



ANNUAL SURVIVAL OF RED KNOTS (*CALIDRIS CANUTUS RUFUS*) WINTERING IN FLORIDA

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ABSTRACT.—Populations of Red Knots (*Calidris canutus rufa*) have declined an estimated 80% in the past 25 years. Declines are primarily attributed to dwindling food resources in Delaware Bay, their last migratory stopover before the breeding grounds. Red Knots wintering in Florida also decreased in numbers, prompting the need to estimate local vital rates to determine whether local factors contribute to declining trends. We estimated age-specific annual survival rates and compared them with estimates from populations of Red Knots wintering in South America using the Barker model. Adult annual survival rates between 2005 and 2010 averaged 0.89 ± 0.02 [SD]; range: 0.86–0.94) and were similar to estimates reported for Delaware Bay (0.87–0.92). Juvenile survival (0.95 ± 0.06 [SE]) and adult fidelity (0.81 ± 0.05 [SE]) were also high. However, juvenile survival did not include the period between fledging and arrival in Florida, a period of potentially high mortality. Similar adult survival rates suggested that there was no apparent survival cost for adults migrating to and from Florida compared with those migrating elsewhere. Factors that influence adult survival likely affect populations of *C. c. rufa* where they co-occur (e.g., breeding grounds, staging areas). Low year-to-year variation (CV = 2.24%) of adult survival suggests that other vital rates with higher variation (e.g., recruitment) may exert a stronger influence on population growth and partly account for the observed decline. Status projections require estimates of fecundity, year-round juvenile survival, and winter distribution in the United States. Received 7 December 2011, accepted 14 August 2012.

Key words: Barker model, *Calidris canutus*, Florida, Red Knot, survival, site fidelity.

Supervivencia Anual de *Calidris canutus rufa* Invernando en Florida

RESUMEN.—Las poblaciones de *Calidris canutus rufa* han disminuido un 80% en los últimos 25 años. La disminución se atribuye principalmente a la merma de alimentos en la bahía de Delaware (EEUU), la última escala antes de llegar al área de reproducción. Los *Calidris canutus rufa* que invernán en Florida también han disminuido, precipitando la necesidad de estimar tasas vitales para determinar si factores locales contribuyen a la disminución. Estimamos tasas anuales de supervivencia por edad y las comparamos con estimados de poblaciones de *C. c. rufa* que invernán en Suramérica utilizando el modelo Barker. Las tasas anuales de supervivencia de adultos entre 2005 y 2010 fueron, en promedio, de 0.89 (SD = 0.02; rango: 0.86–0.94), y fueron similares a las reportadas para la bahía de Delaware (0.87–0.92). La supervivencia de aves juveniles (0.95 ± 0.06 SE) y la fidelidad de los adultos (0.81 ± 0.05 SE) también fueron altas. Sin embargo, la supervivencia de los individuos juveniles no incluyó el periodo entre el emplumamiento y la llegada a Florida, un periodo potencialmente de alta mortalidad. La similitud entre las tasas de supervivencia de los adultos sugiere que no hubo un costo aparente para la supervivencia de los adultos que migran hacia o desde Florida, comparado con los que migran a otras partes. Los factores que afectan la supervivencia de los adultos posiblemente afectan otras subpoblaciones de *C. c. rufa* donde éstos convergen (e.g., áreas de reproducción o de escala migratoria). La baja variación anual (CV = 2.24%) en la supervivencia de los adultos sugiere la posibilidad de que otras tasas vitales con mayor variación (e.g., reclutamiento) ejerzan una influencia más fuerte sobre el crecimiento poblacional y expliquen parcialmente la disminución observada. Las proyecciones de estado poblacional requieren estimados de fecundidad, de supervivencia de aves juveniles a lo largo del año y del conocimiento de la distribución invernal de *C. c. rufa* en los Estados Unidos.

