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RESEARCH ARTICLE

Repeated count surveys help standardize multi-agency estimates of American Oystercatcher (*Haematopus palliatus*) abundance

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ABSTRACT

The extensive breeding range of many shorebird species can make integration of survey data problematic at regional spatial scales. We evaluated the effectiveness of standardized repeated count surveys coordinated across 8 agencies to estimate the abundance of American Oystercatcher (*Haematopus palliatus*) breeding pairs in the southeastern United States. Breeding season surveys were conducted across coastal North Carolina (90 plots) and the Eastern Shore of Virginia (3 plots). Plots were visited on 1–5 occasions during April–June 2013. *N*-mixture models were used to estimate abundance and detection probability in relation to survey date, tide stage, plot size, and plot location (coastal bay vs. barrier island). The estimated abundance of oystercatchers in the surveyed area was 1,048 individuals (95% credible interval: 851–1,408) and 470 pairs (384–637), substantially higher than estimates that did not account for detection probability (maximum counts of 674 individuals and 316 pairs). Detection probability was influenced by a quadratic function of survey date, and increased from mid-April (~0.60) to mid-May (~0.80), then remained relatively constant through June. Detection probability was also higher during high tide than during low, rising, or falling tides. Abundance estimates from *N*-mixture models were validated at 13 plots by exhaustive productivity studies (2–5 surveys wk^{-1}). Intensive productivity studies identified 78 breeding pairs across 13 productivity plots while the *N*-mixture model abundance estimate was 74 pairs (62–119) using only 1–5 replicated surveys $season^{-1}$. Our results indicate that standardized replicated count surveys coordinated across multiple agencies and conducted during a relatively short time window (closure assumption) provide tremendous potential to meet both agency-level (e.g., state) and regional-level (e.g., flyway) objectives in large-scale shorebird monitoring programs.

Keywords: American Oystercatcher, detection probability, *Haematopus palliatus*, population size, *N*-mixture models

Los muestreos de conteos repetidos ayudan a estandarizar las estimaciones de abundancia de *Haematopus palliatus* realizadas por múltiples agencias

RESUMEN

El extenso rango reproductivo de muchas especies de aves playeras puede hacer que sea problemático integrar los datos de estudio a escalas espaciales regionales. Evaluamos la efectividad de estandarizar los muestreos de conteos repetidos coordinados entre 8 agencias para estimar la abundancia de las parejas reproductivas de *Haematopus palliatus* en el sudeste de Estados Unidos. Los muestreos de la estación reproductiva fueron realizados en 93 parcelas a lo largo de la costa de Carolina del Norte (CN; 90 parcelas) y la costa este de Virginia (VA; 3 parcelas). Las parcelas fueron visitadas en 1 – 5 ocasiones durante abril y junio, 2013. Se usaron modelos *N*-mixtos para estimar la abundancia y la probabilidad de detección en relación a los datos de muestreo, la etapa de la marea y la localización de la parcela (bahía costera vs isla de barrera). La abundancia estimada de *H. palliatus* en el área muestreada fue de 1,048 individuos (95% de intervalo de credibilidad: 851 – 1,408) y de 470 parejas (384 – 637), substancialmente mayor que las estimaciones que no consideraron la probabilidad de detección (conteos máximos de 674 individuos y 316 parejas). La probabilidad de detección estuvo influenciada por una función cuadrática de la fecha de muestreo y aumentó desde mediados de abril (~0.60) hasta mediados de mayo (~0.80), para luego permanecer relativamente constante hasta

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junio. La probabilidad de detección también fue más alta durante la marea alta que durante las mareas baja, creciente o menguante. Las estimaciones de abundancia de los modelos *N*-mixtos fueron validadas en 13 parcelas por estudios detallados de productividad (2 – 5 muestreos semana^{-1}). Los estudios detallados de productividad identificaron 78 parejas reproductivas a lo largo de 13 parcelas de productividad mientras que la estimación de abundancia de los modelos *N*-mixtos fue de 74 parejas (62 – 119) usando solo 1 – 5 muestreos estacionales^{-1} replicados. Nuestros resultados indican que los muestreos de conteos repetidos estandarizados coordinados entre múltiples agencias y realizados durante un período de tiempo relativamente corto (supuesto de cierre) presentan un enorme potencial para alcanzar los objetivos a nivel de agencia (e.g., estado) y de región (e.g., ruta migratoria) en los programas de estudio a gran escala de las aves playeras.

Palabras clave: Haematopus palliatus, modelos *N*-mixtos, probabilidad de detección, tamaño poblacional

INTRODUCTION

Accurate information on population size and status are necessary for shorebird management and conservation efforts (Howe et al. 1989, Brown et al. 2005). Collaborative multi-agency monitoring programs can be especially beneficial for wide-ranging shorebird species that use areas under the jurisdiction of multiple local, state, or federal agencies. Survey methods that are standardized across collaborating agencies increase spatial coverage and improve inference of population-level dynamics (Lyons et al. 2012). Cooperative multi-agency monitoring programs provide tremendous potential to increase understanding of shorebird population dynamics, estimate range-wide abundance, and improve population-level conservation efforts (Howe et al. 1989, Brown et al. 2001, Davis et al. 2001, Brown et al. 2005, Lyons et al. 2012).

