



Research Article

Sufficiency of Horseshoe Crab Eggs for Red Knots During Spring Migration Stopover in Delaware Bay USA

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ABSTRACT Horseshoe crab (*Limulus polyphemus*) eggs are a dietary staple of the red knot (*Calidris canutus*) during its spring stopover on the Delaware Bay. Numbers of knots stopping in Delaware Bay declined in the 1990s concurrent with a decline in horseshoe crabs, leading to the hypothesis that reduced horseshoe crab egg abundance limited the red knot population. Management efforts, including a seasonal harvest moratorium in the Delaware Bay, have been instituted to restore crab populations to levels of sustainable use by multiple users, including migratory birds. Our objective was to evaluate the sufficiency of horseshoe crab eggs in Delaware Bay in May–June 2004 and 2005 for knots to refuel for their migratory flight to the Arctic breeding grounds. We examined egg counts to determine if there were fewer high egg-density sites later than earlier in the day and season, as migrating birds might deplete this resource. We studied foraging rates at red knot locations to determine if foraging probes increased with time of day and season as birds depleted surface eggs by pecking, then began probing for subsurface eggs. Finally, we experimentally tested whether red knots and their competitors depleted horseshoe crab eggs. Crab egg numbers at knot foraging sites did not decline throughout the day or season in 2004. In both years, we found no evidence that knots switched from pecking to probing with increases in time since sunrise or start of the stopover. Egg numbers were similar in enclosed and accessible plots on crab nesting depressions and in areas of open intertidal zone, but were significantly lower in accessible than in enclosed plots in the wrack line. Our results indicate that horseshoe crab eggs in Delaware Bay were sufficient to support the refueling of the present-day stopover population of red knots. If an increase in the availability of crab eggs to foraging birds does not result in an increase in knot numbers, managers must prioritize mitigation of limiting factors at other historically important spring stopovers and on the poorly understood breeding and wintering grounds in addition to the Delaware Bay. © 2011 The Wildlife Society.

KEY WORDS *Calidris canutus*, conservation, Delaware Bay, horseshoe crab, *Limulus polyphemus*, migration, prey depletion, red knots, shorebirds, stopover.

The red knot (*Calidris canutus*) population wintering in Tierra del Fuego (TDF) and stopping in Delaware Bay during northward migration has declined. Knots at wintering sites in Patagonia and TDF dropped from 67,500 in the mid-1980s to 16,260 birds in 2009 (Morrison et al. 2004; Niles et al. 2008, 2010). Concurrently, a decreasing proportion of red knots stopping in Delaware Bay reached the weight required to complete northward migration, leading to the hypothesis that the Delaware Bay stopover population of knots is food limited (Baker et al. 2004). During spring

stopover in Delaware Bay, red knots eat primarily horseshoe crab (*Limulus polyphemus*) eggs and red knot distribution is determined by these eggs (Karpanty et al. 2006, Haramis et al. 2007). Horseshoe crab eggs have been an abundant food for red knots and other shorebirds to replenish fat supplies depleted from earlier stages of migration before departure to the Arctic breeding grounds (Wander and Dunne 1981, Shuster and Botton 1985). The fat that shorebirds deposit during this stopover refueling must sustain them on the northerly migration and often provide energy for a week or more upon arriving at the breeding grounds if there is still snowpack (Morrison and Hobson 2004).

Concurrent with declines in wintering red knot numbers and proportions of knots reaching required pre-departure weights in Delaware Bay, fisheries biologists raised concerns that horseshoe crabs may have been overexploited for bait

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and biomedical uses (Berkson and Shuster 1999, Atlantic States Marine Fisheries Commission (ASMFC) 2004). These concerns led to the predominant working hypothesis that the Delaware Bay stopover population may be limited by the amount of horseshoe crab eggs available to shorebirds (Haramis et al. 2007) and to management efforts to restore crab populations and to limit crab harvests to sustainable levels (Niles et al. 2009). It has been hypothesized that the decline in TDF knots may also have been driven by the lack of sufficient horseshoe crab eggs in Delaware Bay (Baker et al. 2004). Our study and other recent work explores this hypothesis linking red knot and crab declines as well as other possible hypotheses such as limiting factors at other northerly stopover sites (Cohen et al. 2009, 2010*b*). Much work remains to be done to explore possible limiting factors on the knots' Arctic breeding grounds (Niles et al. 2008).

Prey depletion via exploitative competition is one strong line of evidence that a population is food-limited (Goss-Custard et al. 2001, Newton 2006). Exclosure experiments have commonly been used to determine if declines in invertebrate prey were caused by predators (e.g., Rosa et al. 2008). Such experiments have shown prey depletion by shorebirds at many wintering and migratory stopover sites (Quammen 1984, Alerstam et al. 1992, Mercier and McNeil 1994). Red knots and their competitors depleted crab eggs placed in experimental trays on a beach in Mispillion Harbor on Delaware Bay (Gillings et al. 2007). However, no egg density was found at which knots left the experimental feeding trays to move onto another feeding area with equal or greater egg density (i.e., giving-up density) as would be predicted by optimal foraging theory if eggs in the feeding trays were insufficient. Density-dependent prey depletion during spring migration may lead to population limitation if some birds do not accumulate sufficient reserves to initiate migration, to survive migration, or to survive the often harsh arrival conditions on the breeding grounds (Newton 2006). Red knots feeding during spring migration in the Delaware Bay must consume approximately 24,000 eggs/day to replenish fat stores lost during the previous migratory stage for a successful migration to the Arctic breeding grounds (Haramis et al. 2007). This daily crab egg requirement may be met if knots feed for most of the daylight hours in areas where egg densities are ≥ 360 surface eggs/m² or 19,200 buried eggs/m² (Gillings et al. 2007). If prey is depleted to below these thresholds by foraging birds, it would indicate that horseshoe crab egg abundance is still too low to support the populations of predators that use them, including red knots.

Our objective was to determine if horseshoe crab eggs in the Delaware Bay in 2004 and 2005 were sufficient to sustain red knots and to refuel them for their migratory flight to the Arctic breeding grounds. We first examined egg counts in May–June 2004 and predicted that if horseshoe crab eggs were insufficient, there would be 1) fewer high egg-density sites ($\geq 19,200$ buried eggs/m²) later in the day than earlier (most crab spawning activity occurs during the nocturnal high tide) and 2) fewer high egg-density sites later in the season than earlier, as migrating birds forage on the eggs throughout their stopover. Second, we studied foraging rates

at red knot locations and predicted that the proportion of foraging attempts as probes, instead of pecks, would increase as the time of day and the stopover season progressed in both 2004 and 2005, because foraging birds deplete surface eggs by pecking, then begin probing for subsurface eggs (Gillings et al. 2007). Finally, we tested whether red knots and their competitors depleted horseshoe crab eggs in the Delaware Bay in May–June 2005 by counting eggs in bird-excluded and bird-accessible plots. We predicted that if egg resources were insufficient, eggs would be depleted in bird-accessible control plots compared to plots from which birds were excluded. We measured the numbers and behavior of birds using experimental beach sections so we could understand whether any observed changes in crab egg numbers could be attributed to the intensity of bird foraging.

STUDY AREA

Our study area in May–June 2004 and 2005 was the Delaware Bay in Delaware and New Jersey, USA. The region contained sandy beaches, peat beaches, mudflats, creeks, tidal cordgrass (*Spartina alterniflora* and *S. patens*) marshes, agricultural land, and residential developments. Delaware Bay is about 50 km long and 50 km across at its widest point (Fig. 1).

We assisted the New Jersey Endangered and Nongame Species Program and the Delaware Division of Fish and Wildlife in capturing red knots with cannon nets on 5 beaches in New Jersey (Reed's, Fortescue, Kimbles, Gandy's, Rutgers' Biological Station) and 3 beaches in Delaware (Mispillion Harbor, Port Mahon, South Bowers; Fig. 1) in May 2004.

