

Nocturnal roost on South Carolina coast supports nearly half of Atlantic coast population of Hudsonian Whimbrel *Numenius hudsonicus* during northward migration

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Hudsonian Whimbrel *Numenius hudsonicus* are rapidly declining and understanding their use of migratory staging sites is a top research priority. Nocturnal roosts are an essential, yet often overlooked component of staging sites due to their apparent rarity, inaccessibility, and inconspicuousness. The coast of Georgia and South Carolina is one of two known important staging areas for Atlantic coast Whimbrel during spring migration. Within this critical staging area, we discovered the largest known Whimbrel nocturnal roost in the Western Hemisphere at Deveaux Bank, South Carolina. Surveys in 2019 and 2020 during peak spring migration revealed that Deveaux Bank supports at least 19,485 roosting Whimbrel, which represents approximately 49% of the estimated eastern population of Whimbrel and 24% of the entire North American population. The high concentrations of Whimbrel at Deveaux Bank may allow nocturnal roost counts to efficiently track population trends and add greater accuracy to current population estimates. We found that dates within two days of the full moon, when civil twilight and high tide are 30–60 minutes apart, enable more complete and accurate counts. We thus recommend joint consideration of tide and lunar phase for future surveys. The discovery of Deveaux Bank has conservation implications throughout the flyway and presents a unique opportunity to improve our understanding of the role nocturnal roost sites play in the staging ecology of Whimbrel.

Keywords

site fidelity
stopover
staging area
population estimate
management
conservation

INTRODUCTION

North American shorebirds have experienced steep declines, with an overall 37% decrease across species from 1970–2018 (Rosenberg *et al.* 2019). Hudsonian Whimbrel *Numenius hudsonicus* (hereafter Whimbrel) are experiencing an even sharper decline: peak numbers in the Atlantic flyway decreased nearly 50% over a 15-year period beginning in the early 1990s (4.2% per year; Watts & Truitt 2011). This precipitous decline may be partly attributable to the degradation and loss of staging areas (Watts *et al.* 2019), and studies to better understand the role these areas play in Whimbrel ecology are considered a top research priority (Wilke & Johnston González 2010).

Whimbrel breed across much of Arctic and sub-Arctic North America (Gill & Rasmussen 2020). Published

literature describes two distinct breeding populations with disjunct ranges: the eastern population breeds west and south of Hudson Bay and the western population breeds from coastal Alaska east to the Northwest Territories (Skeel & Mallory 2020), but recent work has divided the western population into two separate breeding populations (B. Watts pers. comm.). Genetic analyses and satellite tracking of Whimbrel from both their eastern and western breeding areas suggest they are separate populations, although mixing may occur, especially at non-breeding sites (Watts *et al.* 2008, Skeel & Mallory 2020).

During northbound migration, the eastern population of Whimbrel are highly site-faithful to a few key staging areas, perhaps relying exclusively on only two regions along the mid-Atlantic seaboard of the United States: the