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THE RED KNOT (*Calidris canutus*; hereafter “knot”) is a long-lived migratory sandpiper species that occurs worldwide and is divided into six recognized subspecies (Harrington 2001). *Calidris c. rufa* occurs in the Western Hemisphere, and the majority winter in Tierra del Fuego (about 14,000–17,000 individuals). Smaller groups winter in Brazil and the United States (about 3,000–6,000 and 2,500–3,000, respectively; Niles et al. 2008, L. J. Niles unpubl. data). The *rufa* population has decreased an estimated 80% over the past 25 years (Niles et al. 2008). Declining trends are also exhibited by the *rufa* population wintering in Florida (L. J. Niles et al. unpubl. data). Florida is home to the largest concentration of wintering *rufa* in the United States, with the main concentration occurring in the greater Tampa Bay region. Aerial surveys conducted during 1980–1982 estimated approximately 6,500–10,000 wintering knots from Cape Romano to Anclote Key (Harrington et al. 1988, Morrison and Harrington 1992). Surveys conducted over the past 5 years suggested that this population had dwindled to approximately 1,000–1,500 knots (L. J. Niles et al. unpubl. data).

At least eight shorebird species, in addition to the knot, exhibit significant declining trends in the North Atlantic region (Bart et al. 2007). Negative trends are also evident for species migrating through the continental United States (Thomas et al. 2006) and at the breeding grounds (e.g., Page and Gill 1994; Gratto-Trevor et al. 1998, 2001; Jehl and Lin 2001). The pervasive nature of declines prompted efforts not only to identify the underlying ecological mechanisms behind them, but also to improve the statistical foundation used to monitor and derive population trends (Brown et al. 2001). A substantial body of work has recently been published on the intricacies and challenges posed by monitoring shorebirds at multiple scales (e.g., Bart et al. 2005, 2007; Brown et al. 2007). Identifying the mechanisms that regulate shorebird populations continues to be a challenge (Colwell 2010), but advances in methodology are helping to address and unravel this question, central to shorebird conservation (e.g., Harrington et al. 2002, Sandercock 2003, Thomas et al. 2006, McGowan et al. 2011).

Identifying the underlying mechanism behind the knot’s population decline, as with other species, has been hampered by a lack of information on vital rates. In recent years, interest has focused on the relationship between adult survival rates and foraging habitat quality at Delaware Bay, where wintering populations converge prior to migration to the breeding grounds (Baker et al. 2004). A steep reduction in the knots’ primary food source at the bay, Horseshoe Crab (*Limulus polyphemus*) eggs, had been singled out as a contributor of the species’ decline (Tsipoura and Burger 1999, Karpanty et al. 2006, Haramis et al. 2007). Purportedly, deteriorating foraging conditions at the bay hamper the ability of adults to gain the body mass needed to survive and breed successfully. For many avian taxa, especially longer-lived species, adult survival is the vital rate that is most influential on changes in population growth (Pfister 1998, Sæther and Bakke 2000, Stahl and Oli 2006). In a recent study, McGowan et al. (2011) found support for a positive relationship between Horseshoe Crab spawning abundance and the probability of gaining mass. However, support for the link between mass gain and adult survival was poor. Instead, McGowan et al.’s (2011) study raised the possibility that other factors, such as arctic weather conditions on the breeding grounds, exerted a stronger influence on adult survival.

There have been no estimates of vital parameters for distinct populations such as those wintering in Florida. Without

population-level estimates, it is difficult to identify threats and potential actions at local levels that might affect population size and persistence. Here, for knots wintering in southwestern Florida, we report annual survival of adults and of individuals banded as juveniles. Our survival estimates are based on mark-resight data collected from 2005 to 2010 and analyzed using the Barker model (Barker 1997). Estimates of survival can be biased low because traditional Cormack-Jolly-Seber models confound emigration with mortality (Lebreton et al. 1992). The Barker model (Barker 1997, 1999) can separate survival from emigration, provided that birds emigrating from Florida wintering sites were available to be resighted elsewhere in their breeding, wintering, or migratory ranges. These data were readily available because knots are intensively banded and monitored throughout the eastern coast of the Western Hemisphere. This approach has been used successfully with migratory species such as waterfowl (e.g., Sedinger et al. 2002) and several shorebird species (Sagar et al. 2002, Cohen et al. 2006, Stenzel et al. 2007, LeDee et al. 2010). We also determined whether annual survival rates of adults banded in Florida differed from estimates obtained at Delaware Bay. We assumed that annual survival estimates reported by McGowan et al. (2011) represented rates of the *rufa* populations wintering in South America, given that these birds comprise $\geq 90\%$ of annual migrants at Delaware Bay (Niles et al. 2008). Similar survival rates would indicate that factors that impinge on survival rates act largely on the whole subspecies, likely where populations of knots co-occur (e.g., northbound migration, breeding grounds). Lower rates for Florida would indicate that knots contend with local factors not encountered by populations wintering elsewhere. Conversely, higher rates in Florida could be a function of different migration strategies among the populations, where the trade-off would be between adult survival and reproductive success (Belthoff and Gauthreaux 1991). Hypotheses to account for the observed population decline of *rufa* center on adult survival and its relationship with food resources at Delaware Bay (Baker et al. 2004, McGowan et al. 2011). We discuss the support for this hypothesis in light of our results and explore alternatives that merit formal consideration. We also discuss how other factors (e.g., distance traveled, foraging habitat quality) might influence migration and wintering distribution of knots and how these might influence survival of adults in Florida.