American Oystercatcher (*Haematopus palliatus*) is listed as a species of high concern in the U.S. Shorebird Conservation Plan (Brown et al. 2001) and a Focal Species by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2014). Schulte et al. (2007) outlined a conservation action plan for the eastern subspecies of American Oystercatchers (*H. palliatus palliatus*) that includes goals to monitor population status and estimate statewide and range-wide breeding season abundances. Numerous state, federal, and nongovernmental agencies monitor American Oystercatcher populations across their Atlantic and Gulf Coast breeding range (Davis et al. 2001, American Oystercatcher Working Group et al. 2012). Comprehensive range-wide breeding season abundance surveys, however, require collaboration among multiple agencies and organizations (Brown et al. 2001, Schulte et al. 2007). Doing so will require the development of breeding season survey methods that are easily standardized, scientifically sound, and address logistical constraints of the numerous participants.

Estimating the size of American Oystercatcher breeding populations (i.e. the number of breeding pairs; Davis et al. 2001) is difficult due to widely dispersed habitat, sparsely distributed breeding pairs, remote nesting locations, and time-intensive nest searching (Davis et al. 2001, Sanders et al. 2004, Wilke et al. 2005). Extrapolating well-designed local studies of American Oystercatchers into regional or range-wide estimates has also proven problematic due to discrepancies in survey methods and metrics among agencies (Davis et al. 2001, Wilke et al. 2005). For instance, American Oystercatcher breeding surveys do not consistently differentiate between confirmed and unconfirmed breeding pairs (Wilke et al. 2005). Confirmation of breeding requires intensive nest searching, which is often logistically limiting for large-scale breeding season surveys of solitary nesting shorebirds. Less intensive approaches (e.g., counts of territorial pairs using physical or behavioral cues; Wilke et al. 2005, Sanders et al. 2008) may provide useful information, but have yet to be validated as adequate approximations for the number of breeding pairs.

Recently developed *N*-mixture models using spatially and temporally replicated counts (Royle 2004) have shown tremendous potential for large-scale avian abundance studies (Royle 2004, Kéry et al. 2005), including studies of the related Black Oystercatcher (*H. bachmani*; Lyons et al. 2012). These models are useful for estimating abundance, detection probability, and covariate relationships using relatively easily collected replicated count data. We evaluated the effectiveness of repeated count surveys conducted by multiple cooperating agencies to estimate American Oystercatcher breeding pair abundance. Our objectives were to (1) estimate abundance of American Oystercatcher breeding pairs across areas of North Carolina and Virginia surveyed by multiple agencies, (2) evaluate covariates thought to influence abundance and detection processes during breeding season surveys, and (3) evaluate the use of less intensive count metrics (i.e. metrics that do not require nest searching) as approximations of breeding pairs, which require highly intensive nest searching surveys.

METHODS

Study Species

American Oystercatchers breed throughout eastern North America, from Maine to Florida on the Atlantic Coast and along the Gulf of Mexico (American Oystercatcher Working Group et al. 2012). North Carolina and Virginia are considered important breeding areas for American

