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ARTICLE
Coastal and Marine Ecology

The effects of spatiotemporal variation in marine resources on the occupancy dynamics of a terrestrial avian predator

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Abstract

Identifying how species respond to system drivers such as weather, climate, habitat, and resource availability is critical for understanding population change. In coastal areas, the transfer of nutrients across the marine and terrestrial interface increases complexity. Nesting populations of bald eagles (*Haliaeetus leucocephalus*) along the Pacific coast of North America, although terrestrial, are largely dependent on marine resources during the breeding season and therefore represent a good focal species for understanding the linkages of nutrients between terrestrial and marine systems. Due to their location, coastal eagle populations are susceptible to a variety of climate-induced perturbations, from both land and sea. The northeast Pacific Marine Heatwave (PMH) of 2014–2016 had wide-ranging impacts on the marine ecosystem and provided an opportunity to explore how marine conditions can impact terrestrial wildlife populations. We used a spatially explicit multistate occupancy modeling framework to analyze >30 years of bald eagle nest occupancy data collected in four large national parks along a coastal interior gradient in Alaska, USA. We assessed occupancy state in relation to weather conditions, salmon abundance, access to alternate prey resources, and the PMH event to help elucidate the factors affecting bald eagle occupancy dynamics over time. We found that occupancy probability was higher in areas where prey resources were concentrated (e.g., near seabird colonies, where bears facilitate access to salmon carcasses). We also found that the probability of reproductive success was higher during warmer, drier springs with higher-than-average salmon abundance. After the onset of the PMH, success declined in the areas most dependent on non-salmon marine resources. These findings confirm the importance of spring weather conditions and access to salmon resources during the critical chick-rearing period, but also reveal that marine heatwaves may have important secondary effects through a reduction in the overall quantity or quality of prey available to bald eagles. Given ongoing warming at high

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latitudes and the expectation that marine heatwaves will become more common, our findings are useful for understanding ongoing and future changes in the transfer of nutrients from marine to terrestrial ecosystems and how such changes may impact terrestrial species such as bald eagles.

KEYWORDS
bald eagles, climate, marine heatwave, occupancy dynamics, salmon, spatial autocorrelation

INTRODUCTION

Spatial and temporal heterogeneity in resource availability plays a large role in determining the distribution of animals in space and time (Deacy et al., 2016; Masello et al., 2017; Wilson et al., 2012). This heterogeneity can impact fitness-related traits of individuals, and by extension, population dynamics (Long et al., 2016; Masello et al., 2021; Middleton et al., 2018). Therefore, further understanding of the processes by which energy is transmitted through ecosystems can provide important insights into observed patterns in the dynamics of populations of interest. In coastal areas, marine-derived nutrients can contribute significantly to freshwater and terrestrial ecosystems. For example, nesting seabirds and anadromous fish deposit large quantities of nutrients in coastal systems (Harding et al., 2004; Schindler et al., 2005; Walters et al., 2009), a portion of which is integrated into the terrestrial food web (Field & Reynolds, 2011; Gende et al., 2004; Hilderbrand et al., 1999; Merz & Moyle, 2006; Monson et al., 2023; Schindler et al., 2003). These linkages are important for ecosystem function, and understanding how variation in marine resources may affect terrestrial systems can help predict the potential cascading effects on system components.

Weather conditions impact vital rates and population trajectory in a variety of taxa, and extreme weather events can cause punctuated changes in ecosystems and populations (Hansen et al., 2014; Parmesan et al., 2000; Rattenbury et al., 2018; Schmidt et al., 2018; Walsh et al., 2020). Weather may also indirectly affect populations by altering the availability of prey resources during critical periods within a species' life history (Arbeiter et al., 2016; Gangoso et al., 2020; Stirling & Derocher, 2012). These effects can in turn alter survival, reproduction, and recruitment. For species that rely on both marine and terrestrial ecosystems, understanding the drivers of population change is further complicated by the responses of these two systems to long-term variation in climate.

At high latitudes, climate change is occurring quickly and represents a major driver of changes to ecosystem dynamics (Wassmann et al., 2011). The effects of climate warming are pronounced (Park et al., 2020; Post et al., 2018) and can lead to variability in weather patterns across arctic and subarctic ecosystems (Meng et al., 2023). Between 2014 and 2016, the northeast Pacific Ocean experienced a prolonged marine heatwave, a phenomenon where sea-surface temperatures warm above the long-term average (Hobday et al., 2018). Centered near the Gulf of Alaska, the effects extended from the eastern Bering Sea south to the Pacific Northwest (Belkin & Short, 2023). The Pacific Marine Heatwave (PMH) had wide-ranging impacts on the marine ecosystem (Di Lorenzo & Mantua, 2016; Gentemann et al., 2017) that resulted in large-scale changes in the distribution and abundance of marine species (Suryan et al., 2021; Szuwalski et al., 2023). Specifically, several seabird species experienced mass die-offs related to changes in the availability of forage fish (Arimitsu, Piatt, et al., 2021; Arimitsu, Schoen, et al., 2021; Jones et al., 2018; Piatt et al., 2020), and reduced prey availability likely contributed to the declines in humpback whale (*Megaptera novaeangliae*) survival and reproductive success (Gabriele et al., 2022). The effects of the PMH were not restricted to offshore marine environments (Danielson et al., 2022). Dramatic changes in community structure were observed in the rocky intertidal zone as declines in macroalgal cover, followed by increases in invertebrate abundance, suggesting a decline in coastal primary productivity (Weitzman et al., 2021). The systemic impacts of the PMH were large and persistent, suggesting a prolonged disruption of ecosystem function (Schoen et al., 2022; Suryan et al., 2021), which in many cases, still persists (Suryan et al., 2023). The disruptive nature of the PMH provides a unique opportunity to further investigate the connection between marine and terrestrial ecosystems, as well as the potential implications of climate change for these systems.

Bald eagles rely heavily on marine-derived resources throughout much of the Pacific Northwest and Alaska (Buehler, 2022), thereby representing a potential indicator for impaired transfer of marine-derived nutrients into freshwater–terrestrial ecosystems. Bald eagles are long-lived and often reuse nesting sites, facilitating monitoring of breeding dynamics through time (e.g., Schmidt et al., 2020; Wilson et al., 2018; Wilson, Phillips, et al., 2017;

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Wilson, Weiss, et al., 2017). Existing research suggests that reproductive success is broadly related to prey availability (Elliot et al., 1998; Gende & Willson, 1997; Hansen, 1987; Hoff et al., 2004) and weather conditions (Gende et al., 1997; Steidl et al., 1997; Swenson et al., 1986; Wilson et al., 2018), although these relationships can be complex (e.g., Schmidt et al., 2020). When food availability varies spatially, we might expect eagles to concentrate on the highest value food sources that are readily available (MacArthur & Pianka, 1966), and some foraging sites with high prey quality and availability may provide an outsized boost to fitness. For example, although salmon (*Oncorhynchus* spp.) abundance might be important for bald eagles in general, access to salmon may be greater in areas where a high concentration of bears (*Ursus* spp.) actively feed on salmon, leaving numerous carcasses on shore (Field & Reynolds, 2013). In other sites, marine resources such as herring (*Clupea* spp.) and other fishes, seabirds, and waterfowl provide high-quality food for eagles (Anthony et al., 2008; Buehler, 2022; Ofelt, 1975; Rechsteiner et al., 2018). Marine mammals may also provide food resources in the form of beach-cast carcasses (Gerraty, 2023) or sea otter (*Enhydra lutris*) and seal (e.g., *Phoca vitulina*) pups (Anthony et al., 2008; Hayward et al., 2010). A large reliance on marine-derived resources and a variety of potential pathways to consumers in terrestrial systems suggests long-term data on bald eagle reproductive patterns could facilitate the investigation into how conditions in the marine environment can influence terrestrial systems in areas with dynamic energy landscapes.

Bald eagle breeding occupancy dynamics have been monitored for multiple decades in four subareas in Alaska, USA (Putera & Miller, 2018; Wilson, Weiss, et al., 2017). The studied populations represent a gradient from fully coastal (Kenai Fjords National Park [KEFJ]), partially coastal (Lake Clark National Park and Preserve [LACL]), coastally influenced (Katmai National Park and Preserve [KATM]), to interior (Wrangell-St. Elias National Park and Preserve [WRST]), all of which rely on marine-derived nutrients during the nesting and chick-rearing periods. Using spatially explicit multistate occupancy models, we explored spatial and temporal variation in reproductive parameters of eagles in each subarea, thereby providing a broad assessment of how marine resources may affect breeding dynamics. Our primary objectives were to (1) investigate how weather and prey accessibility influence bald eagle occupancy dynamics; (2) assess changes in temporal patterns in occupancy state in relation to the PMH; and (3) model unexplained spatial pattern in occupancy state that may help identify additional sources of variation in marine-derived food availability. Based on past work, we expected weather conditions and prey availability would be related to nest occupancy state. In turn, we also expected the PMH would have a lasting impact on occupancy dynamics due to reductions in the availability and/or quality of marine-derived resources for breeding eagles. Finally, we suspected unexplained spatial patterns in occupancy state may be associated with unmeasured factors affecting habitat quality. Identifying spatial patterns may provide further insight into variation in the energy landscape that affects the transfer of marine resources into the terrestrial system. Meeting these objectives would help us to better understand the drivers of bald eagle reproductive dynamics, while also providing broad and unique insight into the potential mechanisms affecting the linkages between the transfer of nutrients from marine-to-freshwater-terrestrial ecosystems.

