Kiawah and Seabrook islands are a critical site for the *rufa* red knot (*Calidris canutus rufa*)

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ABSTRACT

The *rufa* red knot (*Calidris canutus rufa*) is a migratory shorebird that performs one of the longest known trans-hemispheric migrations of any bird species — from their breeding grounds in the Canadian Arctic to their nonbreeding grounds as far south as Tierra del Fuego — and they have experienced a population decline of over 85% in recent decades. During migration, they rest and refuel at stopover sites along the Atlantic Coast, including Kiawah and Seabrook islands in South Carolina. Here, we document the importance of Kiawah and Seabrook islands for knots by providing population and stopover estimates during their spring migration. We conducted on-the-ground surveys between 19 February - 20 May 2021 to record the occurrence of individually marked knots. In addition, we quantified the ratio of marked to unmarked knots and deployed

geolocators on knots captured in the area. Using a superpopulation model, we estimated a passage population of 17,247 knots (~41% of the total *rufa* knot population) and an average stopover duration of 47 days. Our geolocator results also showed that knots using Kiawah and Seabrook islands can bypass Delaware Bay and fly directly to the Canadian Arctic. Finally, our geolocators, combined with resighting data from across the Atlantic Flyway, indicate that a large network of more than 70 coastal sites mostly concentrated along the coasts of Florida, Georgia, South Carolina, and North Carolina provide stopover and overwintering habitat for the knots we observed on Kiawah and Seabrook islands. These findings corroborate that Kiawah and Seabrook islands should be recognized as critical sites in the knot network and, therefore, a conservation priority. As a result, the threats facing the sites — such as prey management issues, anthropogenic disturbance, and sea level rise — require immediate attention.

INTRODUCTION

Migration is the process whereby individuals move from one area to another to exploit alternative resources or environments that fluctuate in suitability (Winger et al. 2019). Migration can range from short-distance movements to those that cover tens of thousands of kilometers (Alerstam, Hedenström and Åkesson, 2003). The *rufa* Red Knot (*Calidris canutus rufa,* hereafter, 'knot') is a long-distance migratory shorebird that performs one of the longest migrations of any bird species (Piersma et al. 2005, Conklin et al. 2017), with some individuals traveling ~30,000 km from their breeding grounds in the Canadian Arctic (70°N) to nonbreeding grounds in the southeastern U.S. (Niles et al. 2012, Lyons et al. 2018) and as far south as Tierra del Fuego at the southern tip of South America (53 – 54°S; Niles et al. 2008, Burger et al. 2012). Knots face numerous threats along their migratory route (Burger et al. 2012) and, in 2015, were

listed as a threatened species in both Canada and the United States due to a steep population decline of 85% over the past few decades (U.S. Fish and Wildlife Service 2014).

Knots migrate between their breeding and nonbreeding grounds along the Atlantic Flyway and undertake several nonstop flights of thousands of kilometers without feeding or resting (Niles et al. 2008). To endure the energetic demands of such long flights, knots rely on stopover sites where they can rest and refuel (Baker et al. 2004, Atkinson et al. 2007). The annual cycles and migratory strategies of knots, in turn, require that knots time their migrations to coincide with the occurrence of superabundant but ephemeral resources at their stopovers (Piersma and Baker 2000, Lyons et al. 2016). Delaware Bay — one of the best studied stopover sites for knots — exemplifies this dependency. Knot arrival at Delaware Bay coincides with the spawning of the horseshoe crabs (*Limulus polyphemus)* on which they feed in order to refuel and continue their migrations to the Arctic (Niles et al. 2008, McGowan et al. 2011, Tucker et al. 2021). Delaware Bay, however, represents only one site within a larger network of beaches, estuaries, and barrier islands (Cohen et al. 2009, 2010a,b, Tuma and Powell 2021) that share a suite of pressures including anthropogenic disturbance (Burger et al. 2007), coastal development (Buler & Moore, 2011), and unsustainable prey harvest practices (Niles et al. 2009). As a result, knots' foraging efficiency has decreased at some sites, and they have failed to reach the minimum threshold of mass gain to complete their migrations in some years (Baker et al. 2004). Given that climate change and sea level rise will continue to exacerbate the pressures on stopover sites that support knots and other shorebirds (Iwamura et al. 2013, Rakhimberdiev et al. 2018), there is an urgent need to identify all the critical stopover sites for these at-risk species.

Within North America, the network of sites used by knots spans much of the Atlantic Coast. In addition to Delaware Bay, the Eastern Shore of Virginia is known to support upwards

of 5,000 knots during spring migration (Cohen et al. 2010a). Recent evidence suggests that more than two dozen coastal sites in the southeastern U.S. (i.e., from Texas to South Carolina) also support knots during migration and the nonbreeding season (Tuma and Powell 2021). In Georgia, for instance, estimates indicate that between 8,000 - 24,000 knots stop during fall migration (Lyons et al. 2018). Intriguingly, flocks of up to 8,000 knots have been recorded in spring as well on the Kiawah-Seabrook Island complex in South Carolina (Thibault 2013) — a relatively small site in comparison to most others in the network. Kiawah and Seabrook islands, however, have received relatively little attention and much remains to be learned about how (and how many) knots use them over the course of the year (Smith et al. 2019).

Population estimates of overwintering and migrating shorebirds are traditionally difficult to quantify because of fluctuating numbers of birds as they enter and exit a site during the season (Lyons et al. 2016, Lok et al. 2019). We aim to build on the count data collected on Kiawah and Seabrook islands in previous studies to assess its importance to knots by accounting for the flow-through nature of stopover sites. To do this, we used a mark-resighting approach following Lyons et al. (2016) to estimate the: (1) population size, (2) stopover duration, (3) connectivity, and (4) overwintering status of knots using the Kiawah-Seabrook Island complex. We complemented these analyses by assessing stopover site usage along the Atlantic Flyway by knots carrying light-level geolocators and using the online www.bandedbirds.org database to link the knots we resighted in South Carolina with resightings from other sites across the flyway. Ultimately, we believe that our study can contribute to a broader understanding of the knot annual cycle and efforts to conserve knots wherever they occur throughout the year.

