FACTORS AFFECTING THE REPRODUCTIVE SUCCESS OF AMERICAN OYSTERCATCHERS *HAEMATOPUS PALLIATUS* ON THE OUTER BANKS OF NORTH CAROLINA

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SUMMARY

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We used an information-theoretic approach to assess the factors affecting the reproductive success of American Oystercatchers *Haematopus palliatus* on the Outer Banks of North Carolina. We evaluated survival with respect to nesting island, year, time of season, brood age, distance to tide (m), presence of off-road vehicles and proximity of foraging habitat. The daily nest survival (mean 0.981, standard error [SE] 0.002) was affected by year and island, and declined over the nesting season. Mammals were responsible for 54% of identified nest failures. Daily brood survival (mean 0.981, SE 0.002) varied by island and increased non-linearly with age, with highest mortality in the seven days after hatching. Model results indicate direct access to foraging sites has a positive effect on brood survival, whereas presence of off-road vehicles has a negative effect. We studied chick behavior and survival using radio telemetry and direct observation and found that vehicles caused mortality and affected behavior and resource use by oystercatcher chicks. We identified the source of mortality for 37 radio-tagged chicks. Six (16%) were killed by vehicles, 21 (57%) by predators, and 10 (27%) by exposure and starvation. From 1995 to 2008, 25 additional oystercatcher chicks were found dead, 13 (52%) killed by vehicles. Chicks on beaches closed to vehicles used beach and intertidal zones more frequently than chicks on beaches open to vehicles. Chick predators included Great Horned Owls *Bubo virginianus*, Fish Crows *Corvus ossifragus*, cats *Felis catus*, mink *Mustela vison*, raccoons *Procyon lotor*, and ghost crabs *Ocypode albicans*. The factors affecting reproductive success differed between the incubation and chick-rearing stages. Management actions that influence chick survival will have a larger effect on total productivity than actions affecting nest survival.

Key words: American Oystercatcher, breeding success, nest predation, North Carolina

INTRODUCTION

The American Oystercatcher *Haematopus palliatus* is listed as “threatened” in the US states of Georgia and Florida and as a “species of special concern” in North Carolina (North Carolina Wildlife Resources Commission 2008). The American Oystercatcher Conservation Plan lists the species as high priority (American Oystercatcher Working Group 2012), in part because of significant threats from development and heavy recreational use of coastal breeding habitats. Human population density in the United States, which is growing, is highest in coastal regions (Crossett *et al.* 2004). As more humans inhabit the coastal zone, recreational use of beaches, salt marshes and waterways will continue to rise. Many visitors to the coast seek undeveloped beaches. As coastal islands and beaches are developed, more visitors are concentrated onto the remaining undeveloped areas. Coastal development, recreational activity and altered predator communities have substantially reduced the amount of suitable nesting and foraging habitat for beach-nesting birds on the Atlantic Coast. Roads and artificial dunes along nesting beaches can limit access to foraging habitats for beach-nesting species such as Piping Plovers *Charadrius melodus* and American Oystercatchers. Nesting and roosting sites can also be lost when jetties and hardened shorelines alter the normal process of longshore sand transport and accelerate erosion of adjacent beaches (Dugan & Hubbard 2006).

Like many long-lived species, oystercatcher reproductive rates tend to be highly variable but generally low. On the Atlantic Coast, annual nest survival can range from 0.2 to 0.75 chicks per pair in a given year (Evans 1991, Davis *et al.* 2001, Wilke *et al.* 2005, McGowan *et al.* 2005, Traut *et al.* 2006, American Oystercatcher Working Group 2012). Mammalian predators are consistently identified as a major source of nest failure, along with storm washover, avian predators and other sources (Davis 1999, McGowan 2004, George *et al.* 2004, Sabine *et al.* 2006). Humans account for relatively few cases of direct nest loss, but there is evidence for an interaction effect between disturbance and increased nest loss (Novick 1996, Davis 1999, McGowan 2004, Sabine *et al.* 2005, McGowan & Simons 2006).

The factors affecting shorebird chick survival are more challenging to understand than those affecting nest survival (Nol 1989, Ens *et al.* 1992). Shorebird chicks are precocial or semi-precocial, and they often leave the nest within a few hours of hatching, after which they are cryptic and highly mobile. Chicks may be eaten by predators, and those that die for other reasons are quickly scavenged or washed away by the tide, which further reduces the chance of learning the cause of death. Studies of other shorebird species have identified chick age, mass at hatching, human disturbance, habitat quality, access to foraging sites, rainfall and an array of predator species as factors affecting chick survival (Dinsmore *et al.* 2002, Ruhlen *et al.* 2003, Ruthrauff & McCaffery 2005, Colwell *et al.* 2007). Like the threatened Piping Plover, American Oystercatchers nest and raise chicks in coastal environments that are heavily used and altered by human activity. Because many breeding attempts fail during the chick-rearing stage, several studies have stressed the need for a better understanding of the factors affecting American Oystercatcher chick survival (Davis *et al.* 2001, McGowan *et al.* 2005). The objectives of this study were to identify patterns of chick behavior and habitat use, quantify the effects of off-road vehicles (ORVs) on oystercatcher chick behavior and compare the effects of two management actions (closed beach versus partial beach closures).

We developed hypotheses to explain variation in nest and brood survival on the Outer Banks of North Carolina from 1999 to 2008 with respect to age, season, year, island, presence of ORVs and habitat quality.

METHODS

Study area

The barrier island habitat of Cape Lookout and Cape Hatteras National Seashores (Fig. 1) stretches over 160 km in North Carolina. The islands are characterized by wide barrier beaches with a primary and secondary dune complex broken by flats and overwash fans. The dunes transition to scrub characterized by wax myrtle *Myrica cerifera* and then to salt marsh bordering the back bays and sounds. This system is subject to periodic washover events, followed by recolonization by dune grasses. Cape Lookout and Cape Hatteras support approximately 90 breeding pairs of oystercatchers, which nest on the sand flats and dunes and forage along the beach and salt marsh. ORVs are permitted on beach and interdune roads in both parks, except in designated wilderness areas or sensitive bird or turtle nesting areas. Cape Hatteras has a permanent road system and several small towns along the length of the islands.

