

Conservation implications of reproductive success of American Oystercatchers in an urbanized barrier island complex

Thomas Virzi¹, Julie L. Lockwood², David Drake³, Steven M. Grodsky⁴ & Todd Pover⁵

¹*Ecostudies Institute, P.O. Box 735, East Olympia, Washington 98540, USA. tvirzi@ecoinst.org*

²*Department of Ecology, Evolution, and Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, New Jersey 08901, USA*

³*Department of Forest and Wildlife Ecology, University of Wisconsin – Madison, 1630 Linden Drive, Madison, Wisconsin 53706, USA*

⁴*Fisheries, Wildlife, and Conservation Biology Program, North Carolina State University, Raleigh, North Carolina 27695, USA*

⁵*Beach Nesting Bird Project, The Conserve Wildlife Foundation of New Jersey, P.O. Box 400, Trenton, New Jersey 08625, USA*

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Urbanization on the barrier islands along the Atlantic coast of North America has severely altered the traditional breeding habitat for many ground-nesting waterbirds in this region, including the American Oystercatcher *Haematopus palliatus*. We used an information-theoretic approach to analyze various human-induced effects on oystercatcher daily nest survival rates and overall reproductive performance in an urbanized coastal ecosystem. We used explanatory variables including habitat type, level of human disturbance, presence of mammalian predators, proximity to gull colonies and nest height above sea level as nest-specific covariates in our models to explore their effects on the daily survival rates of clutches and broods separately. We found an overall reproductive success rate of 7%, which is far below the level necessary to sustain the population. The principal factor negatively influencing daily survival rates of clutches and broods was the presence of predators, with mammalian predators affecting clutches and gulls affecting broods. The reproductive success rate on predator-free inlet and back-bay islands (25%) was an order of magnitude greater than the rate reported on barrier islands (2%), which have relatively high densities of predatory mammals. Ours is one of the few studies to comprehensively evaluate the breeding success of American Oystercatchers within alternative breeding habitats such as inlet and back-bay islands. Our results confirm the management conclusions of others that the best way to ensure the long-term population viability of American Oystercatchers is to concentrate management on these alternative habitats. This protection strategy likely also has benefits for other ground-nesting waterbirds.

Keywords

American Oystercatcher
Haematopus palliatus
 brood survival
 clutch survival
 dredge-spoil islands
 nest success
 predator-free islands
 program MARK

INTRODUCTION

Beach-nesting birds are in sharp decline worldwide, in large part because of increasing loss or alteration of critical breeding habitat, human disturbance of breeding grounds, and mammalian predation pressure (Patterson *et al.* 1991, Erwin *et al.* 2001, Lowney *et al.* 2005). In North America, these declines began between 1930–1970, coinciding with the first period of intensive coastal development (Nisbet & Spendelow 1999). Coastal development

pressure continues to increase, so much so that coastal counties currently make up 17% of the total land area in North America but account for 53% of the total human population (Crossett *et al.* 2004). Given such intense development pressure on coastal ecosystems, with all the attendant ecological issues, beach-nesting bird populations may not be able to persist without sustained intensive management efforts. American Oystercatchers *Haematopus palliatus* are a prime example of a species facing this

dilemma. They are a species of high conservation concern in North America because of their low population numbers and rapid range-wide population decline (Nol *et al.* 2000, Davis *et al.* 2001, Clay *et al.* 2014). Recently, the Atlantic coast population in North America has benefited from a large-scale conservation effort focused on increasing reproductive success (i.e., nest and brood survival), which is the vital rate often managed in the context of habitat loss and degradation.

Prior to World War II, the coastline of the United States remained in a relatively natural state with more than 90% of barrier island complexes undeveloped and largely inaccessible to the public. This situation changed dramatically over the next several decades and perhaps nowhere more pronounced than in the Mid-Atlantic region. In the state of New Jersey, USA total urbanized coastal barrier acreage reached 37% by 1950 and 47% by the mid-1970s (USFWS 1996). Coastal development in New Jersey has slowed in some areas in recent years, but the condition of coastal habitats has already been altered so severely in many instances that the species utilizing these habitats for breeding have experienced severely reduced reproductive success. Since the population consequences of reproductive failure are postponed in long-lived species with delayed maturity (Hernandez-Matias *et al.* 2003), a trait shared by many of the beach-nesting species in the order Charadriiformes, North American beach-nesting birds such as the American Oystercatcher warrant high conservation concern.

