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Managing American Oystercatcher (*Haematopus palliatus*) Population Growth by Targeting Nesting Season Vital Rates

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Abstract.—In populations of long-lived species, adult survival typically has a relatively high influence on population growth. From a management perspective, however, adult survival can be difficult to increase in some instances, so other component rates must be considered to reverse population declines. In North Carolina, USA, management to conserve the American Oystercatcher (*Haematopus palliatus*) targets component vital rates related to fecundity, specifically nest and chick survival. The effectiveness of such a management approach in North Carolina was assessed by creating a three-stage female-based deterministic matrix model. Isoclines were produced from the matrix model to evaluate minimum nest and chick survival rates necessary to reverse population decline, assuming all other vital rates remained stable at mean values. Assuming accurate vital rates, breeding populations within North Carolina appear to be declining. To reverse this decline, combined nest and chick survival would need to increase from 0.14 to ≥ 0.27 , a rate that appears to be attainable based on historical estimates. Results are heavily dependent on assumptions of other vital rates, most notably adult survival, revealing the need for accurate estimates of all vital rates to inform management actions. This approach provides valuable insights for evaluating conservation goals for species of concern. Received 10 October 2015, accepted 23 June 2016.

Key words.—American Oystercatcher, component vital rates, *Haematopus palliatus*, population viability, stage-based matrix model.

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Wildlife managers are often faced with taking action to protect threatened species even when little is known regarding the efficacy of these actions in restoring threatened populations. Actions targeting different age classes within a population can provide very different contributions to overall population growth (λ). In long-lived species, vital rates associated with adult survival often have the greatest influence on population growth (Crouse *et al.* 1987; Saether and Bakke 2000). However, vital rates with the greatest influence on population growth (i.e., with the greatest elasticity) are characteristically less variable (Gaillard *et al.* 1998; Pfister 1998). Vital rates with the greatest elasticity may be the most difficult for management actions to change due to their canalization, while the high variability of vital rates with lower elasticity may be more difficult to predict but more easily manipulated. Knowledge of each vital

rate and its influence on overall population growth is key to maximizing the efficacy of management actions.

American Oystercatchers (*Haematopus palliatus*) are subject to numerous threats existing in coastal habitats, each varying in its degree of impact to the species' various life stages. A population viability analysis (PVA) on the American Oystercatchers in North Carolina, USA, from 1998 to 2007 revealed a declining population ($\lambda < 1.0$; Schulte 2012). Adult survival was identified as having the greatest effect on population growth rates (Davis 1999; Schulte 2012). However, American Oystercatcher adult survival is often high (≥ 0.92) and not easily manipulated (Davis 1999; Schulte 2012; Ens and Underhill 2014).

Managers in North Carolina and throughout the American Oystercatcher's range often focus on increasing fecundity, defined as the number of chicks fledged

per pair (American Oystercatcher Working Group and National Fish and Wildlife Foundation 2008; Clay *et al.* 2010). Such management actions (e.g., predator removal and beach closures) target specific components (i.e., component vital rates) of fecundity, such as nest survival and chick survival. Increased recreational activity and predator abundance on beaches negatively influences both nest and chick survival (McGowan *et al.* 2005b; McGowan and Simons 2006; Sabine *et al.* 2006; Martin *et al.* 2010).

Here, we developed a demographic PVA to investigate the influence of nesting season

vital rates (nest survival and chick survival) on North Carolina's American Oystercatcher population growth rate (λ). Based on historic estimates of nest and chick survival in the region, we evaluated the effectiveness of targeting these vital rates in reversing the decline of the American Oystercatcher population in North Carolina.

METHODS

Study Area

American Oystercatcher breeding season studies were conducted across coastal North Carolina, USA, from 1995 through 2013 (Fig. 1). Monitoring locations