Nest survival

Surveys of breeding oystercatchers on the Outer Banks began in late March each year. Nests were located by walking or slowly driving along the barrier beach and back-road system. When an adult oystercatcher was located, observers watched for behavioral cues that indicated the bird had a nest. Although nesting oystercatchers do not usually employ “broken-wing” distraction displays typical of smaller shorebirds, they do exhibit easily identifiable behaviors such as false incubating and alarm calling. When breeding behavior was observed, scrapes were found by following the tracks of the adult birds, or by systematic searches. Once located, nests were either marked with a small wooden stick placed at least 5 m from the nest and concealed to prevent detection by predators, or located using adjacent natural landmarks such as driftwood and shells as a reference. The location of each nest was recorded with a handheld global positioning system (GPS). Nests were checked every one to four days until hatching or failure. We made every effort to minimize disturbance and reduce any effect of our observations on nesting success. If a bird was seen incubating, the nest was considered active and was checked only periodically to determine whether the chicks had hatched. We avoided walking directly to nest sites and spent a minimal amount of time in the vicinity of the nest to minimize cues for predators. If a nest failed, we attempted to determine the cause of failure by searching the area for signs of predators, storm overwash or other sources of nest failure. For example, when a storm event washes out a nest, the nest scrape is usually gone and a debris line is evident above the nest’s original location. Unfortunately, such evidence does not last long on a barrier beach, so it was not always possible to determine the causes of nest failure.

Brood and chick survival

When a nest hatched, the young were observed every one to four days until fledging, or until all the chicks had died or disappeared. We documented habitat use and behavior of oystercatcher broods on Cape Hatteras National Seashore from 2004 to 2007 in an observational study of oystercatcher behavior. We observed broods for hour-long intervals, recording instantaneous observations of habitat use at two-minute intervals. Broods were observed through spotting scopes at distances where observer presence did not affect the birds’ behavior. Habitats were designated as below the tide line, open beach or dune/grass. Observations continued if the birds disappeared from sight, as long as it was possible to determine habitat type. This prevented a negative bias affecting observations in dune and grass habitats, where the birds were less visible. We observed chicks of all ages from hatching through fledging at all times of day and stages of the tide cycle. We were unable to conduct behavior watches at night, but we did periodically check on the location of broods at night to document habitat use. Observation windows were assigned randomly to active oystercatcher broods throughout the nesting season.

With careful monitoring, it was possible to determine annual productivity, or the number of chicks fledged per pair, per year, although we were often unable to determine the cause or exact timing of chick mortality. Adult oystercatchers exhibit markedly different behavior patterns when they are tending their chicks. They are much more aggressive toward intruders, and give distinct alarm calls. Thus, we determined whether a pair of adult birds had chicks by observing adult behavior, even if we could not observe the chicks directly. In most cases, chicks were located by observing adults

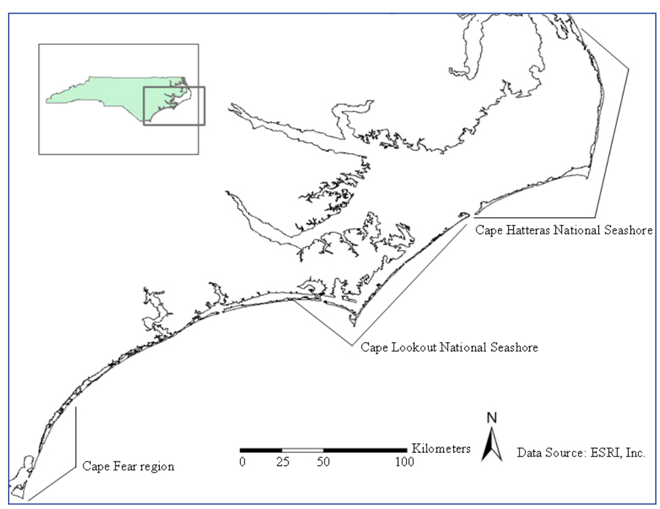

Fig. 1. American Oystercatcher study sites in North Carolina.

from a distance using a spotting scope and occasionally a portable blind. When we found dead chicks or observed predation events, we recorded the cause of death.

In addition to analyzing brood survival, we examined factors affecting individual chick survival and sources of mortality for a subset of chicks using radio telemetry. From 2005 to 2007 we radio-tagged a total of 121 chicks on Hatteras Island, Cape Hatteras National Seashore, and North Core Banks, Cape Lookout National Seashore. Chicks were radio-tagged as soon as they were mobile, usually within 24–48 hours of hatching. We attached ATS A2420 transmitters (1.3 g) to the scapular region of the chick using surgical-grade skin glue (Fig. 2). Chicks were checked every 24 hours for the first week, and every one to three days thereafter. Transmitter range was 400–1 000 m, depending on terrain. When a chick died, we tried to locate the remains and determine the cause of death. In 2005 and 2006 we exchanged the ATS transmitters for larger PD2 model transmitters from Holohil Systems when the chicks reached four weeks of age. These transmitters were designed to last at least six months and were attached to a permanent leg band (Fig. 2).

Statistical analyses

We analyzed our nest survival data from1999 to 2008 using the nest survival module in Program MARK (White & Burnham 1999, Dinsmore *et al.*, 2002). Daily nest survival is defined as the probability of surviving from day i to i + 1. Program MARK uses a maximum likelihood method to estimate the nest failure date when the time between nest checks is greater than one day, and it allows for modeling covariates to explain variations in nest success and comparing alternative models using Akaike's information criteria (AIC) (Burnham & Anderson 2002).

Covariates used in analyses

Year: Year-to-year variation in weather patterns, timing of storms, prey abundance, predator abundance and numerous other factors that were not explicitly measured could affect oystercatcher nest survival.

Island: The study area is composed of six islands in two National Parks. Human use of the seashores varies considerably from island to island, along with predator composition and abundance. Differences in these and other factors could explain variations in nest survival.

Presence of off-road vehicles: Vehicle activity can affect nesting behavior (McGowan & Simons 2006) and nest survival for beach-nesting birds (Buick & Paton, 1989, Novick 1996, Davis 1999). Although many of the nests in the study area were protected from direct impact by signs and symbolic fencing, we hypothesized that the indirect effects of adjacent vehicle traffic would lower nest survival on beaches open to ORVs. We considered a beach open for vehicle traffic if ORVs were allowed to pass above or below the nest, even if the nest itself was in a closed area ("partial beach closure"). We did not attempt to include distance from nests to ORVs or the number of ORVs using the beach, as these data were unavailable for most of the nests. Presence of ORVs was recorded for each nest based on beach closure records from the National Park Service. ORVs were considered to be present if any part of the beach above or below the nest was open to vehicle traffic, regardless of whether the nest itself was in a vehicle exclosure. We did not account for differences in traffic volume or exclosure size, as these data were not available for the majority of our nests.

