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Substrate-level Nest Site Selection of Sympatric Piping Plovers (*Charadrius melodus*) and American Oystercatchers (*Haematopus palliatus*) in New Jersey, USA

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Abstract.—Piping Plovers (*Charadrius melodus*) and American Oystercatchers (*Haematopus palliatus*) are shorebird species of conservation concern that breed sympatrically along the U.S. Atlantic coast, facing substantial anthropogenic habitat loss and disturbance. Interspecific aggression has been increasingly observed in overlapping habitat, potentially resulting in diverting time and energy that would be available for breeding activities. Because nests are camouflaged against the substrate, nest site habitat is important to fitness. Understanding habitat selection disparities could inform management of both species while ameliorating agonistic interactions. Nest sites in New Jersey were compared with paired random sites based on median proportions of substrate covered by rock, shell, wrack, plant, and other items (including peat and plastic litter). Both American Oystercatchers ($n = 37$ nests) and Piping Plovers ($n = 42$ nests) selected certain substrate features in amounts disproportionate to their availability, and interspecific differences were present. For American Oystercatchers, wrack constituted 17.7% of the substrate at nest sites versus 2.0% at paired sites. Piping Plover nest sites had greater proportions of shells, and medium fragments (2-64 mm) alone represented 18.9% of nest substrate versus 6.3% at paired sites. Results indicate that substrate management may be effective in creating ecological separation between these species. *Received 2 January 2019, accepted 22 May 2019.*

Key words.—American Oystercatcher, breeding behavior, *Charadrius melodus*, ecological separation, habitat selection, *Haematopus palliatus*, nest substrate, New Jersey, Piping Plover, shorebirds.

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Piping Plovers (*Charadrius melodus*) and American Oystercatchers (*Haematopus palliatus*) are two shorebird species of conservation concern that nest sympatrically on the east coast of North America. It is common for the two species to nest on the same beaches in their overlapping breeding ranges throughout the mid-Atlantic and northeastern United States (Elliott-Smith and Haig 2004; Nol and Humphrey 2012). Wherever species need similar habitat for critical life stages such as breeding, competition may affect fitness of one or both species and is an important consideration for management and conservation (Zanchetta *et al.* 2016). Hogan *et al.* (2018), who investigated agonistic interactions between Piping Plovers and American Oystercatchers in New York, suggested that plovers are more likely than oystercatchers to experience a reduction of fitness due to these interactions and that the number of interactions may be positively correlated to the nest density of these species. Maxson (2000) observed that Piping Plovers experience agonistic interactions frequently with several other sympatrically breeding species, like Killdeer (*Charadrius vociferus*), noting the impacts these aggressive encounters may have on survival and breeding success. These potentially harmful interactions may be mitigated by exploiting species-specific, fine-scale nest site preferences that are amenable to substrate management to create ecological separation.

Barrier islands provide breeding sites for Atlantic coastal populations of both species (Elliott-Smith and Haig 2004; Nol and Humphrey 2012; Schweitzer *et al.* 2017). A 2001 census demonstrated that among Atlantic populations, barrier islands hosted 39.2% of Piping Plovers recorded (Haig *et al.* 2005). American Oystercatchers are traditionally considered to be barrier island nesters, but in the last three decades, they have increasingly nested in marshes or other locales adjacent to barrier island systems, possibly indicating saturation and loss of habitat on the barrier islands (Lauro and Burger 1989; Shields and Parnell 1990; McGowan *et al.* 2005). However, habitat loss and degradation in either system may push oystercatchers to nest on whatever is most available given their demonstrated behavioral plasticity in breeding. When both species co-occur, American Oystercatchers may harass Piping Plovers, especially if plover broods enter their territory (Nol and Humphrey 2012). Agonistic interactions between closely related species may be detrimental for fitness of one or both species as it diverts time and energy from foraging and reproduction (Orians and Willson 1964). Both Piping Plovers and American Oystercatchers are of conservation concern, with the former being federally threatened (USFWS 2018). Thus, reducing agonistic interactions may be important for managing the two species where they co-occur.

