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# Temporal not foraging factors affect reproductive success for American Oystercatchers (*Haematopus palliatus*) on two barrier islands in Virginia, U.S.A.

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**Abstract.**—Barrier islands in Virginia, U.S.A. support the most breeding American Oystercatchers (*Haematopus palliatus*) throughout their range; however reproductive success remains low. This study focused on how the food supply might influence reproductive success on two barrier islands in coastal Virginia. From 2022–2024, 821 observations were made on foraging adults and brood provisioning to assess food profitability, distances to foraging areas, diets of breeding pairs, and brood provisioning rates. Two hundred fifty-four nests were monitored, 102 of which hatched 215 chicks. Overall, foraging factors did not affect breeding success at the study site. Instead, daily nest survival was best explained by year. Interannual variation in predator and storm activity determined hatching success. In 2024, a lack of storm overwash and limited predator activity led to higher hatching success compared to 2023 and 2022 when nor'easters flooded nests and there was high nest predator activity by foxes, avian predators, and ghost crabs. Daily brood survival was best explained by age, where daily survival decreased with age. Older chicks tended to be of larger body size and hide less from predators, which likely increased their predation risk. Efforts to control predators and increase nesting habitat elevation can support American Oystercatcher reproductive success. *Received 1 Mar 2025, accepted 20 Oct 2025.*

**Key words.**—Breeding performance, Brood survival, Diet specialization, Foraging, Individual specialization, Nesting success, Predation, Overwash, Shorebirds

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The American Oystercatcher (*Haematopus palliatus*) is an obligate coastal bird that nests on beaches and in adjacent coastal marshes of the U.S. Atlantic Coast (American Oystercatcher Working Group *et al.* 2020). The American Oystercatcher is a species of conservation concern and is listed as state threatened in Georgia and Florida (Schulte and Simons 2015). American Oystercatchers inhabit a complex marine ecosystem with multiple factors contributing to the breeding success including the food supply, predation, storm overwash, and human disturbance (Nol 1989; Schulte and Simons 2015; Vitale *et al.* 2022).

Brood survival is tightly connected to the food supply for *Haematopus* spp. (Nol 1989; Ens *et al.* 1992; Robinson *et al.* 2019; Vitale *et al.* 2022). *Haematopus* spp. provide biparental care, where both adults provision broods (Nol 1989). Because of the handling skills and musculature required to successfully open bivalve prey (Kersten 1996; Hand *et al.* 2010), *Haematopus* spp. chicks must be provisioned one month past the age of fledging until they

are 60 days old and can forage for themselves (Kersten 1996). This lengthy provisioning period means that factors affecting foraging including the distance to the foraging area from the nest, brood provisioning rates, diet, and food profitability (food mass/handling time) can influence fledging success (Safriel 1985; Nol 1989; Ens *et al.* 1992; Hazlitt *et al.* 2002).

The state of Virginia in the U.S.A. has the highest concentration of breeding American Oystercatchers throughout their range (Wilke *et al.* 2005). On two barrier islands in Virginia, from 2016–2021, breeding productivity (chicks fledged per breeding pair) was lower (range: 0–0.32 chicks fledged per breeding pair) than the level required to maintain the population and balance adult mortality (0.5 chicks fledged per breeding pair) (Walters *et al.* 2020). Assateague Island and Assawoman Island, Virginia, U.S.A. are managed by the U.S. Fish and Wildlife Service as a part of Chincoteague National Wildlife Refuge. Current management efforts include predator trapping and closing nesting areas to human disturbance. Despite current

management efforts, breeding productivity remained low, so other factors like the food supply could be involved. Our aim was to understand the role of the food supply on American Oystercatcher breeding productivity at Assateague Island and Assawoman Island. Specifically, we investigated how food profitability, distance to the foraging area, diet, and brood provisioning rates might impact nest and brood survival.

METHODS

Study Area

The study was conducted on Assateague Island (37° 51' 7.2" N, 75° 22', 55.2" W; 753 ha) and Assawoman Island (37°, 48', 3.6" N, 75°, 31', 4.8" W; 129 ha) in coastal Virginia, U.S.A. We collected data during the American Oystercatcher breeding season from April to August of 2022–2024. From 2022–2024, Assateague Island supported 20–26 breeding pairs and Assawoman Island supported 26–31 breeding pairs. Our study population consisted of banded breeding birds with unique alphanumeric coded leg bands, so breeding pairs were distinguishable from one another. We regularly banded adults, so that at least one breeding pair member was banded (Table 1). Breeding pair members tend to spend time together, so if one adult was banded, the pair was distinguishable (L. A. Brown unpublished data). We also recognized distinct breeding pairs based on their location, since American Oystercatchers are highly territorial and defend nesting territories (Nol 1985).

The two islands are 10 km apart and provide nesting habitat for American Oystercatchers consisting of sand-shell substrate and sparse to no vegetation. On both islands, nesting areas are closed to the public. Both islands experience similar weather patterns with nor'easters and hurricanes occurring in late summer and into the fall (McPherran et al. 2021). Foraging habitats on both islands include oceanside shorelines with marine invertebrates including Atlantic Mole Crabs (*Emerita talpoida*), and bayside mudflats and marshes with natural populations of Atlantic Ribbed Mussels (*Modiolus demissus*), Eastern Oysters (*Crassostrea virginica*), Northern Quahog Clams (*Mercenaria mercenaria*), and Atlantic Razor Clams (*Tagelus plebeius* and *Ensis directus*), as well as commercially seeded populations of Eastern Oysters and Northern Quahog Clams (Fig. 1 and Fig. 2). Assateague Island supports breeding pairs that feed primarily on Atlantic Mole Crabs from oceanside beaches, as well as breeding pairs that have a generalist diet of Atlantic Mole Crabs and bivalves including Atlantic Ribbed Mussels, Eastern Oysters, Northern Quahog Clams, and Atlantic Razor Clams. Assawoman Island only has breeding pairs with a generalist diet. For the two islands, both adults of a breeding pair had

Table 1. American Oystercatcher (*Haematopus palliatus*) breeding productivity (chicks fledged per breeding pair) from 2022–2024 at Assateague Island and Assawoman Island, Virginia, U.S.A.