Distance to the high tide line (m): Oystercatchers nest anywhere from within a few meters of the high tide line to hundreds of meters away on large sand flats. Overwash from storms and spring tides is a major source of nest failure. In addition, the majority of vehicle traffic is located near the high tide line. We hypothesized that nest survival would increase with distance from the high tide line. The individual covariate "distance to high tide line" was measured by calculating the distance between nest locations and recorded high tide lines in ArcMap (ESRI 2006).

Direct access to foraging habitat: Although oystercatchers do forage on the ocean beach, most birds maintain primary foraging territories in the creeks and mudflats on the back side of the barrier islands. If nesting oystercatchers have to fly a long way to

Fig. 2. Radio-tagged American Oystercatcher chicks: recently hatched chicks with glue-on transmitter (right) and post-fledging immature with leg-band transmitter (left).

get to their foraging site, they are unavailable to help their mates defend nests from predators. Perhaps more importantly, nest sites adjacent to foraging territories may be very important during chick rearing (Ens *et al.* 1992, Heg & van der Velde 2001, Kersten & Brenninkmeijer 1995, van de Pol 2007). Older, more experienced birds are likely to occupy these prime territories, so this covariate may be an indirect measure of adult quality. We hypothesized that direct access to primary foraging habitat would increase nest survival. Foraging access was a binary individual covariate based on access to foraging sites for nesting pairs. The covariate was positive if a pair had direct walking access to a primary foraging site.

Time of the nesting season: The nesting season on the Outer Banks of North Carolina spans approximately five months. We fit linear and quadratic time trend models to the null model of constant survival to evaluate temporal variation in nest survival within the nesting season. For the linear model, we predicted that survival would decrease through the season. The quadratic model allowed for a non-linear change in nest survival to account for more than one survival peak or valley.

We used a three-step hierarchical process to evaluate different models. In the first step, we created models with linear and quadratic time trends as well as a null model of constant survival. We then added the effects of year and island to the best model(s) (ΔAICc ≈ <2.0), and found the best model with these added effects. Finally, we added covariates for tide distance, foraging and presence of ORVs to the new best model(s).

Our analyses of factors affecting chicks during the pre-fledging period considered chick survival and brood survival separately. Chick survival was defined as the probability of a single chick surviving from hatching to fledging, while brood survival was defined as the probability of at least one chick in a brood surviving to fledging. Because of the difficulty in determining the status of individual chicks during each monitoring check, we developed hypotheses and analyzed covariates associated with brood survival, rather than individual chick survival. We developed models incorporating these hypotheses using the nest survival module in Program MARK. Our hypotheses about factors affecting brood survival were similar to those concerning nest survival. However, we did not include an effect of distance to high tide because oystercatcher chicks are highly mobile. We also examined the effect of brood age on survival, hypothesizing that daily survival would increase with brood age. Covariates included in the brood survival models were year, island, presence of ORVs, direct access to foraging habitat, time of the nesting season (linear and quadratic trends) and age of the brood (linear and quadratic trends).

We used a multi-step approach in developing our chick survival models, similar to our nest survival analysis. In the first step, we ran models with linear and quadratic time and brood age trends as well as a simple null model of constant survival. We then added the effects of year and island to the best model(s), and found the best model with these added effects. Finally, we added covariates for presence of ORVs and foraging access to the best model to see whether they contributed any useful information.

In addition to modeling nest and brood survival, we used *t*-tests to compare habitat use on beaches where driving was permitted to habitat use on beaches closed to vehicles. We estimated survival probability for radio-tagged chicks using the Kaplan-Meier known fate procedure. Day zero was defined as the day of hatching, regardless of capture date. Multiple chicks from the same brood were tagged and followed, which violates the assumption of independent observations. As a result, our survival estimates are unbiased, but standard errors (SEs) are likely underestimated (Pollock *et al.* 1989). Values reported in the Results section are means ± SE.

Total productivity (P) was defined as the number of fledged chicks per nesting pair (pair that laid at least one egg). Productivity is a function of nest survival (S_N), chick survival (S_C), chicks hatched per successful nest (H_C) and total nests per breeding pair. Because the number of nests per pair is a function of nest survival (Fig. 6), we can summarize total productivity as: $S_N * S_C * H_C *$

TABLE 1
Model selection results for factors affecting survival of American Oystercatcher nests on Cape Hatteras and Cape Lookout National Seashores from 1999 to 2008

Model[a]	ΔAICc[b]	Number of parameters, k	Model weight, Wi	Deviance
Day + Year + Island	0	16	0.294	4 807.560
Day + Year + Island + Vehicle	0.015	17	0.291	4 805.570
Day + Year + Island + Forage	0.851	17	0.192	4 806.406
Day + Year + Island + Tide	1.465	17	0.141	4 807.020
Day + Year + Island + Tide + Forage + Vehicle	2.534	19	0.083	4 804.080
Day + Year	51.755	11	0	4 869.332
Day + Island	56.952	7	0	4 882.540
Day	116.954	2	0	4 952.548
Day^2	118.750	3	0	4 952.342
Constant	121.374	1	0	4 958.968

[a] Model factors include linear and quadratic daily variation over the nesting season (Day and Day^2), year, island, presence of off-road vehicles, access to foraging areas and distance to the high tide line.
[b] The lowest AICc score in this model set was 4 839.594. Models are ranked by ΔAICc.

$(-0.04139(\text{LN } S_N) + 1.1099) = P$. This formulation is useful because it separates out the effects of individual components of productivity on overall nesting success.

RESULTS

Nest survival

This analysis is based on a sample of 1 172 nests monitored on six islands from 1999 to 2008 for which sufficient data were collected for nest survival analysis. Nests were monitored during a 126-day window (April 2 to August 6) during the 10-year period, for a total of 15 736 exposure days. Overall observed hatching success from the beginning of egg laying to hatching for all years and locations was 0.280 (0.013). The single estimate of daily survival from Program MARK (null model) was 0.950 (0.002). The average incubation period for oystercatcher nests is 27 days (American Oystercatcher Working Group 2012). To obtain the probability of nest survival to hatching (period nest survival) we raised estimates of daily survival rates (DSR) to the 27th power. Period survival for the null model was $0.950^{27} = 0.250$ (0.011).