Coinciding with rapid coastal development the American Oystercatcher began to utilize non-traditional habitat to breed (Post & Raynor 1964, Humphrey 1990, Clay *et al.* 2014). The oystercatcher population in New Jersey utilizes a mosaic of habitats for breeding including barrier beach strands, saltmarsh, natural inlet islands and artificial dredge-spoil islands, many of which are severely altered and subject to high levels of human disturbance (Virzi 2010). A similar shift in habitat has been observed for several waterbirds along the Atlantic coast of North America; however, there have been few detailed investigations into the reproductive performance of individuals that utilize these alternative habitats (Erwin & Beck 2007). Very few studies have been able to track the success of broods of young for American Oystercatchers (or many other shorebirds) after they hatch, thus leaving a critical gap in our understanding of how these alternative habitats function in terms of population persistence. There is consistent evidence that the young of precocial species face drastically different survival pressures once they hatch, and this observation presents the possibility that what is good for clutch survival may not be good for juvenile survival. For example, McGowan *et al.* (2005) examined the difference in American Oystercatcher reproductive success between barrier beach and river island habitats in North Carolina and found that hatching success was significantly greater on river islands; however, fledging success was lower resulting in no significant difference in overall reproductive output. Gaining a better understanding of the effects of this habitat shift on oystercatcher reproductive success is paramount in developing conservation strategies for the species.

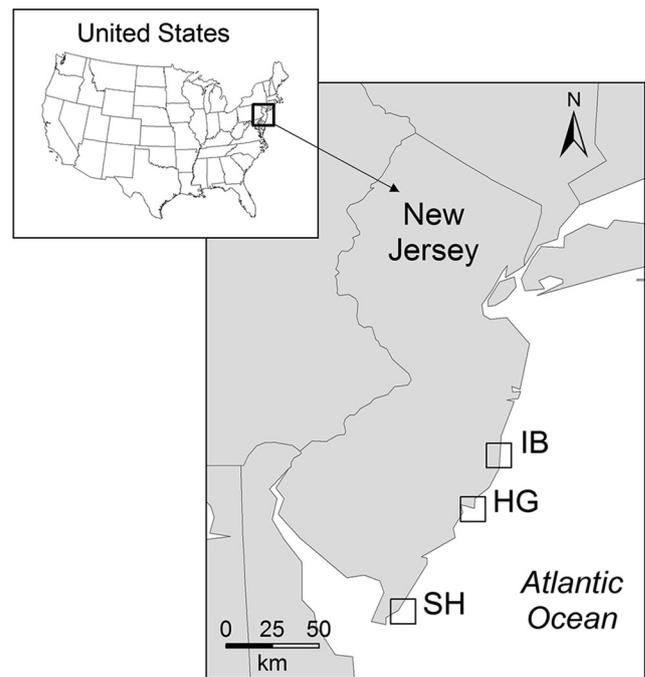


Fig. 1. Location of three breeding areas included in our 2005–2007 study of breeding American Oystercatchers in coastal New Jersey, USA. Study sites shown on map include: Island Beach State Park (IB), the Holgate Division of the Edwin B. Forsythe National Wildlife Refuge (HG), and Stone Harbor Point (SH).

Here we evaluate the breeding success of American Oystercatchers within a highly urbanized coastal barrier island ecosystem. Specifically, we test for effects of habitat characteristics, predator abundance, and human disturbance on daily survival rates of nests and broods. Our study provides important information about oystercatcher habitats that have less commonly been studied, and is the first to consider the effect of habitat on brood survival.

METHODS

Study areas

We collected reproductive data at three study areas located near the northern limit of the breeding range of the American Oystercatcher in New Jersey, USA: (1) Island Beach State Park (IB; 39°46'12"N, 74°05'60"W), (2) the Holgate Division of the Edwin B. Forsythe National Wildlife Refuge (HG; 39°30'00"N, 74°17'60"W), and (3) Stone Harbor Point (SH; 39°01'48"N, 74°46'48"W; Fig. 1). Available breeding habitat at each site included barrier beach strands, adjacent saltmarsh systems, and nearby inlet or dredge-spoil islands providing replicates for each habitat type. Habitat at IB included 3.3 km of undeveloped barrier beach, a 1.6-km inlet beach along a man-made dike, 197 ha of adjacent saltmarsh, and an 8-ha artificial dredge-spoil island located within Barnegat Inlet. Habitat at HG included 6.0 km of undeveloped barrier beach, 74 ha of

saltmarsh located directly adjacent to the barrier beach strand, and a 5-ha naturally-forming inlet island located within Little Egg Inlet. Habitat at SH included 1.8 km of partially developed barrier beach, 23 ha of saltmarsh located directly adjacent to the barrier beach strand, a 126-ha nearby saltmarsh island connected to the mainland by automobile bridges, and an 11-ha naturally-forming inlet island located within Hereford Inlet. The three study areas also represented a gradient of human disturbance from low- to high-use areas allowing analysis of the effects of human disturbance on oystercatcher reproductive rates. IB was the most heavily disturbed site, HG was the least disturbed site, and SH had an intermediate level of human disturbance on breeding oystercatchers.

