

HABITAT SELECTION AND BEHAVIOR OF RED KNOTS ON THE NEW JERSEY ATLANTIC COAST DURING SPRING STOPOVER

JONATHAN B. COHEN¹, SARAH M. KARPANTY, AND JAMES D. FRASER

Department of Fisheries and Wildlife Sciences, Virginia Tech, Blacksburg, VA 24061-0321

Abstract. Delaware Bay is an important spring stopover site for the Western Atlantic Red Knot (*Calidris canutus rufa*), which has suffered a recent population decline. Stable-isotope evidence suggests Red Knots from different wintering areas partially segregate at the site, with short-distance migrants concentrating on the Atlantic coast of New Jersey rather than in Delaware Bay itself. The Red Knot has been little studied on the Atlantic coast, and our objectives were to determine the extent to which birds captured on the coast used Delaware Bay and to characterize their habitat use and behavior. In 2006, we radio-tracked birds captured on an Atlantic beach and collected behavioral data and prey samples for comparison to those at randomly selected plots within Red Knot habitat. Depending on tidal stage, the distribution of Red Knot locations was skewed toward either Atlantic marshes or beaches. It was skewed away from Delaware Bay on the falling tide. Red Knots observed in Delaware Bay were foraging, whereas birds on the Atlantic coast were equally likely to forage or rest on rising and high tides. On the Atlantic coast, Red Knot locations had significantly more prey items than did random points, but this was not so on Delaware Bay beaches. Our results support the idea of partial segregation between Red Knots stopping on New Jersey's Atlantic coast and those in Delaware Bay, at least in some years. Whatever the cause of this partial segregation, conservation of Red Knots depends on protecting a complex of stopover habitats.

Key words: *Calidris canutus*, Delaware Bay, habitat selection, New Jersey, Red Knot, shorebirds, stopover.

Selección de Hábitat y Comportamiento de *Calidris canutus* en la Costa Atlántica de Nueva Jersey durante la Parada de Primavera

Resumen. La Bahía de Delaware es un sitio de parada de primavera importante para *Calidris canutus rufa*, quién ha sufrido recientemente una disminución poblacional. La evidencia de isótopos estables sugiere que los individuos de *C. canutus* de diferentes áreas de invernada se segregan parcialmente en este sitio, y que los individuos que realizan migraciones de corta distancia se concentran en la costa atlántica de Nueva Jersey más que en la misma Bahía de Delaware. La especie *C. canutus* ha sido poco estudiada en la costa atlántica, por lo que nuestros objetivos fueron determinar el grado con que las aves capturadas en la costa usan la Bahía de Delaware, como también caracterizar su uso de hábitat y comportamiento. En 2006, seguimos con radio transmisores a las aves capturadas en una playa atlántica y colectamos datos de comportamiento y muestras de presas en esos sitios para compararlas con las de parcelas seleccionadas al azar dentro del hábitat de *C. canutus*. Dependiendo de la altura de la marea, la distribución de las localizaciones de *C. canutus* fue sesgada hacia las marismas o hacia las playas del Atlántico. Las aves se alejaron de la Bahía de Delaware en la marea menguante. Los individuos de *C. canutus* observados en la Bahía de Delaware estuvieron siempre forrajeando, mientras que las aves de la costa atlántica tuvieron la misma probabilidad de estar forrajeando o descansando durante las mareas creciente o alta. En la costa atlántica, las localizaciones de *C. canutus* presentaron significativamente más tipos de presa que los sitios al azar, pero este no fue el caso en las playas de la Bahía de Delaware. Nuestros resultados apoyan la idea de segregación parcial entre los individuos de *C. canutus* que paran en la costa atlántica de Nueva Jersey y los de la Bahía de Delaware, al menos en algunos años. Cualquiera que sea la causa de esta segregación parcial, la conservación de *C. canutus* depende de proteger un complejo de hábitats de parada.

INTRODUCTION

A decline in the number of northbound Western Atlantic Red Knots (*Calidris canutus rufa*) stopping in Delaware Bay has been attributed to overharvest of horseshoe crabs (*Limulus polyphemus*), the eggs of which provide abundant food for migrating shorebirds (Baker et al. 2004, Niles et al. 2008, 2009).

Concurrently, diminishing sizes of winter flocks in Tierra del Fuego, at the southern extreme of South America, suggest that the Red Knot population has truly declined, rather than having shifted either its stopover or wintering locations (Morrison et al. 2004).

A second smaller group of Western Atlantic Red Knots winters in the Caribbean and along the coasts of the Gulf of

Manuscript received 14 October 2009; accepted 9 May 2010.

¹E-mail: jocohen1@vt.edu

Mexico and southern Atlantic states (Niles et al. 2008). Stable-isotope analyses of feathers collected in the Delaware Bay region have indicated that birds from both sections of the winter range stop there (Atkinson et al. 2005), but the northern-wintering group is more heavily represented on New Jersey's Atlantic coast (Atkinson et al. 2006). This difference suggests that Red Knots using the Delaware/New Jersey region during the spring stopover may partially segregate, at least in some years. If so, one segment of the subspecies may not benefit from conservation that focuses solely on horseshoe crabs, depending on what resources are used by birds on the coast. These may include bivalves (Haramis et al. 2007), which are the staple of nonbreeding Red Knots on stopover in nearby Virginia and around the world (Piersma et al. 2005, Cohen et al. 2010).

