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Day and Night Foraging of Red Knots (*Calidris canutus*) During Spring Stopover in Virginia, USA

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Abstract.—Long-jump migrant shorebirds have brief windows during spring stopover to acquire the energy needed to complete migration. Red Knots (*Calidris canutus*) refueling on Horseshoe Crab (*Limulus polyphemus*) eggs in Delaware Bay can meet their energy needs foraging only by day. In nearby Virginia, thousands of Red Knots stop over, but primarily low-quality, hard-shelled prey are available. One tactic Red Knots may use to meet their energy demands with such prey might be to extend their foraging time by feeding at night. To estimate the length of the foraging day in Virginia, daylight feeding was studied during three spring stopover periods (2008 to 2010), and night feeding was studied in 2010. Red Knots foraged 76 ± 3 SE% of the time in 2008 and 2009 combined, and 59 ± 3 % of the time in 2010, during 3-minute observations. In 2010, Red Knots foraged 51 ± 7 % of the time during a continuous 7-h daytime observation and 77 ± 5 % of the time during a continuous 8-h night time observation on the same island. Given constraints on energy intake, night foraging by Red Knots in Virginia may be necessary for birds to attain sufficient mass to complete migration. Received 10 December 2010, accepted 25 April 2011.

Key words.—barrier islands, *Calidris canutus*, foraging, migration, Red Knot, shorebird, stopover, Virginia.

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Long-jump migrant shorebirds make energetically costly flights between stopover sites (Piersma 1987). Arrival of western Atlantic Red Knots (*Calidris canutus*, hereafter knots) at spring stopover sites coincides with peaks in prey abundance (Niles *et al.* 2008; Cohen *et al.* 2010), approximately one month before the knots' Arctic nesting season. They must gain mass rapidly to reconstitute their organs and accumulate enough fat to complete migration (van der Meer and Piersma 1994).

Tide, day length, prey quality (digestible energy:shell mass) and prey abundance limit refueling rates of shorebirds foraging on benthos (Zwarts 1990; van Gils *et al.* 2005a; van Gils *et al.* 2005b; van Gils *et al.* 2006). Comparisons of knot body mass among spring stopover sites suggested that mass gain in Delaware Bay, Delaware and New Jersey, where birds forage on Horseshoe Crab (HSC, *Limulus polyphemus*) eggs, was greater than at sites where they refueled on bivalves (Piersma *et al.* 2005). Birds consuming soft prey can maintain high energy intake rates without large gizzards (van Gils *et al.* 2003), alleviating physiological constraints to rapid

mass gain. Gillings *et al.* (2007) estimated that knots eating HSC eggs could meet their energy needs by foraging from sunrise to sunset for fifteen hours per day for approximately two weeks.

One hundred kilometers south of Delaware Bay, the Eastern Shore of Virginia hosts peak spring numbers of 5-8,000 knots (Cohen *et al.* 2009). Their prevalent prey are hard-shelled bivalves (Cohen *et al.* 2010), which require shorebirds to take digestive breaks to crush the shells (van Gils *et al.* 2005a). Western Atlantic Red Knot numbers declined substantially in the past two decades and research has focused on the role of diminished HSC egg supplies, a critical knot food resource (Niles *et al.* 2008). However, Red Knots worldwide forage primarily on molluscs (Piersma *et al.* 2005). Thus, sites like Virginia where bivalves are abundant might provide a viable alternative to Delaware Bay, if knots can gain enough weight there to complete migration.

We hypothesized that knots stopping in Virginia would forage at night to facilitate rapid mass gain. Night foraging has been observed in shorebirds during migration and

winter (Robert *et al.* 1989; Rompre and McNeil 1994; Dodd and Colwell 1998). Knots foraged at night in Argentinian and Wadden Sea stopover sites (van Gils and Piersma 1999; Sitters *et al.* 2001). Nocturnal foraging increases foraging period length, can be more profitable than diurnal foraging if prey are more abundant or active at night (McNeil and Rodriguez 1996), and may allow avoidance of diurnal predators (McNeil and Rodriguez 1996).

Our objectives were to determine 1) the proportion of time knots foraged during daytime and nighttime in Virginia, and 2) the interaction between tide and time of day in affecting foraging behavior. Our results shed light on the potential for migrant knots to gain weight on low quality prey.

METHODS

Study Area

We studied knots on the barrier islands off the Eastern Shore of Virginia, USA (37°23.7'N, 75°42.5'W). The site contains twelve islands, approximately 100 km in aggregate length, bounded by the Atlantic Ocean to the east and a shallow marsh/lagoon system to the west. The islands are undeveloped and experience little human activity. Knots foraged primarily in the ocean intertidal zone, which contains sandy stretches punctuated by peat banks.

