

DEMOGRAPHIC RATES AND ENERGETICS OF RED KNOTS WINTERING IN
FLORIDA

By

AMY C. SCHWARZER

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To the red knot and all of its feathered kin and to all the people who inspired me to work
with them and for them

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TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS.....	4
LIST OF TABLES.....	8
LIST OF FIGURES.....	9
ABSTRACT	10
CHAPTER	
1 INTRODUCTION	12
2 ANNUAL SURVIVAL AND BODY MASS OF RED KNOTS (CALIDRIS CANUTUS) WINTERING IN FLORIDA.....	16
Methods.....	19
Field Methods.....	19
Data Analysis	20
Results.....	25
Discussion	26
3 LOCAL SURVIVAL, MOVEMENT RATES, AND PLASMA METABOLITES OF RED KNOTS WINTERING IN THE TAMPA BAY REGION	38
Methods.....	40
Study Area.....	40
Capture Methods.....	41
Resighting Methods.....	42
Invertebrate Sampling Methods.....	43
Plasma Metabolite Laboratory Analysis Methods.....	43
Data Analysis	44
Residency and movement rates.....	44
Prey and plasma metabolites.....	48
Results.....	49
Discussion	50
4 CONCLUSION.....	66
Management Recommendations	68
Recommendations for Further Research.....	69

APPENDIX

A PREY SELECTION IN WINTERING RED KNOTS IN THE TAMPA BAY REGION..... 71

 Methods 71

 Study Area..... 71

 Invertebrate Sampling 72

 Reference sampling 72

 Foraging sampling 72

 Stomach contents 73

 Data Analysis 73

 Results..... 74

 Reference Sampling 74

 Foraging Sampling 74

 Stomach Contents..... 74

 Discussion 75

B PREY AVAILABILITY AND SELECTION IN MIGRATORY RED KNOTS IN THE CEDAR KEY REGION 80

 Methods 80

 Study Area..... 80

 Reference Sampling 81

 Foraging Sampling 82

 Red Knot Surveys 82

 Data Analysis 82

 Results..... 83

 Discussion 84

LIST OF REFERENCES 90

BIOGRAPHICAL SKETCH..... 96

LIST OF TABLES

<u>Table</u>	<u>page</u>
2-1 Model selection for annual survival for adult and juvenile Red Knots banded in Florida from 2005-2010.	33
2-2 Parameter estimates from the top model {S(HY(.), AHY*t) p(t) r(=0) R(.) R'(=0) F(age) F'(HY(=0), AHY) PIM} listed in 2-1.	34
2-3 Comparison of seasonal averages of weights for Florida birds with South American estimates reported in the literature.	35
3-1 Model selection for daily, local survival of Red Knots in the Tampa Bay region (winters 2008-2009 and 2009-2010).....	57
3-2 Model selection for survival and movement rates of Red Knots wintering in three sub-regions within the Tampa Bay region	58
3-3 Beta parameter estimates for the multi-state model for Red Knots wintering in the Tampa Bay Region.....	59
3-4 Results of plasma metabolite analysis from the Tampa Bay region.	60
A-1 Comparison of reference and foraging samples from the Anna Maria, Indian Shores and Longboat regions in Tampa Bay during the winter and spring..	76
A-2 Number of items and percentage of total items by prey type found in 16 Red Knot stomachs from the Tampa Bay region.....	77
B-1 Mean horseshoe crab egg/larvae counts by site for 2008-2010.	86
B-2 Differences in horseshoe crab eggs/larvae buried compared to eggs available.	87

LIST OF FIGURES

<u>Figure</u>	<u>page</u>
2-1 Map showing primary study area (inset map) and secondary study area (main map).	36
2-2 Population trends predicted by heuristic model.	37
3-1 Map of Tampa Bay region	61
3-2 Daily survival probabilities across season for three locations in the Tampa Bay region.	62
3-3 Daily transition probabilities between sub-regions in the Tampa Bay region.....	63
3-4 Plasma metabolites levels with standard error for the Tampa Bay region	64
3-5 Weekly mean densities of preferred prey over the winter and spring at three sub-regions within Tampa Bay	65
A-1 Weekly mean densities of all preferred prey over the winter and spring at three sub-regions within Tampa Bay	78
A-2 Weekly mean densities of <i>Donax</i> , <i>Emerita</i> and <i>Spionidae</i> over the winter and spring at three sub-regions within Tampa Bay.....	79
B-1 Map of Cedar Key region with major resighting and invertebrate spawning locations.	88
B-2 Example invertebrate reference sampling plot.....	89

Abstract of Thesis Presented to the Graduate School
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Amy C. Schwarzer

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Chair: H. Franklin Percival
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The *rufa* subspecies of red knot (*Calidris canutus*), a long-distance migrant shorebird, has undergone drastic declines in the last 25 years. In this study I examined the Florida wintering population of this subspecies and assessed possible vulnerabilities faced by the population on its wintering grounds. I estimated annual survival and size-adjusted body mass for knots wintering in Florida and compared them to estimates derived from the entire subspecies. Comparisons between Florida and South American birds indicated that annual survival rates between 2005 and 2010 were similar (FL = 0.86-0.94 vs. SA = 0.87-0.92), and that they had similar or higher body mass. My findings do not suggest local factors are the primary explanation for declines of Florida populations, nor do they indicate that adult mortality is the likely mechanism of decline during 2005-2010. Evaluating alternative mechanisms and vital parameters, such as fecundity, during other portions of their annual cycle is necessary.

Multiple theories abound for the distribution of non-breeding migrants. Through the comparison of Florida and South American populations, I assessed the likelihood of these theories as they apply to the global red knot subspecies. Although my work was

not definitive, I demonstrated how ecological conditions such as food resources were a more likely determinate of winter red knot distribution than evolutionary based theories of fitness and dominance.

I also modeled local residency and movement rates among three sites in the Tampa Bay region as a function of prey, body mass index, and distance. Knots remained in traditionally used areas unless conditions (e.g., human recreation) changed markedly. However, mean length of stay (MLS) varied greatly among the three sites during the core winter months (28d at Indian Shores, 44d at Longboat, 69d at Anna Maria). Although I did not measure human disturbance directly, smaller MLS corresponded with higher anthropogenic development and vice versa. Transition probabilities between areas were minimal (<0.08). Finally, I used plasma metabolites to evaluate the energetic state of wintering birds. Plasma metabolites were consistent with maintenance to a slightly positive energy budget and showed no significant differences between years or sites.

CHAPTER 1 INTRODUCTION

Red Knots (*Calidris canutus*) consist of at least six subspecies world-wide, representing both long-distance and short-distance migrants. In the Americas three subspecies exist (*C.c. roselaari*, *C.c. islandica* and *C.c. rufa*). The *C.c. rufa* subspecies (hereafter referred to as *rufa*) is then subdivided into three distinct over-wintering populations found in southern South America (Tierra del Fuego), Brazil, and the southeastern United States. The bulk of the *rufa* population winters in Tierra del Fuego (~14,000-16,000 individuals). Smaller groups are found in Brazil (~3,000) and the United States (~2,000 in Florida) (Niles et al. 2008a). Historically Tierra del Fuego hosted an even larger proportion of the wintering population (up to ~100,000 birds during the mid 1980's as compared to ~20,000 in Brazil and parts north combined) (Niles et al 2008b).

Over the past 25 years the *rufa* subspecies has declined approximately 80% (Niles et al. 2008a). This decline has been linked to a steep reduction in the knots' primary food source, horseshoe crab (*Limulus polyphemus*) eggs (Haramis et al. 2007, Karpanty et al. 2006, Tsipoura and Burger 1999), at the final north bound migratory stopover in Delaware Bay. Available data also suggest that the *rufa* population in Florida is declining (Niles et al. 2008c). Florida is home to the largest wintering knot population in the southeastern United States (Niles et al. 2006). This prompted the Florida Fish and Wildlife Commission in 2005 to support research designed to determine the status of the species within the state and identify factors that could be managed to curb further declines.

An assessment of the status of the subspecies wintering in Florida must start with the recognition of the possible interplay between habitat quality and survival rates of the species' throughout its annual cycle. Understanding this relationship may be complicated by the range of migratory strategies exhibited by segments of the *rufa* subspecies. Post-breeding Red Knots migrate south along a gradient of available habitat from the United States to southern South America, similar to some other Arctic breeding shorebirds (Myers et al. 1986). Within this range, higher concentrations of birds occur at more southerly latitudes. Several hypotheses have been advanced to account for this non-uniform distribution pattern. These include greater food resources, less competition for food, and decreased predator pressure in southern latitudes (Myers et al. 1986). Piersma (1997, 2007) suggested that lower disease and parasite loads at non-tropical latitudes may also attract more birds. Myers et al. (1986) hinted at other hypotheses, some of which have been documented in other avian taxa. These include sex-specific resource dominance (e.g. Marra 2000), leap-frogging (e.g. Kelly et al. 2002), and the presence of sedentary and migrant segments in a population (e.g. Lauber and Langenberg 1998, Jahn et al. 2004).

The presence of short and long-distance migrants within the subspecies leads to several possible mechanisms that might account for population declines. For example, if one assumes that Tierra del Fuego, the migratory terminus of the species, represents the strategy that maximizes annual survival and reproduction, then lower annual survival rates for Florida Red Knots would be consistent with a marginal population at the extreme northern edge of the species wintering range (e.g., Piersma 1997, 2007). As such the status of knots wintering in Florida could be particularly vulnerable

(sensitive) to variations in habitat quality and anthropogenic pressures. Conversely, if differences in annual survival are negligible along the north-south gradient, then population declines reported by Niles et al. (2008a) for all *rufa* populations might be related to factors shared across selected migratory stopovers or the breeding grounds.

The objective of this study was to assess the status of Florida Red Knots by examining and contrasting evidence of selected vital parameters and energetic status of the population on a global (hemispheric) and local (Florida) scale. Examining evidence at multiple scales offers opportunities to decouple the species' annual cycle and requirements, providing a better foundation to formulate conservation schemes. In Chapter 2, I compare annual survival rates and body condition of knots wintering in Florida with their counterparts wintering in South America. This comparison also provides a basis for reasonable speculation about migratory strategies and trade-offs. I obtained estimates of annual survival from knots banded in Florida from 2005 to 2010, and from the populations of *rufa* wintering in South America from capture-resight studies conducted at Delaware Bay (McGowan et al. 2011). I also compare size-adjusted estimates of body mass between knots wintering in Florida and South America as a means to assess their relative energetic state or condition. Size-adjusted mass estimates have received a great deal of attention in recent years as a tool to assess trade-offs associated with migratory strategies and habitat quality (Atkinson et al. 2007, Niles et al. 2008b, Baker et al. 2004). Recently, the metric was a focal parameter used to gauge whether knots migrating through the Delaware Bay area had met physiological and energy thresholds required for survival and prospective reproductive performance (Niles et al. 2008b, Smith et al. 2008, McGowan et al. 2011).

In Chapter 3, I document local dynamics of knots wintering in Florida. Specifically, I estimate residency and movement rates for and among three traditionally used wintering areas in the Greater Tampa Bay region--Indian Shores (which includes birds from Indian and Reddington Shores and Indian Rocks Beach), Anna Maria (which includes Anna Maria Island, Ft. De Soto County Park and Shell Key Preserve), and Longboat (which includes Longboat and Lido Keys). I examine *a priori* predictions regarding the influence of size-adjusted body mass, prey levels and distance on the aforementioned parameters. I also examine temporal trends in body condition and levels of plasma metabolites as means to assess the energy state of wintering birds. Plasma metabolites were of particular interest in this assessment because, unlike values of size-adjusted mass, they provide an indication of the energetic state of birds for a time-window of 2-5 days (Williams et al. 1999, Guglielmo et al. 2005, Acevedo Seaman et al. 2006). Seasonal changes in levels of triglyceride, glycerol and β -OH butyrate indicate whether overwintering birds were on a path of energetic maintenance, fat loss (catabolism) or fat production (anabolism).

In Chapter 4, I present my concluding remarks and discuss their potential conservation implications. I also suggest several topics for future research that may further our understanding of Red Knots and causes of decline. Finally, I include two appendices, summarizing prey types, levels and seasonal fluctuations at the Tampa Bay and Cedar Key regions respectively. Results represent a broad-based attempt to document seasonal patterns of prey with particular interest in documenting the presence and abundance of horseshoe crab eggs and determining prey preferences for Red Knots in Florida.

CHAPTER 2
ANNUAL SURVIVAL AND BODY MASS OF RED KNOTS (*CALIDRIS CANUTUS*)
WINTERING IN FLORIDA

The Red Knot (*Calidris canutus*) is a globally distributed sandpiper that breeds in the high Arctic and makes short to long distance migrations to its non-breeding sites. There are six recognized subspecies: *canutus*, *islandica*, *piersmai*, *rogersii*, *roselaari*, and *rufa*. Three of these subspecies occur in North America and demonstrate alternative migration strategies. *Islandica* breeds in the eastern Canadian Arctic and migrates along a trans-Atlantic route to Europe for the non-breeding season (Harrington 2001). *Rufa* breeds in the central-eastern Canadian Arctic and migrates south along the Atlantic Flyway (Niles et al. 2008b, Harrington 2001). The *rufa* subspecies winters along a gradient, with wintering populations in the southeastern United States, Brazil, Argentina and Chile (Niles et al. 2008b). The majority of the subspecies is found at this migratory extreme. On the other hand, it has been suggested that the majority of *roselaari*, while migrating south from their Alaskan Arctic breeding grounds do not attempt such long-distance migrations, wintering instead in Mexico and Central America (Niles et al. 2008b).

Since the early 1990's declines in numbers of the *rufa* subspecies have been well documented at both wintering and migratory stopover locations (Morrison et al. 2004, Niles et al. 2008b). Previous hypotheses to account for these declines include: a) direct mortality to underweight individuals during migration (Baker et al. 2004), or b) inability of underweight birds to breed successfully due to physiological constraints (Morrison et al. 2005). Attention has primarily focused on Delaware Bay where knots congregate in large numbers to build up energy reserves for both migration to the breeding grounds and subsequent initiation of breeding activities. Hypotheses on the subspecies' decline

have linked seasonal changes in body mass, as a proxy for energy reserves, with food resources, particularly horseshoe crab (*Limulus polyphemus*) eggs (Haramis et al 2007, Karpanty et al. 2006, Tshipoura and Burger 1999). Studies examining the relationship between food availability and the species status have shown that as the available supply of horseshoe crab eggs has declined the percentage of birds reaching sufficient weight for migration, or at least a theoretical threshold of 180 grams, has decreased (Baker et al. 2004). This threshold has been hypothesized as a predictor of the knots' annual survival (Baker et al. 2004, Niles et al. 2008b). There was strong support in the data for this hypothesis (McGowan et al. 2011). However, including climatic conditions on the breeding grounds (i.e., snow fall) improved model support substantially, suggesting that other ecological and anthropogenic factors (i.e., climate change) may contribute to declines in knot populations.

Identifying mechanisms for the species' decline has been limited by lack of information on vital parameters. This is partly due to difficulties in obtaining reliable estimates of reproductive success across the vast and remote geographic extent of the breeding grounds. Survival estimates have only recently become available (McGowan et al. 2011, Baker et al 2004). Most estimates come from Delaware Bay, where the majority of birds from all wintering populations converge prior to migration to the breeding grounds (Harrington 2001). No estimates exist for distinct populations such as those wintering in Florida. Florida supports one of the largest wintering concentrations of Red Knots in the southeastern U.S. (Niles et al. 2008c). Cumulative data since 2005 are adequate to estimate selected vital parameters, providing an opportunity to explore mechanisms of decline.

I report annual survival for adults and for birds banded as juveniles, and body condition estimates for wintering knots in southwestern Florida. Estimates were used to determine if birds wintering in Florida differed from other *rufa* populations. Lower estimates in Florida than elsewhere would lend support to the possibility that population declines in Florida have a local demographic or physiological component. Specifically I explored whether annual survival rates of Florida adults differed from estimates for other populations obtained at Delaware Bay. Although Florida knots pass through Delaware Bay along with South American populations they likely represent less than 10% of total migrants in the bay. Therefore I viewed survival estimates from Delaware Bay as being representative of annual survival for the South American wintering populations. I also examined whether body mass, adjusted for body size (i.e., culmen), was similar to that from birds wintering in South America during the same time period. I focused on this metric because it is commonly used as an indicator of the energetic status and health of individuals (Baker et al. 2005, Niles et al. 2006) and as a predictor of survival and reproduction (Baker et al. 2004, McGowan et al. 2011).