METHODS

Study area

Our study area encompassed known bald eagle nesting habitat within four subareas encompassed within National Park Service units in Alaska, USA: KEFJ, LACL, KATM, and WRST. Collectively, these parklands cover nearly 9 million ha and contain large breeding bald eagle and spawning salmon populations. In each subarea, we considered shorelines of the ocean, large lakes, and specific rivers and streams to provide potential nesting habitat for bald eagles and surveyed these areas as shown in Figure 1.

Kenai Fjords National Park

KEFJ covers 0.27 million ha on the southern coast of the Kenai Peninsula in southcentral Alaska. The maritime climate in this coastal subarea is characterized by cool (~5–23°C) rainy summers and stormy winters (~100–200 cm of precipitation annually). In this area, bald eagle habitat occurs along the extensive coastline, which consists of multiple islands and fjords. Salmon spawning habitat and returns are limited in KEFJ aside from a small run in McCarty Fjord (~10,000–20,000 fish). Given the relative lack of salmon, other marine fishes and numerous seabird colonies provide possible prey resources throughout the subarea. In addition, sea otters may provide a consistent, alternate resource for eagles in the form of pups, as well as beach-cast carcasses. The sea otter population along the KEFJ coastline has been stable for over two decades at approximately 2000 animals, although overall density is considered to be somewhat low, likely due to the lack of shallow-water sea otter habitat in the fjords of the park

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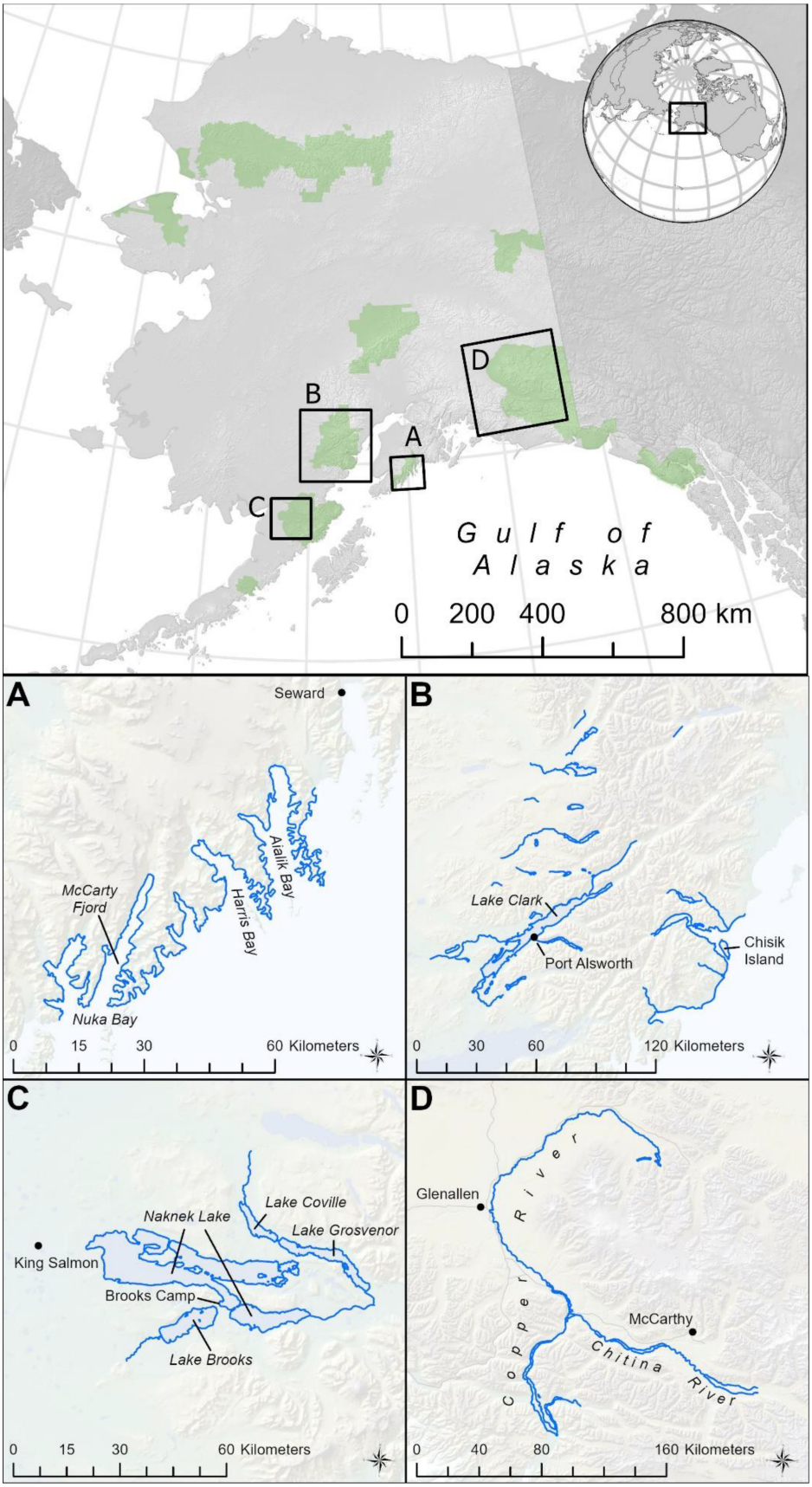

FIGURE 1 Legend on next page.

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(Esslinger et al., 2021). Bald eagles typically nest in Sitka spruce (*Picea sitchensis*) and mountain hemlock (*Tsuga mertensiana*) in coastal forests, occasionally building ground nests on sea stacks, points, and islands (Wilson, Weiss, et al., 2017).

Lake Clark National Park and Preserve

LACL covers 1.63 million ha at the base of the Alaska Peninsula in southcentral Alaska and has two different climate areas: coastal and interior. The coast is foggy and wet, with ~100–200 cm of precipitation annually. The interior is much drier, with ~43–66 cm of precipitation falling annually. Inland temperatures range from 10 to 18°C in summer and can drop to −40°C in winter. Eagles typically nest in white spruce (*Picea glauca*) and cottonwood (*Populus balsamifera*) trees located along the shores of inland lakes, islands, and streams, as well as along the coastline. Sockeye salmon (*Oncorhynchus nerka*) are abundant in the inland areas, with 3.2 million fish returning to the Kvichak River annually (2000–2018 average). Salmon runs also occur on the Nushagak and Kuskokwim River systems. Along the coast, salmon are less plentiful, although there are a variety of other marine resources available. There are several small seabird colonies on the LACL coast, with larger colonies in Tuxedni Channel and on Chisik Island. The large Chisik colony consists of common murres (*Uria aalge*) and black-legged kittiwakes (*Rissa tridactyla*) that may provide marine-derived prey resources to some nesting bald eagles. Although numbers may have approached 20,000 total individuals in 1995, seabird populations in this colony have declined by ≥70% since that time (Arimitsu, Schoen, et al., 2021).

Katmai National Park and Preserve

KATM covers 1.66 million ha on the Alaska Peninsula, north of Kodiak Island. The area has a subarctic climate with cool summers (−1 to 27°C) and cold winters (−37 to 10°C). Approximately 50 cm of precipitation falls annually. Surveyed habitat included the entire shoreline of Naknek Lake, Brooks Lake, Coville Lake, Lake Grosvenor, the American River, from the outlet of Lake Grosvenor to the junction with the Savonoski River, and then along the Savonoski to Naknek Lake. In some years, the shoreline of Lake Coville was also surveyed. Nesting habitat primarily consists of large white spruce and cottonwood, as in LACL. Sockeye salmon represent an abundant resource with an average of 1.7 million fish returning annually from 2000 to 2018 to the Naknek River. Unique to this subarea, large numbers of bears congregate at Brooks Falls to feed on the salmon migrating into Brooks Lake. This concentrated feeding results in numerous discarded carcasses deposited along the shoreline.

