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Exploring Differences in Adult Survival and Site Fidelity of Migratory and Non-migratory American Oystercatcher (*Haematopus palliatus*) Populations

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Abstract.—The conservation of a species is reliant on identifying threats to critical vital rates such as survival and dispersal. Accurate estimates of these vital rates and the factors that affect them can be used to better manage populations. The USA Atlantic Coast population of American Oystercatchers (*Haematopus palliatus*) benefits from a large-scale conservation effort, but this long-lived species remains especially sensitive to fluctuations in adult survival. The model used here and 8 years of mark-resight data from three breeding populations with varying migration strategies from the United States (migratory: Massachusetts and New Jersey; non-migratory: South Carolina) were used to estimate adult survival and site fidelity. Results indicated a resident population in South Carolina with 100% of the breeding population wintering in that State, a migratory population in Massachusetts with the majority of individuals wintering in Florida (42%), and a partially migratory population in New Jersey with a portion of the breeding population overwintering in that State (33%). Annual adult survival did not vary among populations. Although the average estimate of adult survival was high (0.89), there was an apparent decline in adult survival (from 0.94 to 0.83) over the study period. Given strong site fidelity (0.91), adult mortality is a critical factor for the viability of local populations. *Received 3 October 2015, accepted 8 March 2016.*

Key words.—American Oystercatcher, Barker model, *Haematopus palliatus*, migratory connectivity, migratory strategies, partial migration, site fidelity, survival.

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Annual survival is often the most influential demographic parameter affecting population viability and growth rate in long-lived species (Doak *et al.* 1994; Davis 1999; Crone 2001; Roche *et al.* 2010). For long-lived shorebirds, survivorship may be the single most challenging parameter to accurately estimate under field conditions because individuals must be marked and followed for many years (Sandercock 2003). Even more challenging is attempting to relate migratory connectivity to annual survival because individuals must be marked and resighted in breeding and wintering areas that are often separated by very large distances. Annual survival may be even more influential in affecting fitness and population viability for migratory populations of shorebirds due to the costs associated with migration and threats experienced over a large geographic area (Pérez-Tris and Tellería 2002).

Survival between breeding seasons for migratory populations may be reduced because of the costs associated with migration, including high energy demands, increased risk of predation during migration, exposure to habitat changes over a larger geographic area, and exposure to inclement weather (Alerstam *et al.* 2003; Newton 2006; McKinnon *et al.* 2010; Alves *et al.* 2013). Further, intra-specific competition on limited stopover and wintering sites might be greater for migratory birds because resident individuals have a competitive advantage due to local territoriality, knowledge of sites, timing of arrival, or a combination of these factors (Drent *et al.* 2003; Newton 2006). Thus, survival of migratory populations may be expected to suffer due to intra-specific competition with resident populations at stopover and wintering sites (Pérez Tris and Tellería 2002). However, the benefits of migration may include increased reproduction or higher survival rates during the breeding period (Duriez *et al.* 2012; Sanz-Aguilar *et al.* 2012).

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Survival is typically estimated using Cormack-Jolly-Seber (CJS) models (Cormack 1964; Jolly 1965; Seber 1965). These models rely on resightings of live, marked individuals to estimate apparent, or local, survival (φ). Estimates of φ based on CJS models depend on the probability that an individual returns to the study area and is available for capture. Thus, estimates of survival (*S*) are confounded by the joint probability of apparent survival (φ) and site fidelity (*F*). This drawback of traditional CJS models can be dealt with using more advanced modeling approaches such as robust design models, multi-state models, and joint probability models (Sandercock 2006). Another model is one such joint probability model developed to remove the effect of permanent emigration from survival estimates (Barker 1997; hereafter Barker model). This model takes advantage of three sources of information: 1) resightings of birds during the capture period (e.g., breeding season); 2) resightings during the open interval between capture periods (e.g., nonbreeding season); and 3) recoveries of dead birds during the open interval. Recently, the Barker model has been used to estimate survival and site fidelity for a number of shorebird species (Sagar *et al.* 2002; Cohen *et al.* 2006; Stenzel *et al.* 2007; Ledee *et al.* 2010).