Understanding habitat and prey selection during stopover is important to conserving the Red Knot, which is a candidate species for listing under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2006) and was recommended for designation as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2007). Little is known about the habitat use and prey selection of Red Knots stopping over on the Atlantic coast of New Jersey. Sanderlings (*Calidris alba*) collected from New Jersey's Atlantic beaches contained a high percentage of polychaetes, as well as horseshoe crab eggs (Tsipoura and Burger 1999), indicating that horseshoe crab eggs may be available to Red Knots along the coast as well as in Delaware Bay. During the spring stopover, especially at high tide, several species of shorebirds forage in the Atlantic marshes of New Jersey, which are adjacent to the coastal beaches (Burger et al. 1997).

The current habitat on the Atlantic coast likely represents a small and degraded remnant of what was once available to Red Knots (MacKay 1893). Over the last century, Atlantic beaches and marshes have been heavily affected by human development and recreation (U.S. Commission on Ocean Policy 2004). Such habitat loss at stopover sites is believed to account for shorebird declines globally (Thomas et al. 2006). If a distinct subset of the Red Knot's population concentrates in migration on beaches and marshes along the Atlantic coast, then the factors affecting its distribution and abundance on the coast merit further attention. Our objectives were (1) to describe the habitat distribution of Red Knots radio-tagged on New Jersey's Atlantic coast during spring stopover, including the effect of tidal stage, (2) to determine whether the Red Knot's behavior differs by habitat at different tidal stages, and (3) to determine if the species' distribution within various habitats is associated with particular prey. Our results will shed light on whether Red Knots using the Atlantic coast are segregated to any degree from those using Delaware Bay and will help to highlight resources important to the birds on the coast that might warrant protection.

METHODS

STUDY AREA

We studied Red Knots on the Atlantic coast of New Jersey (39° 03' N, 74° 46' W) and in the Delaware Bay estuary. The Atlantic portion of the study area consists of narrow barrier islands and tidal shoals, bounded by the Atlantic Ocean to the east and salt marshes and lagoons to the west (Fig. 1). The barrier islands are characterized by sandy beaches and adjacent intertidal flats and are punctuated by tidal inlets that allow the ocean to flush into the marsh/lagoon. Except for protected sanctuaries near the inlets, the islands are covered by dense human development. The marsh/lagoon system consists of islands of saltmarsh cordgrass (*Spartina alterniflora*) and sandbars, some of which are inhabited by blue mussels (*Mytilus edulis*). The Delaware Bay estuary portion of the study area contains the shoreline of Delaware Bay in both New Jersey and Delaware and is composed of salt marsh and tidal creeks edged with beaches of peat or sand (Fig. 1). Much of the latter are covered by moderate to dense human development, and in some places the shoreline is armored with bulkheads. Red Knots typically start arriving at these stopover sites during the last week of April and build to peak numbers by late May; most are gone by the second week of June (Clark et al. 1993).

FIELD METHODS

Using cannon nets, biologists with the New Jersey Endangered and Nongame Species Program captured Red Knots at Stone Harbor Point, a barrier spit on New Jersey's Atlantic coast, on 18 May 2006. We trimmed the feathers down to the stubble in a 2-cm × 2-cm patch between the scapulae on 19 Red Knots and attached 3.1-g radio transmitters (American Wildlife Enterprises, Monticello, FL) to the patch with cyanoacrylate glue. We flew daily radio-tracking surveys, weather permitting, in a Cessna-172 fixed-wing aircraft from 20 May to 1 June 2006. We followed the shoreline of the Delaware Bay from Cape Henlopen to Bombay Hook, Delaware, and from Ben Davis Point to Cape May, New Jersey, and the shoreline of the New Jersey Atlantic coast from Cape May to Corson's Inlet. We also flew a transect down the center of the Atlantic marsh/lagoon system. During each flight we attempted to relocate all radio-tagged Red Knots. Our surveys included all areas on the Delaware Bay shoreline Red Knots are known to use. We flew at 112 km hr⁻¹ between 150 and 300 m elevation. To detect radio signals, we used one H-antenna on each wing strut, connected to a left/right switchbox in the plane that allowed us to receive signals from either or both antennae, and a combiner/splitter that directed the signal to the receivers of each of two observers. Each receiver contained half of the radio frequencies and was set to cycle through one frequency every 2 sec. When we detected a signal, we recorded the location and time of detection on a map.