Wrangell-St. Elias National Park and Preserve

WRST covers 5.34 million ha in southcentral Alaska. Surveyed habitat included the riparian corridor along most of the Copper River, as well as the Chitina and Bremner Rivers. Most of the Copper River drainage is glacial in origin, with high turbidity, and it drains an area of 68,600 km^2. An average of ~900,000 sockeye salmon enter the system annually, representing the primary prey item for nesting bald eagles during the chick-rearing period. Other potential food resources include salmon carcasses discarded by humans and bears, freshwater fish, and waterfowl. Freshwater fish and waterfowl can be found in abundant wetland habitat bordering much of the Copper River. Nesting habitat is typically dominated by white spruce and cottonwood in the north, with cottonwood becoming the common nesting tree in the south. In the lowest reaches of the Copper River drainage, black cottonwood (*Populus trichocarpa*), Sitka spruce, and mountain hemlock also occur. Temperatures for interior WRST during winter range from −15 to −30°C and 5 to 12°C during the growing season. Precipitation levels in the interior of WRST range from 27 to 37 cm.

Field methods

We conducted two surveys each year, a nest occupancy survey during the nesting season (typically mid-May), and a productivity survey prior to the fledging period to determine reproductive success (mid-July to early August). The specific survey protocols varied through time and among subareas, although the basic approaches were similar. In KATM, LACL, and WRST, we used a tandem-seat fixed-wing aircraft to search potential habitat for nests. During each survey, the pilot-observer team

FIGURE 1 The blue lines depict the potential habitat searched during the bald eagle (*Haliaeetus leucocephalus*) occupancy surveys in (A) Kenai Fjords National Park, (B) Lake Clark National Park and Preserve, (C) Katmai National Park and Preserve, and (D) Wrangell-St. Elias National Park and Preserve. The location of each park and survey area within the state of Alaska are shown in the top panel. The green polygons represent National Park units.

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traversed all linear habitat features (e.g., shoreline, river) searching for bald eagle nest structures. During the occupancy survey, each detected nest was classified as occupied if a nest contained eggs or adults were observed in an incubation posture (except in WRST where occupancy was also defined as two adults perched on or near the nest tree). In KATM and WRST, the identified habitat was searched completely for known and new nests. In LACL, only known nest locations were searched each year; however, any new nests detected while transiting between known nest locations were included and revisited during the subsequent productivity survey. Survey platforms varied through time in KEFJ. In the 1980s and 1990s, a combination of ground-based, boat-based, and aerial survey approaches were used to locate nests and determine nest status. Starting in 2009, surveys were conducted using a helicopter, and from 2010 to 2017, the survey area was divided into a series of transects, a subset of which were surveyed annually (see Wilson, Weiss, et al., 2017). During the productivity survey (all subareas), the pilot-observer team only revisited nests that were determined to be occupied during the initial survey. Upon revisiting each nest, they assigned it to one of two states: occupied but unsuccessful (no chick present) or successful (i.e., ≥1 chick present). In some subareas in some years additional survey protocols were implemented to allow us to assess detection probability (Wilson et al., 2014; Wilson, Phillips, et al., 2017). Here we collapse that information into a single value for each survey (i.e., nest occupied or empty) to create a uniform dataset across the four subareas through time. We acknowledge that our dataset therefore represents apparent nest state and contains some amount of observation error, which we expected to remain consistent through time.

Analytical methods

We used a spatially explicit, multiseason multistate occupancy model for analysis. We used the implicit dynamics formulation (MacKenzie et al., 2018), but in contrast to previous work (Schmidt et al., 2020; Wilson et al., 2018), here we divided the linear habitat into ~1-km segments and then treated the segment as the sample unit. Doing so allowed us to reformulate the analysis in a fully spatial context. We chose 1 km for segment length based on the estimated home range size of nesting bald eagles (Buehler, 2022) with the goal of minimizing overlap among occupied territories. Based on the nest-specific occupancy data we collected during the surveys, we assigned each segment the highest occupancy state observed among the nests within it. For example, if a segment happened to contain two nests, one of which was occupied, the segment would be considered to be occupied. For analysis, we then assumed each segment could exist in one of four possible occupancy states: empty (no nest structure detected), nest present (nest observed, but no evidence of occupancy), occupied (adult observed at a nest in incubation posture [see WRST exceptions above]), and successful (≥1 chick present in a nest). Following the notation of Kéry and Schaub (2012) and the presentation of Schmidt et al. (2020), the probability of the state, z, of segment i in year j is modeled using a categorical distribution

$$z_{ij} \sim \text{categorical}\left(\mathbf{\Omega}_{ij}\right)$$

where $\mathbf{\Omega}_{ij}$ is the state vector. Then

$$\mathbf{\Omega}_{ij} = \begin{bmatrix} 1-\Psi_{1,ij} \\ \Psi_{1,ij}\left(1-\Psi_{2,ij}\right) \\ \Psi_{1,ij}\Psi_{2,ij}\left(1-\Psi_{3,ij}\right) \\ \Psi_{1,ij}\Psi_{2,ij}\Psi_{3,ij} \end{bmatrix}$$

where Ψ_1 is the probability a given segment contains a nest, Ψ_2 is the probability that a given segment is also occupied, Ψ_3 is the probability that an occupied segment is successful, and $1-\Psi_{1,ij}$ is the probability that a segment does not contain a nest. The observed states, y_{ij}, come from a categorical distribution

$$y_{ij} \sim \text{categorical}\left(\mathbf{\Theta}_{1\ldots O,i,k}\right)$$

where $\mathbf{\Theta}$ is the observation array, O is the total number of states, and k indicates visit. Because the two visits to each segment in our study occurred during different portions of the breeding season, $\mathbf{\Theta}$ is

$$\begin{array}{r} \\ \text{no nest} \\ \text{empty nest} \\ \text{occupied nest} \\ \text{successful nest} \end{array} \begin{array}{c} \begin{array}{cccc} \text{no nest} & \text{empty nest} & \text{occupied nest} & \geq 1 \text{ chick} \end{array} \\ \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 1 & 0 \end{bmatrix} \end{array}$$

for $k = 1$ and

$$\begin{array}{r} \\ \text{no nest} \\ \text{empty nest} \\ \text{occupied nest} \\ \text{successful nest} \end{array} \begin{array}{c} \begin{array}{cccc} \text{no nest} & \text{empty nest} & \text{occupied nest} & \geq 1 \text{ chick} \end{array} \\ \begin{bmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{bmatrix} \end{array}$$

for $k = 2$. The first survey occurs prior to hatch; therefore, the successful state is not yet observable. During the

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second survey, the true state is assumed to be observed without error. The observation matrix for $k = 1$ is generally only relevant when a given nest is not observed during the second survey, thereby acknowledging the potential for state classification error.

We can model the effects of covariates on each state as follows:

$$\text{logit}(\Psi_{1,ij}) = \boldsymbol{x}'_{ij}\boldsymbol{\alpha}$$

$$\text{logit}(\Psi_{2,ij}) = \boldsymbol{x}'_{ij}\boldsymbol{\beta}$$

$$\text{logit}(\Psi_{3,ij}) = \boldsymbol{x}'_{ij}\boldsymbol{\gamma}$$

where $\boldsymbol{x}'_{ij}$ is a vector of i covariate values and $\boldsymbol{\alpha}$, , and γ are the associated coefficients. For logistical reasons, we analyzed the data from each of the four subareas separately. However, we used the same basic model structure among them to provide similar inference and allow us to compare covariate relationships among subareas.

For the submodel for Ψ_1, we included a trend through time and a measure of habitat availability representing the proportion of the area within 1 km of the segment that contained trees at least 10 m tall. In LACL and KATM, we treated this as a binary variable for proportions >0.05. We did this because a large proportion of segments had values <0.05. KEFJ and WRST are much more vegetated, so we treated the habitat variable as continuous. This mainly helped to account for areas without trees so that the model would be less likely to predict nest occurrence in areas without nesting habitat. The trend term allowed the probability of nest occurrence to change through time.

For the submodel for Ψ_2, we included proximity to seabird colonies (LACL, KEFJ), pond area (WRST), and/or an inland versus coast indicator (LACL) as indices of the availability of possible food resources to explain variability in occupancy probability among segments. The primary large colony in LACL is located on Chisik Island (Arimitsu, Schoen, et al., 2021), so we used a binary variable indicating whether a segment was within 5 km of the colony center. In KEFJ, multiple colonies were present. Here we considered a binary variable representing whether each segment was within 2 km of a colony of ≥100 individuals (based on Parsons et al., 2012). Bald eagles will eat eggs, chicks, and adult seabirds when available and will steal food from other predators, so we expected that segments near colonies would be more likely to contain occupied nests. In WRST where marine-derived resources other than salmon are not available, we hypothesized that small ponds may provide a useful index of alternative prey resources (e.g., waterfowl, freshwater fish). Therefore, we included the area covered by ponds within 1 km of each segment as a covariate in that subarea. Finally, the LACL survey area is divided geographically into inland and coastal areas. We included an indicator variable to explore the possibility that the two broad areas may have different probability of occupancy. These metrics did not vary by year, so we expected them to be more relevant for predicting areas where eagles may choose to attempt breeding. In addition to the segment-specific covariates, we also included a trend through time with a changepoint in 2014, the beginning of the PMH. Doing so allowed us to broadly assess whether the probability of occupancy changed after the onset of the heatwave. Finally, we included a spatial random effect term to account for any remaining spatial autocorrelation in the data. We did so using a series of basis functions that smooth predictions across the collection of segments within a subarea. We accomplish this by distributing some number of knots (i.e., spatial locations over which predictions are smoothed: 30 in this application) throughout the study area and then model spatial autocorrelation based on the distance from each segment to each knot as has been done in similar applications (Collier et al., 2012; Crainiceanu et al., 2005; Gimenez et al., 2009; Kéry & Royle, 2021; Schmidt et al., 2022).

