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RESEARCH ARTICLE

# Flooding and a complex predator community drive American oystercatcher nest and chick survival in Virginia

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## Abstract

On the Atlantic and Gulf coasts of the United States, conservation efforts for the American oystercatcher (*Haematopus palliatus*) commonly focus on improving reproductive success by identifying and managing key threats to nest and chick survival. However, these threats have the potential to change over time. We monitored the reproductive success of American oystercatchers in the Virginia barrier island system, a significant breeding site where annual American oystercatcher productivity has been low since 2016, suggesting evolving drivers of nest and chick survival. We routinely surveyed the nests and broods of breeding pairs from 76 active American oystercatcher territories on Metompkin Island in 2021–2022 and Fisherman Island in 2023. Additionally, we used radio-telemetry to track one chick per brood ($n = 45$ chicks) and improve our chances of identifying fate. Using models of age-specific daily survival rates, we found that the probability of a nest surviving to hatching was high (0.91 ± 0.08 [SD]), relative to the probability of a chick surviving to fledging (0.51 ± 0.14 [SD]), indicating that low chick survival may be limiting reproductive success at sites in Virginia. Overall, American oystercatcher reproductive success was

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affected by a complicated set of factors, including flooding from tidal inundation and storm surge during the nesting stage, and the threat of predation from a complex predator community during the nesting and brood-rearing stages. As threats to American oystercatcher reproductive success change in response to climate change and human activities, natural resource managers will need to consider ecosystem-based management strategies to address those threats, such as habitat restoration to assist behavioral adaptation of nesting American oystercatchers to flooding, and control of threats from both mammalian and non-mammalian predators.

**KEYWORDS**

American oystercatcher, chick survival, coastal flooding, *Haematopus palliatus*, predation, productivity, nest survival, reproduction, Virginia

Shorebirds (order Charadriiformes) face population declines on the global and continental scale (Koleček et al. 2021, Smith et al. 2023). Conservation efforts focus on long-term population monitoring and identification of extrinsic factors that limit population growth, with the goal of developing management strategies that address those limiting factors by reducing their effects on population vital rates (Brown et al. 2001, Colwell 2010). On the breeding grounds, research and monitoring efforts often track annual breeding pair numbers and productivity (a combined metric of nest and chick survival; Boettcher et al. 2007, Wilke et al. 2017), attempt to identify factors that limit reproductive success, such as predation and human disturbance (Sutherland et al. 2012), and implement management actions to control threats to reproductive success (Hunt et al. 2019, Mengak et al. 2019).

The threats to shorebird reproductive success may vary between stages of reproduction (e.g., clutch incubation, brood rearing), across space, and over time. Shorebirds, such as those from families Charadriidae (e.g., plovers) and Haematopodidae (i.e., oystercatchers), have precocial or semi-precocial chicks that are highly mobile shortly after hatching (Winkler et al. 2020*a*, *b*). Thus, brood rearing often occurs in a different location than clutch incubation (Cohen et al. 2009, Schulte and Simons 2015), resulting in variation in the threats to clutch and brood success. Additionally, many shorebirds breed in dynamic systems where threats may constantly change or evolve. In coastal landscapes where beach-nesting shorebirds breed, the landscape may rapidly change in response to human activities such as development and coastal engineering (Schupp et al. 2013), short-term events such as storms and high-water events (Robinson et al. 2019, Zeigler et al. 2019), and long-term drivers such as sea-level rise (Von Holle et al. 2019, van de Pol et al. 2024). As the landscape changes, the factors affecting clutch and brood success are also expected to be dynamic.

The American oystercatcher (*Haematopus palliatus*) is a long-lived shorebird that undergoes intense monitoring and management within its range on the Atlantic and Gulf coasts of the United States (Clay et al. 2014, American Oystercatcher Working Group et al. 2020). Management efforts for this species often target reproductive success, as adult survival is high (Schulte 2012, Felton et al. 2017). Across the species' range, breeding season management efforts involve monitoring the survival of nests and semi-precocial chicks, and aim to increase productivity rates by identifying and addressing key threats to nest and chick survival (Schulte et al. 2010).

Virginia is a significant breeding location for American oystercatchers, supporting the largest breeding population on the Atlantic and Gulf coasts of the United States (Wilke et al. 2005, American Oystercatcher Working Group et al. 2020). The barrier island system on the Atlantic coast of Virginia's Delmarva Peninsula provides a large expanse of contiguous undeveloped habitat. As a result, it supports a majority of the Virginia breeding population of American oystercatchers (Wilke et al. 2005) and historically high average reproductive success rates relative to other locations in the United States (American Oystercatcher Working Group et al. 2020). Long-term monitoring and research have identified flooding from high water events and predation by mammals (e.g., red fox [*Vulpes vulpes*], northern raccoon [*Procyon lotor*]), avian species (e.g., crows [*Corvus* spp.], grackles [*Quiscalus* spp.], gulls [Laridae], peregrine falcons [*Falco peregrinus*]), and Atlantic ghost crabs (*Ocypode quadrata*) as common causes of clutch loss and mortality of newly hatched chicks in Virginia (Nol 1989, Wilke et al. 2005, Denmon et al. 2013, Call et al. 2023). Management efforts in Virginia have addressed these locally identified threats and other range-wide threats (e.g., disturbance from beach recreation, habitat loss; Schulte et al. 2010, Clay et al. 2014) when possible by removing mammalian predators, limiting disturbance from humans through restrictions on access and recreational activities, and preserving nesting and foraging habitat through the widescale protection of beaches and saltmarshes.

The Virginia barrier island system is highly dynamic (Hayden et al. 1991). Despite ongoing management efforts, natural resource managers have observed low annual productivity rates in Virginia since 2016, indicating that the threats to nest and chick survival in this system may be changing such that current management practices alone are not as effective. In 2016–2020, American oystercatcher productivity on monitored islands within the Virginia barrier island system averaged 0.34 ± 0.04 (SE) fledged chicks per pair, compared to 0.70 ± 0.03 (SE) fledged chicks per pair in the 5 years prior, 2011–2015 (The Nature Conservancy, unpublished data). This reduction in average productivity occurred despite the number of monitored breeding pairs remaining relatively stable, with 282.8 ± 6.79 (SE) pairs monitored in 2016–2020, compared to 272.4 ± 15.34 (SE) pairs monitored in 2011–2015. While American oystercatchers have high annual survival rates and a long lifespan, and thus low productivity may be sufficient for maintaining a stable population (McGowan et al. 2005, Sabine et al. 2006), average productivity in the barrier island system from 2016–2020 was lower than the estimated rate needed for population stability in Virginia (approximately 0.4 fledged chicks per pair; Wilke et al. 2017). In 2019, camera monitoring at nests and brood-rearing sites on a Virginia barrier island with approximately 100 breeding pairs of American oystercatchers provided some insight into the threats to reproductive success by characterizing the predator community and documenting nest failure events. However, these efforts failed to provide a complete picture of what may be causing low productivity, as cameras did a poor job of documenting chick survival and capturing sources of mortality of mobile chicks that had left the nest site (Call et al. 2023).

The objective of this study was to assess the cause of declining American oystercatcher productivity in the Virginia barrier islands by identifying sources of nest failure and chick mortality through routine surveys and tracking of radio-tagged chicks at select study sites in 2021–2023. Additionally, we aimed to identify which stage of reproduction was driving low reproductive success in American oystercatchers to guide adaptive management decisions. We hypothesized that both nest and chick survival in Virginia were negatively associated with a complex set of environmental conditions (e.g., extreme weather events, vulnerability to flooding) and biotic factors (e.g., presence of predators, competition with neighboring pairs). Additionally, we predicted that low chick survival, rather than low nest survival, was driving low productivity rates based on a prior camera-trapping study that found high hatching success (Call et al. 2023).

## STUDY AREA

We monitored American oystercatcher reproductive success during the breeding season (late-March through July) within study sites on Metompkin Island (37.75° N, 75.54° W) in 2021–2022 and Fisherman Island (37.09° N, 75.96° W) in 2023. Average mean daily air temperature during the study period was 20.04 ± 0.03°C (SE; range = 3.33–31.11°C). Average daily precipitation was 0.30 ± 0.04 cm (SE; range = 0–5.82 cm). Both islands were part of the Virginia barrier island system, a 100-km expanse of largely undeveloped islands located on the Atlantic coast of

Virginia's Delmarva Peninsula (Figure 1). The Virginia barrier islands were a semidiurnal tidal system with a mean tidal range of approximately 1.2 m (National Oceanic and Atmospheric Administration 2025). Combined, Metompkin Island and Fisherman Island were representative of the range of geomorphological and ecological conditions within the Virginia barrier island system.