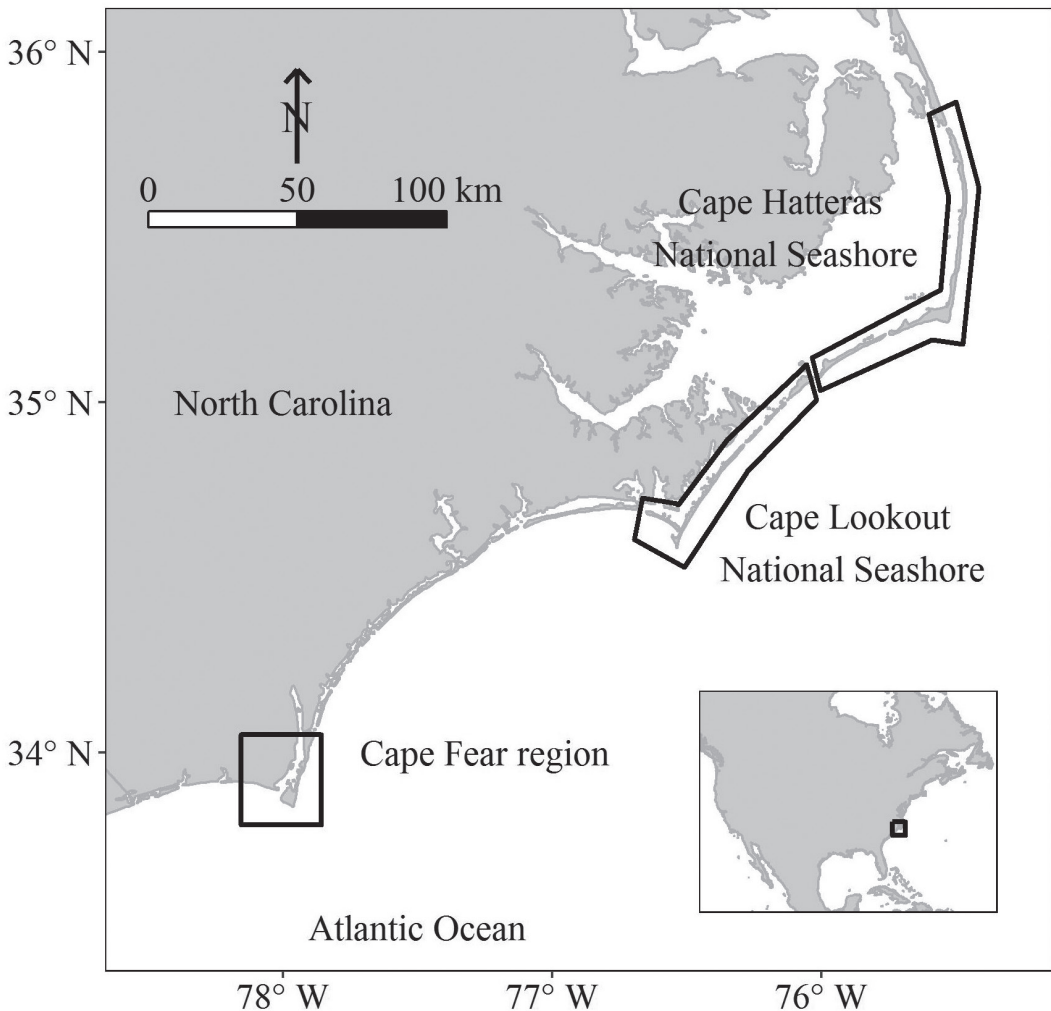


Figure 1. Regions of coastal North Carolina, USA, surveyed for breeding American Oystercatchers for ≥ 1 season, 1995–2013. Monitored islands were generally classified into one of three regions: Cape Fear, Cape Lookout National Seashore, or Cape Hatteras National Seashore.

were divided into three general regions: Cape Fear, Cape Lookout National Seashore, and Cape Hatteras National Seashore (Fig. 1). Monitored islands were primarily barrier islands, but also included a small number of sound-side and coastal bay islands (Simons and Stocking 2011).

Life-stage Model

Young American Oystercatchers that fledge here may return to their natal region as second-year birds, following their first winter. However, there are no records of individuals breeding until year three, with many individuals not breeding until after their third year (Ens *et al.* 1995; McGowan *et al.* 2005a). We developed a three-stage, female-based matrix model to summarize demographic rates for American Oystercatchers breeding in North Carolina (Table 1). Life stages included: 1) immature (2nd year birds); (2) sub-adult (> 2nd year, non-breeding birds); and (3) adults (breeders) (Table 1). Overall, eight component vital rates were included as part of the matrix (Table 1), with mean estimates of stage-specific vital rates compiled from the literature or estimated as part of this study (Tables 2 and 3). Where possible, component vital rates were derived from studies in North Carolina (Table 2). Data for several vital rates, however, were unavailable, in which case literature sources were used to provide approximate values (Table 2).