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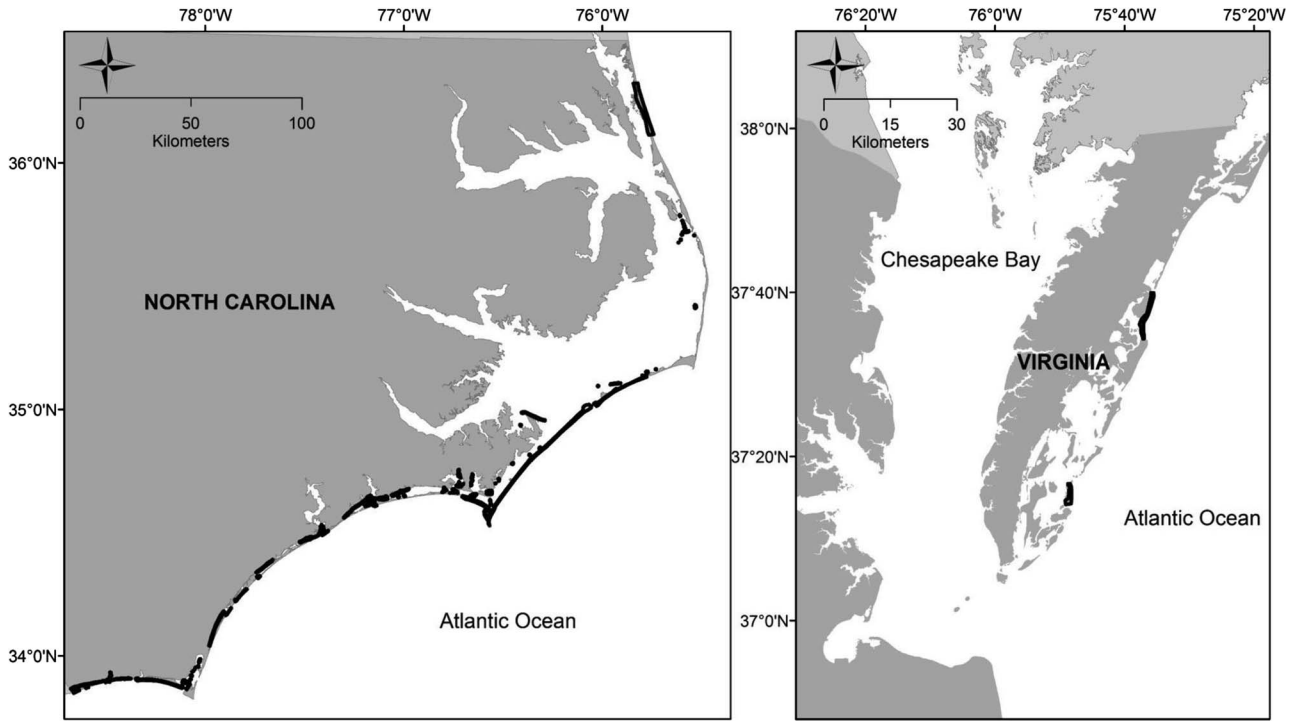


FIGURE 1. Areas surveyed for American Oystercatchers (black) in coastal North Carolina (left) and the Eastern Shore of Virginia (right), USA, during 2013.

Oystercatchers with some of the largest breeding populations for the species (Davis et al. 2001).

The first spring migrants to North Carolina and Virginia generally arrive during the last week of February to first week of March, with breeding activity initiated in early to mid-April (Davis et al. 2001, American Oystercatcher Working Group et al. 2012, Borneman et al. 2014). Average incubation is 27 days and pairs may renest if nests are lost. Average age of fledging is 35 days, with juveniles remaining dependent on adults for approximately 60 days post hatch (American Oystercatcher Working Group et al. 2012). Premigration flocks generally form during July and August (American Oystercatcher Working Group et al. 2012).

Study Area

Our study was conducted at 93 plots across coastal North Carolina (90 plots) and the Eastern Shore of Virginia (3 plots; Figure 1). Plots were selected based on published information of oystercatcher distribution in North Carolina and Virginia (Davis et al. 2001, Wilke et al. 2005) and ongoing shorebird monitoring programs in North Carolina and Virginia. Plots were located on barrier islands (31 plots) and coastal bays (62 plots) and included discrete islands, clusters of small islands, and sections of larger areas (large islands and mainland) that contained potential nesting habitat (Figure 1). Plots were delineated to allow a complete shoreline survey to generally be conducted in <3 hrs, but specific plot sizes varied from 3 to 1,097 ha (median $= 105$ ha). Plot boundaries were delineated by GPS coordinates. To facilitate standardization across repeated surveys, plot boundaries were often associated with identifiable landmarks (e.g., piers, buildings, access ramps).

Repeated Surveys

Multiple agencies collaborated to survey all 93 plots during the 2013 American Oystercatcher breeding season (April–July). Protocols for oystercatcher surveys generally followed those of the North Carolina Wildlife Resources Commission (R. Boettcher personal communication) and the Virginia Department of Game and Inland Fisheries (S. H. Schweitzer personal communication) with a few minor modifications to standardize methods across multiple agencies and address study-specific objectives (see below). In brief, observers conducted area searches of suitable nesting habitat within the plot boundaries and recorded oystercatcher detections. Breeding season surveys for American Oystercatchers often focus on quantifying the number of breeding pairs (Davis et al. 2001, Wilke et al. 2005, Traut et al. 2006, Wilke et al. 2007, Sanders et al. 2008). Confirmation of breeding, however, requires extensive nest searching that is logistically limiting for large-scale breeding surveys (Wilke et al. 2005). In this study, observers did not spend extra time to confirm breeding (e.g., search for eggs or chicks), but instead

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recorded 2 count statistics within each plot: total number of observed oystercatcher individuals and observed oystercatcher pairs. Oystercatcher individuals were simply the number of unique individuals observed during a survey. Oystercatcher pairs were defined as 2 birds that appeared associated with one another in space, or when a solitary oystercatcher was displaying nesting behavior indicating it was part of a pair. Behavioral cues used to identify pairs included observations of nesting (e.g., opportunistic observation of eggs or chicks) or nesting behavior, where nesting behavior included scraping, copulation, defensive behavior, or displaying (American Oystercatcher Working Group et al. 2012).