Recently, the Atlantic Coast population in the United States has benefited from a large-scale conservation effort with the goal of increasing the American Oystercatcher population. The focus has been primarily to increase reproductive success by managing human disturbance and predators, but the long-lived species remains especially sensitive to fluctuations in adult survival. In the first published account of apparent survival (φ) for American Oystercatchers, Nol *et al.* (2012) used CJS models to estimate φ from a historical dataset (1978-1983) for American Oystercatchers breeding in coastal Virginia. Nol *et al.* (2012) indicated that direct mortality and emigration likely both affected the survival rates in their study and suggested that the inclusion of movement data in analyses would be critical in understanding the role of site fidelity on survival. The large-scale conservation effort in recent years has led to an abundance of mark-recapture data for American Oystercatchers, and these data are especially suited for the Barker model to explore the effect of emigration on survival since it includes data from several sources spanning a large spatiotemporal scale.

Our main objectives were to: 1) estimate American Oystercatcher survival using a large dataset (8 years of mark-resight data) collected from three breeding populations: Massachusetts, New Jersey and South Carolina; 2) use a Barker model to separate survival (*S*) from site fidelity (*F*); and 3) explore differences in survival and site fidelity between migratory (Massachusetts and New Jersey) and non-migratory (South Carolina) populations of American Oystercatchers.

METHODS

Study Area

We studied American Oystercatcher breeding populations in three States along the Atlantic Coast of the United States: Massachusetts, New Jersey, and South Carolina. From early March into August, American Oystercatchers breed along the sparsely vegetated coastal zone, placing nests on sand and shell beaches, dunes, and salt marshes. During the nonbreeding season, American Oystercatchers primarily inhabit shell rakes and sand islands (Brown *et al.* 2005).

The Massachusetts portion of the study was conducted in Nantucket County (41° 14′ to 41° 23′ N, 69° 57′ to 70° 18′ W), which is made up of three islands: Nantucket, Tuckernuck, and Muskeget. This population represents one of the northernmost breeding populations of American Oystercatchers occurring along the Atlantic Coast of the United States (Murphy 2010). Breeders from the Massachusetts population are entirely migratory with no individuals overwintering within the State (Clay *et al.* 2014). The New Jersey portion of the study was conducted at breeding aggregations found in all coastal counties including Monmouth, Ocean, Atlantic, and Cape May (39° 04′ to 40° 11′ N, 74° 04′ to 74° 77′ W). Some breeders from the New Jersey population are migratory while others overwinter in the southern portion of the State. The South Carolina portion of the study was conducted in the Cape Romain Region, in Charleston County, defined as the coastal area of the State from Cape Romain National Wildlife Refuge south to Isle of Palms (32° 49′ to 33° 05′ N, 79° 20′ to 79° 45′ W). This entire region can be accessed only by boat. The Cape Romain Region supports about one-fifth (1,900 individuals) of the wintering American Oystercatcher population on the Atlantic and Gulf Coasts of the United States (Sanders *et al.* 2004;

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Brown *et al.* 2005). Migratory American Oystercatchers arrive in South Carolina in late August and leave as late as the beginning of April. American Oystercatchers from every Atlantic Coast State north of South Carolina with breeding season banding programs have been observed in the Cape Romain Region during the winter, and American Oystercatchers that breed in the Cape Romain Region apparently remain year round (Sanders *et al.* 2004).

Data Collection

In Massachusetts and New Jersey, surveyors identified breeding pairs by searching historical, known, and potential nesting areas for adult American Oystercatchers. Sites were visited regularly (every 2-7 days) except for locations with poor accessibility, and effort was comparable among States. After breeding pairs were discovered, nests were monitored until failure or young fledged. In South Carolina, most territories were only visited twice during the breeding season to band and search for previously banded birds. Nest monitoring did not occur. Breeding adults were banded on the territory using decoy, playback, and leg-hold noose mats (McGowan and Simons 2005) and whoosh net systems (Hawkseye Nets). In South Carolina, 33 individuals were captured using a cannon net during the nonbreeding season when American Oystercatchers were in flocks. We fitted each bird with a U.S. Geological Survey band on the tarsometatarsus and two identically coded Darvic wraparound color bands (Haggie Engraving, Inc.) on each tibiotarsus. In South Carolina, 23 American Oystercatchers were fitted with only one wraparound color band. The engraved codes were unique for every bird banded, and band colors were State-specific (Massachusetts = yellow, New Jersey = orange, South Carolina = blue) following protocols established by the American Oystercatcher Working Group (AOWG). Although American Oystercatchers exhibit sexual dimorphism, there was sufficient overlap in the morphometric characters to preclude separating males and females by body size (Carlson-Bremer *et al.* 2010). Consequently, we pooled sexes together. Nol *et al.* (2012) reported no support for sex effects on survival.