METHODS

Study area.—Knots were captured and banded along the southwest Gulf coast of Florida from October to March between 2005 and 2010. Banding locations included Sanibel Island, North Captiva Island, and the greater Tampa Bay area, including Longboat Key and Lido Key (Fig. 1). Not all locations were trapped each year, but captures took place at two or more locations per winter. Resight data were collected across multiple locations and grouped into two sampling phases for analysis with the Barker model (Barker 1997; see below). Any bird seen within Florida in any given year was defined as coming from the primary sampling area, and any bird seen outside the state during the same period or the remainder of the year was defined as being in the secondary sampling area. Secondary sampling areas included Delaware, New Jersey, Georgia, Virginia, Massachusetts, North and South Carolina, and Ontario (Fig. 1).

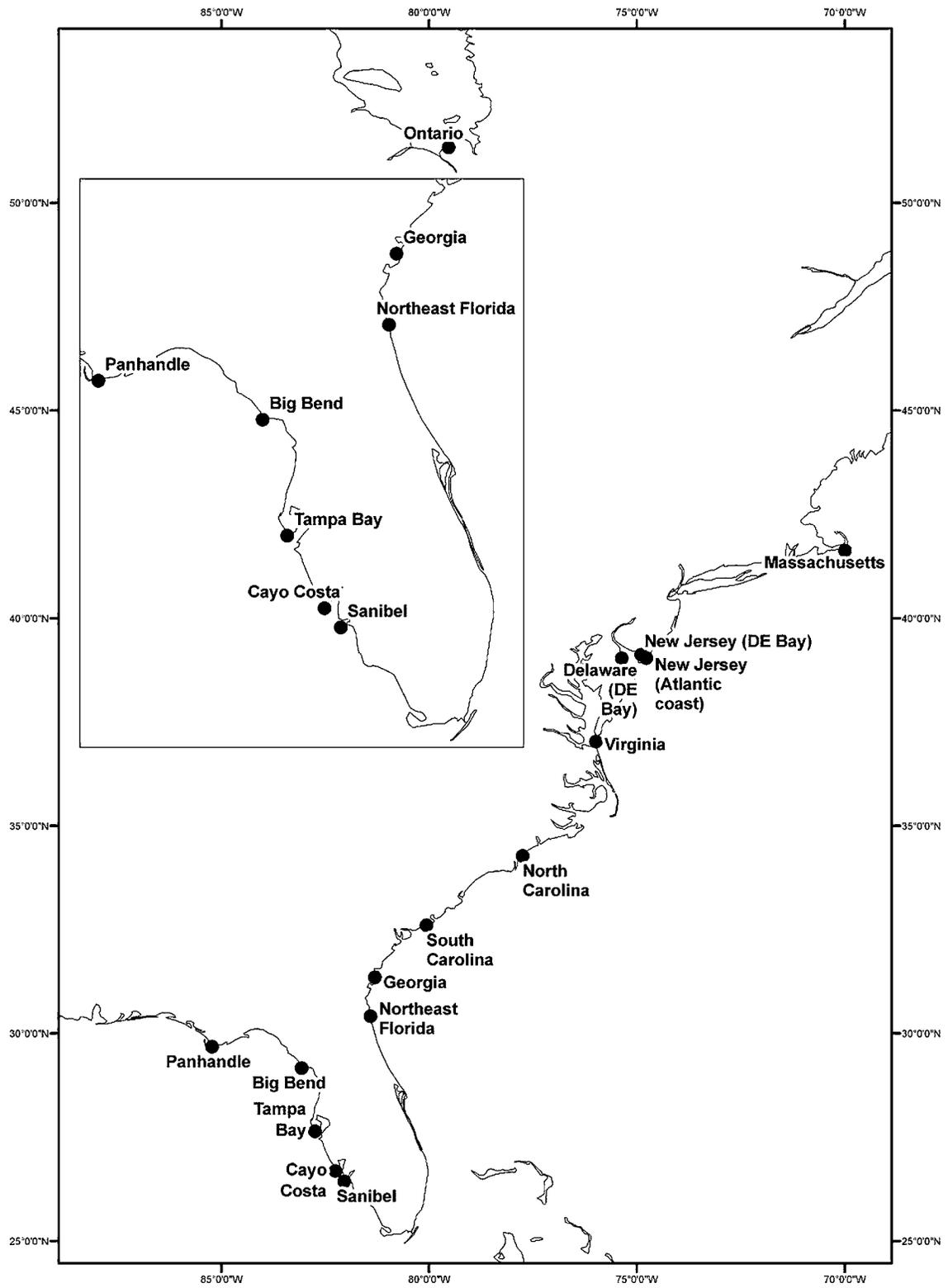


FIG. 1. Banding and resighting locations for Red Knots in Florida within the primary study area (inset), as well as the resighting locations in the secondary study area along the Atlantic coast.

Field methods.—At least 90 knots were captured per winter, exceeding 1,700 captures for the 5-year period. Birds were captured using cannon nets, banded with a federal incoloy band, and marked on the tibiotarsus with a plastic flag engraved with a unique alphanumeric code. Each bird was aged (when unambiguous) as adult (after-hatching-year [AHY]) or juvenile (juvenile captured in Florida [HY_{FL}]), weighed to the nearest gram, and the culmen (exposed bill from base to tip) was measured to the nearest 10th of a millimeter. In addition, we collected blood samples from a subset of captured birds for plasma metabolite analysis during the winters of 2008–2009 and 2009–2010. During the winter of 2008–2009, we bled 50 birds (11.7% of total captures). During 2009–2010, we bled 148 birds (49.2% of total captures). We do not believe that bleeding birds for this purpose was a source of