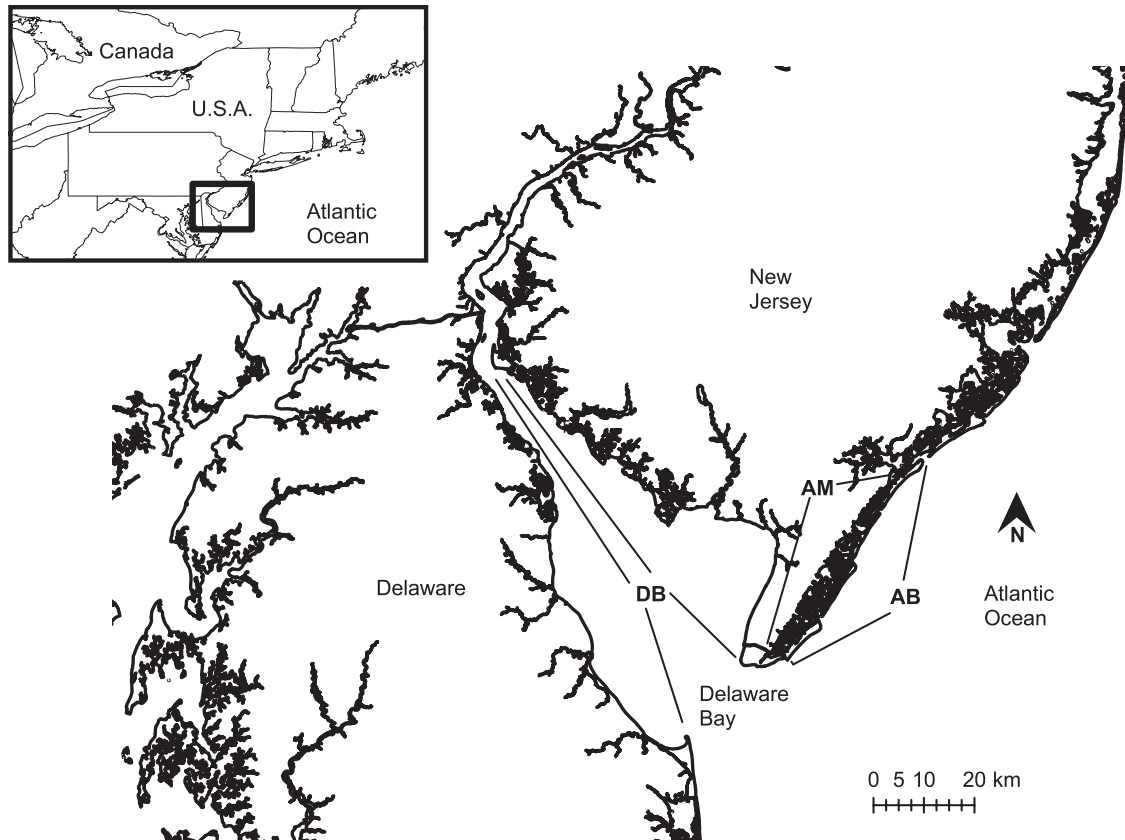


FIGURE 1. Map of study area where we tracked Red Knot habitat use, New Jersey and Delaware, 2006. The three habitat zones we recognized in the study were Atlantic beaches (AB), Atlantic marshes (AM), and Delaware Bay beaches and marshes (DB).

We randomly selected a subset of birds located on aerial surveys each day to be sampled on the ground for behavior and habitat use. We used a stratified random-sampling scheme in which the strata were Atlantic coast beach (AB), Atlantic coast marsh (AM), and Delaware Bay beach or marsh (DB). Within strata, we sampled the birds without replacement until all of them were sampled once, after which we replaced them all and started sampling again. This procedure resulted in some birds being sampled multiple times through the season. When we detected a target bird on an aerial survey, we relayed the location to a ground crew, which scanned the vicinity for the target frequency with a hand-held receiver and a three-element Yagi antenna. We attempted to identify the target bird visually by looking for the antenna with a spotting scope. If we could not find the target bird, we randomly selected a focal bird from its flock by counting a random number of birds in from the left edge of the flock. We recorded the behavior of the target bird every 10 sec for 3 min (Altmann 1974) as feeding, walking, standing, sleeping, preening, flying, or other. We categorized the focal bird as "foraging" if it fed for >50% of the 10-sec observation. We categorized the bird as "resting" if it was sleeping, preening, or standing for >50% of the 10-sec observation. We categorized the tide during our observations

as high of within 1 hr of the predicted high, falling from 1 hr after the predicted high to 1 hr before the predicted low, low if within 1 hr of the predicted low, and rising from 1 hr after the predicted low to 1 hr before the predicted high.

If few or no birds were foraging during our observations of behavior, our sampling ended at that point. Otherwise, we collected three sediment samples on a transect perpendicular to the shoreline that passed through the location of the bird. Using a PVC corer, diameter 10 cm, depth 3 cm, we collected the samples at the seaward edge of the flock, the center of the flock, and the landward edge of the flock, then placed the sample in a 1-L plastic bottle, which we filled with 100% ethanol upon return from the field. We also collected sediment samples from randomly chosen plots in each of the three strata, by generating random latitudes and longitudes within the boundaries of each stratum. At each random point we collected three samples from the seaward edge, center, and landward edge of the wet intertidal zone (i.e., the portion of the intertidal zone that is wet from recent tidal and wave action but not actively being hit by waves), where Red Knots typically forage. We counted the number of items of Red Knot prey in the samples, considering as potential prey polychaete worms, crustaceans, insect larvae, horseshoe crab eggs, blue mussel spat (i.e.,

juveniles), coquina clams (*Donax variabilis*), other clams, and gastropods (Harrington 2001). For both points used by Red Knots and random points, we used the average counts of prey in the three subsamples at each plot as our indicator of prey abundance. If we collected two or more samples per individual Red Knot within a stratum through the season (because after sampling all birds without replacement we restarted the sampling), we averaged prey abundance within a bird's locations to avoid including nonindependent observations in our analyses as if they were independent samples.