I use annual survival estimates to inform a discussion about differing migratory strategies and distributions of various knot populations. Florida birds are short-distance migrants compared to other populations of *rufa* red knots. One school of migration theory would suggest that there will be a trade-off between survival and reproductive success (i.e. closer access to the breeding grounds and higher reproductive success is balanced by higher adult mortality) (ex. Belthoff and Gauthereaux 1991, Ketterson and Nolan 1976), another suggests that immunological factors such as disease and parasites determine distribution (i.e. more diseases and parasites are present at more

tropical latitudes) (Piersma 1997, 2007), while a third suggests that ecological factors such as prey availability, predator presence, etc. determines the distribution of birds among populations (Myers et al.1986). In the first two theories, Florida birds should suffer higher adult mortality than their South American counterparts. In the last theory however, one would expect that birds from all populations would show similar levels of survival. Thus by comparing survival estimates from different populations I explore these theories and discuss possible mechanisms for the distribution and size of *rufa* knot populations. Finally, I discuss results and conservation implications for the species in Florida and for *rufa* as a whole.

Methods

Field Methods

Birds were captured and banded as part of this project (2007-2010) and previous projects (2005-2007) along the southwest Gulf coast of Florida at locations including Sanibel Island, Cayo Costa Island, and the greater Tampa Bay area including Longboat and Lido Keys (Figure 2-1). Banding took place each winter between 2005 and 2010. Not all locations were trapped each year, but captures took place at two or more locations per winter. At least 90 Red Knots were captured per winter, exceeding 1,700 captures total for the five year period. Birds were captured using cannon nets. Upon capture, each knot was banded with a standard Incoloy U.S. Fish and Wildlife Service band and marked each with a field-readable leg flag inscribed with a unique alpha-numeric code. Before release each bird was weighed, measured (i.e., wing chord, culmen length, and combined head/bill length), and aged as a hatch year (HY) or after hatch year (AHY). Banding protocols were sanctioned under the University of Florida IFAS Animal Research Committee, protocol number 004-08SNR and US Fish and

Wildlife Service Banding Permit 21980. Marked birds were resighted in both a structured and an opportunistic fashion. I conducted resighting efforts following a pre-determined schedule during the winters of 2007-2010 in the greater Tampa Bay region. Additionally I obtained data from other organized resighting efforts both within and outside of Florida as well as opportunistic sightings by the general birding public (Figure 2-1). I obtained these data through the bandedbirds.org database.

Data Analysis

I modeled age-specific survival using the Barker model in Program MARK (Barker 1997, White and Burnham 1999). This modeling framework uses encounter histories from multiple sources, particularly from sampling units that are greater than the primary sampling unit (e.g., peninsular Florida). In this study, the secondary sampling unit encompassed primarily the Atlantic coast (Figure 2-1). I constructed encounter histories for 1,348 individual Red Knots marked in the primary sampling area and resighted in the primary and/or secondary sampling area. Resightings predominantly came from Delaware, New Jersey and Georgia, although birds were also seen in Virginia, Massachusetts, North Carolina, Ontario (Canada).

Use of this data structure (i.e. multiple data sources with nested primary and secondary sampling units) with the Barker model permits estimation of true survival, the complement of which includes only deaths. This stands in contrast to the traditional mark-resight (recaptures only) analyses used in most shorebird studies (e.g., Fernandez et al. 2003, Rice et al. 2007) that produce estimates of apparent survival, the complement of which includes both deaths and permanent emigration from the sampled areas. Estimates of apparent survival in these traditional analyses are biased low when taken as estimates of true survival because they combine survival and fidelity.

I selected this analytical framework, as opposed to a multi-state framework, because the Barker model focuses on survival while allowing for the testing of a variety of emigration patterns. The use of a multi-state model gives state-specific survival (e.g., survival for each major sampling location, including FL), but also requires estimates of state-specific (specific to each location) detection probabilities and transition probabilities to other locations. In addition, because of the temporal asymmetry in sampling (e.g., Delaware Bay sampled at later time than Florida), the multistate approach would need seasonal survival probabilities for the periods that separated these different sampling periods/places. I felt that estimation of these additional parameters were not germane to my main objective, estimation of annual survival, and could probably introduce undue complexity and precision problems.

I defined adult and juvenile annual survival as the probability that a bird of either age class banded in Florida between October and March of a given winter i was present in either the primary (peninsular Florida) or secondary sampling area (Atlantic seaboard) during year $i+1$ (Barker 1997). Juvenile survival in this work refers to the probability that a wintering juvenile will survive to the next winter. I used the notation HY_{FL} to distinguish survival during this period from true juvenile survival, estimated from the time of hatching or fledging.

Barker models estimate 7 parameters (Barker 1997). Of relevance to this study were survival (S_i ; the probability an animal alive at i is alive at $i+1$), recapture (or in this study, resight) probability (p_i ; the probability an animal at risk of capture at i is captured at i), and two parameters that relate to movement: F_i (the probability an animal at risk of capture at i is at risk of capture at $i+1$) and F' (the probability an animal not at risk of

capture at i is at risk of capture at $i+1$). These parameters concern the probability of being exposed to sampling efforts in the primary study area (e.g., peninsular Florida) depending on location during winter the previous year. Parameter r_i is the probability an animal that dies in i , $i+1$ is found dead and the band reported) and R_i' is the probability an animal that dies in i , $i+1$ without being found dead is resighted alive in i , $i+1$ before it died. Several parameters were fixed ($r_i = 0$, $R_i' = 0$, $F'_{HY} = 0$) because they were not interpretable or necessary in our analysis because data consisted of only live birds (W. Kendall; Colorado State University; R. Barker, University of Otago, New Zealand, pers. comm.). F'_{HY} was fixed because HY_{FL} become AHY and there were no birds marked outside the primary study area to estimate the transition between sampling units. The remaining parameter, R_i , that a marked animal that survives from i to $i+1$ is resighted alive at some time between i and $i+1$.

I created a candidate set of 14 models to evaluate evidence in the data for constant or time-specific survival rates, detection rates, and movement rates for HY_{FL} (hatching year at Florida) and AHY (after hatching year). The standard parameterization in MARK for movement is Markovian (no constraint), that is, the availability of a knot to be captured is conditioned on the state (available or not) during the previous occasion. However, I included two other parameterizations in the candidate set to assess their support in the data and influence on parameter estimates. These tested for random movements between sampling units ($F_i' = F_i$) and permanent emigration ($F_i' = 0$). I applied these tests to the model with the highest Markov support. Parameters \pm SE are reported.

Careful consideration of assumptions is important to interpret results. As indicated before, I assumed that annual survival estimates reported by McGowan et al. (2011) represented rates of the *rufa* populations wintering in South America based on their representation at Delaware Bay (i.e., 90-95%; Niles 2008a). We also assumed that survival rates obtained at Florida (wintering grounds) and at Delaware Bay (stopover) had similar biological interpretation as they represent estimates based on a complete annual cycle. Finally, the Barker model makes three assumptions. It assumes that every color-marked bird had the same probability of being resighted in sampling period i given that it was present in the population at the time the survey was conducted and that every marked bird present at the primary sampling area in year i had the same probability of being present on the primary sampling area in sampling period $i+1$. Second, marks (i.e., color bands) were not lost and that color bands were correctly recorded. Third, the reporting rate of marks of dead animals depends only on the stratum in which the animal was during the immediately preceding live observation. The second assumption was met as banding techniques and color schemes have long history of use and dependability. Meeting the third assumption was not necessary because data in this study did not include dead recoveries. Assumptions about emigration were tested using three movement parameterizations (i.e., permanent, random, Markov; Barker 1997). There was no evidence for permanent emigration, but not all birds had the same probability of returning to the primary sampling area (Florida) annually (assumption 1). Moreover, I cannot claim that every bird in peninsular Florida and elsewhere had equal probability of being captured (resighted). Thus, I used the

median \hat{c} procedure in MARK to estimate a variance inflation factor to adjust for possible assumption violations.

I used Akaike's Information Criterion to select the most parsimonious model (Burnham and Anderson 2002). Due to the use of the median \hat{c} procedure, models were ranked by QAICc, instead of AICc, where the model with the minimum QAICc was the model with the most support in the data. The difference in QAICc units between the best supported model and any other model (ΔQAICc) was used to calculate model weights (QAICc w_i), which indicate the relative likelihood of the model given the data (Burnham and Anderson 2002). Models with $\Delta\text{QAICc} \leq 2$ were considered models with highest support.

Finally, I compared average body mass (gr) of knots captured in Florida with reported values for knots captured in South America during December-January (core of winter) and late February-early March (spring). Birds in Florida were captured in 2005, 2006, 2008 and 2009; those from South America were captured between 2000-2005 (Niles et al. 2006, Baker et al. 2005). Averages from South America were adjusted for sex, molt pattern (complete or not), culmen (35 mm) and season (winter and spring). While I was unable to sex Florida individuals due to lack of molecular data, tests were restricted to birds that had completed molt, had a culmen of 35-35.9 mm, and were captured either in winter or spring. Comparisons consisted of one-sample t-tests, because standard errors for South American birds were not reported in the literature. Accordingly, I treated the average body mass from South America as the hypothesized value (μ) and asked whether the body mass from the sample of birds captured in Florida came from a bird population with the hypothesized mean value. I used a grand mean \pm

SE (all years) for the Florida estimates. This was done to incorporate annual variation given that hypothesized means came from data collected in different years. Tests were 2-tailed, favoring a more conservative test (non-directional). Test significance was set at $\alpha = 0.05$.

Results

Model selection was adjusted for overdispersion; median $\hat{c} = 1.29$. Survival of adults and juveniles banded in Florida (HY_{FL}) was best explained by a model that featured constant survival for juveniles banded in Florida (HY_{FL}), time-specific survival for adults (AHY), time-specific detection probability, and age-specific movement probability (Table 2-1). There was additional support for two other models. One included permanent emigration instead of an age-specific movement probability (QAICc $w_i = 0.19$) and the other featured the same model terms as the top model except that it supported the inclusion of time-specific survival rates for both adults and juveniles marked in Florida (QAICc $w_i = 0.15$).

I will focus on the model with highest support (QAICc_{*w_i*} = 0.62) to summarize parameter estimates and subsequent discussion of results. Under this model, annual adult survival rates varied between 0.85 ± 0.02 and 0.94 ± 0.03 (Table 2-2), for an average survival rate of 0.91 ± 0.01 over 5 years. Survival rate for juveniles marked in Florida was 0.94 ± 0.06 . Capture probability varied between 0.50 ± 0.05 and 0.99 ± 0.07 . The probability of birds banded as juveniles in Florida to return as adults was 0.70 ± 0.08 . Similarly, the probability for adults captured in peninsular Florida to return the following year was 0.81 ± 0.05 . The probability of adults moving into peninsular Florida, given that they were outside peninsular Florida the year before was 0.22 ± 0.08 (Table 2-2).

Average, size-adjusted body mass (g) for Florida and South American birds are summarized in Table 2-3. Florida birds averaged 128.8 ± 0.79 g during winter and 120.3 ± 1.26 g during spring. Average, size-adjusted body mass of Florida birds was significantly higher than average values reported for South America ($P < 0.001$) with the exception of birds captured in Chile. Body mass from Florida birds could have come from a population with a mean of 128.5 g ($P > 0.05$, Table 2-3).

Discussion

The 5-year average survival estimate for knots wintering in Florida was 0.91 ± 0.01 . The 95% confidence intervals of this estimate encompassed the survival rates reported for two body mass groups for Delaware Bay from 1997 to 2007 (McGowan et al. 2011). Survival rates of heavy (≥ 180 g) and light (<180 g) birds were 0.92 and 0.91, respectively. Similarities between rates also existed for the period of overlap between studies. Between 2005 and 2007, survival for heavy birds in Delaware Bay ranged between 0.91 and 0.92, and between 0.87 and 0.90 for light birds. Florida estimates varied between 0.86 and 0.94 during those years. Admittedly, the presence of knots from Florida in Delaware Bay may have contributed to similarities. This possibility leads to two possible interpretations, albeit both coincident with our fundamental inference. Either annual survival rates of Florida knots came from a distribution of rates represented by knots at Delaware Bay (predominantly from South America) or they did not, in which case they still experienced similar survival rates to birds wintering elsewhere.

The application of the Barker framework was particularly insightful in that it provided estimates of fidelity, which were quite high (0.70-0.81). Conversely, there is a portion of *rufa* that does not return to Florida in any given year. Accounting for these

patterns of emigration and fidelity is one reason why my estimates were, on average, higher than the 0.84 reported previously for the overall *rufa* population (Baker et al 2004). I cannot claim, however, that my estimates are completely unbiased because some birds might have still occurred in areas the network of observers or I did not sample.

The annual survival rate of juveniles banded in Florida (HY_{FL}) was 0.94. The high rates of survival could be accounted by the fact that my estimate does not include the portion of the juvenile annual cycle associated with highest levels of mortality (Martin 1995, Oppel and Powell 2010). Banding takes place in winter after this period of high mortality has already passed. High rates could also be explained by the possibility that knots often do not breed until their second adult year, many skipping migration to and from the breeding grounds during their first adult year or exhibiting only partial migration. Thus, juveniles banded in Florida could also exhibit high survival rates by avoiding the risks of migration during their first year of adult life.

Florida birds were equal to and often significantly heavier than their South American counterparts sampled at various locations across their wintering grounds. Florida birds on average are morphometrically larger than Chilean or Argentine birds and overlap in size with the Brazilian population (Niles et al. 2008b). However I accounted for this by comparing birds of similar size based on culmen measurements (~35 mm), molt and season (Baker et al. 2005, Niles et al. 2006).

Comparisons of adult survival estimates and wintering weight estimates among Florida and South American birds point towards two important conclusions. First, Florida knots did not have a lower annual survival than birds wintering in South

America. If there is a tradeoff(s) between staying in Florida and migrating to South America, it does not seem to be at the annual survival parameter level. Second, given that body mass can exert an influence on survival and reflect the physiologic state of the individual (sensu McGowan et al. 2011), then Florida birds were not at a disadvantage relative to birds wintering in South America.

All together my results suggest that decline in population numbers in Florida is not a uniquely local phenomenon, although some variation in annual survival has to have a local component. Adult survival rates and those of juveniles banded in Florida (HY_{FL}) are reasonably high, making it unlikely that direct mortality during migration or on the breeding grounds are the main causes of declines (Baker et al 2004). The question then becomes what are plausible mechanisms that could explain population declines in Florida and elsewhere for *rufa* over the last twenty years? One possibility is that declines are linked to a process(es) or cause(s) that may impinge the subspecies across portions where their populations overlap. Recently, increasing attention has been given to two other vital parameters: breeding productivity and recruitment rates. McGowan et al. (2011) found that adult survival is positively influenced by annual snow cover on the breeding grounds. These researchers suggested that higher levels of snowfall provide the moisture needed in this water-limited system for sufficient production of insects (Noy-Meir 1973), the knots' main food source on the breeding grounds. Depressed food levels might reduce fecundity either by precluding birds from breeding or producing low fledging rates (McGowan et al. 2011). Unfortunately, researchers have been unable to obtain reliable estimates of fecundity and recruitment for *rufa*, largely because breeding grounds occur in remote locations and over a vast

landscape. Thus researchers have resorted to using fecundity estimates from the *islandica* subspecies for current models.