Given how critical barrier islands are for both species, more information about specific nest sites selected on barrier islands is important for future conservation efforts. Piping Plovers nesting on Atlantic beaches typically have been observed adjacent to dunes, where vegetation is sparse, and on open sand, gravel, or cobble (Elliott-Smith and Haig 2004). Barrier island-breeding American Oystercatchers in North Carolina and New Jersey have nested on similar substrate, preferring sandy sites near salt marshes with varying vegetation density on ocean beaches, sand flats, and dunes (Lauro and Burger 1989; McGowan *et al.* 2005; Virzi 2008). In New Jersey, American Oystercatchers also have nested in tidal wrack deposits associated with marshes (Virzi 2008). Periodic flooding is common at oystercatcher nest sites which include open, flat sand, interdunal areas, overwash flats, and dune slopes. Habitat loss has brought nesting populations of these species closer together, possibly exacerbating competition and agonistic interactions. However, fine-scale habitat selection by both species may facilitate coexistence, and differences in nest site selection may make substrate-level management strategies viable in reducing negative interactions.

American Oystercatcher peak nest initiation occurs from late April to May in New Jersey (Virzi 2010). This onset is earlier than for Atlantic populations of Piping Plovers that demonstrate peak courtship initiations in early May with peak egg laying in New Jersey around mid-May (Burger 1987; Elliott-Smith and Haig 2004). Because oystercatchers arrive on the breeding grounds first, they may select their nest sites before plovers establish nests, thus possibly leading to exclusion of Piping Plovers from preferred habitat if species requirements are the same or very similar. Burger (1987) found that Piping Plovers in New Jersey tended to nest close to vegetation (mean distance ≤ 10 m) and dunes (mean distance ≤ 30 m) on flatter areas with 5-20% shell cover far from the high tide line (mean distance > 150 m). Beach-nesting American Oystercatchers in New Jersey have typically nested on high, sandy sites, often in tidal wrack deposits near salt marshes (Bent 1929; Lauro and Burger 1989; Virzi 2008).

Both Piping Plovers and American Oystercatchers deserve special attention because their breeding habitat is vulnerable and subjected to myriad human activities. Increasing shoreline development, pollution and litter, and direct human contact are of major concern for the conservation of critical coastal habitat and all species that depend on it (National Audubon Society 2016). Habitat loss for shorebirds is associated with coastal development, beach erosion due to sea-level rise, and artificial barriers to flooding that reduce intertidal habitat and decrease low tide exposure times (Ferns 1992; Jones *et al.* 2009; Sutherland *et al.* 2012). Additionally, peak times for human activity on beaches correspond with peak times of Piping Plover and American Oystercatcher breeding in these areas. Human disturbance could influence shorebird adult and chick behavior at nest locations and directly harm nests through trampling (Finney *et al.* 2005; Liley and Sutherland 2007; Sabine *et al.* 2008). Anthropogenic disturbance will likely escalate in the future as beach recreation becomes increasingly popular (Davenport and Davenport 2006). Limiting coastal development, human disturbance, and predation are major aims of coastal conservation efforts (Elliott-Smith and Haig 2004; Nol and Humphrey 2012).

The Holgate Unit of Edwin B. Forsythe National Wildlife Refuge is a barrier island in New Jersey that is designated as a federal wilderness area and hosts sympatric Piping

Plovers and American Oystercatchers. In 2017, 22 Piping Plover pairs nested on Holgate, 3 pairs less than in 2016, but above the 14.3 10-year mean number of pairs since 2008 (Heiser and Davis 2017). However, the fledging rate dropped from 1.44 fledglings/pair in 2016 to 1.05 fledglings/pair in 2017 (Heiser and Davis 2017). On the refuge, American Oystercatcher mean density was 2.7 ± 0.4 individuals/km^2 on average from 2005-2011, but between 2009 and 2011, no pairs on Holgate successfully fledged chicks (USFWS 2013). Conservation of Piping Plovers is particularly pressing in New Jersey where the population has not grown since being federally listed as threatened in 1986. Furthermore, an overall negative population growth ($\lambda = 0.91$) has been recorded for 20 years post-listing, which is unlike trends reported in most surrounding states (Hecht and Melvin 2009). Because our study site was closed to public use, it provided an opportunity to examine habitat separation between Piping Plovers and American Oystercatchers without human presence. Our goal was to understand differences in nest substrate selection between Piping Plovers and American Oystercatchers to inform conservation of the two species where they may be in conflict.

