A Historical Estimate of Apparent Survival of American Oystercatcher (*Haematopus palliatus*) in Virginia

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A Historical Estimate of Apparent Survival of American Oystercatcher 
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Abstract.—Using mark-recapture models, apparent survival was estimated from older banding and re-sighting data (1978-1983) of American Oystercatchers (Haematopus palliatus) nesting on beaches and in salt marshes of coastal Virginia, USA. Oystercatchers nesting in salt marshes exhibited higher apparent survival (0.94 ± 0.03) than birds nesting on beaches (0.81 ± 0.06), a difference due to variation in mortality, permanent emigration, or both. Nesting on exposed barrier beaches may subject adults and young to higher risk of predation. These early estimates of adult survival for a species that is heavily monitored along the Atlantic and Gulf Coasts can be used to (1) develop demographic models to determine population stability, (2) compare with estimates of adult survival from populations that have reached carrying capacity, and (3) compare with estimates of survival from other oystercatcher populations and species. Received 24 February 2012, accepted 17 July 2012.

Key words.—American Oystercatcher, apparent survival, Haematopus palliatus, mark-recapture, shorebirds, Virginia.


The American Oystercatcher (Haematopus palliatus), a Species of High Concern in the eastern United States (Brown et al. 2001), has an estimated Atlantic Coast population of 10,971 ± 298 individuals (Brown et al. 2005). Survival estimates of banded individuals are critical to the development of demographic models (Hitchcock and Gratto-Trevor 1997) that can be used to determine trajectories of local or regional populations. Survival estimates of marked individuals in the past are rare but comparisons across historical timeframes can also help to inform and assess management actions and future risks, especially in long-lived organisms (De La Mare and Kerry 1994; Beissinger and Westphal 1998).

The American Oystercatcher, although small in numbers relative to other North American shorebirds, has re-colonized from near extirpation (Mawhinney et al. 1999), and increased over the last 50 years in the northern part of its range, reaching over 800 birds in the states of Massachusetts and New York (Melvin 2007; New York State Department of Environmental Conservation). During this recovery period, populations appear to be declining in the core, Mid-Atlantic breeding areas including Virginia and South Carolina (Davis et al. 2001; Sanders et al. 2008; Wilke et al. 2005). In many states numbers of birds nesting on beaches has declined, possibly due to human disturbance (McGowan and Simons 2006; Sabine et al. 2008), while numbers of birds nesting in salt marshes and shell rakes have increased, comprising the majority of nesting pairs in eastern North America (Lauro and Burger 1989; Wilke et al. 2005; Virzi 2010). Herein, we present a survival estimate of the American Oystercatcher from a Virginia study population that was derived from a banded breeding population from 1978-1983 nesting on coastal beaches and salt marshes in Virginia.

Study Area and Methods

From 1978 to 1983, field work was conducted from March through July in salt marshes and beaches to the south of Chincoteague, VA, (37° 50' N, 75° 35' W; Nol et al. 1984). From 1978 to 1981, breeding adult oystercatchers were captured during the incubation period using drop traps placed over the nest (Mills and Ryder 1979). Birds were banded with a federal aluminum band and a unique combination of 2-3 spiral color bands on the tarsometatarsus. Observations of color-banded oystercatchers were conducted over the breeding seasons of 1979 to 1983. Sex of each bird was determined by size and weight with females both larger and heavier (Nol et al. 1984). The study area and survey effort remained constant over the study period.
We used Cormack-Jolly-Seber (CJS, Cormack 1964; Jolly 1965; Seber 1965) models using Program Mark 6.0 (White and Burnham 1999) to estimate apparent survival \((q)\) and encounter probability \((p)\) from live encounter data. This open population model assumes: 1) capture has no effect on survival or encounter probability; 2) every oystercatcher has an equal chance of survival; 3) color bands are not lost; 4) capture periods are instantaneous relative to the intervals between them; 5) fates are independent, and 6) emigration is permanent (White and Burnham 1999). Observations during this study support these assumptions. To reduce the risk of violating assumption 4, capture periods were held constant (15 April-15 June) over the study period. Apparent survival is the product of true survival and site fidelity and, as a result, is negatively biased. We included time-dependence \((t)\) and sex \((s)\) in our models of \(q\) and \(p\) because both parameters are known to vary between sex and across years in several shorebird species (Sandercock 2003). Because habitat is also known to impact survival (Van de Poel et al. 2006), nesting habitat \((\text{habitat})\) was grouped into two categories, beach or salt marsh.

We assessed the fit of competing models using an information-theoretic approach (Burnham and Anderson 2002). Selection of the best-fit model was done using corrected quasi-Akaike’s Information Criterion adjusted for small sample size \(\text{QAIC}_c\) (Burnham and Anderson 2002; Arnold 2010). Apparent survival \((\hat{q})\) was grouped into two categories, beach or salt marsh.

We conducted a goodness-of-fit (GOF) test for the global model \(\phi_{\text{habitat}} p_{t, \text{sex}}\) 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 variation inflation factor, \(\hat{\epsilon}\), which corrects the data (Gooch and White 2009).