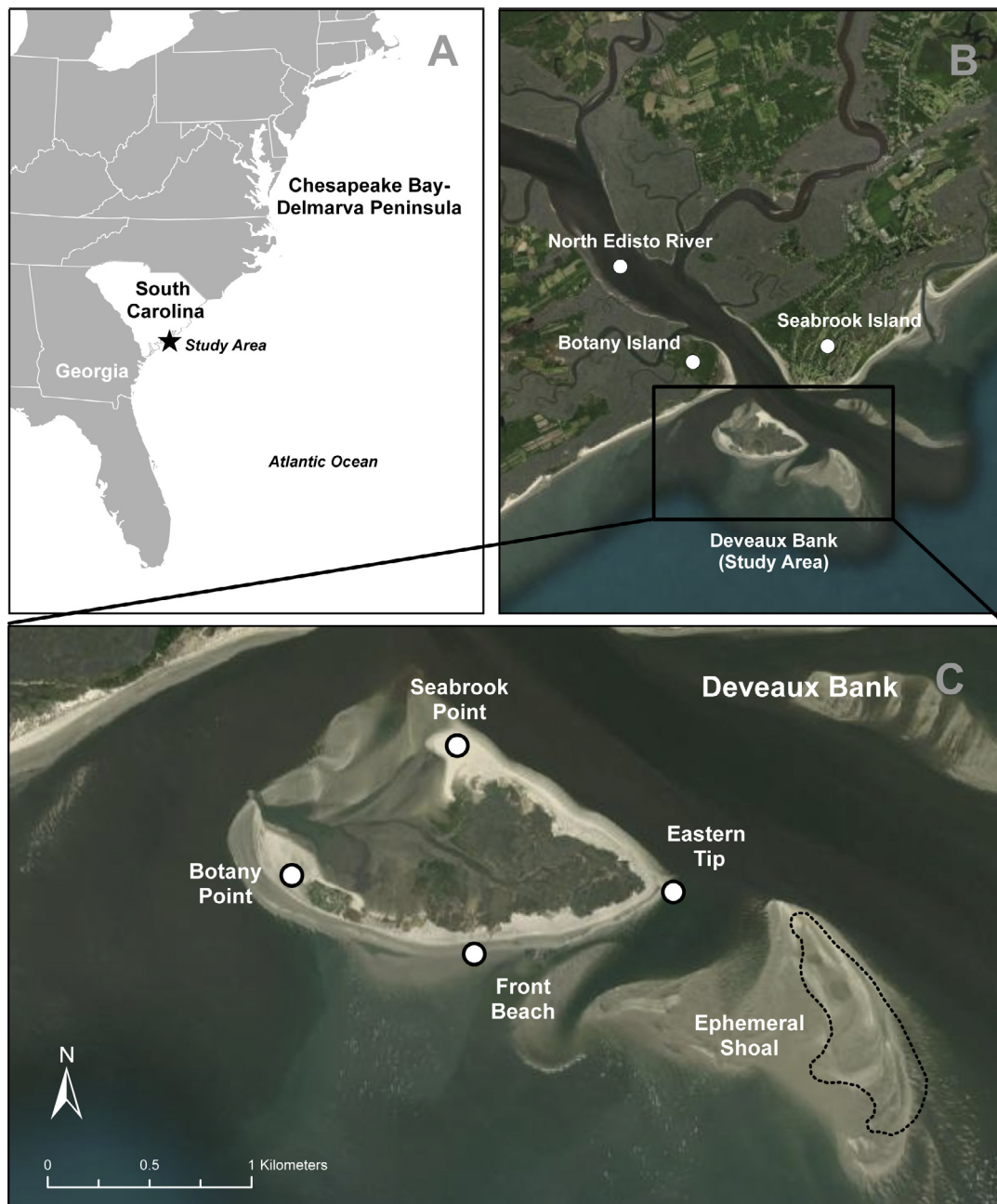


Fig. 1. Map showing the location of Deveaux Bank, Charleston County, South Carolina ($32^{\circ}33'10''\text{N}$, $80^{\circ}10'53''\text{W}$). (a) Deveaux Bank's location along Atlantic seaboard of southeastern United States, (b) Deveaux Bank's location on the South Carolina coast, and (c) locations of four distinct Whimbrel roosts on the island.

Chesapeake Bay-Delmarva Peninsula and the coast of Georgia and South Carolina (Fig. 1). Whimbrel stage in these regions from late April to the end of May (26–40 d; Johnson *et al.* 2016) and maintaining their habitat quality is thought to be critical to Whimbrel population dynamics. These staging areas must provide abundant and high-quality food resources to not only fuel a final jump to Arctic breeding grounds (Warnock 2010), but also sufficient reserves to allocate to territory acquisition and egg-development upon arrival (Hobson & Jehl 2010). Accordingly, individuals in other shorebird species departing staging areas in poor condition often have low subsequent survival

and reproductive success (Tulp *et al.* 2009, Rakhimberdiev *et al.* 2018).

In addition to prey-rich foraging areas, staging areas must include suitable roost sites that provide a safe place to rest away from predators and other disturbances when feeding areas are inundated or inaccessible (Rogers *et al.* 2006a). However, little is known about the physical and environmental factors that determine the suitability of safe roost sites. This is especially true for nocturnal roosts, because they are often distinct from, and more remote than, daytime roosts and thus more difficult to locate and access (Dickens 1993, Sitters *et al.* 2001, Rogers *et al.* 2006b).

Safe nocturnal roost sites are often farther from mainland beaches and forests than diurnal sites to reduce the risk of predation by nocturnal predators such as owls (Piersma *et al.* 2006). The availability of these sites is thus more limited than that of diurnal roosts, and shorebirds are often more faithful to nocturnal than diurnal roosts (Conklin & Colwell 2007). This site-fidelity heightens the importance of identifying and protecting key nocturnal roosts.

In 2014 we discovered a large nocturnal roost of eastern Hudsonian Whimbrel at Deveaux Bank, South Carolina in one of the two known critical staging areas: the coasts of Georgia and South Carolina. In the following years, we visited Deveaux Bank in the evening during April and May, observing large roosting flocks, with over 10,000 Whimbrel roosting at Deveaux Bank on 1 May 2018. In 2019 and 2020 we conducted surveys to: (1) document the size of the nocturnal roost at Deveaux and (2) improve our protocol for counting Whimbrel by examining tide timing and lunar phase in relationship to our ability to estimate the size of the nocturnal roost. Given their high inter-annual fidelity to staging areas, as well as to specific foraging and roosting sites within these staging areas (Watts *et al.* 2021), documenting this important Whimbrel nocturnal roost site offers an opportunity to improve our ability to monitor population sizes, further our understanding of the use of nocturnal roost sites for Whimbrel, and inform conservation actions.