Observations of marked individuals were collected using three approaches. During the nesting season (March-July), trained monitors searched for breeding pairs and recorded the presence of marked individuals. Across the species' range, nonbreeding season surveys are conducted at various times throughout the year (August-February) along the Atlantic and Gulf Coasts of the United States (Brown *et al.* 2005). Although consistent breeding and nonbreeding season surveys represent the vast majority of observations collected, birdwatchers and citizen scientists also contributed a small number of incidental observations by submitting records to the AOWG website. If the report did not include a photo of the marked bird, researchers carefully scrutinized records for accuracy, redundancy, and completeness before being entered into the AOWG dataset. For this study, we excluded any incomplete or dubious records.

Analytical Approach

We calculated adult survival and site fidelity from all American Oystercatchers banded and resighted between the nesting season of 2005 and through the nonbreeding season of 2012-2013. We used the Barker (1997) model in Program MARK (White and Burnham 1999), a mark-recapture method that uses multiple types of encounter data for joint-analysis. Encounter categories were: 1) local encounters – banded birds captured or encountered within a breeding population during the breeding season (1 March-31 July); 2) nonbreeding encounters – banded birds encountered during the open interval (1 August-28 February); and 3) dead recoveries – bands collected from dead birds during any period. The Barker model estimates seven parameters as follows (Barker and White 2001): survival (S_i, probability that a bird alive at time i is alive at time $i + 1$, where i and $i + 1$ represent successive breeding seasons), breeding season detection probability (p_i, probability that a bird is captured or reported, given that it is alive at time i and within the study area), recovery probability (r_i, probability that a marked bird dies between time i and time $i + 1$ is reported), nonbreeding season resighting probability (R_i, probability that a bird remains alive between time i and time $i + 1$ is reported), resighting probability of nonsurvivors (R'_i, probability that a bird dies between time i and time $i + 1$ is reported before it died), site fidelity (F_i, probability that a bird at risk of capture at time i is at risk of capture at time $i + 1$), and temporary emigration (F'_i, probability that a bird not at risk of capture at time i is at risk of capture at time $i + 1$).

Our data included few dead recoveries and emigrants. For this reason, we only considered the corresponding parameters, r, R', and F', as constant through time. Following the model notations of Lebreton *et al.* (1992), we use subscripts: (t) to represent full temporal variation, (T) to include a linear trend across years, (c) to represent the absence of annual variation, and (state) to represent differences between breeding populations. Temporal models with a breeding population effect were incorporated as interactions, (state *t) and (state *T).

We defined a process of model selection of 100 *a priori* candidate models. For survival (S) and site fidelity (F), we considered all parameterization alternatives. There are no standardized protocols for breeding and nonbreeding season surveys of American Oystercatchers along the USA Atlantic and Gulf Coasts; however, protocols have been established in each of the States included in our study. As part of State protocols, the American Oystercatcher breeding populations in Massachusetts and New Jersey are consistently monitored with similar effort. The majority of breeding pairs in each State are regularly checked from the time they arrive (March) until they leave the area or join a nearby nonbreeding flock (August and September), thus increasing the chance of observing a marked individual. In South Carolina, breeding populations are surveyed and monitored by way of large scale single surveys corresponding with peak nesting intervals. The resightings

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of marked individuals were collected during the breeding season surveys. Nonbreeding season resightings of marked birds were primarily amassed from winter surveys that varied spatiotemporally in extent and methods throughout the species' range. However, the Barker model allows for this variation in obtaining 'incidental' resights during the open interval. Still, due to this variation in effort we considered parameterizations including a population effect, (state) and (state*t), for detection probabilities, p and R.

