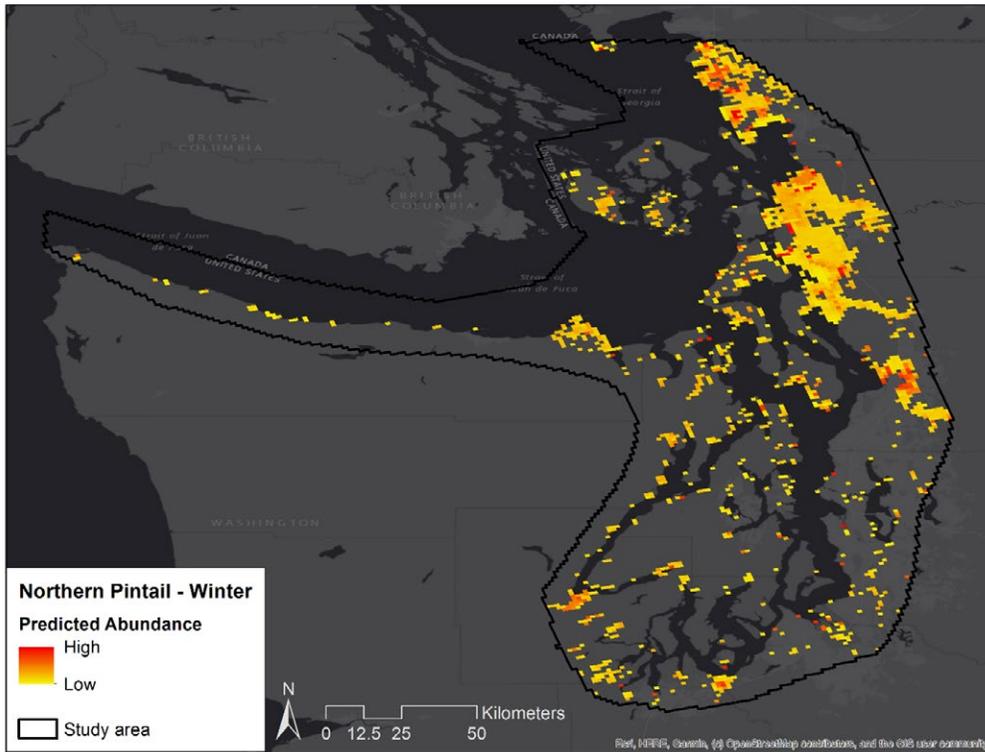


Figure S10. Relative abundance map of Northern Pintail in winter across the Puget Sound study area from habitat suitability models.