METHODS

Site description

Deveaux Bank, Charleston County, South Carolina (32°33'10"N, 80°10'53"W; hereafter Deveaux) is an ephemeral, horseshoe-shaped, vegetated sandbar at the mouth of the North Edisto River on the northeastern edge of the ACE Basin, a 142,000 ha multi-use conservation area (SCDNR 2009) – one of the largest wetland estuarine systems on the Atlantic coast of the U.S. (Fig. 1). Deveaux is owned and managed by the South Carolina Department of Natural Resources (SCDNR) as a Seabird Sanctuary and Heritage Preserve. Deveaux supports thousands of nesting waterbirds and, in recent years, the largest Brown Pelican *Pelecanus occidentalis* rookery on the Atlantic coast of the U.S. (SCDNR unpubl. data). The island is approximately 100 ha at low tide, although it is constantly shifting and changing in a cycle of erosion and accretion. It has approximately 3.7 km of sandy beach and a shallow tidal bay. Average elevation on the island is 1 m, with some areas being completely submerged during high tide (mean high tide during study: 1.9 m; NOAA 2020) leaving approximately 26 ha of dry roosting area. In addition, approximately 0.5 km east of Deveaux is a recently accreted 10 ha intertidal sandbar that is exposed at lower tides, but underwater when tides are over approximately 1.7 m. Deveaux is closed year-round above the high-water line, except for a section on its north side that is designated for limited recreational use. Additionally, a portion of the intertidal beach zone is closed seasonally to protect seabird nesting colonies.

Roost counts

We conducted five surveys on Deveaux during the peak of northbound Whimbrel migration in South Carolina: three in 2019 (4, 16, and 17 May) and two in 2020 (4 and 5 May). Prior to this study, we observed Whimbrel arrival at Deveaux on nights when high tide occurred after midnight and tide height was low enough to leave the nearby shoal exposed. On these nights, we saw few Whimbrel arrive at Deveaux before civil twilight. For example, on 9 May 2018, when high tide was at 04:20 hrs, we observed approximately 50 Whimbrel at Deveaux before twilight. Thus, we selected survey dates near the spring tide, when foraging areas are inundated near sunset, and high tide and civil twilight are no more than 125 minutes apart.

We conducted our surveys from four distinct locations on the island: Botany Point, Seabrook Point, Eastern Tip, and Front Beach (Fig. 1c). All members of the team had previous experience conducting shorebird surveys and practiced flock size estimation before counting in the field. One to two counters were stationed at each location to watch all directions for arriving Whimbrel and help corroborate count estimates in real time. Any researcher on their own at a location used a voice recorder to document counts. To ensure no birds were double counted, each team logged when birds that had already been counted left their area (i.e., due to disturbance, such as flyovers by Bald Eagles *Haliaeetus leucocephalus*) and subtracted these from their totals. If these flocks subsequently settled at a different roost area, they were counted at that location. Due to logistical challenges, we were only able to count Whimbrel at two or three locations each night.

We began counting birds as soon as flocks flying towards Deveaux were visible over the water (~0.5 km). Most groups were made up entirely of Whimbrel, although occasionally Willet *Tringa semipalmata* and dowitchers *Limnodromus* sp. were interspersed in the flocks. These two species are clearly distinguished by their bright white wing stripe and much smaller body size, respectively, and were excluded from our counts. Whimbrel continued to arrive at the island after dark, making it extremely challenging to get a complete count. On each survey night we continued counting until Whimbrel stopped arriving or it became too dark to count accurately (i.e., civil twilight). All but one count date (4 May 2019) was within three days of a full moon, maximizing our ability to count as late as possible by moonlight.

RESULTS

Abundance

Total nightly Whimbrel counts ranged from 8,974–19,485 (Table 1). The highest one-night total (17 May 2019) was tallied from only two roost locations (Front Beach and Botany Point), but the waxing gibbous moon was nearly full, at 98%, and the sky was clear, providing better visibility and more moonlight than other survey nights.

Patterns of arrival

During each survey, the first flocks of Whimbrel arrived from the mainland, primarily flying out of the mouth of the North Edisto River and nearby inland marshes. The last flocks arrived only from across the ocean to the southwest. Although we did not always quantify arrival directions, we consistently witnessed this pattern. For example, on 17 May 2019, all Whimbrel that arrived in the last hour (21:00–22:00 hrs) came from the southwest.