Vital rates. Mean component vital rates are presented in Table 2. Mean American Oystercatcher clutch size in North Carolina (β ; the average number of eggs per breeding female) was 2.35 (Schulte and Simons 2015). Nest survival (ϕ_n) was defined as the probability of a nest surviving from when the first egg was laid through hatching (successful if ≥ 1 egg hatched). Simons and Stocking (2011) estimated a mean nest survival probability of 0.29 using data from 13 islands across North Carolina from 1995 to 2011. Re-nesting probability (R_i) was defined as the proportion of failed nests that resulted in a subsequent nest attempt. American Oystercatchers in North Carolina will occasionally re-nest up to four times within a season (Schulte 2012). We considered three nesting attempts (two re-nests; Murphy 2010). Though Murphy (2010) found that survival rates for re-nests in Massachusetts, USA, were significantly lower than survival rates for initial nests of the season, this has not been observed in North Carolina's American Oystercatchers (Appendix). We maintained consistent nest survival across all three nest attempts (Tables 1 and 2). Hatching rate (H) was defined as the proportion of eggs in successful nests that hatched (Taylor *et al.* 2012). We used the same dataset as Simons and Stocking (2011) supplemented with additional 2012-2013 data to calculate hatching rates (Tables 2 and 4). In total, 934 successful nests were monitored from 1999 to 2013, with a mean annual hatching rate of 0.75 (Tables 2 and 4). Mean chick survival (probability of survival from hatch to fledging [35 days post hatching]) averaged 0.48 for American Oystercatchers nesting in North Carolina from 1995 to 2011 (Table 2; Simons and Stocking

Table 1. American Oystercatcher three stage life-history component vital rate matrix (pre-birth pulse census) and baseline (mean) matrix element values. Component vital rates included mean clutch size (β), hatching rate (H), nest survival (ϕ_n), probability of re-nesting after first failed nest (R_1), probability of re-nesting after second failed nest (R_2), chick survival (ϕ_c), juvenile survival (ϕ_j), immature survival (ϕ_i), sub-adult survival (ϕ_s), adult survival (ϕ_a), and sub-adult to adult transition probability (ψ_a ; see Table 2 for mean component vital rate values). Fecundity, or chicks fledged per breeding female, is defined by the formula $\beta * [\phi_n + (1 - \phi_n)R_1\phi_n + (1 - \phi_n)^2R_1R_2\phi_n] * H * \phi_c$. Life-stages included immature (birds that successfully survived their 1st year), sub-adult (year 2+ non-breeding birds), and adults (year 3+ breeding birds).

Element Type	Stage			Sub-adult		Adult	
Vital Rate Formulas	Immature	Sub-adult	Adult	0		$0.5 * (\beta * [\phi_n + (1 - \phi_n)R_1\phi_n + (1 - \phi_n)^2R_1R_2\phi_n] * H * \phi_c) * \phi_j$	
				ϕ_i		0	
				0		ϕ_a	
Baseline Values	Immature	Sub-adult	Adult	0		$0.5 * (0.38) * 0.50$	
				0.80		0	
				0		0.92	

Table 2. Mean component vital rates for American Oystercatchers breeding in North Carolina, USA. We provide the standard deviations (SD) for each estimate, as available, though these values are not used in the model. The regions where data were collected and sources for those results are also provided. Where values are not applicable, “N/A” is written within the cell.

Parameter	Definition	Mean	SD	Region	Source
β	Clutch size	2.35	0.01	North Carolina, USA	Schulte and Simons (2015)
ϕ_n	Nest survival (27 days)	0.29	0.01	North Carolina, USA	Simons and Stocking (2011)
R_1	Re-nesting probability 1	0.60	0.11	North Carolina, USA	This study ^a ; Simons and Stocking (2011)
R_2	Re-nesting probability 2	0.34	0.13	North Carolina, USA	This study ^a ; Simons and Stocking (2011)
H	Hatching rate	0.75	0.06	North Carolina, USA	This study ^b ; Simons and Stocking (2011)
ϕ_c	Chick survival (35 days)	0.48	0.01	North Carolina, USA	Simons and Stocking (2011)
ϕ_j	Juvenile survival (10 months)	0.50	N/A	Europe	Ens and Underhill (2014)
ϕ_i	Immature survival (annual)	0.80	N/A	Europe	Ens and Underhill (2014)
ϕ_s	Sub-adult survival (annual)	0.92	N/A	N/A ^c	N/A ^c
ψ_{sa}	Transition from sub-adult to adult (annual)	0.15	0.13 ^d	Europe	0.11 from Safriel <i>et al.</i> (1984); 0.19 from Ens <i>et al.</i> (1995)
ϕ_a	Adult survival (annual)	0.92	0.03	North Carolina, USA	Schulte (2012)

^aSee Table 3.

