

The effect of benthic prey abundance and size on red knot (*Calidris canutus*) distribution at an alternative migratory stopover site on the US Atlantic Coast

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Abstract A population decline of the western Atlantic red knot (*Calidris canutus rufa*) has been linked to food limitation during the spring migratory stopover in Delaware Bay, USA. The stopover ecology at potential alternative sites has received little attention. We studied factors affecting red knot habitat selection and flock size at a coastal stopover site in Virginia in 2006–2007. The most common potential prey items were coquina clams (*Donax variabilis*) and crustaceans. Red knot foraging sites had more clams and crustaceans than unused sites in 2006. Prey abundance increased during the 2007 stopover period and remained high after the red knot peak. Red knot flock size in 2007 increased with mean clam shell length, and probability of flock presence decreased with increasing distance from night use locations. Our results suggest that red knots preferred coquina clams and that these clams were not depleted during the stopover period in 2007. Thus prey abundance did not appear to be a population-limiting factor at this coastal stopover site in Virginia in that year. Protection of coastal sites outside of Delaware Bay, many of which have been altered by human development, would likely benefit red knot population recovery, as they can apparently provide abundant food resources during at least some years.

Keywords *Calidris canutus* · Barrier islands · Habitat selection · Red knots · Shorebirds · Virginia

Introduction

The western Atlantic red knot (*Calidris canutus rufa*) has declined substantially in recent years. This subspecies winters in Tierra Del Fuego (TDF), northeastern Brazil, and the southeastern United States (Morrison et al. 1980; COSEWIC 2007; Harrington et al. 2007; Niles et al. 2008). The TDF subpopulation has recently declined 68–80% (Morrison et al. 2004; Niles et al. 2008). The Brazilian and southeastern US wintering subpopulations have been less studied than the TDF knots, but they also may be in decline (Niles et al. 2008). The entire western Atlantic subspecies is a candidate for listing under the US Endangered Species Act (Federal Register 2006), and was recommended for endangered status by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2007).

During the northward migration, more than half of the western Atlantic *rufa* knots stop for a final refueling in the Delaware Bay region (Niles et al. 2008). Like the TDF population, this stopover population has declined substantially in recent years (Baker et al. 2004; Niles et al. 2008). This decline has sparked concern about the supply of horseshoe crab (*Limulus polyphemus*) eggs which are a key food for red knots and other shorebirds during northward migration at this stopover site (Berkson and Shuster 1999; Tsipoura and Burger 1999; Baker et al. 2004; Haramis et al. 2007; Niles et al. 2009). The red knot distribution in the Delaware Bay can be predicted by the distribution and abundance of horseshoe crab eggs (Botton et al. 1994; Karpanty et al. 2006), and a decline in horseshoe crab abundance has been related to decreased annual survival and

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lower pre-departure body mass of knots stopping in Delaware Bay (Baker et al. 2004). Based on high depletion rates of horseshoe crab eggs by red knots foraging on experimental feeding trays, Gillings et al. (2007) supported the hypothesis that horseshoe crab eggs are a red knot population-limiting factor. Haramis et al. (2007) demonstrated that red knots in Delaware Bay rely almost entirely on horseshoe crab eggs to support their weight gain, which is the most rapid of any known stopover population of red knots (Piersma et al. 2005; Atkinson et al. 2007).

Like Delaware Bay, the barrier islands of Virginia host thousands of red knots during spring migration. This has long been the case, as knots were known to stop in coastal Virginia in the 1800s (Mackay 1893). In the mid-1990s, nearly 9,000 were counted in coastal Virginia during the spring stopover (Watts and Truitt 2000). Currently, Virginia supports approximately 25% of the population of red knots stopping in the mid-Atlantic region of the United States (Cohen et al. 2009). The Virginia stopover appears to be independent from the Delaware Bay stopover, as there is little crossover ($\leq 5\%$) within seasons (Cohen et al. 2009) though the two areas are only 100 km apart. Birds may change stopover sites between years (New Jersey Nongame and Endangered Species Program and Delaware Natural Heritage Program, unpublished data).

With the Delaware Bay stopover population declining, Virginia's importance to the conservation of the species has increased, but little is known of the factors that limit the numbers of knots stopping in Virginia or what determines the distribution and abundance of the species in Virginia, where horseshoe crabs and their eggs are scarce. The intent of this study was to begin to explore these issues. Our objectives were (1) to determine what food resources were available to red knots on the Virginia coast, (2) to explore whether red knots were depleting prey resources in Virginia, and (3) to determine if the red knot distribution in Virginia was determined by the distribution, abundance, and size of their prey. We also investigated the influence of night-use sites on the distribution and abundance of knots, since the cost of commuting between night roost locations and foraging sites may constrain habitat use in European red knots (*C. c. islandica*, van Gils et al. 2006). This is the first systematic study of red knots at a spring migration stopover site on the US Atlantic coast outside of the Delaware Bay, and will be important in the management of the recovery of the western Atlantic red knot.