METHODS

Study Area

We conducted our study at the Holgate Unit (39° 30′ 44.3″ N, 74° 17′ 13.8″ W) of the Edwin B. Forsythe National Wildlife Refuge, an undeveloped portion of a barrier island in New Jersey that has an inlet at the southern tip. In total, there were 332 ha of barrier beaches, dunes, and tidal salt marsh at the Holgate Unit, providing habitat for beach-nesting birds such as Piping Plovers and American Oystercatchers (New Jersey Audubon 2014).

Field Methods

We collected data on nest site selection for Piping Plovers and American Oystercatchers from June to August of 2017. To measure substrate-level selection of nest sites for these two species, we located known nest attempts for the season by foot using GPS coordinates collected by local nest monitors. We collected data after a nest attempt was complete (either failed or hatched with chicks moved away from the nest site) to avoid disturbing nesting birds. We are aware that dynamic weather can alter substrate composition rapidly at such a small scale, so we tried to take measurements at nest sites as soon as we knew a nest attempt was complete, usually no longer than a week, to minimize alterations that could occur in the vicinity between attempt completion and measurement. For successful nests, measurements were recorded approximately 32 to 34 days after nest initiation.

Once at the location of the former nest, we placed a 1-m^2 quadrat made of string and PVC piping over the site, centered on the nest location. The frame consisted of two parallel string grids with 64 intersections spaced at 10 cm, with legs 0.5 m in length at each corner to minimize direct contact with the substrate. At each grid intersection, we used a straight metal stake (diameter = 5 mm) to indicate the point at which we recorded substrate type. Categories we included were sand (< 2 mm), pebble (2-64 mm), or cobble (> 64 mm), and small (< 2 mm), medium (2-64 mm), or large (> 64 mm) shell fragments for the rock and shell substrate respectively. We measured substrate size for these categories of rock and shell with a 30-cm ruler marked every 1 mm. We also recorded individual plants and pieces of wrack (washed up algae and nonwoody plant debris) in their own categories when found at the grid intersections and pooled other substrate items into an "other" category consisting of woody debris, peat, and plastic litter. We did not take measurements at the center four intersections of the grid because they surrounded the nest; in total, the area at the center of the quadrat that was excluded measured 900 cm^2. The center area is most susceptible to manipulation by the bird and therefore is the most likely portion to have substrate characteristics that are a product of the nesting bird's behavior post-selection. Thus, the substrate present at each intersection measured was calculated as 1/60$^{\text{th}}$ of the total substrate composition at the site.

To obtain an estimate of habitat availability, we sampled a paired point at a random bearing and distance from each nest within a 24-m radius around the sampled nest sites. We believed a 24-m radius would balance our sampling goal of sufficiently representing the surrounding available habitat on the beach with minimizing the chance of encountering another nest site of either species or an inaccessible area. We used a random number generator on a TI-84 Plus graphing calculator (Texas Instruments Inc., Dallas, Texas) to acquire a random bearing from 0 to 359 degrees and a random distance from 1 to 24 m. We repeated the procedure for placing the grid and recording the substrate at the 60 intersections (excluding the center four intersections).