^bSee Table 4.

^cValue assumed to be equal to adult survival as per Schulte (2012).

^dSome variation in this estimate may be due to differences in sampling methods between studies.

Table 3. Observed re-nesting probabilities for monitored American Oystercatcher nests in North Carolina, USA, 1997-2013. Re-nesting probability was defined as the number of pairs that laid an additional nest, following the failure of their previous nest prior to hatching, divided by the total number of failed nests (Murphy 2010). The annual means are the arithmetic means of annual re-nesting probabilities. Data are from Simons and Stocking (2011) and supplemented with North Carolina 2012-2013 nest records.

Year	Initial Nests	Initial Nests Failed	First Re-nests	Probability of First Re-nest (R_1)	First Re-nests Failed	Second Re-nests	Probability of Second Re-nest (R_2)
1997	23	21	9	0.43	8	2	0.25
1998	58	53	28	0.53	26	9	0.35
1999	108	83	47	0.57	42	10	0.24
2000	91	58	29	0.50	25	2	0.08
2001	95	71	47	0.66	33	12	0.36
2002	109	79	60	0.76	48	12	0.25
2003	133	93	58	0.62	45	17	0.38
2004	81	34	24	0.71	14	3	0.21
2005	80	53	22	0.42	10	5	0.50
2006	73	42	24	0.57	16	3	0.19
2007	85	65	39	0.60	25	9	0.36
2008	80	61	33	0.54	26	10	0.38
2009	178	99	47	0.47	37	7	0.19
2010	167	85	50	0.59	36	16	0.44
2011	109	59	40	0.68	31	15	0.48
2012	85	41	32	0.78	28	14	0.50
2013	211	142	101	0.71	69	38	0.55
Annual mean (SD)				0.60 (0.11)	0.35 (0.13)		

2011). Together, these values resulted in an average fecundity of 0.38 (often referred to as chicks fledged per pair; Table 1; Simons and Stocking 2011).

Table 4. Annual hatching rate (H) for monitored American Oystercatcher nests in North Carolina, USA, 1999-2013. Hatching rate was defined as the proportion of eggs in successful nests that hatched (Taylor *et al.* 2012). The annual mean is the arithmetic mean of all annual hatching rates. Data are from Simons and Stocking (2011) and supplemented with North Carolina 2012-2013 nest records.

Year	Successful Nests	Successful Nest Eggs	Total Chicks	Hatching Rate
1999	30	66	48	0.73
2000	41	117	96	0.82
2001	42	94	77	0.82
2002	44	109	81	0.74
2003	58	141	108	0.77
2004	59	155	125	0.81
2005	45	104	85	0.82
2006	40	106	80	0.75
2007	36	86	66	0.77
2008	30	73	54	0.74
2009	98	260	171	0.66
2010	108	294	218	0.74
2011	122	321	225	0.70
2012	83	233	166	0.71
2013	114	275	176	0.64
Annual mean (SD)				0.75 (0.06)

No published estimates of American Oystercatcher juvenile survival (ϕ_j), immature survival (ϕ_i), or sub-adult to adult transition probabilities (ψ_{sa}) were available, so we supplemented these values with those published for Eurasian Oystercatchers (*H. ostralegus*) (Ens and Underhill 2014). This species is well studied (Ens *et al.* 2014) and shares many life-history traits with American Oystercatchers. Both exhibit delayed maturity (not breeding until year three), long-distance winter migration, variable natal-site fidelity as immature individuals, and high adult survival (Ens *et al.* 1995, 2014; McGowan *et al.* 2005a; Ens and Underhill 2014). Ens and Underhill (2014) recently published estimates for juvenile (ϕ_j) and immature (ϕ_i) survival probabilities to be 0.50 and 0.80, respectively, based on continuing studies of banded Eurasian Oystercatchers beginning in 1983. Mean estimates of sub-adult survival (ψ_i), sub-adult to adult transition probabilities (ψ_{sa}), and adult survival (ϕ_a) are similar to those of Schulte (2012). Mean sub-adult and adult apparent survival probabilities were 0.92 (Schulte 2012). Adult survival probabilities were based on mark-resight data collected across coastal North Carolina from 2001 to 2008 (Schulte 2012). There was also no information available on sub-adult survival for American Oystercatchers, thus sub-adult and adult survival were assumed equal (Schulte 2012). Finally, transition probability of sub-adult to adult was averaged across two studies of Eurasian Oystercatchers (Safriel *et al.* 1984; Ens *et al.* 1995). Mean sub-adult to adult transition probability was 0.15, which is supported by the average age of first breeding reported for Eurasian Oystercatchers (3-11 years; Schulte 2012).