Variation in nest survival was best explained by a model with a linear within-season time trend and added covariates for year and island (Table 1). The quadratic time effect was not supported (it yielded an approximately one unit increase in AICc, for a one parameter increase, lower model weights, and 95% confidence interval (CI) for the beta coefficient overlapping zero). A linear time effect was supported in all the top models, indicating that nest survival declined over the nesting season (β = -0.005, CI -0.008 to -0.001). The 95% CIs for the beta coefficients of five of the 10 years (2000, 2001, 2003, 2007 and 2008) overlapped zero, indicating no significant difference in survival from the baseline year (1999). In contrast, the entire confidence interval for the coefficient for 2002 was below zero, while the intervals for 2004, 2005 and 2006 were all above zero. The 2004 breeding season had the highest beta coefficient of any year (β = 0.882, CI = 0.522 to 1.241). Nests on the island of South Core Banks had lower overall survival (β = -0.327, CI -0.499 to -0.156) than North Core Banks, while Ocracoke (β = 0.407, CI 0.136 to 0.677) and Hatteras (β = 0.323, CI

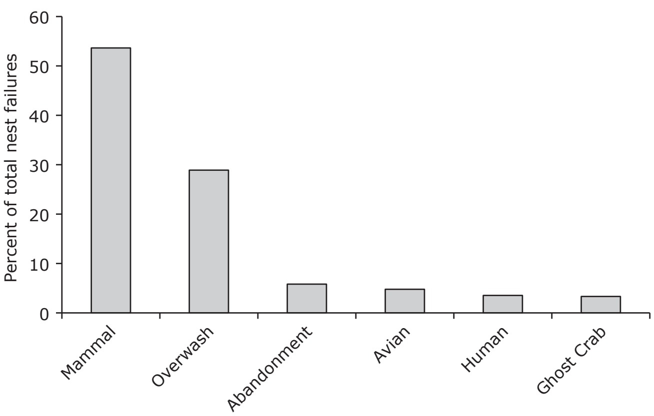

Fig. 3. Sources of American Oystercatcher nest failure on the Outer Banks of North Carolina from 1998 to 2008, when cause of failure could be determined (n = 481). Cause could not be determined for 49% of nest failures (n = 464).

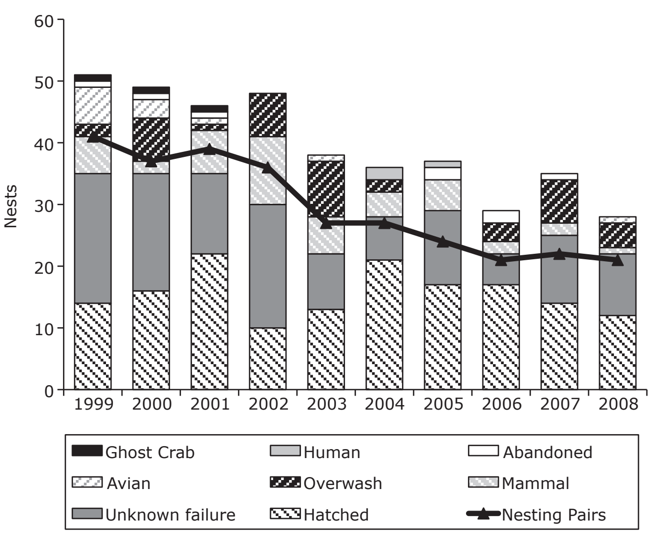

Fig. 4. Nest fates for American Oystercatcher nests on Cape Hatteras National Seashore from 1999 to 2008. Column segments represent the number of nests in each outcome category.

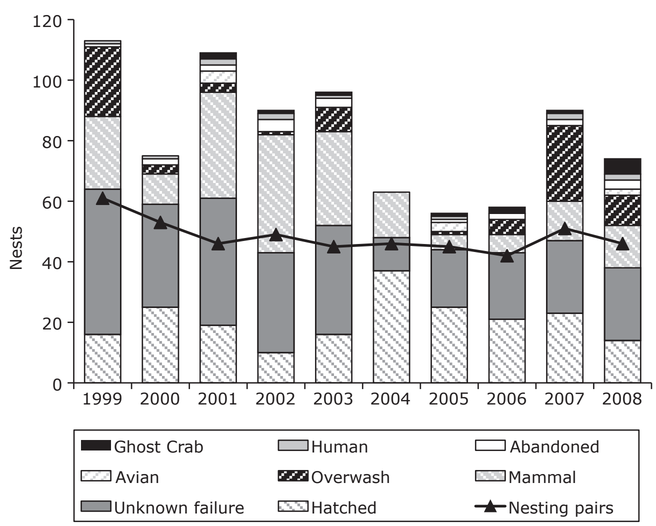

Fig. 5. Nest fates for American Oystercatcher nests on Cape Lookout National Seashore from 1998 to 2008. Column segments represent the number of nests in each outcome category.

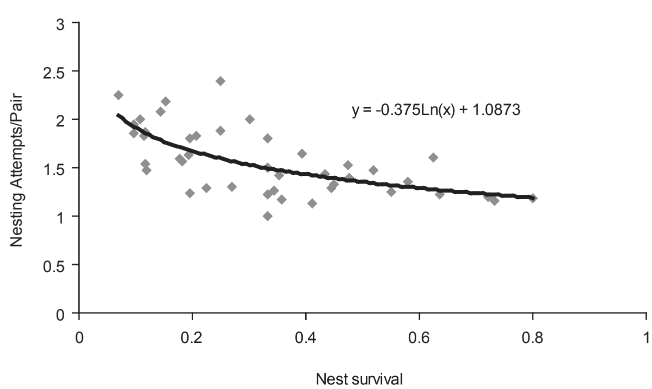

Fig. 6. The number of nesting attempts per pair as a function of nest survival on Cape Lookout and Cape Hatteras National Seashores, 1998–2008; n = 44 location/years, 1 234 nesting attempts.

0.107 to 0.538) were higher than North Core Banks over the course of the study. The 95% CIs for the beta coefficients of Middle Core Banks and Bodie Island overlapped zero, indicating no significant difference in survival from North Core Banks.

One of the top two models by AICc rank included a covariate for ORV presence. In this model, nests with ORV access had a lower survival rate, but support for the ORV covariate was weak, as the 95% CI for the beta coefficient included zero (β = -0.196, 95% CI -0.472 to 0.080), and there was no change in AICc. Models that included covariates for access to foraging habitat, and distance to tide line also received some support (ΔAICc <2), but the confidence interval of the beta coefficient for each of the covariates also included zero.