Field Methods

We stratified sampling over peat banks and sandy beaches. We visited randomly-selected sampling points on the peat banks between 18 to 21 May each year from 2008-2010. The first point was selected by walking a random distance (m), selected using a random number table, from the edge of the first peat bank encountered on a transect parallel to the waterline. We then walked parallel to the shore 300 m to each successive point, using a GPS unit to mark points and measure distances. If peat banks were separated by > 300 m of open sand, the random number table was used at the next peat bank encountered to select the next point.

A second group of randomly-selected points was sampled in the sandy ocean intertidal zone. We collected behavioral data between 22 and 28 May (typically the week of peak knot abundance, Clark *et al.* 1993) and once between 29 May and 4 June in each year, 2008 - 2010. We generated 100 random points inside polygons digitized from orthophoto quarter quads in ArcGIS 9.3 (ESRI, Redlands, CA) using the Hawth's Tools extension (Beyer 2004), constraining the points to be at least 500 m apart.

In 2008 and 2009, whenever we encountered one or more knots within 100 m of a point, we selected one focal individual for sampling (Altmann 1974), counting a random number of birds from the left edge of the flock.

Every 10 sec for 3 min, we recorded whether the bird was foraging, using a 60× spotting scope (Bushnell Corporation, Overland Park, KS). In 2010, every 30 sec for 3 min we instead recorded the proportion of the flock foraging.

In 2010, overnight sampling was conducted using a 10× Generation 2 night vision scope with external infrared illuminator (American Technologies Network Corp, San Francisco, CA). For comparison, we sampled from sunrise to sunset on a subsequent day, using a spotting scope. Radio-tagged birds available from a different study facilitated the location of flocks at night using a handheld radio-telemetry receiver and a three-element Yagi antenna (Advanced Telemetry Systems, Inc., Isanti, MN). Every 10 min we recorded the behavior of a focal bird, selected by counting a random number of birds from the left edge of the flock. We also sampled the behavior of radio-tagged birds, if present.

Statistics

The proportion time foraging in 2008 and 2009 was calculated as "number of 10-sec sub-samples where the focal bird was foraging"/"total observation time", dropping observations that lasted <2 min. Our study was only three weeks long due to the short Red Knot stopover period, and given that the tide cycle shifted by twelve hours a week during that period, tide and week were confounded. The sampling was not aimed at separating these effects and, thus, we only calculated an overall mean of percent time foraging. For the 2010 data, we estimated the average proportion of the flock that was foraging, using a mixed model with "observation" as a random effect with temporally-autocorrelated errors, because each observation consisted of six sub-samples taken in a 3-minute time period (Diggle 1988).

Logistic regression was used to estimate the proportion of observations that knots were foraging in the sunset to sunrise, and sunrise to sunset, samples in 2010. We examined the effects of tide and time of day, and an interaction between survey sampling period (day or night) and time, including time². Appropriateness of the binomial model was tested using the Hosmer and Lemeshow Goodness-of-Fit test (Hosmer and Lemeshow 1989). We compared the fit of models containing subsets of the variables of interest, as well as a null intercept-only model, using information-theoretic criteria, and considered any model with a likelihood >0.125 to fit the data well enough to be worth further consideration (Burnham and Anderson 2002).

RESULTS

Based on 87 daytime observations (collected between 1.1 and 11.1 hr after sunrise), knots spent an average of 76 ± 3 SE% of their time foraging in 2008 and 2009 combined. Based on 41 daytime observations (collected between 3.6 and 12.1 hr after sunrise), 59 ± 3 % of knots in flock scans were observed foraging in 2010.

We recorded knot behavior from 21:00 to 05:00 on 25 May 2010, under a full moon

and no cloud cover. Knots were observed on peat banks and spent $77 \pm 5\%$ of their time foraging ($n = 77$). One radio-tagged bird in our sample had been captured and radio-tagged in the daytime while foraging on sand on a different island. We returned to the nighttime sampling site for a daytime observation on 29 May. Knots were using the peat banks, and foraged $51 \pm 7\%$ of the time ($n = 55$) between 09:00 and 16:00. The model containing an interaction between sampling period and time² had strong support ($\omega_i = 0.86$). No other model had a likelihood > 0.125 . Foraging activity increased over time during the day but not at night, but tide and time of day were confounded given that we only sampled once by day and night and tide changes with time of day (Fig. 1).