Methods

Study area

We studied red knots in the barrier island system on the Eastern Shore of Virginia, USA (37°23.7' N, 75°42.5' W).

The site (VA) consisted of approximately 100 km of narrow barrier islands and marsh islands between the mainland and the Atlantic Ocean (Fig. 1). There are 12 barrier islands in the chain from Fisherman's Island in the south to Assateague Island in the north. A shallow lagoon system with open water, mudflats, and *Spartina* spp. marsh separates the barrier islands, which are largely undeveloped, from the mainland. Red knots typically begin to arrive at their spring migratory stopover sites in the last week of April, and build to a peak population size by about 28 May. Most are gone by the second week of June (Clark et al. 1993; Watts and Truitt 2000).

Red knot capture and tagging

We captured red knots with cannon nets in the sandy ocean intertidal zone on the rising tide throughout the migration season. We marked each red knot on the upper left leg with a lime green plastic flag (a United States-specific marker) etched with a field-readable alphanumeric code, a Darvic orange band on the upper right leg, and a US Geological Survey Incoloy band on the lower right leg. We plucked or cut feathers from a 1 cm × 2 cm patch of skin on the back between the scapulae, and attached a 3-g radio transmitter (2006: American Wildlife Enterprises, Monticello, FL, USA; 2007: Advanced Telemetry Systems, Inc., Isanti, MN, USA) with cyanoacrylate glue. Radios were $< 3\%$ of the average red knot body mass.

Radio-tracking

To locate day-use areas of radio-tagged red knots, we conducted daily aerial telemetry flights in 2006, weather permitting, using a Cessna 172 aircraft (Cessna Aircraft Company, Wichita, KS, USA) equipped with a two-element H-antenna on each wing. We flew at between 152 and 214 m altitude and at 120–136 km/h along the entire shoreline of the study site and through the marsh lagoon system. We split the signal from the antenna using a combiner/splitter, and used two observers. Each observer operated a receiver (Advanced Telemetry Systems, Inc., Isanti, MN, USA) and searched for one half of the deployed transmitters. If repeated relocations suggested that a bird had lost its radio tag, we searched for the tag on the ground using a handheld receiver and antenna.

To identify night use sites of red knots in 2007, we attempted to detect each radio-tagged bird after sundown at high tide twice during the peak migration week (see below). We focused on night roosts because red knots did not appear to have set day roosts in our study area, but rather roosted in flocks adjacent to their foraging sites during daylight high tides, as has been reported in Australia (Rogers et al. 2005).

