

Shorebirds Forage Disproportionately In Horseshoe Crab Nest Depressions

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Abstract.—Horseshoe Crab (*Limulus polyphemus*) eggs are an important shorebird food during the Delaware Bay spring stopover, and shorebird management plans aim to increase and monitor this resource. If shorebirds focus their foraging on Horseshoe Crab nesting depressions they may find richer food supplies than if they forage randomly on the beach. The amount of shorebird sign in quadrats centered on Horseshoe Crab nest depressions was compared with the amount of sign in paired beach areas with no Horseshoe Crab nests. Horseshoe Crab nest depressions had more pecks, probes, digit marks, Ruddy Turnstone excavations, Horseshoe Crab eggs and a greater coverage by shorebird sign than paired beach plots with no Horseshoe Crab nests. Foraging disproportionately within Horseshoe Crab nesting depressions may facilitate the rapid mass gain needed to prepare shorebirds for their flight to the breeding grounds. Horseshoe crab egg monitoring currently estimates mean egg abundance per beach. However, birds are able to find patches with high egg densities even when foraging on beaches with lower average densities. Received 27 January 2009, accepted 29 November 2009.

Key words.—*Arenaria interpres*, *Calidris alba*, *Calidris alpina*, *Calidris canutus*, foraging, Horseshoe Crab, *Limulus polyphemus*, Red Knot, Ruddy Turnstone, shorebirds.

Waterbirds 33(1): 96-100, 2010

During northward migration, tens of thousands of shorebirds stop in Delaware Bay in May and June and feed primarily on eggs of spawning Horseshoe Crabs (*Limulus polyphemus*). Semipalmated Sandpipers (*Calidris pusilla*), Ruddy Turnstones (*Arenaria interpres*), Red Knots (*Calidris canutus*), Sanderlings (*Calidris alba*) and Dunlin (*Calidris alpina*) are the most common species (Clark *et al.* 1993).

Most Horseshoe Crabs come ashore during the night high tide near the full and new moons. Female crabs dig nest burrows and deposit egg masses containing an average of 3,650 2-3 mm-diameter eggs at 0-20 cm below the beach surface (Shuster and Botton 1985; Brockman 1990; Botton *et al.* 1994). They depart, leaving a semi-circular depression in the sand. On most days after spawning, a line of nest depressions stretches across the beach just below the high water mark, parallel to the water's edge. Some crab eggs are distributed on the beach because they are dislodged from the egg mass by the laying female, because a laying female excavates the eggs of another crab, or due to scouring by waves, while others remain buried (Botton *et al.* 1994; Kraeuter and Fegley 1994; Jackson *et al.* 2002).

Food intake rate is important to shorebirds stopping in Delaware Bay because they have a limited time to store the fat required for their flight onto the breeding grounds (Atkinson *et al.* 2007). Gillings *et al.* (2007) showed that birds can ingest surface eggs faster than buried eggs, and that ingestion rate is positively correlated with egg density. Using functions derived from feeding experiments, they predicted that Red Knots could meet their daily energy requirements by feeding for 15 h d⁻¹ on surface eggs at 360 eggs m⁻² or buried eggs at 19,200 eggs m⁻². They referred this to mean egg densities on eleven beaches and noted that only seven beaches had mean egg densities \geq 19,200 eggs m⁻², and concluded that "the opportunities for feeding on buried eggs are limited."

We agree that this conclusion is warranted if eggs are distributed uniformly or randomly and if birds cannot detect patches of high egg density. But if high density patches exist, and birds can readily detect those patches, birds may be able to forage in high egg densities more often than suggested by beach average densities. One place where birds may be able to find high egg densities is Horseshoe Crab nest depressions. We tested the hypothesis that shorebirds preferen-

tially foraged in Horseshoe Crab nest depressions in comparison to nearby beach areas without visible crab nest depressions.

METHODS

The hypothesis that shorebirds use Horseshoe Crab nest depressions preferentially was examined by comparing evidence of shorebird foraging activity (bird footprints, peck and probe marks, and Ruddy Turnstone excavations) in nest depressions with similar evidence in paired control plots. Control plots had no evidence of crab nesting, were the same distance from the water as the nesting depression, and were ± 75 cm from the nest plot. If shorebirds were not using Horseshoe Crab nests preferentially, the number of bird footprints and peck, probe, and excavation marks should be similar in nest depressions and control plots.