Mammalian depredation was the major cause of nest failure at our study sites, accounting for approximately 54% of identified nest failures (Fig. 3). Overwash and other weather-related causes accounted for 29% of identified failures. The remaining identified failures (17%) were caused by human activity, avian predators, ghost crabs or unknown reasons (Fig. 3). Human activity was defined as a human action directly leading to nest failure, such as physical destruction of the eggs, and did not include indirect effects of disturbance. We were unable to identify the causes of failure for 52% of failed nests. The sources of nest mortality were similar on Cape Hatteras and Cape Lookout, but the relative proportion of nests lost to each source varied by year and location (Figs. 4 and 5).

Clutch size averaged 2.35 (0.01) eggs per nesting attempt. A nesting attempt was defined as a nest with at least one egg. Pre-nesting scrapes were not considered nesting attempts. When a nest failed, oystercatcher pairs waited 9–14 days before initiating a new clutch. If a nest hatched successfully, pairs did not re-nest unless the chicks were lost while still very young (<7 days). Oystercatcher pairs initiated between one and five nests per season with an average of 1.55 (0.01) nests per pair. The average number of clutches per pair (y) was logarithmically related to overall nest survival (x) according to the equation $y = -0.375\text{Ln}(x) + 1.0873$ (Fig. 6).

Brood and chick survival

Our analysis of factors affecting brood survival is based on a sample of 306 broods on Cape Lookout and Cape Hatteras National Seashores from 1999 to 2008. Mean brood size at hatch was 1.99 chicks (0.042), while the mean daily brood survival was 0.981 (0.002). Mean period survival for the 40 day pre-fledging period was 0.471 (0.030).

Our best model of factors affecting brood survival included covariates for the age of the brood, island, presence of ORVs, and access to foraging habitat. This model was the only supported model in our set (model weight = 0.991, ΔAIC of next model = 9.443). Within-season time trends and year effects were not useful in explaining variability in brood survival rates. The best model included a quadratic term for brood age (Table 2), with daily survival rates increasing rapidly for the first two weeks, and then leveling off (Figs. 8 and 9). Brood survival varied among islands. Survival was highest on Middle Core Banks, Cape Lookout National Seashore (β = 0.722, CI -0.379 to 1.823) and lowest on

TABLE 2
Model selection results for factors affecting survival of American Oystercatcher chicks on Cape Hatteras and Cape Lookout National Seashores from 1999 to 2008

Model[a]	ΔAICc[b]	Number of parameters, k	Model weight, Wi	Deviance
Age^2 + Island + Vehicle + Forage	0.000	10	0.991	1 018.194
Age^2 + Island + Vehicle	9.442	9	0.009	1 029.641
Age^2 + Island + Forage	24.476	9	0.000	1 044.675
Age^2 + Island	32.170	8	0.000	1 054.374
Age^2 + Year + Island	34.334	17	0.000	1 038.474
Age^2 + Year	40.623	12	0.000	1 054.804
Age^2	42.491	3	0.000	1 074.711
Day + Age^2	44.139	4	0.000	1 074.356
Day^2 + Age^2	45.220	5	0.000	1 073.435
Age	47.293	2	0.000	1 081.515
Day + Age	48.958	3	0.000	1 081.178
Day^2 + Age	50.779	4	0.000	1 080.997
Day	77.079	2	0.000	1 111.300
Day^2	79.076	3	0.000	1 111.296
Constant	91.888	1	0.000	1 128.111

[a] Model factors include linear and quadratic daily variation over the nesting season (Day and Day^2), linear and quadratic age (Age and Age^2), year, island, presence of off-road vehicles and access to foraging areas.
[b] The lowest AICc score in this model set was 1 038.223. Models are ranked by ΔAICc.

Bodie Island, Cape Hatteras National Seashore (β = -0.72597, CI -1.819 to 0.367). The within-island variability in survival was very high, however, and only South Core Banks had a beta coefficient with a CI that did not include zero (β = -0.688, CI -0.213 to -0.164). Predicted brood survival was lower when ORVs were present (β = -0.991, CI -1.381 to -0.601; Fig.7) and higher when broods had direct access to foraging areas (β = 0.717, CI 0.277 to 1.156; Fig. 8).

Individual chick survival and sources of chick mortality were determined from the radio telemetry study. One hundred and twenty-one chicks were tracked from hatching to fledging or death. We were able to determine the cause of death for 37 chicks. Predators accounted for 54% (n = 21) of chick loss, and these included Great Horned Owls *Bubo virginianus*, Fish Crows *Corvus ossifragus*, feral cats *Felis catus*, raccoons *Procyon lotor*, American Mink *Mustela vison* and ghost crabs *Ocypode albicans* (Fig. 9). Vehicle traffic was directly responsible for 16% (n = 6) of chick deaths. Environmental factors, including starvation and storm events, claimed 30% (n = 10). We were unable to determine the cause of death for 51% (n = 39) of the mortality events. Dead chicks were quickly carried off by predators and scavengers or washed away by the tide, so even with radio transmitters we could not always find and retrieve dead chicks. The highest chick mortality rates occurred in the first week after hatching and during the week before fledging (Fig. 10). The cumulative probability of surviving the pre-fledging period varied with the definition of "fledged." Thirty-five days is the minimum age we observed chicks achieving sustained flight (>100 m). Survival to 35 days was estimated at 0.438 (0.0459). A few chicks took up to 46 days to fledge, however, which reduced the survival probability to 0.280 (0.168). The wide confidence interval after 40 days is a result of the very few chicks in the sample still alive and unfledged at this age.

After fledging, radio-marked chicks were tracked daily until mid-August, when field personnel were no longer available. No fledgling mortality was documented during this time. Survey flights in late August and early September in 2005 and 2006 covered the Outer Banks from Nags Head to Morehead City. The oldest chicks began to migrate out of the study area by the end of August, but several still remained at their natal sites on the last survey flights on 18 September 2005 and 25 September 2006.