Insights about the importance of parameters that comprise fecundity might be gained if the ratio of juveniles (HY) to adults (AHY) in wintering grounds was a suitable index of breeding productivity. Although timing of migration for juveniles and adults differs, it appears that juveniles and adults share the same wintering grounds in Florida. The value of the index would also depend on meeting the assumption that juvenile and adult capture probability is similar (Bart et al. 1999). Here I assumed that the ratio was a suitable index and used it to explore the importance of fecundity with a heuristic, deterministic model. I did so by calculating the predicted population change (positive or negative) of a population of 10,000 individuals (or the estimated Red Knot population in Florida during the mid-1980s) based on the percentage of juveniles in the population of 1% to 13%, at 0.5% increments. This range was derived from empirical estimates of the percent of juveniles in catches over the past 5 years, which ranged from 1.65 to 13.86, for an average of 7.34. Population response was modeled with the model presented below. I used my estimates of adult and juvenile (HY_{FL}) survival. The use of HY_{FL} assumed that the observed age ratio reflected mortality rates from the time of fledging to arrival in Florida.

$$\text{Population in year } t+1 = ((\text{pop in year } t \times \% \text{ adults} \times \text{adult survival}) + (\text{pop in year } t \times \% \text{ juveniles} \times HY_{FL} \text{ survival})) / \% \text{ adults}$$

A population containing 2-3% juveniles (HY/AHY) closely matched the actual declines observed in the Florida population. Even the observed average of ~ 7% produced a decline, albeit of less severe proportions. The population became stable at

~8.75% and increased at the highest observed level of 13% (Figure 2-2). This exercise, while heuristic, was useful in demonstrating that observed declines could be reproduced with low juvenile percentages in light of my estimates of survival for adults and HY_{FL} . I also ran simulations under another scenario. On a second set of simulations, I used the 0.84 adult survival rates previously reported by Baker et al. (2004). Results strongly suggested that at that rate of survival, and even using plausible but biologically high fecundity and juvenile recruitment rates, population declines would have been much sharper and would not conform to the magnitude of observed decline. Thus, these simulations hint at the possibility that the demographic basis of observed declines may indeed include a strong fecundity component.

I also used annual estimates of survival to gain insights about the migration strategies exhibited by subpopulations of *rufa* staying in Florida or going further to South America. Myers et al. (1986) advanced several hypotheses aimed at assessing why sub-populations of Sanderlings (*Calidris alba*) exhibited a similar situation, including higher numbers wintering in South America. These were: a) milder climatological conditions further south resulting in lower physiological stress, b) lower predation rates on far-south wintering grounds, c) resource availability is higher on southern wintering grounds, and d) resources are more stable further south providing greater predictability. Of these, Myers et al. suggested that availability and/or the predictability of food resources were stronger determinants of the distribution of wintering Sanderlings. Put in another way, fewer Sanderlings occurred on northern shores (e.g., California) because the food resources did not exist to support a larger population. Admittedly,

Myers et al. were not able to completely discount the possibility that the threat of predation also played a role in influencing the observed distribution of Sanderlings.

Red Knots resemble Sanderlings in very important ways and my estimates of annual survival provided a basis for reasonable speculation. First, similar survival estimates between birds wintering in Florida and the population converging in Delaware Bay lends support to one of Myers' contentions. That is, ecological conditions, not annual survival constraints, were stronger determinants of the differing migratory strategies of knots. Moreover, as they contended for Sanderlings, the availability of food resources likely played a strong role in influencing numbers of knots across its wintering range. While direct comparisons of food availability among wintering locations are not currently possible, reports from South America (Harrington 2001) and Florida (Appendix A, Chapter 3) suggest that prey items sought by knots, particularly the clam *Donax*, are more abundant in southern South America during the core of winter (December-February). Certainly, the core winter months have the lowest availability of prey items for *rufa* in Florida (Appendix A). Anecdotal evidence suggests that predation by avian predators may be higher in South America than in Florida (L. Niles, pers. comm.), but research is needed before discarding this competing hypothesis. It is interesting to note that Florida and Brazilian birds are morphometrically larger than the Tierra del Fuego birds. This may allow these populations to stay further north for one of two reasons. One is that larger birds may be more adept at competing for scarce food resources and therefore able to dominate northern beaches, where presumably food resources are scarcer (Ketterson and Nolan 1976). Another is that a larger body size may allow birds to persevere under physiologically demanding conditions, either due to

lower food resources or more variable weather patterns (Ketterson and Nolan 1976, Belthoff and Gauthreaux 1991). Sex ratio differences between populations are likely not an influence on average size for a given population since previous studies have found that the Florida and South American populations have a sex ratio of roughly 50:50 (Niles et al. 2006).

I assessed the status of knots in Florida using a broad geographic framework and two metrics, annual survival rates and body condition. Results suggested that knots wintering in Florida were not at a disadvantage when compared to the rest of the hemispheric population. Rather my results suggested that the underlying factors behind observed population declines are affecting the whole population, likely in stages of their annual cycle where all segments of the population could be similarly influenced. This possibility advocates for obtaining, for example, reliable estimates of fecundity and the early trajectory of juvenile survival (i.e., fledging to wintering grounds). Efforts to decouple annual survival rates across the species' annual cycle would facilitate a more complete demographic and vulnerability assessment of the species. Such data gain added importance in the advent of climate change and exploration of the knots' ability to adapt to this change.

Table 2-1. Model selection for annual survival for adult and juvenile Red Knots banded in Florida from 2005-2010.

Model	QAICc	Δ QAICc	QAICc Weights	Model Likelihood	Num. Par	QDeviance
{S(HY(.), AHY*t), p(t), r(=0), R(.), R'(=0), F(age), F'(HY(=0), AHY) PIM}	5695.16	0.00	0.62	1.00	13.00	650.73
{S(HY(.), AHY*t), p(t), r(=0), R(.), R'(=0), F, F'=0 (permanent emigration)}	5697.49	2.33	0.19	0.31	12.00	655.08
{S(age*t), p(t), r(=0), R(.), R'(=0), F(age), F'(HY(=0), AHY) PIM}	5697.95	2.79	0.15	0.25	16.00	647.46
{S(HY(.), AHY(t), p(t), r(=0), R(.), R'(=0), F(HY(.), AHY(t)) F'(HY(=0), AHY(t))}	5701.14	5.98	0.03	0.05	18.00	646.61
{S(age), p(t), r(=0), R(.), R'(=0), F(age), F'(HY(=0), AHY (.))}	5719.51	24.35	0	0	10.00	681.13
{S(age), p(age*t), r(=0), R(.), R'(=0), F(age), F'(HY (=0), AHY (.))}	5725.07	29.91	0	0	13.00	680.64
{S(HY(.), AHY*t), p(.), r(=0), R(.), R'(=0), F(age), F'(HY (=0), AHY (.))}	5769.43	74.27	0	0	10.00	731.05
{S(HY(.), AHY*t), p(t), r(=0), R(.), R'(=0), F=F'} (random movement)}	5781.10	85.94	0	0	12.00	738.69
{S(HY*t, A=(.)), p(.), r(=0), R(.), R'(=0), F(age), F'(HY (=0), AHY (.))}	5803.37	108.21	0	0	9.00	767.00
{S(HY (.), AHY (.)), p(.), r (=0), R (.), R' (=0), F (HY (.), AHY (.)), F' (HY= 0, AHY (.))}	5803.86	108.70	0	0	9.00	767.50
{S(HY(.), AHY*t), p(t), r(=0), R(.), R'(=0), F(age), F'(HY=0, AHY) PIM}	7337.17	1642.01	0	0	12.00	650.73
{S(age*t), p(t), r(=0), R(.), R'(=0), F(age), F'(HY=0, AHY) PIM}	7339.00	1643.84	0	0	15.00	647.46
{S(HY(.), AHY(t)), p(t), r(=0), R(.), R'(=0), F(HY(.), AHY(t)) F'(HY(=0), AHY(t))}	7341.94	1646.78	0	0	17.00	646.61
{S(age), p(age*t), r(=0), R(.), R'(=0), F(age), F'(HY (=0), AHY (.))}	7377.49	1682.33	0	0	13.00	680.43

Model parameters were: S = survival probability from period i to $i+1$, p = capture probability, r = probability of dead encounters (fixed to zero in these models since data only relied on live encounters), R = probability of live encounters outside the study area, R' = probability of dead encounters outside the study area (also fixed to zero), F = probability that a bird banded in the study area will remain in the area in the next period, F' = probability that a bird seen outside the primary study will return to the study area, t = variation over time. Lower QAICc weight indicates better support for a model.

Table 2-2. Parameter estimates from the top model {S(HY(.), AHY*t) p(t) r(=0) R(.) R'(=0) F(age) F'(HY(=0), AHY) PIM} listed in Table 2-1.

Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI
Juvenile survival for 2005-2010	0.9462	0.067674	0.564754	0.995829
Adult survival (2005-2006)	0.9368	0.031946	0.837347	0.977115
Adult survival (2006-2007)	0.8597	0.023143	0.80803	0.899328
Adult survival (2007-2008)	0.9166	0.024765	0.853536	0.954077
Adult survival (2008-2009)	0.8796	0.024143	0.823766	0.91953
p (2005-2006)	0.4981	0.051233	0.399121	0.597298
p (2006-2007)	0.6881	0.039864	0.605291	0.760568
p (2007-2008)	0.6962	0.039726	0.61336	0.768141
p (2008-2009)	0.9980	8	1	1.000000
R	0	0	0	0
R	0.3181	0.01105	0.296863	0.340158
R'	0	0	0	0
Juvenile F	0.6996	0.082881	0.518136	0.834607
Adult F	0.8083	0.02381	0.757283	0.85071
Juvenile F'	0	0	0	0
Adult F'	0.2218	0.059403	0.126782	0.358785

Model parameters were: S = survival from time t to t+1, p = capture probability, r = probability of dead encounters (fixed to zero in these models since data only relied on live encounters), R = probability of live encounters outside the study area, R' = probability of dead encounters outside the study area (also fixed to zero), F = probability that a bird banded in the study area will remain in the area in the next period (fidelity), F' = probability that a bird seen outside the primary study will return to the study area. S for 2009-2010 was not estimable. F' for juveniles was fixed (=0) because juveniles become adults in year t+1 and none were not banded in the secondary sampling area. All birds were banded while wintering in Florida.

Table 2-3. Comparison of seasonal averages of weights for Florida birds with South American estimates reported in the literature.

Winter Florida Average: 128.8g +/- 0.795 SE (n = 121)							
Location	Year	Season	Mean (g)	Sample Size	Complete molt	p-value	Source
Argentina	2000	winter	124.5	441	Na	<.0001*	Baker et al. 2005
Argentina	2001	winter	124	447	Na	<.0001*	Baker et al. 2005
Argentina	2002	winter	121.5	250	Na	<.0001*	Baker et al. 2005
Argentina	2003	winter	124	137	Na	<.0001*	Baker et al. 2005
Argentina	2004	winter	120	94	No	<.0001*	Baker et al. 2005
Chile	2005-2006	winter	128.5	102	Yes	0.698	Niles et al. 2006
Spring Florida Average: 120.3 g +/- 1.265 SE (n = 36)							
Brazil	2004-2005	spring	114	38	Yes	<.0001*	Baker et al. 2005

Florida averages derived from birds with complete molt and culmen length of 35.0-35.9 mm. Winter (Dec-Jan) Florida averages include data from 2005-2006, 2006-2007, 2008-2009, and 2009-2010. Early spring averages include data from 2008-2009 and 2009-2010. Birds from winter 2007-2008 were excluded because molt data were unavailable. All South American estimates are model predictions for birds with a culmen length of 35.0-35.1 mm. Contrasts were made with one-sample t-tests.

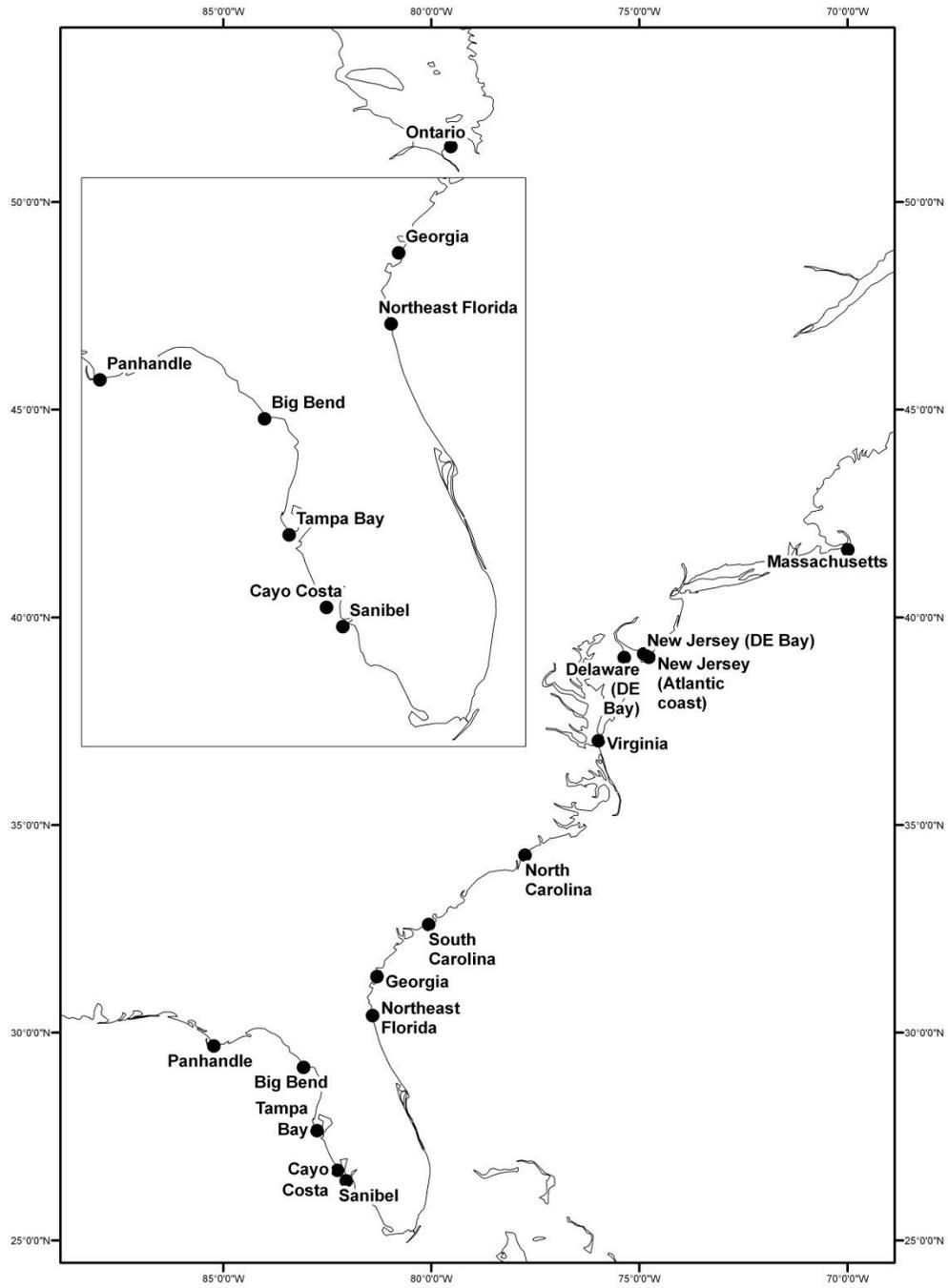


Figure 2-1. Map showing main Florida banding and resighting locations within the primary study area (inset map), as well as the major resighting locations in the secondary study area (main map).