Nest searches and monitoring

We conducted weekly surveys for territorial pairs of American Oystercatchers at each study site from 1 April to 31 July during each year of our study (2005–2007). We conducted surveys by walking line transects following barrier beaches and the perimeters of inlet and dredge-spoil islands. We searched for pairs in saltmarsh habitat by boat, following all navigable shorelines and tidal creeks. In all interior saltmarsh habitat that was not accessible by boat, we also conducted surveys by walking line transects spaced 100 m apart. We located nests by intensively searching areas where we observed breeding behavior by adult oystercatchers. Typically, we located nests during the egg stage ($n = 284$); however, we did locate reproductive attempts during the brood stage as well ($n = 8$). Most nests located during the egg stage were found prior to clutch completion ($n = 206$; mean number of eggs when found = 1.9, SD = 0.8).

We monitored nests and broods every 3–7 days (mode = 3.0, mean = 5.1, SD = 3.3) until either at least one young successfully fledged or all nest contents were lost to predation or flooding. A brood was considered to have fledged if it survived >35 days, or sooner if flight capability of chicks was observed. Clutch failure was determined when eggs disappeared and chicks were not observed, or if there was an absence of behavioral cues that would indicate hatching (described below) after the expected hatch date and/or when the entire clutch had disappeared. We considered a clutch to have hatched upon the observation of at least one chick in or near the nest. We considered a brood as successful when at least one chick fledged, and we considered a reproductive attempt to have failed when the entire brood was lost. We considered a brood lost when no chicks were observed or when we observed no behavioral cues over two consecutive visits. In these instances, we determined the date of failure as the first date that chicks or behavioral cues were not observed. We determined the cause of failure for clutches based on evidence observed at the nest site, such as signs of predation or flooding, the former including presence of broken eggshells in nests or animal tracks leading to failed nests. Causes of failure for broods were difficult to identify since chicks often disappeared from territories without evidence.

We used a modeling approach that required accurate determination of transitions between reproductive stages (see below), thus we intensified nest visits near predicted hatch dates (i.e., 28 days after estimated clutch completion). We determined transition between these stages by observation of at least one chick in the nest or by observation of certain behavioral cues by adults indicating that a clutch had hatched. The use of behavioral cues as an indication of hatching was necessary in order to obtain the most accurate estimate of transition date since chicks could not be located during every visit. The behavioral cues included an increased vigilance by adults, with adults exhibiting much more aggressive behavior in defense of territories upon approach. The aggressive behavior included a circling flight around observers while calling loudly with a unique, rapid, four-note staccato call that is used by adults predominantly when there is an active brood. We observed a few occasions where this behavior was used when clutches were near their expected hatch dates; however, in most instances this behavior was only observed after clutches had hatched. In all cases where we relied on these behavioral cues to indicate transition between the egg and brood stages, we later confirmed hatching on subsequent visits by the observation of at least one chick.

Factors influencing reproductive success

We recorded year, site, and habitat as basic descriptors of oystercatcher breeding success. We also collected four nest-specific variables that index nest height (i.e., likelihood of flooding), predation pressure, and level of human disturbance. We did not include information on age of eggs or chicks because we could not always age them accurately.

We assigned all breeding territories into one of three habitat categories: beach, marsh or island. Beach sites were those located on major barrier island beach strands. Marsh sites were those located in *Spartina*-dominated saltmarsh. Island sites were those located on isolated natural inlet islands or artificial dredge-spoil islands. We hypothesized that clutch and brood survival rates would be higher in alternative habitats, primarily due to protection from high mammalian predation rates likely to be found in traditional habitats (McGowan *et al.* 2005, Sabine *et al.* 2006), but also possibly due to a lower level of human disturbance expected in alternative habitats (Virzi 2010). Since oystercatcher nests are susceptible to flooding (Lauro & Burger 1989, Nol 1989), we assigned each nest one of three rankings of height above sea level: (1) low, (2) medium and (3) high. Low nests were those located in areas that we considered susceptible to flooding caused by monthly spring tides (e.g., nests located below wrack lines on beaches and nests located on wrack deposits in low marsh areas dominated by *Spartina alterniflora*). Medium-height nests were those located in areas that we expected to be safe from flooding caused by monthly spring tides, but susceptible to flooding from storm tides (e.g., nests located in areas on beaches with evidence of recent overwash events and nests located in high marsh areas dominated by *S. patens*). High nests were those located in areas that we expected to be safe from flooding

from all but the most severe storm tides (e.g., nests located on primary dunes). We hypothesized that broods would also be susceptible to flooding, especially young broods, as many of the breeding territories in our study were located on isolated islands distant from higher areas where chicks could swim to safety during high tide events.

Gulls are known to depredate eggs and young of a variety of waterbirds (Harris & Wanless 1997, Tjorve & Underhill 2008). Abundant gull species found at our study sites during summer months included Great Black-backed Gulls *Larus marinus*, Herring Gulls *L. argentatus* and Laughing Gulls *L. atricilla*, all of which were observed breeding in close proximity to oystercatchers. In order to assess the effect that gulls have on oystercatcher reproductive success, we recorded the location of all gull breeding colonies at our study sites with a handheld GPS device. These data were later used to measure the Euclidean distance from each oystercatcher nest to the center of the nearest gull colony, providing a proxy for the expected level of predation pressure from breeding gulls at each nest site.