STATISTICAL ANALYSES

We determined whether aerial radio locations were evenly distributed among AB, AM, and DB within each tidal stage with a multinomial logistic regression (SAS PROC NLMIXED) to model habitat used by tidal stage, which provides results identical to those of a χ^2 test when the explanatory variables are categorical fixed effects. However, modeling habitat use in this way allowed us to include the random effect of individual, to determine if using some individuals' locations multiple times resulted in overdispersion (e.g., allowed us to test for the effect of pseudoreplication). We compared the fit of the mixed model with an effect of individual bird to a fixed model without such an effect by using Akaike's information criterion corrected for small sample size (AIC_c , Burnham and Anderson 2002), where a difference of 2 or less indicates that including the individual-bird effect was not necessary because it did not improve the model's fit. Because our number of behavioral observations when broken down by habitat and tidal stage was small, we did not statistically compare activity budgets but rather present in a table the number of observations in each stratum/tide/behavior combination.

Although we did not have data to determine how the area of AB, AM, and DB changed with tidal stage, we calculated the total area of each habitat type from land-use/land-cover data to provide some reference for their relative availability. For Delaware, the data came from the 2007 Delaware Land Use and Land Cover dataset, which was based on aerial photographs taken in 2007 and contained land-cover classes relevant to shorebirds (DataMIL 2008). For New Jersey, the data came from a 1992 classification of shorebird habitat, based on aerial photographs taken in 1986 (New Jersey Department of Environmental Protection 1992). More recent land-use/land-cover data for New Jersey did not have a classification system fine enough to be useful for mapping shorebird habitat. We considered all cover classes of beach, coastal open sand, and unvegetated tidal land to be useful for Red Knot foraging and/or roosting, and we added the area of all such classes within AB, AM, and DB. The results of this exercise provided only an index of habitat availability, given that the New Jersey data were old and the tidal stage at which the aerial photographs were taken was unknown. However, we believe the index roughly represents habitat availability around low tide because the full extent of tidal flats and creeks appeared to be delineated.

We compared the average number of prey items in the random samples from AB, AM, and DB with the multiresponse permutation procedure (MRPP, Cade and Richards 2005). MRPP is a nonparametric permutation test that can be used in lieu of ANOVA when sample sizes are small. We compared the abundance of prey at locations Red Knots used and random locations with the multiresponse blocked permutation procedure (MRBP), with individual Red Knots as blocks (Cade and Richards 2005). Like MRPP, MRBP is a nonparametric permutation test for comparing responses by group, and the blocking allowed us to compare use data from individual animals to availability data for the whole population.

RESULTS

We radio-tagged 19 Red Knots and obtained 110 aerial radio locations. We relocated each bird 1–9 times (mean 5.8, median 7). The average percentage of locations in each habitat type, tidal stages pooled, was 37% on Atlantic beaches, 41% in Atlantic marshes, and 21% on Delaware Bay beaches. According to a test with fixed-location transmitters, our classifications of Red Knot relocations were accurate within 200 m, which would easily separate the birds among the three habitat strata.

The fit of the mixed model of Red Knot distribution among habitats by tide ($AIC_c = 232$) was worse than the fixed-effects model that lacked an effect of individual birds ($AIC_c = 229$). Thus, we found no evidence of nonindependence of radio locations caused by repeated measures of individual birds and proceeded to analyze the radio locations as if they were independent observations. At high and low tide, most radio locations were on Atlantic beaches and only one was in the Atlantic marshes (Table 1). When the tide was rising, most locations were in the Atlantic marshes (Table 1). On the falling

TABLE 1. Distribution of Red Knot radio locations ($n = 110$ locations of 19 birds) among Atlantic beaches (AB), Atlantic marshes (AM) and Delaware Bay beaches and marshes (DB) by tidal stage, New Jersey and Delaware, 2006.

Tide ^a	Habitat	Number	%	Partial χ^2	χ^2_2	P^b
High	AB	12	66	6.0	10.3	0.006
	AM	1	6	4.1		
	DB	5	28	0.2		
Falling	AB	20	48	2.5	6.1	0.046
	AM	15	36	0.1		
	DB	7	17	3.5		
Low	AB	0	0	6.0	14.3	0.001
	AM	13	72	8.1		
	DB	5	28	0.2		
Rising	AB	4	13	4.1	10.9	0.004
	AM	19	59	6.5		
	DB	9	28	0.3		
All	AB	49	44	4.1	7.3	0.026
	AM	35	32	0.1		
	DB	26	24	3.1		

^a High, ± 1 hr of predicted high tide; low, ± 1 hr of predicted low tide.

^b Test of equal distribution among habitats.

tide, most locations were on the Atlantic beaches and marshes (Table 1). Only four of 26 (15%) radio locations in Delaware Bay were on the Delaware side; the rest were in New Jersey. The areas and percentages of the total area of the three habitats, based on land-use and land-cover data, were AB = 579 ha (30%), AM = 872 ha (44%), and DB = 508 ha (26%). Because the tide affects habitat availability, we did not attempt to compare use to availability on the basis of these maps but provide the percent availability around low tide for reference. Because we never relocated Red Knots in Delaware Bay marshes, the value for DB included Delaware Bay beaches only, and we excluded the marshes from further analyses.

In Delaware Bay Red Knots were foraging, regardless of tidal stage, and in Atlantic marshes they were usually foraging (Table 2). They always foraged on the falling tide, regardless of habitat (Table 2). On Atlantic beaches, the few Red Knots we observed at high tide were closely divided between resting and foraging (Table 2).