The Web of ScienceTM and unpublished sources are used to extract other estimates of adult survival for oystercatchers of the world.

Results

We uniquely marked 58 (31 in 1978; twelve in 1979; four in 1980; eleven in 1981) nesting adult American Oystercatchers (16 marsh-nesting females, 13 beach-nesting females, 17 marsh-nesting males, twelve beach-nesting males) from 1978-1981 and collected 222 unique live encounters from 1979-1983. Using the global model \(\phi_{\text{habitat}} p_{t, \text{sex}}\), we detected minor overdispersion in the live encounter data \((\hat{\epsilon} = 1.57)\), adjusted \(\text{AIC}_c\) (QAIC\(_c\)) by dividing the observed deviance of the global model by the mean expected deviance, and proceeded with model selection. The model that minimized QAIC\(_c\), for our analysis included apparent survival as a function of nesting habitat and detection that varied annually \((\phi_{\text{habitat}} p_{t, \text{sex}}); \text{Table 1})

Model 2, the only other candidate model within two QAIC\(_c\) units, included an effect of habitat on apparent survival and retained a time- and sex-dependent encounter rate \((\phi_{\text{habitat}} p_{t, \text{sex}}))\). This model differed by only a single parameter, so does not improve model fit (Burnham and Anderson 2002; Arnold 2010). Apparent survival \((\phi_{\text{beach}})\) for American Oystercatchers nesting on Virginia beaches was 0.81 (95% CI: 0.67-0.90), whereas adults nesting in salt marshes exhibited higher apparent survival \((\phi_{\text{marsh}} = 0.94, 95\% \text{ CI}: 0.85-0.98)\). Encounter probability \((p)\) was high but varied annually (range 0.93-1.00; \text{Table 2}).

<table>
<thead>
<tr>
<th>Model(^{a})</th>
<th>QAIC(_c)</th>
<th>ΔQAIC(_c)</th>
<th>(w_i)</th>
<th>Model Likelihood</th>
<th>K</th>
<th>Dev</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\phi_{\text{habitat}} p_t)</td>
<td>110.70</td>
<td>0.00</td>
<td>0.17</td>
<td>1.00</td>
<td>4</td>
<td>41.82</td>
</tr>
<tr>
<td>(\phi_{\text{habitat}} p_{t, \text{sex}})</td>
<td>110.20</td>
<td>0.50</td>
<td>0.13</td>
<td>0.78</td>
<td>5</td>
<td>40.22</td>
</tr>
<tr>
<td>(\phi_t p_t)</td>
<td>111.70</td>
<td>2.00</td>
<td>0.06</td>
<td>0.37</td>
<td>6</td>
<td>39.58</td>
</tr>
<tr>
<td>(\phi_{\text{habitat}} p_{t, \text{sex}})</td>
<td>112.15</td>
<td>2.45</td>
<td>0.05</td>
<td>0.29</td>
<td>7</td>
<td>37.88</td>
</tr>
<tr>
<td>(\phi_t p_t)</td>
<td>112.27</td>
<td>2.57</td>
<td>0.05</td>
<td>0.28</td>
<td>3</td>
<td>46.48</td>
</tr>
<tr>
<td>(\phi_{\text{habitat}} p_{t, \text{sex}})</td>
<td>112.36</td>
<td>2.66</td>
<td>0.05</td>
<td>0.26</td>
<td>4</td>
<td>44.49</td>
</tr>
<tr>
<td>(\phi_{\text{habitat}} p_t)</td>
<td>112.49</td>
<td>2.79</td>
<td>0.04</td>
<td>0.25</td>
<td>6</td>
<td>40.38</td>
</tr>
<tr>
<td>(\phi_{\text{habitat}} p_{t, \text{sex}})</td>
<td>112.64</td>
<td>2.93</td>
<td>0.04</td>
<td>0.23</td>
<td>6</td>
<td>40.52</td>
</tr>
<tr>
<td>(\phi_{\text{habitat}} p_{t, \text{sex}})</td>
<td>112.78</td>
<td>3.08</td>
<td>0.04</td>
<td>0.21</td>
<td>8</td>
<td>36.33</td>
</tr>
<tr>
<td>(\phi_t p_{t, \text{sex}})</td>
<td>113.03</td>
<td>3.33</td>
<td>0.03</td>
<td>0.19</td>
<td>7</td>
<td>38.76</td>
</tr>
<tr>
<td>(\phi_{t, \text{sex}} p_{t, \text{sex}})</td>
<td>114.24</td>
<td>4.54</td>
<td>0.05</td>
<td>0.10</td>
<td>15</td>
<td>21.84</td>
</tr>
</tbody>
</table>

\(^{a}\)Model factors included: \text{habitat} = nesting in barrier beach or marsh habitat, \(t\) = annual variation, \(\epsilon\) = constant, and \text{sex} = male or female.
DISCUSSION

All oystercatcher species are characterized as having high survival (Table 3) and breeding-site fidelity (Tomkins 1954; Hockey 1996). Thus, apparent survival of adult oystercatchers is a credible estimate, and similar to that reported for American Oystercatchers in Massachusetts (Murphy 2010). The Virginia population was at a much lower breeding density than the Massachusetts population (Lauro et al. 1992; Murphy 2010), so density, at least, with this limited sample, does not appear to impact adult survival. Our final model did not include the variable sex, a result that contrasts with those for the similar Eurasian Oystercatcher (H. ostralegus, Durell 2007). By contrast, our final model suggested that adult survival was 13% greater for birds nesting in salt marsh habitat than for those nesting on coastal beaches. As apparent survival estimates are the product of true survival and the probability that an individual returns to the breeding site (i.e. breeding site-fidelity), these differences may be attributed to habitat effects on survival, breeding-site fidelity or a combination of these two life-history characteristics.

