Effects of White-Tailed Deer (Odocoileus virginianus) on the Maritime Forest of Bald Head Island, North Carolina

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Abstract.—Overabundance and associated impacts of deer on mainland forests of the United States have been topics of extensive investigation and management discussion. Conversely, deer populations on barrier islands have been less studied with few investigations of their impacts on maritime evergreen forest. We investigated how deer influenced understory vegetation and oak seedling survival following culling of deer. In 2007 twenty 10 m × 10 m paired exclosure and control plots were established within a 77.3 ha protected area on Bald Head Island, North Carolina. Vegetation was sampled in 2011. We determined deer did not affect understory vegetation and oak survival was low and not influenced by deer. Chronic over-browsing (i.e., ‘ghost of herbivory past’) was unlikely because deer were not abundant on Bald Head Island until the 1990s, oak seedlings were observed where light was abundant, and deer were observed using other cover types on the island. Continued monitoring of the forest understory and maintenance of deer at the current population level will help conserve maritime forest on Bald Head Island.

Introduction

Throughout the eastern United States, the abundance of white-tailed deer (Odocoileus virginianus) has increased dramatically over the last century (McShea et al., 1997; Russel et al., 2001). This could have occurred because of increased habitat fragmentation from land development or reduced predators and hunting pressure (Augustine and DeCalesta, 2003; Knight et al., 2009). Regardless of the cause, high deer densities can have significant effects on plant communities (Côté et al., 2004) and have changed floristic compositions by over-browsing of understory vegetation or selective browsing of species that inhibited forest succession (Augustine and Frelich, 1998; Russell et al., 2001; Horsely et al., 2003; Côté et al., 2004; Long et al., 2007; Baiser et al., 2008; Knight et al., 2009; Aronson and Handel, 2011).

Plant communities on southeastern U.S.A. barrier islands have been particularly susceptible to browsing because they grow in nutrient-poor soils and are subjected to additional physical stress such as salt spray and shifting sediments (Au, 1974; Ray et al., 2001). Maritime forest regeneration and maintenance of community structure has occurred in response to the physical environment and disturbance regime (Au, 1974; Turner and Bratton, 1987; Conner et al., 2005). Despite increases in deer abundances on southeastern barrier islands (Osborne et al., 1992; Ray et al., 2001), few studies investigated how herbivores influenced maritime forest dynamics (Turner and Bratton, 1987; Forrester et al., 2006).

Deer presence on Smith Island in North Carolina (Fig. 1) has been relatively recent as deer were not recorded in mammalian surveys conducted in 1964 (Cooper and Satterthwaite, 1964) or 1970 (Parnell and Adams, 1970). Deer colonized the island in the mid-1980s and established a viable population in the early 1990s (Ray et al., 2001). Studies have suggested barrier islands can sustain deer populations ≤19 deer/km² (Stransky, 1969;
Osborne et al., 1992; Sherrill et al., 2010). Since 1999 surveys showed deer densities on the Bald Head Island portion of Smith Island increased dramatically, fluctuated considerably, and exceeded 19 deer/km² most years (Sherrill et al., 2010; Bald Head Island Conservancy, 2012; Table 1). Complaints of browsing damage to residential plantings and several deer deaths from vehicular accidents (e.g., construction trucks) during 1999–2002 prompted the local government, Bald Head Island Village Council (2014), to hire sharpshooters for culling (Bald Head Island Conservancy, 2012). Culls were conducted in 2002, 2005, 2006, 2008, and 2011, but the village council was concerned about deer impacts on the local forest preserve. Our objective was to determine if deer influenced dynamics of a protected maritime evergreen forest – south Atlantic subtype (Schafale, 2012) on a barrier island in the southeastern U.S.A.
STUDY AREA

The study area was within the Bald Head Woods Coastal Reserve (33°51’10.80”N, 77°58’30.68”W), a 77.3 ha maritime forest preserve located on Bald Head Island in North Carolina (Fig. 1). Bald Head Island consists of approximately 620 ha of ocean beach to sound communities on a barrier island where the majority of uplands are occupied by privately-owned tracts with special attention paid to protection of natural features. This area represents the southern portion of Smith Island, a complex which also encompasses Middle Island, Bluff Island, and other beaches/marshes in private and public ownerships.