On the basis of randomly collected samples, polychaetes were less abundant on Atlantic beaches than in other habitats, and horseshoe crab eggs were more abundant in Delaware Bay than in Atlantic habitats (Table 3). In Atlantic beaches and marshes, several potential prey items were more abundant at points Red Knots used than at random points; in the marshes these included crab eggs, although they were not very

TABLE 2. Frequency of Red Knots observed foraging and resting on Atlantic beaches (AB), Atlantic marshes (AM), and Delaware Bay beaches and marshes (DB) at various stages of the tide, New Jersey, 2006.^a

Habitat	Behavior ^b	Tide				
		High	Falling	Low	Rising	All
AB	Foraging	1	6	1	1	9
	Resting	1	0	0	2	3
AM	Foraging	— ^c	6	3	—	9
	Resting	—	0	1	—	1
DB	Foraging	2	4	2	3	11
	Resting	0	0	0	0	0
All	Foraging	3	16	6	6	31
	Resting	1	0	1	2	4

^a Sample size of birds (high, falling, low, rising tides, respectively) for AB = 2, 5, 1, 3; for AM = 0, 6, 4, 0; for DB = 2, 4, 2, 3.

^b Foraging, bird recorded as feeding for >50% of 10-sec intervals during 3 min of observation; resting, bird sleeping, standing, or preening for >50% of 10-sec intervals.

^c No observations.

abundant (Table 3). Most striking was blue mussel spat, which was virtually absent from sites not used by Red Knots but very abundant at some used sites (Table 3). In Delaware Bay, most prey items were less abundant at points Red Knots used

TABLE 3. Abundance of prey items at plots (samples were means of 3 10-cm diameter × 3.0-cm deep subsamples) used by Red Knots and randomly-selected plots ($n = 29$ – 30 per habitat type) in Atlantic beaches (AB), Atlantic marshes (AM) and Delaware Bay beaches and marshes (DB), New Jersey, 2006.

Habitat	Prey	Used points			Random points			MRBP ^b		Selection index ^c
		n	\bar{x}	SE	n	\bar{x} ^a	SE	S	P	
AB	Polychaetes	10	4.67	1.95	29	0.17 B	0.09	−4.1	0.005	+
	Insect larvae		0.02	0.02		0.01	0.01	−3.0	0.016	+
	Crustaceans		4.41	1.51		0.75	0.30	−4.0	0.008	+
	Mussel spat		125.64	41.11		0.43	0.36	−3.3	0.012	+
	Clams		1.02	0.36		1.39	0.50	−0.6	0.187	0
	Horseshoe crab eggs		1.17	1.01		0.00 B	0.00	−1.6	0.058	0
AM	Polychaetes	10	1.82	0.52	30	2.55 A	0.83	−0.5	0.211	0
	Insect larvae		0.05	0.03		0.01	0.01	−2.9	0.018	+
	Crustaceans		5.45	1.60		1.44	0.83	−1.7	0.067	0
	Mussel spat		132.88	29.88		2.50	1.59	−5.3	0.002	+
	Clams		1.48	0.74		0.15	0.08	−3.1	0.012	+
	Horseshoe crab eggs		0.07	0.07		0.01 B	0.01	−4.0	0.008	+
DB	Polychaetes	10	2.26	1.08	29	14.69 A	11.44	−6.3	0.001	−
	Insect larvae		0.00	0.00		0.11	0.07	−2.7	0.027	−
	Crustaceans		0.18	0.12		0.35	0.13	−6.7	0.001	−
	Mussel spat		0.14	0.08		1.11	0.62	−6.4	0.001	−
	Clams		0.08	0.03		4.95	4.23	−6.7	0.001	−
	Horseshoe crab eggs		25.83	10.21		48.37 A	27.33	−1.8	0.062	0

^a Within categories of prey, means of habitats with the same capital letter are the same; multiresponse permutation procedure, $\alpha = 0.05$. No capital letters are shown if the habitats did not differ.

^b Results of comparison by the multiresponse blocked permutation procedure of mean number of prey items at used and random points, where S = Pearson type III test statistic and P = significance value of the test.

^c + = mean greater at used than at random points, 0 = mean at used and random points equal, − = mean lower at used than at random points.

than at random points, but there was no statistical difference between counts of horseshoe crab eggs at used and random points (Table 3).

DISCUSSION

Like Red Knots tagged in Delaware Bay in 2004, those tagged on the New Jersey Atlantic coast in 2006 concentrated in areas with a high abundance of their prey (Karpanty et al. 2006). Cohen et al. (2010) demonstrated similar associations between Red Knot distribution and prey abundance during migration in Virginia. Unlike Red Knots tagged in Delaware Bay in 2004, which did not use coastal beaches, on the Atlantic side Red Knots remained largely coastal and their distribution was not related to horseshoe crab eggs. This difference represents either an opportunistic response of Red Knots to a change from 2004 to 2006 in the distribution and composition of prey or partial segregation between populations that use Delaware Bay and the Atlantic coast during migratory stopover.