In 2005, we conducted a foraging shorebird exclosure experiment on 8 sandy beaches spread around the perimeter of Delaware Bay (Big Stone, Slaughter, and Ted Harvey Reserve in Delaware and Dyer's Cove, Moore's, Pierce's Point, Raybin's, and Reed's in New Jersey, Fig. 1). Our criteria for beach selection included: 1) known use by spawning horseshoe crabs and large numbers of foraging shorebirds, including red knots, 2) distribution throughout Delaware Bay, 3) ≥ 250 m of continuous sandy beach-front for experiment placement, and 4) minimal use by people, dogs, and other sources of shorebird disturbance. Our sample of beaches included most of the beaches used in high numbers by red knots during their stopover in Delaware Bay, with the exception of Mispillion Harbor beach in Delaware, which was not accessible due to restrictions on research at that site.

METHODS

Field Methods

Egg counts and behavior at foraging sites.—We radio-tagged a total 65 knots from one capture at each of the 8 beach locations, placing 7–9 radio-tags on birds per capture to evenly distribute tag placement on birds from around the Delaware Bay. We marked each knot with a lime green plastic flag with a field-readable alphanumeric code on the upper left leg and a United States Geological Survey Incoloy

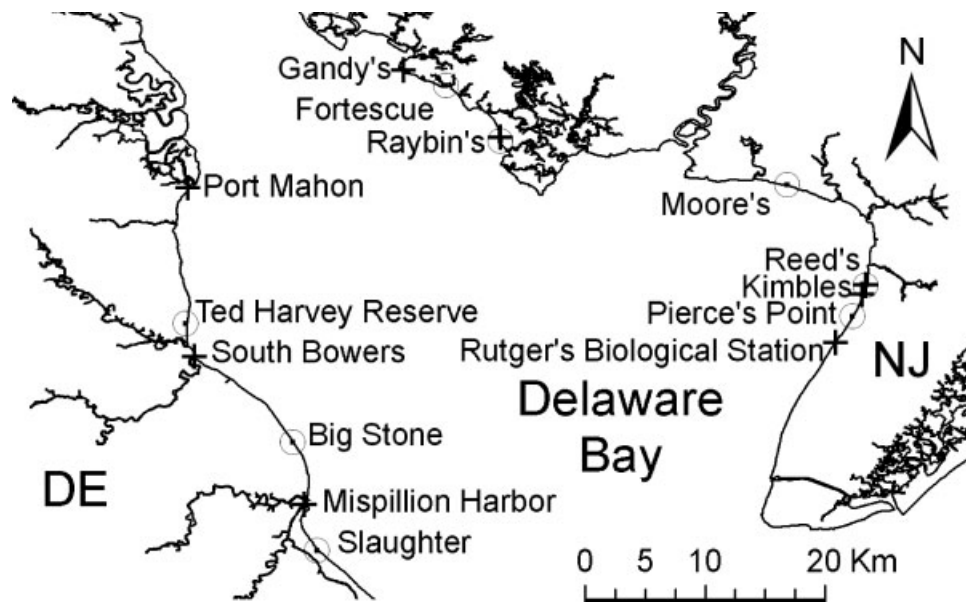


Figure 1. We studied red knots in Delaware Bay in May–Jun 2004 and 2005. We captured and radio-tagged red knots at Reed's, Fortescue, Kimbles, Gandy's, Rutger's Biological Station, Mispillion Harbor, Port Mahon, and South Bowers beaches in 2004 (+ on map). We conducted a foraging shorebird enclosure experiment on Big Stone, Slaughter, Ted Harvey Reserve, Dyer's Cove, Moore's, Pierce's Point, Raybin's, and Reed's beaches in 2005 (O on map).

band on the lower right leg. We picked a random sample of birds from each capture upon which to place the radio-tags to study the habitat selection and foraging behavior of these birds (Karpanty et al. 2006). We plucked or cut feathers from a 1 cm × 2 cm patch of skin on the back between the scapulae, and we attached a 3-g radio transmitter (<3.0% of bird's body weight; Holohil Model no. PD-2, Ontario, Canada) with gel-consistency cyanoacrylate glue.

We conducted daily aerial surveys, weather permitting, from 12 May 2004 to 4 June 2004, to relocate radio-tagged birds. Our sampling included the peak of red knot migration through Delaware Bay and the new moon on 19 May and full moon on 3 June. Annual horseshoe crab spawning normally peaks during the nightly high tides associated with the May or early June new and full moons and thus horseshoe crab egg densities available to birds often peak at these times. We flew over the entire Delaware Bay coastline and Atlantic Ocean marshes and beach from Cape May, New Jersey to Corson's Inlet, New Jersey in a Cessna 172 (Cessna Aircraft Company, Wichita, KS) aircraft equipped with 2-element H-antenna on each wing. We systematically varied the direction of the flight and flight start time relative to tidal stage. We flew at 150–220 m altitude at 130–170 km/hr. Transmitter range was 1,100 m from the aircraft at these altitudes. We communicated bird locations to observers on the ground, who used handheld receivers to find randomly selected birds for observations and prey sampling (Karpanty et al. 2006).

We selected radio-tagged birds for daily prey and behavioral sampling using simple random sampling without replacement, repeating once all birds had been sampled. When we approached a radio-tagged bird's location, we attempted to visually discern it. If we could not distinguish it from other flock members, we selected a focal knot from the flock as close as possible to the apparent location of the

tagged bird. Two observers used spotting scopes and recorded the number and species of all birds in the flock. Observers then watched the focal knot continuously for 5 min and described behavior as resting (including standing, sleeping, preening), foraging, or locomoting (including walking, running, flying) every 10 s and all pecks and probes continuously while the second observer recorded the data (Altmann 1974). After collecting the behavioral sample, we collected 3 sediment core samples (10.5-cm diam, 3.5-cm deep) centered on the location of the focal knot and spread evenly across the estimated flock width, perpendicular to the tide line. The core depth corresponded to the length of a red knot bill. To collect these samples, one observer walked slowly toward the target location. In most cases the bird flock would simply walk away from the observer to an adjacent spot 5–10 m down the beach and continue to forage; only rarely did the flock flush and fly to another section of beach. We collected all core samples with a section of polyvinyl chloride pipe and stored them in 95% ethanol in a 1-L jar. We later separated eggs and invertebrates from sand and other inorganic material by elutriation and flushing with water through a series of screens and then counted the horseshoe crab eggs.

Depletion experiment.— We visited each beach every other day from 15 May to 3 June 2005, encompassing the peak of bird migration through Delaware Bay. This period included the full moon on 23 May during which horseshoe crab spawning and egg availability was at or near its peak for the stopover season. During each visit, we placed 2 1-m × 1-m enclosed plots and 2 bird-accessible control plots on randomly selected horseshoe crab nests and clumps of wrack and one enclosed plot and one control plot on randomly selected sites in the open intertidal zone away from crab nests and wrack. We spread the plots across the intertidal zone at the elevation containing most of the previous night's horse-

shoe crab spawning depressions (depressions left in the sand surface as a laying female crab retreats from her nest).