Mammals are known to be efficient nest predators for ground-nesting species and are regularly cited as having significant negative effects on oystercatcher nest success rates (McGowan *et al.* 2005, Virzi 2008, Schulte & Simons 2015). Mammalian species regularly observed at our study sites included Red Fox *Vulpes vulpes*, Striped Skunk *Mephitis mephitis* and Raccoon *Procyon lotor*. In order to assess the effect that mammals have on oystercatcher nest survival, we conducted surveys for mammal tracks or other signs within a 100-m radius of all oystercatcher nests during each periodic nest visit. This was done during our approach to check nest contents, which generally took 1–2 minutes per visit to collect all data. During each visit, a binary code was recorded indicating the presence (1) or absence (0) of mammal tracks or

signs. We used these data to calculate the proportion of visits over the course of the monitoring period that we recorded mammal activity at each territory.

The effects of human disturbance on oystercatcher nest or brood survival is unknown; however, McGowan *et al.* (2006) and Sabine *et al.* (2008) provided evidence that human disturbance can alter oystercatcher incubation behavior. It is probable that high rates of human activity on breeding grounds can disrupt oystercatcher incubation behavior leading to lower nest survival rates by inducing lethal incubation temperatures or increasing nest predation due to exposure of nests during forced departures. We also predict that high levels of human disturbance could reduce brood survival due to a disruption of brood rearing activities. In order to assess the effect of human disturbance on oystercatcher reproductive success, we assigned an index for human activity to each nest site. During each nest visit, a binary code was recorded indicating the presence (1) or absence (0) of human activity within a 100 m radius surrounding each oystercatcher nest. We used these data to calculate the proportion of visits over the course of the monitoring period that we recorded human activity on or near each territory.

Data analysis

We measured reproductive success as the daily survival rate (DSR) following Mayfield (1975). Recent incarnations of Mayfield's estimator allow investigators to evaluate the influence of factors on DSR using information-theoretic algorithms (Johnson 2007). We estimated daily survival rates of oystercatcher nests and broods using the nest survival model (Dinsmore *et al.* 2002) in program MARK (White & Burnham 1999). This software uses generalized linear models within a maximum likelihood approach to estimate DSR (Rotella *et al.* 2004). We used a hierarchical approach to generate a candidate set of *a priori* models

Table 1. Hypothesized effects of model covariates on daily survival rates of American Oystercatcher clutches and broods in coastal New Jersey, USA (2005–2007).

Covariate/Interaction	Clutch Survival	Brood Survival
Year	High variation in survival rate between years	Same hypothesis
Site	No effect – other variables account for site differences	Same hypothesis
Habitat type	Higher survival rate in alternate habitats than on barrier beaches	Same hypothesis
Nest height	Lower nests have reduced survival rates	Same hypothesis
Avian predators (gulls)	High level reduces survival rate moderately	High level reduces survival rate substantially
Mammalian predators	Mammal presence reduces survival rate substantially	Mammal presence reduces survival rate moderately
Human disturbance	High level reduces survival rate substantially	Same hypothesis

for use in our analyses, similar to other recent studies using program MARK (Colwell *et al.* 2007, Hood & Dinsmore 2007). We began our analyses by examining the effect of nest stage on DSR by coding our data into two groups and running models comparing constant and time-varying DSR with and without a group (stage) effect, excluding any additional nest-specific covariates.

As expected, we found large differences in DSR between the two stages (clutch and brood). Thus, we generated a set of *a priori* models examining the effects of various explanatory variables (covariates) on oystercatcher DSR during the clutch and brood stages separately. All generalized linear models that incorporated one or more covariates used the logit link function and all other models used the sine link function (Burnham & Anderson 2002). We ranked competing models that describe the relationship between DSR and explanatory variables using Akaike's Information Criterion (AIC_c) corrected for small sample size (Burnham & Anderson 2002). We judged models with ΔAIC_c values <2.0 as having substantial support, ΔAIC_c values from 2.0–7.0 having considerably less support, and ΔAIC_c values >7.0 indicating essentially no support (Burnham & Anderson 2002). The effect of each explanatory variable on clutch or brood survival is represented by the importance value (Ψ) and beta (β) estimate for each covariate provided by program MARK. Strong effects were inferred by high importance values (Ψ approaching 1.0) and beta estimates with confidence intervals that do not cross zero (Burnham & Anderson

2002). All parameter estimates and effect sizes were based on model-averaged estimates from the best-supported models (i.e., models with $\Delta AIC_c < 2.0$).

Due to high predation rates at our study areas, it was difficult to accurately determine whether nests were in the egg-laying or incubation stages. As such, we combined all nests with eggs, regardless of timing within the egg stage, into our clutch survival models. Additionally, since individual chicks were difficult to observe during each visit, we modeled brood survival rather than individual chick survival, which is more appropriate in such cases (Colwell *et al.* 2007). We were able to accurately determine the fate of broods based on direct observation of chicks or behavioral cues, as described previously.