Data Analysis

We used multiresponse randomized block permutation procedures (MRBP), a nonparametric analog of MANOVA that controls for block effects, to determine statistical significance in differences between nest sites and their associated random points with respect to proportions of selected substrate categories, where nest-random point pairs were the blocks. We conducted the MRBP with Blossom Statistical Software provided by the

United States Geological Survey (Cade and Richards 2008). For American Oystercatchers, we analyzed differences in proportions of rock, shell, plant, wrack, and other categories between nest sites and random points. Because plant and wrack were minimal (< 5%) in nest and random point plots for Piping Plovers, these categories were pooled into other. Thus, the analysis for Piping Plovers was based on rock, shell, and other.

For each species, we also conducted MRBP analyses to test for differences in proportion of the substrate covered by rocks and shells of different grain size between nest sites and random points. Categories included in the rock grain size analyses were sand, pebble, cobble, and other (representing any substrate that was not rock). Categories for the shell grain size analyses were small shell, medium shell, large shell, and other (representing any substrate that was not shell). For Piping Plovers, because rock constituted the major portion of substrate in the other category at both nests and random sites, we separated it out for the shell grain size analysis. Thus, the categories in this MRBP analysis were small shell, medium shell, large shell, rock, and other (representing any substrate that was not rock or shell).

We considered all tests to be significant at the α = 0.05 level. If we detected an overall difference in substrate composition between nest points and random points, we ran another MRBP on individual substrate components, using a Bonferroni adjusted α level of 0.05 divided by the number of comparisons (i.e., substrate components). We calculated multivariate median proportions of cover types using the MEDQ procedure in Blossom. We calculated univariate first and third quartiles in each substrate category to represent variation in proportion cover.

We also analyzed the distances that Piping Plovers and American Oystercatchers nested from the bay and ocean shorelines and the toe of the primary dune. Using perpendicular measurements taken in ArcMap 10.6.1 (Environmental Systems Research Institute 2018) from each nest to either shoreline and the dune line, we compared distances nests were established from the shorelines and dunes between the two species. We categorized nests as within 1,000 m ("near") of the inlet center or those farther than 1,000 m ("far") from the inlet center because the barrier island physiography was nonlinear within 1 km of the inlet, and distances to shorelines would be expected to be different near the inlet than far from it. We modeled the effect of species and proximity to inlet on nest-shoreline distances using two-way factorial ANOVA using the l m function in R (R Development Core Team 2016). We also used one-way ANOVA to analyze the species effect on distances nests were established from dunes (R Development Core Team 2016).

RESULTS

We collected data at 37 nest sites and paired random points for 18 pairs of American Oystercatcher and at 42 nest sites and paired random points for 22 pairs of Piping Plovers on Holgate. All nest attempts occurred during the 2017 breeding season and included renests. For American Oystercatchers, substrate composition differed between nests and random points (Pearson Type III Test Statistic = -10.6, $P < 0.001$; Fig. 1). Wrack comprised a greater proportion of ground cover at nest sites than random sites, while rocks made up a larger proportion of the substrate at random sites than nest sites (Fig. 1). We found no difference in the proportion of the substrate composed of particular grain sizes of rock or shell, and both used and unused locations lacked pebbles and cobbles.

For Piping Plovers, substrate composition also differed between nests and random points (Pearson Type III Test Statistic = -11.3, $P < 0.001$; Fig. 2). Rocks made up a larger proportion of the substrate at random sites than at nest sites, and shells composed a larger proportion of the substrate at nest sites than at random sites, but the "other" category did not differ in median proportions between nest and random sites (Fig. 2). There were no differences in substrate composition based on rock grain size. However, Piping Plovers did appear to select nest sites with more medium and large shells (Fig. 2).