We fashioned enclosures of bird netting fastened to 4 2-cm × 4-cm wooden stakes, which we pounded into the sand in a square, 1 m on a side, with 2 sides parallel to the water's edge. We marked bird-accessible control plots only with a 2-cm × 4-cm wooden stake 5 m landward from one corner. We placed one control for each enclosure to ensure a balanced design, but enclosures and controls were not paired spatially on the beach. Rather, we enforced >10 m separation between all plots to prevent spatial autocorrelation. This set of plots and inter-plot spacing covered only about 250 m of each experimental beach. We set up these plots on each experimental beach after the night high tide but before sunrise and the arrival of any foraging birds. We did not observe birds foraging at night as we established plots on each experimental beach, and we remained at the site until the start of and for the duration of each sample, and thus we were confident that eggs were not eaten between the nightly spawn and the arrival of foraging birds at sunrise. We allowed the experiment to run for 2–6 hr daily on each beach, from sunrise when the birds began to arrive until the rising tide approached our enclosures. Most horseshoe crab spawning occurs during the night high tide (Rudloe 1980, Brousseau et al. 2004), thus our sampling was focused in the morning after the nightly high tide spawn. Because we collected our samples prior to the daytime high tide, egg numbers in our experiment were not subject to any replenishment that may arise from tidal disturbance of the substrate (Nordstrom et al. 2006).

At the beginning and end of each experimental period, we collected 7.6-cm diameter × 3.5-cm deep sediment cores. We chose the locations for the cores by drawing lines in the sand dividing the plot into 4 equal quadrants. The initial core was placed within a randomly selected quadrant of the plot close to the plot center, such that the quadrant axes were tangent to the sample core. The post-experiment core was taken from a different randomly selected quadrant and was similarly placed near the plot center. We divided the cores into 2 sections: surface (<0.3 cm) and subsurface (0.3–3.5 cm). We stored the sediment samples in 95% ethanol until we could later count the horseshoe crab eggs.

While the experiment was running, 2 observers watched the plots from vantage points about 100 m from the plots, hiding behind dunes, vegetation, or other cover. Every 15 min and using a spotting scope, we counted all birds in the 250 m section of each experimental beach where the plots were established. We classified birds as being in the swash zone (the zone of active wave action), the open intertidal zone between the swash and the previous night's spawning depressions, the spawning depression zone (i.e., the high elevation part of the intertidal zone where crabs nested), and the dry backshore above the intertidal and spawning depression zones. Between each bird count, we conducted 2 or 3 3-min focal samples of random birds of the target species close to the center of the foraging flock in the experimental zone, sampling ≥1 red knot each hour and as many other species as time permitted. We sampled behavior

in the same manner as in 2004, except we used 3-min focal samples this season as opposed to the 5-min focal samples in 2004, as shortening the sample 1) does not significantly change results or inferences and 2) allowed us to sample more unique individuals and species in a shorter time period.

Data Analyses

Egg counts and behavior at foraging sites.— We determined the maximum horseshoe crab egg count from 3 subsamples collected at each knot foraging location in 2004. We used the maximum egg count because we were interested in testing if hotspots with high egg densities remained at the end of the day of foraging, or late in the migration season, and the maximum egg count was an indication of whether such hotspots existed. We converted maximum egg count to crab eggs/m² of beach 5 cm deep to be comparable to data contained in management plans for the Delaware Bay and to other analyses of this system, assuming uniform distribution of eggs in the top 5 cm of sand (e.g., Gillings et al. 2007). We modeled the number of eggs per core as a function of time since sunrise and date using negative binomial regression (Hilbe 2007). Time since sunrise is an index of time exposed to foraging by birds, as we did not observe birds foraging at night. We obtained overdispersion factor estimates (deviance/df) for the model (Proc Genmod, SAS Institute, Cary, NC) and considered the negative binomial model assumptions to be met if this factor was approximately 1. The negative binomial model is useful for patchily distributed count data such as crab egg counts and is an alternative to the use of a Poisson distribution when there is overdispersion of the data (Hilbe 2007).

We modeled the effects of date (before or after peak crab spawn), tide, time since sunrise, number of horseshoe crab eggs, and all 2-way interactions on the proportion of foraging attempts made as pecks, instead of probes, and compared with a null (intercept-only) model for data collected in both 2004 and 2005. We used all-possible-subsets linear regression and Akaike's Information Criterion (AIC_c) to select the best model. We fit models using a trust region algorithm (SAS 2010; Proc NLMixed, SAS Institute).

Depletion experiment.— We modeled the effect of experimental enclosures on post-experiment egg counts using negative binomial regression (Hilbe 2007). We built separate models for surface and subsurface egg counts. We examined 52 models containing all possible combinations of several variables that we hypothesized could affect post-experiment egg counts (Table 1). In all models, we used site × date as a random blocking variable, as all plots on the same beach on a given date are subject to the same tide, weather, and spawn conditions; this procedure improved the AIC_c of the global model over a fixed-effects only model. We included pre-experiment egg counts in every model to control for plot effects, and we included microhabitat type (horseshoe crab nest, wrack, open intertidal zone) in every model because our experiment was nested within these microhabitats. We used a nested analysis (i.e., plots nested within microhabitat type) because we did not randomly place plots across the experimental beaches, but rather placed them randomly only

Table 1. Variables included in models of post-experiment subsurface and surface horseshoe crab egg counts from sediment core samples collected at sites of foraging red knot, dunlin, sanderling, semipalmated sandpiper, ruddy turnstone, short-billed dowitcher, and laughing gulls, Delaware and New Jersey, USA, May–June 2005.

Variable	Definition
Horseshoe crab nest ^a	A microhabitat indicator variable (1 = yes, 0 = no)
Wrack ^a	A microhabitat indicator variable
Open intertidal zone	A microhabitat indicator variable, not explicitly included in models (serves as reference level)
Treatment (horseshoe crab nest)	The effect of experimental treatment (control vs. enclosure) nested within the horseshoe crab nest indicator variable
Treatment (wrack)	The effect of experimental treatment (control vs. enclosure) nested within the wrack indicator variable
Treatment (open intertidal zone)	The effect of experimental treatment (control vs. enclosure) nested within the open intertidal zone indicator variable
Number of eggs pre-experiment ^a	Horseshoe crab egg counts from cores taken at the start of experimental runs
Interaction nest × eggs	Interaction between horseshoe crab indicator variable and pre-experiment egg count as metric of variation in pre-experiment egg numbers related to microhabitat type
Interaction wrack × eggs	Interaction between wrack indicator variable and pre-experiment egg count as metric of variation in pre-experiment egg numbers related to microhabitat type
Total shorebird minutes	Sum of shorebird counts taken during the experimental run × 15 (the count interval in min) as metric of foraging intensity during experiment
Total gull minutes	Sum of gull counts taken during the experimental run × 15 (the count interval in min) as metric of foraging intensity during experiment
Experiment run time	Minutes from sunrise and the associated arrival of foraging birds to dismantling; we established experiment during the night after the high tide but before the arrival of any birds
Interaction shorebirds × time	Interaction between shorebird minutes and experiment run time
Interaction gulls × time	Interaction between gull minutes and experiment run time
Site × date ^a	Random block effect of study site × date

^a Included in every model tested.

within each of these microhabitat strata to control for habitat. Using this design and analysis, we could explore differences between bird-accessible and enclosed plots within a habitat type but not across habitat types. We fit models using a trust region algorithm (Proc NLMixed, SAS 2010). We obtained overdispersion factor estimates (deviance/df) for the fixed effects model as described above and considered the negative binomial model assumptions to be met if this factor was approximately 1 (Hilbe 2007).

We model-averaged parameter estimates and standard errors across all models and calculated unconditional confidence intervals on them (Burnham and Anderson 2002). We considered a variable important if the unconditional confidence interval on its regression parameter estimate did not contain zero. We calculated model-averaged least squares means and standard errors for post-experiment egg counts in all microhabitat × treatment (bird-accessible control vs. bird-excluded enclosure) combinations. We calculated model-averaged predicted percent reduction in post-experiment egg counts between controls and enclosures as $[1 - (\text{control/exclosure}) \times 100]$. We considered egg counts in controls to differ from egg counts in enclosures if their unconditional confidence intervals overlapped <50% (Cumming and Finch 2005).