Within our stage-specific models, we generated separate sets of *a priori* candidate models that described competing hypotheses (Table 1). We developed a set of 24 *a priori* models explaining DSR of clutches and broods independently. We hypothesized that oystercatcher reproductive success would vary between year and habitat type. We also hypothesized that predator activity would be the major factor to negatively affect survival rates at both reproductive stages; however, we expected there to be different effects at each stage depending on type of predator (e.g., avian vs. mammalian). We considered examining the effect of time of season on DSR of clutches and broods; however, since oystercatcher nests in our study were initiated synchronously among study sites

Table 2. Model selection results for top 10 clutch survival models for American Oystercatchers in coastal New Jersey, USA (2005–2007).

Model ^a	AIC_c^b	ΔAIC_c	w^c	K^d	Deviance
Global Model	685.06	0.00	0.55	11	662.96
Gull + Mammal + Nest Height	686.54	1.48	0.26	4	678.53
Gull + Mammal + Disturbance + Nest Height	687.74	2.68	0.14	5	677.72
Mammal + Nest Height	690.87	5.81	0.03	3	684.86
Mammal + Disturbance + Nest Height	692.05	6.98	0.02	4	684.03
Gull + Mammal	713.13	28.07	0.00	3	707.13
Gull + Mammal + Disturbance	714.10	29.03	0.00	4	706.08
Mammal	717.38	32.31	0.00	2	713.37
Year + Site + Habitat	717.89	32.83	0.00	7	703.85
Mammal + Disturbance	717.95	32.89	0.00	3	711.94

^aModels ranked by ΔAIC_c in ascending order. Additive models indicated by +.

^bAkaike's Information Criterion adjusted for small sample size.

^cAIC model weight.

^dNumber of parameters.

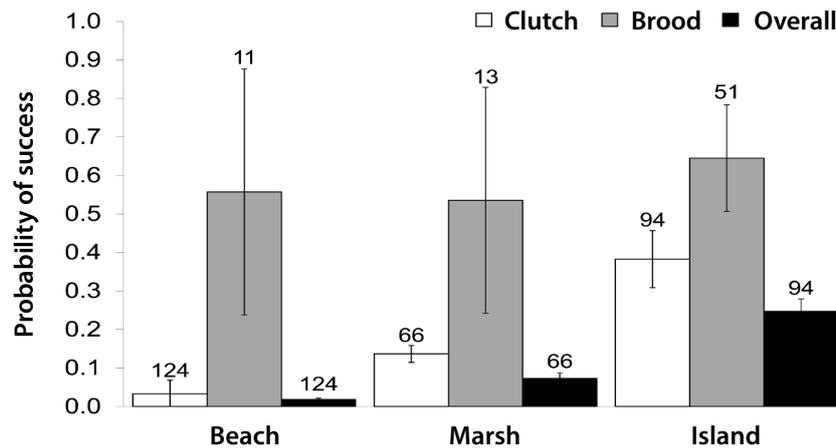


Fig. 2. American Oystercatcher reproductive rates by habitat type in coastal New Jersey, USA (2005–2007). Probability of clutch or brood success (hatch or fledge) based on model-averaged daily survival rate (DSR) for clutches or broods and number of exposure days until success at each stage. Clutch success = $DSR_{clutches}^{28}$; brood success = DSR_{broods}^{35} ; overall reproductive success = clutch success \times brood success. Error bars represent 95% confidence intervals based on standard errors calculated using the delta method. Numbers above error bars represent sample sizes of clutches and broods included in nest survival models.

and were tied more closely with tidal fluctuations than time of season we did not feel the need to include this covariate in our models.

To illustrate the effects of various covariates on overall oystercatcher reproductive success, we portrayed DSR of clutches and broods separately (Johnson 1979). We raised the DSR estimate based on the best approximating model(s) for each stage to a power representing the total number of exposure days of each stage (clutch = 28 days; brood = 35 days) based on the mean days to clutch hatching and brood fledging observed in our data. Reproductive success was calculated by multiplying clutch and brood success rates (Johnson 1979). Standard errors for clutch and brood success rates were calculated by multiplying the standard error reported by program MARK for each stage-specific DSR estimate by the derivative of the DSR estimate (Powell 2007). The standard error for reproductive success was calculated using the delta method (Seber 1982, Powell 2007).

RESULTS

We monitored 284 American Oystercatcher clutches and 75 broods during 3 years, with reasonably large numbers of nests distributed across all habitats (Fig. 2). The proportion of clutches monitored that hatched (i.e., apparent nest success) was 24%. Apparent nest success was substantially lower on barrier beaches (9%; $n = 124$) and marshes (20%; $n = 66$) compared to isolated islands (54%; $n = 94$). The number of chicks fledged per breeding pair (i.e., apparent productivity) was also substantially lower on barrier beaches (0.02; $n = 77$ pairs) and marshes (0.13; $n = 47$ pairs) compared to isolated islands (0.33; $n = 71$ pairs). Nests tended to be somewhat higher above sea level on beaches (mean nest height index = 2.0) compared to islands (1.6) and marshes (1.2). The level of human

disturbance was lower on beaches (mean disturbance index = 0.07) compared to islands (0.10) and marshes (0.20). Predator presence/activity varied substantially among habitats: mammalian activity was much higher on beaches (mean mammal index = 0.46) compared to islands (0.01) and marshes (0.15); mean gull density counted within 100 m of oystercatcher nests was highest on isolated islands ($n = 76$), where large gull colonies tended to occur within our study sites, compared to beaches ($n = 8$) and marshes ($n = 7$).