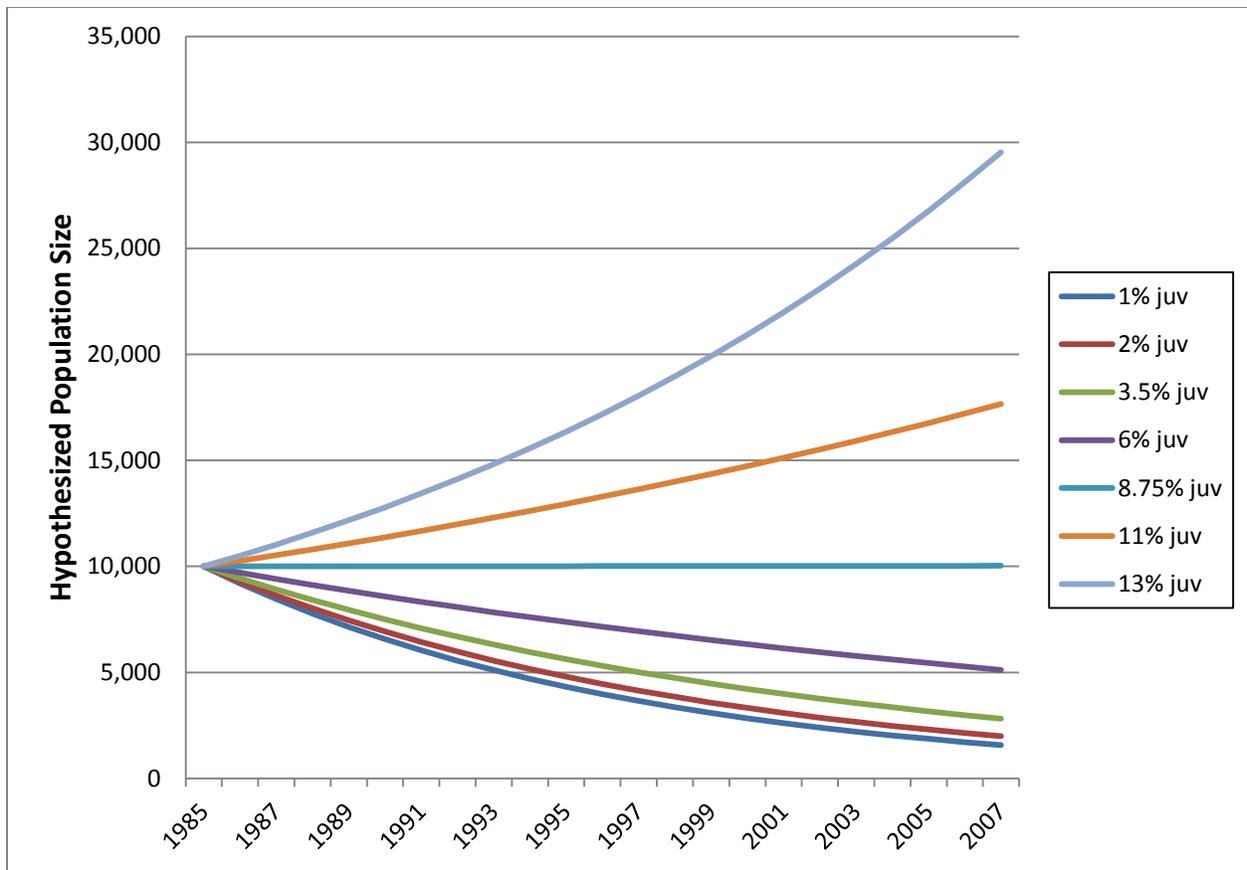


Figure 2-2. Red knot population trends predicted by heuristic model based on percentage of hatch year birds seen within wintering population and differential survival of hatch year (0.94) and adult birds (0.91). Starting population of 10,000 was based on estimates from surveys conducted in the mid-1980's.

CHAPTER 3 LOCAL SURVIVAL, MOVEMENT RATES, AND PLASMA METABOLITES OF RED KNOTS WINTERING IN THE TAMPA BAY REGION

Over the past ten years the Red Knot (*Calidris canutus*) has been the focus of intense interest by researchers across the globe. This shorebird species is a long-distance migrant and in Europe has been frequently used for studies regarding migratory strategies and migration-related physiology (e.g., Piersma 2007, van Gils and Piersma 2004, van Gils et al. 2005a and 2005b). Many studies within the Americas have been more conservation focused, developed to explain the decline in numbers of the *rufa* subspecies seen at winter and migratory stopover sites over the past 30 years (e.g., Morrison et al. 2004, Baker et al. 2004, Karpanty et al. 2006, Atkinson et al. 2007, Niles et al. 2009). However, much of this research has ignored the *rufa* population that winters in the southeastern United States, instead placing emphasis on the population wintering in South America (particularly in Argentina and Chile).

Florida is home to the largest concentration of wintering *rufa* knots in the United States. The main concentration of knots on the southwest Florida coast is found in the greater Tampa Bay region. Aerial surveys conducted during 1980-1982 estimated approximately 6,500-10,000 wintering knots from Cape Romano in the south to Anclote Key in the north (Harrington et al. 1988, Morrison and Harrington 1992). Aerial surveys conducted over the past five years suggested that this population had dwindled to approximately 1,000-2,500 knots (Niles et al. 2008c). This decline has emphasized the importance of information that may help highlight threats and pressures facing these birds during their stay in Florida.

I combined trapping and resighting data with sampling of the intertidal invertebrate community to augment our understanding of the winter dynamics of knots in the Tampa

Bay region. Specifically, I estimated local daily survival probability for the Tampa Bay region. I also estimated local daily survival probability and movement probabilities among three areas (states) known to harbor wintering knots in the greater Tampa Bay region. I used residency rates to gauge the strength and duration (mean length of stay) with which birds used areas over winter, and assessed evidence in the data in support of hypothesized influence of a body-mass index and prey levels on residency rates. High residency rates are associated with areas where shorebirds meet energetic requirements (Alerstam and Lindstrom 1990, Lyons and Haig 1995, Rice et al. 2007). I also determined the extent of exchange or movement between the three traditionally used areas in the region by wintering knots. Beach habitats are linear and do not present obvious barriers that might curtail connectivity. However, wintering knots in Florida encounter higher levels of coastal development and anthropogenic disturbance. A greater understanding of the extent of movement and how distance might impinge on it is of value to conservation planners. The ability or willingness of individuals to move among areas can provide wintering knots the means to access alternative foraging areas, ameliorate predation risks, and avoid or minimize anthropogenic disturbance (Farmer and Parent 1997, Skagen 1997, Belisle 2005).

I also assessed plasma metabolites to quantify the physiological state of knots as a means to explore further the condition of knots wintering in Florida. Body mass has been used in many studies of Red Knots as to assess body condition and energetic state in knots (e.g., Baker et al. 2004, Niles et al. 2006, Atkinson et al. 2007) and, more recently, to examine the implications of different body mass levels on survival (McGowan et al. 2011). By this standard I demonstrated that knots wintering in Florida

are in similar or better condition than their South American counterparts (Chapter 2). However, body mass estimates only represent a point estimate, often derived from capturing an individual once in a season (Fernandez et al. 2003, Dinsmore and Collazo 2003, Rice et al. 2007) and the energetic trajectory of the individual is not clear. It is possible, for example, that heavier birds may be physiologically stressed and burning energy, while lighter birds may be rapidly assimilating energy sources. Plasma metabolites provide insights into the short-term (2-5 days) energetic path of knots post-capture (Cersale and Guglielmo 2006, Guglielmo et al. 2005, Williams et al. 1999). Here I report levels of three metabolites collected from birds during three periods over the wintering season and asked if there was any evidence that birds were on a path to a positive or negative energy balance. Samples were collected in late October/early November, early January, and late February/early March, spanning the core of winter in southwestern Florida. As a reference and large scale context in the knots' annual cycle, I also report metabolite levels at Delaware Bay where birds are building up fat reserves to complete the last leg of their migration to the breeding grounds and assist with the onset of reproduction (McGowan et al. 2011). Finally, I discuss the conservation implications of my findings for knots wintering in Florida.

Methods

Study Area

The Tampa Bay region (Figure 3-1) along the Gulf Coast of Florida encompasses ~74 linear kilometers of ocean-side beaches. These beaches are predominantly composed of fine-grained sand, face the Gulf of Mexico, and are generally subject to low-energy wave action and small tidal amplitude (~0.25-0.75 m). Only two locations, Gulfport and Shell Key, contain broad tidally-exposed sand or mud flats that were also

regularly surveyed. The locations represent a wide range of human activity, including the highly developed, tourist rich Clearwater Beach to the less developed, private beaches of Longboat Key to the multi-use publicly owned preserves of Ft. De Soto County Park and Shell Key Preserve. In this study I grouped all data for analyses into three sub-regions of roughly equal extent: 1) Indian Shores which included all territory from Clearwater Beach to Madeira Beach and Gulfport, 2) Anna Maria which included Shell Key Preserve, Ft De Soto County Park and Anna Maria Island, 3) and Longboat which included Longboat and Lido Keys (Figure 3-1). I used these three areas as state variables in the multi-state models.

Capture Methods

I trapped knots during four periods during winter 2008-2009 and 2009-2010. The periods were late October/early November, early January, late February/early March and mid-April. I spaced trapping efforts to establish weight and plasma metabolite profiles for the Tampa Bay population while minimizing trap stress on the birds. Birds were trapped using a cannon-net array consisting of two cannons and an 8 x 25 m net specifically for shorebird trapping. I trapped opportunistically on beaches where birds were present and in catchable conditions. Catchable conditions were defined as the time when beach topography allowed sufficient access and area to set up equipment without forcing birds from the beach. I distributed capture locations throughout the region each period to capture variation among beaches. Upon capture, each knot was banded with a standard Incoloy U.S. Fish and Wildlife Service band and marked each with a field-readable leg flag inscribed with a unique alpha-numeric code. Before release each bird was weighed, measured (i.e., wing chord, culmen length, and combined head/bill length), and aged as a hatch year (HY) or after hatch year (AHY).

I collected blood from a subset of birds at each capture. Samples were collected from up to 30 individuals. All birds were processed within 30 minutes of the time of initial capture to minimize the possibility that stress altered plasma metabolite levels (Guglielmo et al. 2002, Dietz et al. 2009). I bled birds following the standard method of piercing the brachial vein and collecting blood in one or two 70 μ l heparinized capillary tubes. I used cotton swabs and applied pressure to stop bleeding and held birds for approximately two minutes to assure bleeding had stopped. I kept the blood chilled on ice. Each night I spun the blood to separate the plasma using a centrifuge set at 3000 rpm for ten minutes. I then transferred the plasma into micro-centrifuge tubes and stored it at -80° F until lab analysis. All birds were banded under a US Fish and Wildlife Service Bird Banding permit held by the Florida Fish and Wildlife Conservation Commission, and the capture, handling, and blood-sampling protocols were approved by the University of Florida IFAS Animal Research Committee permit 004-08SNR.

Resighting Methods

I surveyed all beaches for marked birds at the following locations: Clearwater Beach to Madeira Beach (including Indian Shores), Gulfport, Shell Key Preserve, Fort De Soto County Park, Anna Maria Island, Longboat Key and Lido Key (Figure 3.1). Surveys occurred during October to mid-May of winter 2008-2009 and 2009-2010. There were 17 total survey periods and time intervals between surveys were 69, 14, 14, 10, 7, 7, 7, 7, 7, 7, 7, 7, 7, 8, 6, 10, and 3 days, respectively. During each survey I would cover all locations within the study area within a consecutive 3-day period. I scanned all beaches for the presence of Red Knots. If knots were located, a second observer (if present) and I recorded general data including start time, weather conditions, number of

knots present, number of knots banded, knot activity (e.g., foraging, roosting), tide stage, and estimated numbers of other bird species present. After recording general information, I scanned flocks using a spotting scope (Vortex Skyline 80mm with 20-60x zoom or Kowa TSN 660 with 20-60x zoom). I recorded all band and flag code information on individuals within the flock. I scanned the flock multiple times and if possible from several angles to maximize the leg flags detected. When two complete scans produced no new flags for either observer, we ended the scanning session and recorded the end time.

Invertebrate Sampling Methods

I sampled for invertebrates at Ft. De Soto, Shell Key, Lido Key, Longboat Key and Indian Shores in 2010. I selected these locations based on the consistent presence of foraging Red Knots in previous years. I established two reference transects at each of the five locations. Each transect consisted of a fixed starting point, with four points total spaced ten meters apart. Transects were placed randomly along selected beaches and were at least 200 m apart. I sampled both transects weekly at each location starting the third week of January. I sampled in the surf zone, parallel to the waterline. At each point I collected sediment cores 5 cm deep and 10 cm in diameter and stored them in a lock-seal plastic bag for future analysis. After sample collection, I sieved each sample with a 1mm wide mesh sieve. I collected, identified to family (or genus if possible) and counted each invertebrate in the sample. I measured common invertebrates in order to create an index of biomass.

Plasma Metabolite Laboratory Analysis Methods

I analyzed plasma samples at the facilities of Dr. Chris Guglielmo at the University of Western Ontario. I assayed lipid metabolites in a microplate spectrophotometer. I

measured total triglyceride and free glycerol sequentially by endpoint assay (Sigma-Aldrich glycerol reagents A and B; Williams et al. 1999). True triglyceride concentration was calculated by subtracting glycerol from total triglyceride. β -OH butyrate was measured by kinetic assay (R-Biopharm β -OH butyrate kit and Stanbio standards; Williams et al. 1999). I chose these metabolites because they are easily measured and have a strong relationship with the rate of change in fat levels (Guglielmo et al. 2005, Williams et al. 1999). Triglyceride is a product of fat production and β -OH butyrate and glycerol are products of fat metabolization. Comparison of the three indicates whether a bird is actively laying down fat, maintaining current conditions, or burning fat (Guglielmo et al. 2005).

Data Analysis

Residency and movement rates

I used two types of modeling frameworks in program MARK (White and Burnham 1999) to estimate residency and movement rates. I used the “recaptures only” model in program MARK (White and Burnham 1999) to estimate residency rates for the Tampa Bay Region. Residency rates (\hat{S}) were defined as the probability that a knot, banded in the Tampa Bay Region on day i , remained in the area until day $i+1$. I examined 18 models of residency and recapture rates, which included the four basic models (i.e., constant and time-specific residency and recapture rates). Daily residency probabilities were calculated to account for unequal time-interval length between capture periods. The daily probability is the n th root of the period’s residency probability, where n is the number of days in the interval. Shorebird mean length of stay (MLS), expressed in

days, was estimated using the mean life expectancy equation derived by Brownie et al. (1985): $MLS = -1/\ln(\text{daily residency probability})$.

In addition, I used a multi-state analytical framework to estimate daily survival and transition probabilities within the Tampa Bay Region (Kendall and Nichols 2004).

Residency rates (\hat{S}) were defined as the probability that a knot, banded at state j on day i , remained at state j to day $i+1$. Movement rates (Ψ , $\hat{\psi}$) were defined as the probability that a knot, banded in state j on day i , moved to another state on day $i+1$. States in the model were: Indian Shores (I), Anna Maria (A), and Longboat (L). The extent of each state is provided in the study area section above. I examined 10 models of residency and recapture rates, which included basic models (i.e., constant and time-specific residency, recapture and movement rates). Both model sets included year effects (2009, 2010; code=g), seasonal terms (i.e., linear or quadratic) and a body-mass index as an individual covariate. Multi-state models included two additional covariates (i.e., distance, prey density) and interaction terms. Below I describe all model terms and covariates, and when appropriate, I provide the hypothesized influence of the covariate on residency or movement rates. Unless indicated, covariates were modeled as additive factors.

Body Mass Index – This index is a size-adjusted value (BMI) calculated as body mass divided by culmen length of the individual used in the two model sets. In the knot literature body mass is often used as a proxy of body condition or health of the individual (e.g., Baker et al. 2004, Niles et al. 2008b). Adjusting for size allowed us to use all birds across sites. I hypothesized that residency rates should be positively influenced by BMI as birds in good body condition would chose to remain to exploit

resources and minimize unnecessary risks accrued with movements (Alerstam and Lindstrom 1990, Taft and Haig 2006a, b).

Seasonal Variation – I evaluated evidence for seasonal patterns in daily survival probability using two terms, a linear (T) and quadratic trend (TT). Previous studies have shown that a variety of factors, such as timing of arrival or departure from Florida, may cause variation in daily survival probability (e.g., Dinsmore and Collazo 2003).

Inter-State Distance – This covariate was defined as the nearest neighbor distance from the perimeter of each sampling or beach state as defined in the study area section to the closest point of a neighboring sampling state. I used Google Earth to calculate these distances. The distance between Anna Maria and Longboat was 13 km, between Anna Maria and Indian Shores was 38 km, and between Longboat and Indian Shores was 53 km. The hypothesized influence of this covariate on movement rates was negative. Because there are no shorebird studies assessing connectivity in linear, coastal habitats, I used two salient findings from Farmer and Parent (1997) and Taft and Haig (2006a, b) to help me interpret results. These were that connectivity should occur among states that are ≤ 2 km apart, and that movement rates ≤ 0.08 were associated with states that were effectively isolated. Accordingly, I hypothesized that all states would be isolated, with the greatest degree of connectivity occurring between Anna Maria and Longboat.

Prey Density – I calculated prey levels as the average number of prey per sample per season for a given sub-region (392.5 cm^2 per sample). I included all possible prey items. Preferred prey sources for the knots in Tampa Bay included *Donax* clams, mole crabs (genus *Emerita*) and marine worms. Although other items were included in the

estimated means, non-preferred items account for only 0.31% of the overall prey found in samples. The sampling period was divided into four seasons: fall, winter, early spring and late spring. Increased residency in suitable habitat not only is beneficial energetically, but reduces the risks of mortality incurred as birds move among wetlands (Farmer and Parent 1997). I hypothesized that prey density would have a positive influence on residency rate and negative on movement rates (Weber and Haig 1996).