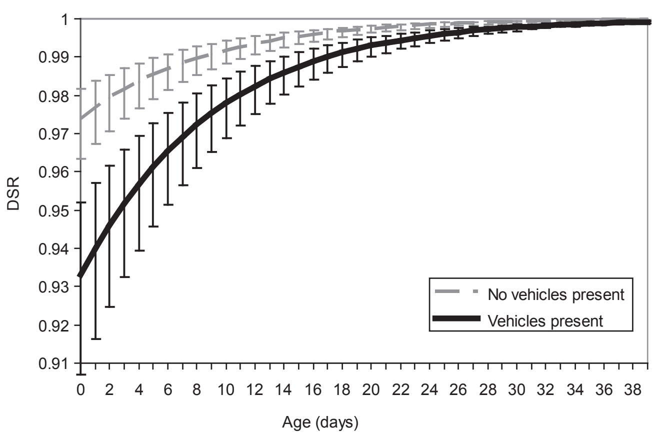

Fig. 7. Survival curves for American Oystercatcher broods on beaches with and without off-road vehicles. Daily survival rates (DSR) and confidence intervals (error bars) were estimated from the model with the lowest ΔAICc score (Table 2).

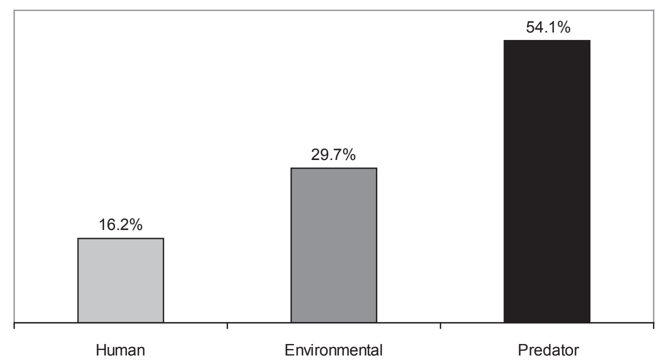

Fig. 9. Sources of pre-fledging American Oystercatcher chick mortality at Cape Hatteras and Cape Lookout National Seashores from 2005 to 2007 (n = 37). Source of mortality could not be determined for 51% of chick deaths (n = 39 chicks).

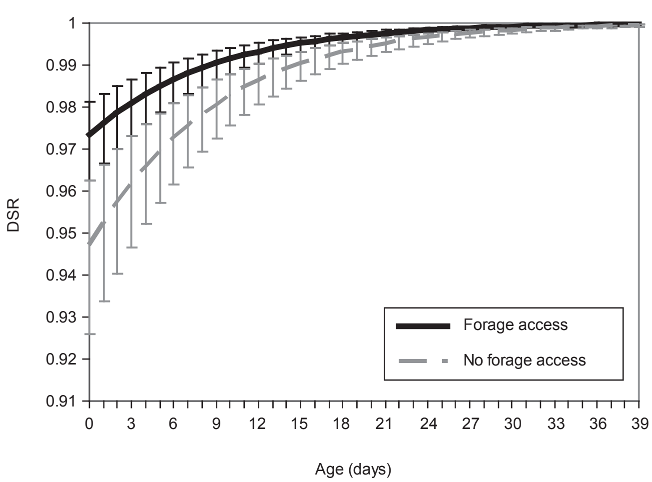

Fig. 8. Survival curves for American Oystercatcher broods with and without direct access to foraging sites. Daily survival rates (DSR) and 95% confidence intervals (error bars) were estimated from the model with the lowest ΔAICc score (Table 2).

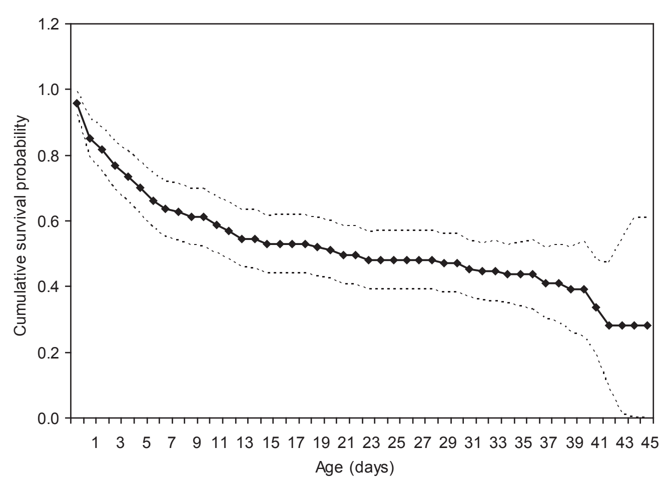

Fig. 10. Kaplan-Meier survival curve and 95% confidence interval (dashed lines) for pre-fledging American Oystercatcher chicks on Cape Hatteras and Cape Lookout National Seashores from 2005 through 2007 (n = 121 chicks).

We conducted 169 h of behavioral observation on 63 chicks on Cape Hatteras National Seashore over four years (2004–2007). Over 90% of the observations were of chicks in full-beach closures, because most of the locations where chicks hatched were subsequently closed under Park Service management policies. Chicks on beaches where vehicles were present spent significantly more time hiding in the dunes and less time at or below the high tide line than chicks on beaches closed to vehicles (Fig. 11, t = 2.00, P = 0.047). Chicks on beaches with partial vehicle closures spent 74% (44.6 min/h, SE 7.78 min/h) of their time hiding in dunes and vegetation and did not use the intertidal zone. Chicks on closed beaches spent 43% (25.8 min/h, SE 3.64 min) of their time in the dunes and 20% (12.0 min/h, SE 3.64 min) in the intertidal zone (Fig. 11). Chicks on beaches where driving was permitted often ran back and forth from the beach to the dunes in response to vehicles, humans and dogs. Oystercatchers with chicks showed a stronger reaction to humans with dogs than to humans alone. We did not document any dog-related mortality, but dogs were observed chasing adult oystercatchers on several occasions. Most adults began to bring their chicks to the waterline to forage within 24 h of hatching. Broods ranged up and down the beach from their nest sites, often moving 500 m or more each day. This pattern continued throughout the chick-rearing stage. Night observations of chicks invariably found the broods on the open beach or below the tide line on both open and closed sections of beach. During the day chicks spent most of their time hiding in the dunes, particularly in areas open to vehicles. Parents always brought their chicks to the beach around sunset. We observed oystercatchers of all ages that became disoriented by vehicle headlights at night and walked, ran, or flew toward the light source. We also observed adult oystercatchers that were startled and apparently disoriented by headlights and abandoned their chicks until the vehicles had passed. In some cases adults returned quickly to their chicks, but in at least one case the adults were kept away by multiple vehicles passing, which resulted in the deaths of their young chicks from exposure and depredation by ghost crabs.