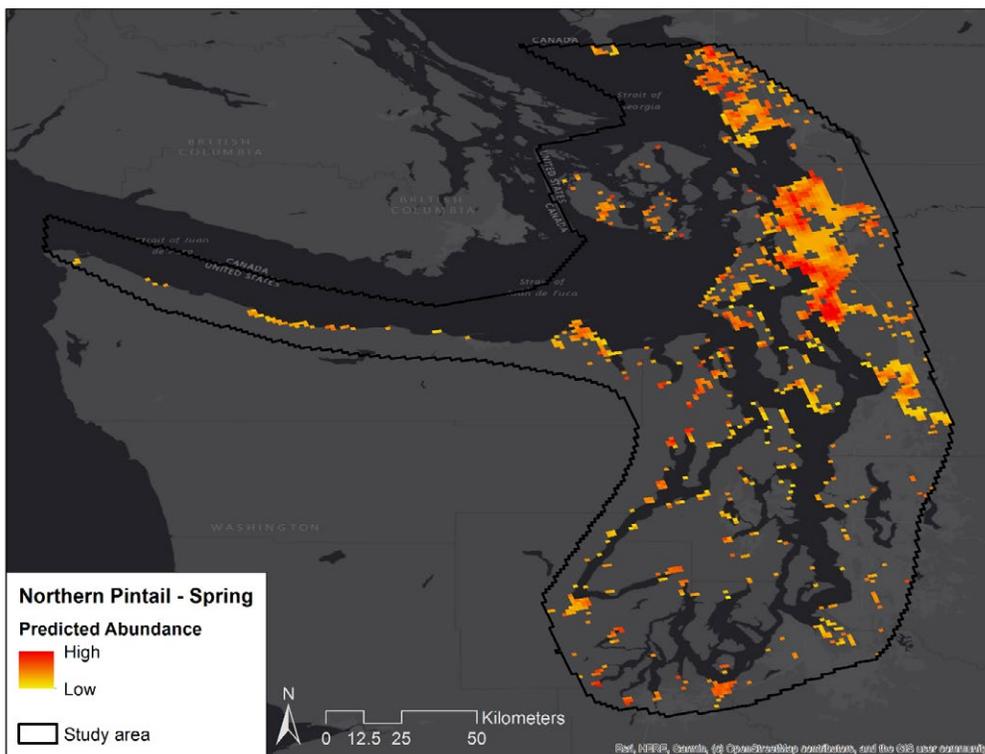


Figure S11. Relative abundance map of Northern Pintail in spring across the Puget Sound study area from habitat suitability models.

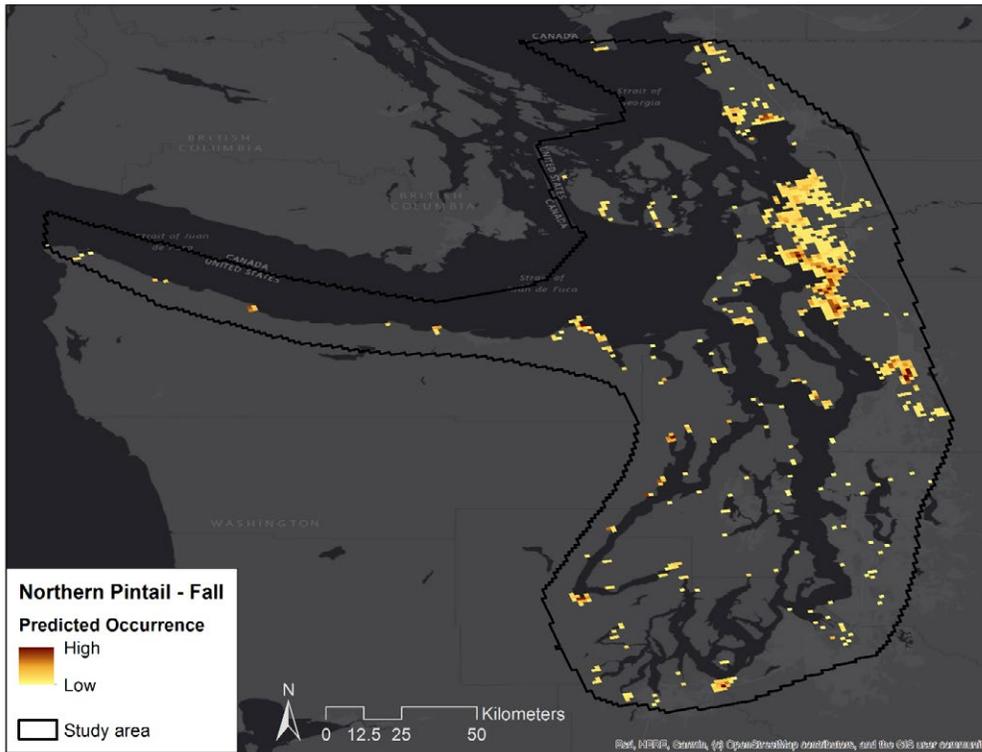


Figure S12. Occurrence probability map of Northern Pintail in fall across the Puget Sound study area from habitat suitability models.



**Avian Habitat Suitability Models
for Puget Sound Estuary Birds**