Matrix model. For our model, we assumed a pre-birth pulse breeding census. Recruitment was only from adult females and was the product of 0.5 (assuming equal sex ratio), fecundity (0.38), and juvenile survival (0.50; Table 1). We included both immature and sub-adult life stages because American Oystercatchers may begin breeding as early as their third year, but not before (McGowan *et al.* 2005a). Thus, a bird in her second year (immature) can survive and become a third year bird (sub-adult) with probability 0.80 (immature survival; Table 1). A non-breeding third year bird (sub-adult) can either remain a non-breeding sub-adult the following year [with probability $\phi_s * (1 - \psi_{sa})$] or transition into a breeding adult (with probability $\phi_s * \psi_{sa}$; Table 1).

Baseline and Management Alternatives

We used baseline (mean) values to calculate population growth rate (λ) and elasticity values. There was insufficient information to estimate and remove sampling variance from several of the published component vital rates. As such, we evaluated mean component vital rates and manipulations to those means (Crowder *et al.* 1994). Specifically, we investigated the required increase in nest survival, chick survival, or the product of the two probabilities required to increase $\lambda \geq 1.0$ while holding all other vital rates at their mean values. We used an isocline approach to evaluate population growth rate using all possible combinations of nest and chick survival probabilities. Minimum levels of nest and chick survival probabilities required for $\lambda \geq 1.0$ are easily identified across a wide range of possible values.

Finally, we investigated how assumptions regarding mean adult survival probabilities affect both population growth rate and subsequent efficacy of increasing nest and chick survival to achieve $\lambda > 1.0$. The mean adult survival applied in this study was 0.92, which was an adjusted estimate from mark-resight studies to estimate apparent survival in North Carolina (Schulte 2012). Similar studies in coastal Virginia, USA, estimated mean apparent survival probabilities of 0.81 and 0.94 depending on nesting habitat type (Nol *et al.* 2012). Currently, Nol *et al.* (2012) and Schulte (2012) provide the most likely set of adult survival estimates for American Oystercatchers in the southeastern USA. We did not feel these three values were adequate to develop a distribution for adult survival probabilities but recognize that this amount of variation has important implications for estimates of λ and the importance of management actions directed at nest and chick survival. We therefore repeated our previously described approaches of targeted manipulations when adult survival was 0.81 (Nol *et al.* 2012), 0.92 (Schulte 2012), or 0.94 (Nol *et al.* 2012).

Implementation

Baseline and alternate matrix models were fitted in statistical program R (R Development Core Team 2015). For the baseline model, we evaluated the population growth rate (λ ; dominant eigenvalue) and proportional sensitivity (elasticity) of the dominant eigenvector λ to changes in matrix elements.

RESULTS

Baseline Model

Under baseline conditions, American Oystercatcher population growth rate (λ) in North Carolina was 0.975. Elasticity values were greatest for adult survival, followed by sub-adult survival and transition probabilities (Table 5; Schulte 2012).