There was no difference in the distance Piping Plovers and American Oystercatchers nested from the ocean shoreline regardless of whether nests were established near the inlet or far from it (ANOVA, $F_{3,75} = 2.7$, $P = 0.051$; Table 1). We also found no difference between Piping Plovers and American Oystercatchers in the distance from the nest to the bay shoreline, regardless of proximity to the inlet (ANOVA, $F_{3,75} = 1.4$, $P = 0.246$; Table 1). Moreover, there was no difference in the distance from nests to the dune line (ANOVA, $F_{1,77} = 1.4$, $P = 0.248$) between American Oystercatchers (n = 37, mean ± SE = 123.2 ± 20.9 m) and Piping Plovers (n = 42, mean = 91.9 ± 16.8 m). Active plover nests were located an average of 156.0 m (± 20.9) from the closest active oystercatcher nest with a minimum distance of 31.4 m. Piping Plovers, on average, nested closer to conspecifics (155.5 ± 19.7 m) than American Oystercatchers (386.6 ± 56.4 m).

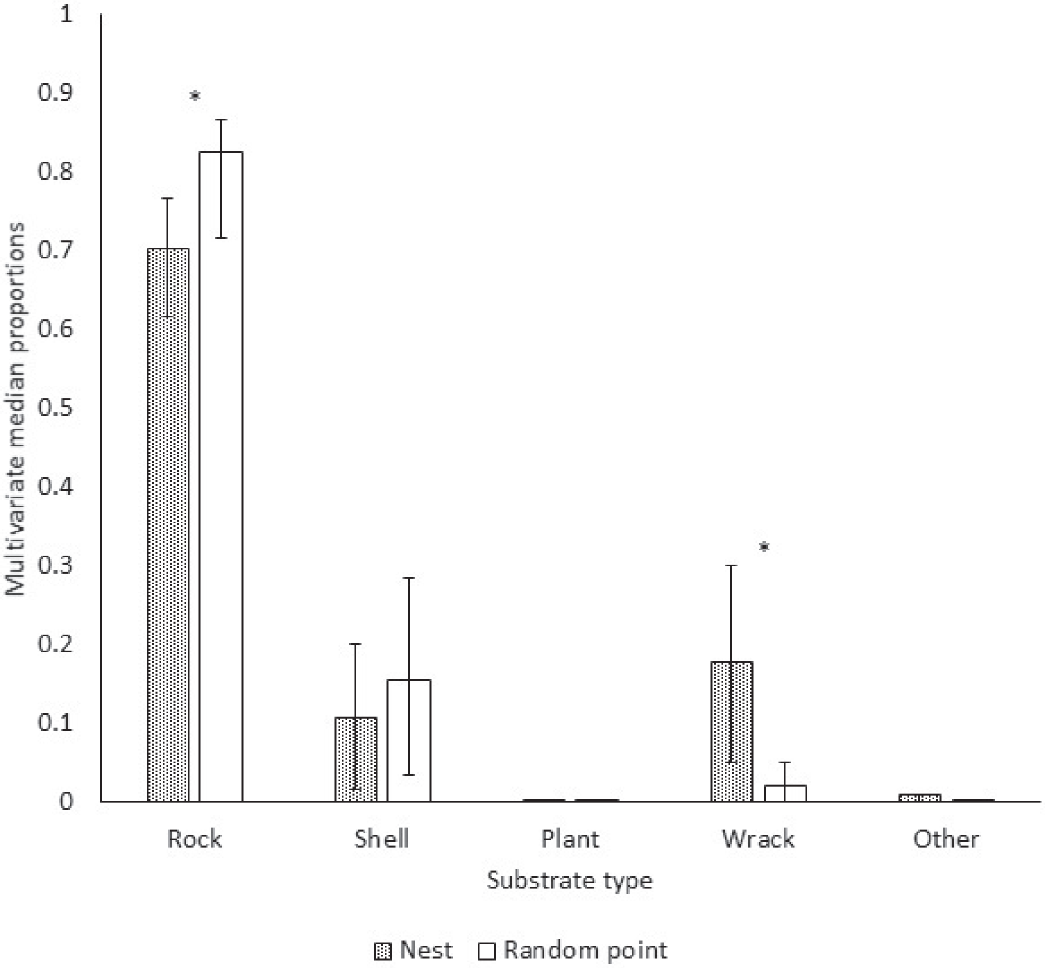

Figure 1. Median proportions of rock, shell, plant, wrack, and other substrate types combined at nest sites and random points for American Oystercatchers (*Haematopus palleatus*) on the Holgate Unit of Edwin B. Forsythe National Wildlife Refuge, New Jersey, USA in 2017. Error bars represent univariate interquartile ranges. Asterisks indicate pairs of medians that are significantly different at $\alpha = 0.05$, after a Bonferroni correction for multiple comparisons. (Multiresponse Randomized Block Permutation Procedure, Bonferroni-adjusted $\alpha < 0.01$).