mortality, given that the amount of blood was ~ 70 μ L, an amount successfully and widely used in other shorebird studies (Guglielmo et al. 2005, Lyons et al. 2008). We obtained data from organized resighting efforts both within and outside of Florida, as well as opportunistic sightings by the general birding public obtained through the bandedbirds.org database. Additional data were collected during the winters of 2007–2010 in the Tampa Bay region. Banding protocols were sanctioned under the University of Florida IFAS Animal Research Committee, protocol number 004-08SNR, and the Florida Fish and Wildlife Conservation Commission's U.S. Fish and Wildlife Service Bird Banding Permit 21980.

Data analysis: Survival estimates.—We estimated age-specific survival using the Barker model in Program MARK (Barker 1997, White and Burnham 1999). We opted for this analytical framework instead of other mark–recapture frameworks because the Barker model focuses on obtaining an apparent survival estimate that approaches true survival by separating permanent emigration from true mortality and relaxing the assumption of no permanent emigration. We 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 year i was present in either the primary (peninsular Florida) or secondary (Atlantic seaboard) sampling area during year $i + 1$ (Barker 1997). “Juvenile survival” refers to the probability that a wintering juvenile will survive to the next winter. We used the notation “ HY_{FL} ” to distinguish survival during this period from “true” juvenile survival, estimated from the time of hatching or fledging. We used encounter histories of 1,348 individually marked knots captured and resighted within the primary sampling area of Florida and resighted within the secondary sampling area along the Atlantic coast. These data permitted 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., Fernández 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 are biased low when taken as estimates of true survival because they combine these two parameters.