Lunar phase dictated how long we could continue counting after civil twilight. On all nights except 17 May 2019, Whimbrel continued to arrive after we finished counting; our totals are thus minimum estimates. On 4 May 2019, the only survey that took place on a new moon, we could hear Whimbrel continuing to land on Deveaux, but our inability to see forced us to end the survey at civil twilight. On 17 May 2019, just one night before the full moon, we were able to continue for 80 minutes after civil twilight. With the aid of these brighter moonlight conditions, 17 May 2019 was the only night that the survey ended because birds stopped arriving, with only 10 individuals counted in the last 40 minutes of the survey. On this night, 34% of all Whimbrel counted arrived after civil twilight. On all nights, more Whimbrel arrived during the half-hour survey intervals that started just before or after civil twilight than during any other time interval (Fig. 2).

DISCUSSION

Nocturnal roost sites are a vitally important, yet often underappreciated and inconspicuous component of migratory staging sites. Our surveys revealed that Deveaux Bank, South Carolina – a previously unknown nocturnal roost site – supports at least 19,485 roosting Whimbrel during peak spring migration. This is the largest nocturnal roost known for this species and our counts represent 22–49% of the estimated eastern population of Whimbrel (40,000) and 11–24% of the entire North American population (80,000; Andres *et al.* 2012). Whimbrel have been steadily declining for the past three decades (Watts & Truitt 2011) and mortality rates during migratory periods are five times higher than other periods of the year (Watts *et al.* 2019). Northward migration staging sites may therefore be especially crucial in the Whimbrel annual cycle. Although Deveaux Bank presents an opportunity to focus research on one island that may benefit an entire population, the unprecedented concentration of Whimbrel on an ephemeral sandbar is of concern and a reminder that a network of suitable roosting sites is crucial for long-term conservation of this species.

Conservation implications

To address global shorebird population declines, one key conservation strategy is to identify networks of key sites that host significant proportions of populations to effectively focus conservation efforts. The Western Hemisphere Shorebird Reserve Network (WHSRN) currently recognizes 107 sites in 17 countries that range from Regional ($\geq 10\%$

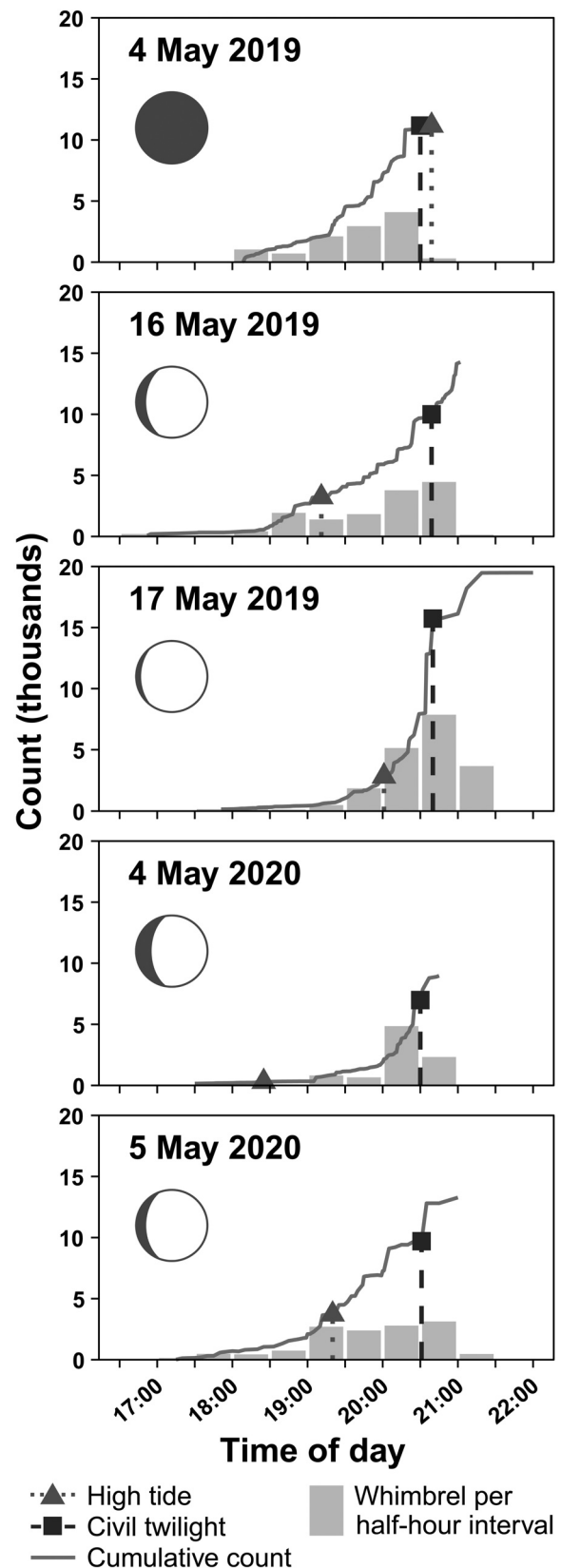


Fig. 2. Timing of Whimbrel arrival at the Deveaux Bank nocturnal roost in relation to high tide and civil twilight. Plotted line shows cumulative Whimbrel count over the course of each survey and bars represent the number of birds counted in each half hour. Vertical dotted and dashed lines show time of high tide and civil twilight, respectively. Moon icons in upper left corners indicate lunar phase on each survey night.