Interaction Terms –I evaluated a linear and a quadratic term to account for the fact that prey undergoes marked seasonal fluctuations (Appendix A for prey). I wanted to sort the effects of this factor given that migration (arrival or departure), at the beginning and end points of the winter season, also influence daily residency rates.

I used Akaike's Information Criterion to select the most parsimonious model (Burnham and Anderson 2002). Models were ranked by AICc, where the model with the minimum AICc was the model with the most support in the data. The difference in AICc units between the best supported model and any other model (ΔAICc) was used to calculate model weights ($\text{AICc } w_i$), which indicate the relative likelihood of the model given the data (Burnham and Anderson 2002). Models with $\Delta\text{AICc} \leq 2$ were considered models with highest support.

I used the median \hat{c} procedure in MARK to estimate the variance inflation factor and Akaike's Information Criterion to select the most parsimonious model using recaptures only data (Burnham and Anderson 2002). There is no procedure in MARK to obtain an estimate \hat{c} to adjust models for overdispersion in multi-state models. Thus careful consideration of model assumptions was important to interpret multi-state results. First, I assumed that every color-marked bird had the same probability of being

resighted in sampling period i and that every marked bird had the same probability of surviving from sampling period i to $i+1$, assuming that it was alive and present in the population at the time the survey was conducted. Second, I assumed that emigration (i.e., departure) was permanent. I believe that this assumption was met because there was support in the data used to estimate annual survival for a model testing for permanent emigration (QAICc $w_i = 0.19$; Chapter 2). Third, I assumed that marks (i.e., color bands) were not lost and all correctly recorded. Parameter estimates were reported as estimate \pm standard error. A covariate was considered significant within a given model if the 95% confidence intervals of the beta value for the covariate did not overlap zero.

Prey and plasma metabolites

I compared estimates of prey density using a linear model (PROC MIXED, SAS 2002). Model terms were region (Anna Maria, Long Boat, Indian Shores), week (16 weeks, week 8 was excluded due to lack of samples), and interaction terms (i.e., week*region, week*week, week*week*region, week*week*week). This model treated site [region] and transect [region*site] as random effects. The response variable, prey density, was log-transformed prior to running the model. I also compared plasma metabolites levels across the winter (seasons = late October/early November, early January, late February/early March). For triglyceride I used a linear model using PROC MIXED (SAS 2002). Model terms were season, year, and BMI (adjusting for ddfm). Due to problems with normality in the data for β -OH butyrate and glycerol, I used a non-parametric model (PROC npar1way, SAS 2002). Differences in means between groups were tested using the Wilcoxon two-sample test. Test significance was set at $\alpha = 0.05$. Response variables were each of three metabolites measured in this study.

Results

Model selection for the residency models was adjusted for overdispersion; median $\hat{c} = 1.18$. Residency rates were best described by a model that accounted for variation in survival rates by year (QAICc $w_i = 0.61$; Table 3-1). Encounter probabilities were influenced by year, varying by time within year (g^*t). A plausible alternative was a model that featured the same terms but included body mass ($\Delta QAICc \leq 2$; QAICc $w_i = 0.38$). Body mass had a positive effect on daily survival, as predicted, but its influence was weak (Beta = 0.208 ± 0.178 ; 95% CIs overlapped zero).

Daily survival and movement rates were best described by a model that accounted for variation in survival rates with a linear trend term (T) for every site, prey abundance and its interaction with time of season, and distance between sites (AICc $w_i = 0.62$; Table 3-2). Encounter probabilities were influenced by year (yr 1 = 0.21, yr 2 = 0.36), but within year detection probability were similar across states. A plausible alternative was a model that featured the same terms influencing daily survival but included body mass (AICc $w_i = 0.38$). Body mass had a negative effect on daily survival, but its influence was weak (Beta = -0.113 ± 0.177 ; 95% CIs overlapped zero).

Daily survival rates among sites were similar (95% CIs overlapped, Figure 3-2). Rates declined linearly as the season progressed, but were positively and strongly influenced by seasonal prey abundance (T*Prey Beta = 0.026 ± 0.002 ; 95% CIs did not overlap zero; Table 3-3). While daily survival at Anna Maria and Longboat Key remained relatively high and roughly equal throughout the season, daily survival probabilities at Indian Shores dipped substantially during weeks 10-14 (Mar 22-Apr 23). The probability of moving in or out of each site was negatively, but weakly influenced by

distance among sites (Beta 95%CI's overlapped zero). Daily transition probabilities were low between all three sites (Figure 3-3). Only one value, the transition probability of birds moving from Longboat Key to Anna Maria, was higher than 0.08 (Figure 3-3).

There were no significant differences for metabolites when examined among areas and years in Florida. Therefore results from both years and multiple areas were lumped together for the final analysis. Plasma metabolite levels decreased across the season for triglyceride, glycerol and β -OH butyrate (Figure 3-4). Concentrations of triglyceride, β -OH butyrate, and glycerol were significantly higher in October/November than in January or March (Table 3-4). There were no significant differences between January and March for any metabolite. The elevated concentrations of all three metabolites in October/November may be a residual effect from migration, with birds arriving with both higher energy stores (triglycerides) and signs of higher energy expenditure (β -OH butyrate, glycerol). While triglyceride levels in Florida ranged from 1.08 to 2.07, concentrations in Delaware Bay averaged 9.59 (SE \pm 4.82), far more typical for a refueling site. Similarly concentrations of glycerol averaged 2.54 (SE \pm 2.24) and β -OH butyrate averaged 0.58 (SE \pm 0.31), compared to 0.03-0.05 and 0.70-0.83 respectively. Elevated glycerol is also expected at high levels of refueling since it is a by-product of high triglyceride production.

Discussion

Knots overwintering in Florida are a sedentary population that conserves energy and maintains body condition. Residency rates in the greater Tampa Bay region translated to a mean length of stay of 52 d in 2008-2009 and 99 d in 2009-2010. Annual differences likely reflected local variations on the internal state of knots (e.g., body condition) or habitat quality, which could encompass prey fluctuations, weather

and anthropogenic factors (e.g., human disturbance). To explore how body condition, prey levels and distance might operate, I modeled daily survival and movement rates for three locations known to harbor wintering knots. I found that estimates of daily survival were high for all three locations, albeit exhibiting a seasonal negative trend. The negative trend is consistent with a resident population that eventually transitions to a migratory phase. Residency was highest in the Anna Maria region, followed by Longboat and Indian Shores, respectively. During the core of winter (January-March), mean length of stay was 69 d for Anna Maria, 44 d for Longboat and 26 d for Indian Shores. Despite the sedentary nature of birds at all three locations, estimates of daily survival were consistently lower at Indian Shores, falling to their lowest value (0.75) during April 5-April 14. At this point mean length of stay was only 3.47 days.

As hypothesized, residency rates were positively and strongly influenced by average prey density at each location. Prey levels, however, were lowest at Indian Shores and may explain why the pattern of daily survival at Indian Shores was lower than the other two locations (Figure 3-5). Previous studies have linked body condition to residency at stopover and wintering sites (Skagen and Knopft 1994, Lyons and Haig 1995). As body mass is an expression of energetic state, it is reasonable to assume that it would affect whether birds chose to remain at or vacate from a location. Yet body mass exerted only a weak influence on residency. Similar findings were reported for wintering Semipalmated Sandpipers in the eastern Caribbean (Rice et al. 2007).

Body mass is a valuable proxy for bird condition, but because it is almost invariably based on a single capture estimate, it is hard to discern if the bird is on a positive, sustaining or negative energetic path. In this sense, my assays of plasma

metabolites addressed an important void in our understanding of the condition of knots during winter in Florida. Analyses revealed two salient results: a) there were no significant differences between locations during any of the sample periods, and b) despite a general trend of dropping triglyceride levels across the seasons, catabolic metabolites remained low and stable during the core of winter. This indicated that knots at all three locations, while consuming less energy during the core winter months, were not undergoing a severe or even moderate fast despite differences in prey availability at each location. Winter birds, unlike migratory birds, are likely concerned with maintaining body condition and minimizing predation risks rather than improving it through building fat and muscle (Warnock and Bishop 1998, Van Der Veen and Sivars 2000, Gentle and Gosler 2001). Body mass may not always be the best indicator of energetic state, and thus, may not illuminate the relationship between residency and energetic state. This work suggested that a lighter bird would have no more or less incentive to move than a heavier bird.

Residency patterns hinted at the role that human disturbance may play within the Tampa Bay region. Among the three areas, Indian Shores is the most highly developed area with condos and motels just behind the dune area, high levels of human foot traffic, and a narrow beach that impairs birds' ability to avoid human interaction. Throughout the winter, birds at Indian Shores had lower daily survival probabilities than knots at other locations. Longboat, which has significantly less land development and human foot traffic, had the second best survival and Anna Maria, which encompasses areas closed to human access, had the highest daily survival rates. In addition, birds at Indian Shores underwent a period of greatly reduced daily survival between mid-March and

mid-April, while the other locations did not. This period coincided with a marked increase in human activity (e.g., recreational), culminating in a surge of presence and activities along the coast during spring break (pers. obs). I surmised that the drop in daily survival was caused by either knots temporarily or permanently vacating the area in response to this surge. Although this inference is speculative, it is noteworthy that estimates of food availability actually increased during the period in question. Therefore it weakens the possibility that prey played a major role based on the strong and positive relationship between residency and prey levels reported in this study.

Results thus far suggested that movements out of an area can be triggered by changes in habitat quality (e.g., prey levels, human activity). This process highlights the importance of alternative areas where knots can continue to meet overwintering needs. Proximity of good quality sites reduces exposure to predation risks and energetic costs (Skagen 1997, Farmer and Weins 1999). In this study, I assessed this process and found that distance among locations exerted a negative, but weak influence on movement rates. Still, average transition probabilities between locations within Tampa Bay were quite low (Figure 3-3). Previous studies on shorebirds suggested that transition probabilities ≤ 0.08 between sites and at distances greater than 2 km are perceived by shorebirds as effectively isolated (Farmer and Parent 1997, Taft and Haig 2006b). It follows that locations within Tampa Bay area might be perceived by knots in a similar fashion. The highest transition probability was from Longboat to Anna Maria (0.14), and this movement was uni-directional (transition probability in the opposite direction was 0.06) despite Longboat's greater abundance of food resources. I speculate that knots from Longboat may take advantage of the protected areas within

Anna Maria as reflected by high movement rates and daily survival at Anna Maria. This possibility can be viewed as an example of functional connectivity (Belisle 2005). The implications of my results were particularly relevant to areas like Indian Shores. It suggested that the Anna Maria and Long Boat areas provided little functional value (e.g., place to reside) when birds at Indian Shores were displaced. My results indicate that birds remained in the area at high rates and seemed reticent to move long distances to other traditionally used areas. As such, displaced birds could incur unnecessary energetic costs and may undermine their overwinter survival (Tarr et al. 2010). The magnitude of these costs will largely depend on whether displaced knots engage on short-distance movements and continue to meet their needs. I did not address this possibility in this study.

The topic of movement rates, that is, how far and how frequently an individual moves is of conservation interest for other reasons. Knots use linear habitats (beaches), which in the context of other landscape studies, present few barriers to movement. Yet knots seem to rely on traditional areas with low exchange rates among them, at least in Tampa Bay. Obvious benefits from returning to these areas include familiarity with resources and threats, particularly if favorable in years past. Indeed evidence at a larger scale indicated that adults and juveniles (0.81 and 0.70, respectively) return annually to Florida (Chapter 2) and knots in at least one other wintering population show high inter-annual site fidelity (Leyer et al. 2006). Traditionally used areas, therefore, serve a demographic function, providing overwinter requirements to multiple segments of the *rufa* population wintering in Florida. These areas in Florida could be viewed as the more discrete units (e.g., wetlands) used to formulate the

conservation underpinnings of the Hemispheric Shorebird Reserve Network (Myers et al. 1987).

Generally, it is believed that persistence of a species is a function of its numeric strength provided the fate of individuals is independent. With shorebirds, however, the numeric strength of the population is undermined because they aggregate in few, traditionally used areas both during migration and the non-breeding season. Thus persistence effectively becomes a function of the availability of such areas (Myers et al. 1987). Beach areas in Florida will likely become more discretized in the advent of climate change (e.g., sea level rise causing fragmentation and erosion of coastal habitat) and continued human encroachment. Even though coastal beaches facilitate structural connectivity, I have presented evidence that functional connectivity is dependent on inter-site distance and habitat quality. Additional attention should be given to elucidating the scales at which these processes operate in coastal beach habitats so that increased knowledge could inform conservation design and planning.

In this study I documented important aspects of the local dynamics of wintering knots. I found that most birds reside for extended periods of time in traditional winter areas, seemingly moving only if necessary. I also documented that birds are maintaining themselves energetically. Of the locations under consideration, knots at Indian Shores were most vulnerable to high human disturbance and low prey densities. Exchange among these traditional areas was minimal, emphasizing the importance in maintaining the integrity of traditionally used areas. Thus, attention should also be given to the geographic context within which traditional areas are imbedded to determine if some measures of protection could be implemented (e.g., alternative

habitats). As suggested above, unnecessary movements could expose these birds to increased predation, loss of foraging opportunities and perhaps higher mortality (Parent and Farmer 1997). This work showed how variation in site quality and other factors could account for the differences in mean length of stay. But even during a year of low mean length of stay (i.e., 2009), presumably caused by birds that permanently emigrated from the region, annual survival for that winter was not the lowest estimate available over a five year period (Chapter 2). This lends support to the belief that local dynamics contribute to annual survival variation, but cannot fully account for recent population declines.

Table 3-1. Model selection for daily, local survival of Red Knots in the Tampa Bay region (winters 2008-2009 and 2009-2010).

Model	QAICc	Δ QAICc	QAICc Weights	Model Likelihood	Num. Par	QDeviance
{Phi(g) p(g*t) PIM}	3614.286	0	0.6159	1	33	3546.710
{Phi(g+BC) p(g*t) PIM}}	3615.230	0.9444	0.3841	0.6236	34	3545.558
{Phi(g*t) p(t) PIM}	3668.002	53.7162	0	0	37	3592.022
{Phi(g*TT+BC) p(t) PIM}	3741.341	127.0552	0	0	21	3698.698
{Phi(g*T) p(t) PIM}	3754.162	139.8761	0	0	19	3715.633
{Phi(g*t+TT) p(g) PIM}	3773.527	159.2409	0	0	8	3757.427
{Phi(g*t+TT+BC) p(g) PIM}	3775.549	161.2627	0	0	9	3757.424
{Phi(g*TT) p(g*TT) PIM}	3790.720	176.4346	0	0	8	3774.621
{Phi(g*TT+BC) p(g*TT) PIM}	3792.720	178.4340	0	0	9	3774.596
{Phi(g*t+T) p(g) PIM}	3799.422	185.1361	0	0	6	3787.364
{Phi(g*T) p(g*T) PIM}	3815.113	200.8274	0	0	6	3803.055
{Phi(g) p(g) PIM}	3865.412	251.1259	0	0	4	3857.384
{Phi(g) p(g*T) PIM}	3866.445	252.1593	0	0	5	3856.404
{Phi(.) p(.) PIM}	3894.693	280.4073	0	0	2	3890.685
{Phi(g) p(t) PIM}	3896.658	282.3720	0	0	17	3862.233

Parameters were: Phi = daily survival, g = year, p = detection probability, t = time, BMI = body mass index, T = linear trend in time, TT = quadratic trend in time. Lower QAICc weight indicates better support for a model. $\hat{c} = 1.18$

Table 3-2. Model selection for survival and movement rates of Red Knots wintering in three traditionally used sub-regions within the Tampa Bay region (winters 2008-2009 and 2009-2010).