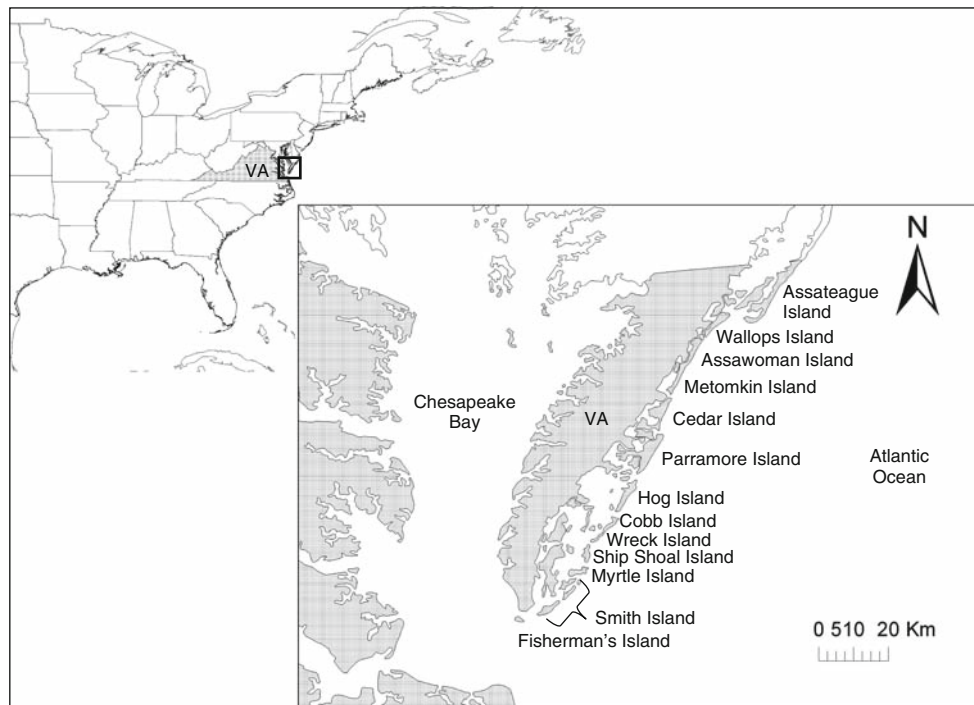


Fig. 1 Study area map of Virginia (VA). We studied red knots during the spring stopover between Fisherman's Island in the south and the Virginia portion of Assateague Island in the north

Habitat selection, flock size, and prey abundance

Each day in 2006, we attempted to locate a sample of radio-tagged birds on the ground for prey and habitat sampling. We selected radio-tagged birds using simple random sampling without replacement, repeating this procedure until all tagged birds believed to be remaining in the study area had been sampled, at which time we replaced all the birds and restarted the sampling protocol. When we approached a radio-tagged bird's location, we attempted to visually identify it. If we could not distinguish it from other flock members, we selected a focal red knot from the flock as close as possible to the apparent location of the tagged bird. We recorded the number of birds in the flock and collected a sediment core sample (10-cm diameter \times 3.5-cm deep, the approximate length of a red knot's bill) centered on the location of the focal knot. All core samples were collected with a section of PVC pipe and stored in 100% ethanol in a 1-L jar (Nalgene Nunc International Corporation, Rochester, NY, USA). We also collected sediment cores halfway between the water and the top of the swash zone (where most red knots were found) at randomly-selected locations without red knots. These locations were chosen using a random-number generator to select latitudes, as the study area was more or less linear along a north–south axis.

In 2007, we sampled red knot flock sizes and behavior at randomly-selected sites along a transect running the length

of the study area. We generated 100 random points along this transect using the Hawth's Tools (Beyer 2004) extension in ArcGIS 9.1 (ESRI, Redlands, CA, USA), constraining each point to be at least 500 m from its nearest neighbor. We counted red knots in flocks within 100 m of the random points. We performed these counts at all 100 random points three times during the migratory stopover: 25 April–4 May, 21 May–28 May, and 29 May–7 June. These sampling periods were chosen in advance to reflect a typical red knot stopover phenology, and we refer to them as 'arrival,' 'peak,' and 'post-peak.' At each point, we collected a 10-cm diameter \times 3.5 cm-deep core sample, using the same techniques as in 2006.

During each sampling period, we collected sediment samples where we encountered red knot flocks away from the random points, provided that these flocks were at least 300 m from the nearest random point. We took the sediment core at the approximate center of the flock, in the swash zone. We collected a paired sediment sample 100 m from the center of such flocks at the same elevation on the beach to examine habitat selection at the patch scale.

In both years, we sorted and counted the number of invertebrates in the sediment samples by category [coquina clams (*D. variabilis*, hereafter "donax"), blue mussels (*Mytilus edulis*), crustaceans (Class Crustacea), polychaete worms (Class Polychaeta), other bivalves (Class Bivalvia), and other organisms]. We dried each sample at 60°C for 48 h, and measured the dry mass within each category.

In 2007, we measured the long shell axis of each bivalve (± 0.1 mm) under a microscope using an SAC-410A color camera (Samsung, Mount Arlington, NJ, USA) with Image Pro Plus 4.1 software (Media Cybernetics, Inc., Bethesda, MD, USA). We measured the distance from red knot night locations to each random point using the Hawth's Tools extension for ArcGIS 9.1.

Statistical analyses

We compared prey abundance in 2006 between used and randomly selected plots using the Multiresponse Blocked Permutation Procedure (MRBP) in Blossom (Cade and Richards 2001), a randomization test analogous to a MA-NOVA. For that analysis, we compared the average prey abundance at sites used by each bird to the average prey abundance across all the randomly selected sites not used by red knots (so the model input contained two lines for each bird, the second of which was the same for all birds).

We compared prey abundance among the three sample periods in 2007 using negative binomial regression (Hilbe 2007). We modeled bivalve length as a function of time period using a mixed model linear regression, with plot as the random effect. We also compared the proportion of donax in different length classes among the three time periods, and between sites near and far from presumed night roosts (with the cutoff distance determined post hoc by the distribution of red knots), using multinomial logistic regression (McFadden 1974) with plot as a random effect. We used Akaike's information criterion corrected for sample size (AIC_c , Burnham and Anderson 2002) and model weights (ω_i , Burnham and Anderson 2002) to determine the best-fitting model (i.e., time period only, distance to night locations only, time period and distance to night locations, and intercept only).