The study was conducted on six Delaware Bay beaches (Cook's, Kimble's, Pierce's Point, Reed's, Slaughter, and Ted Harvey Beaches) known for Horseshoe Crab spawning and shorebird use (Smith and Michels 2006). On each sampling occasion, a crab nesting depression was randomly selected for examination. Thereafter, every fifth crab nest depression on a path parallel to the water was examined. Sampled nest depressions were spaced such that all nest depression quadrats were > 2 m apart. After examining a crab nest depression, we placed a control plot 2 m away at the same distance from the water as the nest. If there was a crab nesting depression at the 2-m mark, the control quadrat was placed further down the beach so that it was at least 0.75 m from the edge of the nearest crab nesting depression. A maximum of ten nesting depressions and ten controls were examined on any beach on any day.

A $0.75 \text{ m} \times 0.75 \text{ m}$ quadrat was centered on each nest depression and control point. Within this quadrat, each hole in the substrate that was made by a digging, pecking, or probing shorebird was counted. Because bill-created holes and holes created by shorebird toes were sometimes indistinguishable, we summed all holes and assumed they constituted an index to shorebird activity in the quadrats. In addition to probing in the sand, Ruddy Turnstones often excavate holes. We counted these separately. The percent of the quadrat covered by signs of bird activity (bird footprints, pokes, and excavations) was visually estimated. Two people independently assessed each site at the same time. The independent assessments of number of holes and excavations and total coverage by bird sign were averaged. We excavated a cylindrical hole 25 cm in diameter in the center of the depression or control quadrat and recorded the number of Horseshoe Crab eggs in the top 5 cm of the excavated cylinder.

Statistical Analyses

We estimated mean responses using generalized linear mixed models where the fixed effects were treatment (nest vs. control) and block (sampling occasion, i.e. a beach on a particular day) and the random effect was plot (the nest-control pair). The block variable was included to control for variance associated with environmental variables (e.g. tidal stage, time of day, weather, intensity of crab spawning, density of foraging birds). Analyses were performed in SAS version 9.1.3 (SAS In-

stitute 2004). Continuous data that conformed to assumptions of normality and heteroscedasticity were analyzed with a linear model, and count data were analyzed with a Poisson model, except for the number of eggs in the top 5 cm of sand, which was analyzed with a negative binomial model because the negative binomial was a better fit (AIC_c negative binomial model = 860 vs. AIC_c mixed Poisson model = 1677) due to many zero values that led to overdispersion.

RESULTS

Sixty-six pairs of Horseshoe Crab nest depressions and controls were examined during eight sampling occasions between 12 May and 1 June, 2005. All sample plots were available to birds from first light until sampling began. Sample collection began 3.3-5.2 (mean = 4.1 hours) hours after sunrise. From sunrise to the beginning of sampling the plots were exposed for 0.0-5.1 h of falling tide (mean = 2.4 h) and 0.0-3.7 h of rising tide (mean = 1.3 h).

We found egg masses in 55 of 66 nest plots and 34 of 66 control plots ($\chi^2_1 = 15.2$, $P < 0.01$). Compared to control plots, nest plots had more shorebird-created holes, Ruddy Turnstone digs and Horseshoe Crab eggs in the top 5 cm (Table 1). Compared to control plots, a higher percentage of nest plots were covered by shorebird holes and ruddy turnstone excavations (Table 1).

DISCUSSION

The greater concentration of shorebird activity sign in the Horseshoe Crab nest plots compared to the control plots supports the hypothesis that shorebird foraging activity was higher in crab nest depressions than elsewhere on the beach. The greater number of eggs in the top 5 cm of the crab nests compared to control plots indicates that birds foraging in Horseshoe Crab nest depressions were likely to find richer food supplies than birds foraging on random beach plots. The range of Ruddy Turnstone excavation depths in nest plots was sufficient for them to find entire egg masses, an energetic reward that may offset the cost of deep excavations.