Model	AICc	Δ AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{S(T/site+prey+T*prey), p (By YR but = site), Psi (Dist)}	5277.45	0	0.675	1	14	5249.16
{S(T/site+prey+T*Prey+BMI), p (By YR but = sites), Psi (Dist)}	5279.09	1.634	0.298	0.441	15	5248.76
{S(TT/site+prey+TT*Prey), p (By YR but = sites), Psi (Dist)}	5285.55	8.098	0.012	0.017	15	5255.22
{S(TT/site+prey+TT*Prey+BMI), p (By YR but = sites), Psi (Dist)}	5287.23	9.773	0.005	0.007	16	5254.85
{S(T/site+prey), p (By YR but = sites), Psi (Dist)}	5287.35	9.890	0.004	0.007	13	5261.09
{S(TT/site), p (By YR but = sites), Psi (Dist)}	5288.09	10.636	0.003	0.004	13	5261.84
{S(TT/site+prey), p (By YR but = sites), Psi (Dist)}	5289.96	12.503	0	0.002	14	5261.67
{S(T Indian, constant for other sites), p (BY YR but = sites), Psi (constant/year)}	5300.59	23.138	0	0	12	5276.38
{S(yr), p (yr), Psi (yr)}	5303.52	26.069	0	0	23	5256.75

Parameters were: S = daily survival, p = detection probability, Psi = transition probability, BMI = body mass index, prey = average prey levels, Dist = distance between sub-regions, T = linear trend in time, TT = quadratic trend in time, "By YR but =" = variation by year but equal across sub-regions. Lower AICc weight indicates better support for a model.

Table 3-3. Beta parameter estimates for the multi-state model with highest support for Red Knots wintering in the Tampa Bay Region (winters 2008-2009 and 2009-2010).

Parameter	Estimate	SE	LCI	UCI
Anna Maria daily survival	6.013789	0.331431	5.364183	6.663394
Indian Shores daily survival	-1.27312	0.287554	-1.83672	-0.70951
Longboat daily survival	1.94492	0.348822	1.26123	2.62861
T (linear trend in daily survival)	-0.21452	0.027629	-0.26867	-0.16037
Prey	-0.34361	0.095803	-0.53138	-0.15583
T*prey (interaction term)	0.026613	0.006395	0.014078	0.039148
capture probability, yr 1	-1.32266	0.086013	-1.49125	-1.15408
capture probability, yr 2	-0.56768	0.06731	-0.6996	-0.43575
Intercept	-0.69139	0.87467	-2.40575	1.022962
Dist Group (Indian Shores)	-0.75223	0.413734	-1.56315	0.058687
Dist Group (Anna Maria & Long Boat)	-0.44065	0.864196	-2.13447	1.253175
Distance among sites	-0.02858	0.028742	-0.08491	0.027754
Dist*area (Indian Shores)	-0.01167	0.019834	-0.05055	0.027202
Dist*areas (Anna Maria & Long Boat)	-0.02263	0.026364	-0.0743	0.029044

The top model was S(T/state+prey+T*prey), p (By year but equal among states), Psi (Distance).

Table 3-4. Results of plasma metabolite analysis conducted on plasma collected within the Tampa Bay region during late October/early November, January and late February/early March of winters 2008-2009 and 2009-2010.

Metabolite	Seasonal Comparison	Pr > t or Pr> Z
Triglyceride	Oct-Jan	<0.0001* (t=6.08, DF=192)
	Oct-Mar	<0.0001* (t=6.87, DF=192)
	Jan-Mar	0.0971 (t=1.67, DF=192)
β-OH Butyrate	Oct-Jan	0.0012* (Z=3.25, n=117)
	Oct-Mar	0.0010* (Z=2.58, n=115)
	Jan-Mar	0.0785 (Z=1.77, n= 162)
Glycerol	Oct-Jan	0.0092* (Z=2.61, n=115)
	Oct-Mar	0.0266* (Z=2.22, n=116)
	Jan-Mar	0.2553 (Z=-1.14, n=163)

* - indicates significance at $\alpha=0.05$. Tests for triglyceride were conducted using ANOVA, t values and degrees of freedom (DF) are reported; tests for the other two metabolites were conducted with a non-parametric test Z scores and sample size are reported.



Figure 3-1. Study area – Tampa Bay region. Labeled locations indicate main sites for resighting and invertebrate surveys and yellow outlines indicate sub-regions (states) for resident and multi-state models.

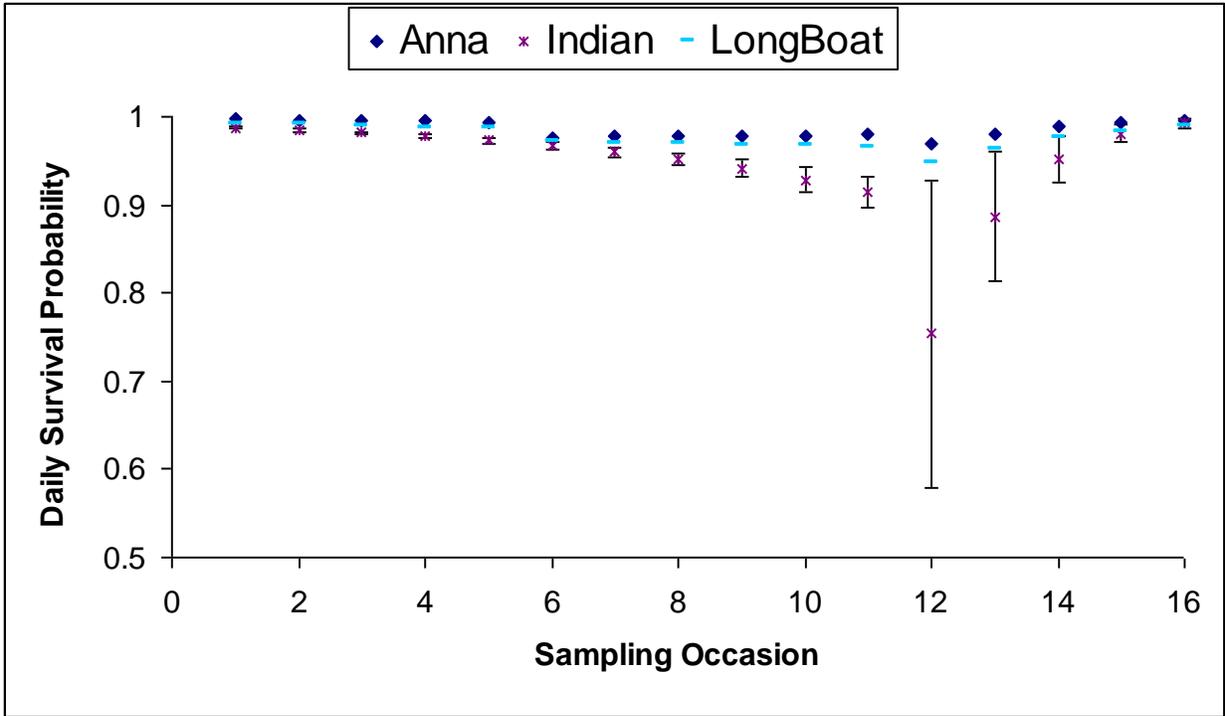


Figure 3-2. Daily survival probabilities across season for three locations in the Tampa Bay region. Estimates were obtained from the top multi-state model: $S(T/state+prey+T^*prey)$, p (by year but equal among states), Ψ (Distance).

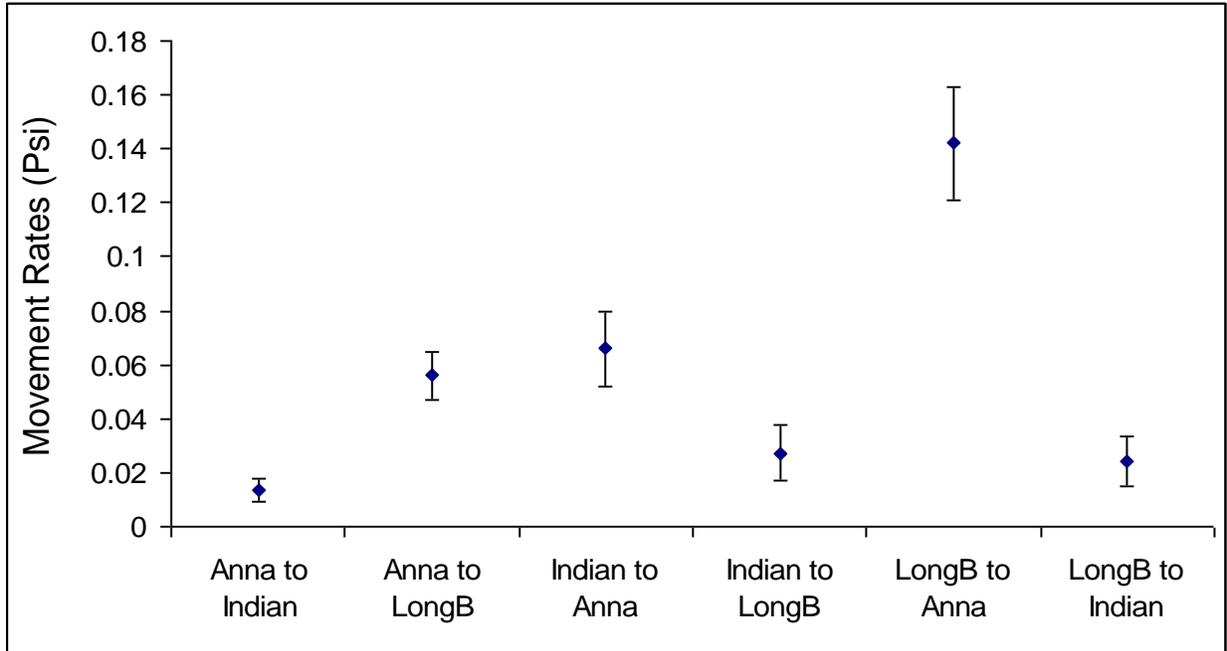


Figure 3-3. Daily transition probabilities between sub-regions in the Tampa Bay region. Indian corresponds to the Indian Shores or northern sub-region, Anna corresponds to the Anna Maria or central sub-region, and LongB corresponds to the Longboat or southern sub-region. Estimates were obtained from the top multi-state model: $S(T/state+prey+T*prey)$, p (by year but equal among states), Ψ (Distance).

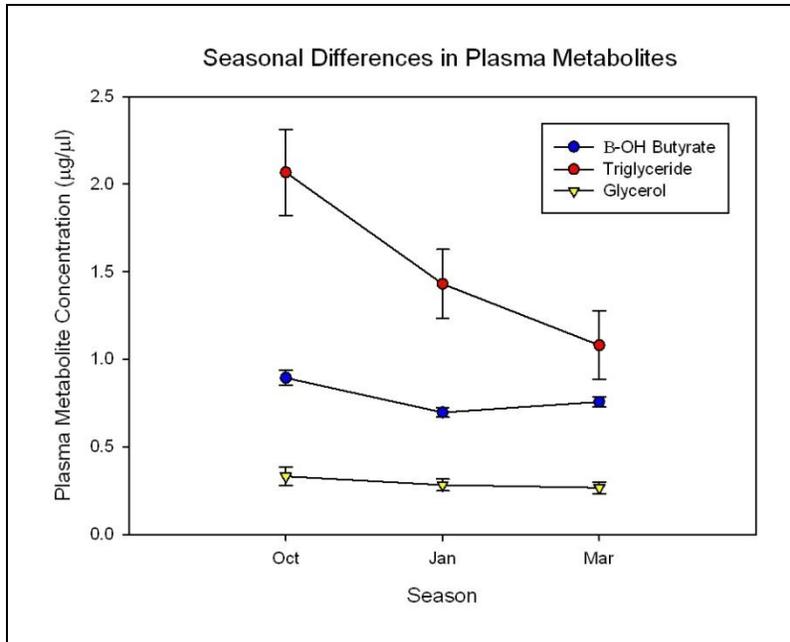


Figure 3-4. Plasma metabolites levels with standard error for the Tampa Bay region over the seasons. 2008-2009 and 2009-2010 data and data from all locations pooled.

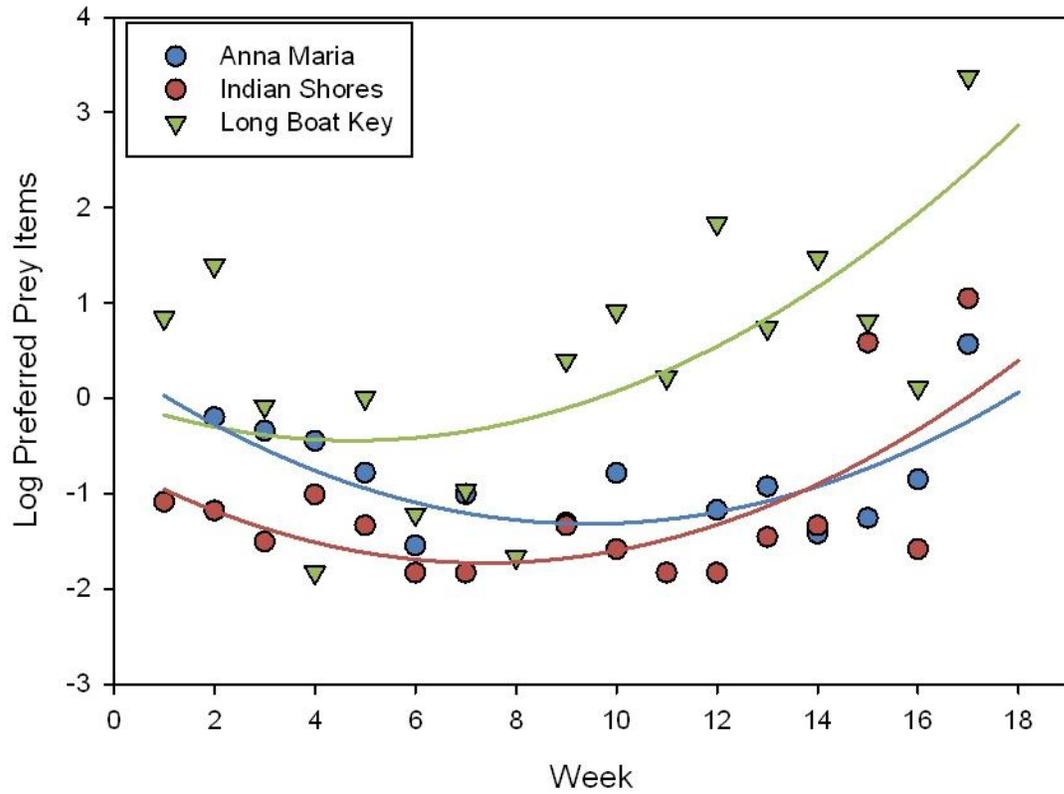


Figure 3-5. Weekly mean densities of preferred prey over the winter and spring (January 18 – May 11, 2010) at three sub-regions within Tampa Bay. Lines represent the model predictions from each location.

CHAPTER 4 CONCLUSION

I examined demographic and physiological aspects of Red Knots (*Calidris canutus rufa*) wintering in Florida. I adopted a multi-scale approach in an attempt to decouple their annual cycle and differentiate between local and global (hemispheric) factors that might influence population changes. This distinction provides a stronger basis to formulate local conservation strategies. The strongest impetus for the study was the sharp decline in numbers recorded in Florida in the last 30 years. Winter counts have dropped from ~10,000 (1980s) to ~1,200 (2010). The relevance of this study is further strengthened because the remainder of the hemispheric population of Red Knots, which winters in South America, also exhibits a declining population trend. Assessments at multiple spatial and temporal levels are needed to develop a comprehensive conservation strategy to curb the species' decline.

At the broadest scale, I estimated annual survival of juveniles and adults, and compared them to similar estimates from the remaining populations of *rufa*. I also tested for differences in size-adjusted body mass between Florida birds and other wintering populations as a measure of relative health. Comparisons of adult annual survival rates indicated that birds wintering in Florida survived at similar rates (0.91) as birds from the remaining populations of *rufa* (0.91-0.92). Comparisons of body mass between birds wintering in Florida and South America were either similar or favored Florida birds. These findings suggest that the mechanism(s) behind the observed population decline were likely acting on all populations of *rufa*, not just the segment wintering in Florida. In addition this work and recent work at Delaware Bay leads me to suggest that adult mortality was not the primary mechanism for population declines, at

least between 2005-2010, and plausible alternatives should be considered. Among these depressed reproductive or recruitment rates should be given greatest attention. These findings also suggest that despite their smaller numbers and northern wintering grounds relative to the core wintering population in South America, knots wintering in Florida should not be viewed as a marginal population. Ecological factors such as availability of food resources may explain the unequal distribution of the populations, instead of trade-offs in annual survival.