In total, 216 surveys were conducted from April 16 through July 31, 2013. Preliminary investigations, however, suggested that surveys in July may not have met the closure assumption required for single-season *N*-mixture models (see Results). Surveys in July were therefore excluded from all further summaries and analyses. The final dataset included 188 surveys conducted from April 16 through June 28, 2013. Plots were surveyed on 1–5 occasions (i.e. temporally replicated counts), with a mean of 2.0 surveys per plot. Personnel from 8 agencies collaborated to complete surveys: Audubon North Carolina, Cape Hatteras National Seashore, Cape Lookout National Seashore, North Carolina State University, North Carolina Wildlife Resources Commission, The Nature Conservancy of Virginia–Virginia Coast Reserve, U.S. Geological Survey–North Carolina Cooperative Fish and Wildlife Research Unit, and Virginia Department of Game and Inland Fisheries.

Statistical Analysis

We summarized the data such that $y_{i,j}$ is the count at plot i during survey j, or an NA for sites without full replication. The maximum number of repeat visits to any site was J=5. Following methods used for Black Oystercatcher surveys (Lyons et al. 2012), we used an *N*-mixture model with overdispersion in both detection probability and local abundance (Kéry and Royle 2010, Kéry and Schaub 2012, Lyons et al. 2012) due to the sparse and highly variable count data observed in this study. We ran the model described below twice, once where $y_{i,j}$ was the count of pairs and once where it was the count of individuals.

We modeled abundance (of pairs or individuals) as function of plot location (barrier island or coastal bay) and area (in hectares) such that:

$$N_i \sim Poisson(\lambda_i)$$

$$\log(\lambda_i) = \alpha_0 + \alpha_1 PL_i + \alpha_2 Log(A_i) + \varepsilon_i$$

$$\varepsilon_i \sim Normal(0, \sigma_\lambda^2)$$

where N_i is the local abundance at plot i, α_0 is the intercept, PL_i is the plot location (barrier island or coastal bay) for plot i, A_i is the area of plot i, and ε_i is a random error term for each site (Kéry and Royle 2010, Kéry and Schaub 2012).

Detection probability was modeled as a function of tide and date:

$$y_{i,j} \sim Binomial(N_i, p_{i,j})$$

$$\text{logit}(p_{i,j}) = \beta_0 + \beta_1 TR_{i,j} + \beta_2 TF_{i,j} + \beta_3 TL_{i,j} + \beta_4 DOY_{i,j} + \beta_5 DOY_{i,j}^{\ 2} + \delta_{i,j}$$

$$\delta_{i,j} \sim Normal(0, \sigma_p^2)$$

where $p_{i,j}$ is the survey and site-specific detection probability, β_0 is the logit-scale estimate of detection probability when all covariates were at zero (reference condition was high tide and mean survey date [May 24]); $TR_{i,j}$, $TF_{i,j}$, and $TL_{i,j}$ are the covariate values for rising, falling, and low tides, respectively, at site i during survey j; $DOY_{i,j}$ is the day of year at site i during survey j; and $\delta_{i,j}$ is a random error term for each site visit (Kéry and Royle 2010, Kéry and Schaub 2012).

We included tide as a 4-point categorical variable: high (+/− 1 hour from high tide), low (+/− 1 hour from low tide), rising (between low and high tide stages), or falling (between high and low tide stages), which were assigned at the beginning of each survey. Survey date (day of year [*DOY*]) was included as a quadratic term to investigate potential nonlinear trends in detection probability. For instance, detection of oystercatcher pairs may be reduced during early- and late-season surveys due to reduced occurrence of behavioral cues used to determine nesting (e.g., copulation, defensive behavior, displaying). Plot location was included as a categorical variable on abundance as previous studies suggested American Oystercatcher abundance may vary among barrier islands and coastal bay locations (Wilke et al. 2005). Day of year and log of plot area were treated as continuous variables and standardized by subtracting the mean and dividing by the standard deviation.

Implementation

N-mixture models were analyzed in a Bayesian framework using JAGS (Plummer 2003, Plummer 2012) accessed through R version 3.0.1 (R Core Team 2014). Vague priors were used for all parameters. Specifically, *Normal*(0,1000) priors were used for all regression parameters (α_x and β_x) and uniform distributions were used to constrain priors for σ_p(0,10) and σ_λ(0,10). We ran 3 parallel Markov chain Monte Carlo (MCMC) simulations. Each chain contained

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TABLE 1. Naïve (counted) and *N*-mixture abundance estimates (mean and 95% credible interval) of American Oystercatcher pairs and individuals for 93 surveyed plots across North Carolina and the Eastern Shore of Virginia. Naïve abundance estimates (Counted) are the sum of maximum plot counts.