All models were created using a logit-link function, which constrains the parameter estimates between [0, 1]. During the model fitting process, the logit-link function fails to include parameters that approach the boundaries (White and Burnham 1999). For these cases, we manually adjusted the parameter number to appropriately reflect the model tested. We assessed the fit of these competing models using an information-theoretic approach (Burnham and Anderson 2002). To identify the best fitting model, we used Akaike's Information Criterion (AIC_c) adjusted for small sample size and overdispersion (quasi-likelihood AIC_c [$QAIC_c$]), which calculates the log-likelihood of the observed encounter histories given the model (i) and the number of parameters (K). We evaluated goodness-of-fit (GOF) between fitted models and the encounter data using a parametric bootstrap procedure (White and Burnham 1999). The bootstrap GOF test compares the observed deviance to 1,000 randomly generated replications, detects overdispersion in the data, and estimates a variance-inflation factor ($\hat{c}$) to correct the data. Although we apply a GOF test, it can lead to estimates of $\hat{c}$ that are biased high (White 2002). We used the model selection strategy recommended by Burnham and Anderson (2002) for selecting the best model from a set of candidate models. This approach recommends considering all models that are within two units ($\Delta AIC_c < 2$) from the model that minimized AIC_c. For parameters with temporal variation, we used a variance components approach to derive an estimate of the mean and the amount of process variation (σ) (White and Burnham 1999).

To investigate the migratory connectivity among breeding populations and winter locations, we defined the winter period from 1 December to 28 February (29 in leap years), inspected the location (i.e., State) of each encounter, and summed the total number of marked individuals observed. During the winter period, American Oystercatchers move between multiple sites within regions for roosting and foraging. We assumed that American Oystercatchers encountered during this window were observed as part of an overwintering statewide location.

RESULTS

Encounter Histories

We compiled the capture events and subsequent resightings for 396 (Massachusetts = 118; New Jersey = 128; South Carolina = 150) banded, breeding adult American Oystercatchers along the Atlantic Coast from the breeding season of 2005 to the nonbreeding season of 2012-2013 (Table 1). Our captures and resights included 2,280 encounters throughout the annual cycle from Massachusetts south to Florida; 949 of these encounters were during the breeding season. We only recovered six dead, adult American Oystercatchers over the study period. A portion, 12% (n = 346), of the individuals resighted during the nonbreeding season came from the fall period (August-November) in which marked individuals were observed in postbreeding flocks located in proximity to breeding territories or during southward migration.

Table 1. Number of captured and resighted American Oystercatchers observed in breeding populations from 2005-2012. Captures = number of birds trapped during the breeding season in year *i*; Resighted = number of birds trapped in year *i*-1 and resighted during the breeding season of year *i*; Total = total number of marked birds observed in the breeding population in year *i*.

	Massachusetts			New Jersey			South Carolina		
Year	Captures	Resighted	Total	Captures	Resighted	Total	Captures	Resighted	Total
2005	26	0	26	11	0	11	48	0	48
2006	32	22	54	11	10	21	33	30	63
2007	22	52	74	6	16	22	9	56	65
2008	15	62	77	30	19	49	22	50	72
2009	7	46	53	10	40	50	7	62	69
2010	6	52	58	25	46	71	6	64	70
2011	5	55	60	17	48	65	15	57	72
2012	5	45	50	18	52	70	10	65	75

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Parameter Estimation

The model selection process was corrected for small sample size and overdispersion using the estimated variance-inflation factor ($\hat{c}$ = 1.09). Model fitting indicated support for two models with $\Delta QAIC_c < 2$ and model weights of 0.58 and 0.39 (Table 2). The model that minimized $QAIC_c$ for our analysis included adult survival as a linear trend across years (S_T). Model 2, the only other candidate model within two $\Delta QAIC_c$ units, varied adult survival annually (S_t). This model differed by six additional parameters, so does not improve model fit (Burnham and Anderson 2002; Arnold 2010). Differences in breeding season detection probability varied among populations; however, the probability of detection during the nonbreeding season varied among populations and years.

Average adult survival across all years of the study was high (S = 0.89, σ = 0.013), but our parameter estimates revealed a decline over the study period (βs = -0.19, SE 0.056, CI = -0.29 – -0.076) (Table 3). This represents a 0.10 decline in adult survival from 2005-2011. Site fidelity, the probability that a marked American Oystercatcher returned to the same population to breed in the following year, was high (F = 0.91, SE = 0.016). The complement to site fidelity is permanent emigration (1-F). Therefore, this estimate indicates that approximately 9% of the breeding American Oystercatchers permanently emigrated from the study populations to regions where they were no longer detectable. The annual return of emigrants (F') was 0.24 (SE = 0.059).