METHODS

In 2007 we established paired 20 plots that each consisted of a 10 m × 10 m exclosure and a 10 m × 10 m control. This plot size and square configuration has been shown to provide sufficiently detailed information on terrestrial vegetation composition and structure for diverse applications and compatibility with data derived from commonly used methods (Peet et al., 1998). We selected sites for paired plots to represent variation in species composition, physical structure of forest regeneration phases, and environmental gradients that trended from southwest to northeast (i.e., a gradient direction that included younger to older dunes, increasing moisture availability, and decreasing salt spray) (Brewer, 2008). Each exclosure was surrounded by a black polypropylene mesh (4.4 cm × 4.4 cm) deer fence 2.13 m in height and 12 m × 12 m in area to avoid edge effect on the interior 100 m² sample. At least one gap (10 cm high × 25 cm long) was created along the bottom of each side to allow small animal access. This design was consistent with deer exclosures of this size (Nicholas et al., 2007; Deer Facts, 2009) and successfully prevented deer access.

In 2011 we sampled each plot to acquire tree, shrub, and vine data. We used Weakley (2012) as the plant identification guide and deposited a voucher specimen in the University of North Carolina Wilmington Herbarium (WNC) for each vascular plant species sampled. Trees, shrubs, and vines were divided into three height classes: small (<50 cm), medium (51–130 cm), and large (>131 cm). We measured diameter at breast height of all other

### Table 1.—Deer Population Estimates for Bald Head Island 1999–2011 (Sherrill et al., 2010; Bald Head Island Conservancy, 2012). Estimates from Sherrill et al., 2010 are listed first for 2008 and 2009; others are from Bald Head Island 2012

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of deer</th>
<th>Number culled</th>
<th>Density (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>93</td>
<td></td>
<td>15.0</td>
</tr>
<tr>
<td>2000</td>
<td>185</td>
<td></td>
<td>29.8</td>
</tr>
<tr>
<td>2001</td>
<td>316</td>
<td></td>
<td>51.0</td>
</tr>
<tr>
<td>2002</td>
<td>257*</td>
<td>149</td>
<td>41.5</td>
</tr>
<tr>
<td>2003</td>
<td>54</td>
<td></td>
<td>8.7</td>
</tr>
<tr>
<td>2004</td>
<td>332</td>
<td></td>
<td>53.5</td>
</tr>
<tr>
<td>2005</td>
<td>359*</td>
<td>100</td>
<td>57.9</td>
</tr>
<tr>
<td>2006</td>
<td>256*</td>
<td>145</td>
<td>41.3</td>
</tr>
<tr>
<td>2007</td>
<td>134</td>
<td></td>
<td>21.6</td>
</tr>
<tr>
<td>2008</td>
<td>107/148*</td>
<td>71</td>
<td>17/23.9</td>
</tr>
<tr>
<td>2009</td>
<td>93/97</td>
<td></td>
<td>15/15.6</td>
</tr>
<tr>
<td>2010</td>
<td>141</td>
<td></td>
<td>22.8</td>
</tr>
<tr>
<td>2011</td>
<td>155*</td>
<td>73</td>
<td>25.0</td>
</tr>
<tr>
<td>2012</td>
<td>76</td>
<td></td>
<td>12.3</td>
</tr>
</tbody>
</table>

* - herd reduction performed
species >1.3 m. Herb occurrences in exclosures and throughout the maritime forest were sparse and not included. The lack of herbaceous vegetation in North Carolina maritime forests was reported by Bordeau and Oosting (1959) and Au (1974). Paucity of herbs in this forest was likely due to low light conditions under the closed canopy. In a vegetation survey conducted on this island prior to deer colonization, Bordeau and Oosting (1959) reported: “…the herb layer was sparse, except below openings in the canopy.”

We used paired \( t \)-tests to determine overall density of woody species, density of the most abundant woody understory species, and understory diversity of woody species (Shannon index). We examined the influence of deer on understory composition by permutated analysis of variance (PERMANOVA). We conducted all analyses in R version 2.15.0 (R Development Core Team, 2012).