DISCUSSION

Our results suggest that Piping Plovers and American Oystercatchers select nest sites based on different substrate characteristics. Plovers nested in areas with greater proportions of shelly substrate compared to the surrounding area, and most of these shell grains were of medium size. This finding is consistent with previous research indicating that Piping Plovers tend to nest in areas with debris such as shells (Cairns 1982; Burger 1987; Espie *et al.* 1996). Vegetation and wrack appear to have been avoided in nest site selection by Piping Plovers, possibly even at the scale of the nesting area as indicated by the low proportion of such items at random sites within 24 m of the nests. Past studies also indicate that Piping Plovers nest in areas with little vegetation (Cairns 1982; McIntyre *et al.* 2010), although Burger (1987) demonstrated that they will nest near vegetation at certain sites in New Jersey. The Holgate Unit had limited vegetation apart from the dunes at the interior and marshy areas on the bay side of the barrier island, but most of the nest attempts were located outside the dunes in shelly sand flats. The nest site selection we observed was

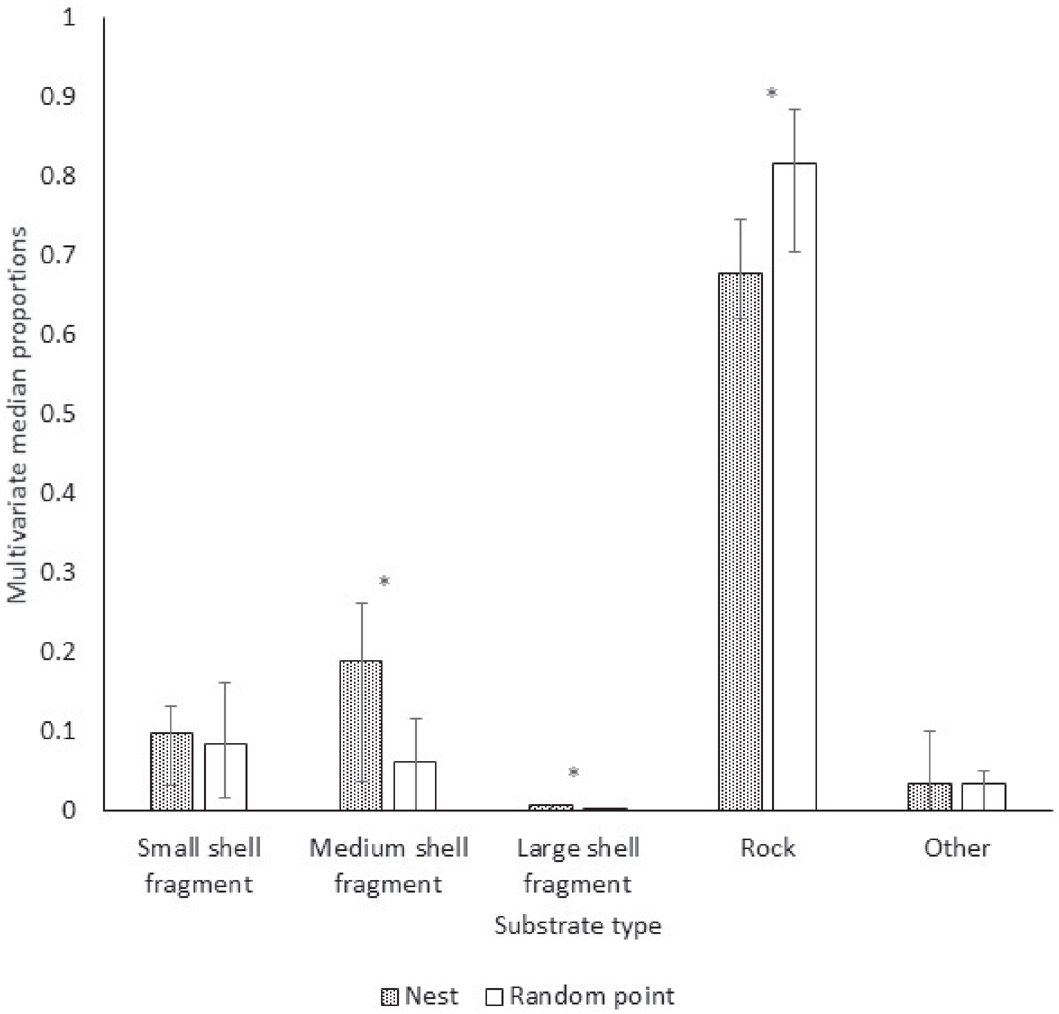

Figure 2. Median proportions of small shell fragments (<2 mm), medium shell fragments (2-64 mm), large shell fragments (>64 mm), rocks, and other substrate types combined at nest sites and random points for Piping Plovers (*Charadrius melodus*) on the Holgate Unit of Edwin B. Forsythe National Wildlife Refuge, New Jersey, USA in 2017. Error bars represent univariate interquartile ranges. Asterisks indicate pairs of medians that are significantly different at $\alpha = 0.05$, after a Bonferroni correction for multiple comparisons. (Multiresponse Randomized Block Permutation Procedure, Bonferroni-adjusted $\alpha < 0.01$).

consistent with their behavior when constructing nests. Piping Plovers scrape in sandy substrate and tend to line their nests with broken shells that they accumulate during courtship and incubation if present (Cairns 1982). This shelly debris may aid in concealing the nest to some extent, and greater nest crypsis has been shown to increase nest success in various plover species (Nguyen *et al.* 2007; Wiltermuth *et al.* 2009; Hardy and Colwell 2012).