METHODS

Study Area

Our study area comprises 24 kilometers of sandy beach in the Kiawah-Seabrook Island complex (hereafter, KSI) on the coast of South Carolina (32°35'10.6"N, 80°07'47.6"W; Fig. 1). Seabrook and Kiawah islands are bordered by the North Edisto and Stono rivers, respectively. The islands are divided by Captain Sam's Inlet, which is critical to local fauna, including strand feeding common bottlenose dolphins (*Tursiops truncates*; Dybas 2021), foraging seabirds, and a variety of roosting shorebirds, including knots. This area also provides critical overwintering habitat for Piping Plovers (*Charadrius melodus*) and nesting habitat for Wilson's Plovers (*C. wilsonia*), American Oystercatchers (*Haematopus palliatus*), and Least Terns (*Sternula antillarum*), all of which are species of conservation concern in South Carolina (U.S. Fish and Wildlife Service 2001; South Carolina Department of Natural Resources 2015). Due to its unusual hydrodynamic regime, the inlet experiences frequent shifts and geomorphological changes. It has also been intentionally relocated several times, most recently in 2015 (Doyle and Adams 2015). A semi-diurnal tide results in shorebirds using the inlet twice each day to roost during high tide.

At low tides, shorebirds occupy the complex's sandy beaches where they feed primarily on invertebrate prey. Benthic core and knot fecal samples suggest knots' diet on KSI consists primarily of coquina clams (*Donax variabilis*; Thibault and Levisen 2013). Both islands are popular tourist destinations with fully developed coastlines containing golf courses, several resorts, and popular public beach access points with high levels of human and dog disturbance. At the south end of the study area, South Carolina Department of Natural Resources owned Deveaux Bank — an ephemeral offshore sand bank — provides additional undeveloped habitat for shorebirds and marine birds. Knots move back and forth between KSI and Deveaux Bank, especially during spring horseshoe crab spawning events, with horseshoe crab eggs comprising

an additional important component of their diet (Thibault and Levisen 2013, South Carolina Department of Natural Resources 2018). As Deveaux Bank requires boat access, it was not surveyed during our study.

Banding

Standardized shorebird banding was implemented in the Western Hemisphere beginning in the mid-1980s (Pan American Shorebird Group 2016). Across the Atlantic Flyway, 3-6% (Smith et al. 2019) of the knot population is estimated to be marked with flags consisting of a unique alphanumeric code that allows for the identification of each marked bird. Flags are colored according to the Pan American Shorebird protocol, with colors corresponding to the area in which the bird was marked (Pan American Shorebird Group 2016). These possible areas are: Canada, the United States, Mexico, Central America, the Caribbean, northern South America, Argentina, and Chile. By resighting knots that have been previously marked by other researchers, we estimated their passage population and stopover duration. Compiling resighting data from other sites in North America also allowed us to identify connections between South Carolina and stopover sites throughout the knot migratory network.

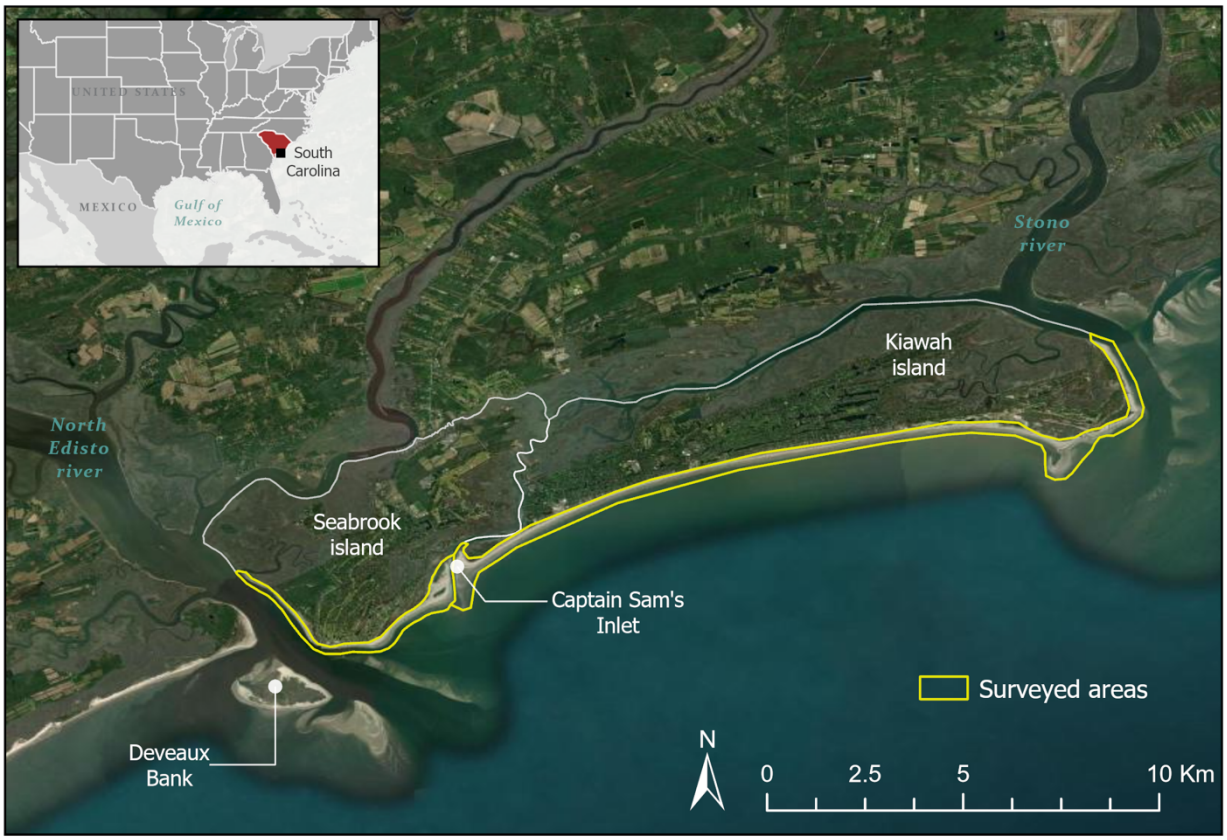

Figure 1. The Kiawah-Seabrook Island Complex, South Carolina consists of 24 kilometers of sandy beaches and an estuarine inlet.

Data Collection

We collected data from 19 February - 20 May 2021 — a period during which migrating knots were likely to be present in KSI. After a two-week period of observer training, KSI was surveyed 2-4 times a week by two separate observers between February-March. In April and May — the period of expected peak knot presence — we increased our sampling effort to 4-6 times a week. These observations resulted in 13 weeks of total effort. Due to restricted access, flag readings and scan samples were collected from Seabrook, but not Kiawah, from 14-20 May.