Metompkin Island was an approximately 10-km-long, 107–831-m-wide barrier island (approximately 504 ha) located 1.5–2.5 km from the mainland and oriented parallel to the mainland's shoreline. Average elevation was 1.64 m above sea level (asl; Robbins et al. 2022). Habitat on Metompkin Island varied across the island in regard to the dominant geomorphological and ecological processes and abundance of nesting, chick-rearing, and foraging habitat (Figure S1). The northern half of Metompkin Island was dominated by widespread overwash disturbance that maintained low elevation (i.e., mean elevation approximately 1.0 m asl) and a hummocky dune system punctuated by overwash fans, providing access to mudflats and saltmarsh on the island's bayside. The beach, dunes, and overwash fans were sparsely vegetated with herbaceous species such as saltmeadow cordgrass (*Spartina patens*), American beachgrass (*Ammophila breviligulata*), and bitter panicum (*Panicum amarum*). In contrast, the southern half of Metompkin Island had a relatively tall dune ridge as a result of localized disturbance processes. The dune ridge protected an interior vegetation community dominated by saltmeadow cordgrass, American beachgrass, bitter panicum, and thickets of southern wax myrtle (*Morella cerifera*) that collectively restricted access to the island's bayside mudflats and shallow lagoon.

Fisherman Island was an approximately 880-ha round barrier island located 0.8–1.5 km from the Delmarva Peninsula in the mouth of the Chesapeake Bay. Average elevation was 1.45 m asl (Robbins et al. 2022). Habitat on the eastern side of Fisherman Island included a wide ocean-facing beach and a narrow low-energy beach and sand spit that were sheltered by inlets on the northeastern side of the island (Figure S2). The sandy beaches were backed by a hummocky dune system, grasslands primarily composed of saltmeadow cordgrass, American beachgrass, and bitter panicum, dense shrub thickets dominated by northern bayberry (*Morella pensylvanica*), a maritime forest containing black cherry (*Prunus serotina*) and scattered loblolly pine (*Pinus taeda*), and saltmarsh.

During our study, Metompkin Island and Fisherman Island were managed to protect imperiled species, such as the American oystercatcher, a species of very high conservation need in Virginia, the federally threatened piping plover (*Charadrius melodus*), and the state endangered Wilson's plover (*Charadrius wilsonia*; Virginia Department of Wildlife Resources 2015). Metompkin Island was primarily owned and managed by The Nature Conservancy, though a small portion of the island at its northernmost extent was owned by the United States Fish and Wildlife Service. Fisherman Island was entirely owned and managed by the United States Fish and Wildlife Service. Both islands had public access restrictions that limited human use of the island. On Metompkin Island, public access was restricted to low-disturbance recreational activities (e.g., walking, fishing, sunbathing) in the intertidal zone. No public access was allowed on Fisherman Island.

Additionally, natural resource managers conducted seasonal trapping for mammalian predator species (northern raccoon, red fox, and coyote [*Canis latrans*]) on both islands before and during the shorebird breeding season. Trapping allowed for complete or near-complete removal of mammalian predators on Metompkin Island, which lacks dense vegetation to support persistent mammal populations. In contrast, trapping only served to reduce the number of mammalian predators on Fisherman Island (including complete removal of red fox and coyote, if present), which had a robust population of northern raccoons because of its dense vegetation, proximity to the mainland, and connection to the Delmarva Peninsula via US Route 13. Additional shorebird predators (Hunt et al. 2019) known to be present on Metompkin Island and Fisherman Island included herring gull (*Larus smithsonianus*), great black-backed gull (*Larus marinus*), laughing gull (*Leucophaeus atricilla*), gull-billed tern (*Gelochelidon nilotica*), black-crowned night heron (*Nycticorax nycticorax*), American crow (*Corvus brachyrhynchos*), fish crow (*Corvus ossifragus*), boat-tailed grackle (*Quiscalus major*), common grackle (*Quiscalus quiscalus*), great horned owl (*Bubo virginianus*), peregrine falcon, and Atlantic ghost crab.

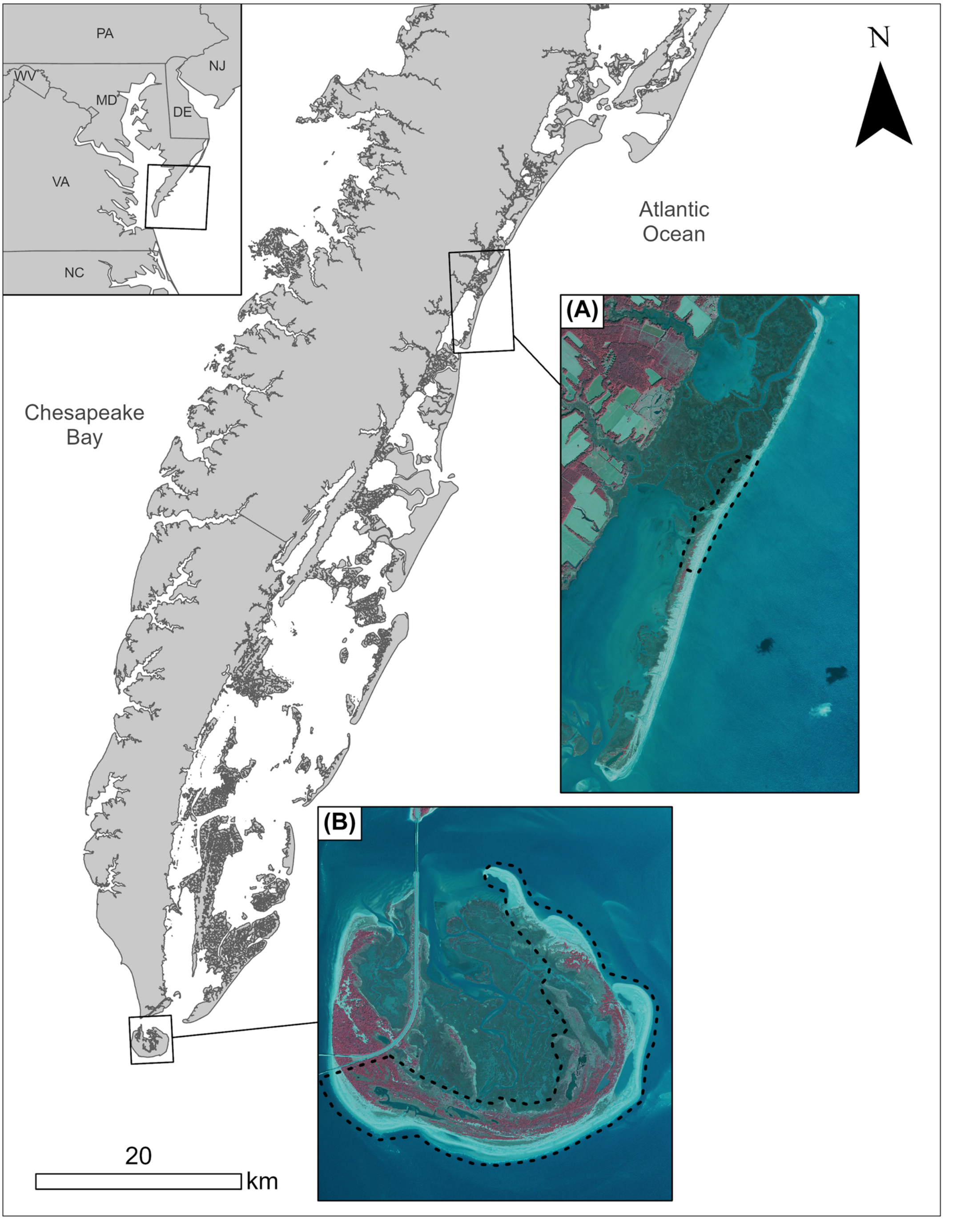


**FIGURE 1** The Virginia barrier island system is a chain of 14 barrier islands located on the Atlantic coast of the Delmarva Peninsula in the United States. We tracked American oystercatchers in study areas (outlined by dashed polygons) located within a 3-km extent centered around the middle of Metompkin Island in 2021–2022 (A) and on the ocean-facing side of Fisherman Island (B) in 2023.

# METHODS

## Field methods

We used walking surveys to monitor nest and brood survival and radio-tracking to monitor individual chick survival. We initiated monitoring in early spring as American oystercatchers began establishing territories (i.e., 25 March in 2021, 8 April in 2022, and 14 April in 2023) and proceeded until all breeding pairs successfully fledged young or stopped defending their territories (i.e., 18 July in 2021, 22 July in 2022, and 11 July in 2023). We attempted to conduct surveys every 1–3 days, though monitoring intervals varied (average = 2.09 ± 0.85 days, range = 1–9 days) depending on our ability to access remote sites due to weather and tides.

### Nest and brood surveys

To monitor nest survival, we conducted routine nest surveys during each site visit. We searched all dry, sandy portions of the study area for evidence of nesting activity and identified pair territories and nest sites by observing birds for territorial or defensive behavior (e.g., alarm calling, sneaking behavior) and noting the presence of dense tracks, scrapes, or eggs. Once we found a nest or scrape, we recorded the location in ArcGIS Collector or ArcGIS Field Maps (Esri, Redlands, CA, USA) and confirmed the status of the nest as active, failed, or hatched at nest checks during subsequent surveys. We monitored all nests until we determined success or failure. We considered a nest successful if at least one egg from the clutch hatched. If no eggs hatched, we considered a nest to be failed. When possible, we identified sources of egg loss using available signs around the nest (e.g., predator tracks).