Barker models estimate seven kinds of parameters (Barker 1997). Of relevance to the present study were survival (S_i), recapture probability (p_i , the probability that an animal at risk of capture at trapping occasion i is captured), and two movement-related parameters: F_i (fidelity, the probability that an animal at

risk of capture in the primary study area at i is at risk of capture at $i + 1$) and F'_i (re-emigration, the probability that an animal not at risk of capture in the primary study area at i is at risk of capture at $i + 1$). In our study, birds were physically captured first, with a small percentage being physically recaptured on an additional occasion ($\sim 15\%$). All other “captures” refer to visual resightings. These parameters are related to the probability of being available for sampling in the primary study area (e.g., peninsular Florida), depending on location during winter the previous year. Parameter r_i is the probability that an animal that dies in $i, i + 1$ is found dead and reported; R'_i is the probability that 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 in our analysis or because the data consisted of live birds only (W. Kendall, Colorado State University; R. Barker, University of Otago, New Zealand, pers. comm.). F'_{HY} was fixed because HY_{FL} become adults and there were no birds marked outside the primary study area to estimate this transition between sampling areas. The remaining parameter, R_i , is the probability that a marked animal that survives from i to $i + 1$ is resighted alive between i and $i + 1$.

We created a candidate set of 14 models to evaluate the evidence for constant or time-specific survival rates, detection rates, and emigration or re-emigration rates for HY_{FL} and adults. The standard parameterization in MARK for movement is Markovian (i.e., the availability of a knot to be captured is conditioned on the state [available or not] during the previous occasion). However, we 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 ($F'_i = 0$). We applied these tests to the Markovian model with the highest support.

We used Akaike's information criterion corrected for small sample sizes (AIC_c) to select the most parsimonious model (Burnham and Anderson 2002). Models were ranked by AIC_c , and the model with the minimum AIC_c value was the model with the most support in the data. The difference in AIC_c values (ΔAIC_c) between the best-supported model and any other model was used to calculate model weights (w_i), which indicate the relative likelihood of the model given the data and the model set (Burnham and Anderson 2002). Models with $\Delta AIC_c \leq 2$ were considered models with highest support, provided that such models were not more complex versions of a simpler and better-supported model (Burnham and Anderson 2002). Parameter estimates are reported \pm SE, except for the average adult survival rate. We report the average adult survival of the four annual estimates and the estimated standard deviation (SD) owing only to process variance. We used the variance components option in MARK to estimate the underlying process variance for adult survival (Lande 1988, Gould and Nichols 1998, Gaillard et al. 2000).

We assumed that annual survival estimates reported by McGowan et al. (2011) represented rates of the *rufa* populations wintering in South America because 90–95% of birds staging in the Delaware Bay overwinter there (Niles et al. 2008). We also assumed that survival rates obtained at Florida wintering sites and at Delaware Bay stopover sites had similar biological interpretation because they represent estimates based on a complete annual cycle. Finally, we followed assumptions of the Barker and standard

mark–recapture models. However, we cannot claim that every bird in peninsular Florida and elsewhere had equal probability of being captured. Therefore, we used the median \hat{c} procedure in MARK to estimate a variance inflation factor to adjust for the possibility of violating the assumption 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 $i + 1$. Double-observer surveys and secondary readings of already-recorded bands were used to reduce the possibility of recording errors.

RESULTS

Model selection was adjusted for overdispersion; median $\hat{c} = 1.29$. Survival of adults (AHY) and HY_{FL} was best explained by a model that featured constant survival for HY_{FL} , time-specific survival for adults, time-specific detection probability, and age-specific emigration and re-emigration probabilities ($w_i = 0.62$; Table 1). There was also some support for models that recognized similar fidelity probability between juveniles and adults ($w_i = 0.19$) and for time-specific survival rates for adults and juveniles (QAIC_c $w_i = 0.15$).

The model with the highest support yielded estimates of adult survival that ranged from 0.860 ± 0.023 to 0.937 ± 0.032 (Table 2); the average annual adult survival rate was 0.89. The estimated standard deviation owing to process variance for adult survival was 0.02 (95% confidence interval: 0–0.12). Survival rate for HY_{FL} was 0.946 ± 0.067 . The estimated probability of birds banded as juveniles in Florida returning as adults during the following winter was 0.70 ± 0.08 (F HY_{FL}). The estimated probability of winter-to-winter fidelity for adults banded in Florida was 0.81 ± 0.05 (FAHY). The estimated probability of adults returning to

Florida, given that they were outside Florida the year before, was 0.22 ± 0.08 (F'AHY; Table 2). Model-averaged parameters of adult and juvenile (HY_{FL}) survival and fidelity parameters (F HY_{FL} and F) were nearly identical to estimates from the top-ranked model. For example, model-averaged juvenile survival was 0.925 ± 0.041 ; for adults it ranged from 0.859 ± 0.022 to 0.937 ± 0.031 .