We used negative binomial regression to estimate the total number of red knots and of all other shorebirds and gulls we observed that feed on horseshoe crab eggs in each of 4 microhabitat types (swash zone, open intertidal zone, spawning depression zone, backshore), nested within tides (high = within 1 hr of lunar high tide, low = within 1 hr of lunar low tide, rising or falling in between), and controlling for the site × date effect. We included all bird species present on the beach, including shorebirds and gulls, in these analyses because all feed on horseshoe crab eggs. We calculated the proportion of time focal red knots, ruddy turnstones

(*Arenaria interpres*), sanderlings (*Calidris alba*), and laughing gulls (*Larus atricilla*) spent foraging during different tidal stages using mixed logistic regression, where the site × date combination was the random effect. In the binomial model, the number of trials was the number of 10-s behavioral subsamples during the 3-min focal period, and we considered an event any subsample where we recorded the focal bird foraging.

RESULTS

Egg Counts and Behavior at Foraging Sites

We found no significant decrease in crab egg numbers as a function of time since sunrise or date. The number of horseshoe crab eggs at red knot foraging sites in 2004 did not significantly decrease as minutes since sunrise, and the associated arrival of the birds for foraging from their night roost sites, increased (Fig. 2), either before or after the observed peak horseshoe crab spawn on 19 May (Karpanty et al. 2006). The intercept-only model of egg counts was the most supported model with the lowest AIC_c and an Akaike weight (w_i) of 0.56; we found mild overdispersion ($\hat{c} = 1.34$) and thus we scaled variance by \hat{c} . We found samples with >19,200 eggs/m² throughout the day both before and after the peak horseshoe crab spawn, with some samples having high egg densities even after 10 hr of exposure to foraging (i.e., >10 hr since sunrise).

The proportion of foraging attempts made as pecks, instead of probes, did not change through the stopover season in 2004 or 2005 (Fig. 3). Most samples in both years showed a high proportion (>0.70) of foraging attempts made as pecks (Fig. 3a,b). There were no effects of date, time since sunrise, and number of horseshoe crab eggs on the proportion of foraging attempts as pecks. In both years, the intercept-only model was the most supported model with the lowest AIC_c.

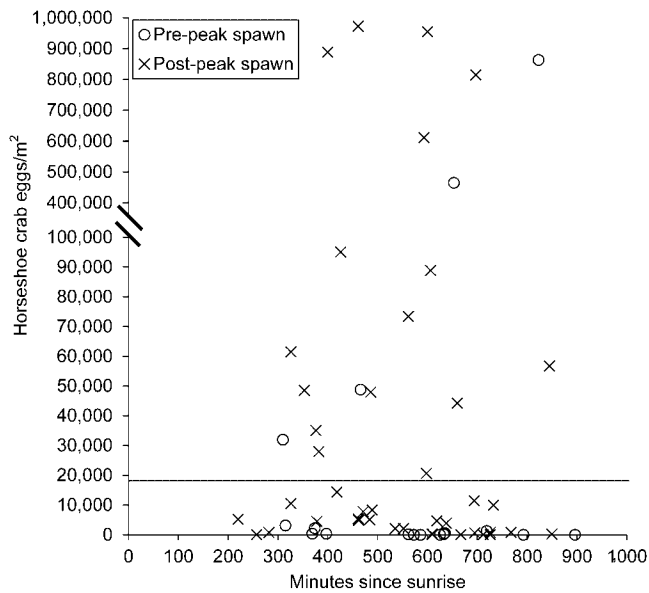


Figure 2. Maximum counts from 3 subsamples of horseshoe crab eggs (no./m²), 5 cm deep, remaining in sediment core samples (as calculated from 10.5-cm-diam × 3.5-cm-deep cores) collected at sites of radio-tagged foraging red knots in Delaware Bay, May–Jun 2004, both before and after the peak in horseshoe crab spawning activity on 19 May. We found no significant decrease in crab egg numbers as a function of time since sunrise and the associated arrival of foraging birds, or date, using negative binomial regression. The horizontal line represents horseshoe crab egg densities (19,200 eggs/m²) required for red knots to achieve necessary pre-migration weight gains if all eggs were subsurface (Gillings et al. 2007).

and the highest model weight ($w_i > 0.82$). In 2005, we collected all samples before the peak in spawning, thus we could only include time since sunrise and starting egg count in 2005. Residual plots indicated no violation of the assumptions of normality and heteroscedasticity.

Depletion Experiment

Crab nesting depressions had more post-experiment eggs than did other microhabitats in both subsurface (Tables 2

Table 2. Model of subsurface horseshoe crab egg counts (7.6-cm-diam × 3.5-cm-deep cores, excluding top 0.3 cm) post-experiment, Delaware and New Jersey, USA, May–Jun 2005. We model-averaged values from 52 negative binomial regressions, $n = 438$ plots.

Variable ^a	Estimate	SE	95% lower CL	95% upper CL
Intercept	-0.20	1.06	-2.28	1.88
Horseshoe crab nest (yes or no) ^b	2.83	0.36	2.13	3.54
Wrack (yes or no)	0.53	0.35	-0.16	1.22
Treatment (horseshoe crab nest)	-0.26	0.31	-0.86	0.34
Treatment (wrack) ^b	-0.76	0.27	-1.30	-0.22
Treatment (open intertidal zone)	0.32	0.38	-0.42	1.06
Number of eggs pre-experiment ^b	0.80	0.31	0.19	1.41
Interaction nest × eggs ^b	-0.74	0.31	-1.34	-0.14
Interaction wrack × eggs	0.31	0.40	-0.47	1.10
Shorebird minutes	0.35	1.85	-3.28	3.98
Gull minutes	0.95	1.60	-2.18	4.08
Experiment run time	0.49	0.39	-0.28	1.26
Interaction Shorebirds × time	-0.06	0.69	-1.42	1.30
Interaction gulls × time	-0.06	0.28	-0.61	0.50
Variance of site × date effect ^b	1.64	0.48	0.69	2.59
Negative binomial dispersion factor ^b	2.60	0.22	2.18	3.02

^a Variables are defined in Table 1.

^b Significant effect on number of eggs post-experiment (95% confidence bounds do not contain zero).

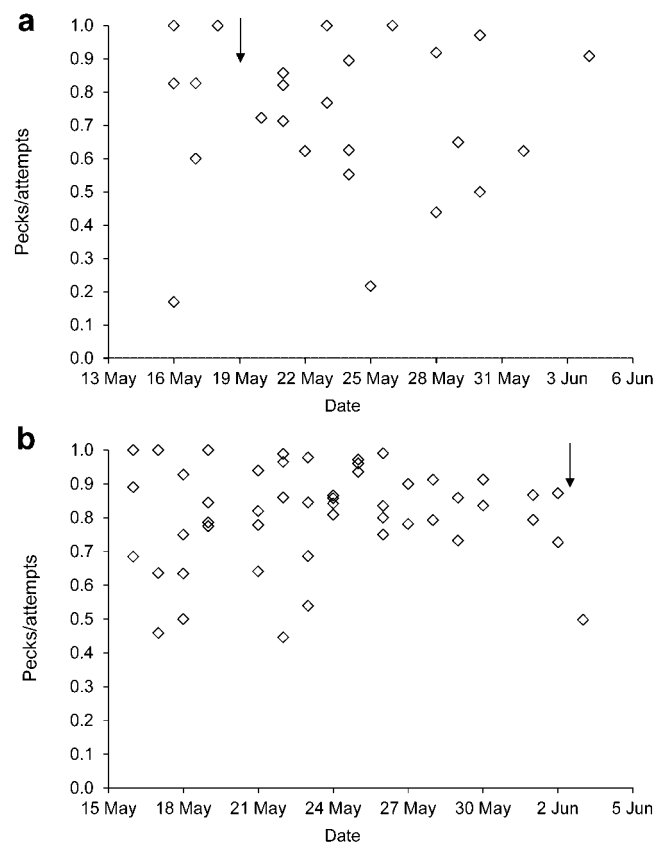


Figure 3. Proportion of foraging attempts made as pecks (instead of probes) by foraging red knots in Delaware Bay, May–Jun in (a) 2004 ($n = 27$) and (b) 2005 ($n = 50$). The arrow indicates the days of peak horseshoe crab spawning activity during our study, 19 May 2004 and 4 Jun 2005. Of 24 models tested (including date, tide, time of day, and number of horseshoe crab eggs), none were better than an intercept-only model in either year.