Year	Island	Breeding pairs	Breeding pairs with at least one		Breeding pairs with two unbanded adults	Nesting density (nests/hectare)	Nests laid	Hatched nests	Hatched chicks	Broods that fledged at least one chick		Chicks fledged per breeding pair	
			banded adult	unbanded adult						fledged	one chick	fledged	breeding pair
2022	Assateague Island	20	5	15	15	0.07	52	5	9	3	5	0.25	
2023	Assateague Island	25	21	4	4	0.04	33	14	31	7	9	0.36	
2024	Assateague Island	26	22	4	4	0.04	33	19	46	10	16	0.62	
2022	Assawoman Island	31	8	23	23	0.33	43	22	45	4	5	0.16	
2023	Assawoman Island	32	28	4	4	0.39	50	19	33	5	9	0.28	
2024	Assawoman Island	29	26	3	3	0.33	43	23	51	11	24	0.83	

Note that nests laid includes initial nests and re-nests.



**Figure 1.** 2022–2024 American Oystercatcher (*Haematopus palliatus*) nests and prey distribution at Assateague Island, Virginia, U.S.A.

the same diet in all cases, except for one pair on Assateague Island where one adult had a specialist diet and the other had a generalist diet (Brown and Nol unpublished data).

On both islands, Chincoteague National Wildlife Refuge contracts the U.S. Department of Agriculture to trap mammals prior to and during the breeding season. The main predators include Red Foxes (*Vulpes vulpes*), Raccoons (*Procyon lotor*), Virginia Opossums (*Didelphis virginiana*), crows (American Crows (*Corvus brachyrhynchos*) and Fish Crows (*Corvus ossifragus*)), gulls (*Larus spp.*), Peregrine Falcons (*Falco peregrinus*), and Atlantic Ghost Crabs (*Ocyropsis quadrata*). In 2023 only, due to changes in staffing levels, the U.S. Fish and Wildlife Service set up Reconyx and Browning game cameras at some nests to capture predation events. The U.S. Fish and Wildlife Service programmed game cameras to take three photos 30 seconds apart after being motion activated. We used the number of trapped predators by the U.S. Department of Agriculture and the number of depredated nests to indirectly assess predator activity. Across years, we made more predator trapping requests and trapping effort on Assateague Island (3,469 nights and 88 days) than on Assawoman Island (200 nights and 16 days; Table 2).

#### Data Collection

**Nest Monitoring.** We assisted the U.S. Fish and Wildlife Service with monitoring American Oystercatcher breeding activities from April 1–August 31 from 2022–2024. American Oystercatchers typically laid 1–3 eggs per clutch,

and re-nested up to two times within a breeding season if initial nests failed (Nol *et al.* 1984). Incubation takes 27 days (American Oystercatcher Working Group *et al.* 2020). For determining nest initiation dates, we typically knew the exact date because we found nests during egg-laying before clutch completion. If a nest was found after clutch completion, we calculated the nest initiation date by counting backwards from the hatch date. We visited nests 2–3 times per week until nests hatched/failed and recorded the number of eggs and GPS coordinates for the nest. To determine hatch dates, we used actual hatch dates, ages of the chicks, or the median (middle) date between two nest visits. We attributed nest failures to overwash, predation, abandonment, infertility, or unknown cause of failure. We defined overwash as when wrack (organic material defining the high tide line) was located above the nest site. We determined predation from unique tracks and signs around the nest, and we used game camera photos. We defined nest abandonment as unhatched nests that passed their hatch dates and were no longer being incubated. We checked eggs from abandoned nests for infertility by checking the yolk content. If an egg had a bloody yolk, it indicated no fertilization.

We monitored broods 1–3 times per week until all chicks fledged (reached 35 days old) or were lost from a brood, and recorded the number and age of chicks during each visit. We considered the brood as fledged if the breeding pair fledged at least one chick. Chicks from a brood are kept as one unit with both parents typically



**Figure 2.** 2022–2024 American Oystercatcher (*Haematopus palliatus*) nests and prey distribution at Assawoman Island, Virginia, U.S.A.

watching over the brood, unless one parent is off defending the territory or foraging (L. A. Brown unpublished data). Most chicks disappear for unknown reasons (Schulte and Simons 2015). We were able to attribute chick mortality to predation if a depredation event was directly observed.

**Foraging Metrics.** We used a combination of behavioral observations of foraging and brood provisioning behaviors as well as GPS tracking data to measure foraging variables for each breeding pair, including diet, food profitability, distance to the foraging area, and brood provisioning rate. For behavioral observations, we used  $10 \times 42$  binoculars and  $60\times$  spotting scopes to observe a foraging adult from a breeding pair for 10 minutes or brood provisioning for one hour using focal animal sampling (Altmann 1974). Observations on foraging adults occurred throughout incubation and chick rearing until chicks fledged. Brood provisioning observations occurred from the time chicks hatched until they fledged. We timed our observations to occur during falling and low tide when foraging habitat is most available. We rotated which breeding pairs/nests we visited, so that we could make observations on foraging adults 1–3 times per week

for each breeding pair throughout the months of April to August. We made brood provisioning observations 2–3 times per week for each brood from the hatch date to fledging at day 35. We usually stationed ourselves to do observations from a tall dune, where we could simultaneously see the nesting area and foraging area(s) of a focal breeding pair. This let us continuously track a focal breeding pair and tie specific foraging behaviors to them. During adult foraging observations and brood provisioning observations we recorded the identity of the breeding pair, prey species eaten/provisioned, prey handling time (time from the initial dart probe when the bill is fully inserted into the substrate, until the prey is swallowed; Tuckwell and Nol 1997), and foraging location. We determined breeding pair ID based on the unique bands of the breeding pair members, foraging location, and brood age. Foraging behaviors could be tied to a pair even when one adult was unbanded because pair members tend to forage together in similar locations (L. A. Brown unpublished data). To identify the breeding pair when both pair members were unbanded, we relied on the territoriality of American Oystercatchers, where breeding pair members tend to stay near nests to defend