Fig. 3. Video frame of Whimbrel at Deveaux Bank, South Carolina. This clip was recorded during pre-dawn conditions in May 2019 as Whimbrel departed the roost *en masse* for foraging grounds (video: Matt Aeberhard/Cornell Lab of Ornithology).

of a species' biogeographic population) to Hemispheric Importance (>30% of a biogeographic population).

The largest number of Whimbrel reported at any site in the WHSRN network is 10,880 (~27% of the biogeographic population) from the 2.7 million ha Reentrâncias Marenhenses State Protected Area in Maranhão, Brazil (WHSRN 2019), which is likely a core wintering area for Whimbrel that use Deveaux (Johnson *et al.* 2016). There are eight other sites in the Network that were designated based on their importance to Whimbrel, however all qualified at the level of Regional Importance (WHSRN 2020). Deveaux would thus be the first site of Hemispheric Importance proposed for WHSRN nomination for this species. Such recognition would increase regional awareness of the roost and cultivate the public support needed to ensure Deveaux's continued protection.

Limited roost availability

The large concentration of Whimbrel at a single roost site suggests that suitable nocturnal roosts are rare in South Carolina and, perhaps, Georgia. Combined with our observation that individuals arrived first from nearby inland marshes and hours later from the south, evening observations of large flocks of Whimbrel flying in the direction of Deveaux from 50 km to the south in Port Royal, South Carolina further suggest roost sites are limited (FJS unpubl. data). Long-term monitoring of shorebirds on the South Carolina coast also shows that Deveaux is one of only three Whimbrel nocturnal roosts in the state used during spring migration and that the others host far fewer Whimbrel than Deveaux (e.g., 1,100–2,000 individuals; FJS unpubl. data).

There appear to be few spring nocturnal roost sites in any of the other Whimbrel staging areas on the Atlantic Americas flyway as well. For instance, a recent satellite tracking project identified only 12 nocturnal roosts used by Whimbrel during their spring migration from Brazil to the breeding grounds, although some sites could have been missed (Watts *et al.* 2021). Importantly, the satellite

tracking studies that discovered these sites showed that individual Whimbrel are highly faithful to specific roosts both during staging periods and across repeated migration seasons. Roost availability may thus strongly constrain shorebird distributions within staging areas (Rogers *et al.* 2006a) and studies are needed to uncover the specific combination of factors that determine the suitability of nocturnal roost sites for Whimbrel. Ultimately, identifying active roost sites and protecting a network of offshore habitats in known critical staging areas may be a key conservation measure to increase the survival of Whimbrel and other shorebirds during migration.

Coastal management implications

In South Carolina, the limited number of Whimbrel roosts may be the result of human alteration of coastal areas. Shifting islands and shoals, such as Deveaux, form naturally at river mouths from sediment deposits (Eisma *et al.* 1998). However, human activities, such as the placement of physical structures to protect against coastal erosion, mining intertidal sand for beach renourishment projects, and dredging shipping channels can alter natural shoreline processes (Dugan *et al.* 2011). Much of the Atlantic coast of the United States now has hard structures that limit coastal migration and the natural accretion of islands (Pilkey & Wright 1988, Rice 2015). This has important implications for Deveaux: we first discovered large numbers of Whimbrel using Deveaux in 2014 but are unsure how long the island has been an important roost site. Deveaux was known to be important for nesting waterbirds in the 1930s, then disappeared after Hurricane David in 1979 (SCDNR unpubl. data). To mitigate the potential ephemerality of the island, identifying or creating (e.g., Burton *et al.* 1996, Lilleyman *et al.* 2020) a network of alternative roost sites is a necessity.

Survey method implications

A key priority for Whimbrel conservation is estimating their population size and trends (Wilke & Johnston González 2010). South Carolina has approximately 200,000 ha of

saltmarsh, more than any other Atlantic coast state (SCDNR 2015). During both diurnal high and low tides, Whimbrel are dispersed throughout these vast marshes and are therefore difficult to census during the day (Wallover *et al.* 2015). Although evening counts are also challenging, we observed Whimbrel arriving to Deveaux over the span of only a few hours, thus enabling more accurate flock estimates. High concentrations of shorebirds at nocturnal roosts thus offer unique opportunities to assess population trends of Whimbrel and other saltmarsh shorebird species (Fig. 3).