Unfortunately for the evaluation of the opportunism hypothesis, longitudinal aerial surveys of shorebird abundance in the region have not historically included New Jersey's Atlantic coast, and horseshoe crab eggs have been the sole focus of long-term monitoring of prey (Niles et al. 2008, Niles et al. 2009). It is possible that bivalves were lacking on the Atlantic coast in 2004, as they cycle through years of boom and bust (Beukema and Dekker 2007). However, numbers of horseshoe crab eggs in Delaware Bay in 2004 and 2006 were similar (Niles et al. 2009). On the basis of a limited number of counts from the ground, there were Red Knots on New Jersey's Atlantic coast in 2004, but they were scarce in comparison to 2003 and 2006 (Delaware Department of Natural Resources and Environmental Control and New Jersey Department of Environmental Protection, unpublished data). More substantially, in Delaware Bay peak aerial counts in 2004 and 2006 were virtually identical (Niles et al. 2008), which would seem to counter the notion of a habitat shift by the Delaware Bay population.

We believe our results are therefore consistent with partial habitat segregation of different populations while stopping over during migration, but it is possible that such segregation occurs only in years when prey is abundant on the coast. Intraspecific habitat segregation in birds was first described as a means to reduce competition between males and females (Sclander 1966). In songbirds, however, segregation in the nonbreeding period has been shown to result from dominance of a particular sex or age or of residents over migrants (Lynch et al. 1985, Catry et al. 2004, Perez and Hobson 2009), sometimes to the detriment of the fitness of subordinates (Marra and Holmes 2001). Fernandez and Lank (2006) showed habitat segregation of the Western Sandpiper (*Calidris mauri*) to be based on sex and age also. Additionally, the Western Sandpiper's latitudinal habitat segregation is associated with

birds with different bill lengths migrating different distances (Mathot et al. 2007). Differential migration may also lead to sex- and age-based latitudinal habitat segregation (Ketterson and Nolan 1976, Marques et al. 2009). Therefore, proximate (dominance) and evolutionary (habitat specialization) factors can lead to segregation by nonbreeding habitat at different spatial scales.

Whether the partially segregated stopover of Western Atlantic Red Knots represents different wintering populations, as suggested by Atkinson et al. (2006), and whether these populations consist of the same birds from one year to the next, needs further study. Both questions are possibly resolvable with the current database of resightings of banded birds (Shorebird Project 2009). It also may be possible to partially resolve the question of dominance-mediated segregation with available data on morphology and age from cannon-net captures, although identifying sex-based segregation during stopover will require molecular techniques.

An alternative, evolutionary explanation also is credible, given the potentially different migration strategies of northern- and southern-wintering Red Knots. Atkinson et al. (2006) advanced the hypothesis that short-distance migrants from Florida may not be reliant on horseshoe crab eggs for rapid weight gain, as they may migrate in short hops and thus refuel on the way. Elsewhere in the world, for fuel for migration, Red Knots rely on bivalves (Piersma et al. 2005, Morrison et al. 2007), such as those found on New Jersey's Atlantic coast. Therefore, Red Knots migrating short distances could avoid competition in Delaware Bay with birds from the southern-wintering group, which rely on fast rates of weight gain from consuming abundant horseshoe crab eggs, by using the Atlantic coast. If so, early in the spring stopover period Red Knots should be in better body condition on the Atlantic coast than in Delaware Bay because they would not be emaciated from a nonstop long-distance flight from South America, another issue that could be resolved with available morphology data. Puzzling for evolutionary explanations is the lack of documentation of the Red Knot in Delaware Bay before 1980 (Clark et al. 1993), despite accounts of Ruddy Turnstones (*Arenaria interpres*) foraging on horseshoe crabs there (Stone 1937) and large numbers of Red Knots along the Atlantic coast of several states (MacKay 1893).

A comparison of prey samples at sites where Red Knots foraged highlighted differences in prey abundance among Atlantic coast beach, Atlantic coast marsh, and Delaware Bay that were not evident from our random samples alone. Random sampling may not have captured the difference in prey abundance among sites as well as sampling at foraging locations because benthic prey is patchily distributed (Hewitt et al. 1993), and our random sample was small enough to have missed the high-quality patches where Red Knots apparently concentrate. Mussel spat illustrated this point the best, as at random sites we found almost none, but at some sites Red

Knots used mussel spat was very dense. On sandy beaches of Delaware Bay, sites where tagged birds foraged in 2004 likewise contained a greater abundance and diversity of prey items than random points, with horseshoe crab eggs making up 91% of the prey biomass (Karpanty et al. 2006). Birds tagged on the Atlantic coast in 2006, however, did not appear to be in "hot spots" for eggs when foraging on Delaware Bay. This difference may have arisen because eggs were not patchily distributed, or because competition kept Red Knots tagged on the Atlantic coast away from the "hot spots" or because the birds were simply not selecting habitat on the basis of egg abundance, but our data cannot distinguish among those possibilities.

Regardless of how the segregation during stopover arose, and whether it occurs in only some years, our results support the idea that a comprehensive conservation strategy should include coastal habitat protection as well as horseshoe crab management. The latter is certainly critical, but at least in some years, part of the population stopping over in the Delaware Bay region uses a complex of habitats and prey items. Salt marshes and beaches will continue to be lost to coastal development and rising sea levels (Crossett et al. 2004, Cooper et al. 2008). Thus protecting all components of the Red Knot's stopover habitat remains a challenge for the conservation of this species.