The 24 km of KSI beaches were surveyed by randomly selecting beach-walking access points, which served as the survey starting point for a given island. We performed surveys within ~2.5 hours of high tide when knots were likely to be relatively stationary. When a flock was found, we performed a series of flag ratio scans using spotting scopes by recording the number of individuals with and without leg flags. We sampled without replacement as much as possible by scanning from one end of the flock to the other. Efforts were also made to avoid recounting flocks in the same day by not taking samples from flocks that we had already encountered and from which we therefore recognized flag combinations. Additionally, we ensured that we had adequate coverage of birds on KSI to the best of our ability by randomly selecting sites to survey and having two observers working separately during the week. If birds in a scan had flags, we recorded the flag color, alphanumeric code, and presence of any other device that it might carry. We also recorded the specific location, time, wind, and tide of the sighting.

Flag and Geolocator Deployment

Between April 2015 and May 2016, we deployed geolocators on knots captured in South Carolina. Knots were captured using cannon nets on Bird Key Stono Seabird Sanctuary on 21 April 2015; in Cape Romain National Wildlife Refuge at Marsh Island on 16 October 2015; and on Deveaux Bank Seabird Sanctuary on 10 May 2016. Captures were made at high tide roosts at Bird Key and Marsh Island, and while feeding on horseshoe crab eggs as the tide fell on Deveaux Bank. Upon capture, birds were immediately removed from the net and placed in keeping cages for processing. All birds were measured and fitted with a uniquely inscribed 3-character leg flag and U.S. Geological Survey metal band. Migrate Technology Ltd. geolocators weighing 1.1 g were attached to leg bands as described in Niles et al. (2010). The units record the maximum light level every minute and conductivity (i.e., contact with alkaline water) every 3

seconds. A total of 33 geolocators were deployed, but only three were retrieved. One knot captured at Deveaux Bank was recaptured on Tierra del Fuego on 13 January 2018. A geolocator deployed at Bird Key was retrieved from a dead knot (presumably from red tide, a harmful algal bloom) found in the Tampa Bay, Florida region. And, finally, a geolocator from Marsh Island was retrieved from a knot recaptured at Seabrook Island on 29 April 2017.

Mark-Resighting Analysis

We reconstructed mark-resighting data for each marked knot on a weekly basis by combining all observations within one week into a single observation, beginning 19 February. We used the www.bandedbirds.org database to verify our resightings. For those marking schemes that had been input into the database (e.g., from the United States and Canada), we removed observations of flag codes that had no corresponding capture history. Some marking schemes did not appear in the database, however; in these cases, we retained all observations with a high degree of observer certainty. We then used an open population Jolly-Seber (JS) modeling framework to explore the flow of arriving, stopped over, and departing knots during the spring migratory period. Specifically, we used the superpopulation parameterization of the JS model — a hierarchical, state-space parameterization that incorporates data augmentation (Crosbie and Manly 1985, Royle and Dorazio 2008, Kéry and Schaub 2012) — to estimate the probabilities of entering (β) the study site, staying (ϕ) to the next week, and resighting (ρ). These parameters are analogous to the demographic parameters of recruitment, survival, and recapture in conventional mark-recapture JS models, respectively. We implemented methods from Lyons et al. (2016) to add a binomial model for flag ratio scan samples, which also enabled us to estimate total passage population, or the number of knots estimated to use KSI during the spring migratory period.

More recently developed models additionally allow for the statistical identification of groups that might pass through a site separately (e.g., Lok et al. 2019). However, knot local- and regional-scale movements, and the resulting resighting heterogeneity early during our study period (see below), precluded us from employing these models, meaning that we could only estimate a single, average stopover duration for all knots using KSI.

We verified that the JS model fit our data using goodness-of-fit tests developed for capture-recapture models in the R Programming Environment (version 4.1.1; R Core Development Team 2016) and package 'R2ucare' (Gimenez et al. 2018). Omnibus testing of the null hypothesis that the model was an adequate fit for the data was non-significant ($p = 0.11$, χ^2=43.34, df = 33), indicating that we did not need to adjust the model for transience or trap-dependence. We also explored support for time-varying versus constant parameters. In a stopover context, entry probabilities (β) are commonly allowed to vary over time, since individuals may be less likely to arrive at a stopover site during some weeks (e.g., the last week) than others. We compared various models that constrained the probabilities of staying (ϕ) and resighting (ρ) to be constant and/or allowed them to vary with sampling occasion (week). Models were fit using encounter histories and the POPAN model in program MARK (White and Burnham 1999) *via* the R package 'RMark' and compared using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). The most parsimonious model (AIC_c< 2 and with the fewest parameters) consisted of a constant staying probability and weekly variation in resighting probability (Table 1).

Table 1 Model comparison for time-varying versus constant ϕ and p parameters. K = number of parameters; Weight = Akaike weight.

Model	K	AIC_c	ΔAIC_c	Weight	Deviance
$\beta_t \phi_c \rho_t$	27	856.594	0.000	0.999	-711.943
$\beta_t \phi_t \rho_t$	38	879.294	22.700	<0.001	-716.126
$\beta_t \phi_c \rho_c$	15	897.980	46.385	<0.001	-643.268
$\beta_t \phi_t \rho_c$	26	905.934	49.339	<0.001	-660.251

We performed a Bayesian analysis integrating the superpopulation JS model with the binomial scan sample model, using the approach outlined in Lyons et al. (2018). The JS model estimates stopover duration using encounter histories and a latent state variable that reflects arrival in and departure from the study site (Lyons et al. 2016). The latent state variable ($z_{i,t}$) is a time-specific Bernoulli random variable for each individual *i* in the population (i.e., flagged and unflagged) at time *t*, where $z_{i,t}$= 1 while using the stopover site and $z_{i,t}$= 0 before arrival and after departure. The posterior latent states are then summed across individuals to estimate the stopover duration (Lyons et al. 2018). In this way, the calculation of mean stopover duration is robust to variations in resighting probability, which were pronounced during weeks when knots roosted and foraged on Deveaux Bank or moved among sites in the southeastern U.S.