and 3) and surface samples (Tables 4 and 5, see Appendices SA and SB for supported model details for subsurface and surface samples, available online at www.onlinelibrary.wiley.com). There were more post-experiment eggs in wrack

Table 3. Least squares (LS) mean of subsurface horseshoe crab (HSC) egg counts (7.6-cm-diam × 3.5-cm-deep cores, excluding top 0.3 cm) post-experiment, Delaware and New Jersey, USA, May–Jun 2005. We model-averaged values from 52 negative binomial regressions, $n = 438$ plots.

Cover type	Plot type	n	LS \bar{x}	SE	95% lower CL	95% upper CL	Overlap ^a
HSC nest	Exclosure	74	75.1	21.7	32.5	117.7	0.79
	Control	74	59.2	16.9	26.0	92.3	
Wrack	Exclosure	95	8.7	2.4	4.1	13.3	0.11
	Control	95	3.0	0.9	1.2	4.8	
Open beach	Exclosure	50	4.4	1.4	1.6	7.2	1.22
	Control	50	5.9	1.9	2.1	9.7	

^a Proportion overlap of 95% confidence bounds on exclosure and control LS means, within microhabitat types. An overlap of ≤ 0.25 indicates a significant difference between treatments (Cumming and Finch 2005).

Table 4. Model of surface horseshoe crab egg counts (7.62-cm-diam × 0.3-cm-deep cores) post-experiment, Delaware and New Jersey, USA, May–Jun 2005. We model-averaged values from 52 negative binomial regressions, $n = 424$ plots.

Variable ^a	Estimate	SE	95% lower CL	95% upper CL
Intercept	-1.20	0.99	-3.13	0.73
Horseshoe crab nest (yes or no) ^b	2.77	0.47	1.86	3.68
Wrack (yes or no) ^b	2.01	0.43	1.16	2.85
Treatment (horseshoe crab nest)	-0.16	0.30	-0.75	0.43
Treatment (wrack)	-0.55	0.54	-1.61	0.51
Treatment (open intertidal zone)	1.19	1.95	-2.62	5.00
Number of eggs pre-experiment	-0.53	1.99	-4.45	3.38
Interaction nest × eggs	0.51	2.02	-3.45	4.46
Interaction wrack × eggs	-0.04	1.30	-2.59	2.51
Shorebird minutes	0.05	0.62	-1.16	1.27
Gull minutes	0.14	0.34	-0.53	0.81
Experiment run time	0.10	0.51	-0.90	1.11
Interaction shorebirds × time	0.001	0.11	-0.22	0.22
Interaction gulls × time	-0.008	0.31	-0.61	0.59
Variance of site × date effect ^b	1.45	0.56	0.35	2.54
Negative binomial dispersion factor ^b	3.82	0.43	2.98	4.67

^a Variables are defined in Table 1.

^b Significant effect on number of eggs post-experiment (95% confidence bounds do not contain zero).

Table 5. Least squares (LS) mean of surface horseshoe crab (HSC) egg counts (7.62-cm-diam × 0.3-cm-deep cores) post-experiment, Delaware and New Jersey, USA, May–Jun 2005. We model-averaged values from 52 negative binomial regressions, $n = 424$ plots.

Cover type	Plot type	n	LS \bar{x}	SE	95% lower CL	95% upper CL	Overlap ^a
HSC nest	Exclosure	73	11.4	3.7	4.2	18.7	0.74
	Control	73	8.2	2.6	3.2	13.2	
Wrack	Exclosure	90	5.9	2.0	2.0	9.8	0.61
	Control	90	2.9	1.9	-0.9	6.7	
Open beach	Exclosure	49	0.5	0.2	0.1	0.9	1.00
	Control	49	0.5	0.2	0.1	0.9	

^a Proportion overlap of 95% confidence bounds on exclosure and control LS means, within microhabitat types. An overlap of ≤ 0.25 indicates a significant difference between treatments (Cumming and Finch 2005).

subsurface samples in the exclosure plots than in bird-accessible control plots (Tables 2 and 3). This effect was not significant in the surface stratum (Tables 4 and 5). There were no differences in egg numbers between exclosed and accessible plots in horseshoe crab nests or in open beach, in either surface or subsurface samples. Neither experiment run time nor number of bird-minutes on the experimental section of beach affected post-experiment egg counts even though gull-minutes and experiment run time were in models with $\Delta AIC_c < 2$ (Tables 2 and 4, see Appendices SA and SB, available online at www.onlinelibrary.wiley.com). The model-averaged predicted percent reduction in mean subsurface egg density between exclosures and controls was 26% in nest depressions, 67% in wrack, and 0% in open

intertidal zone. For surface eggs, the percent reductions were 39% in nest depressions, 74% in wrack, and 20% in open intertidal zone.

There were fewer red knots in the dry backshore than in moist cover types where we placed experimental plots during all tidal stages, controlling for time since sunrise ($F_{5,204} = 7.88$, $P < 0.001$, Fig. 4; $\hat{c} = 0.34$ indicating underdispersion for which the negative binomial model provides a conservative overcorrection of the variance). Total bird counts (including all species foraging on horseshoe crab eggs; mainly red knot, dunlin [*Calidris alpina*], sanderling, semipalmated sandpiper [*Calidris pusilla*], ruddy turnstone, short-billed dowitcher [*Limnodromus griseus*], and laughing gulls) were likewise lowest in the backshore but did not differ

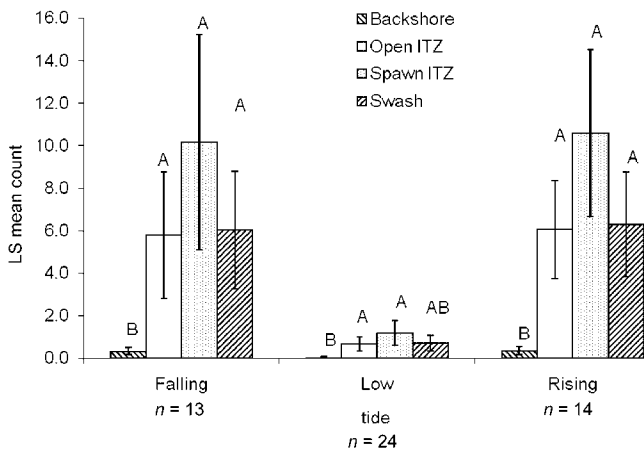


Figure 4. Least squares (LS) mean red knot counts and standard error in 4 microhabitats within 3 tidal stages, Delaware and New Jersey, USA, May–Jun 2005. Swash = swash zone, Spawn ITZ = horseshoe crab nest depressions located in intertidal zone, Open ITZ = lower elevation intertidal zone between the Spawn ITZ and the swash zone, Backshore = dry beach above the intertidal zone. Within tidal stages, counts with the same capital letter are not significantly different (negative binomial regression, $\alpha = 0.05$). n = number of counts.

among intertidal cover types where we placed the plots ($F_{11,204} = 18.99$, $P < 0.001$, Fig. 5; $\hat{c} = 0.96$). Red knot numbers were high after sunrise when birds began to arrive on the beaches and remained steady as long as the tide was falling, but red knots departed our sampling sites approximately 3 hr after sunrise if the tide was low (± 1 hr of low) or rising ($F_{3,52} = 5.49$, $P = 0.002$, Fig. 6a). The total number of shorebirds and gulls feeding on crab eggs on the beach remained steady in our experimental area throughout the morning if the tide was falling or low, but most birds departed our sites by 5 hr after sunrise if the tide was rising ($F_{3,52} = 10.69$, $P < 0.001$, Fig. 6b).