To monitor chick survival, we conducted routine brood surveys during each site visit. When possible, we used resighting of adults marked with plastic field-readable alphanumeric bands to identify broods. However, not all adults monitored in our study were uniquely marked, so we also identified broods based on breeding pair territories and assumed that territory mixing rarely, if ever, occurred. Once a nest hatched, we confirmed the status of the brood (active, failed, or fledged) and the number of chicks present at brood checks during subsequent surveys. To avoid double-counting chicks, we only counted the maximum number of chicks seen at one time. If we did not observe chicks but observed adult behavior that indicated chicks were present (e.g., alarm calling, provisioning behavior), we assumed the brood was active, but the number of chicks was unknown. We monitored all broods until confirmed failure or fledging, which we assumed to occur at 35 days based on the minimum age of fledging for American oystercatchers (American Oystercatcher Working Group et al. 2020) and anecdotal observations of flight in chicks in Virginia. We estimated chick ages based on their hatch dates, which we considered to be day 0.

### Radio-tracking chicks

American oystercatchers are often mobile within 12–48 hours after hatching (American Oystercatcher Working Group et al. 2020). This mobility, combined with their cryptic coloration and tendency to hide to avoid detection, makes them difficult to relocate once they have left the nest site (Schulte and Simons 2015). Radio-tracking improves the chances of relocating highly mobile and camouflaged chicks, making it a useful method for understanding the factors that affect the survival of shorebird chicks (Whittier and Leslie 2005, 2009). Additionally, radio-transmitters are a way to uniquely mark chicks when they are still too small to mark with plastic field-readable bands; thus, they were useful for identifying individual chicks and their broods.

For broods that survived long enough to have dry, mobile chicks available for capture, we radio-tagged one chick per brood using a battery-powered digitally coded radio-transmitter (i.e., PowerTag; Cellular Tracking Technologies, Rio Grande, NJ, USA) weighing less than 1.0 g (<3% of average mass at hatching; American Oystercatcher

Working Group et al. 2020). We captured chicks using hand nets and attached a radio-transmitter to the intrascapular region of the chick using a cyanoacrylate adhesive (VetBond Tissue Adhesive, 3 M Animal Care Products, St Paul, MN, USA, or Super Glue Ultra Gel Control, Loctite, Hartford, CT, USA; Warnock and Takekawa 2003, Stantial et al. 2018). We released all chicks within 15 minutes of capture and monitored them after release from a distance using spotting scopes to ensure no adverse effects due to capture, handling, or radio-transmitter attachment, and that an adult returned to attending the chick.

We monitored the survival of all radio-tagged chicks until mortality or fledging. To relocate the chicks, we used a tracking system that combined continuous, long-range tracking conducted by a grid of stationary receivers, with fine-scale tracking using a handheld antenna and receiver (Figure 2). This system allowed us to combine automated radio-telemetry with telemetry surveys, which is demonstrated to perform similarly to satellite telemetry when monitoring breeding shorebirds (Loring et al. 2017).

The grid of stationary receivers included 2 components: 1) a solar-powered base station (Generation II SensorStation; Cellular Tracking Technologies) connected to an approximately 6-m tower equipped with 1 omnidirectional antenna and 2 Yagi antennas (hereafter, referred to as tower) that could detect signals from our radio-transmitters within an approximately 1.5-km radius, and 2) a grid of 27–37 solar-powered receivers (Generation II Nodes; Cellular Tracking Technologies) equipped with omnidirectional antennas, mounted on approximately 2.5-m conduit poles. The tower and receivers were equipped with anti-perching devices to minimize perching by avian predators. The receivers were placed approximately 150 m apart, as recommended by the manufacturer for the study site, and positioned so that they were centered around the tower to cover the beach, dune, grassland, shrubland, and saltmarsh edge. The number of receivers used depended on the width of the study area. The study area on Fisherman Island was wider than the study area on Metompkin Island because of the shape and size of the islands. Both the tower and the receivers recorded the digital ID, time stamp, and signal strength of all detected signals from the radio-transmitters, which were programmed to send a signal every 15 seconds. The receivers communicated these data to the tower base station, which uploaded the data to an online data portal hourly, allowing us to access data remotely. We viewed and analyzed automated telemetry data in the statistical computing environment R, versions 4.0.5–4.3.1 (R Core Team 2023), using functions from the package celltracktech (Gorzo 2022).

We combined automated radio-telemetry with in-person telemetry surveys using a handheld antenna and receiver during our brood surveys. The data we received from the automated telemetry grid aided our ability to identify when transmitters were not moving or no longer within range of the receivers. If we found a transmitter during telemetry surveys with chick remains or other signs of chick mortality (e.g., plucked feathers), we attempted to determine the cause of mortality using surrounding field sign. If we relocated the transmitter without chick remains or other signs of mortality, or if we resighted a chick without its transmitter during brood surveys, we assumed the transmitter had fallen off the chick. Chicks often lost transmitters because the cyanoacrylate adhesive failed before the chick reached minimum age of fledging (transmitter retention time ranged from 2–31 days). When a chick lost its transmitter, we attempted to recapture the chick so that we could reapply the transmitter. We identified previously tagged chicks from untagged chicks based on the area of missing feathers where the base of the transmitter was attached within their intrascapular region.

## Statistical analyses

We conducted all analyses in the statistical computing environment R, version 4.3.1 (R Core Team 2023). To quantify survival for all nest attempts and radio-tagged chicks, we developed logistic-exposure models (Shaffer 2004) implemented within a Bayesian framework (Schmidt et al. 2010). We used a modeling framework with age-specific estimates of daily survival rate, rather than a constant estimate, to account for sampling bias and changes in survival as a nest or chick aged (Weiser 2021).

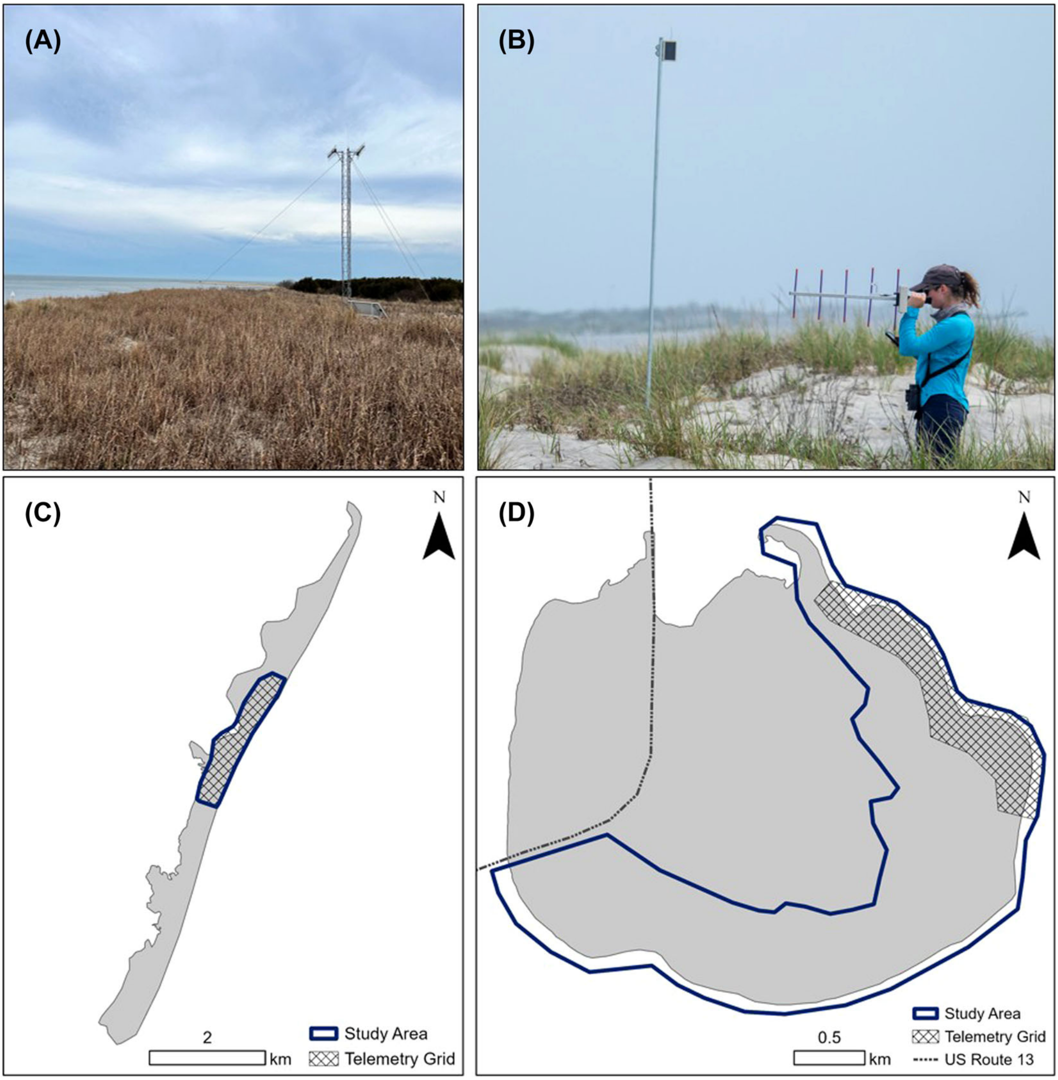


**FIGURE 2** The radio-telemetry system used to track American oystercatcher (*Haematopus palliatus*) chicks at study sites on Metompkin Island, Virginia, USA, in 2021–2022 and Fisherman Island, Virginia, in 2023 combined automated radio-telemetry with radio-telemetry surveys. The automated radio-telemetry system included a 6-m tower equipped with 3 antennas (A) and a grid of 27–37, 2.5-m receivers equipped with a single omnidirectional antenna (B). We also used a handheld antenna and receiver for fine-scale tracking of radio-transmitters (B). The automated radio-telemetry system spanned our entire 3-km-long study area on Metompkin Island (C) and a 3-km area in our larger study area on Fisherman Island (D).