**Table 2. Predator take and trapping effort by the U.S. Department of Agriculture at Assateague Island and Assawoman Island, Virginia, U.S.A. from January 1–September 30 in 2022, 2023, and 2024.**

	Predators trapped					Trapping effort	
	Red Fox ( <i>Vulpes vulpes</i> )	Raccoon ( <i>Procyon lotor</i> )	Opossum ( <i>Didelphis virginiana</i> )	Fish Crow ( <i>Corvus ossifragus</i> )	American Crow ( <i>Corvus brachyrhynchos</i> )	Trapping nights	Trapping days
Assateague Island							
2022*	25	13	0	0	3	1,149	34
2023	20	8	0	2	0	1,034	24
2024	25	17	0	3	0	1,286	30
Assawoman Island							
2022	0	0	0	0	0	0	0
2023	1	0	0	0	0	112	7
2024	1**	0	2	0	0	88	9

\* No trapping requests were made for Assawoman Island in 2022.

\*\* 1 Red Fox was found as roadkill in late May at the south end of Wallops Island (the island immediately north of Assawoman Island). After this roadkill event, no Red Fox signs were reported.

territories (Nol 1985). In this way, we associated the nest/brood location to the closest unbanded pair that was defensive/territorial, and then we continuously watched that pair during the observation to tie individual foraging behaviors to them. We used prey handling times to calculate food profitability as wet food mass (g)/handling time (s), as per (Nol 1989). We had determined wet food mass by collecting sizes of individuals of each prey species that American Oystercatchers would take (their shells were opened) and measuring the wet mass. Average wet mass  $\pm$  SE for each prey species was Atlantic Mole Crab:  $2.51 \pm 0.48$  g,  $n = 19$ , Atlantic Ribbed Mussel:  $6.31 \pm 1.01$  g,  $n = 19$ , Eastern Oyster:  $3.44 \pm 0.50$  g,  $n = 19$ , Northern Quahog Clam:  $1.82 \pm 0.15$  g,  $n = 10$ . We calculated a brood provisioning rate for each breeding pair as the sum of the number of prey items delivered to the brood by both pair members/observation duration (h).

**GPS Tracking.** In 2023 and 2024, we deployed 12 GPS tags (PathTrack Ltd Nanofix® GEO + RF, 9 g) on American Oystercatcher breeding adults on Assawoman Island ( $n = 6$  in 2023,  $n = 1$  in 2024) and Assateague Island, Virginia ( $n = 4$  in 2023,  $n = 1$  in 2024; Supplementary Table S1). To distinguish individuals, we banded birds with black Darvic bands that had unique alphanumeric codes. A single member of a breeding pair received a GPS tag. We attached GPS tags to birds using leg loop harnesses made of Teflon ribbon (Bally Ribbon Mills). The GPS tag sat above the bird's rump and was elevated with a 5 mm neoprene patch to prevent abrasion. We strengthened the Teflon harnesses by inserting 1.5 mm Stretch Magic™ inside the Teflon, and then crimped, glued, and sewed the harness ends onto the harness. The GPS tag and harness mass was 15 g. We recaptured individuals after one year to remove GPS tags.

In 2023, we programmed 9 GPS tags to take a GPS fix every 15 minutes during the breeding season from April to August 0400–2059 EST, using the solar-driven mode. One GPS tag was scheduled to take a GPS fix every half hour from 0000–2459 during the breeding

season, so that nocturnal movements could be examined as part of a different study. In 2024, we programmed 2 GPS tags to take a GPS fix every 15 minutes from April to August 0400–2059 EST. We downloaded GPS data remotely using Bluetooth with a PathTrack Ltd base station. We rotated the GPS base station across nests of tagged individuals to download data from each individual every 2–3 weeks.

We processed GPS data by removing GPS fixes taken with fewer than five satellites; removing duplicate timestamps; and visually checking for outliers. We used the R packages 'amt', 'move', and 'moveVis' to import and visualize the GPS data in R (Signer *et al.* 2019; Schwalb-Willmann *et al.* 2020; Kranstauber *et al.* 2023).

**Diet Classification.** We used different methods to classify individual's diets based on whether they had a GPS tag or not. For individuals without a GPS tag, we used data from foraging observations to define specialists as individuals who primarily ate Atlantic Mole Crabs (>90% of their diet) with a small allowance for Coquina (*Donax variabilis*) (<10% of their diet), another ocean intertidal-dwelling invertebrate (Brown and Nol unpublished data). Coquina was only temporarily available for three weeks in the summer of 2022, and a few days in 2023, so individuals did not incorporate this prey species regularly in their diet. We defined generalists as individuals who ate any prey species in addition to Atlantic Mole Crabs or Coquina, including Atlantic Ribbed Mussels, Eastern Oysters, Northern Quahog Clams, and Atlantic Razor Clams (Brown and Nol unpublished data). For GPS tagged individuals, we classified diet based on movements to foraging habitat. Specialists only visited the oceanside shoreline to feed, and generalists foraged at both the oceanside shoreline and bayside mudflats (Brown and Nol unpublished data). We defined breeding pairs as a specialist if both breeding pair members were specialists, and generalist if either breeding pair member was a generalist. Across both islands, we classified breeding pairs as having a generalist diet for 84 nests and 44 broods, and as having a

specialist diet for 63 nests and 21 broods (Supplementary Table S2).