Using flag scan samples, we modeled the number of flagged individuals in a scan sample as a binomial random variable

$$m_s \sim \text{Binomial}(C_s, \pi_t)$$

where m_s is the number of flagged individuals in the scan sample s, C_s is the number of individuals checked for flags, and π_t is the proportion of flagged individuals in the population during the corresponding week. This modification for weekly variation in the proportion of the population that is flagged (π_t) suits the pulsed arrivals of two or more migratory groups that may differ in the proportion flagged, which we expected to find at our study site. The total passage population was then calculated as the sum of the arrivals at each sampling occasion, adjusted for the flagged proportion at the corresponding occasion

$$\widehat{N} = \sum B_t/\pi_t$$

where $\widehat{N}$ is the total passage population, B_t, is the number of entries/arrivals at a sampling occasion t, and π_t is the proportion of the population carrying alphanumeric flags at occasion t. In this way, the integrated model thus estimated both stopover dynamics (e.g., stopover duration, mean staying probability, weekly resighting probability) and the derived weekly and total passage population.

The full model incorporating the JS model and flag scan sample ratios was implemented in R using the package 'jagsUI' (Kellner 2016) as an interface with JAGS software (Plummer 2003). We followed guidance from Kéry and Schaub (2012) for parameter-expanded data augmentation (PX-DA; Royle and Dorazio 2012) in order to fix the parameter space for analysis, adding potential unobserved individuals as all-zero encounter histories (n = 600) to our dataset.

253 We checked that this value was sufficiently large by visually inspecting the posterior distribution
254 of the estimated number of total marked individuals ($\widehat{M}$) to verify that it was not truncated.
255 Following Lyons et al. (2018), we used uniform priors (0,1) for the staying and resighting
256 probabilities and uninformative priors for arrival probability. We simulated three MCMC chains
257 of 90,000 iterations each, with burn-in periods of 30,000 iterations and a thinning rate of 3. We
258 assessed convergence of the chains visually and *via* the Brooks-Gelman-Rubin statistic ($\hat{R}$;
259 Brooks and Gelman 1998), where models with parameter values < 1.1 were considered to have
260 converged. All values are presented as means and 95% credible intervals unless otherwise noted.

261

262 ***Geolocator and Connectivity Analysis***

263 To corroborate our mark-resighting results, we used our geolocation data to answer three
264 questions: (1) How long did knots stopover in South Carolina during their northward migration?
265 (2) How many stops did knots make after departing from South Carolina for the breeding
266 grounds? and, (3) Where were those stops? Geolocators were analyzed using the R package
267 *FLightR* (Rakhimberdiev et al. 2017) — which has been shown to successfully delineate the
268 movements of migratory shorebirds (Rakhimberdiev et al. 2016) — and followed the workflow
269 outlined in Lisovski et al. (2019). Briefly, before deploying our geolocators, we placed them
270 outside for a ~7-day long period that we then used within *FLightR* to calibrate the data from each
271 geolocator. We otherwise used the default package settings, but constrained the locations
272 identified as stopover sites to coastal areas. We included all sites at which an individual was
273 estimated to stop for at least 2 days with a (movement) probability of 0.8 and considered an
274 individual to have stopped in South Carolina if a stopover was recorded between 30-33°N. Using
275 this approach, we estimated the mean dates of arrival and departure from South Carolina, the

number of stops an individual made after departing South Carolina on its way northward, and the location of those stops.

To further assess migratory connectivity, we searched the online database www.bandedbirds.org and retrieved the capture and resighting history for every knot that we resighted during our study. With this information, we mapped the network of sites used by knots during their passage through the U.S. and Canada. We eliminated sites that were less than 10 km from each other using a rarifying filter in R (Brown et al. 2014).

RESULTS

Resighting Results

We recorded 217 uniquely flagged knots during our 13-week study period. Resightings occurred in all weeks except for the week beginning 26 March, when knots in the KSI area were observed only on nearby Deveaux Bank (N.R. Senner pers. obs.). We recorded flag scan samples in all weeks except for the two-week period beginning 19 March, also due to temporary knot roosting and foraging on Deveaux Bank. Resightings and scan samples occurred throughout KSI but were most common near Captain Sam's Inlet, shortly before or after high tide. Most resighted individuals carried dark green or lime green flags indicative of having been flagged in the United States. Other individuals flagged in South America appeared later in the season (Fig. 2) and during this period we observed flocks of at least 4,000 individuals on multiple occasions. While new resightings occurred up until the final week, our study period was nonetheless a good approximation of the full duration of knot stopover, as nearly all knots had departed by 21-27 May (M. Andrews and R. Mercer, pers. obs.).

Our model estimated a total passage population of 17,247 knots (95% CI: 13,548, 22,099) during our study period. Of this passage population, 2.4% (95% CI: 1.9, 2.9) on average were estimated to be flagged. This estimate is approximately 41% of the total global population of 42,000 *rufa* knots (Andres et al. 2012). On average, individuals spent 47 days (95% CI: 40.1, 54.8) at the study site.

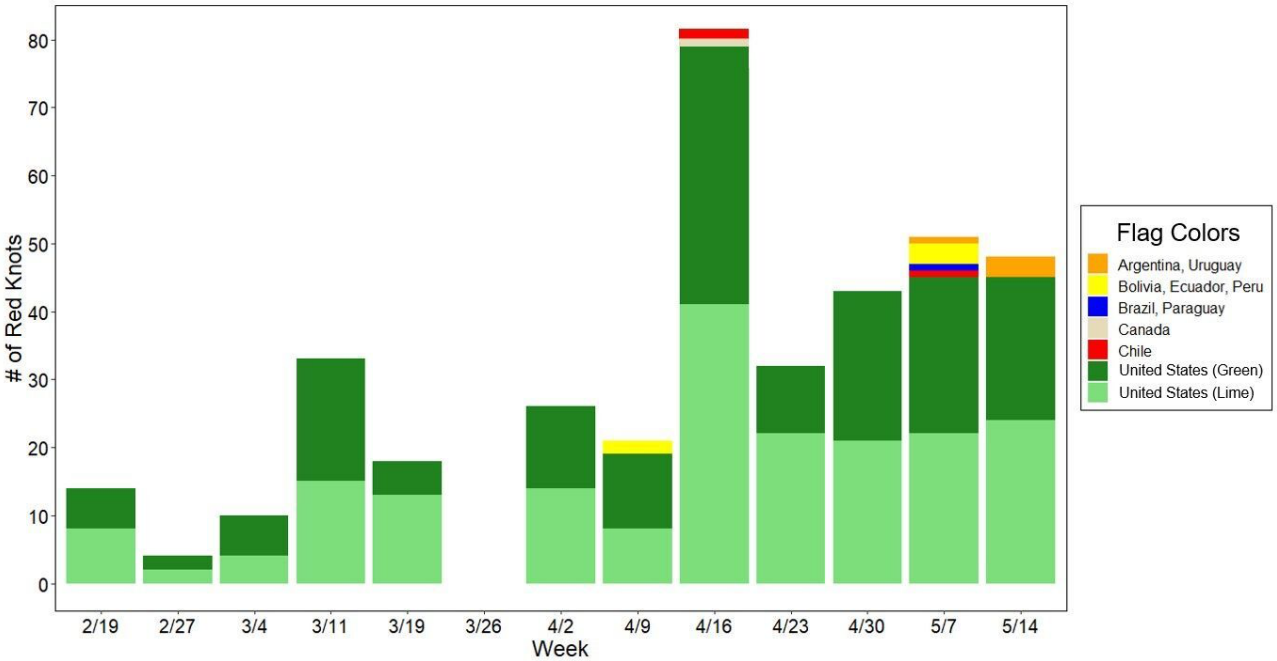

Figure 2: Number of uniquely flagged Red Knots and the corresponding flag colors encountered each week from February-May 2021 on Kiawah and Seabrook islands, South Carolina. Dates shown represent the start of each week.