Management Alternatives

To achieve $\lambda \geq 1.0$, fecundity (or chicks fledged per pair) had to increase from 0.38 to 0.63, when all other vital rates were held at their mean values (Fig. 2). Under this scenario, the product of nest and chick survival must increase from its current value of 0.14 ($0.29 * 0.48$) to ≥ 0.27 for λ to be ≥ 1.0 (assuming mean values for all other vital rates). There are an infinite number of possibilities to increase the product of nest and chick survival to ≥ 0.27 , from increasing only one rate (e.g., nest survival) to any combination of increases in both rates (Fig. 3). For instance, increasing nest survival from 0.29 to ≥ 0.58

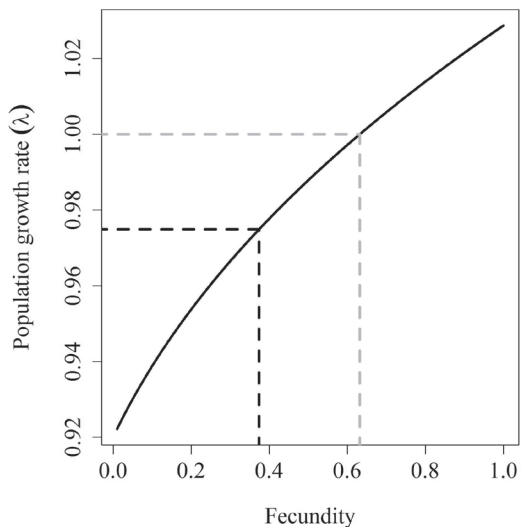


Figure 2. Population growth rate (λ) as a function of possible fecundity values when all other matrix elements were held at their mean values (Table 2). Black dashed lines denote current values of fecundity (0.38 chicks fledged pair⁻¹ year⁻¹) and λ (0.975). Gray dashed lines denote the value of fecundity (0.63 chicks fledged pair⁻¹ year⁻¹) required for $\lambda = 1.0$.

resulted in $\lambda \geq 1.0$, when all other component vital rates were held constant (Fig. 3). Conversely, chick survival would need to be raised from 0.48 to ≥ 0.81 to raise $\lambda \geq 1.0$ (Fig. 3). All combinations of increased nest and chick survival that result in $\lambda \geq 1.0$ are shown as isoclines in Fig. 3.

The alternative baseline scenarios, in which adult survival was changed to 0.81 or 0.94, led to similar results: λ was < 1.0 under baseline conditions, but could potentially be increased to $\lambda \geq 1.0$ with increased nest and chick survival. The amount of increase required to reach $\lambda \geq 1.0$, however, varied by assumptions of adult survival probabilities (Fig. 3). When adult survival decreased from 0.92 to 0.81 (resulting $\lambda = 0.904$), the chick * nest survival needed to increase from 0.14 to ≥ 0.81 to achieve $\lambda \geq 1.0$ (Fig. 3). Conversely, if adult survival increased from 0.92 to 0.94 (resulting $\lambda = 0.990$), the product of chick and nest survival only needed to increase from 0.14 to 0.19 (Fig. 3).

Finally, we used annual island-specific nest and chick survival probabilities provided in Simons and Stocking (2011), supple-

mented with data from 2012 to 2013, to evaluate if North Carolina's historical nest and chick survival probabilities from the 1999–2013 records achieved levels required for $\lambda \geq 1.0$ under the above scenarios (Fig. 4). In total, there were 119 annual island-specific estimates of nest survival, 129 annual island-specific estimates of chick survival, and 119 annual island-specific estimates of the product of nest and chick survival (nest * chick). Results indicated that under baseline conditions required nest (0.58), chick (0.81), and nest * chick (0.27) survival probabilities were occasionally observed in historical records, though the minimum value required for chick survival was greater than the upper quartile (Fig. 4). When adult survival was increased to 0.94, levels of nest, chick, and nest * chick survival probabilities required to reach $\lambda \geq 1.0$ were observed more frequently (Fig. 4). Conversely, if adult survival was decreased to 0.81, required increases to nest and chick survival probabilities were beyond values observed in North Carolina from 1999 to 2013 (Fig. 4). In this latter scenario (i.e., adult survival = 0.81), increasing

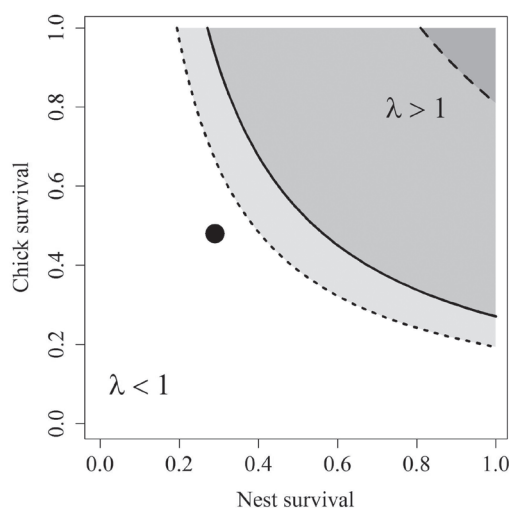


Figure 3. Values of American Oystercatcher nest survival and chick survival required for population growth rate (λ) to be ≥ 1.0 when all other vital rates were held at their mean values (Table 2). Dashed, solid, and dotted lines denote minimum values required when adult survival was 0.81 (Nol *et al.* 2012), 0.92 (Schulte 2012), or 0.94 (Nol *et al.* 2012), respectively. Point denotes current mean values for nest and chick survival.