ACKNOWLEDGMENTS

This research was funded by the National Marine Fisheries Service of the National Oceanic and Atmospheric Administration, United States Department of Commerce. Field work was conducted by V. D'Amico, D. Fraser, M. M. Griffin, K. Guerna, C. C. Kontos, B. McLaughlin, G. Moore, and R. Rydlewicz. Assistance with capture of Red Knots was provided by A. Dey, C. D. T. Minton, M. Peck, L. Niles, S. Taylor, A. Watts, and D. Veitch. Laboratory assistance was provided by K. Ballagh, C. Hitchens, K. Minton, and J. Stiles. Telemetry flights were piloted by Jim Strong Aviation.

LITERATURE CITED

- ALTMANN, J. 1974. Observational study of behavior: sampling methods. *Behavior* 69:227–263.
- ATKINSON, P. W., A. J. BAKER, R. M. BEVAN, N. A. CLARK, K. B. COLE, P. M. GONZALEZ, J. NEWTON, L. J. NILES, AND R. A. ROBINSON. 2005. Unravelling the migration and moult strategies of a long-distance migrant using stable isotopes: Red Knot *Calidris canutus* movements in the Americas. *Ibis* 147:738–749.
- ATKINSON, P. W., A. J. BAKER, K. A. BENNETT, N. A. CLARK, K. B. COLE, A. DEY, A. G. DUIVEN, S. GILLINGS, P. M. GONZALEZ, B. A. HARRINGTON, K. KALASZ, C. D. T. MINTON, J. NEWTON, L. J. NILES, R. A. ROBINSON, I. DE LIMA SERRANO, AND H. P. SITTERS. 2006. Using stable isotope ratios to unravel shorebird migration and population mixing: a case study with Red Knot *Calidris canutus*, p. 535–540. *In* G. C. Boere, C. A. Galbraith, and D. A. Stroud [EDS.], *Waterbirds around the world*. Scottish Natural Heritage, Edinburgh.
- BAKER, A. J., P. M. GONZALEZ, T. PIERSMA, L. J. NILES, I. DE SERRANO DO NASCIMENTO, P. W. ATKINSON, N. A. CLARK, C. D. T. MINTON, M. PECK, AND G. AARTS. 2004. Rapid population decline in Red Knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society of London B* 271:875–882.
- BEUKEMA, J. J., AND R. DEKKER. 2007. Variability in annual recruitment success as a determinant of long-term and large-scale variation in annual production of intertidal Wadden Sea mussels (*Mytilus edulis*). *Helgolander Marine Research* 61:71–86.
- BURGER, J., L. NILES, AND K. E. CLARK. 1997. Importance of beach, mudflat, and marsh habitats to migrant shorebirds on Delaware Bay. *Biological Conservation* 79:283–292.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. *Model selection and inference: a practical information-theoretic approach*, 2nd edition. Springer, New York.
- CADE, B. S., AND J. D. RICHARDS. 2005. *User manual for Blossom statistical software*. U.S. Geological Survey, Fort Collins, CO.
- CATRY, P., A. CAMPOS, V. ALMADA, AND W. CRESWELL. 2004. Winter segregation of migrant European Robins *Erithacus rubecula* in relation to age, sex, and size. *Journal of Avian Biology* 35:204–209.
- CLARK, K. E., L. J. NILES, AND J. BURGER. 1993. Abundance and distribution of migrant shorebirds in Delaware Bay. *Condor* 95:694–705.
- COHEN, J. B., S. M. KARPANTY, J. D. FRASER, AND B. R. TRUITT. 2009. 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. *Journal of Ornithology* 151:355–364.
- COOPER, M. J. P., M. D. BEEVERS, AND M. OPPENHEIMER. 2008. The potential impacts of sea level rise on the coastal region of New Jersey, USA. *Climatic Change* 90:475–492.
- CROSSETT, K. M., T. J. CULLITON, P. C. WILEY, AND T. R. GOOD-SPEED [ONLINE]. 2004. Population trends along the coastal United States: 1980–2008. NOAA/National Ocean Service. <http://www.oceanservice.noaa.gov/programs/mb/supp_cstl_population.html> (10 July 2009).
- COSEWIC. 2007. *Canadian Species at Risk*. Environment Canada, Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario.
- DATAMIL [ONLINE]. 2007. 2007 Delaware land use and land cover. <<http://datamil.delaware.gov/geonetwork/srv/en/main.home>> (12 October 2009).
- FERNANDEZ, G. AND D. B. LANK. 2006. Sex, age, and body size distributions of Western Sandpipers during the nonbreeding season with respect to local habitat. *Condor* 108:547–557.
- HARAMIS, G. M., W. A. LINK, P. C. OSENTON, D. B. CARTER, R. G. WEBER, N. A. CLARK, M. A. TEECE, AND D. S. MIZRAHI. 2007. Stable isotope and pen feeding trial studies confirm the value of horseshoe crab *Limulus polyphemus* eggs to spring migrant shorebirds in Delaware Bay. *Journal of Avian Biology* 38:367–376.
- HARRINGTON, B. A. 2001. Red Knot (*Calidris canutus*), no 563. *In* A. Poole and F. Gill [EDS.], *The birds of North America*. Birds of North America, Inc., Philadelphia.
- HEWITT, J. E., G. B. MCBRIDE, R. D. PRIDMORE, AND S. F. THRUSH. 1993. Patchy distributions: optimizing sample size. *Environmental Monitoring and Assessment* 27:95–105.
- KARPANTY, S. M., J. D. FRASER, J. BERKSON, L. J. NILES, A. DEY, AND E. P. SMITH. 2006. Horseshoe crab eggs determine Red Knot distribution in Delaware Bay. *Journal of Wildlife Management* 70:1704–1710.
- KETTERSON, E. D., AND V. NOLAN JR. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern wintering Dark-eyed Juncos (*Junco hyemalis hyemalis*). *Ecology* 57:679–693.