We estimated total productivity as the number of chicks fledged per nesting pair per year, from 1 036 pairs and 1 581 clutches monitored between 1995 and 2008. Productivity was highly variable among years and among locations (Appendix A, available on the website). A total of 320 chicks fledged from all study sites between 1995 and 2008. On average, 0.309 (0.020) chicks fledged per nesting pair.

DISCUSSION

The factors affecting American Oystercatcher reproductive success on the Outer Banks of North Carolina differed between the incubation and chick-rearing stages. This is not particularly surprising, given the semi-precocial nature of oystercatcher chicks. One would expect different sources of mortality after the chicks leave the nest and begin to move about their environment. It is instructive, from both an ecological and a management standpoint, to examine where the differences occur and how different factors influence overall reproductive success. Nest survival through the incubation period was primarily influenced by the date of nest initiation, the nesting island, and year-to-year variation in nesting conditions. Nest survival showed a linear decline over the nesting season. There was little support for a quadratic model in which the rate of change in nest survival could vary across the season. Numerous studies have found trends in daily survival rates when they relax the common assumption of constant survival over the season or the age of the nests (Dinsmore *et al.* 2002). The decline in nest survival over the season could be the result of multiple factors. Heat stress, human activity and predator abundance and distribution may all change over the course of the season. Predators were directly responsible for the majority of failures (61%) for which the source of nest loss could be determined. Differences in nest survival among islands and years may be largely a result of differences in the suite of nest predators and changes in predator abundance. In the absence of comprehensive data on predator populations, this explanation is hypothetical, but there is some evidence to support the idea. On Hatteras Island, Cape Hatteras National Seashore, the nest survival rate fell from 0.272 (0.048) in 1999–2001 to 0.030 (0.023) in 2002, after foxes colonized the island. Predator control measures were initiated in 2003, and the nest survival rate increased to 0.506 (0.050) from 2003 to 2008. On North Core Banks, Cape Lookout National Seashore, the proportion of nests positively identified as lost to predators dropped from 0.31 to 0.10 after Hurricane Isabel flooded the island in September 2003 and apparently reduced predator populations (Schulte & Simons, unpub. data).

Given the importance of predation as a source of nest failure, human actions that affect predator populations or the ability of predators to locate nests will have the greatest effect on nest survival. McGowan & Simons (2006) found that oystercatcher nests that were frequently disturbed were more likely to be depredated. Frequent disturbance may make the nest more visible to avian predators and increase the number of scent trails leading to the nest. We hypothesized that nests on beaches with vehicle traffic would have a lower survival rate, as oystercatchers often move away from their nests in response to vehicle traffic. We considered a beach to permit vehicle traffic if any part of the shoreline was open, even if the upper beach was closed off with symbolic fencing. One of our top two models indicated support for this hypothesis, showing a negative correlation between the presence of ORVs and nest survival. This covariate had a large amount of variability, and the 95% CI of the beta coefficient just included zero. Much of this variability likely stems from differences in physical conditions, human activity and oystercatcher behavior across the islands of the Outer Banks. The effect of vehicle traffic on nest survival could be quite different for a nest on a low-traffic, wider beach where birds are flushed off the nest infrequently than

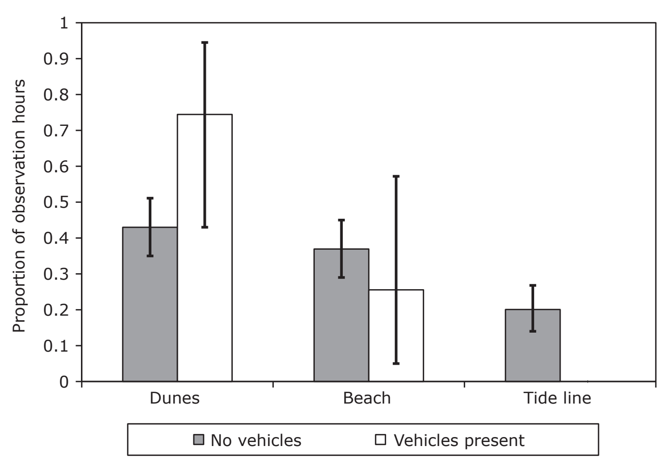

Fig. 11. Habitat use by American Oystercatcher chicks on Cape Hatteras National Seashore on beaches with and without vehicles present (2004–2007): 54 chicks, 157 observation hours on beaches closed to vehicles; nine chicks, 12 observation hours on beaches with vehicle traffic. Bars represent standard errors.

for a high-traffic narrow beach where birds are frequently disturbed. Oystercatcher behavioral responses may also vary from pair to pair, with some birds habituating to human activity and others becoming more sensitized. Finally, the linkage between disturbance and nest failure should vary with the local predator population. The negative effect of disturbance should be greater in areas with higher predator populations. Our beach closure status covariate is not sensitive to these potentially interacting factors, but it does provide a general measure of the correlation between the presence of ORVs and nest survival. An experimental approach that manipulated disturbance levels and controlled for other factors could effectively reduce the uncertainty in this relationship. Tarr *et al.* (2010) used this approach to evaluate the effect of vehicle disturbance on shorebird roosting and foraging behavior during fall migration on Cape Lookout National Seashore and found that disturbance reduced shorebird abundance and use of the beach during roosting.

Storms and high tides are another source of nest failure. Breeding season storms can result in significant nest loss as nests are flooded out or sanded over. A strong storm at the wrong time of year can eliminate most of the active nests, which sets back the reproductive cycle by two to six weeks. Hurricanes and strong winter storms do not directly affect nest success because they usually occur outside of the breeding season. These storms can have beneficial effects, as they create new nesting habitat and may reduce predators. We predicted that nest survival would increase with distance from the high tide line. This hypothesis was not supported by our data. Models with the tide covariate received less support than the same models without the covariate, and the CI of the beta coefficient for the tide covariate encompassed zero. Height above high tide may be a better predictor of success, as some nests on low-lying flats may be hundreds of meters from the high tide line but still flood during storms. Unfortunately, measurements of height above high tide were not available for our nests.

We predicted that nesting pairs with access to sound-side foraging habitats would have higher nest survival than those pairs without this access. Birds with nearby foraging habitat should spend less time and energy commuting to foraging sites and have more time to defend their nests and territories. European Oystercatchers *Haematopus ostralegus* may wait years for the chance to establish a territory in high-quality habitat adjacent to feeding areas (Ens at al 1995, Heg & van der Velde 2001, van de Pol 2007). Nevertheless, we found no effect of proximity to sound-side foraging habitats on nest survival.