The model estimated three parameters on a weekly basis: entry probability, resighting probability, and population size. Entry probability was highest in the first week and remained relatively consistent thereafter (Fig. 3A). Resighting probability increased in the fourth week, was lower during the weeks that knots spent most of their time on Deveaux Bank, and increased again later in the season (Fig. 3B). The estimated weekly population size increased throughout

the season, starting at 2,411 (95% CI: 858, 5,050) in the first week and ending at 13,852 (95% CI: 9,764, 19,254) the week of 14 May (Fig. 3C).

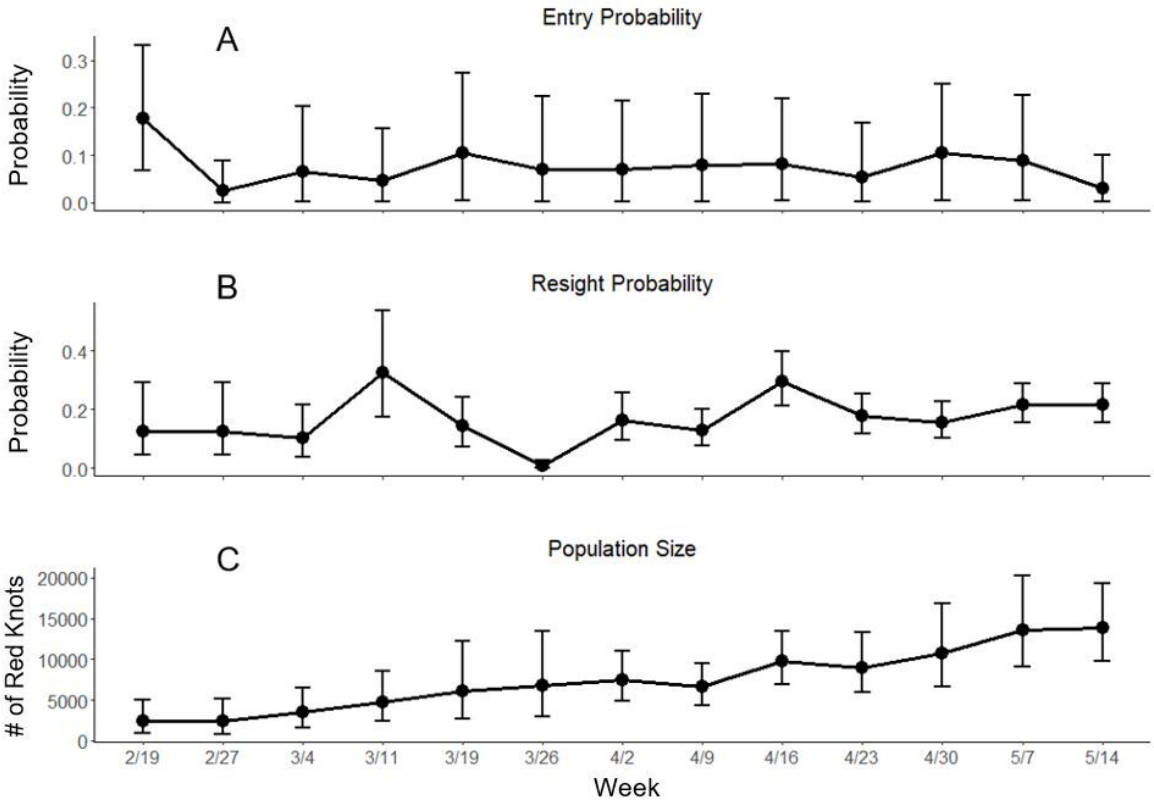

Figure 3. Model-derived estimates of the weekly entry probability (A), resighting probability (B), and population size (C) for Red Knots on Kiawah and Seabrook islands, South Carolina. Bars around estimates represent model generated 95% credible intervals.

Geolocator Results

Each of our three geolocator-carrying individuals spent the nonbreeding season in a different region: one on Tierra del Fuego (50.54°S; Fig. 4A, B); one along the Atlantic Coast, moving among sites from Georgia to North Carolina (30.3-35.1°N; Fig. 4C); and one on the Gulf Coast

of Florida (27.2-29.2°N; Fig. 4D). Of the two individuals that did not spend the nonbreeding season in or close to South Carolina, both arrived in the region 2-5 May and departed approximately three weeks later (μ = 20 ± 1 d), between 23 May-1 June (n = 3 departures). Across all three individuals and all years during which they were tracked, northward departure from South Carolina averaged 24 May ± 5 d (n = 5 departures). Once departing South Carolina, the three individuals stopped on average 1.8 ± 1 times, with those stops occurring north of 49°N, mostly along the western shore of either James or Hudson bays, Canada (49.3-55.4°N; Fig. 4A). Because of the nature of geolocation data and Arctic summers, we were unable to identify the breeding areas used by any of the individuals.