We assessed deer impacts on young live oaks (\textit{Quercus virginiana}) by transplanting seedlings and saplings derived from acorns harvested on Bald Head Island. In 2010 we evenly divided and planted 144 seedlings and 72 saplings (2 to 3 y old) within six exclosures and six control plots. In 2011 we evenly divided another 110 seedlings between an exclosure and a single control. We identified initial transplants by individual tags (\textit{i.e.}, coded ‘twist ties’) and small survey flags for groups of three seedlings. We planted all other seedlings in rows identified by numbered plant stakes. Twelve months following transplantation, we attempted to locate seedlings and saplings for assessment of survival.

To sample ages of canopy recruitment, we obtained tree cores from dominant oaks in all plots (0.4 ha total area). Live oaks were too large in diameter and contained decomposed heartwood inadequate for age determination, but we sampled all sand laurel oaks (\textit{Q. hemisphaerica}). We sanded and examined each core with a dissecting microscope to determine tree age.

**RESULTS**

Understory tree, shrub, and vine species densities were similar between exclosure and control plots in the small \( [t (19) = 0.64, P = 0.53] \), medium \( [t (19) = 0.14, P = 0.89] \), and large size classes \( [t (19) = 0.52, P = 0.60] \) after 4 y of exclusion (Fig. 2). The understory was dominated by yaupon (\textit{Ilex vomitoria}) with lesser amounts of red bay (\textit{Persea borbonia}) and cabbage palmetto (\textit{Sabal palmetto}) (Table 2). Yaupon density was similar in all size classes \( [t (19) = 0.92, P = 0.37 \text{ for small}, t (19) = 0.88, P = 0.39 \text{ for medium}, t (19) = 0.81, P = 0.42 \text{ for large}] \). Shannon diversity was similar between exclosures and controls in all size classes of understory species \( [t (19) = -1.24, P = 0.23 \text{ for small}, t (19) = -1.78, P = 0.09 \text{ for medium}, t (19) = -1.55, P = 0.14 \text{ for large}, \text{Fig. 3}] \). Species composition was similar for small (F Model = 0.43, \( r^2 = 0.01, P = 0.78 \)), medium (F Model = 0.62, \( r^2 = 0.02, P = 0.60 \)), and large size classes (F Model = 0.28, \( r^2 = 0.01, P = 0.81 \), Fig. 4).

The canopy consisted of oaks with only sporadic occurrences of American holly (\textit{Ilex opaca} \textit{var. opaca}), southern red cedar (\textit{Juniperus virginiana} \textit{var. silicicola}), and Carolina laurel cherry (\textit{Prunus caroliniana}) (Table 3). Although cabbage palmetto was common in the understory, it was absent from the canopy within plots.

Only six of the 127 transplanted seedlings survived in the control plots and none of the 127 survived in the exclosures. Three of the 36 transplanted saplings survived in the controls, while zero survived in the exclosures. Evidence of approximately 30 plants removed or killed by digging, presumably by small animals, was observed during monitoring. Of 17 sand laurel oak canopy and subcanopy trees cored, ring counts indicated a mean of 46 y (SE = 3.38) and tree age ranged from 23 to 73 y.
Overabundance and associated impacts of deer on mainland forests of the United States have been topics of extensive investigation and management discussion (Harlow et al., 1970; Stromayer and Warren, 1997; Russell et al., 2001; Rooney and Waller, 2003; Côté et al., 2004; Webster et al., 2005; Tanentzap et al., 2011). Deer populations on barrier islands, however, have been considerably less studied (Stransky, 1969; Epstein et al., 1983, 1985; Miller, 1988; Rowland, 1989; Osbourne et al., 1992; and Ray et al., 2001), with few studies concerning impacts on maritime evergreen forest (e.g., Bratton and Kramer, 1993). Because maritime forest area has been drastically reduced in recent decades by development and other land conversion activities, protection and stewardship of remaining tracts was a priority in southeastern coastal states (Lopazanski et al., 1988; Bellis, 1995; North Carolina Coastal Reserve, 2014). Our results indicated the deer population on Bald Head Island had
TABLE 2.—Relative abundances of each species found in maritime forest understory by size class, Bald Head Island, 2011. There were 14,842 individuals in the small size class, 6246 in the medium size class, and 3293 in the large size class.