At the local scale, I estimated daily survival and mean length of stay for each of three historically wintering locations within the greater Tampa Bay region. These were Anna Maria, Indian Shores and Longboat. These areas spanned a range of habitat quality conditions as reflected by food resource abundance and degree of development. I also estimated transition probabilities among the three traditionally used locations to assess connectivity among them. Results indicated that daily survival was influenced by prey abundances and by location. Daily survival was highest at Anna Maria and lowest at Indian Shores. Temporal fluctuations in daily survival probabilities at Indian Shores suggested that time-specific increases in disturbance, such as spring break, could have an impact on daily survival. Transition probabilities among locations was low (< 0.08), with only one transition (from Longboat to Anna Maria) suggesting that locations could be functionally connected. Knots tend to reside in traditionally used areas unless conditions change markedly. Low transition probabilities, however, indicate that birds were reticent to move between traditionally used areas. As such, they are not perceived as potential alternatives or *refugia* by knots.

Management Recommendations

The mechanisms behind the decline of *Calidris canutus rufa* are not entirely understood despite the severe magnitude of decline. The parameters and scales used to assess the status of the species in Florida did not point at local factors as the major drivers behind observed declines over the past five years. However, managers in Florida should be cognizant of several patterns highlighted in this study. First, the probability of returning to Florida on an annual basis was high (0.70-0.81). Second, birds consistently reside in and return to historically used areas unless conditions change markedly or they are forced out. Third, low transition probabilities among traditionally used areas suggested that they are not viewed by birds as alternative habitats. The latter was exemplified by displacements recorded in Indian Shores, likely caused by spikes in human recreational activities during spring.

These patterns underscore the importance of preserving the integrity of traditionally used areas, but also foster the implementation of measures to protect or buffer other areas from anthropogenic disturbance. These measures will gain importance as the coastal zone and beaches of Florida becomes increasingly segmented as a result of continued development and sea level rise. The creation of protected areas or other *refugia* should take into account the scale at which birds perceive the landscape. *Refugia* will only be effective if knots can transition to the locations easily. Their reluctance to travel greater distances, such as those between the three study areas, would limit the usefulness of a protected area if it is beyond the range that knots perceive as being connected to their wintering grounds.

Recommendations for Further Research

On a hemispheric scale, obtaining estimates of reproductive success and recruitment rates is imperative. These vital parameters are emerging as the possible source of demographic vulnerability for *C. c. rufa* and perhaps the underlying cause of recent population declines. While juvenile to adult ratios may be useful for inference in some areas, such as Florida, they are likely inadequate for larger regions such as the wintering grounds in southern South America. Other research could also explore the effects of sub-lethal factors, such as disease. While my study did not find evidence of increased adult mortality within Florida compared to South America, Florida knots seem to show a higher incidence of avian influenza antibodies than South American birds (A. Howey, pers. comm.), suggesting that they may still be vulnerable to increased disease and parasite pressure. Broader immunological studies could examine potential differences between and impacts on the wintering populations.

In Florida, understanding the scale at which knots consider the landscape to be connected is an important next step. My work highlighted the discrete nature of these historical wintering areas, yet the distance within these areas that knots will willingly travel is unknown. Estimating the upper limit for this distance will be key in designing adequate protections for knots within each of these areas. Additionally, research directed at separating the effect of anthropogenic disturbance from the effect of resource abundance on overwinter survival would be useful in determining the level of influence each factor exerts and understanding better how local factors might impinge on population demography. Finally, estimating site fidelity, both within a winter and between winters, could improve our understanding of local dynamics and may help

elucidate if habitat alterations within the wintering season are more or less detrimental than impacts on habitat quality between years.

APPENDIX A PREY SELECTION IN WINTERING RED KNOTS IN THE TAMPA BAY REGION

Red Knots forage in a variety of habitats and on a variety of prey items throughout their annual cycle, from terrestrial invertebrates on the breeding grounds to intertidal invertebrates on migration and on the wintering grounds. Within the *rufa* subspecies most wintering and migratory populations consume primarily small mollusks within the intertidal zone, particularly the clam genus *Donax* (Harrington 2001). The goals of this study were: 1) document temporal patterns in preferred prey items (*Donax*, mole crabs – genus *Emerita*, marine worms - family *Spionidae*), 2) determine prey preferences within Florida wintering knots by comparing background levels of available prey with prey levels found at foraging locations and 3) provide additional evidence through examination of stomach contents obtained through incidental catch mortality.

Methods

Study Area

This study was conducted in the Tampa Bay region on the Gulf Coast of Florida. Tampa Bay is home to approximately half of Florida's wintering knot population (Niles et al. 2008a). Knots arrive in late October and early November and stay through late March to mid-April. A small number of birds (<50), most likely juveniles, stay in the Tampa Bay area over the summer. Shorebird habitat in Tampa Bay consists of sandy beaches on barrier islands with a narrow intertidal zone. At lower tides, sand or mud flats are exposed and provide additional foraging habitat. I divided the Tampa Bay region into three main sites (Anna Maria, Indian Shores, and Longboat) which each represent distinct historical wintering areas.

Invertebrate Sampling

For this study I used two types of invertebrate sampling. “Reference” sampling refers to sampling conducted every week at the same locations to develop a picture of changes in the invertebrate community over time. “Foraging” sampling indicates sampling at locations where birds are actively feeding.

Reference sampling

I sampled for invertebrates at Ft. De Soto, Shell Key, Lido Key, Longboat Key and Indian Shores in 2010. I selected these locations based on the consistent presence of foraging Red Knots in previous years. I established two reference transects at each of the five locations. Each transect consisted of a fixed starting point, with four points total spaced ten meters apart. Transects were placed randomly along selected beaches and were at least 200 m apart. I sampled both transects weekly at each location starting the third week of January. I sampled in the surf zone, parallel to the waterline. At each point I collected sediment cores 5 cm deep and 10 cm in diameter and stored them in a lock-seal plastic bag for future analysis. After sample collection, I sieved each sample with a 1mm wide mesh sieve. I collected, identified to family (or genus if possible) and counted each invertebrate in the sample. I measured common invertebrates in order to create an index of biomass.

Foraging sampling

When I located a flock of foraging I placed a linear transect through the foraging area, typically along the waterline. I took the first sample at the near edge of the flock and continued sampling every ten meters until I reached the far edge of the flock. Since flocks often abandoned feeding while I sampled, I noted the location of the near and far

edges before we sampling. I took cores 10 cm in diameter and 5 cm deep and processed them in the same manner as described for the reference samples.

Stomach contents

Trapping efforts, regardless of precautions taken, inevitably result in some minimal level of mortality. During 2008-2010, trapping efforts produced 16 mortalities which were collected for later analysis under the Florida Fish and Wildlife Conservation Commission's salvage permit (MB745817-0). I collected all 16 stomachs and preserved their contents in ethanol. I then attempted to identify all prey items and determine the number of each prey type found in each stomach.

Data Analysis

In order to examine temporal trends I compared estimates of prey density using linear model (PROC MIXED, SAS 2002). For the combined preferred prey items model terms were region (Anna Maria, Long Boat, Indian Shores), week (16 weeks, week 8 was excluded due to lack of samples), and interaction terms (i.e., week*region, week*week, week*week*region, week*week*week). This model treated site [region] and transect [region*site] as random effects. The response variable, prey density, was log-transformed prior to running the model. The *Donax* model differed from the overall model by including an additional interaction term (week*week*week*region) and removing transect [region*site] from the random effects. The *Emerita* model included all terms from the overall model but also removed transect [region*site] from the random effects. The *Spionidae* model included all the terms and random effects from the overall model but also included the additional week*week*week*region term.

Differences between reference and foraging samples were analyzed using a non-parametric test due to the non-normal distribution of the data (PROC npar1way, SAS

2002). Data from each group was separated by month (January-May) and region within Tampa Bay and differences in means between groups was tested using the Wilcoxon two-sample test. Test significance was set at $\alpha = 0.05$.

Results

Reference Sampling

All items increased in all areas over time, although the magnitude of change for each item differed by area (Figures A-1 and A-2). By the end of the season *Donax* and *Emerita* were most abundant in the Longboat region while *Spionidae* worms were most abundant in the Indian Shores region. The Indian Shores region consistently showed lower levels of *Donax* throughout the season, the knots most preferred item (see “Stomach Contents” results below).

Foraging Sampling

Comparing reference samples to foraging samples showed few significant differences in available prey between the two types of samples, and several significant results indicated a higher presence of items in the reference samples than in the foraging samples (Table A-1). The notable exception is that *Spionidae* worms were present in significantly larger numbers in foraging samples than in reference samples at Indian Shores during every month in which foraging samples were taken (January-March). No foraging samples were taken at Indian Shores during April and May, since birds had largely vacated the area during these months. No foraging samples were taken in the Anna Maria area during April due to a lack of observed foraging behavior.

Stomach Contents

Donax were found in 93.8% of the stomachs, *Cypraeidae* in 18.8%, and all other item types in 12.5% or less. Only one stomach did not contain *Donax*. *Cypraeidae*, a

type of snail, was found in large quantities (38 individuals) in one stomach, but all individuals were less than 2mm. After discounting items smaller than 2mm, *Donax* represented 69.7% of all items found in the stomachs, with *Crassatellidae* clams being the next most frequent at 10.6% (Table A-2). Birds from the Longboat region showed a focus on *Donax* while birds from Ft. De Soto in the Anna Maria region had a more diverse diet, although sample sizes from both regions were small. No birds were collected from the Indian Shores region.

Discussion

Based on stomach sampling, *Donax* clams seem to be the most preferred prey item in the Tampa Bay region. In addition, larger flocks regularly gathered in the Longboat and Anna Maria regions than in Indian Shores (pers. obs., resighting surveys), indicating that knots may select areas with higher *Donax* concentrations. However it is also clear that knots will utilize a variety of mollusks including clams other than *Donax*, snails, and mussels. In addition, non-systematic foraging observations indicate that *Spionidae* worms are eaten by red knots in the Tampa Bay area, and the invertebrate sampling results from Indian Shores may indicate that they provide an important alternative in a region where the normally preferred *Donax* are scarce. Two reasons that *Spionidae* were likely under-represented in the stomach samples are: 1) no incidental mortality came from Indian Shores and 2) *Spionidae* are soft-bodied and thus quickly digested, suggesting that they may be less likely to be detected depending on length of time from last meal for each individual bird.

Table A-1. Comparison of reference and foraging samples from the Anna Maria, Indian Shores and Longboat regions in Tampa Bay during the winter and spring (January 18 – May 11, 2010).

		January	February	March	April	May
Anna Maria	Donax	0.0084* (n=17, Z=2.64)	0.0689 (n=58, Z=-1.82)	0.2077 (n=78, Z=1.26)	n/a	0.0599 (n=41, Z=-1.88)
	Emerita	1.0000 (n=17, Z=0)	0.4368 (n=58, Z=-0.78)	0.6641 (n=78, Z=-0.43)	n/a	0.0624 (n=41, Z=-1.86)
	Spionidae	0.0036* (n=17, Z=-2.91)	<.0001* (n=58, Z=4.01)	0.8467 (n=78, Z=-0.19)	n/a	0.0345* (n=41, Z=-2.11)
Indian Shores	Donax	0.4160 (n=22, Z=-0.81)	0.6755 (n=41, Z=0.42)	0.3641 (n=41, Z=-0.91)	n/a	n/a
	Emerita	0.2066 (n=22, Z=-1.26)	0.7576 (n=41, Z=-0.31)	1.0000 (n=41, Z=0)	n/a	n/a
	Spionidae	0.0011* (n=22, Z=3.27)	<.0001* (n=41, Z=4.80)	0.0038* (n=41, Z=2.90)	n/a	n/a
Longboat	Donax	0.7430 (n=20, Z=-0.34)	0.1768 (n=75, Z=1.35)	0.5773 (n=114, Z=.56)	0.7852 (n=65, Z=-0.27)	0.3248 (n=35, Z=-0.98)
	Emerita	0.0476* (n=20, Z=-1.98)	0.2618 (n=75, Z=-1.12)	0.1170 (n=114, Z=-1.57)	0.1621 (n=65, Z=1.40)	0.9247 (n=35, Z=-0.09)
	Spionidae	0.4002 (n=20, Z=0.84)	0.2424 (n=75, Z=-1.17)	0.9228 (n=114, Z=-0.10)	0.2613 (n=65, Z=1.12)	0.2539 (n=35, Z=-1.14)

P-values, sample sizes and Z-scores for a Wilcoxon two-sample, two-tailed test of means from reference and foraging samples, broken down by item type. * - indicates significant result. n/a – indicates no foraging sample available for that month.

Table A-2. Number of items and percentage of total items by prey type found in 16 Red Knot stomachs from the Tampa Bay region.

Location	Date	Donax	Crassatellidae	Cassidae	Cypraeidae	Mytilidae	Spionidae	Unknown snail
Ft. De Soto	3/19/2008	1	6			1		
Ft. De Soto	3/19/2008	2						
Ft. De Soto	3/19/2008	1		2	2			
Ft. De Soto	3/19/2008	3						
Ft. De Soto	3/19/2008			2				
Ft. De Soto	3/19/2008	1					2	
Ft. De Soto	3/19/2008	2						
Ft. De Soto	3/19/2008	3			3			1
Ft. De Soto	3/19/2008	1						
Ft. De Soto	3/19/2008	4						
Ft. De Soto	3/19/2008	3						
Ft. De Soto	3/19/2008	3						
Ft. De Soto	3/19/2008	3	1					
Longboat Key	10/25/2009	9						
Longboat Key	1/7/2010	6						
Longboat Key	1/7/2010	4						
FREQUENCY		46	7	4	5	1	2	1
% all items		69.7	10.6	6.1	7.6	1.5	3.0	1.5

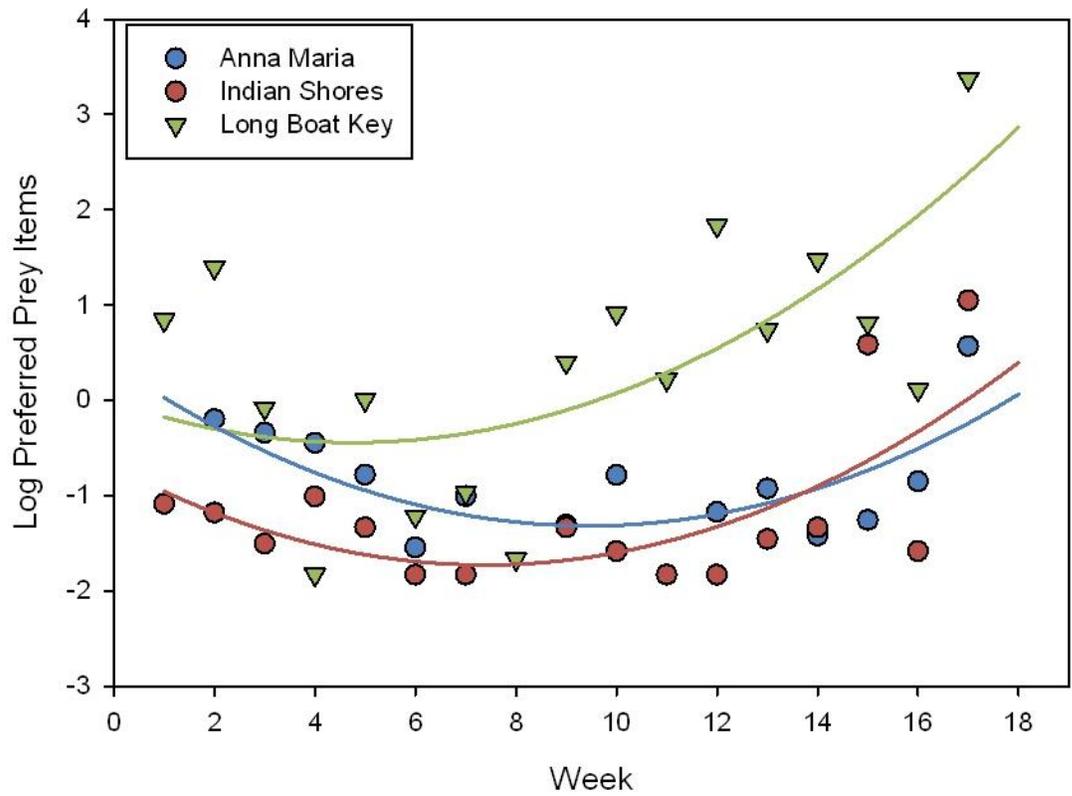


Figure A-1. Weekly mean densities of all preferred prey over the winter and spring (January 18 – May 11, 2010) at three sub-regions within Tampa Bay. Lines represent the model predictions from each location.