Over the course of our study, we improved our knowledge of how to accurately count Whimbrel at Deveaux and, likely, nocturnal roosts more generally. Joint considerations of both tide timing and lunar phase are essential for choosing count dates. For example, our lowest count occurred on 4 May 2020. On that date, high tide was earlier than for other survey dates (at 18:25 hrs, 125 min before civil twilight). Early arrivals foraged as the tide fell prior to twilight and we heard flocks of Whimbrel arriving after the survey. We hypothesize that these conditions may have allowed Whimbrel to wait at dispersed diurnal roosts for the tide to recede to forage before departing to Deveaux closer to civil twilight. The results of this survey indicate there may be a threshold at which high tide occurs too early in the evening to enable a complete count, but this relationship needs further investigation.

However, synchronous nightfall and high tide may shorten the arrival period for Whimbrel at high tide roosts. Our surveys on 16 May 2019 and 5 May 2020, for instance, shared identical lunar phases, had similar intervals between high tide and civil twilight (88 and 71 min, respectively), had similar survey end times, and yielded similar counts (14,271 and 13,278 Whimbrel, respectively; Table 1). Furthermore, our highest count on 17 May 2019, not only had the brightest moonlight conditions, but a high tide that was only 39 minutes before civil twilight. The combination of close synchrony between high tide and civil twilight – with high tide occurring first – may therefore be the optimal counting conditions at nocturnal roosts.

Tide height is an additional factor to consider when selecting count dates. A study in South Carolina's Cape Romain National Wildlife Refuge that examined the use of another nocturnal roost similar in size and vegetation structure to Deveaux found that American Oystercatchers *Haematopus palliatus* used a nearby intertidal sandbar at night when it was exposed (Sanders *et al.* 2013). The oystercatchers only used the larger vegetated island on nights when tides were high enough to flood the sandbar. We found that Whimbrel also roost on the intertidal shoal just east of Deveaux (Fig. 1c) if it is exposed at night (MCH & FJS unpubl. data). These shoals do not have vegetation and this open space may be preferable to shorebirds at night (Handel & Gill 1992). To get accurate counts at vegetated nocturnal roosts, we therefore recommend selecting dates near spring tide within two days of the full moon when civil twilight and high tide are 30–60 minutes apart.

Logistical challenges also resulted in variation in our counts. Limited boat access on the Eastern Tip and efforts to reduce disturbance to roosting birds made it impossible to station counters at all known roost locations on each survey night. Some of the obstacles associated with this study may be overcome by exploring tools such as telemetry, radar, and night vision technology.

Given their apparent rarity and frequent inaccessibility, simply finding nocturnal roost sites must become a priority to incorporate these insights into monitoring and management protocols. Continuing to fine-tune nocturnal roost survey methods, however, could provide an efficient way to track shorebird population trends and add greater accuracy to current population estimates.

Human disturbance

One of the major threats to Whimbrel during migration is human disturbance (Wilke & Johnston González 2010). Deveaux Bank is located within Charleston County, which has a growing human population nearing half a million residents (U.S. Census Bureau 2019), and is just 1 km from

Table 1. Number of Whimbrel counted during evening surveys at Deveaux Bank in relation to high tide and civil twilight. Whimbrel continued to arrive after the end of the survey, except on 17 May 2019, and roosted at four locations on the island thus survey results are minimum estimates.

Date	Whimbrel	Survey start time	Survey end time	Moon phase	Locations # surveyed	High tide	Civil twilight	Whimbrel counted after twilight (% of total)
4 May 2019	11,178	18:08	20:30	new moon	2	20:39	20:30	3
16 May 2019	14,271	16:52	21:02	2 d before full moon	3	19:11	20:39	30
17 May 2019	19,485	17:51	22:00	1 d before full moon	2	20:01	20:40	34
4 May 2019	8,974	17:30	20:45	3 d before full moon	3	18:25	20:30	26
5 May 2019	13,278	17:15	21:00	2 d before full moon	3	19:20	20:31	26

Seabrook Island, a vacation destination. Deveau's sandy beaches are a popular place for fishing and swimming, and human disturbance includes beach recreation, dogs, and plane and helicopter flyovers. Since 2014, most of the island's beaches have been closed during spring and summer to protect migratory and nesting birds. Although dogs and camping are prohibited, enforcement is needed for compliance, and these rules and regulations must be renewed every five years. The use of Deveau by Whimbrel, however, is not widely known as they arrive at the roost at dusk and leave before dawn (Fig. 3). Broadening recognition and appreciation of Deveau Bank's importance to Whimbrel will cultivate the public support needed to ensure its continued protection. We hope that sharing our finding fuels enthusiasm for protecting Deveau Bank and other barrier islands in the region, as well as elsewhere. Targeted research and conservation action at this and other nocturnal sites could have significant positive impacts on efforts to turn the tide for declining shorebird populations.