DISCUSSION

Annual adult survival rates of knots wintering in Florida were as high as or higher than rates reported in other shorebird species. Sagar et al. (2002) reported an average survival rate of 0.89 for Finsch's Oystercatcher (*Haemetopus finschi*), whereas Cohen et al. (2006) and LeDee et al. (2010) found average rates of 0.70 and 0.76, respectively, for different populations of Piping Plovers (*Charadrius melodus*). All three studies used the Barker model in their analyses. Annual survival rates of knots wintering in Florida were also similar to rates of knots staging at Delaware Bay, predominantly winterers from South America. The 95% confidence intervals about the average survival estimate for knots wintering in Florida overlapped the survival rates reported for heavy (≥ 180 g = 0.92) and light (< 180 g = 0.91) birds from Delaware Bay during 1997 to 2007 (McGowan et al. 2011). Between 2005 and 2007, survival estimates for heavy birds in Delaware Bay ranged from 0.91 to 0.92, and from 0.87 to 0.90 for light birds while Florida survival estimates ranged from 0.86 to 0.94 for the same years.

Similar adult survival rates lead to several important implications. First, they did not indicate an obvious and adverse consequence for adults that migrated to and from Florida compared with birds that migrated elsewhere. Second, given the similar survival rates of birds that migrated to different locations, it is likely that factors that influence adult survival do so where populations of *rufa* co-occur (e.g., Atlantic migratory flyway, breeding grounds). This possibility would be consistent with

TABLE 1. Top models for annual survival of banded adult Red Knots (after-hatch-year [AHY]) and of banded juvenile Red Knots captured in Florida (HY_{FL}), 2005–2010. Model parameters^a: S = survival probability from period i to $i + 1$, p = capture probability, R = probability of live encounters outside the study area, F = probability that a bird banded in the study area will remain in the area in the next period, F' = probability that a bird that emigrated from the primary study will re-emigrate to the study area; (.) = constant. QAIC_c for the top model = 5,695.16. k = number of parameters. w_i = model weight.

Model	Δ QAIC _c	w_i	k	QDeviance
S(HY_{FL} (.), AHY(year)), p(year), R(.), F(age), F'(HY _{FL} =0, AHY)	0.00	0.62	13	650.73
S(HY_{FL} (.), AHY(year)), p(year), R(.), F(.), F'=0	2.33	0.19	12	655.08
S(age*year), p(year), R(.), F(age), F'(HY _{FL} =0, AHY)	2.79	0.15	16	647.46
S(HY_{FL} (.), AHY(year)), p(year), R(.), F(HY_{FL} (.), AHY(year)), F'(HY _{FL} =0, AHY(year))	5.98	0.03	18	646.61
S(age), p(year), R(.), F(age), F'(HY _{FL} =0), AHY(.))	24.35	0	10	681.13
S(HY_{FL} (.), AHY*year), p(.), R(.), F(age), F'(HY _{FL} =0), AHY(.))	29.91	0	13	680.64
S(age), p(age*year), R(.), F(age), F'(HY _{FL} =0), AHY(.))	74.27	0	10	731.05
S(HY_{FL} (.), AHY*year), p(t), R(.), F=F'	85.94	0	12	738.69
S(HY_{FL} *year, AHY=(.)), p(.), R(.), F(age), F'(HY _{FL} =0), AHY(.))	108.21	0	9	767.00
S(HY_{FL} (.), AHY(.), p(.), R(.), F(HY_{FL} (.), AHY(.)), F'(HY _{FL} =0, AHY(.))	108.70	0	9	767.49
S(HY_{FL} (.), AHY*year), p(t), R(.), F(age), F'(HY _{FL} =0, AHY(.))	1,642.00	0	12	650.73
S(age*year), p(year), R(.), F(age), F'(HY _{FL} =0, AHY(.))	1,643.83	0	15	647.46
S(HY_{FL} (.), AHY(year)), p(year), R(.), F(HY_{FL} (.), AHY(year)), F'(HY _{FL} =0), AHY(year))	1,646.78	0	17	646.61
S(age), p(age*year), R(.), F(age), F'(HY _{FL} =0), AHY(.))	1,682.33	0	13	680.43

^ar and R' (probability of encountering dead animals inside and outside of primary study area) set to zero because we did not use dead encounters.