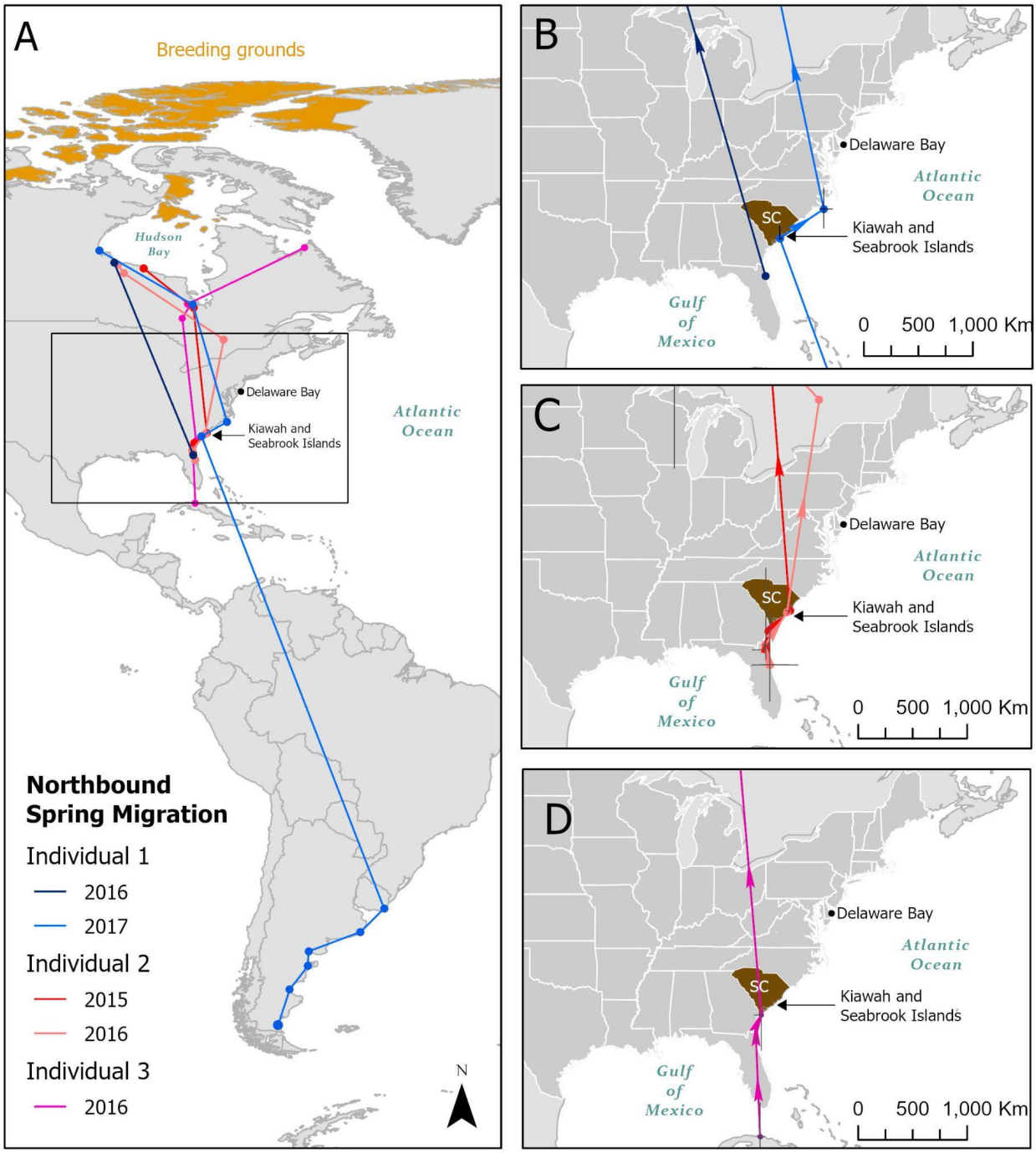

Figure 4: Northbound migratory tracks obtained using light-level geolocators attached to three Red Knots (blue, red, and purple lines, respectively) from 2015-2017 (map inset A). Map inset B, C, and D show northbound movements of individuals 1, 2, and 3 along the Atlantic Coast of the

United States, respectively. Vertices show latitudinal and longitudinal 95% confidence intervals (black lines). Kiawah and Seabrook islands, as well as Delaware Bay, are highlighted to show when birds made a stopover at each site, respectively.

The capture history of the birds with dark or lime green flags that we resighted indicates that they were captured at 18 sites along the U.S. Atlantic Coast (1 in Texas, 4 in Florida, 4 in South Carolina, and 8 in Delaware Bay). Furthermore, based on their resighting history, the knots we resighted have used a network of at least 74 sites, including beaches, barrier islands, estuaries, inlets, and sandbar spits. These resightings came from Texas, Louisiana, Florida, Georgia, South Carolina, North Carolina, Virginia, Maryland, Delaware, New Jersey, Connecticut, and Massachusetts in the U.S., as well as Ontario (James Bay) and Quebec in Canada.

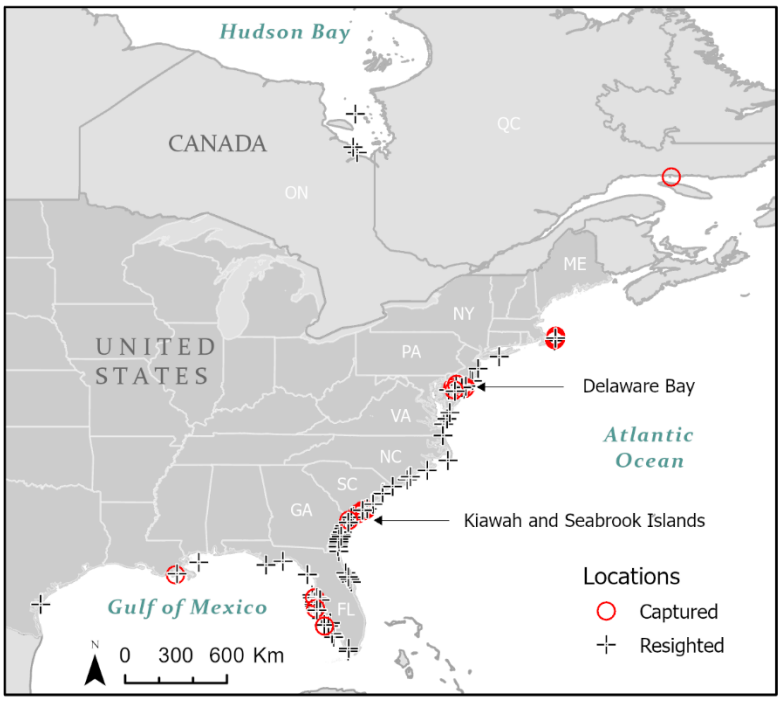

Figure 5. Network of sites where the Red Knots resighted on Kiawah and Seabrook islands, South Carolina were initially flagged (red circles) and where they were subsequently resighted (black crosses) along the Atlantic Coast of Canada and the U.S.