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REFERENCES

- Andres, B.A., P.A. Smith, R.I.G. Morrison, C.L. Gratto-Trevor, S.C. Brown & C.A. Friis. 2012. Population estimates of North American shorebirds. 2012. *Wader Study Group Bulletin* 119: 178–194.
- Burton, N.H.K., P.R. Evans & M.A. Robinson. 1996. Effects on shorebird numbers of disturbance, the loss of a roost site and its replacement by an artificial island at Hartlepool, Cleveland. *Biological Conservation* 77: 193–201.
- Conklin, J.R. & M.A. Colwell. 2007. Diurnal and nocturnal roost site fidelity of Dunlin (*Calidris alpina pacifica*) at Humboldt Bay, California. *Auk* 124: 677–689.
- Dickens, R.F. 1993. A golden plover roost. *Buckinghamshire Bird Club Bulletin*: 5–6.
- Dugan, J.E., L. Airolidi, M.G. Chapman, S.J. Walker & T. Schlacher. 2011. Estuarine and coastal structures: Environmental effects, a focus on shore and nearshore structures. Pp. 17–41 in: *Treatise on Estuarine and Coastal Science* (E. Wolanski & D. McLusky, Eds.). Academic Press, Waltham, UK.
- Eisma, D., P.L. de Boer, G.C. Cadée, K. Dijkema, H. Ridderinkhof & C. Philippart. 1998. *Intertidal Deposits: River Mouths, Tidal Flats, and Coastal Lagoons*. CRC Press, Boca Raton, FL, USA.
- Gill, F. & P. Rasmussen. 2020. *IOC World Bird List (v10.2)*. Accessed 28 Sep 2020 at: doi 10.14344/IOC.ML.10.2.
- Handel, C.M. & R.E. Gill. 1992. Roosting behavior of pre-migratory Dunlins (*Calidris alpina*). *Auk* 109: 57–72.
- Hobson, K.A. & J.R. Jehl. 2010. Arctic waders and the capital-income continuum: Further tests using isotopic contrasts of egg components. *Journal of Avian Biology* 41: 565–572.
- Johnson, A.S., J. Perz, E. Nol & N.R. Senner. 2016. Dichotomous strategies? The migration of Whimbrels breeding in the eastern Canadian sub-Arctic. *Journal of Field Ornithology* 87: 371–383.
- Lilleyman, A., D.I. Rogers, M.V. Jackson, R.A. Fuller, G. O'Brien & S.T. Garnett. 2020. An artificial site provides valuable additional habitat to migratory shorebirds in a tropical harbour. *Pacific Conservation Biology* 26: 249–257.
- National Oceanic & Atmospheric Administration (NOAA). 2020. *Tides and Currents*. NOAA, Charleston, SC, USA. Accessed 16 Nov 2020 at: <https://tidesandcurrents.noaa.gov/map/index.html?region=South%20Carolina>
- Piersma, T., R.E. Gill, Jr., P. de Goeij, A. Dekinga, M.L. Shepherd, D. Ruthrauff & L. Tibbitts. 2006. Shorebird avoidance of nearshore feeding and roosting areas at night correlates with presence of a nocturnal avian predator. *Wader Study Group Bulletin* 109: 73–76.
- Pilkey, O.H. & H.L. Wright. 1988. Seawalls versus beaches. *Journal of Coastal Research*: 41–64.
- Rakhimberdiev, E., S. Duijns, J. Karagicheva, C.J. Camphuysen, V.R.S. Castricum, A. Dekinga, R. Dekker, A. Gavrilov, J. ten Horn, J. Jukema, A. Saveliev, M. Soloviev, T.L. Tibbitts, J.A. van Gils & T. Piersma. 2018. Fuelling conditions at staging sites can mitigate Arctic warming effects in a migratory bird. *Nature Communications* 9: 4263.
- Rice, T.M. 2015. *Habitat Modifications in the U.S. Atlantic Coast Breeding Range of the Piping Plover (Charadrius melodus) prior to Hurricane Sandy: A Synthesis of Tidal Inlet and Sandy Beach Habitat Inventories*. U.S. Fish and Wildlife Service, Hadley, MA, USA.
- Rogers, D.I., T. Piersma & C.J. Hassell. 2006a. Roost availability may constrain shorebird distribution: Exploring the energetic costs of roosting and disturbance around a tropical bay. *Biological Conservation* 133: 225–235.
- Rogers, D.I., P.F. Battley, T. Piersma, J.A. van Gils & K.G. Rogers. 2006b. High-tide habitat choice: insights from modelling roost selection by shorebirds around a tropical bay. *Animal Behaviour* 72: 563–575.
- Rosenberg, K.V., A.M. Dokter, P.J. Blancher, J.R. Sauer, A.C. Smith, P.A. Smith, J.C. Stanton, A. Panjabi, L. Helft,