		Pairs			Individuals		
	Plots	Counted	Mean	95% BCI	Counted	Mean	95% BCI
North Carolina	90	192	307	244–418	416	714	561–975
Virginia	3	124	164	129–251	258	334	266–527
Total	93	316	470	384–637	674	1,048	851–1,408

1,000 adaptation iterations, followed by 20,000 burn-in iterations, and 80,000 posterior iterations. Chain convergence was visually evaluated and verified using the Gelman-Rubin statistic ($\hat{R}$; Gelman et al. 2004). Posterior predictive checks (Kéry and Royle 2010, Kéry and Schaub 2012) indicated adequate model fit. We report results as posterior means and 2.5 and 97.5 percentiles of the posterior distribution for credible intervals (95% BCI).

Field Validation

A primary objective of this study was to evaluate the use of replicated counts of a proximate metric to estimate the actual number of breeding pairs. As part of this objective, we compared abundance estimates from *N*-mixture models to abundance estimates from independent territory mapping and productivity studies. Productivity studies were conducted independently from replicated count surveys and occurred at 13 of the same plots used during replicated count surveys (hereafter productivity plots). Productivity plots were located on the southern and central coast of North Carolina and included islands monitored by Audubon North Carolina, Cape Hatteras National Seashore, and Cape Lookout National Seashore. Productivity studies involved labor-intensive nest-searching surveys (2–5 visits per week) conducted throughout the entire nesting season to determine the number and location of oystercatcher breeding pairs in each plot. We compared *N*-mixture abundance estimates to the number of breeding pairs in each productivity plot to evaluate the use of these less-intensive metrics as approximations for the number of breeding pairs. Specifically, we evaluated (1) the proportion of plots where plot-specific *N*-mixture abundance credible intervals included the number of breeding pairs, and (2) if *N*-mixture abundance credible intervals for the sum of all 13 productivity plots included the total number of breeding pairs detected during productivity studies.

RESULTS

Repeated Surveys

Oystercatcher individuals and pairs were detected in 64 and 57 of the 93 surveyed plots, respectively. Naïve estimates of abundance (sum of maximum plot counts) were 674 individuals and 316 pairs (Table 1). Using *N*-mixture models, estimated abundance of individuals and pairs were 1,048 (95% BCI: 851–1,408) and 470 (95% BCI: 384–637), respectively (Table 1). In North Carolina (90 plots), the estimated abundance of individuals and pairs were 714 (95% BCI: 561–975) and 307 (95% BCI: 244–418), respectively (Table 1). In Virginia (3 plots), the estimated abundance of individuals and pairs were 334 (95% BCI: 266–527) and 164 (95% BCI: 129–251), respectively (Table 1).

Covariate effects on abundance were similar for both individual and pair counts (Table 2). Abundance increased as the log of plot area increased for both individuals (0.59; 95% BCI: 0.23–0.95) and pairs (0.59; 95% BCI: 0.21–0.99; Table 2). Mean per-plot abundance was also lower in coastal bay plots compared to barrier island plots for both individuals (–0.26; 95% BCI: −1.03 to 0.51) and pairs (–0.33; 95% BCI: −1.11–0.46), however credible intervals overlapped zero (Table 2). Unexplained variation in abundance (random site effects) was similar between counts of individuals ($\sigma_\lambda = 1.24$; 95% BCI: 0.93–1.61) and pairs ($\sigma_\lambda = 1.31$; 95% BCI: 1.00–1.71; Table 2).

Detection probability for both individuals and pairs was influenced by a quadratic function of survey date (Table 2 and Figure 2A). Mean predicted detection probability was lowest during mid-April surveys ($\leq$0.65) and higher during mid-May through late-June surveys (>0.80; Figure 2A). Effects of tide stage were also noticeable, with detection probability highest during high tide, and lower for all other tide stages (Table 2 and Figure 3). Detection probabilities for rising, falling, and low tide stages were, however, similar and credible intervals often overlapped (Table 2 and Figure 3). Unexplained variation in detection probability was similar for counts of individuals ($\sigma_p = 1.57$; 95% BCI: 0.98–2.20) and pairs ($\sigma_p = 1.23$; 95% BCI: 0.57–1.92; Table 2).

Preliminary analyses that included July surveys found a steep decline in detection probability during July (Figure 2B). Decreased late-season detection probability was consistent with a decline in observed territorial behavior (i.e. pairs still present but not observed). Breeding oystercatchers in this region, however, also form premi-

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TABLE 2. Covariate effects on abundance and detection probability of American Oystercatcher pairs and individuals (95% credible interval). α_0 is the log-scale mean plot abundance under reference conditions (barrier island plot, mean log area). β_0 is the logit-scale mean detection probability under reference conditions (high tide, mean survey day of year [May 24]).