We first estimated daily survival rate for each nest attempt or radio-tagged chick as:

$$\text{logit}(\varphi_{i,\,t}) = \beta_0 + \alpha_i + \beta_{i,t}X_{i,t},$$

where the survival probability (φ) of nest or chick $i$ at time $t$ (i.e., daily survival) was a function of an intercept ($\beta_0$), a random effect for each individual nest attempt or radio-tagged chick ($\alpha_i$) to account for individual heterogeneity, and the effects of individual- or time-specific environmental or ecological covariates ($\beta_{i,t}X_{i,t}$), including a linear effect of age, in days.

We then quantified cumulative survival probability as:

$$\varphi = \text{logit}(\varphi_{i,1})\cdot \cdots \cdot\text{logit}(\varphi_{i,n}),$$

where the cumulative daily survival probability (φ) of a nest attempt or radio-tagged chick to day *n* was the product of age-specific estimates of daily survival rates for all ages from the nest initiation date or chick hatch date (day 1) to day *n*. We quantified the cumulative probability of nest survival until day 29, which was the average length of nest incubation in our study. We quantified the cumulative probability of chick survival until day 35, or the minimum age of fledging in American oystercatchers (American Oystercatcher Working Group et al. 2020).

The models included the effects of time- and nest- or chick-specific covariates on nest and chick survival (Table 1). In addition to age, we included linear effects for time-specific variables related to weather conditions (e.g., temperature, precipitation, water level) and linear effects for individual-specific variables such as distance from the high tide line, distance to nearest neighboring pair, and pair density. We also included quadratic terms for age and temperature, as we suspected the effects of these variables to be non-linear (i.e., age or temperature thresholds that may affect daily survival rates).

We standardized all covariates by centering each variable around the mean and scaling by 2 standard deviations (Gelman 2008). Nest initiation date was highly correlated with temperature ($r = 0.7$), so we regressed the average mean daily temperature for the monitoring interval on the average date of the monitoring interval and used the residuals as the values for the temperature variable in our nest survival model (Table 1; Riggio et al. 2023). To maintain consistency, we used the same procedure with the temperature variable in the chick survival model, despite chick hatch date being only moderately correlated with temperature ($r = 0.4$). This residual variable for temperature was not correlated with nest initiation date ($r = 0$) or chick hatch date ($r = 0$).

To identify informative covariates, we first ran a full model that contained all covariates for nest or chick survival and then examined the 85% Bayesian credible interval (BCI) for each effect. We concluded that a covariate was informative and had an important effect on survival if the corresponding 85% BCI did not overlap zero (Arnold 2010). We dropped all covariates from the model that were uninformative and re-ran that model so that it only included informative covariates. We present estimates using the mean of the posterior distribution and corresponding 85% credible intervals and *f* value (proportion of the posterior distribution that is above or below zero).

We fit our models using Markov chain Monte Carlo methods implemented in JAGS (Plummer 2003) using the R package jagsUI (Kellner and Meredith 2024; code available in Supporting Information). For the random effect, we used a normal prior with a mean of 0 and a uniform standard deviation constrained to the interval of 0 to 10 (Schmidt et al. 2010). We used a weakly informed, regularizing prior ($\mu = 0, \sigma^2 = 2$) for the intercept and all fixed parameters in the model. On the logit scale, a weakly informative prior such as $N(0, \sigma^2 = 2)$ centers survival probabilities around 0.50, while allowing flexibility for probabilities to move towards zero or one (Lemoine 2019, Banner et al. 2020). We chose to use a weakly informed prior, rather than a vague prior with large variance, to avoid producing probabilities heavily biased towards the extremes, as may occur when a vague prior is transformed to the logit scale (Banner et al. 2020).

We ran 3 Markov chains with 100,000 iterations per chain and an adaptation period of 25,000 iterations. We discarded 25,000 iterations at the beginning of each chain as a burn-in to ensure good mixing of the chains and included a thinning factor of 2, resulting in a posterior sample of 37,500 samples per chain, or 112,500 total samples. We checked for convergence by using the Gelman-Rubin diagnostic (Gelman and Rubin 1992) and visually inspecting the trace plots with the package MCMCvis (Youngflesh et al. 2023). We considered convergence achieved when $\hat{R} \leq 1.05$ for all parameters in the model.

## RESULTS

We monitored 76 active American oystercatcher territories and 110 nest attempts across all 3 breeding seasons. From the 110 nest attempts, 54 nests hatched (49.1% of all nest attempts) at least one egg and 29 chicks were assumed to have fledged (25.4% of hatched chicks). Productivity varied between islands and years (Table 2). Overall productivity for all 3 breeding seasons was 0.38 fledged chicks per pair.

**TABLE 1** Predictor variables used in our logistic exposure models to estimate the daily survival rates of American oystercatcher (*Haematopus palliatus*) nests and radio-tagged chicks from study sites on Metompkin Island, Virginia, USA, in 2021 and 2022 and Fisherman Island, Virginia, in 2023.

| Response | Predictor | Definition of predictor |
|---|---|---|
| Nest survival | Nest age | Number of days since nest initiation, at the midpoint of the monitoring interval. Nest initiation is day 0. |
| | $(\text{Nest age})^2$ | Quadratic term for nest age. |
| | Year | Numeric terms representing 2021, 2022, 2023. |
| | Initiation date | Day of the breeding season (i.e., number of days since 1 April) on which the first egg of the clutch was laid. |
| | Temperature | Residual of the average of the mean daily air temperature for the monitoring interval (°C)[a] regressed on the average date of the monitoring interval. |
| | $(\text{Temperature})^2$ | Quadratic term for temperature. |
| | Precipitation | Average daily precipitation for the monitoring interval (cm).[a] |
| | Water level | The average verified water level (relative to the mean highest high water level; MHHW) for the monitoring interval.[b] |
| | Distance to nearest neighbor | Euclidean distance from a breeding pair to the nearest neighboring breeding pair (m).[c] |
| | Pair density | The number of breeding pairs per hectare, within a 106-m radius.[d] |
| | Distance to high tide line | Euclidean distance from nest to nearest high tide line.[e] |
| Chick survival | Chick age | Number of days since hatch, at the midpoint of the monitoring interval. |
| | $(\text{Chick age})^2$ | Quadratic term for chick age. |
| | Year | 2021, 2022, and 2023. |
| | Hatch date | Day of the breeding season (i.e., number of days since 1 April) on which the first egg of the clutch was laid. |
| | Temperature | Residual of the average of the mean daily air temperature for the monitoring interval (°C)[a] regressed on the average date of the monitoring interval. |
| | $(\text{Temperature})^2$ | Quadratic term for temperature. |
| | Precipitation | Average daily precipitation for the monitoring interval (cm).[a] |
| | Water level | The average verified water level (relative to the mean highest high water level; MHHW) for the monitoring interval.[b] |
| | Distance to nearest neighbor | Euclidean distance from a breeding pair to the nearest neighboring breeding pair (m). Same value used for the nest from which the chick hatched.[c] |

**TABLE 1** (Continued)

| Response | Predictor | Definition of predictor |
|---|---|---|
| | Pair density | The number of breeding pairs per hectare, within a 106-m radius. Same value used for the nest from which the chick hatched.[d] |

[a]These data were from the National Weather Service's climatological data for the Wallops Island Area, Virginia (37.84° N 75.47° W).

[b]These data were collected from National Oceanic and Atmospheric Administration station 8631044 in Wachapreague, Virginia (37.60° N 75.68° W). The datum used for the verified water level was the mean highest high water level (MHHW).

[c]The first nest attempt for each pair was used as a reference point for their territory.

[d]The average distance to the nearest neighboring breeding pair for all breeding pairs in the study was 106 m.

[e]The high tide line was mapped on the most recent publicly available aerial imagery collected by the National Agriculture Imagery Program (United States Department of Agriculture, Farm Service Agency Aerial Photography Field Office, Salt Lake City, Utah, USA), at the time of analysis. The most recent imagery for Metompkin Island was collected on 17 October 2021. The most recent imagery for Fisherman Island was collected on 13 September 2021.