Selection of wrack by American Oystercatchers that we observed was consistent with previous studies indicating that oystercatchers prefer areas with plant debris such as eelgrass (*Zostera marina*) and straw (Bent 1929; Lauro and Burger 1989; Virzi 2008). In agreement with Lauro and Burger (1989), we also noted that many of the nest attempts were located at a distance from the waterline where wrack had been deposited and partially covered with sand over time. Perhaps wrack doubles as a tool to enhance camouflage of nests and to ameliorate threats of flooding by acting as a small barrier to encroaching tides, though further research is necessary to determine the extent to which

Table 1. Mean and standard error of distances Piping Plover (PIPL) and American Oystercatcher (AMOY) nests were established from ocean and bay shorelines depending on nest proximity to the inlet center on the Holgate Unit of Edwin B. Forsythe National Wildlife Refuge, New Jersey, USA in 2017.

		PIPL			AMOY		
Shoreline Type	Distance to Inlet (m)	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
Ocean	>1000	35	187.9	10.0	29	188.9	14.8
	<1000	7	271.1	28.8	8	260.6	71.0
Bay	>1000	35	202.3	14.7	29	217.6	28.5
	<1000	7	315.5	55.8	8	226	59.8

wrack may confer these benefits. As with Piping Plover nest sites, beach plants were largely absent near nest sites, which agrees with previous work on the species (Lauro and Burger 1989). Human development and activity along the coastline that affects wrack deposition may have implications for American Oystercatchers. Eriander *et al.* (2017) found that shading in the shallow areas, where development is greatest, reduced eelgrass coverage by an average of 42-64%. Eelgrass constituted a major part of the wrack that we found in and around oystercatcher nests; therefore, its reduction could be detrimental to their breeding success.