Our observations each day took place well after the beginning of shorebird forag-

Table 1. Counts and percent cover of the substrate by shorebird sign, depth of RUTU digs, depths of HSC egg masses, and counts of HSC eggs in the top 5 cm at HSC nesting depressions and paired random points in similar habitat, Delaware Bay, 2005. Means are least square means.

Variable	Treatment	\bar{x}	SE	Test statistic	Test statistic value	P-value	Method*
Number of shorebird-created holes	Nest	5.5	0.7				
	Control	2.1	0.3	$F_{1,65}$	132.8	<0.001	P
% cover by shorebird holes and footprints	Nest	75.1	3.7				
	Control	55.5	3.7	$F_{1,65}$	30.8	<0.001	L
Number of RUTU digs	Nest	3.1	0.4				
	Control	0.5	0.1	$F_{1,65}$	120.1	<0.001	P
% cover by RUTU digs	Nest	86.1	4.2				
	Control	8.5	4.8	$F_{1,23}$	171.7	<0.001	L
RUTU dig depth (cm)	Nest	3.5	0.3				
	Control	1.5	0.4	$F_{1,14}$	31.8	<0.001	L
HSC egg mass depth (cm)	Nest	8.47	0.4				
	Control	9.74	0.5	$F_{1,30}$	3.96	0.056	L
Number of HSC eggs in top 5 cm	Nest	12.4	2.8				
	Control	5.9	1.3	$F_{1,107}$	7.48	0.007	NB

*L = linear mixed model, P = Poisson mixed model, NB = negative binomial model. For mixed models, the random effect was "plot" (i.e., nest-control pair). The NB mixed model would not converge, so the plot effect was not included. The AIC_c of the fixed effect NB model (860) for number of HSC eggs was better than the AIC_c for the mixed Poisson model (1677).

ing. Because foraging birds favored Horseshoe Crab nest depressions, the differences we observed in egg numbers between nest depressions and control quadrats were probably less than the differences that existed at the beginning of the foraging day at twilight. Thus, the benefits conveyed by the foraging pattern described here are understated.

Migrating shorebirds arrive on the Delaware Bay in early May and must depart for their nesting areas by early June to arrive in time for the short northern breeding season (Clark *et al.* 1993; Atkinson *et al.* 2007). Thus, they must gain weight rapidly during the Delaware Bay stopover. Foraging rates of shorebirds ingesting Horseshoe Crab eggs are positively related to egg densities at the chosen foraging sites (Gillings *et al.* 2007). The condition of birds arriving at their northern breeding sites may influence their ability to survive early summer inclemency and to transform their physiological state from a migration state to a breeding state (Morrison *et al.* 2005). Thus, the ability to find areas with the highest egg densities, as indicated in this study, is likely an adaptive trait.

We did not check nests before shorebirds arrived to forage, so we do not know how many eggs were visible on the surface at that time. Whether birds are initially attracted by the morphology of the nest depression or by visible surface crab eggs within the depressions remains to be discovered. Likewise, the role of social facilitation (*sensu* Pomara *et al.* 2003) in promoting disproportionate use of the crab nest depressions is unknown. We often observed Red Knots and Sanderlings foraging in and around Ruddy Turnstone excavations as the Turnstones were actively digging. Gillings *et al.* (2007) experimentally manipulated Horseshoe Crab egg densities in trays, and found that the number of shorebirds using trays and the bird-time spent on the trays was positively correlated with tray egg density. Since the area and dimensions of their trays were similar across egg densities, this suggests that individual bird decisions to enter, stay on, or leave trays were based either on individual experiences with egg densities or on information gained from

watching other birds, not on the images of the trays themselves.