Clutch survival

The best-supported clutch survival models ($\Delta AIC_c < 2.0$) in our set of candidate models included the global model and an additive model with covariates for distance from nearest gull colony, mammal activity and nest height ($w = 0.95$; Table 2). The model-averaged DSR of oystercatcher clutches based on the best-supported models was 0.92 (SE = 0.01). The negative effect of mammals on clutch survival was substantial ($\Psi = 1.00$; $\beta = -2.16$, 95% CI = -2.84, -1.47; Table 4), whereas nest height had a positive effect on clutch survival ($\Psi = 1.00$; $\beta = 0.63$, 95% CI = 0.37, 0.88). Gull density also had a positive effect on clutch survival; however, the effect size was very small ($\Psi = 1.00$; $\beta = 0.007$, 95% CI = 0.002, 0.012). All other covariates included in the global model had minimal effects based on either low importance values or beta estimates with confidence intervals crossing zero.

One of the benefits of using program MARK to model nest survival is that it provides a method to illustrate DSR based on the best-supported model or set of models (Dinsmore & Dinsmore 2007). We examined the effect of different levels of mammal activity on the survival of oystercatcher nests that were susceptible to flooding (low height category) versus those that were not (high height

category) and predicted DSR based on our best-supported models (Fig. 3). Our predictive analysis illustrates the large difference in DSR between nests likely to flood (low nests) versus those that were not (high nests), and more importantly, the substantial decline in DSR as the level of mammal activity increased within oystercatcher territories regardless of nest height (Fig. 3).

Brood survival

The results from our brood survival analysis are less clear than for clutch survival (Table 3). Eight models received substantial support ($\Delta AIC_c < 2.0$), including a model with no covariates ($DSR_{constant}$). The model-averaged estimate for the DSR of oystercatcher broods was much higher than for clutches (0.99, SE = 0.003). All covariates appeared in one or more of the top models, and none had a substantial effect on brood survival based on importance values or beta estimates. Gull density had the highest importance value ($\Psi = 0.53$; Table 4); however, the beta estimate was not significant ($\beta = 0.00$, SE = 0.00). Study site had the next highest importance value ($\Psi = 0.37$); however, the beta estimate ($\beta = 0.43$, SE = 0.22) had a very large confidence interval indicating a low effect size. The covariate for mammal activity showed the highest beta estimate ($\beta = 3.40$, SE = 5.09); however, the large standard error resulted in a confidence interval that crossed zero.

Net reproductive success

Based on model-averaged results from the top models for clutch and brood survival, the overall reproductive success rate for American Oystercatchers breeding in New Jersey, USA was 0.07 (SE = 0.01). Oystercatchers experienced their lowest reproductive rates in traditional barrier beach habitat. The probability of clutch success was lowest on barrier beaches (0.03, SE = 0.1) and highest on isolated islands (0.38, SE = 0.05), where there was an almost complete absence of mammalian predators (Fig. 2). The clutch success rate for marsh-breeding oystercatchers was 0.14 (SE = 0.04), which is a habitat where nests are also exposed to mammalian predators. Brood success was also higher on isolated islands (0.65, SE = 0.07) than in beach habitat (0.56, SE = 0.16) and marsh habitat (0.54, SE = 0.15); however, the difference was not statistically significant. The differential hatching and fledging success rates across habitat types resulted in substantially higher overall probability of reproductive success for island-breeding oystercatchers (0.25, SE = 0.03) compared with marsh-nesting pairs (0.07, SE = 0.01) and barrier beach-nesting pairs (0.02, SE = 0.004).

DISCUSSION

Breeding success for American Oystercatchers in New Jersey was low, especially compared to more southerly breeding areas along the Atlantic coast of the United States (Nol 1989, Davis *et al.* 2001, McGowan *et al.* 2005, Sabine *et al.* 2006). Reproductive attempts were much more likely to fail at the egg stage rather than the brood