At Holgate, landscape-level habitat selection by both species may favor areas that are sandier without coarser grain rocks, as our study area was devoid of pebbles and cobbles. Thus, at this larger scale, the two species are likely attracted to similar habitat. At the substrate level, our results indicate that American Oystercatchers and Piping Plovers should not compete directly for nest sites. However, because American Oystercatchers initiate nesting earlier in the season than Piping Plovers, it is possible that plovers would nest in areas with different proportions of substrate types if the larger oystercatchers were not already present. On Holgate, oystercatchers arrived and initiated nests earlier than plovers and actively nested throughout the entire period plovers nested. Future research on nest survival as a consequence of habitat selection by the two species could shed light on whether current habitat selection is detrimental. Flemming *et al.* (1992) observed Piping Plovers nesting in similar substrate to our study, primarily with rocks and shells where available, on beaches in New Brunswick and Nova Scotia, where American Oystercatchers are not present. However, they also noted that plovers demonstrated some geographic variation in nest site selections despite similarity in substrate availability among sites (Flemming *et al.* 1992). This geographic variation in nest site selection could only be controlled if the same site had both species in one year, did not undergo drastic changes to the habitat, and then only had Piping Plovers in a later year to test if plover nest site selection changed without the presence of the oystercatchers.

We did not observe agonistic interactions between Piping Plovers and American Oystercatchers on our study site during monitoring in 2017, although these have been recorded there previously. Heterospecific nest sites generally were not very close together. Active nests of plovers and oystercatchers were separated by a distance of at least 31.4 m, and most nests were > 100 m away from the closest active nest of the other species. When we saw aggressive interspecific interactions, it was when chicks had already hatched on smaller sites with denser nesting populations compared to Holgate. Holgate provides vast foraging habitat, especially for such low nesting densities, ameliorating congestion and overlap of habitat use on the site. Parents of both species on our study site had fairly well-defined foraging territories with little observed conspecific or heterospecific brood interactions.

Substrate-level differences in nest site selection may not be a matter of present competitive interactions but could be a result of divergence through past competition or separate evolutionary pathways (Connell 1980).

Such divergence would indicate that ecological separation may be beneficial in simultaneous management efforts. Conservation efforts could create areas of greater ecological separation between these beach-nesting bird species through substrate management to reduce agonistic interactions between them. For Piping Plovers and American Oystercatchers, which both already face numerous other threats, agonistic interactions between each other and other sympatric species could create an additional source of productivity impairment. The extent to which these interactions negatively impact reproductive success is an area that has been investigated but should be explored further (Hogan *et al.* 2018). Nevertheless, management actions should be most effective if they promote greater ecological separation between the species to alleviate potential conflict. Fine-scale substrate manipulation could aid in this effort, including the manual distribution of wrack (for oystercatcher nesting) and shells (for plover nesting) in different areas of a breeding site. Wrack should not be moved or removed from breeding sites, as wrack often hosts numerous invertebrate prey species, providing important foraging habitat for plovers (Elias *et al.* 2000; Maslo *et al.* 2012). Removal or movement of wrack already present on the beach would thus adversely impact both oystercatchers and plovers. Instead, adding patches of wrack in certain areas may entice oystercatchers to nest there. In a similar manner, adding medium-sized shell fragment patches may be effective in encouraging nesting in areas conducive for ecological separation.

Further investigation could include manipulative experiments that alter the availability of substrate to observe how site preferences change and should include a focus on breeding success. Similar studies could be conducted on sites with different substrate composition where these species nest sympatrically to determine the behavioral plasticity of each species in choosing nest sites and to compare reproductive success based on nest site substrate. Given the impressive behavioral plasticity demonstrated by American Oystercatchers in selecting nest sites, some even found nesting on rooftops and parking lots in New Jersey, it may prove difficult to influence where they nest through substrate management. However, our results indicate that creation of ecological separation via fine-scale substrate management may be possible, especially through the addition of large patches of medium-sized shells for piping plovers. Further study is necessary to determine the extent of separation needed to effectively ameliorate agonistic interactions to aid in concurrent conservation of both species.

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