If we assume equal survival across nesting habitats, then the discrepancy between apparent survival rates is a function of site fidelity varying by habitat. Using breeding and nonbreeding encounters of oystercatchers in Massachusetts, Murphy (2010) disentangled site fidelity from survival and proposed that local population swings are likely the result of birds emigrating from the study population. Congeneric oystercatchers exhibited higher levels of site fidelity to territories that successfully fledged young (Safriel et al. 1984; Ens et al. 1992; Harris and Wanless 1997; Hazlitt and Butler 2001). Higher apparent survival of Virginia salt-marsh nesting oystercatchers may indicate higher reproductive output relative to those nesting on beaches, as beach-nesting American Oystercatchers experience both high mammalian predation and human disturbance in other parts of their range (McGowan et al. 2005; Sabine et al. 2008). Birds on beaches may have moved into nearby salt marshes (Wasilco 2008) or northward to growing populations of the northeastern U.S.

Alternatively, equal levels of nest-site fidelity suggest a difference in survival between habitats with beach-nesting oystercatchers experiencing direct mortality. At the time of the study, one inlet between two barrier islands used for nesting was closing by movement of sand, reducing saltwater flow to oystercatcher feeding areas. Reductions in food supply could have contributed to lower apparent survival of beach-nesting birds. Additionally, Red Foxes (Vulpes vulpes) denned

Table 2. Estimates of apparent survival for American Oystercatchers nesting on beaches ($\varphi_{\text{beach}}$) and salt marshes ($\varphi_{\text{marsh}}$), encounter probabilities ($p_t$), standard error (SE), lower 95% confidence limit (LCL), and upper 95% confidence limit (UCL) in Virginia from 1978-1983 under the best fit model ($\varphi_{\text{habitat}},p_t$).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>LCL</th>
<th>UCL</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\varphi_{\text{beach}}$</td>
<td>0.81</td>
<td>0.06</td>
<td>0.67</td>
<td>0.90</td>
</tr>
<tr>
<td>$\varphi_{\text{marsh}}$</td>
<td>0.94</td>
<td>0.03</td>
<td>0.85</td>
<td>0.98</td>
</tr>
<tr>
<td>$p_{1979}$</td>
<td>0.93</td>
<td>0.06</td>
<td>0.69</td>
<td>0.99</td>
</tr>
<tr>
<td>$p_{1980}$</td>
<td>1.00</td>
<td>&lt;0.01</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>$p_{1981}$</td>
<td>1.00</td>
<td>&lt;0.01</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>$p_{1982}$</td>
<td>1.00</td>
<td>&lt;0.01</td>
<td>1.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Table 3. Estimated adult survival (SE) of oystercatcher species (Haematopodidae).

<table>
<thead>
<tr>
<th>Haematopodidae</th>
<th>Annual survival</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>H. ostralegus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>male:</td>
<td>0.91 (0.01)</td>
<td>Durell 2007</td>
</tr>
<tr>
<td>female:</td>
<td>0.84 (0.03)</td>
<td>Durell 2007</td>
</tr>
<tr>
<td></td>
<td>0.90 (0.01)</td>
<td>Safriel et al. 1984</td>
</tr>
<tr>
<td></td>
<td>0.92 (0.01)</td>
<td>Harris and Wanless 1997</td>
</tr>
<tr>
<td>H. finschi</td>
<td>0.89 (0.03)$^1$</td>
<td>Sagar et al. 2002</td>
</tr>
<tr>
<td>H. palliatus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>marsh:</td>
<td>0.94 (0.03)</td>
<td>This study</td>
</tr>
<tr>
<td>beach:</td>
<td>0.81 (0.06)</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td>0.92 (0.03)</td>
<td>Murphy 2010</td>
</tr>
</tbody>
</table>

$^1$True survival; all others are apparent survival.
and hunted at beach study sites (Nol, pers. obs.). Emigration in a Massachusetts study population is estimated to be between 0-11% (Murphy 2010). Thus, it is likely that the difference in survival between habitats in Virginia is due to both emigration and direct mortality on adults.

Movement data will be critical to understanding the role of site fidelity on adult survival. Studies estimating inter-annual movements across the U.S. population from Massachusetts to Florida are currently underway (American Oystercatcher Working Group et al. 2012). Movement data linking breeding and wintering populations may also allow study of carry-over effects (e.g., Duriez et al. 2012) and can be incorporated into future, more complex, mark-recapture models (e.g. multi-state models, White et al. 2006).

Acknowledgments

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Literature Cited


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