**TABLE 2** The number of monitored American oystercatcher (*Haematopus palliatus*) territories, number of nest attempts, and productivity (i.e., the number of fledged chicks per pair) within study sites on Metompkin Island, Virginia, USA, in 2021 and 2022 and on Fisherman Island, Virginia, in 2023.

| | | Nest attempts | | | | |
|---|---|---|---|---|---|---|
| Year | Territories monitored | Total | First | Second | Third | Productivity |
| 2021 | 26 | 38 | 26 | 11 | 1 | 0.58 |
| 2022 | 28 | 44 | 27 | 16 | 1 | 0.21 |
| 2023 | 22 | 28 | 22 | 4 | 2 | 0.36 |
| Overall | 76 | 110 | 75 | 31 | 4 | 0.38 |

## Nest survival

Nest loss from flooding and predation were the largest drivers of nest failure (32% and 22% of failed nests, respectively; Table 3), though predation was a widespread event that occurred annually, while flooding predominantly occurred in 2022 from a single coastal flooding event (Figure S3). Suspected predators included mammals (8% of failed nests) and ghost crabs (6% of failed nests). Additionally, 8% of failed nests were suspected to have been predated, but we could not determine the predator. Additional sources of nest failure were eggs failing to hatch because of non-viability or environmental exposure (20% of failed nests) and abandonment (6% of failed nests). We could not identify the cause of failure for 20% of failed nests. We could not determine fate (hatch or failure) for 5.5% of total nests ($n = 6$).

The average time from nest initiation to hatching was 29 days (range = 26–39 days; $n = 101$ nests, after 9 nests were censored from the survival analysis for incomplete data), and the probability of a nest surviving to day 29 was 0.91 ± 0.08 (SD; 85% BCI = 0.77, 0.99; Figure 3; daily survival rates in Table S1). Nest survival progressively decreased as nests aged ($\beta_{\text{linear age}} = -1.07$; 85% BCI = −2.03, −0.28; $f = 0.99$; $\beta_{\text{quadratic age}} = -1.54$; 85% BCI = −2.51, −0.56; $f = 0.99$; Figure 4; Table S2). Nest survival also declined at higher water levels ($\beta = -1.49$; 85% BCI = −1.97, −1.06; $f = 1.00$; Figure 4; Table S2) and as distance from the high tide line increased ($\beta = -0.78$; 85% BCI = −1.51, −0.14; $f = 0.96$; Figure 4; Table S2). Nest survival varied between years and was greatest in 2023 on Fisherman Island ($\beta = 0.86$; 85% BCI = 0.37, 1.45; $f = 1.00$; Figure 4; Table S2).

**TABLE 3** Determined fates and, when relevant, suspected source of failure for American oystercatcher (*Haematopus palliatus*) nest attempts ($n$ = 110 attempts from $n$ = 76 active territories) monitored during the 2021 and 2022 breeding seasons on Metompkin Island, Virginia, USA, and 2023 breeding season on Fisherman Island, Virginia. Fates and suspected sources of failure were determined by trained monitors using the best available field sign or evidence. For example, nest fates were determined using predator tracks, eggshell fragments, yolk remains, and sand or moisture accumulation on or around eggs. Percentages are expressed as proportions of the total number of nests each year ($n$ = 38 in 2021; $n$ = 44 in 2022; $n$ = 28 in 2023; $n$ = 110 total).

| Year | Hatch | Did not hatch | Predated (mammal) | Predated (avian) | Predated (crab) | Predated (unknown) | Flooded | Abandoned | Unknown failure | Unknown fate |
|---|---|---|---|---|---|---|---|---|---|---|
| 2021 | 18 (47.3%) | 5 (13.2%) | 2 (5.3%) | 0 (0%) | 0 (0%) | 2 (5.3%) | 1 (2.6%) | 1 (2.6%) | 5 (13.2%) | 5 (13.2%) |
| 2022 | 20 (45.5%) | 4 (9.1%) | 0 (0%) | 0 (0%) | 2 (4.5%) | 2 (4.5%) | 15 (34.1%) | 1 (2.3%) | 0 (0%) | 0 (0%) |
| 2023 | 16 (57.1%) | 1 (3.6%) | 2 (7.1%) | 0 (0%) | 1 (3.6%) | 0 (0%) | 0 (0%) | 1 (3.6%) | 6 (21.4%) | 1 (3.6%) |
| Total | 54 (49.1%) | 10 (9.1%) | 4 (3.6%) | 0 (0%) | 3 (2.7%) | 4 (3.6%) | 16 (14.5%) | 3 (2.7%) | 10 (9.1%) | 6 (5.5%) |

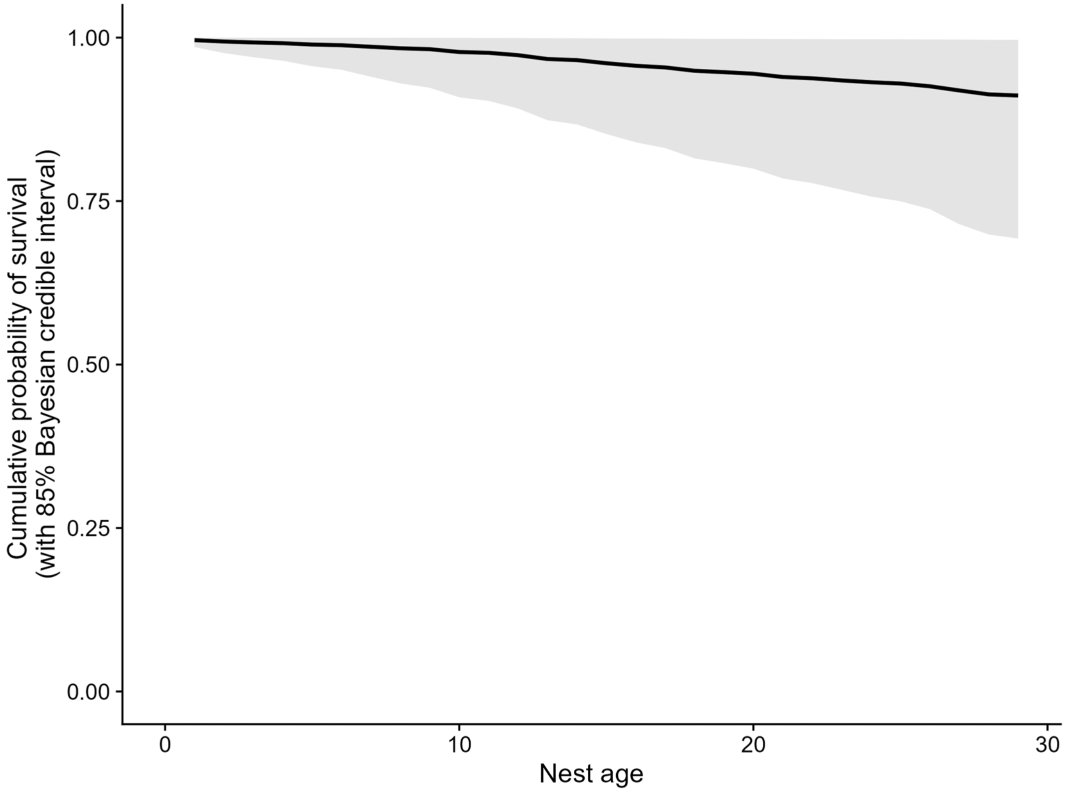


**FIGURE 3** Cumulative probability (curve) with 85% Bayesian credible interval (shaded area) of an American oystercatcher (*Haematopus palliatus*) nest surviving from initiation to the average length of incubation (i.e., 29 days) within study sites on Metompkin Island, Virginia, USA, in 2021 and 2022, and Fisherman Island, Virginia, in 2023. Cumulative survival probability is quantified as the product of daily survival rate estimates that include linear effects for age, temperature, and distance to the high tide line, and a quadratic effect for age.

## Chick survival

We captured and attached radio-transmitters to 45 chicks ($n = 15$ in 2021, $n = 19$ in 2022, and $n = 11$ in 2023). Radio-transmitters allowed us to determine the fate of 95.6% of radio-tagged chicks ($n = 43$; Table 4). In addition to confirming fate, we also identified fledging or cause of mortality for 66.7% of total radio-tagged chicks ($n = 30$). In contrast, we only identified fledging or a cause of mortality for 26.1% of chicks that were untagged (*n* known fate = 18; *n* total = 69).

Predation was the most common suspected source of chick mortality, with 25% of radio-tagged chicks that did not fledge suspected as predated by avian predators and 21.4% of radio-tagged chicks that did not fledge suspected as predated by ghost crabs (Table 4). Additional suspected sources of chick mortality were weather (3.6% of radio-tagged chicks that did not fledge), including flooding from storms, and physical trauma (3.6% of radio-tagged chicks that did not fledge), which we identified in one chick when it presented abnormal posture indicative of neurological issues, including head tilt (Jones and Orosz 1996; Table 4). We were unable to confirm a source of mortality for 46.4% of radio-tagged chicks that did not fledge (i.e., 28.9% of total radio-tagged chicks; Table 4).