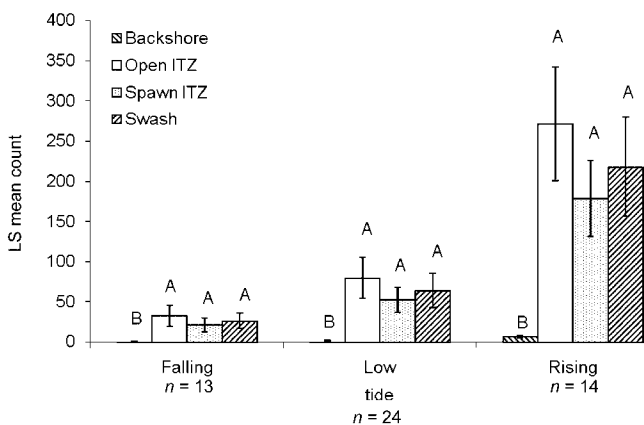


Figure 5. Least squares mean total bird counts (including all species foraging on horseshoe crab eggs; mainly red knot, dunlin, sanderling, semipalmated sandpiper, ruddy turnstone, short-billed dowitcher, and laughing gulls) and standard error in 4 microhabitats within 3 tidal stages, Delaware and New Jersey, USA, May–Jun 2005. Swash = swash zone, Spawn ITZ = horseshoe crab nest depressions located in intertidal zone, Open ITZ = lower elevation intertidal zone between the Spawn ITZ and the swash zone, Backshore = dry beach above the intertidal zone. Within tidal stages, counts with the same capital letter are not significantly different (negative binomial regression, $\alpha = 0.05$). n = number of counts.

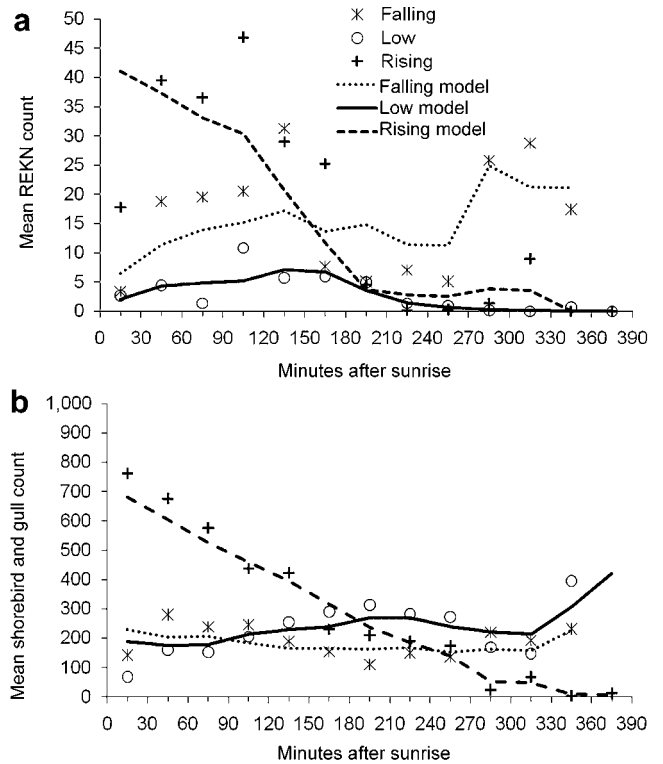


Figure 6. Least squares mean red knot (REKN) counts (a) and total shorebird and gull counts (b, mainly red knot, dunlin, sanderling, semipalmated sandpiper, ruddy turnstone, short-billed dowitcher, and laughing gulls) versus mean time since sunrise, and exposure to foraging birds, in 15-min intervals, by tidal stage, Delaware and New Jersey, USA, May–Jun 2005. Low tide is ± 1 hr of low.

Red knots spent a higher proportion of their time foraging on the falling tide than at low tide ($F_{2,39} = 4.41$, $P = 0.019$, Fig. 7). Ruddy turnstones foraged for an equal proportion of time in all tidal stages ($F_{2,49} = 0.67$, $P = 0.518$, Fig. 7), as did sanderlings ($F_{2,30} = 2.60$, $P = 0.091$, Fig. 7). Laughing gulls spent a higher proportion of time foraging on the falling

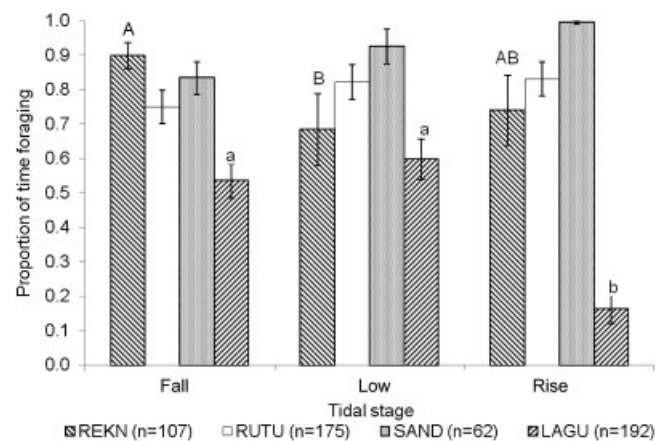


Figure 7. Least squares mean proportion of time birds (red knot [REKN], ruddy turnstone [RUTU], sanderling [SAND], laughing gulls [LAGU]) spent foraging in different tidal stages, Delaware and New Jersey, USA, May–Jun 2005. Means with the same capital letter (red knots) or lowercase letter (laughing gulls) are not significantly different (mixed logistic regression, $\alpha = 0.05$). No letters indicates no differences. n = number of behavioral observations. Low tide is ± 1 hr of low.

and low tides than on the rising tide ($F_{2,50} = 16.34$, $P < 0.001$, Fig. 7).

DISCUSSION

Contrary to our expectations, which we based on literature linking the rapid decline in red knots in the mid-1990s to the decline in horseshoe crabs during that same time period (Niles et al. 2008), we did not find evidence in 2004 and 2005 that there were insufficient numbers of crab eggs for refueling red knots around the Delaware Bay. In 2004, we found high egg numbers after >10 hr of availability to foraging birds. These egg hotspots late in the day and season cannot be explained by replenishment during the daily sampling period, as most spawning horseshoe crabs lay eggs on the beaches during the nocturnal high tide (Rudloe 1980, Brousseau et al. 2004). Thus, eggs would not have become newly available to birds due to spawning or crab-induced perturbation of sand during our daily sample period. Further, the peck to probe ratio of foraging red knots did not significantly decline within or across days in either study season. Finally, we found egg numbers were similar between bird-accessible and exclosed plots in 2 of 3 microhabitat types in 2005. These results from both the exclosure experiment and observations of foraging red knots are congruent and suggest that horseshoe crab eggs were sufficient to support the refueling of the red knot population for their next migratory flight to their Arctic breeding grounds during these seasons on stopover in Delaware Bay.