The probability of detection during the breeding season was high among populations (p_{MA} = 0.98, SE = 0.018; p_{NJ} = 0.97, SE = 0.023; p_{SC} = 0.88, SE = 0.025). The probability of live resightings occurring during the open interval varied among years and populations (Table 4). Mean nonbreeding season detection probabilities varied somewhat among States (R_{MA} = 0.63, σ = 0.058; R_{NJ} = 0.78, σ = 0.039; R_{SC} = 0.53, σ = 0.070) (Fig. 1). Conversely, mean nonbreeding detection of American Oystercatchers that died during the nonbreeding season was considerably lower (R' = 0.34, SE = 0.052).

Migratory Connectivity

Birds breeding in Massachusetts were observed overwintering in every State of the winter range and most often observed in Florida. Over the course of this study, 42% (n = 98) of the resighted population was observed overwintering in Florida, primarily at Cedar Key on the Gulf Coast (Appendix). None of the marked American Oystercatchers breeding in Massachusetts were observed within the State during the winter period. In New Jersey, 33% (n = 106) of the birds breeding in the State remained for the winter period. New Jersey breeders also wintered throughout the range, including Florida (21%), with many individuals wintering at Cedar Key. The South Carolina population of American Oystercatchers appears resident. The South Carolina breeding population was never reported outside of the State at any point during the annual cycle. During the nonbreeding period, only two observa-

Table 2. Best supported and global models developed for estimating survival (*S*), breeding detection probability (*p*), nonbreeding detection probability (*R*), and site fidelity (*F*) for American Oystercatchers along the Atlantic Coast from 2005-2012. For each model, the following information is given: model rank and parametrization, differences in quasi-Akaike's Information Criterion values from the best fit model ($\Delta QAIC_c$), model weights (w_i), model likelihood, the number of parameters (K), and model deviance (QDev). Description of the characteristics for each parameter are the subscripts: c (constant effect), *t* (annual variation), *T* (linear trend), and state (population effect).

Model Rank	Model Parameterization	$\Delta QAIC_c$[a]	w_i	Model Likelihood	K	QDev
1	$S_T\ p_{state}\ R_{state*t}\ F_c$	0.00	0.581	1.000	33	1,727.06
2	$S_t\ p_{state}\ R_{state*t}\ F_c$	0.81	0.387	0.667	39	1,715.46
3	$S_c\ p_{state}\ R_{state*t}\ F_{state*t}$	9.11	0.006	0.011	52	1,696.64
100[b]	$S_{state*t}\ p_{state*t}\ R_{state*t}\ F_{state*t}$	478.31	0.000	0.000	93	2,078.11

[a]Corrected quasi-Akaike's Information Criterion using variance inflation factor ($\hat{c}$ = 1.09).
[b]Global model.

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Table 3. Model estimates, standard errors (SE), and confidence intervals (CI) for survival (S_t) and nonbreeding season detection probability ($R_{state*t}$) for adult American Oystercatchers (n = 396) along the Atlantic Coast from 2005-2012.

	Survival			Massachusetts Nonbreeding Detection			New Jersey Nonbreeding Detection			South Carolina Nonbreeding Detection		
Year	S	SE	CI	R_{MA}	SE	CI	R_{NJ}	SE	CI	R_{SC}	SE	CI
2005	0.938	0.014	0.906-0.960	0.599	0.102	0.393-0.774	0.727	0.140	0.401-0.914	0.542	0.080	0.386-0.690
2006	0.927	0.013	0.898-0.948	0.717	0.063	0.581-0.822	0.556	0.116	0.334-0.758	0.476	0.062	0.358-0.596
2007	0.913	0.011	0.889-0.932	0.763	0.052	0.647-0.850	0.708	0.097	0.492-0.858	0.600	0.062	0.475-0.713
2008	0.897	0.010	0.876-0.915	0.726	0.056	0.604-0.821	0.851	0.054	0.712-0.929	0.158	0.042	0.092-0.259
2009	0.879	0.010	0.857-0.897	0.337	0.060	0.232-0.462	0.850	0.051	0.721-0.925	0.694	0.054	0.580-0.789
2010	0.857	0.014	0.828-0.883	0.543	0.065	0.416-0.665	0.696	0.061	0.566-0.800	0.606	0.060	0.486-0.715
2011	0.833	0.021	0.787-0.871	0.723	0.065	0.581-0.831	0.853	0.047	0.737-0.924	0.644	0.060	0.521-0.751

tions were made of American Oystercatchers outside the study area but still in South Carolina.