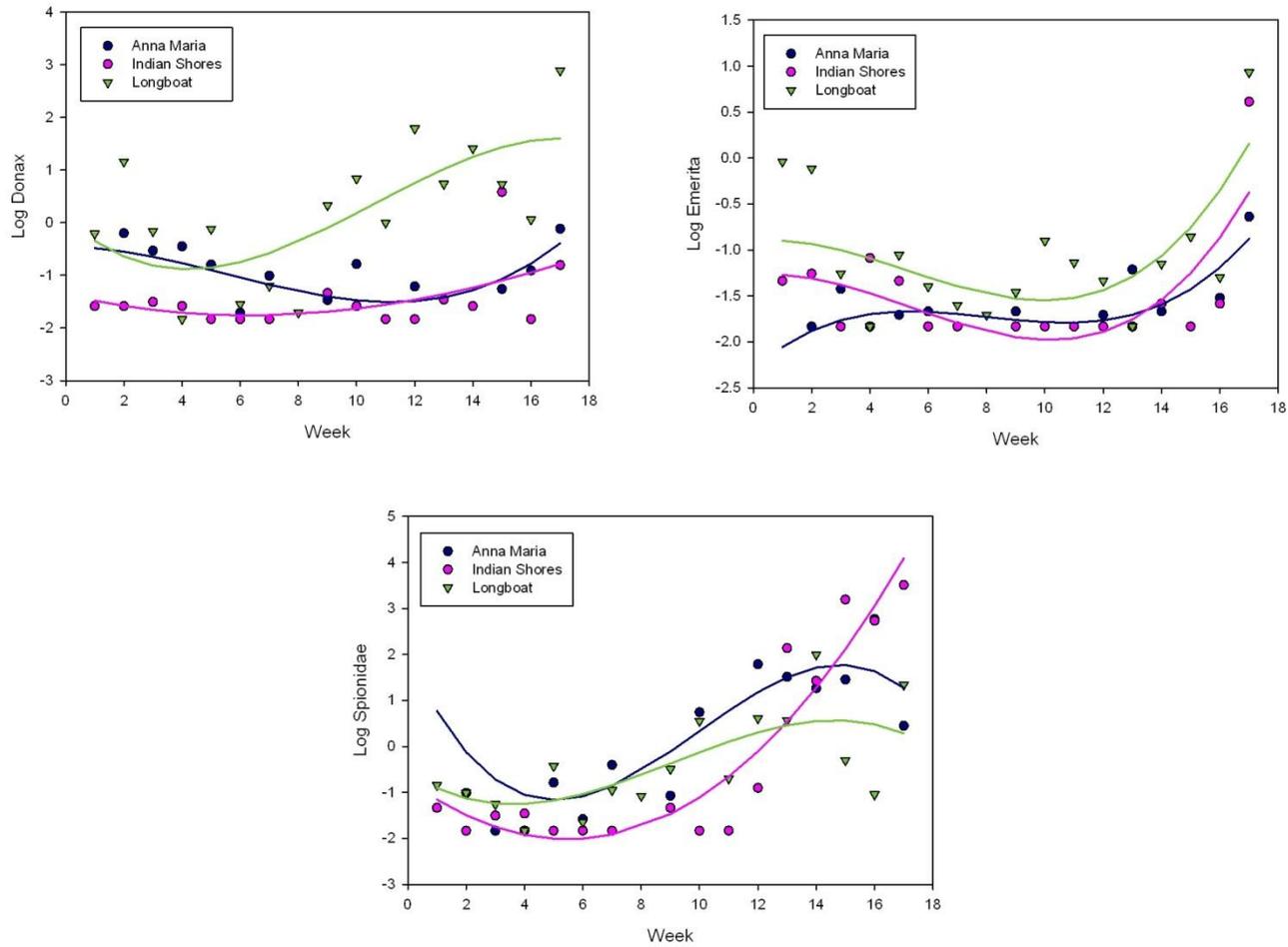


Figure A-2. Weekly mean densities of *Donax*, *Emerita* and *Spionidae* over the winter and spring (January 18 – May 11, 2010) at three sub-regions within Tampa Bay. Lines represent the model predictions from each location.

APPENDIX B PREY AVAILABILITY AND SELECTION IN MIGRATORY RED KNOTS IN THE CEDAR KEY REGION

The vast majority of *rufa* red knots pass through Delaware Bay on their northbound migration to the breeding grounds (Harrington 2001). Here they feed almost exclusively on horseshoe crab (*Limulus polyphemus*) eggs before completing their final non-stop flight to the Arctic breeding grounds (Tsipoura and Burger 1999). Florida supports a healthy breeding population of horseshoe crabs, particularly in the Cedar Key region of the Gulf coast. Although breeding densities do not reach the super-abundance found in Delaware Bay, local breeding concentrations can be high (Gerhart 2007). Migratory red knots are known to pass through the Cedar Key region, located on the north-central Gulf Coast of Florida, during the peak horseshoe crab spawning season. Thus this study was designed with two goals: 1) determine what the availability of eggs within reach of shorebirds is compared to the number laid and 2) examine the importance of horseshoe crab eggs and larvae to migratory knots in Florida.

Methods

Study Area

The Cedar Key area consists of large swaths of saltwater marsh and oyster beds, interspersed with small islands with sandy beaches. Despite the relative limited size of sandy beaches, the shallow waters and low wave action make this region an ideal place for spawning horseshoe crabs. This area has some of the highest spawning crab densities in Florida during the spring months (March-May) (Gerhart 2007). It also provides habitat for wintering and migrating shorebirds. Within the region I chose two

sites, McClamory Key and Atsena Otie, which provided both good habitat for crab spawning and potential foraging habitat for red knots (Figure B-1).

Reference Sampling

I sampled each site weekly, except when weather did not permit access to the islands, during the spring months (late February to mid-May). I sampled each location for three years during 2008-2010. Within each of the sites I chose transect locations at random. In the first year, I chose two transects at Atsena Otie and one transect at McClamory Key. Due to the small amount of suitable habitat I was unable to place two transects on McClamory Key. Severe erosion destroyed one section of beach at Atsena Otie between the first and second years, and thus Atsena Otie was also reduced to one transect for year two and three.

Each transect was 50-m long x 3-m wide along the high-tide line to encompass the area where horseshoe crabs lay their eggs (Collazo et. al 2002). I subdivided each transect into five quadrants (10-m long x 3-m wide), and each quadrant into 30 plots (1-m x 1-m); each quadrant and plot were numbered (Figure B-2). I sampled three plots from each reference site weekly. To identify specific plots to sample, I used a random-number generator to select quadrant and plot numbers; individual plots were not resampled during subsequent sampling periods. I sampled one core with a 10 cm diameter and 25 cm deep within each plot and subdivided each core into a shallow (0-5 cm) and deep (5-25 cm) sample. Additionally, I walked a perpendicular line from the transect starting at the plot down to the waterline and took an additional shallow core (0-5 cm), since this is the area used most frequently for foraging by shorebirds. Using this method allowed us to compare what was available to the birds at the high high-tide line with prey available at the water's edge. I stored each sample in a lock-seal plastic bag

for future analysis. After sample collection, I sieved each sample with a 1mm wide mesh sieve. I collected, identified to family (or genus if possible) and counted each invertebrate in the sample.

Foraging Sampling

For the second methodology I placed a linear transect along the foraging area, typically along the waterline. When I located a flock of foraging knots I took the first sample at the near edge of the flock and continued sampling every ten meters until I reached the far edge of the flock. Since flocks often abandoned feeding while I sampled, I noted the location of the near and far edges before sampling. I took cores 10 cm in diameter and 5 cm deep and processed them in the same manner as described for the reference samples.

Red Knot Surveys

I surveyed shorebirds in the Cedar Key region at weekly intervals from late February to mid-May. Each survey was completed within a day. Survey locations included the Cedar Key Municipal Beach, Atsena Otie, Seahorse Key, North Key (until suitable habitat eroded away in 2009), Rattlesnake Key, McClamory Key, Derrick Key and parts of the Shell Mound area (Figure B-1). Surveys were conducted by boat and/or land, depending on beach topography and accessibility, using two observers when possible to verify species identification and count. Once a flock with red knots was identified, I quantified each species then scanned red knots for leg bands and recorded band information (flag codes and color combinations).

Data Analysis

Availability of horseshoe crab eggs/larvae (i.e. differences between shallow and deep cores) and differences between reference and foraging samples were analyzed

using a non-parametric test due to the non-normal distribution of the data (PROC npar1way, SAS 2002). Data from each group was separated by month (Mar-May) and year and differences of means between groups were tested using the Wilcoxon two-sample test. Test significance was set at $\alpha = 0.05$.

Results

Overall densities of horseshoe crab eggs/larvae in the reference samples available to birds were low (5.61 eggs/larvae per sample or less, Table B-1), although individual samples could contain up to 62 eggs/larvae in shallow samples and 841 eggs/larvae in deep samples. Availability also varied from year to year and site to site. In 2008 more eggs were available on average at McClamory Key than at Atsena Otie, while in 2009 this trend was reversed. In 2010 there were no eggs available to the birds at all at either site. Eggs buried at depths between 5cm and 25cm were significantly more numerous than eggs available to the birds in April of 2009 and 2010 (Table B-2). Otherwise densities at any depth were too low to show significant differences.

Foraging samples had significantly more horseshoe crab eggs/larvae during April and May of 2008 ($p=0.0004$ ($Z=3.56$, $n=50$) and $p=0.0002$ ($Z=3.76$, $n=28$) respectively) but not in April of 2010, since there were no eggs/larvae in either reference or foraging samples ($n=29$). Foraging data is sparse however, with no data available for 2009 or March of any year. Most of these areas covered by this study were sandy beaches where red knot and horseshoe crab habitat would overlap. However the Cedar Key area supports extensive mud flats at low tide and it is likely that knots were utilizing this habitat. The inaccessibility of these flats made it nearly impossible to survey or sample them although knots were observed foraging on flats in the Shell Mound area during 2010 (pers. obs.).

Peak counts for bird surveys in the area ranged from 0-269, with overall peak counts of 121 in 2008, 100 in 2009, and 269 in 2010. Large numbers were only present from mid-April to early May each year. Red knots were only found in the area encompassing McClamory Key, Derrick Key and the Shell Mound area. A total of 28 banded individuals were seen over the three years.

Discussion

The results above demonstrate that although red knots may preferentially choose horseshoe crabs eggs and larvae for food when opportunistically available, horseshoe crab eggs and larvae likely do not serve as an important food item for red knots migrating out of or through Florida. The lack of observed foraging data for multiple months during all three years suggests that knots are regularly using inaccessible mud flats instead of sandy beaches for their foraging. Based on the biology of the horseshoe crab, one can conclude that no eggs or larvae would be available on these flats. Peak counts of knots in the Cedar Key region are very small compared to peak counts at other migratory sites in northeast Florida and southeast Georgia (P. Leary, pers. comm.) suggesting that it is not a primary stopover for migratory knots in Florida. In fact, the peak counts and band resights in Cedar Key constitute only a fraction of the entire southwest Florida knot population (~270 birds versus ~800 birds), indicating that even most “local” knots do not pass through the Cedar Key region. In addition, the majority of banded knots (i.e. 26 out of 28) resighted in Cedar Key come from the southwest Florida area and none were banded outside of the United States, demonstrating that the availability of horseshoe crab eggs does not attract interest from other migratory populations. Furthermore, the knots’ consistent (but low-level) presence in the Cedar Key region even during low spawning years and the complete absence of

knots observed on Seahorse Key, the island with the highest horseshoe spawning densities in the area (J. Brockmann, pers. comm.), provides evidence that knots in this region are selecting for factors other than the horseshoe crab. Although I did not determine what these other factors may be, this conclusion makes sense given that the highly fluctuating levels of horseshoe crab eggs available from year to year would not allow migratory birds to rely on them as a consistent food source. Migratory birds often rely on the predictability of food sources at migratory stopovers (Bairlein and Gwinner 1994) and this resource would be unsuitable for this purpose.

Table B-1. Mean horseshoe crab egg/larvae counts by site for 2008-2010.

Year	Month	Site	Mean	std
2008	March	AO	0	0
		MC	0.58	1.64
	April	AO	0.06	0.24
		MC	0.44	0.78
	May	AO	0.08	0.29
		MC	0.83	1.34
2009	March	AO	0	0
		MC	0.50	0.84
	April	AO	5.67	14.52
		MC	3.44	14.61
	May	AO	0.50	1.24
		MC	0	0
2010	March	AO	0	0
		MC	0	0
	April	AO	0	0
		MC	0	0
	May	AO	0	0
		MC	0	0

Means and standard deviations were obtained from reference samples taken during each month from March to May. Cores were 5 cm deep and had a 10 cm diameter. For site, AO = Atsena Otie and MC = McClamory Key.

Table B-2. Differences in horseshoe crab eggs/larvae buried compared to eggs available.

	2008	2009	2010
March	0.5562 (Z=-0.59, n=81)	0.9425 (Z=0.07, n=18)	1.000 (Z=0.0, n=36)
April	0.3761 (Z=0.89, n=54)	0.1945 (Z=1.30, n=55)	*0.0470 (Z=1.99, n=36)
May	0.3425 (Z=0.95, n=36)	*0.0412 (Z=2.04, n=36)	0.1753 (Z=1.36, n=36)

P-values, Z-scores, and sample sizes for a Wilcoxon two-sample, two-tailed test of means from deep and shallow samples, broken down by month and year. * - indicates significant result.



Figure B-1. Map of Cedar Key region with major resighting and invertebrate spawning locations.

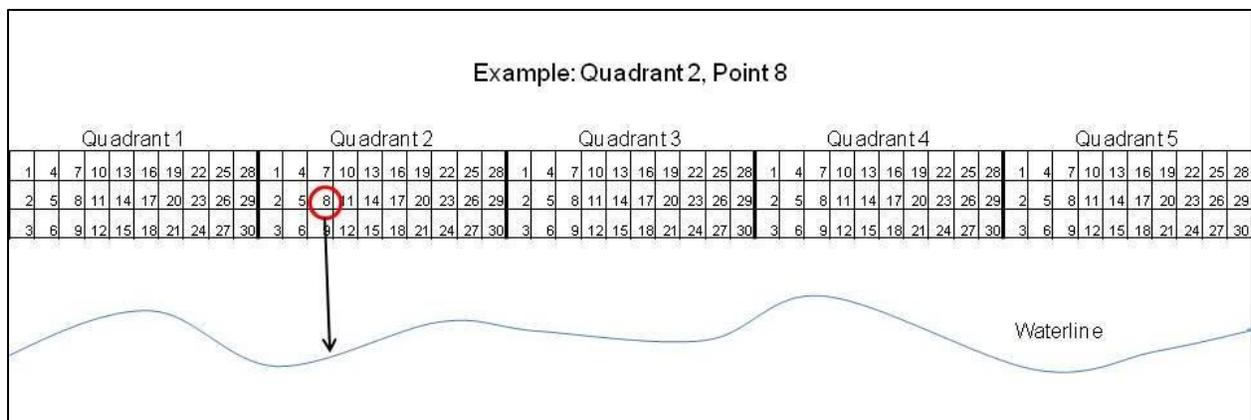


Figure B-2. Example invertebrate reference sampling plot. Two cores (0-5 cm and 5-25 cm) would be taken at the point and a third core (0-5 cm) would be taken at the waterline.

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BIOGRAPHICAL SKETCH

Amy C. Schwarzer was born and raised in the Berkshire Mountains of western Massachusetts. There she cultivated an interest in wildlife in nature through a variety of opportunities provided by family camping trips, the Girl Scouts, the local Audubon Society and even her family's backyard bird-feeders. After moving to Florida with her family she finished high school at the Pine View School in Osprey. She attended the University of Florida and graduated with a Bachelor of Arts in environmental science (policy concentration) from the School of Natural Resources in 2003. From 2000-2007 she worked in a variety of biological field positions, with a heavy emphasis on birds and conservation biology. She rejoined the School of Natural Resources in 2007 and received her Master of Science in interdisciplinary ecology in August 2011.