<table>
<thead>
<tr>
<th>Species</th>
<th>Small</th>
<th>Medium</th>
<th>Large</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Berchemia scandens</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>0</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Carpinis caroliniana</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cartrema americana</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cornus florida</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Gelsemium sempervirens</td>
<td>&lt;0.01</td>
<td>0</td>
<td>0</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Ilex opaca var. opaca</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ilex vomitoria</td>
<td>0.85</td>
<td>0.71</td>
<td>0.66</td>
<td>0.79</td>
</tr>
<tr>
<td>Juniperus virginana var. silicola</td>
<td>&lt;0.01</td>
<td>0</td>
<td>0</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Muscadine rotundifolia</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>0</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Parthenocissus quinquefolia</td>
<td>&lt;0.01</td>
<td>0</td>
<td>0</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Persea borbonia</td>
<td>0.08</td>
<td>0.14</td>
<td>0.08</td>
<td>0.10</td>
</tr>
<tr>
<td>Prunus carolinana</td>
<td>0</td>
<td>0.03</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Quercus hemisphaerica</td>
<td>&lt;0.01</td>
<td>0</td>
<td>0</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Quercus virginiana</td>
<td>&lt;0.01</td>
<td>0</td>
<td>0</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Sabal palmetto</td>
<td>0.06</td>
<td>0.11</td>
<td>0.25</td>
<td>0.10</td>
</tr>
<tr>
<td>Smilax bona-nox</td>
<td>&lt;0.01</td>
<td>0</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Toxicodendron radicans</td>
<td>&lt;0.01</td>
<td>0</td>
<td>0</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

Fig. 3.—Shannon understory diversity within 20 exclosure and control plots located in the Bald Head Island maritime forest, 2011.
relatively little influence on the understory of a maritime evergreen forest. We may have been unable to detect an effect because: (1) over-browsing for many years has eliminated any potential for recovery of plant communities by eliminating the seed bank ("the ghost of herbivory past" sensu, Carson et al., 2005), (2) deer may use the forest as cover, but not browse, and forest dynamics are driven by disturbance, or (3) the deer population has been reduced to levels that allow plants to persist in the understory.

**DOES 'THE GHOST OF HERBIVORY PAST' HAUNT BALD HEAD ISLAND?**

If over-browsing by deer occurs over a sufficiently long time period, highly selected browse species may be eliminated from the understory and seed bank. Over-browsing can lead to "recalcitrant understory layers" dominated by species with low selectivity at the expense of original species diversity (Côté et al., 2004; Royo and Carson, 2006). "The ghost of herbivory past" suggests that in the absence of a seedling and seed bank, it may take years for locally extirpated plant species to recolonize after deer numbers are lowered or deer are excluded from an area (Carson et al., 2005). However, we do not believe this phenomenon contributed to the lack of differences between exclosures and controls in stem density, diversity, and community composition in this study. Yaupon, the dominant understory species, is considered a highly selected browse species and red bay, the second most abundant understory species, is intermediate in palatability (Goodrum and Reid, 1958; Shadow, 2011; U.S. Forest Service, 2012).

Previous surveys of the Bald Head Island maritime forest (Coker, 1918; Wells, 1932; Bourdeau and Oosting, 1959) included the same woody species, sparse herb stratum, and overall characteristics that we detected in this study. Also, the understory composition and structure that we sampled were similar to quantitative data from plots sampled in 1988 by the Carolina Vegetation survey (2013) in the same protected forest. Our sample size (n =

**Table 3.—Relative abundances and average DBHs of canopy species sampled in the Bald Head Island maritime forest, 2011. A total of 28 trees were sampled in all plots (0.4 ha)**

<table>
<thead>
<tr>
<th>Species</th>
<th>Relative abundance</th>
<th>Mean DBH (cm)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ilex opaca var. opaca</em></td>
<td>0.03</td>
<td>54.2</td>
<td>0.00</td>
</tr>
<tr>
<td><em>Juniperus virginiana var. silicicola</em></td>
<td>0.06</td>
<td>40.1</td>
<td>1.65</td>
</tr>
<tr>
<td><em>Prunus caroliniana</em></td>
<td>0.06</td>
<td>24.4</td>
<td>1.66</td>
</tr>
<tr>
<td><em>Quercus hemisphaerica</em></td>
<td>0.61</td>
<td>30.9</td>
<td>6.60</td>
</tr>
<tr>
<td><em>Quercus virginiana</em></td>
<td>0.24</td>
<td>44.9</td>
<td>4.36</td>
</tr>
</tbody>
</table>
20) was much higher than previous studies that found significant results (e.g., n = 6 in Long et al., 2007). The large sample size and paired design suggested, if deer significantly affected understory composition, we would have detected the change. We also noted the lack of herbaceous vegetation in the controls and exclosures likely indicated light limitation because a survey conducted on this island prior to deer colonization (Bourdeau and Oosting, 1959) found herbs were restricted to canopy gaps. The lack of change in browse species (i.e., yaupon and red bay) following deer exclusion, the consistent composition and structure of the understory over the last century, and the recent colonization (and subsequent management) of deer indicated ‘the ghost of herbivory past’ did not haunt Bald Head Island.