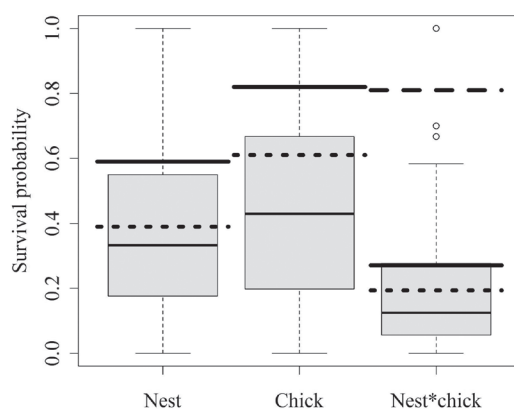


Figure 4. Boxplots of annual island-specific nest survival per pair ($n = 129$ annual island-specific estimates), chick survival ($n = 119$), and the product of nest and chick survival (nest*chick; $n = 119$) at islands in North Carolina, USA, monitored for American Oystercatcher nesting from 1999 to 2013. Black horizontal dashed, solid, and dotted lines denote minimum rate specific values required for statewide population growth rate ≥ 1.0 when adult survival was 0.81, 0.92, and 0.94, respectively, and when all other vital rates were held at their mean values (Table 2). No dashed lines (adult survival = 0.81) are associated with nest and chick survival as required rates were > 1.0 .

Table 5. Elasticity values for matrix elements under baseline conditions (see Table 1).

Stage	Immature	Sub-adult	Adult
Immature	0	0	0.042
Sub-adult	0.042	0.170	0
Adult	0	0.042	0.704

only nest or chick survival to 1.0 would not result in $\lambda \geq 1.0$, and efforts to increase both survival probabilities to extreme historical levels would be required to reverse population declines (Fig. 4).

DISCUSSION

Our research indicates that North Carolina's American Oystercatcher breeding population is declining. In North Carolina and other areas across the species' range, management goals to stabilize American Oystercatcher populations have focused on increasing fecundity, measured as the number of fledged chicks per pair. Our results suggest that management actions targeting the component vital rates associated with fecundity (specifically, nest and chick survival) can reverse population declines. The efficacy of vital rate-specific management alternatives may vary, however, if historical records in North Carolina are any indication of future possibilities. Based on our matrix, mean fecundity must be increased to nearly 150% of current rates to achieve positive population growth. Since 1995, specific islands in North Carolina have occasionally reported yearly nest and chick survival values high enough to establish the fecundity necessary to reach $\lambda \geq 1.0$. However, this does not ensure that managers can effectively maintain chick and nest survival at levels required for population growth using current methods.

In addition to maintaining higher rates of nest and chick survival, management actions targeting more influential vital rates will most likely be necessary to reach $\lambda \geq 1.0$ in North Carolina's American Oystercatcher population. Given that American Oystercatchers are long-lived species, it is not surprising that our results indicated adult

survival as the most influential vital rate to overall population growth. However, adult survival is likely very high (Schulte 2012), so there may be little room to grow this vital rate. Alternatively, managers could aim to increase transition rates of sub-adults to adults, thus increasing the breeding population. Ens *et al.* (1995) have suggested that increasing the amount of high quality habitat can help contribute to an increased transition rate. Unfortunately, we do not always fully understand the habitat requirements of our target species. Further, coastal habitat restoration can be complicated by lack of stakeholder support, funding limitations, decreased land availability due to development, and sea level rise (Zedler 1996; Grayson *et al.* 1999; Simenstad *et al.* 2006; Maslo *et al.* 2011).