- LYNCH, J. F., E. S. MORTON, AND M. E. VAN DER VOORT. 1985. Habitat segregation between the sexes of wintering Hooded Warblers (*Wilsonia citrina*). *Auk* 102:714–721.
- MACKEY, G. 1893. Observations on the Knot (*Tringa canutus*). *Auk* 10:25–35.
- MARQUES, P. A. M., A. M. COSTA, P. ROCK, AND P. E. JORGE. 2009. Age-related migration patterns in *Larus fuscus* spp. *Acta Ethologica* 12:87–92.
- MARRA, P. P., AND R. T. HOLMES. 2001. Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. *Auk* 118:92–104.
- MATHOT, K. J., B. D. SMITH, AND R. W. ELNER. 2007. Latitudinal clines in food distribution correlate with differential migration in the Western Sandpiper. *Ecology* 88:781–791.
- MORRISON, R. I. G., R. K. ROSS, AND L. J. NILES. 2004. Declines in wintering populations of Red Knots in southern South America. *Condor* 106:60–70.
- MORRISON, R. I. G., N. C. DAVIDSON, AND J. R. WILSON. 2007. Survival of the fittest: body stores on migration and survival of Red Knots *Calidris canutus islandica*. *Journal of Avian Biology* 38:479–487.
- NEW JERSEY DEPARTMENT OF ENVIRONMENTAL PROTECTION [ONLINE]. 1992. NJDEP habitat delineations for 12 quadrangles in Cape May and Cumberland counties, New Jersey (South Jersey Marsh). <<http://www.state.nj.us/dep/gis/digidownload/zips/statewide/sjmarsh.zip>> (12 October 2009).
- NILES, L. J., H. P. SITTERS, A. D. DEY, P. W. ATKINSON, A. J. BAKER, K. A. BENNETT, R. CARMONA, K. E. CLARK, N. A. CLARK, C. ESPOZ, P. M. GONZALEZ, B. A. HARRINGTON, D. E. HERNANDEZ, K. S. KALASZ, R. G. LATHROP, R. N. MATUS, C. D. T. MINTON, R. I. G. MORRISON, M. K. PECK, W. PITTS, R. A. ROBINSON, AND I. L. SERRANO. 2008. Status of the Red Knot (*Calidris canutus rufa*) in the western hemisphere. *Studies in Avian Biology* 36:1–185.
- NILES, L. J., J. BART, H. SITTERS, A. D. DEY, K. E. CLARK, P. W. ATKINSON, A. J. BAKER, K. A. BENNETT, K. S. KALASZ, N. A. CLARK, J. CLARK, S. GILLINGS, A. S. GATES, P. M. GONZALEZ, D. E. HERNANDEZ, C. D. T. MINTON, R. I. G. MORRISON, R. R. PORTER, R. K. ROSS, AND C. R. VEITCH. 2009. Effects of horse-shoe crab harvest in Delaware Bay on Red Knots: are harvest restrictions working? *BioScience* 59:153–164.
- PEREZ, G. E., AND K. A. HOBSON. 2009. Winter habitat use by Loggerhead Shrikes (*Lanius ludovicianus*) in Mexico: separating migrants from residents using stable isotopes. *Journal of Ornithology* 150:459–467.
- PIERSMA, T., D. I. ROGERS, P. M. GONZALEZ, L. ZWARTS, L. J. NILES, I. DE LIMA SERRANO DONASCIMENTO, C. D. T. MINTON, AND A. J. BAKER. 2005. Fuel storage rates before northward flights in Red Knots worldwide, p. 262–273. *In* R. Greenberg and P. P. Marra [EDS.], *Birds of two worlds*. Johns Hopkins University Press, Baltimore.
- SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113–151.
- SHOREBIRD PROJECT [ONLINE]. 2009. Shorebird resighting information. <<http://bandedbirds.org>> (10 February, 2010).
- STONE, W. 1937. Bird studies at Old Cape May. Delaware Valley Ornithological Club, Philadelphia.
- THOMAS, G. H., R. B. LANCTOT, AND T. SZEKELY. 2006. Can intrinsic factors explain population declines in North American breeding shorebirds? A comparative analysis. *Animal Conservation* 9:252–258.
- TSIPOURA, N., AND J. BURGER. 1999. Shorebird diet during spring migration stopover on Delaware Bay. *Condor* 101:635–644.
- U. S. COMMISSION ON OCEAN POLICY [ONLINE]. 2004. Conserving and restoring coastal habitat, p. 170–179. *In* An ocean blueprint for the 21st century. Final report. <http://oceancommission.gov/documents/full_color_rpt/11_chapter11.pdf> (10 July 2009).
- U.S. FISH AND WILDLIFE SERVICE. 2006. Endangered and threatened wildlife and plants—proposed critical habitat designations; proposed rule. *Federal Register* 71:53756–53835.