DISCUSSION

The Atlantic Coast of North America hosts a number of critical migratory stopover sites for *rufa* Red Knots, but the majority of scientific and conservation attention has focused on only a few of those sites, such as Delaware Bay (Baker et al. 2004, Atkinson et al. 2007, Niles et al. 2009) and coastal Virginia (Cohen et al. 2009, 2010a,b). Using a superpopulation model, we estimated that the 24-km stretch of sandy beaches on Kiawah and Seabrook islands in South Carolina hosts 17,247 (95% CI: 13,548, 22,099) knots from February-May 2021, representing ~41% of the estimated global *rufa* knot population of 42,000 individuals (Andres et al. 2012). While knot site fidelity to individual sites may exhibit large interannual variation (Piersma et al. 2021, Tucker et al. 2021) depending on the conditions and resource dynamics of the region (van Gils et al. 2005), our study suggests that KSI is a critical site for knots along the Atlantic Coast and deserves increased recognition and conservation attention.

Population Estimates

Across the Atlantic Flyway, a combination of methods has been used to develop estimates of knot population sizes at stopover and nonbreeding sites. These have ranged from: (1) mark-recapture approaches, which led to an estimation of 18,000 knots using Delaware Bay during spring migration in 2004 (Gillings et al. 2010) and 23,400 knots using the Georgia coast in fall 2011 (Lyons et al. 2018); (2) peak count approaches, which resulted in estimates of 5,939 knots

using the Virginia coast from 2004-2007 (Cohen et al. 2010a); and, (3) hybrid approaches, which generated estimates of 8,750 knots using four sites along the South Carolina and Georgia coasts in the spring of 2019 (Smith et al. 2019). This variation in methodologies has led to persistent uncertainty about the number of knots using specific sites, as well as about the total number occurring along the Atlantic Flyway. We hypothesize that our higher estimates of knots using KSI relative to previous estimates from the site and those from other sites along the Atlantic Coast may be a result of either interannual variation in site usage as suggested by Tucker et al. (2021) and our geolocator data (Fig. 4), improved resighting effort and statistical methodologies, an actual shift in site usage by knots, or a combination of the three. Regardless, this variation corroborates the need for more comprehensive estimates to be generated from mark-recapture studies along the entire Atlantic Coast on a regular basis.

KSI Likely Supports Both Overwintering and Migrant Knots

Our resighting (Fig. 1) and geolocator (Fig. 4) data indicate that there are likely two groups of knots using KSI: (1) overwintering knots that stayed on KSI and in surrounding areas or arrived early in the year, as exemplified by the abundance and substantial number of flags we detected at the beginning of our surveys, and (2) spring migrants, as exemplified by the increased population estimates and proportion of flagged individuals we observed as the season progressed. Knots are known to use the southeastern U.S. coast, including South Carolina, during the nonbreeding season (Niles et al. 2012; Burger et al. 2012; Tuma and Powell 2021), and Lyons et al. (2018) estimated that this region alone supports up to 10,400 knots during this period. Our results confirmed that one of our geolocator-carrying individuals moved among Georgia, South Carolina, and North Carolina during the nonbreeding season before ultimately migrating

394 northward from South Carolina in late May. Likewise, during our surveys, we detected knots at
395 KSI as early as 19 February (Fig. 2). We then subsequently detected ~42% of the marked knots
396 we observed during the first two weeks of the study again in May. In contrast, we would expect
397 that longer distance migrants would exhibit later arrivals and shorter stopover durations.
398 Accordingly, our other two geolocator-carrying knots — which spent the nonbreeding season in
399 Florida and southern South America, respectively (Fig. 4) — arrived in South Carolina in early
400 May and departed ~3 weeks later. This suggests that KSI may not only be an important stopover
401 site for spring migrants but an important site for overwintering knots as well.
402 In this respect, our results mirror those of Lyons et al. (2018), who found that during fall
403 migration knots spent an average of 38 days at the Altamaha River Delta, with a group of longer
404 distance migrants (Tierra del Fuego) that stopped over for ~21 days and a group of shorter
405 distance migrants (Southeastern U.S., Caribbean islands, and Brazil) that stopped over for ~42
406 days. Our model, however, was unable to differentiate between the two apparent groups in our
407 study and we could not estimate the difference in the duration of their respective stays on KSI.
408 This is because the methods from Lyons et al. (2016), on which our models were based, are
409 unable to identify the presence of multiple groups and our resighting effort was not great enough
410 to parameterize more complex models (e.g., Lok et al. 2019) that could capture the varying
411 behaviors likely exhibited by the 'overwintering' and 'migrant' groups. A key focus of future
412 research should therefore be to increase resighting efforts in the region, and specifically on KSI,
413 throughout the nonbreeding season (November-May) to try to generate robust estimates of the
414 sizes of these two apparent groups.
415
416 ***Importance of KSI in the Knot Migratory Network***

417 Delaware Bay has historically been regarded as the last steppingstone at which knots can refuel
418 before departing to their Arctic breeding grounds (Baker et al. 2004). Much conservation
419 attention has thus been focused on the site (Clark 1993, Atkinson et al. 2007, Niles et al. 2009,
420 McGowan et al. 2011). However, an increasing body of evidence suggests that knots rely on a
421 suite of stopover sites across the flyway for a variety of purposes (Cohen et al. 2010a, Tuma and
422 Powell 2021). Our survey of the www.bandedbirds.org database to connect the knots we
423 resighted on KSI with other sites across the Atlantic Flyway corroborates these recent studies
424 and revealed a network of more than 70 sites spanning Texas to Maryland (Fig. 5). Our
425 geolocator results also indicate that Delaware Bay is likely not the only terminal stopover site
426 used by knots prior to reaching the Canadian Arctic: the five spring migration departures we
427 obtained from our three geolocator-carrying individuals indicate that they all skipped Delaware
428 Bay after stopping in South Carolina (Fig. 4). These geolocator results are supported by the
429 results of a recent study that used an automated radio telemetry array to track knots from South
430 Carolina on their northward migration (Smith et al. *in prep*.) and which found that the majority
431 of these knots skipped Delaware Bay and went directly to the Arctic from South Carolina.
432 Nonetheless, resighting data from www.bandedbirds.org also suggested that a substantial number
433 of the knots stopping over in South Carolina are subsequently resighted in Delaware Bay in at
434 least some years. Further tracking work, combined with on-the-ground efforts to quantify knot
435 refueling rates and social dynamics, would therefore help clarify the migratory stopover
436 decisions that result in different stopover behaviors being exhibited from year to year (e.g., Chan
437 et al. 2019, Linscott and Senner 2021).
438 Regardless of whether knots are regularly using KSI and the greater South Carolina coast
439 as a terminal stopover site, the comparable importance of KSI as a migratory stopover site for