In our three breeding populations, we observed no marked adults moving from one breeding population to another during subsequent breeding seasons. During the nonbreeding season, 88% (n = 396) of all marked American Oystercatchers were resighted (Appendix). In South Carolina, 95% (n = 150) of the birds were observed during the nonbreeding season. In the more migratory populations of Massachusetts and New Jersey, 89% (n = 248) of the marked individuals were detected during the nonbreeding season.

DISCUSSION

The survival rate for adult American Oystercatchers estimated using the Barker model was high in our study. Although there is no other estimate of survival for this species using the Barker model, breeding American Oystercatchers are characterized as having high site fidelity (Tomkins 1954; Murphy 2010; Schulte 2012), and therefore, discrepancies between survival and apparent survival are likely small. Our estimate of survival is comparable to the recent estimate of adult apparent survival by Nol *et al.* (2012) and is similar to previous survival estimates for other oystercatcher species (Goss-Custard *et al.* 1982; Harris and Wanless 1997; Sagar *et al.* 2002; Durrell 2007). Contrary to our expectations, however, survival was not correlated with migratory tendency as our breeding population covariate (state) did not show up in our top model.

Like many long-lived species, American Oystercatcher populations are greatly affected by small changes to demographic parameters associated with adults, namely survival and site fidelity (Davis 1999; Murphy 2010; Schulte 2012). In this study, adult survival showed a significant decline over the period studied, which could have catastrophic population effects over time. LeDee *et al.* (2010) described a similar trend for

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Table 4. Model estimates, standard errors (SE), and confidence intervals (CI) for site fidelity (F_c) and breeding season detection probability (p_{state}) for adult American Oystercatchers ($n = 396$) along the Atlantic Coast from 2005-2012.

Parameter	Notation	Estimate	SE	CI
Site fidelity	F_C	0.914	0.016	0.877-0.941
Massachusetts breeding detection	p_{MA}	0.978	0.018	0.895-0.996
New Jersey breeding detection	p_{NJ}	0.971	0.023	0.869-0.994
South Carolina breeding detection	p_{SC}	0.881	0.025	0.823-0.921

the Great Lakes population of Piping Plovers (*Charadrius melodus*) and emphasized the need to identify the source of decline. These trends highlight the need for greater understanding of adult survival and the factors acting on shorebirds throughout the annual cycle. Our study is a first step in better understanding American Oystercatcher survival and provides a baseline rate using an advanced modeling approach taking advantage of a unique dataset collected over a large geographic extent. Further analysis using a larger dataset collected over a broader spatiotemporal range could provide a closer look at the suggested decline witnessed in our study.

Breeding season detection probability was high in all populations; however, the rate was much higher for the migratory populations in Massachusetts and New Jersey. The high observed detection rates are likely a function of strong breeding site-propensity and encounter rate, the probability a bird is detected if present in the study area. The lower rate in South Carolina may be a function of reduced survey effort during the breeding season compared to the other States' monitoring programs. Alternatively, the differences in breeding season detection may result from lower breeding-site propensity in South Carolina than in Massachusetts and New Jersey. Intermittent breeding oc-