We censored 2 chicks with unknown fates from the survival analysis, resulting in a sample size of 43 chicks. The probability of a radio-tagged chick surviving to the minimum age of fledging at 35 days old was 0.51 ± 0.14 (SD; 85% BCI = 0.31, 0.70; Figure 5; daily survival rates in Table S3). We found a linear effect for hatch date, with lower

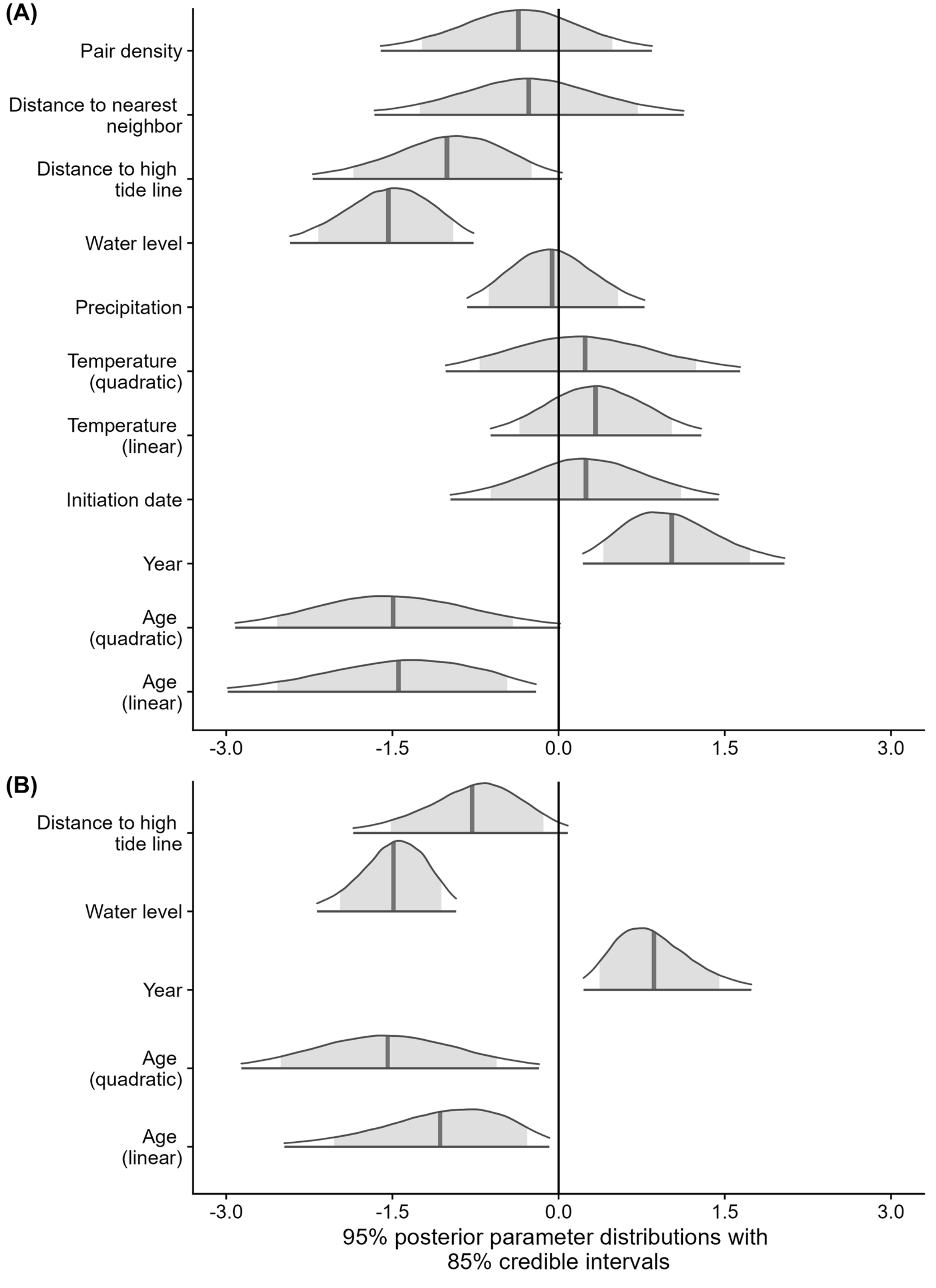


**FIGURE 4** (See caption on next page).

survival rates for chicks hatched later in the breeding season (β = −1.61; 85% BCI = −2.40, −0.91; *f* = 1.00; Figure 6; Table S4). Most mortality events for radio-tagged chicks were recorded in June or July (Figure 7). Additionally, we found a quadratic effect for temperature, with survival increasing quadratically with temperature (β = 1.16; 85% BCI = 0.07, 2.33; *f* = 0.94; Figure 6; Table S4).

# DISCUSSION

While American oystercatcher reproductive success in Virginia is affected by both hatch and fledge success, we found that low rates of chick survival may primarily be driving the low productivity patterns observed on some Virginia barrier islands since 2016. However, both nest and chick survival rates were higher than those reported at American oystercatcher breeding sites on the Atlantic and Gulf coasts in the United States, outside of Virginia. Nest survival rates were also higher than those reported for other oystercatcher species globally.

The cumulative probability of a nest surviving to hatching in our study exceeded 0.90, whereas cumulative nest survival rates (not age-specific) reported elsewhere within the American oystercatcher's breeding range in the United States were all below 0.50, including 0.25 for Cape Hatteras and Cape Lookout in North Carolina (Schulte and Simons 2015), 0.23 for the Cape Romaine region in South Carolina (Jodice et al. 2014), 0.25–0.45 for sites in the southern Big Bend region of Florida (Vitale et al. 2021), and 0.38 for the Texas Gulf Coast region (Koczur et al. 2014). The nest survival rate in our study also exceeded reported cumulative nest survival rates (not-age specific) for Chatham Island oystercatchers (*Haematopus chathamensis*) on Rēkohu-Wharekauri Chatham Island in Aotearoa New Zealand (0.25–0.76; Moore and Reid 2009), African oystercatchers (*Haematopus moquini*) on Robben Island in South Africa (0.22–0.67; Tjørve and Underhill 2008), and black oystercatchers (*Haematopus bachmani*) in Kenai Fjords National Park in Alaska (0.22–0.48; Morse et al. 2006). Additionally, we found that the cumulative probability of a chick surviving to fledging was 0.51, which was greater than American oystercatcher chick survival reported by another study that tracked survival of radio-tagged chicks in North Carolina (0.34; Schulte and Simons 2015). These results suggest that islands in Virginia continue to support above-average oystercatcher nest and chick survival, relative to other oystercatcher breeding locations globally and within the American oystercatcher breeding range on the Atlantic and Gulf coasts of the United States (American Oystercatcher Working Group et al. 2020). However, chick survival will likely need to improve to maintain a stable population in Virginia, as average productivity rates remain below the threshold for stationarity (Wilke et al. 2017).

Flooding and predation accounted for a combined 54% of nest failures in our study. Similarly, predation appeared to be a primary source of chick mortality, with 28.9% of all radio-tagged chicks suspected as predated by avian predators or ghost crabs. Both storm-driven flooding and predation have been previously reported as causes of nest failure for American oystercatchers and other beach-nesting species, such as piping plovers, breeding on the Virginia barrier islands (Nol 1989, Boettcher et al. 2005, Wilke et al. 2005, Denmon et al. 2013). Predation is also often considered to be a major source of American oystercatcher and piping plover brood failure in Virginia and elsewhere along the Atlantic and Gulf coasts (Nol 1989, Boettcher et al. 2005, Schulte and Simons 2015, Collins et al. 2016, Robinson et al. 2023). However, these threats may be evolving in response to climate trends and

**FIGURE 4** The 95% posterior probability distribution with mean estimates (line) and 85% Bayesian credible intervals (shaded area) for standardized covariates in models of American oystercatcher (*Haematopus palliatus*) nest survival within study sites on Metompkin Island, Virginia, USA, in 2021 and 2022, and Fisherman Island, Virginia, in 2023. The models shown are the full nest survival model that includes all possible covariates (A) and the final model that includes only informative covariates (B).

**TABLE 4** Determined fates and, when relevant, suspected source of failure for radio-tagged American oystercatcher (*Haematopus palliatus*) chicks ($n$ = 45) monitored during the 2021 and 2022 breeding seasons on Metompkin Island, Virginia, USA, and 2023 breeding season on Fisherman Island, Virginia. Chick fates were determined using observations of a carcass, carcass location (e.g., in the burrow of an Atlantic ghost crab [*Ocypode quadrata*]) or radio-tag location (e.g., underneath a known raptor perch), and timing of when a radio-tag stopped moving (identified from data collected by the automated telemetry grid). Percentages are expressed as proportions of the total number of radio-tagged chicks each year ($n$ = 15 in 2021; $n$ = 19 in 2022; $n$ = 11 in 2023; $n$ = 45 total).

| Year | Fledged | Predated (mammal) | Predated (avian) | Predated (crab)[a] | Predated (unknown) | Exposure to weather | Physical trauma | Unknown mortality | Unknown fate |
|---|---|---|---|---|---|---|---|---|---|
| 2021 | 7 (46.7%) | 0 (0%) | 1 (6.7%) | 3 (20%) | 0 (0%) | 0 (0%) | 0 (0%) | 4 (26.7%) | 0 (0%) |
| 2022 | 3 (15.8%) | 0 (0%) | 4 (21.1%) | 2 (10.5%) | 0 (0%) | 0 (0%) | 1 (5.3%) | 9 (47.4%) | 0 (0%) |
| 2023 | 5 (45.5%) | 0 (0%) | 2 (18.1%) | 1 (9.1%) | 0 (0%) | 1 (9.1%) | 0 (0%) | 0 (0%) | 2 (18.2%) |
| Total | 15 (33.3%) | 0 (0%) | 7 (15.6%) | 6 (13.3%) | 0 (0%) | 1 (2.2%) | 1 (2.2%) | 13 (28.9%) | 2 (4.4%) |

[a]Chicks were assigned this fate if the carcass was recovered from an Atlantic ghost crab burrow. Chick counts in this category could also include scavenged chicks, as it is difficult to determine scavenging from predation with certainty, without observing the predation or scavenging event.