The submodel for Ψ_2, including the spatial random effect term, can be written as follows

$$\text{logit}(\Psi_{2,ij}) = \boldsymbol{x}'_{ij}\boldsymbol{\beta} + \sum_{k=1}^{30} \mu_k(\text{Segment.loc}_i - \boldsymbol{\kappa}_k)$$

where the spatial effects (μ_k) are modeled as a function of the spatial location of the centroid of each segment (Segment.loc_i) in relation to the placement of the fixed knots ($\boldsymbol{\kappa}_k$). Given the limited number of occupied segments in a given year, we did not index μ by year. The values instead represent the mean spatial pattern over the entire period of observation in each subarea. Note that the effect of the spatial term gets propagated through the other states due to their dependence on one another (see *Results*).

For the submodel for Ψ_3, we included cumulative growing degree-days (GDD) base 0 in April and May, cumulative precipitation in June, the number of salmon entering the system early in the season (i.e., June KATM/LACL, May in WRST), and an interaction between GDD and salmon (WRST only). We expected that these annually varying measures might help explain variation in success. We used long-term weather data from stations located in King Salmon, Port Alsworth, Seward, and

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Gulkana to calculate GDD and precipitation totals for KATM, LACL, KEFJ, and WRST, respectively. We hypothesized that warmer springs would reduce thermal stress during incubation and that drier conditions during the June chick-rearing period would increase chick survival, resulting in higher success. We also included an interaction between GDD and early salmon run size in WRST, based on the findings of Schmidt et al. (2020). Finally, we included a trend through time with the same 2014 changepoint as in the occupancy submodel. This allowed us to assess whether broad trends in success were different before and after the onset of the PMH.

For all surveys with complete coverage, we assumed that all segments were visited during the occupancy survey, meaning that all segments that did not contain a known nest were considered to be empty. In subareas and years where surveys were incomplete, we only assigned state values to a segment that contained an observed nest. All other segments were assigned missing values (i.e., not applicable) so that they did not contribute incorrect information. We treated any nests that were not found or not searched for in a similar manner. Specifically, partial surveys occurred in WRST in 2004–2005 and in KEFJ in 2001. In KEFJ, we only used observed nest information for all nonaerial surveys given that boat and ground-based surveys are more likely to miss nest structures (i.e., segments with no nest information were assigned missing values). Also, from 2010 to 2017, surveys were based on a subset of transects spatially distributed along the coast. We treated all unsurveyed transects as missing data. When the productivity survey was not completed for some subareas in some years, we assigned missing values to those segments for the productivity survey as well. By incorporating missing values in this way, we were able to formally include all the available data together in a single analytical framework without introducing bias due to variation in survey coverage.

We scaled the GDD, precipitation, salmon, and pond area covariates to have a mean of 0 and SD of 1 (for each subarea separately) prior to analysis to improve model convergence. We fit models for each subarea separately using program R 4.2.1 (R Core Team, 2022) as an interface to JAGS 4.3.1 (Plummer, 2022). We used compact priors (i.e., mean = 0, SD = 1.58) on all parameters and ran two chains for 10,000 iterations each, discarding the first 5000 as burn-in and retaining the rest for inference. Testing confirmed that this was sufficient for model convergence given that detection probability was assumed to be one (not shown). We present all parameter estimates as means and posterior probabilities of the estimate being nonzero. We discuss relationships with posterior probabilities >0.8 to provide broader context given the large geographic scope of our study.

RESULTS

Although discontinuous through time, survey effort covered 32-, 34-, 32-, and 19-year timespans in KEFJ, LACL, KATM, and WRST, respectively (Table 1). The number of individual nests monitored in each subarea varied from a low of 26 in KATM to a high of 318 in WRST. Spring temperature, June precipitation, and the size of the early salmon returns were highly variable among subareas (Table 1).

Predictors of occupancy state

As we expected, the forest metric representing the availability of larger trees as potential nesting structures was a strong predictor of nest occurrence within a given segment in all subareas (Table 2). We found mixed evidence for an association between the indices of alternative food resources and occupancy probability (Table 2). In LACL, segments that were near the colony had a lower probability of containing occupied nests. In contrast, segments near colonies in KEFJ were more likely to be occupied. We found no difference in occupancy probability between the inland and coastal segments in LACL, suggesting no fundamental difference in occupancy probabilities between the two parts of the subarea. In WRST, there was no evidence that the proportion of the 1-km area surrounding each segment that was covered by ponds was related to the probability of occupancy, suggesting that access to nearby freshwater resources (e.g., fish, waterfowl) early in the breeding season did not affect nest occupancy.

The factors related to a segment containing a successful nest and the direction of the effects were broadly consistent across subareas (Table 2, Figure 2). The size of the early portion of the salmon run was positively related to success, suggesting that the availability of salmon as a food resource during the chick-rearing period was important for nest success. The relationships between spring GDD and June precipitation also largely corresponded with our expectation that cooler, wetter conditions would be negatively associated with success, presumably due to reduced chick survival (Figure 2A–D). In WRST, we reconfirmed support for an interaction between GDD and early-season salmon abundance reported by Schmidt et al. (2020), suggesting that glacial melt alters salmon availability in this system (see Schmidt et al., 2020). Note the counterintuitive direction of the GDD effect in WRST due to the

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TABLE 1 Summary table showing the number of nests and years monitored, the number of survey segments in each subarea, and the range of the observed annual covariate values.

Subarea	Nests monitored	Years monitored	No. survey segments	April/May GDD	June precipitation (mm)	Early salmon returns
KEFJ	37–91	1986–1998	566	268–480	16–146	NA
	82–149	2001–2002				
	56–99	2009–2017				
LACL	52–75	1988–1990	1164	243–481	2–74	2000–1,509,000
	59–76	1992–1997				
	73–89	1999–2001				
	39–134	2004–2015				
	100–160	2017–2019				
	118	2021				
KATM	26–52	1991–1997	583	219–478	13–83	18,000–1,115,000
	50–56	2011–2013				
	66–93	2015–2019				
	51–83	2021–2022				
WRST	87–154	2004–2005	877	193–426	7–70	27,000–416,000
	270–318	2006–2009				
	273–296	2011–2019				
	277–291	2021–2022				

Note: April/May GDD represents the cumulative number of growing degree-days (base 0) in April and May, June precipitation is the total amount of rainfall in June, and early salmon returns represent the total number of salmon returning to the monitored system through May (WRST) or June (KATM, LACL; note not all runs are monitored). Subareas are organized along the marine-to-freshwater gradient: KEFJ completely coastal/marine, LACL mix coastal and freshwater, KATM freshwater dominated, and WRST completely interior/freshwater.

Abbreviations: KATM, Katmai National Park and Preserve; KEFJ, Kenai Fjords National Park; LACL, Lake Clark National Park and Preserve; WRST, Wrangell-St. Elias National Park and Preserve; NA, not applicable.

interaction between GDD and early-season salmon abundance (Figure 2D).

Temporal patterns relative to the PMH

Our exploration of trend provides insight into how occupancy dynamics in each population changed through time in the context of the major perturbation event represented by the PMH (Table 2, Figure 3). In most coastal subareas, KEFJ, occupancy, and success were largely stable prior to the PMH, followed by a reduction in success and a corresponding increase in occupancy after 2014. In the partially coastal subarea, LACL, the probability of occupancy and success both declined through time, with no meaningful change in relation to the PMH. In coastally influenced KATM, the probability of occupancy decreased after the onset of the PMH. In WRST, the most interior area, success increased slightly after PMH (Figure 3B). The predicted proportions of segments with occupied or successful nests confirm that these trends were manifest as declines in the proportion of segments with successful nests in KEFJ, LACL, and KATM, and as increases in WRST (Table 3).

Spatial pattern

In KEFJ, occupancy and success are most concentrated at the ends of several prominent peninsulas, where the majority of seabird colonies are located, and particularly near McCarty Fjord, where sea otters and small numbers of salmon are also available (Figure 4). In LACL, occupancy and success tended to be higher along the shores of Lake Clark in the vicinity of Port Alsworth and along the southeastern coast where salt marsh habitats occur (Figure 5), both areas where access to salmon may be higher. In KATM, probabilities of occupancy and success were concentrated around the Brooks Falls area where large numbers of returning sockeye salmon congregate, along with high densities of bears that feed on the returning fish. In contrast, occupancy and success along the shores of Lake Grosvenor and Lake Coville were relatively low (Figure 6). And finally, in WRST, the probabilities of

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TABLE 2 Parameter estimates and posterior probability of each estimate being different from zero for each of the four subareas.