	Pairs		Individuals	
	Mean	95% BCI	Mean	95% BCI
Abundance				
α_0 (barrier island, mean log area)	0.82	(0.14, 1.45)	1.69	(1.04, 2.27)
log(area)	0.59	(0.21, 0.99)	0.59	(0.23, 0.95)
Location - coastal bay plot	−0.33	(−1.11, 0.46)	−0.26	(−1.03, 0.51)
σ_λ	1.31	(1.00, 1.71)	1.24	(0.93, 1.61)
Detection				
β_0 (high tide, May 24)	1.50	(0.13, 3.00)	1.45	(0.01, 3.05)
DOY	0.22	(−0.16, 0.62)	0.35	(−0.03, 0.77)
DOY^2	−0.11	(−0.47, 0.26)	−0.15	(−0.52, 0.20)
Tide - rising	−1.85	(−3.34, −0.58)	−1.70	(−3.21, −0.36)
Tide - falling	−0.82	(−2.24, 0.47)	−0.95	(−2.47, 0.39)
Tide - low	−0.64	(−2.06, 0.72)	−1.28	(−2.90, 0.12)
σ_p	1.23	(0.57, 1.92)	1.57	(0.98, 2.20)

gration flocks as early as July (American Oystercatcher Working Group et al. 2012), which may result in individuals leaving a plot (i.e. lack of closure). Either hypothesis may explain the trend of declining detectability in July (Figure 2B). July surveys were therefore excluded from final analyses due to the possible lack of closure.

Validation

The number of breeding pairs in productivity plots ranged from 1 to 26, with a total of 78 breeding pairs across all 13 productivity plots (Figure 4). Naïve estimates of pairs (sum of maximum plot counts unadjusted for detection probability) was 62 pairs across these same plots (Figure 4). Total abundance estimates from *N*-mixture models were 74 pairs (95% BCI: 62–119) (Figure 4). Credible intervals for plot-specific *N*-mixture abundance estimates included the actual number of breeding pairs from territory mapping in 10 of 13 (77%) productivity plots (Figure 4).

DISCUSSION

Abundance estimation using spatially and temporally replicated count surveys and an *N*-mixture modeling framework has proven particularly valuable for large-scale avian abundance studies (Royle 2004, Kéry et al. 2005, Kéry 2008, Lyons et al. 2012). Our study demonstrates the utility of replicated counts, conducted by multiple collaborating agencies across a large geographic area in estimating the abundance of a shorebird of conservation concern. Covariate relationships identified in this work provide important insights for studies designed to estimate oystercatcher abundance. Repeated counts worked especially well in this study due to the ease of standardization across agencies and observers, and the application of *N*-mixture models to account for imperfect detection during surveys.

Imperfect detection is a common challenge in ecological field studies (Williams et al. 2002). Recent studies investigating American Oystercatchers and Black Oystercatchers indicate that detection probability is consistently <1.0 and may also be affected by environmental variables (Brown et al. 2005, Lyons et al. 2012, this study). Tide stage has been cited as a factor influencing detection of oystercatchers (Brown et al. 2005, Sanders et al. 2008). For instance, oystercatchers may be less dispersed across foraging areas during high tide (Sanders et al. 2008). Quantifying the influence of tide stage on detection probability is difficult as tide height varies continuously within a survey, but is only recorded once for a survey. Based on ancillary information and communication with observers, in our study, a small number of surveys would have started in one tide stage but ended in another (e.g., high to falling). This likely reduces our ability to detect differences across tide stages. One method to address this would be to limit survey duration so that tidal stage is more constant within a survey or to subdivide the survey and record tidal information more frequently. Overall, our results support hypotheses of increased detection probability during high tides (Brown et al. 2005, Sanders et al. 2008), but similar to results for Black Oystercatchers (Lyons et al. 2012), differences among tide stages were not always significant.

Survey date was an influential covariate affecting detection probability in our study. Lower detection of oystercatcher pairs during early-season surveys likely reflects oystercatcher nesting chronology. Behavioral cues used to identify oystercatcher pairs (e.g., copulation,

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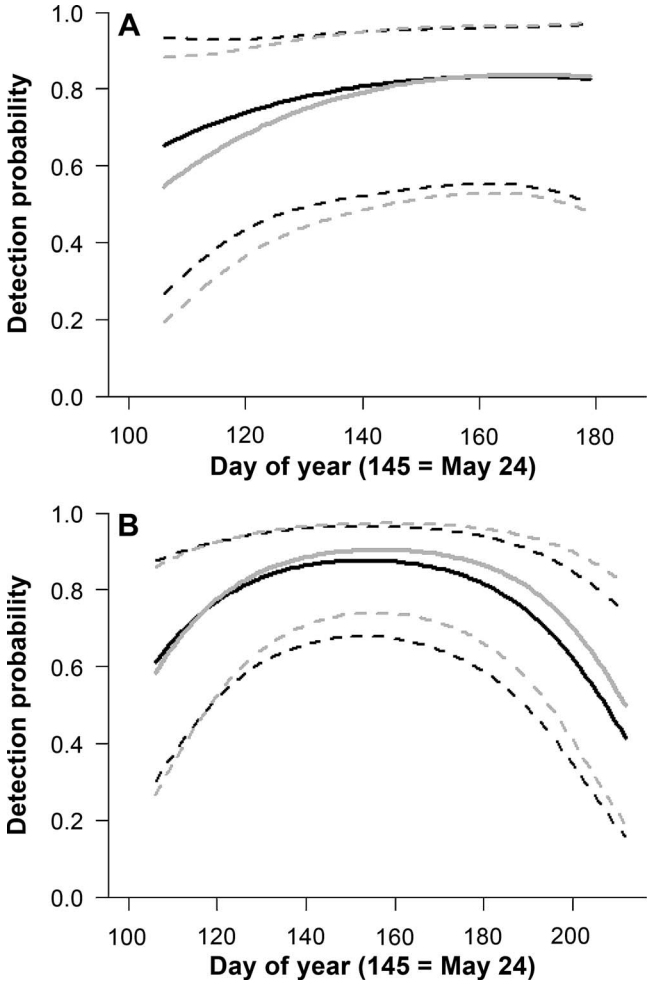