Schneider and Harrington (1981) found shorebird consumption rates on benthic prey during southward migration ranging from 47% to 83% at low shorebird density sites and 80–90% at high density sites and concluded that food during migration could be a factor limiting populations. Consumption rates we observed in 2005 were equivalent to those of Schneider and Harrington (1981) only in the wrack. Interference competition within and across species can result in density-dependent starvation without prey depletion (Goss-Custard et al. 2001). However, we did not observe red knots to be excluded from foraging by aggressive interactions with other red knots or other shorebird or gull species in our experimental sections of beach. Instead, we did observe knots foraging in plots with high egg densities and knots foraging throughout the tidal cycle in all microhabitats. Thus, knots did not appear to be substantially affected by inter- or intra-specific interference competition during our study. This lack of exclusion of red knots from foraging areas, combined with a lack of egg depletion in plots available to all foraging birds, indicates that there were sufficient, accessible eggs on the beach during our study for foraging red knots. We cannot discuss sufficiency of egg densities for other resident or migratory bird species at this time given a lack of knowledge on relationships between food availability and weight gain of those species as is available for the red knot (Haramis et al. 2007).

Our finding of sufficient egg resources on 8 Delaware Bay beaches, which were spread around the entire Bay region in 2005, contrasts with findings from a 2002–2003 study on one Delaware beach (Mispillion Harbor) in which shorebirds

depleted horseshoe crab eggs in trays in as little as 10 min (Gillings et al. 2007). The discrepancy may result from the higher density of shorebirds using the Mispillion artificial trays in that study (up to 167 birds/m² and 210 birds/m²) compared to those in our study (0.3–1.8 birds/m²). Although our study area in 2005 included most major shorebird foraging areas in Delaware Bay outside of Mispillion, we were unable to work in Mispillion that year because management restrictions sought to limit research-related disturbance at that site due to concerns about public perception in light of horseshoe crab harvest restrictions. Mispillion often holds high densities of crab eggs due to its low energy beach, which is ideal for spawning crabs; thus, high densities of shorebirds, including knots, congregate there each year (Niles et al. 2008). Regardless of whether Mispillion hosted higher red knot densities than our experimental beaches did in 2005, we argue that if food were insufficient system-wide at this stopover site during our study, then we would have detected depletion of accessible eggs in our experimental plots as hungry birds from Mispillion and other parts of the Bay sought to find food elsewhere within the stopover area.

Gillings et al. (2007) suggested that 7 of 11 (64%) beaches sampled in Delaware contained the 19,200 subsurface eggs/m² or 360 surface eggs/m² needed by red knots to obtain their daily caloric needs in approximately 15 hr. Those estimates were based on a separate study by Kalasz and Weber (2005), who sampled eggs at randomly selected points within strata across the entire beach and did not account for aggregation of eggs in nest depressions and wrack. We agree with Gillings et al. (2007) that randomly foraging red knots would not, on average, have encountered subsurface egg densities of 19,200 eggs/m² on Delaware Bay beaches in 2005. However, we found depletion of crab eggs in the wrack line, which suggests that birds may key in on these areas of organic matter where crabs eggs get trapped during the falling tide. We also found in a concurrent study in Delaware Bay that shorebirds do not forage randomly on the beach, but rather forage disproportionately in the depressions in the sand left by nesting female horseshoe crabs compared to random locations at the same height above water (Fraser et al. 2010). By moving among crab nests, even at the end of the tidal cycle, shorebirds in 2005 could have found and foraged on egg hotspots with >1,800 eggs/m² on the surface or >16,000 eggs/m² in the subsurface (assuming uniformly mixed eggs in the subsurface and multiplying our results by 1.3 to make them equivalent to results from 5 cm deep cores). This surface egg density alone is 5 times the density required for a red knot to meet its daily nutritional refueling needs in 15 hr (Gillings et al. 2007); our data do not allow us to extrapolate to estimate how many knots the Delaware Bay as a whole might support as we did not measure the available amount of each microhabitat on each experimental beach.

Red knots at stopover sites are expected to forage to maximize their net rate of energy intake, rather than simply meeting their daily energy requirements, because they are building fat reserves for migration (van Gils et al. 2005, Schaub et al. 2008). To maximize net energy intake, birds must switch foraging patches when the value of their current

patch falls below the value of available alternative patches (Nolet et al. 2006). We observed knots and other shorebirds foraging on all parts of the intertidal zone, so they clearly had access to eggs left in nesting depressions and the open intertidal zone at the end of the tidal cycle. The low consumption rate and high density of surface eggs left in nesting depressions in our experiment in 2005 further suggests that the red knot population had excess horseshoe crab eggs available to it. Red knots apparently depleted the subsurface wrack quickly, then foraged on horseshoe crab nesting depressions until about 3 hr after sunrise, only appearing in large numbers later than that if the tide was falling. We are unable to determine from our data where knots went when they left our study beaches. Red knots may have gone to forage on another beach that we did not study (e.g., Mispillion), to consume prey in off-beach marsh or ocean beach habitats (Mackay 1893, Karpanty et al. 2006, Cohen et al. 2010a), or to roost in a safe location to digest their food or convert their newly acquired food into fat (Atkinson et al. 2007). The latter seems most likely, given the abundance of food left at our study sites in both years, the abundance of eggs left late in the day in some samples that were opportunistically collected by our team in Mispillion in 2004, and our finding that other avian species foraged on our experimental beaches later in the day than the knots.

Our findings suggest that the red knot population using Delaware Bay as a spring migratory stopover should remain constant or possibly increase if 1) there has been no decrease in egg availability since our study and 2) food shortage was the cause of the decline in Delaware Bay red knots as reported by Baker et al. (2004). Consistent with this prediction, peak red knot counts in Delaware Bay from 2004 to 2006 were 13,315 knots, 15,345 knots, and 13,445 knots, respectively (Niles et al. 2008). Peak knot numbers in Delaware Bay have continued to hold near steady and possibly increase between 2006 and 2009 according to a recent knot status update (Niles et al. 2010). Similarly, the total red knot passage population size corrected for turnover between weeks did not decrease between 2004 and 2006 in Delaware Bay (Cohen et al. 2009). If the horseshoe crab egg shortage caused the dramatic decline observed in the Delaware Bay stopover counts and TDF wintering counts of knots between the mid 1990s and 2003, and if crab eggs remain the limiting factor, then an increase in eggs available to red knots should result in an increase in the red knot population. If ongoing monitoring of horseshoe crabs, crab eggs, and red knots in the Delaware Bay should indicate that increasing crab egg numbers are not associated with increasing numbers of knots on stopover in Delaware Bay, or on the wintering grounds in TDF, then other causal factors should be explored.

MANAGEMENT IMPLICATIONS

Extensive efforts are underway in Delaware Bay to increase the availability of crab eggs to foraging shorebirds and to restore horseshoe crab populations for the benefits of multiple users. These include beach closures during the migration season, a moratorium on the harvest of horseshoe crabs in Delaware and New Jersey during the shorebird

migration season, and a limited male-only harvest after the stopover season (ASMFC 2008, Niles et al. 2009). Our data suggest that a continuation of these efforts is warranted, as additional eggs in the wrack line and elsewhere on the beaches should result in an increase in the red knot population. If increasing egg densities are not met with increasing knot numbers in Delaware Bay or in TDF, future resources should concentrate on other possible limiting factors in knot recovery. For example, the use of stopovers that were once apparently important final refueling areas for red knots, including coastal New Jersey, New York, and Massachusetts (Mackay 1893), is now much reduced (Niles et al. 2008). The Delaware Bay now serves as the key refueling site for approximately two-thirds of the Western Atlantic red knot population, with coastal Virginia hosting much of the remaining one-third (Cohen et al. 2009). Therefore, managers should also consider factors limiting red knot numbers at these alternate historic stopover sites, at their wintering sites, and on their relatively unknown Arctic breeding grounds in addition to those in Delaware Bay to best facilitate the recovery of red knots to historic numbers.