DISCUSSION

Red Knots in Virginia foraged by day and night during spring stopover. Taking the

highest mean proportion of time we observed Red Knots to forage by day (75%) and night (76%) from 2008-2010, Red Knots could have 18 hr available for foraging in every 24 hours. Non-foraging time could be spent waiting for the tide to uncover prey, and digesting hard-shelled organisms (van Gils *et al.* 2005a, b). Percent time foraging by day during spring stopover also was between 70 and 80% for several shorebird species in Texas playas and North Dakota prairie pot-holes (Davis and Smith 1998; De Leon and Smith 1999). Tidal inundation could limit foraging opportunities in coastal habitats (van Gils *et al.* 2005b). We did not observe knots to forage at high tide, but our data were insufficient to separate this possible effect from time of day.

Our results imply that even if knots stopping in Virginia forage on low quality prey relative to HSC eggs, they can forage throughout much of a 24-hour day, suggesting one manner in which they might obtain

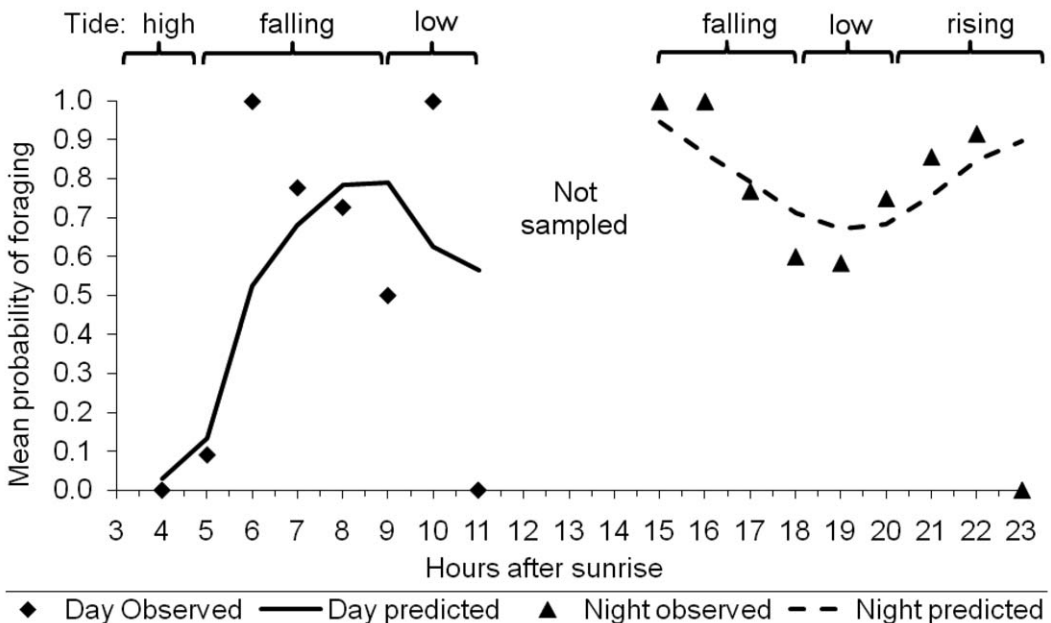


Figure 1. Observed and predicted (logistic regression) proportion of time Red Knots foraged *vs.* time since sunrise ($n = 132$), Virginia, 2010. Observations and model predictions were averaged within 1-h increments to facilitate display, because the observations were 1 = foraging, 0 = not foraging (focal animal observation every 10 min). Tidal stage was not a significant effect in our models, but is provided for reference and to illustrate the confounding of time of day with tidal stage (high tide only occurred early in the morning). Results in the figure are based on the best model ($\omega_i = 0.87$, of 8 models tested) which contained stratum (day and night) interacting with the quadratic effect of hours since sunrise.

adequate fuel to complete migration. The effects of moonlight availability remain to be studied, but Red Knots are known to forage tactilely (Piersma *et al.* 1995; Piersma *et al.* 1998) which could render moonlight unnecessary.

Little attention has been given to conservation of spring stopover habitat for Western Atlantic Red Knots in North America outside of the Delaware Bay, on the assumption that HSC eggs are the primary limiting resource for this species (Niles *et al.* 2008). Bivalves are considered to be lower quality prey than HSC eggs, based on comparative studies of Red Knot body masses among stopover sites (Piersma 2005) and bivalves' low ratio of metabolizable energy to shell (van Gils *et al.* 2005a). However, night foraging may permit the birds to refuel adequately on bivalves in Virginia. Thus, coastal sandy beaches and peat banks might provide valuable alternative prey to HSC eggs. Most U.S. Atlantic beaches that once likely provided similar stopover habitat to the Virginia coast have been altered by human development and recreation that disturbs birds and reduces prey populations (Schlacher *et al.* 2007; Schlacher *et al.* 2008; Tarr *et al.* 2010). Our results support protection of Atlantic beaches from such activities as an important part of any Red Knot recovery strategy.

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