	KEFJ		LACL		KATM		WRST	
Parameter	**Mean**	**Prob**	**Mean**	**Prob**	**Mean**	**Prob**	**Mean**	**Prob**
Nest occurrence								
Intercept	**−1.208**	...	**−3.579**	...	**−3.070**	...	**−1.083**	...
Forest habitat	**0.720**	**1.00**	**0.879**	**1.00**	**0.610**	**1.00**	**0.133**	**0.94**
Trend (nest)	**−0.003**	**0.87**	**0.027**	**1.00**	**0.034**	**1.00**	−0.002	0.67
Occupancy								
Intercept	**−0.069**	...	**0.244**	...	**0.323**	...	**−0.435**	...
Near seabird colony	**0.257**	**0.91**	**−0.290**	**0.90**	...	...		
Inland (LACL)	...	...	0.368	0.77	...	...	...	...
Ponds (WRST)	...	...	...	...	...	...	0.010	0.62
Trend (occ < 2014)	0.002	0.60	**−0.020**	**0.99**	**−0.011**	**0.80**	**0.017**	**0.85**
Trend (occ ≥ 2014)	**0.016**	**0.99**	**−0.017**	**0.99**	**−0.032**	**1.00**	**0.008**	**0.85**
Success								
Intercept (success)	**0.891**	...	**0.888**	...	**−0.188**	...	**−0.325**	...
April/May GDD	**0.208**	**0.95**	−0.037	0.65	0.107	0.75	**−0.141**	**0.92**
June precipitation	**−0.111**	**0.82**	**−0.103**	**0.90**	**0.283**	**0.97**	**−0.116**	**0.96**
Early salmon run	...	...	**0.122**	**0.93**	**0.237**	**0.93**	**0.288**	**0.99**
GDD × salmon inter	...	...	...	...	...	...	**−0.132**	**0.97**
Trend (succ < 2014)	0.004	0.60	**−0.027**	**0.98**	0.016	0.70	0.010	0.62
Trend (succ ≥ 2014)	**−0.027**	**0.99**	**−0.027**	**1.00**	0.006	0.71	**0.024**	**0.97**

Note: Values in boldface indicate parameters that have >0.80 posterior probability (Prob) of being different from zero.
Abbreviations: GDD, growing degree-days; KATM, Katmai National Park and Preserve; KEFJ, Kenai Fjords National Park; LACL, Lake Clark National Park and Preserve; occ, occupancy; WRST, Wrangell-St. Elias National Park and Preserve.

occupancy and success were highest at the headwaters of the system and near the confluence of the Gulkana and Copper Rivers where waters are less turbid (Figure 7). These patterns suggest that there are residual spatial patterns in occupancy dynamics throughout each subarea that are related to prey availability. Also note that although the spatial term is included in the submodel for occupancy, the effects are propagated through the other states because of the conditional nature of the model (e.g., in order for a segment to be successful, a nest must first occur and be occupied).

DISCUSSION

We found that bald eagle reproductive state is linked to variation in weather, climate, and marine-derived resources across four subareas that span a marine-to-freshwater gradient. Although reproductive dynamics are related to weather conditions and prey abundance directly, access to these important prey resources appears to be affected indirectly through complex interactions with weather, climate, and the dynamics of other species (i.e., bears and seabirds) in both space and time. Together, these factors alter local resource availability, which subsequently influences the reproductive dynamics of bald eagles. The natural experiment afforded by the 2014–2016 PMH helped to further clarify the potential impacts of climate-driven changes to marine-derived resources through immediate and lasting impacts to reproductive output in bald eagles. By elucidating some of these important linkages, our work will further the understanding and conservation of populations of bald eagles and other coastal species that might be affected by future changes affecting the marine–terrestrial interface.

We acknowledge that we were required to make a few important assumptions that have a bearing on the interpretation of our results. First, our inability to estimate detection probability forced us to make inference based on apparent rather than true nest state. Apparent data contain noise from the imperfect detection process in the form of false negatives (e.g., an occupied nest misclassified as unoccupied). We expect these observation errors were largely consistent through time and were

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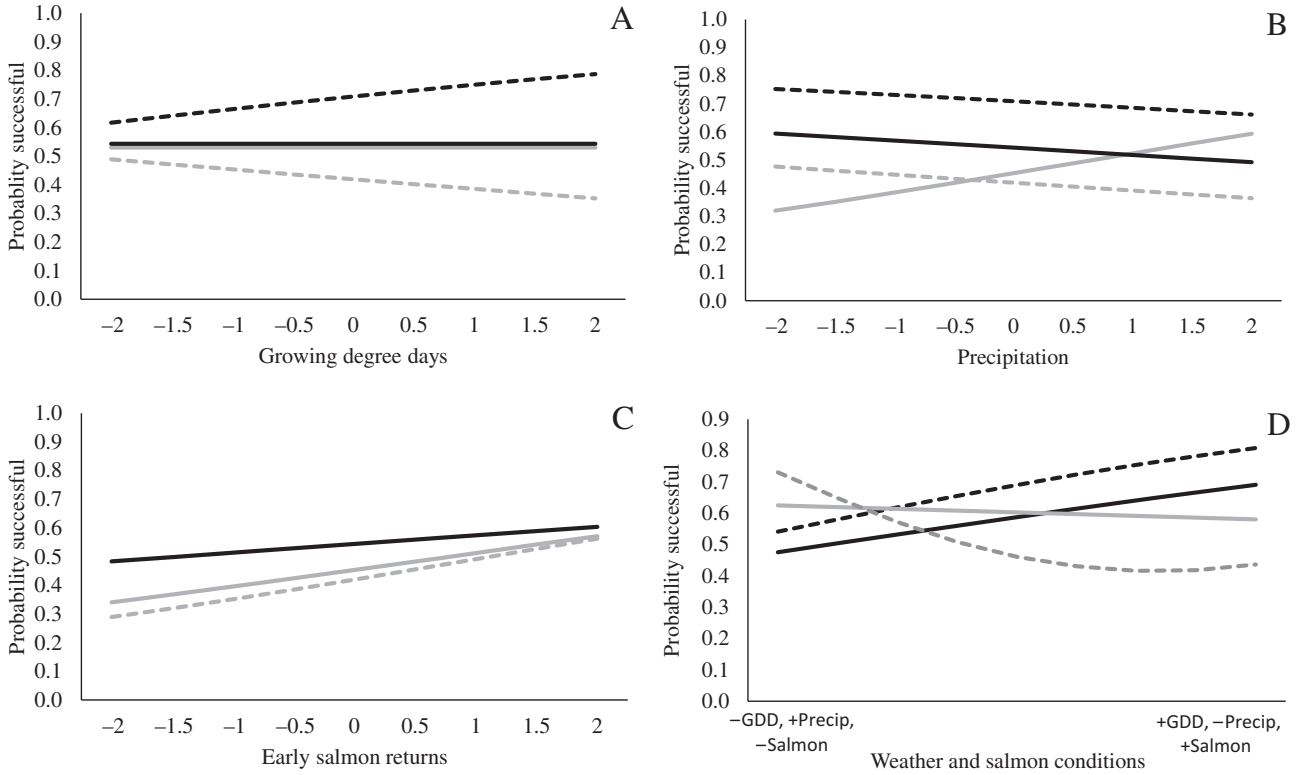

FIGURE 2 Predicted probability of success in relation to (A) cumulative growing degree-days in April/May, (B) total precipitation in June, and(C) total early salmon (*Oncorhynchus* spp.) returns for four subareas: Kenai Fjords National Park (dashed black), Lake Clark National Park and Preserve (solid black), Katmai National Park and Preserve (solid gray), and Wrangell-St. Elias National Park and Preserve (dashed gray), Alaska, USA. (D) The combined effects of weather and salmon returns, from cool, wet, low salmon conditions (left side of *x*-axis) to warm, dry, high salmon conditions (right side of *x*-axis). Note that the values of precipitation are reversed in (D), reflecting the negative effect of precipitation on success. The range of the *x*-axes represents SDs from the mean of the observed values in each area, allowing direct comparison of effects among parks within a single plot.

therefore unlikely to introduce bias. In addition, added noise tends to obscure covariate relationships rather than leading to spurious results, suggesting our findings were conservative. It is also important to consider that although we focused primarily on the importance of marine prey, bald eagles will use terrestrial resources when available. Unfortunately, data on terrestrial resources were unavailable for our subareas, limiting our ability to assess their importance in our system. The use of unidentified alternative terrestrial food sources by bald eagles would be expected to weaken the covariate relationships we investigated by inducing unexplained variation in the observed data. Despite these potential limitations, we were able to identify important associations between the marine environment and bald eagle occupancy dynamics, thereby supporting our conclusion that marine conditions are indeed important drivers of bald eagle reproduction in our study area.