We analyzed the effect of prey abundance, biomass, bivalve length, and distance to night locations on flock size using Δ -lognormal regression. The Δ -lognormal distribution can be used to simultaneously model the probability of a zero value (P_0) in the response variable and the mean of the nonzero values (μ), where the expected value of the response is $(1 - P_0)e^\mu$ (Aitchison and Brown 1957). We performed all-possible-subsets regression with model averaging based on AIC_c to identify variables that were important in explaining flock size. Our candidate variables were donax count, donax mean length, donax dry mass, crustacean count, crustacean dry mass, distance from presumed night roosts, and interactions between donax count and mean length and between crustacean count and dry mass. We used all-possible-subsets logistic regression to determine if red knot use points differed from paired points in prey abundance in 2007.

Results

Sample sizes

We located 21 foraging sites for 13 radio-tagged red knots in 2006. In 2007, we located night-use sites for 18 radio-tagged red knots and used these to calculate distances from our random points to the nearest night-use location. We located these night-use sites near high tide and presumed they were primarily roost sites, but we did not confirm night behavior on the ground. We collected data at 97 sampling locations in 2007, as three of our randomly generated points were in sites that had become unreachable (under water) since our base map was made. We used 92 of these points for our habitat model, because five of them fell on peat banks rather than in the sandy intertidal zone, which was not enough of a sample to include them in an analytical framework. In the peak red knot period in 2007, 78% of the 23 random points where we observed red knots were within 4 km of night locations, and all were within 14 km.

Trends in prey abundance

The most abundant prey items in the ocean intertidal zone during the peak and post-peak red knot periods were donax and crustaceans of various species (Table 1). Blue mussels and other bivalves occurred mainly on outcroppings of peat, which were patchily distributed along the ocean shoreline. We did not detect differences in prey numbers between the peak and post-peak periods in 2006 (Table 1). In 2007, crustaceans and donax increased in abundance over the study period and were most numerous in the post-peak week (Table 1). The average biomass (Table 2), shell length (Table 3), and proportion of large individuals (Table 3) of donax increased over the study period in 2007 (Table 3). Proportion of donax in different length classes did not differ between sites near (<4 or <14 km) and far (≥ 4 or ≥ 14 km) from red knot night use sites; the length class model with time period only fitted the data much better than the models containing distance to night locations, regardless of the distance cutoff used (mixed multinomial logistic regression, AIC_c model weight of the time period-only model = 0.84). Donax shell length ranged from 1 to 10 mm throughout the study.

Factors affecting flock size and presence

With periods pooled, red knot daytime foraging sites had more crustaceans and donax than random points in 2006 (Fig. 2). Donax abundance and mean biomass were highly correlated ($r = 0.87$, $P < 0.001$) in 2007, whereas abundance and mean length were only moderately correlated

Table 1 Mean prey counts and SE of the counts in *rufa* red knot foraging habitat, Virginia, 2006–2007

Year	Period ^a	<i>n</i>	Polychaete		Crustacean		<i>Donax variabilis</i>		<i>Mytilus edulis</i>		Other bivalves	
			\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
2006	Peak	10	0.30 A ^b	0.53	6.20 A	2.34	30.00 A	22.97	0.00	0.00	0.00	0.00
	Post-peak	19	6.05 A	7.32	4.11 A	1.16	20.47 A	11.39	0.00	0.00	0.00	0.00
2007	Arrival	97	0.86 A	0.26	10.55 B	2.84	3.59 C	0.85	10.29 A	8.95	0.97 A	0.76
	Peak	97	0.18 B	0.07	22.37 A	5.98	12.63 B	2.93	0.03 A	0.03	0.02 A	0.02
	Post-peak	97	0.40 AB	0.13	26.86 A	7.17	35.69 A	8.23	0.13 A	0.12	0.21 A	0.17

^a Period is defined as arrival (25 April–4 May), peak migration (21 May–28 May), and post-peak migration (29 May–7 June)

^b Within years, means with the same capital letter within columns (2006 and 2007 analyzed separately) are not significantly different (2007 global tests for polychaetes: $F_{(2,290)} = 5.34, P = 0.005$; crustaceans: $F_{(2,290)} = 7.14, P = 0.001$; *Donax variabilis*: $F_{(2,290)} = 11.61, P < 0.001$; *Mytilus edulis*: $F_{(2,290)} = 0.99, P = 0.373$; other bivalves: $F_{(2,290)} = 1.38, P = 0.253$). There were no significant differences between periods in 2006 (all *P* values > 0.15)