Birds may not be able to take advantage of the high density of crab eggs in nests every day. On windy days, the depressions quickly filled in. On such days the value of eggs found in the swash zone or in windrows on the beach may be relatively more important than on calm days. However, the same winds that cover nest depressions may also create waves that unearth buried eggs (Kraeuter and Fegley 1994; Jackson *et al.* 2002; Nordstrom *et al.* 2006). The annual variation in this phenomenon is unknown. In this study year, 2005, the Horseshoe Crab spawn was largely delayed because of stormy weather (Smith and Michels 2006), and peak Horseshoe Crab spawning did not occur until after this study was completed. Thus, there were likely fewer crab eggs on the study beaches than in other years (Kraeuter and Fegley 1994). In years with more abundant Horseshoe Crab spawning, there might be more eggs on the surface, and the preferential use of nest depressions for foraging might be less pronounced.

The clumped distribution of crab eggs in the swash zone and windrows and the focused nature of shorebird foraging on crab nest depressions, wrack lines and the swash zone (Nordstrom *et al.* 2006; this study), suggest that even when mean densities on a beach are low, birds may be able to find and forage in very high-density patches. Thus, while random sampling of beaches (Pooler *et al.* 2003) can provide useful data on large-scale trends in overall egg abundance to which the availability of eggs to birds may be correlated, assessment of whether birds are able to forage on egg densities high enough to meet their daily energy requirements (Gillings *et al.* 2007) requires an assessment of the distribution and abundance of high egg-density patches, and the density of eggs therein.

ACKNOWLEDGMENTS

We thank the National Marine Fisheries Service for funding. We thank N. Avissar, C. Olfenbuttel, J. Bercome, D. Fraser, J. Trivett, M. Davis, D. Hata, S. Melvin and C. Hitchens for field assistance. We thank S. Melvin

for assistance with project design. Discussion and collaboration with P. Atkinson, K. Bennett, D. Carter, K. Clark, N. Clark, K. Cole, A. Dey, S. Gillings, B. Harrington, K. Kalasz, S. Michels, R. Miller, C. Minton, G. Moore, L. Niles, K. Reynolds, H. Sitters, D. Smith and R. Weber facilitated and improved the work.

LITERATURE CITED

- 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.
- Botton, M. L., R. E. Loveland and T. R. Jacobson. 1994. Site selection by migratory shorebirds in Delaware Bay, and its relationship to beach characteristics and abundance of Horseshoe Crabs. *Auk* 111: 605-616.
- Brockman, H. J. 1990. Mating behavior of Horseshoe Crabs *Limulus polyphemus*. *Behaviour* 114: 206-220.
- Clark, K. E., L. J. Niles and J. Burger. 1993. Abundance and distribution of migrant shorebirds in Delaware Bay. *Condor* 95: 694-705.
- 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.
- Jackson, N. L., K. F. Nordstrom and D. R. Smith. 2002. Geomorphic-biotic interaction on beach foreshores in estuaries. *Journal of Coastal Research* 36: 414-424.
- Kraeuter, J. N. and S. R. Fegley. 1994. Vertical disturbance of sediment by Horseshoe Crabs (*Limulus polyphemus*) during their spawning season. *Estuaries* 17: 228-294.
- Morrison, R. I. G., N. C. Davidson and T. Piersma. 2005. Transformations at high latitudes: why do Red Knots bring body stores to the breeding grounds? *Condor* 107: 449-457.
- 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.
- Pomara, L. Y., R. J. Cooper and L. J. Petit. 2003. Mixed-species flocking and foraging behavior of four neotropical warblers in Panamanian shade coffee fields and forests. *Auk* 120: 1000-1012.
- Pooler, P. S., D. R. Smith, R. E. Loveland, M. L. Botton and S. F. Michels. 2003. Assessment of sampling methods to estimate Horseshoe Crab (*Limulus polyphemus* L.) egg density in Delaware Bay. *Fishery Bulletin* 101: 698-703.
- SAS Institute 2004. SAS/STAT 9.1 users' guide. SAS Institute, Inc., Cary, North Carolina.
- Shuster, C. N., Jr. and M. L. Botton. 1985. A contribution to the population biology of Horseshoe Crabs, *Limulus polyphemus*, in Delaware Bay. *Estuaries* 8: 363-372.
- Smith, D. R. and S. F. Michels. 2006. Seeing the elephant: the importance of spatial and temporal coverage in a large scale volunteer-based program to monitor Horseshoe Crabs. *Fisheries* 31: 485-491.