Spring weather conditions along the North Pacific coast can be cold, wet, and windy, with negative impacts to species that nest in early spring. Inclement weather conditions are tied to reduced reproductive success in a variety of raptor species (Nageli et al., 2022; Steenhof et al., 1997), causing nest failure or chick mortality directly through chilling or wetting. Weather can also indirectly reduce prey availability through delayed break-up of lakes and rivers in spring (Steidl et al., 1997), increased glacial melt (Schmidt et al., 2020), decreases in visibility during rain events (Gende et al., 1997), and changes in prey behavior (Dawson & Bortolotti, 2000; Steenhof et al., 1997), among others. In agreement with these findings, we found that cooler and wetter conditions were generally associated with lower probability of success, except in the turbid, glacially-driven system in WRST where warm conditions may decrease salmon availability through increased glacial melt (see Schmidt et al., 2020). These relationships suggest that both direct and indirect effects of weather influence bald eagle occupancy dynamics in our system.

Salmon are one of the most reliable and abundant food resources available to bald eagles along much of the Pacific coast. Correspondingly, we found a consistent

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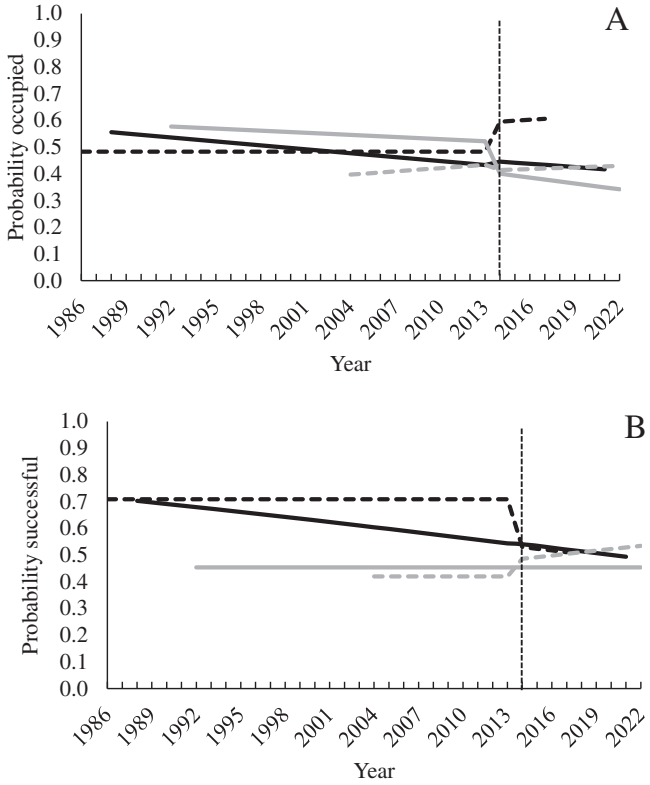

FIGURE 3 Predicted trends in (A) occupancy and (B) success through time in relation to the onset of the marine heatwave event that occurred in 2014 (vertical dotted line) for all four subareas (all continuous covariates were held at their mean values): Kenai Fjords National Park (dashed black), Lake Clark National Park and Preserve (solid black), Katmai National Park and Preserve (solid gray), and Wrangell-St. Elias National Park and Preserve (dashed gray), Alaska, USA.

TABLE 3 Predicted proportion of segments with nests (prop w/nest), proportion of segments with nest that are also occupied (prop occupied), and the proportion of occupied segments that are also successful (prop successful) at three time steps for each subarea: The starting year for each subarea, the year before the onset of the Pacific Marine Heatwave (PMH onset) event, and the final year of the study for each of the four subareas.

Time step	KEFJ	LACL	KATM	WRST
Prop w/nest				
Start of study	0.23	0.03	0.05	0.25
PMH onset	0.21	0.05	0.09	0.25
End of study	0.21	0.06	0.12	0.25
Prop occupied				
Start of study	0.21	0.27	0.43	0.28
PMH onset	0.21	0.26	0.37	0.30
End of study	0.43	0.27	0.22	0.26
Prop successful				
Start of study	0.71	0.70	0.45	0.42
PMH onset	0.73	0.54	0.45	0.45
End of study	0.51	0.49	0.45	0.53

Note: Predictions are based on the trend terms with all other continuous covariates held at mean values. Start and end dates vary among the four subareas.

Abbreviations: KATM, Katmai National Park and Preserve; KEFJ, Kenai Fjords National Park; LACL, Lake Clark National Park and Preserve; WRST, Wrangell-St. Elias National Park and Preserve.

positive association between success and the size of the early part of the salmon runs in LACL, KATM, and WRST. This supports the hypothesis that access to salmon during the chick-rearing period is important for nesting bald eagles (Schmidt et al., 2020), and perhaps explains the lack of a relationship with total salmon returns previously reported for LACL (Wilson et al., 2018). The importance of the timing of salmon availability rather than total abundance is consistent with previous studies showing that prey abundance can be a primary driver of reproductive success in raptors when prey populations fluctuate (McIntyre & Schmidt, 2012; Steenhof et al., 1997). Given that salmon migration timing can be affected by temperature and flow regimes (Anderson & Beer, 2009; Kovach et al., 2015; Quinn et al., 1997), we expect that future warming could indirectly affect bald eagle dynamics through phenological mismatches in the timing of salmon returns and initiation of the nesting season (Visser & Both, 2005).

Access to prey can also be influenced through interactions with other co-occurring species. A prime example in our study is the "occupancy hotspot" in the area around Brooks Falls in KATM where brown bears congregate to feed on migrating salmon. The falls act as a barrier to fish passage, thereby concentrating them in the area where they are more susceptible to predation by both bears and eagles. In addition, bears discard partially consumed salmon carcasses, which are then scavenged by eagles and other animals (Gende et al., 2001; Levi et al., 2020; Lincoln & Quinn, 2019). Higher occupancy in the area surrounding Brooks Falls suggests that eagles are targeting a resource that is augmented by associated bear activity (Figure 6). In LACL, bears are less concentrated, but they may play a similar role in coastal areas and around Lake Clark where bald eagle occupancy probability was higher (Figure 5). In WRST, occupancy was concentrated in the upper reaches of the drainage where clearwater tributaries and human and bear subsidies (i.e., carcasses) may be more available. Given the extremely high silt load in the lower reaches of the Copper River, eagles appear to occupy these upper reaches more frequently, perhaps due to increased foraging efficiency associated with clearer water. Alternative prey sources are

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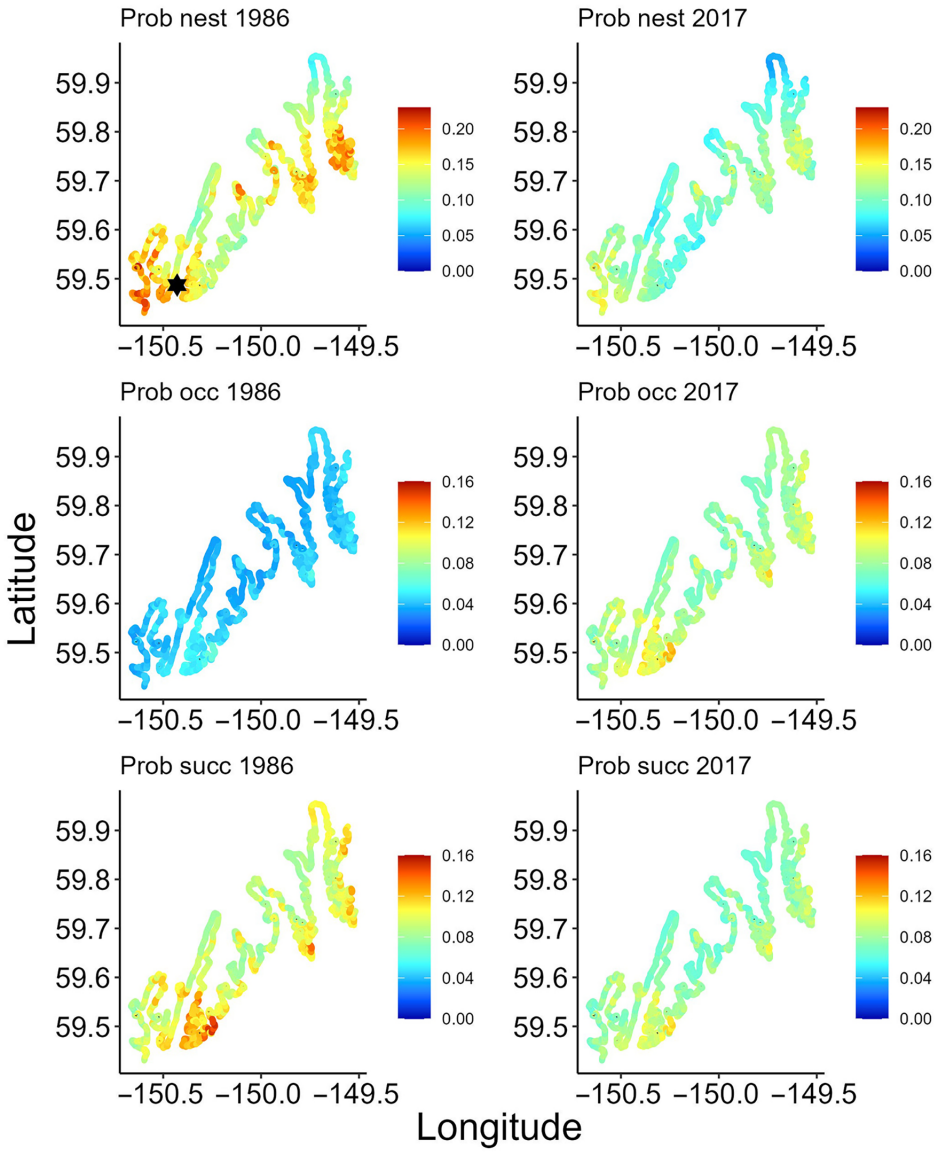