*Foraging Distance from the Nest.* We used a combination of behavioral observations and GPS tracking data to determine distance to the foraging area from the nest. Even though American Oystercatcher chicks are precocial and mobile after hatching (American Oystercatcher Working Group *et al.* 2020), chicks tend to stay near the nest, so we used the nest as a proxy to measure foraging distances. For individuals lacking a GPS tag, we used the behavioral observations to assess foraging distance. Based on the foraging and brood provisioning observations, we delineated feeding areas by drawing polygons around meaningful units of the foraging habitat with the software ArcGIS Pro v. 3.2 (ESRI 2011), as per Brown and Nol (2024). We then calculated the centroid of each feeding area in ArcGIS Pro, from which we measured foraging distance from the nest. For each observation, we measured foraging distance whenever a unique breeding pair member visited a unique foraging area. For example, in one observation, a breeding female might visit three separate foraging areas and a breeding male might visit one foraging area. For GPS tagged individuals, we measured distance to the foraging area from the nest by first distinguishing foraging movements from other movements based on when the movement occurred during the tidal cycle. Most foraging activity occurs during falling tide (one to five hours after high tide) and low tide (one hour on either side of low tide; Brown and Nol unpublished data), so we filtered movements as foraging if they occurred during falling or low tide. We obtained tidal time information from the nearest NOAA tidal gauge station (8630413 for Assateague Island and 8630440 for Assawoman Island). For both the behavioral observations and GPS data, we measured the distance between a foraging location and the nest, using the Haversine method, with the R package ‘geosphere’ (Hijmans 2022).

#### Statistical Analysis

We calculated breeding productivity from 2022–2024 and assigned the cause of failure to each nest when possible. We developed two separate survival models using the program ‘RMark’ (Laake 2022). Each model generally contained the same pairs throughout the study period (Table 1). To examine daily nest survival from incubation to hatching or nest failure, we developed a model considering all nests (effective sample size = 2,561 nest days). To examine daily brood survival to fledging or brood loss, we developed a model considering only nests that hatched (effective sample size = 3,223 nest days). RMark used a generalized linear model (GLM) approach with a logistic-exposure link function to model daily survival rates as a function of foraging and temporal covariates (Rotella *et al.* 2004). Prior to including predictors in candidate models, we tested for collinearity amongst our predictors using Pearson’s correlation test for sets of continuous predictors, biserial correlation tests for sets of categorical and continuous predictors, and chi-square tests for sets of categorical predictors. For daily nest survival we tested if daily nest survival was predicted by diet of the breeding pair (generalist

or specialist), distance to the foraging area from the nest, and/or food profitability. For each nest, we averaged distance to the foraging area from the nest and food profitability across the observations. For daily brood survival, we tested if daily brood survival was predicted by diet, distance to the foraging area from the nest, and/or brood provisioning rate (number of prey items delivered per hour). For each brood, we averaged distance to the foraging area from the nest and brood provisioning rate across the observations. We did not include island as a predictor in either model because island and diet strongly corresponded to one another, since Assawoman Island only supported birds with generalist diets (Supplementary Table S2).

We used a multi-step modeling approach as per Schulte and Simons (2015). In Stage 1 of modeling, we tested if linear and quadratic time and age effects and year should be retained as predictors. If the 95% confidence interval overlapped zero, the predictor was uninformative according to Arnold (2010) and dropped from the model. For informative predictors, we reported the model coefficients ( $\beta$ ). In Stage 2 of modeling, we moved forward with the best model from Stage 1 and added the foraging variables. If year was an informative predictor in Stage 1, we tested for two-way interactions between year and foraging predictors in candidate models. We also tested for year-specific effects by analyzing the data separately for each year. We ranked models using Akaike’s Information Criterion corrected for small sample sizes (AICc). We considered all models  $\leq 2 \Delta AICc$  to be competitive (Burnham and Anderson, 2002).

We calculated daily survival rate and period survival for nests and broods for the null model and significant predictors of the top model. We defined period survival for nests as survival until hatching (27 days after incubation) (American Oystercatcher Working Group *et al.* 2020). We defined period survival for broods as survival until fledging (35 days after hatching) (American Oystercatcher Working Group *et al.* 2020). We performed statistical analyses in R v. 4.3.1 (R Core Team 2023). Codes and data used in the analysis are available at [https://osf.io/dmk4e/?view\\_only=6b85b45054414663bb54b64278278a9b](https://osf.io/dmk4e/?view_only=6b85b45054414663bb54b64278278a9b).

## RESULTS

From 2022–2024 across both islands we monitored 254 nests, 40% ( $n = 102$  nests) of which hatched 215 chicks. Of the 102 broods, 39% ( $n = 40$  broods) fledged at least one chick, and 32% of chicks ( $n = 68$  chicks) fledged in total (Table 1). Breeding productivity peaked in 2024 for both islands with breeding productivity exceeding the goal of 0.5 chicks fledged per breeding pair in 2024 but not in 2023 or 2022 (Table 1). In daily survival models, we included 147 nests and 65 broods that had complete foraging data. From 2022–2024

**Table 3. Summary statistics for foraging predictors of American Oystercatchers (*Haematopus palliatus*) breeding at Assateague Island and Assawoman Island, Virginia, U.S.A. from 2022–2024.**

Reproductive stage	Variable	n	Min	Max	Mean	SE
Incubation	Food profitability (g/s)	131	0.01	1.81	0.42	0.028
Incubation	Foraging distance from the nest (m)	137	38.95	1,618.13	286.30	23.66
Pre-fledging	Foraging distance from the nest (m)	76	38.95	1,058.88	235.03	18.75
Pre-fledging	Provisioning rate (number of prey items delivered to a brood per hour)	71	0.90	15.00	4.27	0.39

For reproductive stage, incubation was defined as the duration when breeding pairs had a nest with eggs, and pre-fledging was defined as the time when chicks hatch at day 0 until day 34 (the day prior to fledging). Variables are presented in units per breeding pair. To best represent the foraging data based on the largest sample size,  $n$  represented the number of nests or broods for which we had foraging data, and could include some nests/broods with partial foraging data (only data for one but not all of the foraging predictors).

across both islands and all breeding pairs, we made 339 observations of foraging adults and 482 observations of brood provisioning. Summary statistics for each foraging predictor are presented in Table 3.