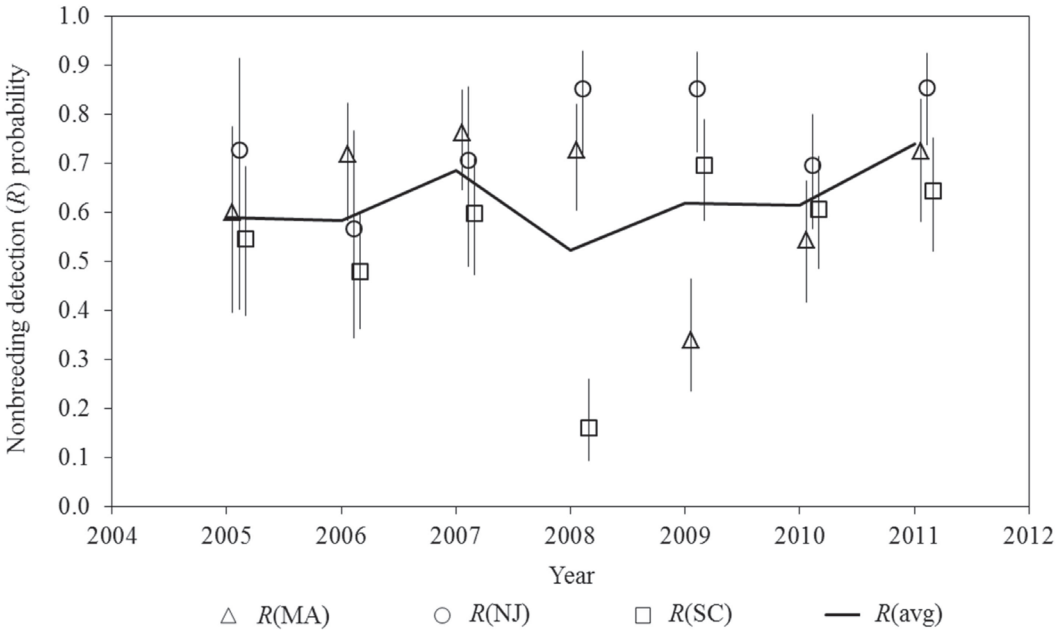


Figure 1. Estimated nonbreeding season detection probabilities for Massachusetts (R_{MA}), New Jersey (R_{NJ}), and South Carolina (R_{SC}) with 95% confidence intervals and average nonbreeding season detection probabilities (R_{AVG}) over time (line) for three populations of American Oystercatchers ($n = 396$) breeding along the Atlantic Coast from 2005-2012.

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curs in South Carolina, confirmed by observations of adults during the breeding season in nonbreeding flocks up to 25 km from the previous year's breeding site. Three banded American Oystercatchers nesting on Sandy Point were never seen again after the island completely eroded. This loss of habitat may decrease detection rates, because American Oystercatchers have to disperse when nesting sites erode, and may result in increased mortality. Detection probability during the nonbreeding season was also substantially lower in South Carolina, which is somewhat surprising since the birds in this population appear to be resident. However, most of the Cape Romain Region is difficult to access and can only be reached by boat. Thus, the large winter population combined with the remoteness of the American Oystercatcher roosts probably reduced detectability. In South Carolina, during the winter of 2008, not all barrier islands were searched for banded American Oystercatchers, thus resulting in lower detectability during that season. The highest nonbreeding detection rate was for the New Jersey population, which may be partially explained by an increase in winter effort to resight banded individuals during the study period both within the State and in Florida. In addition, the winter roost sites located within New Jersey are more accessible than sites in South Carolina and in other parts of the species' wintering range.

Breeding site fidelity was high across all populations following suit for shorebirds as a whole (Oring and Lank 1982; LeDee *et al.* 2010; Cohen and Gratto-Trevor 2011). In contrast, permanent emigration was quite low. Temporary emigration, while perhaps expected to some degree due to differences in breeding habitat quality (Bruinzeel 2007), was somewhat higher than expected (24%). We attribute this high rate to the local movement of American Oystercatchers in response to annual habitat changes on breeding grounds in dynamic coastal landscapes. Breeders, which typically exhibit strong site fidelity, likely move around the landscape as habitat is lost or created, and this local movement may be enough to have individuals move in or out of study plots among years. This has been observed for multiple individuals in New Jersey that shifted from inlet islands lost during storms in one year to saltmarsh islands that were nearby but off plot in the following year (T. Virzi, pers. commun.). Thus, the rate of temporary emigration is affected to some degree by shifts in monitoring effort over time if new sites in proximity to study plots are added into survey areas as the result of habitat changes. If individuals are not observed off-plot, but return to the study plot in a subsequent year perhaps due to improved habitat, the Barker model captures these observations in the estimation of the temporary emigration parameter. These data would lead to lower precision in survival estimates using traditional CJS models either by incorrectly coding the individuals as mortalities or by confounding detection probabilities.