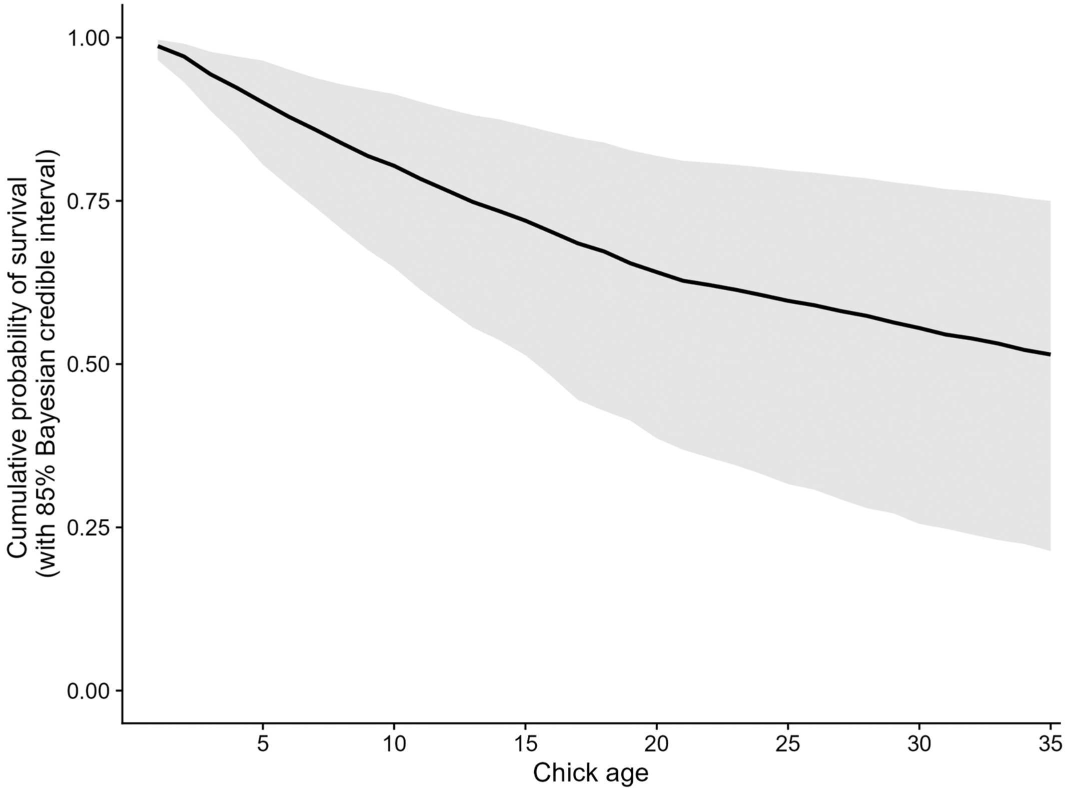


**FIGURE 5** Cumulative probability (curve) with 85% Bayesian credible interval (shaded area) of a radio-tagged American oystercatcher (*Haematopus palliatus*) chick surviving from hatch to the minimum age of fledging for American oystercatchers (35 days) within study sites on Metompkin Island, Virginia, USA, in 2021 and 2022, and Fisherman Island, Virginia, in 2023. Survival estimates include a linear effect for age, to account for variability in daily survival rates, as well as a linear effect for hatch date and a quadratic effect for temperature, both informative covariates.

management actions, as predator and disturbance management efforts have been consistent in the Virginia barrier islands before and after current years of low American oystercatcher productivity.

Low nest survival during periods of verified high water levels is likely the result of nests flooding from tidal or storm surge-driven inundation. Differences in weather patterns between 2021–2023 may, in part, explain the observed effect of year on nest survival. Heavy rain, storm surge, and strong wind gusts as a result of low-pressure storm systems occurred during all 3 years of the study, notably on 29–30 May in 2021, 19 April and 7–12 May in 2022, and 3–4 June and 21–22 June in 2023 (Lapenta et al. 2025). However, the May 2022 storm coincided with peak nesting activity for American oystercatchers in Virginia, which clusters around late-April to early-May (Nol 1989). During the storm, nests were exposed to tidal inundation and overwash, and 55.6% of first nest attempts were lost to flooding. As patterns of regional storminess are altered as a result of global climate change (i.e., longer storm seasons, increased storm intensity, and increased storm-surge-driven flooding; Dolan et al. 1988, Rahmstorf 2017, Truchelut et al. 2022, Dominguez et al. 2024), American oystercatchers and other beach-nesting shorebirds may be exposed to a greater number of flooding events during the breeding season than in the past. The risk of nest failure from high water events may also be further exacerbated by co-occurring changes in habitat as the islands undergo increasing rates of landward migration, shoreline erosion, and inundation as a result of sea-level rise (Mariotti and Hein 2022), and climate-driven ecosystem state change (Zinnert et al. 2019).

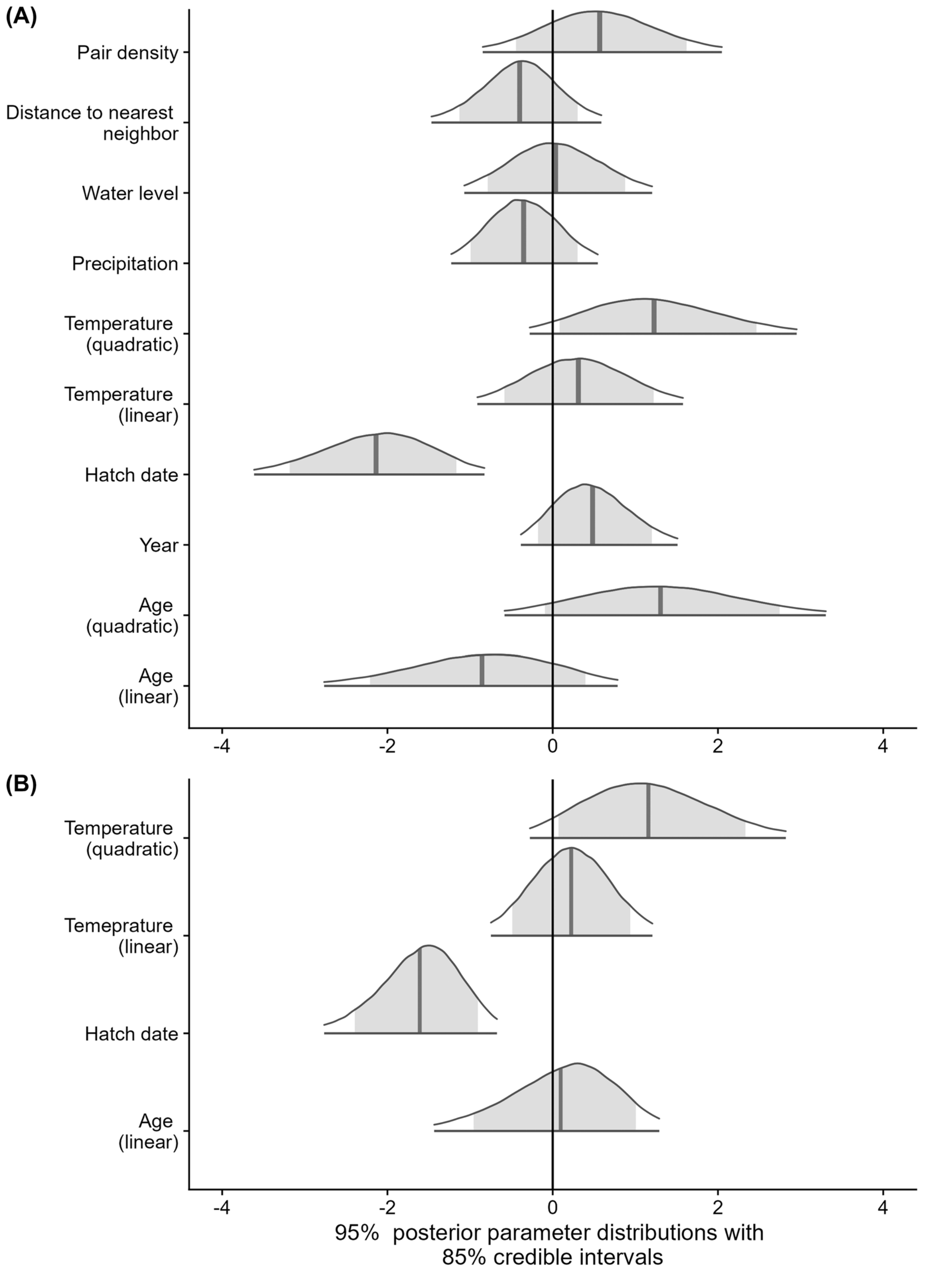


**FIGURE 6** (See caption on next page).

Additionally, our findings indicate that despite removal of some mammalian predators, the predator threat to nests and chicks remains through a complex predator community that includes birds and ghost crabs, in addition to mammals. Only 4 nests in our study (3.6% of all nests) were confirmed as failing because of mammalian predators—2 on Metompkin Island in 2021 when a red fox was temporarily present on the island and 2 on Fisherman Island in 2023 where raccoons remained pervasive despite trapping efforts. An additional 7 nests in