#### Nest Survival

The candidate set of models for nest survival in Stage 2 of modeling included the predictors of diet, food profitability, and year. We considered diet and food profitability as distinct possible predictors, since they were not significantly correlated with one other ( $t_{145} = 0.27$ ,  $P = 0.79$ ,  $r = 0.02$ , 95% CI [-0.14, 0.18]). We dropped distance to the foraging area as a possible predictor from the set of candidate models because distance to the foraging area was significantly associated with diet ( $t_{145} = 2.52$ ,  $P = 0.01$ ,  $r = 0.20$ , 95% CI [0.04, 0.35]). Year was the top predictor of

daily nest survival among temporal variables (Supplementary Table S3), so we retained year in Stage 2 of modeling.

Even though diet and food profitability appeared in models within two AIC<sub>c</sub> units of the top ranked model, the top and most parsimonious model only included the predictor year (Table 4), and year was an informative predictor ( $\beta_{\text{Year}} = 2.935 \pm \text{SE } 0.165$ , 95% CI [2.613, 3.258]). Thus, the food variables did not explain a significant proportion of the variation and were not important predictors of daily nest survival. A separate analysis also indicated there were no year-specific effects of diet or food profitability on daily nest survival. For each study year, the null model was the top model (Supplementary Table S4).

Daily nest survival increased from 2022–2024 (Table 5). Interannual variation in predator and storm activity contributed to yearly

**Table 4. Year best predicted American Oystercatcher (*Haematopus palliatus*) daily nest survival during incubation from 2022–2024 at Assateague Island and Assawoman Island, Virginia, U.S.A.**

Model	$K$	AIC <sub>c</sub>	$\Delta\text{AIC}_c$	$w_i$	Deviance
S(~Year)	3	557.770	0.000	0.432	551.760
S(~Year + Diet)	4	559.126	1.356	0.219	551.110
S(~Year + Food Profitability)	4	559.647	1.877	0.169	551.631
S(~Year + Diet + Food Profitability)	5	561.033	3.263	0.085	551.010
S(~Year + Diet + Year * Diet)	6	561.571	3.801	0.065	549.538
S(~Year + Food Profitability + Food Profitability * Year)	6	563.495	5.725	0.025	551.462
S(~Year + Diet + Diet * Year + Food Profitability + Food Profitability * Year)	9	567.484	9.714	0.003	549.414
S(~Null - intercept only)	1	568.687	10.917	0.002	566.685

Where  $K$  represented the number of parameters; AIC<sub>c</sub> represented the Akaike information criterion corrected for small sample sizes;  $\Delta\text{AIC}_c$  represented the change in AIC<sub>c</sub> information score from the top model;  $w_i$  (model weight) represented the proportion of the predictive power included in the model out of all possible candidate models; and deviance represented the amount of variation in the data that is explained by the model.

Definition of foraging predictors include: diet (specialist or generalist), and food profitability (prey mass in g/handling time of prey in s).

**Table 5. American Oystercatcher (*Haematopus palliatus*) daily and period nest survival during incubation increased with year at Assateague Island and Assawoman Island, Virginia, U.S.A. from 2022–2024.**

Year	<i>n</i>	Daily survival			Period survival		
		Estimate	SE	95% CI	Estimate	SE	95% CI
2022	57	0.95	0.008	0.93, 0.96	0.25	0.055	0.15, 0.36
2023	48	0.97	0.005	0.96, 0.98	0.46	0.069	0.33, 0.59
2024	42	0.98	0.004	0.97, 0.99	0.62	0.074	0.46, 0.75
Null - intercept only	147	0.97	0.003	0.96, 0.98	0.43	0.040	0.35, 0.51

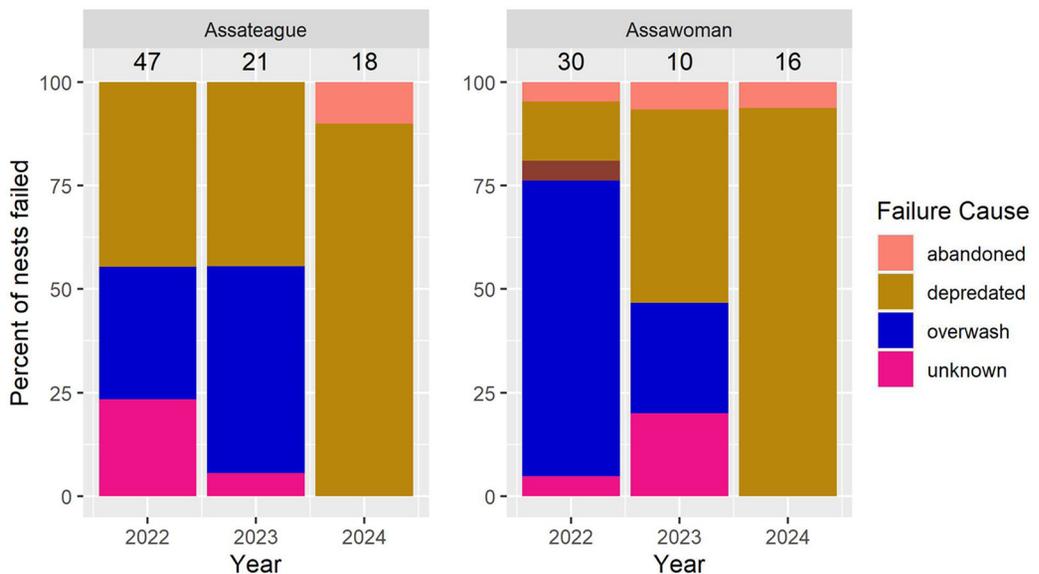
Period survival was the probability that a nest survived until hatching at day 27. *n* represented the number of nests. The null model represented the overall daily and period nest survival rate for all nests across years and islands.

differences in nest survival (Fig. 3 and Fig. 4). Predation and overwash were the leading causes of nest failure on both islands across years, with predation causing 49% of the 142 nest failures, overwash causing 33% of nests failures, abandonment causing 4% of nest failures, infertility causing 1% of nest failures, and unknown reasons causing 13% of nests failures.