- M. Parr & P.P. Marra.** 2019. Decline of the North American avifauna. *Science* 366: 120–124.
- Sanders, F., M. Spinks & T. Magarian.** 2013. American Oystercatcher winter roosting and foraging ecology at Cape Romain, South Carolina. *Wader Study Group Bulletin* 120: 128–133.
- Sitters, H.P., P.M. González, T. Piersma, A.J. Baker & D.J. Price.** 2001. Day and night feeding habitat of Red Knots in Patagonia: Profitability versus safety? *Journal of Field Ornithology* 72: 86–95.
- Skeel, M.A. & E.P. Mallory.** 2020. Whimbrel (*Numenius phaeopus*), v. 1.0. In: *Birds of the World* (S.M. Billerman, Ed.). Cornell Lab of Ornithology, Ithaca, NY, USA. Accessed 28 Sep 2020 at: <https://doi.org/10.2173/bow.whimbr.01>
- South Carolina Department of Natural Resources (SCDNR).** 2009. *The ACE Basin Project*. South Carolina Department of Natural Resources, Columbia, SC, USA. Accessed 19 Nov 2020 at: <https://www.fws.gov/uploadedFiles/Original%20drivingace.pdf>
- South Carolina Department of Natural Resources (SCDNR).** 2015. *Dynamics of the Salt Marsh*. Sea Science: An Information/Education Series from the Marine Resources Division. South Carolina Department of Natural Resources, Columbia, SC, USA. Accessed on 1 Oct 2020 at: <https://www.dnr.sc.gov/marine/pub/seascience/pdf/2015RevisedSalt-Marsh.pdf>
- Tulp, I., H. Schekkerman, R.H.G. Klaassen, B.J. Ens & G.H. Visser.** 2009. Body condition of shorebirds upon arrival at their Siberian breeding grounds. *Polar Biology* 32: 481–491.
- U.S. Census Bureau.** 2019. *U.S. Census Bureau QuickFacts: Charleston County, South Carolina*. Accessed 5 Oct 2020 at: <https://www.census.gov/quickfacts/charlestoncountysouthcarolina>
- Wallover, N.J., M.-C. Martin & F.J. Sanders.** 2015. Monthly abundance and seasonal spatial distribution of shorebirds in Cape Romain National Wildlife Refuge, South Carolina. *Chat* 79: 61–79.
- Warnock, N.** 2010. Stopping vs. staging: the difference between a hop and a jump. *Journal of Avian Biology* 41: 621–626.
- Watts, B.D. & B.R. Truitt.** 2011. Decline of Whimbrels within a mid-Atlantic staging area (1994–2009). *Waterbirds* 34: 347–351.
- Watts, B.D., B.R. Truitt, F.M. Smith, E.K. Mojica, B.J. Paxton, A.L. Wilke & A.E. Duerr.** 2008. Whimbrel tracked with satellite transmitter on migratory flight across North America. *Wader Study Group Bulletin* 115: 119–121.
- Watts, B.D., F.M. Smith, D.J. Hamilton, T. Keyes, J. Paquet, L. Pirie-Dominix, J. Rausch, B. Truitt, B. Winn & P. Woodard.** 2019. Seasonal variation in mortality rates for Whimbrels (*Numenius phaeopus*) using the Western Atlantic Flyway. *Condor* 121: 1–13.
- Watts, B.D., F.M. Smith, C. Hines, L. Duval, D.J. Hamilton, T. Keyes, J. Paquet, L. Pirie-Dominix, J. Rausch, B. Truitt, B. Winn & P. Woodard.** 2021. The costs of using night roosts for migrating whimbrels. *Journal of Avian Biology* 52: jav.02629.
- Western Hemisphere Shorebird Reserve Network (WHSRN).** 2019. *Reentrâncias Maranhenses*. WHSRN, Manomet, MA, USA. Accessed 4 Oct 2020 at: https://whsrn.org/whsrn_sites/reentrancias-maranhenses/
- Western Hemisphere Shorebird Reserve Network (WHSRN).** 2020. *Map of Sites*. WHSRN, Manomet, MA, USA.. Accessed 5 Oct 2020 at: <https://whsrn.org/whsrn-sites/map-of-sites/>
- Wilke, A.L. & R. Johnston González.** 2010. *Conservation Plan for the Whimbrel (Numenius phaeopus) – v. 1.1*. Manomet Center for Conservation Sciences, MA, USA.
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