Table 2 Mean prey dry mass (mg) and SE of the mass in *rufa* red knot foraging habitat, Virginia, 2006–2007

Year	Period ^a	<i>n</i>	Polychaete		Crustacean		<i>Donax variabilis</i>		<i>Mytilus edulis</i>		Other bivalves	
			\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
2006	Peak	10	0.5 A ^b	0.4	2.4 A	0.1	354.6 A	130.0	0.0	–	0.0	–
	Post-peak	19	0.07A	0.01	0.9 B	0.2	188.3 A	111.2	0.0	–	0.0	–
2007	Arrival	97	0.19 A	0.06	3.9 A	1.0	38.7 A	12.0	17.4 A	24.3	3.1 A	2.4
	Peak	97	0.10 A	0.03	5.1 AB	1.2	140.0 B	42.3	1.2 A	2.6	0.7 A	0.8
	Post-peak	97	0.28 A	0.10	8.9 B	2.1	347.6 B	114.6	6.0 A	12.9	5.5 A	5.9

^a Period is defined as arrival (25 April–4 May), peak migration (21 May–28 May), and post-peak migration (29 May–7 Jun)

^b Within years, means with the same capital letter within columns (years analyzed separately) are not significantly different (2006 global tests for polychaetes: $F_{(1,28)} = 3.33, P = 0.0792$; crustaceans: $F_{(1,28)} = 5.29, P = 0.029$; *Donax variabilis*: $F_{(1,28)} = 1.72, P = 0.201$; 2007 global tests for polychaetes: $F_{(2,290)} = 2.11, P = 0.124$; crustaceans: $F_{(2,290)} = 3.04, P = 0.049$; *Donax variabilis*: $F_{(2,290)} = 5.69, P = 0.004$; *Mytilus edulis*: $F_{(2,290)} = 0.25, P = 0.779$; other bivalves: $F_{(2,290)} = 0.72, P = 0.487$)

Table 3 Mean *Donax variabilis* shell length (mm) and distribution of shell lengths in *rufa* red knot foraging habitat, Virginia, 2007

Period ^a	Mean length			Proportion of shells in length category (mm) ^b				
	<i>n</i> ^c	\bar{x}	SE	0–2	2–4	4–6	6–8	8–10
Arrival	35	3.63 A ^d	0.14	0.002	0.828	0.165	0.006	0.000
Peak	45	4.12 B	0.13	0.000	0.553	0.423	0.022	0.000
Post-peak	42	4.90 C	0.14	0.000	0.195	0.696	0.103	0.004

^a Period is defined as arrival (25 April–4 May), peak migration (21 May–28 May), and post-peak migration (29 May–7 Jun)

^b Distributions are significantly different among periods, mixed multinomial logistic regression with random plot effect, $F_{(2,121)} = 15.70, P < 0.001$

^c Number of plots (number of clams measured was 5,035)

^d Means with the same capital letter are not significantly different, linear mixed model with random plot effect, $F_{(2,121)} = 15.96, P < 0.001$

($r = 0.38, P < 0.001$). We therefore dropped donax biomass from further analysis in 2007 to avoid collinearity in our regression models, and used length as our indicator of prey size. As we obtained very few samples with blue mussels, we did not include them in further analyses. Distance to presumed night roosts was moderately correlated with donax count ($r = -0.25, P = 0.013$) and mean length ($r = -0.40, P < 0.001$) in the peak period.

In 2007, red knots were present at 9, 24, and 20% of the random points in the arrival, peak, and post-peak periods, respectively ($n = 92$ points). Red knot numbers within 100 m of random points, at points with at least one knot, were 7.8 ± 1.8 (mean \pm SE), 35.2 ± 10.0 , and 43.7 ± 14.0 in the three periods, respectively.