**DO DEER CONSUME UNDERSTORY VEGETATION IN THIS FOREST?**

Our results indicated deer were not over-browsing understory vegetation. In addition to the maritime forest, Bald Head Island had many other habitats including a golf course, landscaped areas, early successional areas, secondary dunes, and freshwater wetlands. During a study of deer movement and habitat selection on Bald Head Island (Sherrill et al., 2010), animals were observed using a variety of habitats throughout the island (B. Sherrill, pers. comm.), but maritime forest/shrub was used by radio-collared deer at levels greater than other available cover types.

**HAVE DEER BEEN CULLED TO LEVELS THAT DO NOT IMPACT UNDERSTORY VEGETATION?**

Spotlight count estimates of the Bald Head Island deer population were as high as 359 individuals (57.9/km^2) in 2005 but have remained below 150 (24/km^2) individuals since 2007 (Sherrill et al., 2010; Bald Head Island Conservancy, 2012; Table 1). Lack of significant changes in maritime forest vegetation and oak recruitment indicated the forest tolerated, at least in the short term, deer densities higher than predicted by Stransky (1969) for a barrier island system (i.e., 15–17/km^2). Stransky’s estimate assumed a low quality deer habitat, while some southeastern mainland forests were considered able to support approximately 19 deer/km^2 (Stransky, 1969; Osbourne et al., 1992). However, the lack of competition with other barrier island herbivores (e.g., feral horses and hogs), availability of adjacent food sources, and mechanisms of oak recruitment appeared to be important mitigating factors on Bald Head Island. A target density of 15–17 deer/km^2 recommended by Sherrill et al., 2010 was a conservative goal to ensure overall protection of island habitats.

**DEER EFFECTS ON OAK RECRUITMENT**

Similar to other southeastern maritime forests and previous studies on Bald Head Island (Coker, 1918; Wells, 1939; Oosting, 1954; Bourdeau and Oosting, 1959), we determined oaks dominated the Bald Head Island maritime forest canopy. Despite canopy dominance, there was a consistent lack of oak seedlings and saplings on our plots. We counted small numbers of oak seedlings even though several plots encompassed mature trees that produced acorns during this study.

The high mortality of live oak transplants in exclosure and control plots that we observed tended to confirm results of Warbington-Wells (2004) who noted acorns planted at the soil surface in an open field had highest survivorship relative to acorns buried deeper and shaded. Even if acorns were not consumed and successfully germinated, our results indicated seedlings would not survive under a dense canopy. We observed seedling and sapling loss of 96.3% in controls and 100% in exclosures from what appeared to be digging by small animals (e.g., squirrels) and shading (Bourdeau and Oosting, 1959). However, we did observe vigorous oak recruitment along island roadways and in open areas where
sunlight and temperature were conducive for germination/growth despite the opportunities for deer to browse.

Comparisons between exclosure and control plots located within a state-managed protected area did not reveal any significant differences in understory species diversity, stem density, or composition. We believe impacts of deer on the Bald Head Island maritime evergreen forest understory during 2007–2011 were minor. Continuation of the suggested carrying capacity of 100 animals (15–17/km²) (Stransky, 1969; Sherrill et al., 2010) was justified to protect the forest plus adjacent natural communities and to avoid conflicts with residential uses on the island.

Acknowledgments.—We thank staff and volunteers from the Bald Head Island Conservancy for transportation support and vital assistance with field work. Dr. Steven Brewer and his students set up all plots in 2007. The Village of Bald Head Island generously provided funding for the project. The manuscript was improved by thoughtful comments from Myla Aronson, Amy Long, Ian Thompson, and two anonymous reviewers.

LITERATURE CITED