FIGURE 2. Estimated probability of detecting American Oystercatcher pairs (black) or individuals (gray) as a quadratic function of date. The closed period used for final analysis (**A**) included April 16 to June 28. Preliminary investigation of the entire survey period (**B**; April 16 to July 31) suggested a possible lack of closure in July. Values are presented for the high tide stage. Dashed lines denote 95% credible intervals. Note different x-axes.

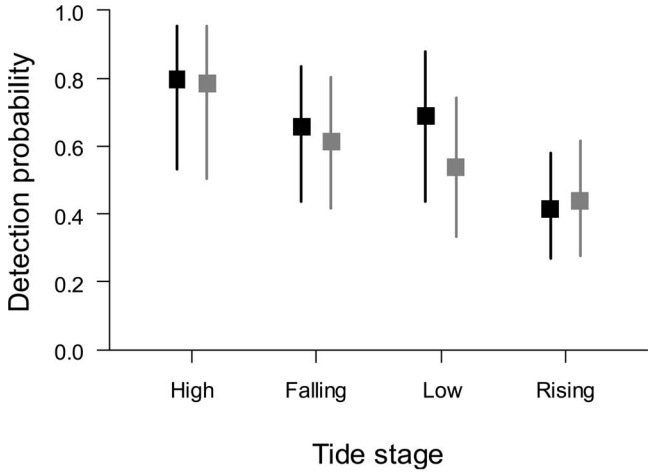


FIGURE 3. Estimated probability of detecting American Oystercatcher pairs (black) or individuals (gray) as a function of tide stage. Values are presented for the average survey date (May 24).

defensive behavior, displaying) may be less obvious before nesting (early season). Similarly, we applied a closed population *N*-mixture model, which assumes closure to changes in abundance during the survey period. We excluded surveys in July as preliminary analyses detected a strong decline in detection probability during July, which may have resulted from reduced territoriality, movements of birds off of plots in preparation for migration (i.e. lack of closure), or a combination thereof. Assumptions of closure in the remaining months (mid-April through June) were supported by the breeding chronology of oystercatchers in this region (Davis et al. 2001, American Oystercatcher Working Group et al. 2012, Borneman et al. 2014) and data from intensive nest monitoring studies that indicated little change during this period. Overall, our results indicate that multiple replicated surveys conducted during a several-week period near the peak of the breeding season provide several advantages in estimating oystercatcher abundance, including increased detection probability and minimizing violations of the closure assumption (Royle 2004, Lyons et al. 2012).

Abundance of breeding pairs is an important management metric in many avian monitoring programs. Breeding season abundance estimates of American Oystercatchers often focus on quantifying the number of breeding pairs (Davis et al. 2001, Wilke et al. 2005, Traut et al. 2006, Wilke et al. 2007, Sanders et al. 2008). Study-specific objectives and logistical constraints, however, often prevent intensive nest searching during oystercatcher breeding season surveys (Wilke et al. 2005, Sanders et al. 2008). Comparisons of exhaustive nest-searching studies and estimates of pairs based on repeated counts suggest that these metrics may be an adequate approximation for breeding pairs. Less intensive count metrics succeeded in covering the total number of breeding pairs in most productivity plots, successfully estimated the total number of breeding pairs, and generally outperformed naïve metrics (e.g., raw count data) at estimating breeding-pair abundance.