On Assateague Island, Red Foxes were the leading trapped nest predator ( $n = 75$  of 121 trapped predators), followed by raccoons ( $n = 38$ ), and crows ( $n = 8$ ). On Assawoman Island, the U.S. Department of Agriculture trapped one Red Fox in 2023 and two Virginia Opossums in 2024. After a Red Fox died as

roadkill in late May of 2024, we stopped observing Red Fox signs on Assawoman Island and all remaining nests hatched.

In 2022, a single nor'easter over Mother's Day weekend (May 5–8, 2022), and high tide events in mid-June and mid-July meant that overwash caused 32% of the 47 nest failures on Assateague Island and 71% of the 21 nest failures on Assawoman Island (Fig. 3). In 2023, overwash from four storms and high tide events in early May, late May, early June, and late June contributed to 50% of the 18 nest failures on Assateague Island and 27% of the 30 nest failures on Assawoman Island. In 2024, a lack of storms meant that no nests failed due to overwash on either island that year.



**Figure 3. Percent of nests failed based on failure cause for American Oystercatchers (*Haematopus palliatus*) at Assateague Island and Assawoman Island, Virginia, U.S.A. from 2022–2024. Labels above each bar represent the total number of nests.**

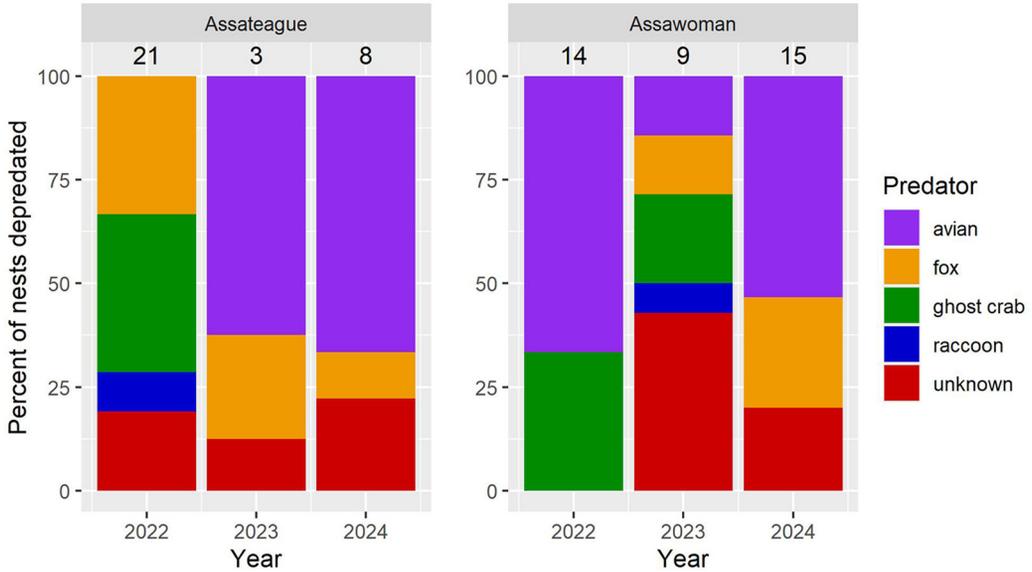


Figure 4. Percent of depredated American Oystercatcher (*Haematopus palliatus*) nests by different predators at Assateague Island and Assawoman Island, Virginia, U.S.A. from 2022–2024. Labels above each bar represent the total number of nests.

### Brood Survival

The candidate set of models for brood survival included the predictors of diet, distance to the foraging area, and brood age. There was no collinearity among the predictors (Supplementary Table S5). Thus, we proceeded with all predictors in Stage 2 of modeling. A linear term for brood age was an informative predictor in the top model among temporal variables

of daily brood survival, so we retained brood age in Stage 2 of modeling (Supplementary Table S6).

Neither diet nor distance to the foraging area were important predictors of brood survival. The top model for daily brood survival contained the predictors of brood age and diet (Table 6), although only brood age was an informative predictor ( $\beta_{\text{Brood age}} = -0.06 \pm \text{SE } 0.01$ , 95% CI  $[-0.08 \text{ to } -0.04]$ ). Daily brood

Table 6. Brood age best predicted American Oystercatcher (*Haematopus palliatus*) daily brood survival from 2022–2024 at Assateague Island and Assawoman Island, Virginia, U.S.A.

Model	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$	Deviance
S(~Brood age + Diet)	3	214.86	0.00	0.28	208.85
S(~Brood age + Diet + Distance)	4	215.43	0.57	0.21	207.41
S(~Brood age)	2	216.45	1.60	0.13	212.45
S(~Brood age + Diet + Brood provisioning rate)	4	216.74	1.88	0.11	208.73
S(~Brood age + Distance)	3	216.85	2.00	0.10	210.85
S(~Brood age + Diet + Distance + Brood provisioning rate)	5	217.41	2.55	0.08	207.39
S(~Brood age + Brood provisioning rate)	3	218.36	3.50	0.05	212.35
S(~Brood age + Distance + Brood provisioning rate)	4	218.62	3.76	0.04	210.61
S(~Null - intercept only)	1	246.66	31.81	0.00	244.66

Where  $K$  represented the number of parameters;  $AIC_c$  represented the Akaike information criterion corrected for small sample sizes;  $\Delta AIC_c$  represented the change in  $AIC_c$  information score from the top model;  $w_i$  (model weight) represented the proportion of the predictive power included in the model out of all possible candidate models; and deviance represented the amount of variation in the data that was explained by the model.