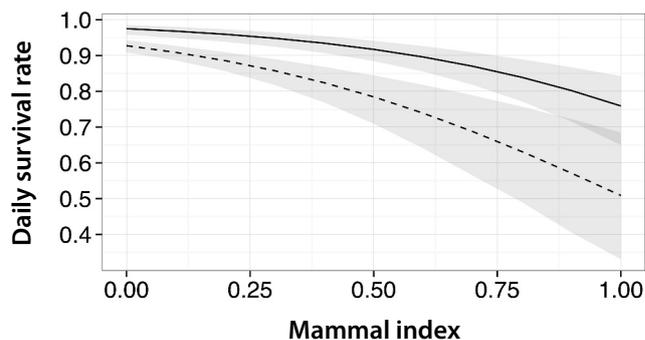


Fig. 3. Predicted daily survival rate of American Oystercatcher clutches in response to mammal activity and nest height in coastal New Jersey, USA (2005–2007). Daily survival rate was based on a clutch survival model that includes the three covariates with the highest importance values (Mammal + Gull + Nest Height). Nest height was set to high (solid line) or low (dashed line); mammal index was allowed to range from 0.0 to 1.0; distance to nearest gull colony was set to zero since the effect size for this covariate on DSR was negligible. Grey shaded areas represent 95% confidence intervals surrounding DSR estimates.

stage. As such, the low reproductive success rates we found were driven primarily by the extremely low nest success rates, which ranged from 3% on barrier beaches to 38% on isolated islands. The nest success rate on barrier beaches was well below rates recently reported further south along the Atlantic coast of the United States. For example McGowan *et al.* (2005) and Sabine *et al.* (2006) reported nest success rates as high as 45% on barrier beaches in North Carolina and Georgia, USA, respectively. The low reproductive success rate we found for oystercatchers breeding on barrier beach strands (7%) was also substantially below that reported on barrier islands in more southern parts of the American Oystercatcher's range (11–14%; Nol 1989, Davis *et al.* 2001, McGowan *et al.* 2005). Based on population viability analyses for North Carolina oystercatchers, Brown *et al.* (2008) show that reproductive success must be above 18% for the population to remain stable over the next 10 years. The reproductive rates we reported for American Oystercatchers breeding along the barrier beach strand in New Jersey, USA are thus far below what might be considered sustainable.

We observed a large difference in reproductive success rates among habitats, and this may provide a potential avenue for conserving this species over the long term. In particular, the chance that a given oystercatcher egg laid on inlet or dredge-spoil islands will result in a fledged juvenile was an order of magnitude higher than what we observed on barrier beaches. The differential reproductive success rate among habitats resulted from a substantially lower DSR of nests during the egg stage in some habitats, with brood success rates being more similar among habitats. The factor that consistently showed a large effect on clutch success, and best explained our observed differences

among habitats, was mammalian predation pressure. Surprisingly, distance from gull colonies did not significantly affect clutch or brood survival rates, with many oystercatchers in our study successfully breeding directly adjacent to large gull colonies (e.g., isolated islands with *L. argentatus* and *L. marinus* colonies). We interpret this as further evidence that isolation from mammalian predation is most important for American Oystercatcher breeding success.

Mammalian predation has been linked to low reproductive success for oystercatcher species worldwide (Hockey 1996, Davis *et al.* 2001, Gill *et al.* 2004). More generally, mammalian predators are associated with reduced reproductive rates, population declines and the extinction of many avian species on oceanic islands due to a lack of defenses in island birds that evolved without the threat of terrestrial predators (Atkinson 1996, Blackburn *et al.* 2004, 2005). Although perhaps not as isolated from continental influences as many oceanic islands, the barrier islands off the Atlantic coast of eastern North America historically functioned as refuges from mainland populations of mammalian predators for many of the region's threatened and endangered waterbird species. Predator movements from the mainland to barrier islands and between islands do occur (Dueser *et al.* 2005). However, historic population levels of mammalian predators on barrier islands may have been lower than current levels due to the harsh conditions on these coastal islands and because of barriers to immigration that existed before automobile bridges were built

connecting many of the barrier islands to the mainland (Patterson *et al.* 1991).

In addition, important native mammalian nest predators have undergone range expansions as a result of coastal development and associated anthropogenic food subsidies (Burger & Lesser 1980). Food subsidies provided by human garbage are often associated with increased predator abundances due to the better physical condition of individuals in the population, decreased mortality rates (especially winter mortality), increased reproductive rates, and higher annual recruitment into predator populations (Burger & Lesser 1980, Patterson *et al.* 1991). Human food subsidies may not only help sustain higher predator populations on barrier islands; subsidies on the extensively developed mainland may help ensure a constant source of migrants onto the barrier islands.

In response to the loss or deterioration of barrier island habitat due to coastal urbanization and heavy predation pressure, many beach-nesting species, including the American Oystercatcher, have already begun to use alternative breeding habitat such as saltmarsh, riverine, inlet or back-bay islands. These small islands are often more isolated than barrier islands and thus often do not have persistent populations of mammalian predators. American Oystercatchers in our study exhibited substantially higher reproductive success in such alternative habitats. Nol *et al.* (2012) found that American Oystercatchers using alternative breeding habitat also reported higher adult survival

Table 3. Model selection results for top 10 brood survival models for American Oystercatchers in coastal New Jersey, USA (2005–2007).