knots is clear. Though KSI is relatively small, we estimate that 41% of the total knot population is passing through during migration. What is more, a nocturnal roost supporting nearly half of the Atlantic Flyway population of Hudsonian Whimbrel (*Numenius hudsonicus*) was recently discovered on Deveaux Bank (Sanders et al. 2021), a site we also observed knots using during our study. Within the framework of the Western Hemisphere Shorebird Reserve Network, KSI (and Deveaux Bank) would therefore qualify as a site of Hemispheric Importance (WHSRN 2021). The fact that KSI only comprises 24 km of beaches — with Deveaux Bank comprising just a few more — underscores its importance and, likely, sensitivity to conservation threats such as those associated with human disturbances, habitat degradation, and outright habitat loss. Results from the loss and degradation of stopover sites used by knots elsewhere in the Atlantic Flyway (Baker et al. 2004) and across the globe (Studds et al. 2017) point to the consequences for the knot migratory network that such changes could cause (Xu et al. 2019). The importance of KSI is amplified even further if knots are indeed not only migrating through KSI but also overwintering there. In such a scenario, knots would be reliant on the site for most of their nonbreeding season (~6 months) and not just the spring migration period (~2-3 months).

Conservation Implications

Because of the variability of knot migratory patterns and their on-going population declines (Piersma et al. 2021, Tucker et al. 2021), it is critical to recognize the threats that knots are facing across the Atlantic Flyway. Delaware Bay, for instance, has suffered a > 75% decline in its use by knots since 1990, which Niles et al. (2009) suggested is likely related to declines in horseshoe crab numbers. To refuel sufficiently, knots need healthy populations of their prey, such as horseshoe crab eggs. At terminal stopover sites like Delaware Bay from which knots

463 leave for their breeding grounds, they must be able to refuel and meet a certain weight threshold
464 (e.g., >180 g) to successfully complete their migrations (McGowan et al. 2011). Female crab
465 abundance at Delaware Bay has thus been shown to positively correlate with an individual's
466 ability to reach this body mass threshold and survive to subsequent years (Baker et al. 2004).
467 Recent results from the Cape Romain National Wildlife Refuge in South Carolina indicate a
468 similar positive correlation between horseshoe crab spawning and knot densities at the refuge
469 (Takahashi et al. 2021). In our study area, knots appear to primarily feed on coquina clams on
470 KSI itself, as horseshoe crabs do not currently occur on the islands, but horseshoe crabs do
471 spawn on Deveaux Bank and knots are known to feed on their eggs there (Thibault and Levinsen
472 2013). Maintaining and understanding the diversity of knot prey used in South Carolina —
473 including both horseshoe crabs and coquina clams — is therefore important in order to enable
474 knots to rapidly refuel and successfully complete their northward migrations.
475 Anthropogenic disturbance also poses a threat to knots that must focus their time and
476 energy on foraging and building up sufficient pre-departure fat reserves to continue their
477 northward migrations (Thomas et al. 2003). Burger et al. (2007) found that knots and other
478 shorebirds using sites with little human disturbance were able to spend 70% of their time
479 foraging, while their foraging efficiency was reduced by more than 40% at high disturbance
480 sites. Because KSI is highly developed, with tourist attractions such as golf courses, public beach
481 access points, and resorts, there is substantial human and dog traffic along its beaches. During
482 our 13-week survey period we observed that, with the onset of spring, increasing numbers of
483 people and dogs led to the frequent disturbance of knots and other shorebirds. Currently both
484 islands do have dog leash laws intended to decrease the disturbance of wildlife: some areas are
485 off limits to dogs year-round, while in others, dogs are allowed either on and/or off leash,

depending on the time of day and year. For large portions of the two islands, however, these latter restrictions do not cover the entirety of the period that knots are likely present. On Kiawah Island, dogs are allowed off leash across much of the island from 1 November - 15 March, while on Seabrook Island, dogs can be off leash in the central portion of the island during the evening and early morning (17:00-09:59), even from 1 April - 30 September (Towns of Kiawah Island and Seabrook Island). Our results suggest that these rules should be extended and enforced throughout the period knots are present on the islands.

Climate change poses an additional variety of unpredictable challenges to knots and their associated coastal habitats. The Mid-Atlantic Coast of the United States has exhibited some of the fastest rates of sea level rise in the world (~4–10 mm y^{-1}; Ezer and Corlett 2012). Because much of the Mid-Atlantic Coast (including KSI) is highly developed, increased inundation may cause the loss of critical habitat by squeezing beaches and mudflats in between existing infrastructure (von Holle et al. 2019). Sea level rise may also alter the geomorphology and hydrodynamic regimes of estuaries (Khojasteh et al. 2021), potentially altering key roosting sites such as Captain Sam's Inlet and Deveaux Bank. Subsequently, a reduction in habitat as a result of sea level rise (and other anthropogenic factors) could further increase human disturbance, as well as inter- and intraspecific competition for roosting and foraging areas (Goss-Custard 1988), thereby constraining the ability of knots to refuel (Baker et al. 2004). Efforts to preserve the integrity of the full suite of habitats currently found on KSI in the face of these potential changes, such as through beach replenishment and habitat migration strategies, is a major priority.

Conclusions

We provide evidence of the critical importance of the Kiawah-Seabrook Island complex as a stopover and (potentially) overwintering site for knots. In order to preserve the site's ability to sustain shorebird populations, increased recognition and protection of the site is a priority. To this end, we recommend the nomination of KSI and neighboring Deveaux Bank as a Site of Hemispheric Importance in the Western Hemisphere Shorebird Reserve Network, as our results show that more than 40% of the *rufa* knot population, as well as 50% of the Atlantic Flyway Hudsonian Whimbrel population (Sanders et al. 2021), use the area. Because KSI may be serving as a terminal stopover site for knots, conservation measures should also focus on maintaining adequate abundances of knot prey to enable them to sufficiently refuel for nonstop flights to the Arctic. Human and dog disturbance on the islands lead to decreased foraging efficiency and use of roosting sites (Koch and Paton, 2013); our study's estimates of knot stopover duration on KSI can be used to help inform the timing of leash laws and other restrictions. Finally, sea level rise is expected to be a source of difficulty for knots in terms of the loss of suitable foraging and roosting habitat, and should remain a factor in management decisions given the critical importance of Captain Sam's Inlet and the adjacent KSI beaches.

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