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LITERATURE CITED

- Alerstam, T., G. A. Gudmundsson, and K. Johannesson. 1992. Resources for long distance migration: intertidal exploitation of *Littorina* and *Mytilus* by knots *Calidris canutus*, in Iceland. *Oikos* 65:179–189.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behavior* 69:227–263.
- ASMFC. 2004. Horseshoe crab 2004 stock assessment report. Atlantic States Marine Fisheries Commission, Washington, D.C., USA.
- ASMFC. 2008. Addendum V to the interstate fishery management plan for horseshoe crab. Atlantic States Marine Fisheries Commission, Washington, D.C., USA.
- Atkinson, P. W., A. J. Baker, K. A. Bennett, N. A. Clark, J. A. Clark, K. B. Cole, A. DeKinga, A. Dey, S. Gillings, P. M. Gonzalez, K. Kalasz, C. D. T. Minton, J. Newton, L. J. Niles, T. Piersma, R. A. Robinson, and H. P. Sitters. 2007. Rates of mass gain and energy deposition in red knot on their final spring staging site is both time- and condition-dependent. *Journal of Applied Ecology* 44:885–895.
- 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 refueling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 271:875–882.
- Berkson, J., and C. N. Shuster. 1999. The horseshoe crab: the battle for a true multiple-use resource. *Fisheries Management* 24:6–9.
- Brousseau, L. J., M. Sclafani, D. R. Smith, and D. B. Carter. 2004. Acoustic-tracking and radio-tracking of horseshoe crabs to assess spawn-

- ing behavior and subtidal habitat use in Delaware Bay. *North American Journal of Fisheries Management* 24:1376–1384.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and inference: a practical information-theoretic approach*. Springer, New York, New York, USA.
- Cohen, J. B., S. M. Karpanty, and J. D. Fraser. 2010a. Habitat selection and behavior of red knots on the New Jersey Atlantic coast during spring stopover. *Condor* 112:655–662.
- Cohen, J. B., S. M. Karpanty, J. D. Fraser, and B. R. Truitt. 2010b. 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.
- Cohen, J. B., S. M. Karpanty, J. D. Fraser, B. D. Watts, and B. R. Truitt. 2009. Residence probability and population size of red knots during spring stopover in the mid-Atlantic region of the United States. *Journal of Wildlife Management* 73:939–945.
- Cumming, G., and S. Finch. 2005. Inference by eye: confidence intervals, and how to read pictures of data. *American Psychologist* 60:170–180.
- Fraser, J. D., S. M. Karpanty, and J. B. Cohen. 2010. Shorebirds forage disproportionately in horseshoe crab nest depressions. *Waterbirds* 33:96–100.
- Gillings, S., P. W. Atkinson, S. L. Bardsley, N. A. Clark, S. E. Love, R. A. Robinson, A. Stillman, and R. G. Weber. 2007. Shorebird predation of horseshoe crab eggs in Delaware Bay: species contrasts and availability constraints. *Journal of Animal Ecology* 76:503–514.
- Goss-Custard, J. D., A. D. West, R. A. Stillman, S. E. A. Le, V. Dit Durell, R. W. G. Caldow, S. McGroarty, and R. Nagarajan. 2001. Density-dependent starvation in a vertebrate without evidence of depletion. *Journal of Animal Ecology* 70:955–965.
- 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 value of horseshoe crab eggs to spring migrant shorebirds in Delaware Bay. *Journal of Avian Biology* 38:367–376.
- Hilbe, J. M. 2007. *Negative binomial regression*. Cambridge University Press, Cambridge, United Kingdom.
- Kalasz, K. S., and R. G. Weber. 2005. Delaware horseshoe crab egg survey project: final report. Delaware Natural Heritage and Endangered Species Program, Division of Fish, and Wildlife, Dover, Delaware, USA.
- Karpanty, S. M., J. D. Fraser, J. Berkson, L. Niles, A. Dey, and E. P. Smith. 2006. Horseshoe crab eggs drive distribution of red knots in the Delaware Bay. *Journal of Wildlife Management* 70:1704–1710.
- Mackay, G. 1893 Observations on the knot (*Tringa canutus*). *Auk* 10:25–35.
- Mercier, F., and R. McNeil. 1994. Seasonal variations in intertidal density of invertebrate prey in a tropical lagoon and effects of shorebird predation. *Canadian Journal of Zoology* 72:1755–1763.
- Morrison, R. I. G., and K. A. Hobson. 2004. Use of body stores in shorebirds after arrival on high-arctic breeding grounds. *Auk* 12:333–344.
- 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.
- Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? *Journal fur Ornithologie* 147:146–166.
- 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.
- Niles, L. J., H. P. Sitters, A. D. Dey, N. Arce, P. W. Atkinson, V. Ayala-Perez, A. J. Baker, J. B. Buchanan, R. Carmona, N. A. Clark, C. Espoz, J. D. Fraser, P. M. Gonzalez, B. A. Harrington, D. E. Hernandez, K. S. Kalasz, R. Matus, B. J. McCaffery, C. D. T. Minton, R. I. G. Morrison, M. K. Peck, W. Pitts, I. L. Serrano, and B. D. Watts. 2010. Update to the status of the red knot *Calidris canutus* in the western hemisphere, April 2010. New Jersey Department of Environmental Protection, Trenton, New Jersey, USA.
- Niles, L. J., J. Bart, H. P. 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 horseshoe crab harvest in Delaware Bay on red knots: are harvest restrictions working? *Bioscience* 59:153–164.
- Nolet, B. A., A. Gyimesi, and R. H. G. Klaassen. 2006. Prediction of bird-day carrying capacity on a staging site: a test of depletion models. *Journal of Animal Ecology* 75:1285–1292.
- Nordstrom, K. F., N. L. Jackson, D. R. Smith, and R. G. Weber. 2006. Transport of horseshoe crab eggs by waves and swash on an estuarine beach: implications for foraging shorebirds. *Estuarine, Coastal and Shelf Science* 70:438–448.
- Quammen, M. L. 1984. Predation by shorebirds, fish, and crabs on invertebrates in intertidal mudflats: an experimental test. *Ecology* 65:529–537.
- Rosa, S., J. P. Granadeiro, C. Vinagre, S. Franca, H. N. Cabral, and J. M. Palmeirim. 2008. Impact of predation on the polychaete *Hediste diversicolor* in estuarine intertidal flats. *Estuarine Coastal and Shelf Science* 78:655–664.
- Rudloe, A. 1980. The breeding behavior and patterns of movement of horseshoe crabs, *Limulus polyphemus*, in the vicinity of breeding beaches in Apalachee Bay, Florida. *Estuaries* 3:177–183.
- SAS. 2010. *SAS 9.2 user's guide*. Second edition. SAS Institute, Cary, North Carolina, USA.
- Schaub, M., L. Jenni, and F. Bairlein. 2008. Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. *Behavioral Ecology* 19:657–666.
- Schneider, D. C., and B. A. Harrington. 1981. Timing of shorebird migration in relation to prey depletion. *Auk* 98:801–811.
- Shuster, C. N. J., and M. L. Botton. 1985. A contribution to the population biology of horseshoe crabs *Limulus polyphemus* (L.), in Delaware Bay. *Estuaries* 8:363–372.
- van Gils, J. A., P. F. Battley, T. Piersma, and R. Drent. 2005. Reinterpretation of gizzard sizes of red knots world-wide emphasizes over-riding importance of prey quality at migratory stopover sites. *Proceedings of the Royal Society B: Biological Sciences* 272:2609–2618.
- Wander, W., and P. Dunne. 1981. Species and numbers of shorebirds on the Delaware bayshore of New Jersey, Spring 1981. *Record of New Jersey Birds* 7:59–64.

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