Definition of foraging predictors include: diet (specialist or generalist); distance (foraging distance from the nest during pre-fledging); and brood provisioning rate (number of prey items delivered to a brood per hour).

Of the predictors, only brood age was informative. All foraging predictors were uninformative because their confidence intervals overlapped with zero.

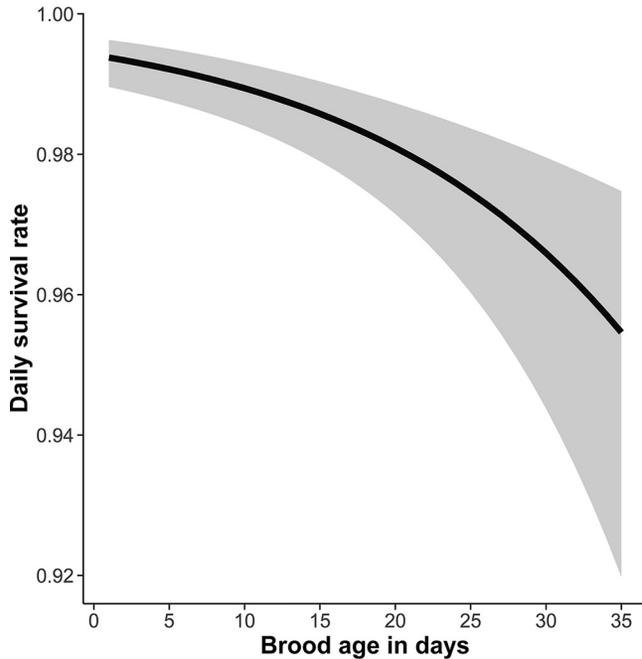


Figure 5. American Oystercatcher (*Haematopus palliatus*) daily brood survival rate decreased with age at Assateague Island and Assawoman Island, Virginia, U.S.A. from 2022–2024. Shading represents the 95% CI.

survival decreased as chicks aged (Fig. 5). In 2022, the cause of chick mortality was unknown in all cases except for three avian depredation events witnessed by observers. Two 3-week-old chicks were killed by Great Black-backed Gulls (*Larus marinus*) on Assawoman Island, and one 7-day old chick was killed by a Peregrine Falcon on Assateague Island. We speculate that Great Black-backed Gulls took additional chicks on Assawoman Island in 2022 because 2–5-week-old chicks kept disappearing from Assawoman Island in the same area as the two witnessed chick depredation events, and a Great Black-backed Gull was frequently observed attacking broods. There were no signs of other sources of depredation, nor major storms when the 2–5-week-old chicks were disappearing from Assawoman Island. In 2023 and 2024, we did not witness any direct chick depredation events. Overall daily survival rate of broods across years and islands for the null model was  $0.992 \pm \text{SE } 0.002$ , 95% CI (0.989, 0.995),  $n = 65$  broods with a period survival until fledging as  $0.763 \pm 0.041$ , 95% CI (0.670, 0.833).

## DISCUSSION

Foraging factors did not limit breeding success of American Oystercatchers at two barrier islands in Virginia, U.S.A. Instead, variation in hatching success was best explained by annual variation in depredation and overwash from the storms/high tide events, and fledging success was most affected by age. Fledging success was similar for breeding pairs regardless of diet. This contrasts with Eurasian Oystercatchers (*Haematopus ostralegus*) at Skokholm Island off of the Irish Sea that provision chicks with worms and arthropods and have three times higher fledging success compared to breeding pairs that provision chicks with limpets (*Patella* spp.; Safriel 1985). Similarly, Slaty-backed Gulls (*Larus schistisagus*) in Japan that provision young with seabirds, have higher fledging success than breeding pairs that provision young with fish or marine invertebrates (Watanuki 1992). Herring Gulls (*Larus argentatus*) in Newfoundland, Canada that specialize on blue mussels (*Mytilus edulis*) also have higher hatching and fledging

success than any other diet because blue mussels provide essential nutrients (calcium and sulfonated amino acids), which aid in bone development and growth (Pierotti and Annett 1990). Our findings that diet did not impact fledging success is consistent with Thick-billed Murres (*Uria lomvia*) in Nunavut, Canada, where brood survival is similar for breeding pairs that specialize provisioning chicks with rare fish species and breeding pairs that provision multiple fish species (Woo *et al.* 2008). In a similar fashion, Brown Skuas (*Stercorarius antarcticus*) in Hermaness, Scotland have similar brood survival regardless of diet, even though breeding pairs that provision birds to chicks have chicks with higher body condition than breeding pairs that provision fish (Votier *et al.* 2004).

Without sufficient prey or provisioning, chicks can die from starvation. American Oystercatcher chicks in Florida, U.S.A. have died of starvation because of severe declines in oyster abundance (Vitale *et al.* 2022). Schulte and Simons (2015) also reported that 27% of American Oystercatcher chicks died from starvation or exposure in North Carolina, U.S.A. For Black Oystercatchers (*Haematopus bachmani*) in Alaska, U.S.A., broods with lower energy intake rates have lower brood survival (Robinson *et al.* 2019). While we did not assess chick body condition directly, we did not find any emaciated chicks on either island across the three years of the study, and we did not attribute any chick mortality to starvation. This suggests that food was probably not a limiting factor at either island.