Red knot flock sizes during the 2007 peak period and post-peak period increased with increasing mean donax

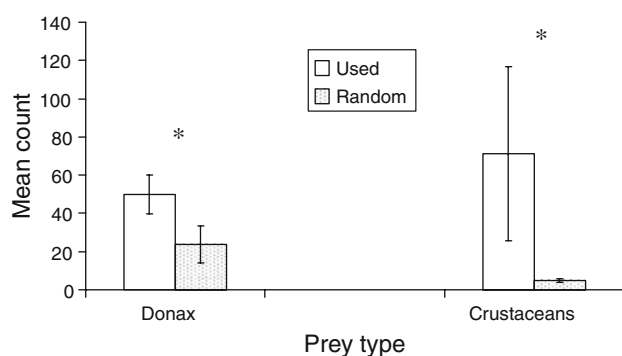


Fig. 2 Mean *Donax variabilis* and crustacean counts at points used by 13 radio-tagged red knots and randomly selected points with no knots, Virginia, May–June 2006. Asterisks indicate that means are significantly greater in used than random points not used by knots (Multiresponse Blocked Permutation Procedure, $P < 0.001$)

length. In the peak period only, probability of flock presence decreased with increasing distance from presumed night roosts (Tables 4, 5). In the peak period, donax count also had a high relative importance index (R_i , Table 4), indicating that it was included in highly-weighted models of flock size, even though it was not a statistically significant factor (i.e., the confidence interval included 0). We did not model habitat use in the red knot arrival period due to low numbers of red knots. We did not identify any variables that determined the probability of red knot presence at used sites compared to paired sites 100 m away in any period; the confidence interval on the model-averaged estimates for every parameter contained zero.

Discussion

We found red knots in Virginia near the best food resources, as in Delaware Bay (Botton et al. 1994;

Karpanty et al. 2006). Selection of larger prey items likely represents the fact that smaller organisms provide too little energy to be worth the handling time (Zwarts and Blomert 1992). Likewise, red knots in Argentina foraged on bivalves between 5 and 20 mm in length out of an available range of 1–28 mm (Gonzalez et al. 1996). Prey patches in our study area were apparently extensive or clustered, as we found no evidence that the abundance or size of donax differed between red knot foraging locations and paired sites 100 m away.

We found no evidence to suggest red knots depleted donax during the stopover period in 2007. Donax reach breeding maturity at a length of 6 mm (Jones et al. 2004), at which time they would be of greatest energetic value to foraging shorebirds (Zwarts 1991). The larger, presumably more energetically valuable, size classes (4–8 mm) of donax increased even into the post-peak period in 2007, suggesting that high-value donax were not consumed during the stopover period faster than they were recruited via immigration or growth. Red knots were present in large numbers in 2007 in Virginia past the typical “peak” portion of the stopover period, perhaps in response to the opportunity to forage on high-quality prey, although there was some evidence from a concurrent band resighting study of a large number of late-arriving red knots in 2007 (Smith et al. 2008). The latter would have encountered abundant donax, and could possibly have compensated for their late arrival with a high-energy intake rate (Atkinson et al. 2007). Although there was a decrease in sample means of donax from the peak to the post-peak period in 2006, the difference was not significant owing in part to small sample size and large variance. However, knots were very unlikely to leave Virginia for Delaware Bay during the spring stopover in either year (Cohen et al. 2009). Migratory shorebirds are predicted to refuel at stopover

Table 4 Model of *rufa* red knot flock presence and size (model average parameter estimates from 47 Δ -lognormal models), Virginia, red knot peak period (21–28 May), 2007 ($n = 92$ plots, 23 used by red knots)

Variable	Flock presence				Flock size where present				R_i^a
	β	SE	Lower 95% CL	Upper 95% CL	β	SE	Lower 95% CL	Upper 95% CL	
Intercept	−0.86	0.10	−1.06	−0.66	2.82	3.17	−3.39	9.03	—
Donax count	0.04	0.04	−0.03	0.11	−0.35	0.25	−0.83	0.14	0.95
Donax mean shell length (mm)	0.19	0.19	−0.19	0.56	6.25 ^b	2.93	0.51	11.98	0.92
Donax count × mean length	0.001	0.005	−0.009	0.011	0.02	0.04	−0.06	0.10	0.16
Crustacean count	0.0006	0.0010	−0.0020	0.0030	−0.004	0.010	−0.024	0.015	0.15
Crustacean mean dry mass (mg)	0.79	2.81	−4.73	6.30	−48.99	129.46	−302.73	204.75	0.10
Crustacean count × mean mass	0.001	0.001	−0.002	0.003	−0.001	0.007	−0.014	0.013	0.00
Distance to nearest night location	−2.33 ^b	0.74	−3.79	−0.87	−1.36	2.93	−7.10	4.38	1.00

^a Relative importance of variable (sum of AIC_c weights of all models containing the variable, ranges from 0 to 1)

^b Significant effect (confidence interval on estimate does not contain 0)