FIGURE 4 Predicted probability (prob) of nest occurrence (nest), occupancy (occ), and success (succ) for each segment of the survey area in the initial (1986) and final (2017) year of the survey in Kenai Fjords National Park, Alaska, USA. The star in the upper left panel indicates the location of McCarty Fjord where sea otter (*Enhydra lutris*) densities are greatest.

also important, particularly when salmon are less available in space or time. For example, occupancy in KEFJ (where comparatively large salmon runs are absent) was spatially concentrated in areas where seabird colonies were more prevalent (Phillips & Curl, 2014) and sea otter abundance was higher (Esslinger et al., 2021), potentially representing spatially concentrated resources for bald eagles (e.g., Henson et al., 2019; Monson, 2021; Schoen et al., 2022; Figure 4). Overall, the spatial patterns in occupancy we observed suggest that the spatial distribution of resources creates a heterogeneous energy landscape driven by a variety of nutrient sources and species interacting among disparate taxa.

The patterns in occupancy dynamics relative to the onset of the PMH suggest a mechanism by which climate can alter population metrics. The impacts of the PMH on reductions of non-salmon prey resources including forage fish (Arimitsu, Piatt, et al., 2021; von Biela et al., 2019) and seabirds (Jones et al., 2018; Piatt et al., 2020; Schoen et al., 2022) have been well documented. In combination with our results, these findings indicate that the PMH affected bald eagle occupancy dynamics, in turn suggesting that the amount and quality of marine prey available to eagles was reduced after the onset of the PMH. Furthermore, climate warming can lead to reductions in body size (Oke et al., 2020), reduced energy

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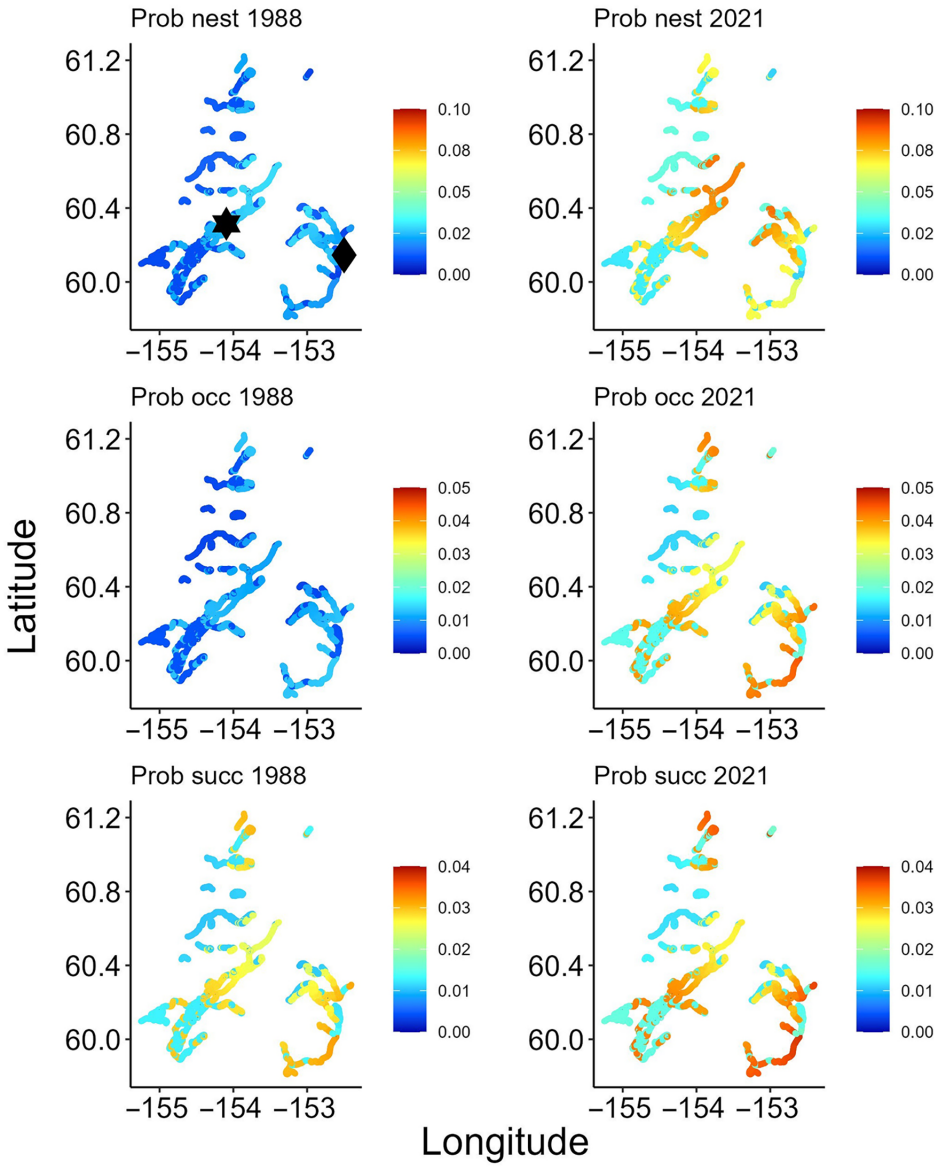

FIGURE 5 Predicted probability (prob) of nest occurrence (nest), occupancy (occ), and success (succ) for each segment of the survey area in the initial (1988) and final (2021) year of the survey in Lake Clark National Park and Preserve, Alaska, USA. Star and diamond in the upper left panel indicate the locations of Lake Clark and Chisik Island, respectively.

content (Carey et al., 2021), and lower spawning migration success (Farrell et al., 2008) in salmon. Together, such changes in ocean temperature can substantially alter the foraging landscape for nesting bald eagles and lead to the patterns we observed. We expect that future marine heatwave events will have negative impacts on bald eagle occupancy dynamics throughout much of our study area.

Access to salmon and other alternative prey types appeared to buffer the effect of the PMH on the occupancy dynamics of bald eagles. Specifically, the fully coastal site, KEFJ, experienced the largest impacts to success in relation to the PMH, as expected. We posit that the impacts in this subarea were magnified because eagles were almost entirely reliant on alternate marine prey resources (e.g., seabirds, herring, and other forage fish) that were severely impacted by the PMH. Without access to large salmon runs or significant terrestrial alternatives to buffer the effects of PMH on food availability, success was reduced. In KATM, where large salmon runs represent the predominant resource, we observed modest declines in occupancy. High salmon abundance appeared to mitigate the impacts of changes to the marine environment, although we suspect an overall reduction in the portfolio of prey available to nesting eagles in the area (e.g., fewer gulls) may have contributed to reductions in occupancy after the onset of the PMH in this coastally influenced site. The temporal pattern in LACL was unique among the sites, exhibiting a steady decline in