We were unable to determine the cause of most nest failures by direct observation and often relied on indirect evidence, such as eggshell fragments or predator tracks, to infer the cause. Nest failure classified as undetermined generally represents nests where wind or rain erased any evidence before the failure was discovered. We believe that the vast majority of our unidentified failures were the result of nest predators. Storm losses were usually easy to identify because the tide line following the storm was often evident above the level of the nest, or the nests were completely sanded over. Identification of different nest predators was much more difficult. Avian predators often leave little or no sign at the nest, and the tracks of mammals such as raccoons and cats are quickly covered by blowing sand. Even during calm weather, predator tracks are often obscured by oystercatcher tracks, as the pair returns and walks around the nest scrape after a predation event. The difficulty of identifying different sources of failure suggests that storm losses may be over-represented in our estimates of identified nest failures (Fig. 3). It is also possible that avian predators are under-represented in these estimates because these predators often leave little evidence. However, avian predators often take only a single egg, reducing the clutch, whereas most nest failures occurred overnight with the loss of an entire clutch, suggesting mammalian depredation.

Oystercatcher brood survival did not change with the date of the nesting season, but survival was affected by the age of the brood. Most brood losses occurred in the first week to 10 days after hatching. This pattern resembles that of other species with precocial young (Colwell *et al.* 2007, Ruthrauff & McCaffery 2005). Young chicks are mobile but cannot fully thermoregulate and are therefore susceptible to temperature and weather extremes. Smaller chicks are also vulnerable to a wider range of predators. Parental behavior may draw attention to younger chicks, which have to be brooded more often and thus stay close to one of the parents. This is particularly true for oystercatchers, as they are one of the only shorebird chicks that are fully dependent on their parents for food (American Oystercatcher Working Group 2012). The oystercatcher's ability to bring food to their young allows them to exploit nesting sites without local food resources. Broods raised at these sites are expected to have generally lower survival because parents must bring food from a separate foraging territory. A long-term study of breeding Eurasian Oystercatchers found that pairs with walking access to foraging habitat had significantly higher productivity than pairs

Fig. 12. Radio-marked American Oystercatcher chicks crushed by a vehicle 16 June 2005, Cape Lookout National Seashore.

that had to fly to their foraging territories (Ens *et al.* 1992). Our best model predicted lower survival for broods without direct access to foraging habitat (Fig. 7), which is consistent with our *a priori* hypothesis.

Brood survival was directly and indirectly affected by the presence of ORVs. Broods on beaches with vehicle traffic had a lower survival rate than broods on closed beaches (Fig. 7). Identifying sources of chick mortality without radio telemetry is extremely difficult. Oystercatcher chicks are well camouflaged, and even live chicks are difficult to locate. Chicks that die below the high tide line are washed away, and predators and scavengers quickly claim the rest. From 1995 to 2008 (excluding the chicks in the telemetry study), 395 oystercatcher chick disappearances were recorded on Cape Hatteras and Cape Lookout. Only 25 dead chicks were found during this period (6.3%). Of these 25 chicks, 13 (54%) were killed by vehicles. However, for the chicks tagged with radio transmitters, we were able to closely track movements and to locate 50% of the chicks that died. We found that very young chicks were much more mobile than previously believed. Movement between the dunes and the intertidal zone places young chicks at considerable risk from beach traffic. We regularly observed chicks hiding in vehicle tracks in response to adult alarm calls and also observed chicks, and even some adults, running or flying directly at the headlights of oncoming vehicles at night. Shortly after we initiated the radio tracking study, we documented the loss of a brood of two-day old chicks to a vehicle on Cape Lookout National Seashore. We had radio-tagged the recently hatched brood at the nest on 16 June 2005. That same evening the chicks were relocated hiding in seaweed at the tide line with the adult pair. The following morning we tracked the transmitter signals to a nearby location and found two of the chicks crushed in a fresh all-terrain vehicle tire track, just above the high tide line (Fig. 12). Over the course of the three-year telemetry study we identified the cause of death for 37 chicks, of which six (16%) were vehicle-related. After reviewing the data on sources of chick mortality, Cape Lookout National Seashore initiated a policy to close sections of beach with unfledged chicks to vehicle traffic, and re-routed traffic around the birds via a back road. After the beach sections were closed, chicks were regularly observed on the open beach and at the tide line during daylight hours, suggesting that vehicle traffic had been altering chick behavior and foraging patterns.

We found that disturbance by vehicles during the chick-rearing phase produces measurable differences in oystercatcher chick behavior, habitat use and survival. In addition to being at risk of direct mortality from vehicles, chicks in areas with ORVs had reduced access to the cooler sand of the intertidal zone, which subjected the chicks to greater heat stress, limited their feeding opportunities, and exposed them to greater risk from predators such as cats, mink and raccoons. The increased risk from nocturnal predators probably explains why adults move their chicks from the dunes to the beach every night even if vehicles are present.

Radio tracking individual chicks allowed us to identify a suite of predators responsible for mortality of chicks before fledging. Although feral cats and raccoons both preyed on chicks, ghost crabs and avian predators such as Great Horned Owls and Fish Crows appeared to play a larger role in chick than in nest predation. The Kaplein-Meier survival curve for radio-tagged chicks showed that chicks were most vulnerable during the first week after hatching when they are most susceptible to exposure and ghost crab depredation (Fig. 10). This result is consistent with the predicted age-related brood survival curve from our best model (Table 2, Figs. 7 and 8).

Total productivity, or the number of chicks fledged per breeding pair, reflects the ability of an oystercatcher population to navigate the hazards associated with reproduction from egg-laying through fledging. Predators, storms, habitat quality and management actions combine to shape the annual success or failure of each breeding pair. Management actions that affect chick survival generally have the greatest effect on overall productivity. In 2008, Cape Hatteras National Seashore increased predator trapping efforts and expanded buffer zones for chicks to 300 m. Chick survival on Cape Hatteras in 2008 was the highest recorded during the study period (0.81), which resulted in a final productivity of 0.714, over twice as high as the average annual productivity in North Carolina. The relative contributions of predator management and vehicle management to this elevated productivity is not clear, but managing both is vitally important for a successful conservation outcome. Given the importance of predators at all stages of the breeding cycle, a better understanding of predator population dynamics would likely go a long way toward explaining temporal and spatial variability in oystercatcher productivity.

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