Estimates of oystercatcher individuals and pairs had similar levels of unexplained variation in abundance and detection. Unexplained variation in detection may have been due to unmodeled differences in weather conditions, observer effects, or variation in survey effort across agencies or personnel (Lyons et al. 2012). Similarly, unexplained variation in abundance could be caused by variation in habitat, predation pressure, or disturbance, which affect oystercatcher breeding populations but are

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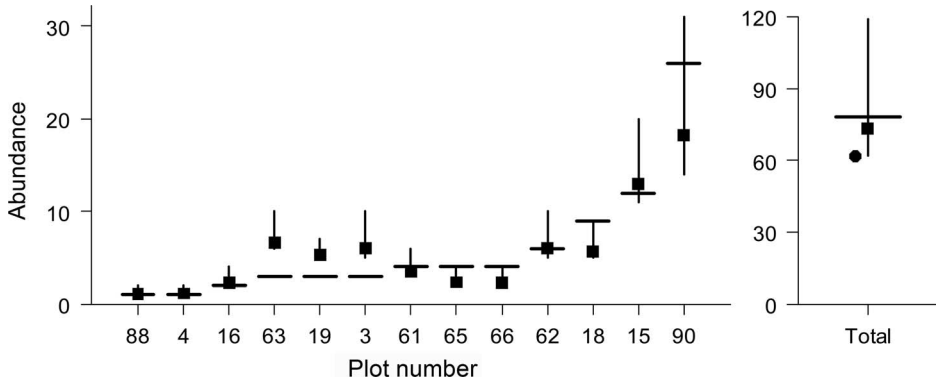


FIGURE 4. Estimated abundance of American Oystercatcher pairs (black squares) from *N*-mixture models and the number of breeding pairs from intensive productivity monitoring (black horizontal bars) at 13 productivity plots in North Carolina. Results are plot specific (left) and the sum of all 13 productivity plots (right). Error bars represent 95% credible intervals of the posterior distributions. Naïve estimates for total breeding pair abundance (sum of maximum count) is shown as a filled circle in the right panel.

difficult to quantify in coastal ecosystems (McGowan et al. 2005, Borneman et al. 2014). Use of previously described plot boundaries (e.g., International Shorebird Survey or other local and regional studies) was logistically helpful, but resulted in noticeable variation in plot size and survey duration. Fitting more complex models was hindered by the low average number of replicated surveys in this study (mean of 2.0 surveys per plot), which was on the lower end of the recommended average number of replicated surveys (2–5 surveys per plot; Kéry et al. 2009). Inclusion of random effects on both abundance and detection provided a reasonable method to address unexplained variation and develop an adequately fitting model, however, this approach resulted in decreased precision of abundance estimates (Kéry and Royle 2010, Kéry and Schaub 2012). Increasing the average number of replicated surveys (Kéry et al. 2009), reducing variation in plot size, standardizing study designs (e.g., similar protocols and training for all agencies; Lyons et al. 2012), and identifying important factors influencing abundance and detection will each improve future estimates of regional and range-wide oystercatcher abundance.

Direct comparisons between our results and previous oystercatcher surveys in the southeastern United States are confounded by 3 important methodological differences: spatial extent, detection probability, and definitions of unconfirmed breeders. First, spatial extent of American Oystercatcher breeding season surveys vary considerably across years and regions (Davis et al. 2001, Wilke et al. 2005). Wilke et al. (2005) demonstrated how expanding the spatial extent of breeding season surveys in Virginia dramatically increased the number of oystercatchers detected. Nonrandom selection of plots in our study prevented inferences beyond the surveyed plots. Future survey designs will need to include random selection of plots to draw inference to the larger population of American Oystercatchers at state or regional levels (Lyons et al. 2012). A second difference in this study was the ability of *N*-mixture models to incorporate imperfect detection, which many previous breeding season American Oystercatcher abundance studies were unable to address (Davis et al. 2001). As shown in this and other studies, maximum counts underestimated breeding pairs and were not equivalent to abundance estimates that accounted for detection probability (Kéry et al. 2005, Lyons et al. 2012). Overall, abundance estimates in this study support previously published estimates of American Oystercatcher abundance in North Carolina (300 pairs in 1999 [Davis et al. 2001]) and Virginia (255 pairs in 1999 [Davis et al. 2001] and 588 pairs in 2003 [Wilke et al. 2007]), 2 states that support a large portion of the eastern U.S. breeding population (Davis et al. 2001, Wilke et al. 2005, Wilke et al. 2007). Statewide oystercatcher abundance during the 2013 breeding season, however, was likely larger than presented in this study as our results only apply to surveyed plots.

Well-designed local studies of American Oystercatchers often meet their intended objectives. Combining results from independent studies may not directly translate into comprehensive range-wide abundance estimates due to differences in study-specific objectives, metrics, and methods (Davis et al. 2001, Wilke et al. 2005). Our results support conclusions of recent studies that indicate a need for standardized methods to estimate statewide and range-wide American Oystercatcher abundance (McGowan et al. 2005, Wilke et al. 2005, Sanders et al. 2008). In this study, standardized surveys involving multiple agencies using relatively inexpensive replicated count data and estimates of detection probability provided abundance estimates that complemented previous breeding season surveys and identified important factors influencing oystercatcher abundance and detection (Mawhinney et al. 1999, Brown et al. 2001, Davis et al. 2001, Wilke et al. 2005).

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Standardized replicated count surveys provide tremendous potential to meet both agency-level (e.g., state) and regional-level (e.g., flyway) objectives in large-scale oystercatcher monitoring programs and are applicable to many other studies investigating abundance and population dynamics.

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