Contrasting with previous studies (Nol 1989; Ens *et al.* 1992; Schulte and Simons 2015) distance to the foraging area was not important for nest or brood survival in our study. In the 1980s in Virginia, distance to the foraging area was important to American Oystercatcher fledging success because foraging proximity reduced time spent away from broods and facilitated increased vigilance over broods, which reduced predation risk of chicks (Nol 1989). Additionally, American Oystercatchers in North Carolina with sound side foraging access have higher fledging success than breeding pairs without sound side foraging access (Schulte and Simons 2015).

Similarly, Eurasian Oystercatchers at Schiermonnikoog, The Netherlands that have foraging grounds adjacent to their nesting areas have 3.5 times greater fledging success than breeding pairs with distant foraging grounds because foraging proximity promotes increased vigilance over broods and higher brood provisioning rates (Ens *et al.* 1992). In our study, brood provisioning rates do not differ based on diet (L. A. Brown unpublished data), so brood provisioning is unlikely to underly a possible relationship with brood survival based on the distance to the foraging area. As for predation risk explaining the possible link between brood survival and distance to the foraging area, even when both parents loafed within 5 m of chicks and were vigilant against predators, we watched a Great Black-backed Gull take a chick from the parents. In our study area, where avian predators are the top predator of chicks, distance to the foraging area might be less important for brood survival than in areas where mammals are the top predators of chicks. It may be that adults close to nests discourage mammalian predators but not avian predators.

We expected that breeding pairs with higher food profitability should be more efficient foragers, which would facilitate their return to the nest sooner, and reduce predation risk of nests, therefore increasing nest survival. However, similarly to Nol (1989), food profitability did not impact nest survival. Food profitability is independent of searching time for prey, so even if individuals are efficient foragers, prey could be widely distributed across the landscape, so individuals might spend more time searching for food and wind up spending a similar time away from the nest.

At our site, hatching success seemed to be most influenced by stochasticity in predator activity and storms. Our findings are consistent with other studies in Virginia (Denmon *et al.* 2013) and North Carolina (Schulte and Simons 2015; Walters *et al.* 2020) that identify predators and overwash from storms as two of the top limiting factors for American Oystercatcher breeding success. In our study, the year 2023 had higher hatching success relative to 2022, and this corresponded with a decrease in predator activity in 2023, which

might have been linked to differences in hurricane activity. Hurricane Ian struck the area in October of 2022 and could have removed nest predators for the 2023 nesting season (Schulte and Simons 2016). In 2024, American Oystercatchers experienced high hatching success due to favorable weather from a lack of strong storms, removal of a depredating Red Fox, and no Atlantic Ghost Crab depredation.

In our study, brood survival decreased with age, which is consistent with American Oystercatchers in Florida. In Florida, insufficient food resources caused older chicks to have lower survival than younger chicks (Vitale *et al.* 2022). Where food did not appear to be a limiting factor, older chicks seemed to experience a higher risk of depredation due to chicks > 3 weeks old seeming to seek cover less when avian predators flew overhead (L. Brown, personal observation). This observation is consistent with age-dependent chick hiding behavior in Mountain Plovers (*Charadrius montanus*; Sordahl 1991) in Colorado, U.S.A. Older American Oystercatcher chicks are also of larger body size and would provide a bigger food reward for predators. In our study, gulls typically attacked and depredated chicks that were at least two weeks old. In contrast, Laughing Gulls (*Leucophaeus atricilla*) in Texas, U.S.A. target attacking and depredating American Oystercatcher chicks younger than two weeks old (Anderson 2014), and in North Carolina, younger American Oystercatcher experience lower survival because younger chicks are less mobile and have more difficulty evading predators (Schulte and Simons 2015).

### Management Recommendations

Since long-term studies are better able to detect multi-year dynamics of prey populations, we note that food might be a limiting factor for American Oystercatcher populations elsewhere, and that the management recommendations presented here are appropriate for this study site, based on a small number of years. Predators and overwash remain the top threats for American Oystercatcher breeding success at our study site. Once depredating Red Foxes were trapped and removed from our study islands, hatching success increased.

As in our study islands, other studies have reported high levels of fox depredation (Schulte 2012) and found increased hatching success after trapping (McGowan 2004). Simply counting trapped animals may not reflect true predation rates, since one Red Fox can depredate all nests on one of our study islands in a single night. More game cameras monitoring nests could better quantify the threat of nest predation at our study site. We reiterate that continued investment in predator control efforts are important to maintain American Oystercatcher breeding success.

Gull harassment or lethal management programs have been attempted to increase reproductive success of shorebirds, but most programs seem to have little to no efficacy (Harris and Wanless 1997; Olijnyk and Brown 1999; Keane 2002). It is more difficult to manage gull predation when gulls are not nesting in the area, as is the case on Assawoman Island. At Eastern Egg Rock, Maine, U.S.A., removal of 18 gulls that specialize fed on terns did not reduce *Sterna* spp. chick depredation because other gulls in the population replaced them (Donehower *et al.* 2007). So far, there do not seem to be any existing cost-effective strategies for reducing gull depredation of American Oystercatcher chicks. Before beginning a campaign against gulls, future research could quantify how problematic gull depredation of shorebird chicks is by identifying the percent composition that shorebird chicks make up in gull diets using behavioral observations of foraging gulls, stomach content analysis, and DNA barcoding of fecal samples.

As climate change increases storm frequency and intensity and sea levels rise (Lee *et al.* 2023), nest flooding will become a greater problem. We echo the management recommendation of Vitale *et al.* (2022) that efforts which increase beach elevation like beach renourishment should help reduce nest losses to overwash. One simple way to increase elevation might be to place used car tires on beaches. In 2022, one breeding pair on Assateague Island nested in a car tire that was partially buried in the sand. When storms occurred the nest in the tire remained dry, even though nests surrounding it were flooded (L. A. Brown, personal observation).

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