The similar survival rates among the breeding populations studied goes against our hypothesis that the non-migratory South Carolina population would exhibit higher adult survival. We expected that this population would exhibit an elevated level of survival by not expending the energetic demands of migration shared by the Massachusetts and New Jersey populations (Duriez *et al.* 2012). Further, the South Carolina resident population might have been expected to have a competitive advantage over the other populations at stopover and wintering sites within the State due to earlier arrival or social dominance (Drent *et al.* 2003; Newton 2006). However, leapfrog migration, where the northernmost breeders migrate the farthest, occurs among shorebirds, including oystercatchers, and presumably the benefit of increased overwinter survival is worth the costs of migration (Pienkowski and Evans 1984; Boland 1990). Presumably, conspecific competition for food is lower and severe winter weather is less frequent at more southern wintering sites (Hulscher *et al.* 1996). Yet oystercatchers that do not migrate benefit from remaining near their nest site, and this may increase reproductive success or lead to positive carry-over effects in annual survival (Duriez *et al.* 2012; Garthe *et al.* 2012). It is also

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possible that migration theory based largely on the study of long-distance migrants does not hold true for partial short-distance migrants such as the American Oystercatcher despite limited evidence that it does (Sanz-Aguilar *et al.* 2012).

Another plausible explanation for the similar survival rates witnessed among our study populations could be the influence of the age structure of the populations. American Oystercatchers have been expanding their range northward in recent years (Mawhinney *et al.* 1999), and it is possible that the range expansion is at least partially driven by the dispersal of young individuals. The juvenile age class would be expected to have the lowest annual survival rates (Goss-Custard *et al.* 1982), but young breeders might show higher survival rates than older individuals. Our data provide some evidence that the Massachusetts and New Jersey populations may be younger because these individuals exhibited lower winter site fidelity, and this may be an indication of a younger population (Lok *et al.* 2011). We did not include age in our survival models because these data were not available for our breeding populations. We cannot rule out the possibility that annual survival for the more northerly populations was positively influenced by their age structure, which might offset the costs of migration. Future studies using a larger dataset might be able to examine the influence of the age structure of populations on survival rates.

The demographic consequences associated with different wintering or migratory strategies plays an important role in population dynamics (Gill *et al.* 2001; Dingle and Drake 2007; Chapman *et al.* 2011). Incorporating migratory connectivity into survival analyses using modern statistical methods allows for the derivation of more precise annual survival estimates, which may better inform demographic models. Our estimate of survival, while high, falls below the predicted estimate from demographic models that would be necessary to increase the American Oystercatcher population. Further, the suggested decline in survival over the study period suggests that despite the efficacy of efforts to increase breeding success, conservation efforts may benefit from improved understanding of the factors affecting adult survival. The recent conservation efforts across the American Oystercatchers' range by members of the AOWG have resulted in a robust dataset available for analysis using advanced mark-recapture methods. Further analysis of these data should help determine if our findings hold true over the species' entire North American range, and possibly identify those factors affecting annual survival.

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Appendix. Marked population, nonbreeding resightings, and State locations of winter resightings of American Oystercatchers (n = 396) breeding in three populations (Massachusetts, New Jersey, South Carolina) from 2005-2012.

			Winter Resightings by State[e]										
Breeding Site	Total Marked[a]	Nonbreeding Resightings[b]	Winter Resightings[c]	Multi-State Winter Resightings[d]	Florida	Georgia	Massachusetts	North Carolina	New Jersey	New York	South Carolina	Virginia	Total
Massachusetts	118	98 (83%)	81 (69%)	8 (10%)	37 (42%)	7 (8%)	0 (0%)	9 (10%)	4 (4%)	0 (0%)	16 (18%)	16 (18%)	89 (100%)
New Jersey	128	106 (83%)	80 (63%)	12 (15%)	19 (21%)	9 (10%)	0 (0%)	3 (3%)	30 (33%)	0 (0%)	15 (16%)	16 (17%)	92 (100%)
South Carolina	150	142 (95%)	142 (95%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	142 (100%)	0 (0%)	142 (100%)

[a]Number of adult American Oystercatchers marked with color leg bands.

[b]Number of marked individuals observed ≥ 1 during the nonbreeding season (August-March).

[c]Number of marked individuals observed during the winter window (1 December-28/29 February) in any State (fall resights excluded from data). Some individuals reported wintering in different States in different years.

[d]Individuals using two to three different States as wintering sites in different years (Massachusetts: birds observed in two States; New Jersey: two birds observed in three States; all others observed in two States).

[e]Number of marked individuals observed during the winter window by States.