TABLE 2. Parameter estimates from the top model $S(HY_{FL}(\cdot), AHY(\text{year}), p(\text{year}), R(\cdot), F(\text{age specific}), F'(HY_{FL}=0, AHY))$ listed in Table 1. Model parameters^a: S = survival, p = capture probability, R = probability of live encounters outside the study area, 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 and p for 2009–2010 were fixed at 1. (\cdot) = constant, t = time-specific.

Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI
$S(HY_{FL})$ 2005–2010	0.9462	0.06767	0.5647	0.9958
$S(AHY)$ 2005–2006	0.9368	0.03194	0.8373	0.9771
$S(AHY)$ 2006–2007	0.8597	0.0231	0.8080	0.8993
$S(AHY)$ 2007–2008	0.9166	0.0247	0.8535	0.9540
$S(AHY)$ 2008–2009	0.8796	0.0241	0.8237	0.9195
p (2005–2006)	0.4981	0.0512	0.3991	0.5972
p (2006–2007)	0.6881	0.0398	0.6052	0.7605
p (2007–2008)	0.6962	0.0397	0.6133	0.7681
p (2008–2009)	0.9980	0.0764	0.000001	1.0000
r	0.3181	0.0110	0.2968	0.3401
$F(HY_{FL})$	0.6996	0.0828	0.5181	0.8346
$F(AHY)$	0.8083	0.0238	0.7572	0.8507
$F'(AHY)$	0.2218	0.0594	0.1267	0.3587

^a r and R' (probability of encountering dead animals inside and outside of primary study area) set to zero because we did not use dead encounters. F' for juveniles was fixed to zero because juveniles become adults in year $t + 1$.

observed declines across all populations of *rufa*. Lastly, the similarity was noteworthy because populations of *rufa* spend much of the non-breeding portion of their annual cycle in different locations. This implies that distance traveled to different wintering grounds may not affect adult annual survival differentially. Ketterson and Nolan (1982) and Varner and Eichholz (2012) found similar patterns in annual survival for short- and long-distance migrant populations of Dark-eyed Juncos (*Junco hyemalis*) and Trumpeter Swans (*Cygnus buccinator*), respectively. These results are also in keeping with those of Myers et al. (1984), who assessed why different populations of Sanderlings (*Calidris alba*) traveled different distances to overwintering grounds. Western populations of Sanderlings exhibit a migration and winter distribution pattern akin to that of the knot, in that one smaller population overwinters in California, whereas the bulk of the species winters in South America. Myers et al. (1984) evaluated four hypotheses that could account for this migration and distribution pattern and concluded that availability and predictability of food resources, not tradeoffs between annual survival and reproductive success, were stronger determinants of migration patterns and distribution of wintering Sanderlings.

Myers et al.'s (1984) findings suggest that the higher numbers of knots wintering in southern latitudes may also be driven by resource availability. Direct comparisons of food availability between wintering sites in Florida and South America are not currently possible; however, reports from South America (Harrington 2001) and Florida (Schwarzer 2011) suggested that prey items sought by knots, particularly the clam *Donax*, are more abundant in southern South America during the core of the non-breeding season (December–February). If this is so, how can knots wintering in the northern extent of the wintering range (e.g., Florida)

offset this differential in foraging quality without a detectable reduction in survival? A plausible mechanism may be that knots wintering in Florida and Brazil are morphometrically larger than those wintering in Tierra del Fuego (Niles et al. 2006). Larger birds may be more adept at competing for scarce food resources and, therefore, dominate northern beaches (Ketterson and Nolan 1976). Larger body size may also allow birds to cope better with physiologically demanding conditions, caused either by lower food resources or more variable weather patterns (Ketterson and Nolan 1976, Belthoff and Gauthreaux 1991).