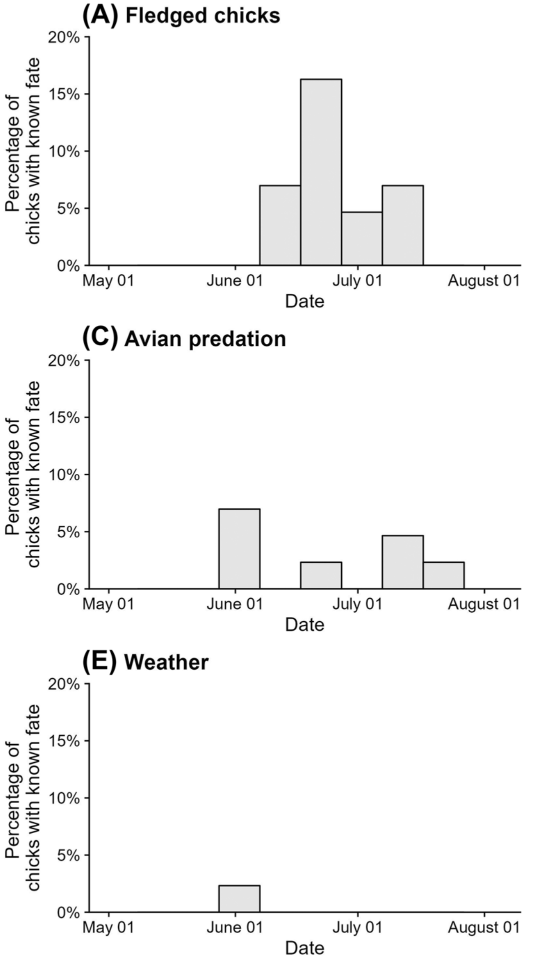


**FIGURE 7** Frequency and timing of fates for 43 radio-tagged American oystercatcher (*Haematopus palliatus*) chicks with known fates within study sites on Metompkin Island, Virginia, USA, in 2021 and 2022, and Fisherman Island, Virginia, in 2023. The ranges of dates during which chicks were radio-tagged and available to fledge or die was 8 May to 18 July. The number of chicks hatched per month were 23 in May, 21 in June, and 1 in July. The number of chicks available to fledge or die per month were 23 in May, 41 in June, and 9 in July.

**FIGURE 6** The 95% posterior probability distribution with mean estimates (line) and 85% Bayesian credible intervals (shaded area) for standardized covariates in models of radio-tagged American oystercatcher (*Haematopus palliatus*) chick survival within study sites on Metompkin Island, Virginia, USA, in 2021 and 2022, and Fisherman Island, Virginia, in 2023. The models shown are the full radio-tagged chick survival model that includes all possible covariates (A) and the final model that includes only informative covariates (B).

the study (6.3% of all nests) were likely predated, though we were unable to determine the direct source, as the ability to identify a nest predator from field evidence alone is limited (Call et al. 2023). Chicks were also predated, though we suspect that avian predators such as peregrine falcons and great horned owls, both abundant raptors on the landscape throughout the breeding season, and ghost crabs were the most likely the source of radio-tagged chick loss, based on field evidence such as the recovery of radio-tags from underneath known raptor perches and inside crab burrows.

Removal of predators, particularly those that are invasive or have artificially inflated populations as a result of human activities, is a common strategy for improving the reproductive success of imperiled bird species (Neuman et al. 2004, Smith et al. 2010, Hunt et al. 2019). However, predator removal does not always eliminate predation pressure, especially in ecosystems with complex predator communities (Doherty and Ritchie 2017), such as the Virginia barrier islands. Predator removal may have unintended consequences, including mesopredator release following the removal of an apex predator (Barton and Roth 2008, Stantial et al. 2021, Wails et al. 2025) and compensatory predation in which predation pressures switch to a different predator guild following partial predator removal (Ellis-Felege et al. 2012). Additionally, the predator threat may vary across the landscape and thus between the stages of American oystercatcher reproduction because brood-rearing often occurs away from the nest site. For example, ghost crab activity may be more abundant where soft, sandy substrate is more conducive to burrowing (Call et al. 2024), and mammalian and avian predator communities may be more active near the island interior, where the stable vegetation community provides suitable habitat for shelter and perching, potentially explaining the pattern of lower nest survival farther from the high tide line.

Complex interactions between drivers of nest and chick survival may also exist. In our study, inundation and flooding during the peak of the American oystercatcher nesting season forced pairs to renest, resulting in a second peak of nesting activity in late May and relatively late hatch dates for chicks. Hatch date had a strong, negative effect on chick survival, resulting in lower chances of surviving to fledging for late-hatching chicks. Late-hatching chicks may face different threats on the beach than chicks hatched earlier in the breeding season. For example, during the shorebird breeding season, ghost crab activity increases with date (Call et al. 2024), likely peaking during the mating and recruitment periods (June to September and June to November, respectively, in the Delmarva region; Lucrezi and Schlacher 2014). As a result, late-hatching chicks may be more likely to overlap with peak ghost crab activity on the island landscape, resulting in higher chick mortality, especially in younger chicks that are smaller and less mobile. Additionally, many juveniles of avian predator species fledge by June or July, including raptors such as peregrine falcons (White et al. 2020). If the flood risk and other factors continue to shift peak oystercatcher nesting and chick-rearing activity later in the breeding season, then chicks may continue to face relatively lower survival rates, resulting in continued low productivity.

Addressing complex and evolving threats to oystercatcher reproductive success will require adaptive management and creative solutions. To mitigate flood risk, natural resource managers may need to consider strategies such as creating and maintaining higher-elevation nesting and foraging habitat. The creation of relatively high-elevation nesting habitat could help long-lived species such as American oystercatchers behaviorally adapt to sea-level rise and coastal flooding, as pairs may increasingly use higher-elevation habitat over time if they can successfully fledge chicks (van de Pol et al. 2010, Bailey et al. 2019). Additionally, natural resource managers will need to adapt predator management strategies to also target the predation threat from non-mammalian predators. Control of a complex predator community is complicated by methodological considerations, including the difficulty of lethally controlling an abundant species such as ghost crabs (Hunt et al. 2019), as well as conservation concerns, such as when the predator of concern is also an imperiled species itself (e.g., peregrine falcons). However, creative approaches, such as ecosystem-based management, where all species are considered during conservation strategy planning, may prove useful (Watts and Truitt 2021). For example, natural resource managers may consider approaches that alter habitat near shorebird breeding sites to be less favorable to predator species (Watts and Truitt 2021), such as increasing shell and wrack cover to obstruct burrowing by ghost crabs (Call et al. 2024), removing perches or nesting habitat for avian predators (Watts and Truitt 2021), or improving the ability for incubating birds to detect predators (i.e., viewshed) by removing vegetation (Dorsey et al. 2025).

## MANAGEMENT IMPLICATIONS

In a rapidly changing world, adaptive management is a useful framework for conservation management because it allows wildlife managers to re-evaluate threats to population growth. The need to continuously monitor and assess threats to nest and chick survival is particularly important for the conservation of beach-nesting shorebird species, which use highly dynamic coastal landscapes throughout the entirety of their annual cycle. Our methods provided useful insight into the potential drivers of low American oystercatcher productivity rates in Virginia since 2016, by improving our ability to confirm nest and chick fate and document potential sources of egg and chick loss, including flooding and predation by species that are not currently lethally managed in Virginia. We emphasize that efforts to monitor the efficacy of existing management actions and evaluate evolving threats to nest and chick survival using both traditional survey techniques and emerging technologies (e.g., automated radio-telemetry) will be a useful management strategy for shorebird conservation as natural resource managers respond to a changing coastline.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

### ETHICS STATEMENT

We conducted all research associated with this project in compliance with the laws of the United States of America. Additionally, we followed all protocols laid out in the following permits: United States Fish and Wildlife Research and Monitoring Special Use Permits 2021-004 (Chincoteague National Wildlife Refuge), 2022-004 (Chincoteague National Wildlife Refuge), and 2023-02 (Fisherman Island National Wildlife Refuge); land access permits granted by The Nature Conservancy Virginia Coast Reserve for 2021 and 2022; the Virginia Department of Wildlife Resources Banding and Research Permit 071013 (for 2021) and the Virginia Department of Wildlife Resources Banding and Research permit granted to customer ID 2558265 (for 2022 and 2023); and the United States Geological Survey's Bird Banding Lab Federal Bird Banding Permit 21446. All research activities were approved by Virginia Tech's Institutional Animal Care and Use Committee (protocol 19-248 FWC). Throughout the study, we adhered to all applicable ethical guidelines for the use of wild birds in research, as presented in the Ornithological Council's Guidelines to the Use of Wild Birds in Research (Fair et al. 2023).

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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