Table 5 Model of *rufa* red knot flock presence and size (model average parameter estimates from 47 Δ -lognormal models), Virginia, red knot post-peak period (29 May–7 June), 2007 ($n = 92$ plots, 15 used by red knots)

Variable	Flock presence				Flock size where present				R_i^a
	β	SE	Lower 95% CL	Upper 95% CL	β	SE	Lower 95% CL	Upper 95% CL	
Intercept	-2.18	0.11	-2.40	-1.97	2.58	1.35	-0.06	5.22	–
Donax count	0.0002	0.0010	-0.0010	0.0020	-0.01	0.02	-0.04	0.03	0.16
Donax mean shell length (mm)	0.20	0.11	-0.03	0.42	3.78 ^b	1.90	0.05	7.51	0.94
Donax count \times mean length	0.000	0.000	0.000	0.000	-0.0001	0.0010	-0.0020	0.0010	0.01
Crustacean count	-0.0005	0.0020	-0.0050	0.0040	0.021	0.051	-0.078	0.121	0.17
Crustacean mean dry mass (mg)	-11.07	23.67	-57.47	35.32	-47.76	349.78	-733.32	637.80	0.27
Crustacean count \times mean mass	-0.024	0.059	-0.140	0.092	-0.532	1.774	-4.009	2.946	0.01
Distance to nearest night location	-0.01	0.05	-0.11	0.08	-0.08	0.26	-0.59	0.43	0.10

^a Relative importance of variable (sum of AIC_c weights of all models containing the variable, ranges from 0 to 1)

^b Significant effect (confidence interval on estimate does not contain 0)

sites where energy intake rates allow them to maximize the overall speed of migration and to leave a site that does not provide sufficient food (Alerstam 2003; Battley et al. 2005; van Gils et al. 2005a). Thus the increase in donax abundance observed during the 2007 season and the long residence times of red knots suggest that there was a food surplus and that additional red knots could likely have been supported at the same level of food intake in that year.

Red knots could have suffered from inadequate food intake even in the midst of abundant prey if they were unable to access the prey. The selection of foraging sites close (mostly within 4 km) to presumed night roosts by red knots indicated that factors in addition to food availability could have influenced habitat selection. Since commuting carries energetic and predation-risk costs, red knots may prefer to forage close to roosting sites even if they are aware of abundant food elsewhere (van Gils et al. 2006). In our study, we did not find evidence of depletion near presumed night roosts, so even if red knots were constrained to forage near roosts they appeared to have adequate food. A more comprehensive study of roost site characteristics that includes distance to prey, safety from predators (Rogers et al. 2005), and shelter from weather would help to discern the relationship between roost and foraging site selection.

Despite the apparent food surplus, knots also could have suffered from inadequate energy intake rates if donax is a very low quality food. Recent results indicate that energy metabolized by red knots may be limited by the amount of undigestible material in their food (van Gils et al. 2005a, b). Gizzard size in red knots changes depending on physiological state (e.g., migrating vs. refueling) and the degree of change may depend on the type of prey available at a stopover site (Piersma et al. 1999b). Red knots consuming shellfish with high shell:flesh ratios require more time and/or larger gizzards to crush and process prey items than do

knots consuming prey with low shell:flesh ratios (van Gils et al. 2003). Migrating knots appear to select stopover sites with high-quality food to allow rapid refueling (van Gils et al. 2005a). The length of stay (similar to nearby Delaware Bay, where knots eat horseshoe crab eggs) and the stopover population trend (recently increasing, Cohen et al. 2009) suggest that Virginia provides adequate food for red knots. Future studies on prey quality and red knot mass gains should shed additional light on this question. Ultimately, the value of this and other sites will best be evaluated by studying the effect of the site on the survival and reproduction of the stopping birds.

Horseshoe crab eggs, a staple for red knots in the nearby Delaware Bay (Niles et al. 2009), were not present in Virginia in appreciable numbers in our study, or in other recent Virginia surveys (Truitt et al. 2001). Niles et al. (2009) suggested that only horseshoe crab eggs are sufficient to fuel the majority of red knots for the final leg of their northward migration, and Buehler et al. (2006) suggested that the presence of abundant horseshoe crab eggs was key to the evolution of the current migratory route of the Western Atlantic red knot. Donax, by implication, would be too low quality to fuel migration from the mid-Atlantic coast to the breeding grounds. However, early ornithological literature in the United States focused on knots eating mollusks, though there also are accounts of them consuming cutworm larvae (Noctuidae), crustaceans, and horseshoe crab eggs (Wilson and Bonaparte 1832; Mackay 1893; Shriner 1897; Forbush 1912). Moreover, donax comprised 98% of the food found in 85 knots collected in Virginia before 1940 (Sperry 1940). This is consistent with the literature for other red knot subspecies, which clearly cast the red knot as a mollusk specialist, whether on migration or wintering (Zwarts and Blomert 1992; Piersma et al. 1994; Battley et al. 2005; van Gils