The relatively high survival rate of HY_{FL} birds (0.95) likely reflects the fact that our estimate did not include the earliest portion of the juvenile annual cycle (fledging and first migration) when mortality is generally high (Martin 1995, Opper and Powell 2010). The high rate also may be explained by some knots not breeding until their second adult year, thus migrating only part way to the breeding grounds during their first adult year or skipping migration altogether. In such cases, mortality risks would be higher for breeding adults (e.g., increased predation risk) than for first-year adults. Therefore, juveniles banded in Florida could also exhibit high survival rates by avoiding the risks of migration and breeding during their first year of adult life.

Interest in discerning the mechanisms that are driving the population declines in knots was the impetus for our study. The effect of dwindling food resources in Delaware Bay on adult survival rates has been the primary focus of hypotheses attempting to explain these declines (Baker et al. 2004, McGowan et al. 2011). The importance of site quality and availability to sustain shorebird populations annually was underscored by the findings of Myers et al. (1987) and Thomas et al. (2006). Yet our results and those of McGowan et al. (2011) indicate that knots have high adult survival, which is difficult to reconcile with the observed declines. The importance of adult survival in the population dynamics of shorebirds is well documented (e.g., Evans 1991) and has been underscored by sensitivity and elasticity assessments (e.g., Hitchcock and Gratto-Trevor 1997, Davis et al. 2001, Stahl and Oli 2006). Sensitivity and elasticity assessments are aimed at identifying the vital rate that produces the greatest change in population growth (λ), and we would expect that such an assessment would single out adult survival in knots as the rate with most influence on growth. Thus, we cannot discard the possibility that historical conditions may have been markedly different, possibly coupled with lower adult survival rates than reported here.

Estimates of adult survival from Florida ranged from 0.86 to 0.94 but exhibited low year-to-year variation ($CV = 2.24\%$). Vital rates whose coefficients of variation are low ($<10\%$) may not have as much of an effect on annual variation in population growth as those with higher temporal variation (Lande 1988, 1993; Gaillard et al. 1998, 2000; Sæther and Bakke 2000). High annual adult survival and its low year-to-year variation suggest that the observed decline of knots could be a consequence of declines of other vital rates, such as low and temporally variable reproduction or recruitment (Sæther and Bakke 2000, Nichols and Hines 2002, Gaillard and Yoccoz 2003). For example, Van Den Hout et al. (2008) reported that falcon predation on knots wintering at Mauritania disproportionately targeted juveniles. Under such circumstances, it is possible that predation could play a

population regulatory function by suppressing recruitment, but not be detectable via the estimation of adult survival rates as in the present study. McGowan et al. (2011) suggested that adult survival was positively influenced by higher levels of snowfall on the breeding grounds, which provide the moisture needed in this water-limited system for sufficient production of insect prey (Noy-Meir 1973). Depressed food levels during migration or on the breeding grounds might also reduce fecundity, either by precluding birds from breeding or by causing fledging rates to be low (Baker et al. 2004, Thomas et al. 2006, McGowan et al. 2011). These possibilities are in concert with the findings of Bart et al. (2007). Their assessment of survey trends of North American shorebirds suggested that the most likely mechanism of population declines was a reduction in the size of breeding populations and poor reproductive output.

We acknowledge that the low temporal variation associated with adult survival rates in the present study could have been an artifact of when data were collected (2005–2010). Link and Nichols (1994) reported marked differences in temporal variation in wintering population sizes of Black-capped Chickadees (*Poecile atricapillus*), depending on the period sampled between 1958 and 1983. Therefore, we suggest that long-term data, such as those used by McGowan et al. (2011), should be used to assess the relative importance of vital rates on population growth of knots. Demographic assessments would benefit from reliable estimates of reproductive success, early juvenile survival (i.e., fledging to wintering grounds), and recruitment, as well as winter surveys across the Atlantic and Gulf coasts to account for possible shifts in the distribution of *rufa*. On this last point, it is pertinent to note that knots banded in Florida between 2005 and 2010 had high fidelity rates ($FHY_{FL} = 0.70$; $FAHY = 0.81$) as well as an adult re-emigration rate ($F'AHY$) of 0.22. Ultimately, comprehensive demographic and vulnerability assessments will require estimates of reproductive rates and age-specific survival throughout the species' annual cycle. Because population growth is influenced by all demographic rates (i.e., survival, reproduction, and movement), conservation strategies should target those rates that can be influenced by management actions (Nichols and Hines 2002).

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