Given the stochastic influences to relevant vital rates for breeding American Oystercatchers, it is important to consider the limitations of our deterministic stage structured growth model. Our analysis aimed to highlight management goals in terms of specific component vital rates to contribute to an average overall positive population growth rate. Using the model provided to project future populations would ultimately underestimate the time required to reach goals of population size because it does not incorporate the effects of stochasticity. Our model did not consider more than three nesting attempts, though American Oystercatchers in North Carolina may attempt up to five nests in a season (Schulte 2012). Not separating these component vital rates ultimately underestimated the fecundity and λ reported here, though not enough to modify our results regarding management alternatives. We did not incorporate the effects of immigration, emigration, and breeding site-fidelity of adults, which is likely to underestimate true survival (Murphy 2010).

At the time of this study, there were no estimates from American Oystercatchers for some of the vital rates shown to be most influential in reversing population decline, leading us to rely on estimates from Eurasian Oystercatchers. Additionally, the adult survival probability used in our analysis was

generated from a capture-mark-recapture analysis from 2002-2008 band resight data, an estimate that may be greatly improved by the additional 6 years of band resight data currently available.

Results from our study provide valuable insight to the current status of American Oystercatchers in North Carolina, the viability of current management priorities, and future research objectives that will improve our understanding of American Oystercatcher population dynamics. While the matrix and values used in our analysis are clearly oversimplifications of complex population dynamics, our results demonstrate the necessity of future efforts to provide accurate vital rates to evaluate the status of American Oystercatcher populations, both locally and regionally.

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Appendix. Observed nest survival and re-nesting probabilities by nest attempt for monitored American Oystercatcher nests in North Carolina, USA, 1997-2013. If nests fail prior to or very soon after hatching, pairs will re-nest up to four times (five total nests) within a single nesting season. For each nest attempt, we determined nest survival by dividing the total number of nests that successfully hatched at least one chick by the total number of nests laid. Re-nesting probability was defined as the number of pairs that laid an additional nest, following the failure of their previous nest prior to hatching, divided by the total number of failed nests (Murphy 2010). Because the pairs never attempted more than five nests in a season, we did not calculate “Nest 5” re-nesting probability. The annual means are the arithmetic means of annual re-nesting and nest survival probabilities. Data are from Simons and Stocking (2011) and supplemented with North Carolina 2012-2013 nest records. In cells for years during which higher value re-nests did not occur, “N/A” is used as a placeholder to indicate these values do not exist and are not applicable.

Year	Nest Survival					Re-nesting Probability			
	Nest 1	Nest 2	Nest 3	Nest 4	Nest 5	Nest 1	Nest 2	Nest 3	Nest 4
1997	0.09	0.11	0.00	N/A	N/A	0.43	0.25	0.00	N/A
1998	0.09	0.07	0.00	0.00	N/A	0.53	0.35	0.33	0.00
1999	0.23	0.11	0.00	N/A	N/A	0.57	0.24	0.00	N/A
2000	0.36	0.14	0.50	1.00	N/A	0.50	0.08	1.00	N/A
2001	0.25	0.30	0.17	1.00	N/A	0.66	0.36	0.10	N/A
2002	0.28	0.20	0.25	0.00	0.00	0.76	0.25	0.22	0.50
2003	0.30	0.22	0.18	0.00	N/A	0.62	0.38	0.14	0.00
2004	0.58	0.42	0.33	0.00	N/A	0.71	0.21	0.50	0.00
2005	0.34	0.55	0.40	N/A	N/A	0.42	0.50	0.00	N/A
2006	0.42	0.33	0.33	N/A	N/A	0.57	0.19	0.00	N/A
2007	0.24	0.36	0.00	0.50	1.00	0.60	0.36	0.22	1.00
2008	0.24	0.21	0.30	N/A	N/A	0.54	0.38	0.00	N/A
2009	0.44	0.21	0.57	0.00	N/A	0.47	0.19	0.33	0.00
2010	0.49	0.28	0.19	0.00	0.00	0.59	0.44	0.23	0.33
2011	0.46	0.23	0.13	0.00	N/A	0.68	0.48	0.08	0.00
2012	0.52	0.13	0.14	0.17	N/A	0.78	0.50	0.50	0.00
2013	0.33	0.32	0.32	0.00	N/A	0.71	0.55	0.04	0.00
Average	0.33	0.25	0.22	0.24	0.33	0.60	0.34	0.21	0.17
SD	0.14	0.12	0.17	0.40	0.58	0.11	0.13	0.27	0.33