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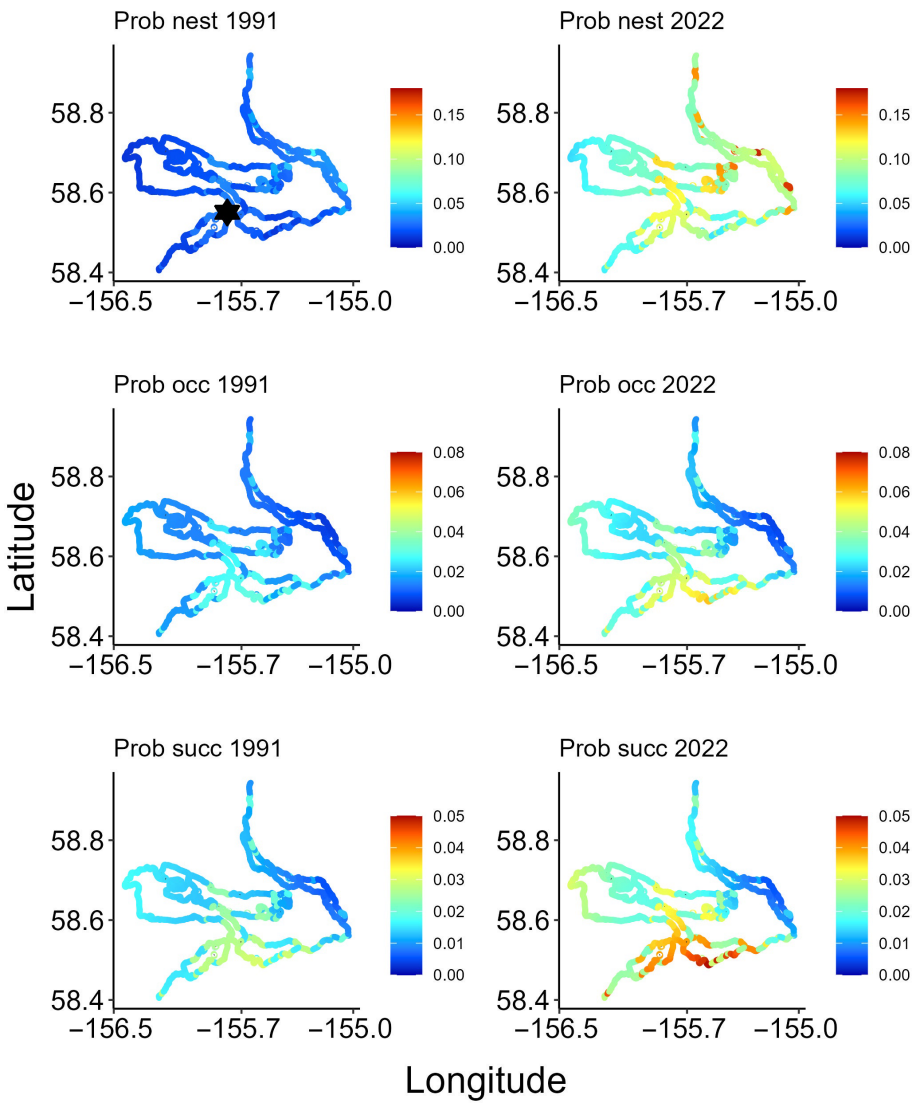

FIGURE 6 Predicted probability (prob) of nest occurrence (nest), occupancy (occ), and success (succ) for each segment of the survey area in the initial (1991) and final (2022) year of the survey in Katmai National Park and Preserve, Alaska, USA. The star in the upper left panel indicates the location of Brooks Falls.

success with no evidence of a PMH effect. We expect these declines are related in part to sampling and a long-term decline in seabird abundance along the coast. In LACL, the continual discovery of unused nests through time may have led to a negative trend if predominantly empty nests were added to the sample through time, thereby driving down the average rate of occupancy and success. In addition, the large (~20,000 adults) seabird colony on Chisik Island declined by ≥70% since the 1990s (Arimitsu, Schoen, et al., 2021), representing a substantial change in a potential prey resource for LACL eagles along the coast and possibly explaining continued declines in success. Combined with the fact that only a subset of nests was located in coastal areas, these factors may explain the lack of a PMH signal in LACL. Finally, in the most interior site, WRST, success showed a slight positive response after the onset of the PMH. Although unexpected, we speculate that the small positive effect may be associated with the positive phase of the snowshoe hare (*Lepus americanus*) cycle, which likely began around the time of the onset of the PMH and peaked around 2020–2021 (Merizon & Carroll, 2023). Hares can be incredibly abundant during the high phase of their cycle and hare abundance is directly related to occupancy dynamics in other raptor species such as golden eagles (McIntyre & Schmidt, 2012). Although fish and birds dominate bald eagle diets, snowshoe hares are certainly taken when available (Cash et al., 1985) and could provide a substantial alternate resource to eagles when abundant. Alternatively, heat stress to salmon during upstream migration (von Biela et al., 2020, 2022) may increase their availability to bald eagles through elevated

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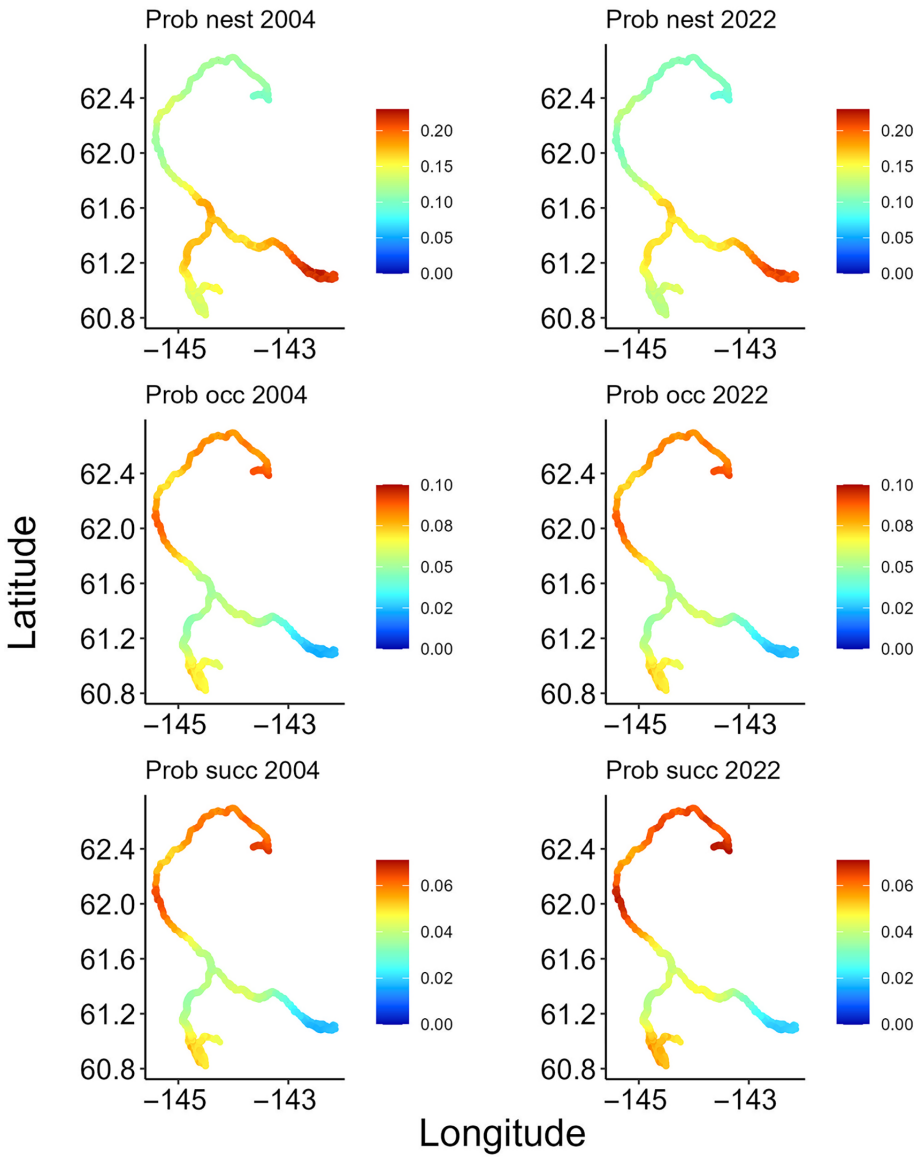

FIGURE 7 Predicted probability (prob) of nest occurrence (nest), occupancy (occ), and success (succ) for each segment of the survey area in the initial (2004) and final (2022) year of the survey in Wrangell-St. Elias National Park and Preserve, Alaska, USA.

mortality (i.e., more carcasses) or increased vulnerability to predation. These possible explanations are important directions for research into understanding how eagle populations may be impacted in the future.

Bald eagle populations were severely depressed by the mid-20th century due to human persecution and exposure to pesticides, although they largely recovered after the ban of DDT (Buehler, 2022). Current populations have rapidly increased throughout a majority of their range in the conterminous United States and are generally stable or increasing in Alaska (Buehler, 2022; Eakle et al., 2015; Hodges, 2011; Zwiefelhofer, 2007). Although currently stable, our findings suggest that populations reliant on marine resources along the Pacific coast could be impacted by variation in ocean conditions, particularly given that large changes in salmon and other fish stocks are expected in relation to heatwave events (Barbeaux et al., 2020; Cheung & Frolicher, 2020; Gallagher et al., 2022; von Biela et al., 2022). With continued climate warming, marine heatwaves will likely become more frequent (Laufkotter et al., 2020; Spillman et al., 2021) with cascading impacts to marine systems and, in turn, bald eagle reproductive dynamics. If subsequent changes to marine food webs occur, more lasting negative impacts on bald eagle populations might be expected.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Schmidt, 2024) are available from the National Park Service (NPS) DataStore: https://doi.org/10.57830/2305284.

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