et al. 2005b). European-wintering red knots (*C.c. islandica*) gained weight rapidly when foraging on bivalves at their Iceland stopover site (up to 5 g/day in the peak of the stopover period, Piersma et al. 1999b), although the average growth rate for the whole stopover period (2.8 g/day) was not as high as in Delaware Bay (4.6 g/day, Piersma et al. 2005; up to a maximum of 18.8 g/day, Atkinson et al. 2007). Nonetheless, a weight gain of 5 g/day would be sufficient for a red knot arriving in Virginia at an emaciated 100 g to reach the 180 g needed to reach the tundra (Baker et al. 2004) in 16 days, the approximate length of time a bird arriving in Virginia in mid-May would be expected to stay (Cohen et al. 2009).

While our results in this study suggest that the Virginia barrier islands could, at least in some years, provide resources for a larger stopover population than we observed in 2007, we do not argue that Virginia is consistently a valuable stopover site. Bivalve populations vary over time and space (Jones et al. 2004; Beukema and Dekker 2007), and there have been years in Virginia in which blue mussels were abundant and clams were sparse during the red knot migration (Truitt et al. 2001). Similarly, storms or cold water can delay horseshoe crab spawning such that peak spawn occurs after red knots have largely departed (Kochenberger 1983; Smith and Michels 2006), indicating that horseshoe crab eggs, like bivalves, are a resource that can vary in time and space. While long-term studies are needed to characterize the interannual variation in red knot prey abundance across stopover areas, it appears likely that protecting as many areas as possible would be in the best interest of the species. Between 1922 and 2003, more than 6,050 km of Atlantic and Gulf of Mexico beaches were subject to the placement of millions of cubic meters of sand to protect human development and enhance recreation (Peterson and Bishop 2005). Such sand placement can reduce populations of donax and other macroinvertebrates which serve as prey to shorebirds, thus reducing their use by shorebirds (Peterson et al. 2006). Protection of red knot stopover sites should include reconsideration of practices that reduce the abundance of their prey and thus the potential size of their stopover range.

Zusammenfassung

Der Einfluss der Abundanz und Größe benthischer Beute auf die Verteilung des Knutts (*Calidris canutus*) in einem Rastgebiet an der US-amerikanischen Atlantikküste während des Frühjahrszuges

Ein Populationsrückgang des westatlantischen Knutts (*Calidris canutus rufa*) ist mit Nahrungsknappheit während einer Rast in der Delaware-Bucht, USA, auf dem

Frühjahrszug in Verbindung gebracht worden. Der Rastökologie an möglichen alternativen Plätzen wurde wenig Beachtung geschenkt. Wir haben Faktoren untersucht, welche die Habitatselektion und Schwarmgröße des Knutts an einem Küstenrastplatz in Virginia in den Jahren 2006 und 2007 beeinflussten. Die häufigsten potentiellen Beuteobjekte waren Florida-Dreiecksmuscheln (*D. variabilis*) und Krebstiere. Die Nahrungsplätze des Knutts wiesen 2006 mehr Florida-Dreiecksmuscheln und Krebstiere auf als ungenutzte Stellen. Die Beuteabundanz stieg während der Rastperiode 2007 an und blieb auch nach der Hauptanwesenheitszeit des Knutts hoch. Die Größe der Knuttschwärme nahm 2007 mit der mittleren Länge der Muschelschalen zu, und die Wahrscheinlichkeit der Anwesenheit eines Schwarms an einer Stelle nahm mit zunehmender Entfernung von den zur Nacht genutzten Plätzen ab. Unsere Ergebnisse deuten darauf hin, dass Knutts Florida-Dreiecksmuscheln bevorzugen und die Muschelvorkommen während der Rastperiode im Jahr 2007 nicht erschöpft wurden. Daher schien die Beuteabundanz kein die Population limitierender Faktor an diesem Küstenrastplatz in Virginia in diesem Jahr zu sein. Der Schutz von Küstengebieten außerhalb der Delaware-Bucht, von denen viele durch menschliche Bautätigkeit verändert wurden, würde sich auf die Erholung der Knuttpopulationen wahrscheinlich positiv auswirken, da sie zumindest in einigen Jahren ergiebige Nahrungsressourcen bereitstellen können.

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