Model ^a	AIC _c ^b	ΔAIC _c	w ^c	K ^d	Deviance
Gull	190.56	0.00	0.16	2	186.56
Year + Site	191.09	0.52	0.12	4	183.06
Gull + Mammal	192.05	1.48	0.08	3	186.04
Site	192.41	1.84	0.06	2	188.40
Site + Habitat	192.42	1.85	0.06	4	184.39
DSRconstant	192.42	1.86	0.06	1	190.42
Gull + Nest Height	192.55	1.99	0.06	3	186.54
Gull + Disturbance	192.55	1.99	0.06	3	186.54
Year + Site + Habitat	192.70	2.13	0.06	6	180.65
Year	193.19	2.63	0.04	3	187.18

^aModels ranked by ΔAIC_c in ascending order. Additive models indicated by +.

^bAkaike's Information Criterion adjusted for small sample size.

^cAIC model weight.

^dNumber of parameters.

rates, which further stresses the importance of alternative habitats for this species.

The availability of high elevation back-bay islands as alternative breeding habitat may become especially important for the population viability of beach-nesting birds if sea levels rise as predicted. Global climate change is predicted to result in sea level rise that would negatively affect shorebird populations worldwide due to loss or alteration of breeding and foraging habitats (Aiello-Lammens *et al.* 2011, Chu-Agor *et al.* 2011, Galbraith *et al.* 2014). The impacts of sea level rise on barrier beaches may be even more severe on heavily developed and armored coastlines (Dugan *et al.* 2008, Sims *et al.* 2013), such as those found along the northeastern coast of the United States. Armoring impedes the retreat of coastal habitats resulting in a disproportionate loss of important upper intertidal habitat and an overall narrowing of beaches, both of which are predicted to have negative effects on beach-nesting birds. Beach-nesting birds may be further threatened by an increase in the frequency, magnitude and timing of extreme climatic events which is also predicted as a result of climate change (Elsner *et al.* 2008, van de Pol *et al.* 2010). In response to climate change, van de Pol *et al.* (2010) predicted that shorebirds

would benefit most from adapting their nest site selection to higher areas, which could partially explain why American Oystercatchers have recently begun using alternative breeding habitat on higher back-bay islands. This apparent plasticity in American Oystercatcher nest site selection should help mitigate the effects of sea level rise to some degree, but only if enough suitable back-bay islands exist.

If beach-nesting birds are already selecting smaller, isolated islands as replacements for large barrier islands for breeding, the protection of these islands becomes central to conservation management. A similarly viable management option over the long term is to create more artificial dredge-spoil islands. Presently, many of these alternative islands are being overlooked in the regulatory process, often excluded from coastal protection programs. The protection of many isolated islands of various types would benefit many species of waterbirds by allowing more colonies to become established thus reducing overcrowding at existing colonies (Lauro *et al.* 1992), reducing competition with other species such as gulls, and spreading the risks associated with stochastic events over more sites. Further, having many isolated islands would make alternative sites available in the event that mammalian predators colonize an existing breeding site. Existing islands should be managed to create

Table 4. Importance values (Ψ) and model-averaged effect sizes (β) for each explanatory variable appearing in the top models ($\Delta AIC_c < 2.0$) that describe the daily survival probability of American Oystercatcher clutches and broods in coastal New Jersey, USA (2005–2007).

Variables	Clutch models					Brood models				
	Ψ	β	SE	LCI	UCI	Ψ	β	SE	LCI	UCI
Year	0.57	–	–	–	–	0.18	–	–	–	–
2006	–	–0.13	0.19	–0.51	0.24	–	0.79	0.46	–0.11	1.69
2007	–	–0.37	0.23	–0.82	0.08	–	1.26	0.57	0.13	2.38
Site	0.57	–	–	–	–	0.37	–	–	–	–
SH	–	–0.30	0.37	–1.12	0.33	–	0.43	0.22	0.01	0.85
IB	–	–0.39	0.37	–1.03	0.44	–	–	–	–	–
Habitat	0.57	–	–	–	–	0.09	–	–	–	–
Island	–	0.86	0.30	0.27	1.45	–	0.00	0.00	0.00	0.00
Marsh	–	0.53	0.26	0.03	1.03	–	0.00	0.00	0.00	0.00
Gull	1.00	0.01	0.00	0.00	0.01	0.53	0.00	0.00	0.00	0.00
Mammal	1.00	–2.16	0.35	–2.84	–1.47	0.11	3.40	5.09	–6.59	13.38
Disturb	0.73	–0.39	0.56	–1.48	0.70	0.09	0.00	0.00	0.00	0.00
Nest height	1.00	0.63	0.13	0.37	0.88	0.09	0.00	0.00	0.00	0.00

optimal breeding habitat for a suite of ground-nesting species (e.g., remove vegetation or increase island height); however, any landscape management should be conducted outside of the breeding season for these species. Further research is needed to better understand site-specific habitat factors that could be managed in such a way as to make individual islands more productive breeding sites for American Oystercatchers and other beach-nesting species.

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