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THE INFLUENCE OF BODY CONDITION ON LOCAL APPARENT SURVIVAL OF SPRING MIGRANT SANDERLINGS IN COASTAL NORTH CAROLINA

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Abstract. Many shorebirds are long-distance migrants, and they depend upon widely spaced stopover sites for refueling during their annual migrations. Two competing hypotheses attempt to explain stopover duration: one predicts departure based on time minimization (time-selection hypothesis) and the other predicts departure on the basis of maximum energy gain (energy-selection hypothesis). During spring 1993, we tested these hypotheses during a mark-resight study of migrant Sanderlings (*Calidris alba*) at Portsmouth Island, North Carolina. We individually color-banded 204 Sanderlings and used capture-recapture methods to estimate local apparent survival during 10 five-day intervals from late April to mid-June. We found that survival rates were best modeled as a decreasing quadratic time trend; a linear time trend and period-specific survival rates received little support. We found no evidence that either body mass or a simple body condition index better explained survival rates. Our estimates of the 5-day local survival rates of Sanderlings at Portsmouth Island remained relatively high ($\phi_i > 0.80$) through late May, after which they dropped rapidly as birds left the area. The period-specific conditional resighting probability was 0.39 (SE = 0.03). Our results do not provide strong support for either the time- or energy-selection hypotheses and hint that studies of migratory behavior need to be conducted even more intensively and across much larger regions in order to better understand the underlying factors.

Key words: body condition, Calidris alba*, North Carolina, Sanderling, shorebird, survival.*

Influencia de la Condición Física sobre las Tasas de Residencia de *Calidris alba* durante la Migración de Primavera en la Costa de Carolina del Norte

Resumen. Muchos playeros migran largas distancias y dependen de áreas ampliamente esparcidas para hacer escalas durante sus migraciones anuales. En estas áreas, los playeros reabastecen rápidamente sus reservas energéticas antes de partir hacia la próxima parada. Existen dos hipótesis principales para explicar la duración de cada escala: una predice que la duración de cada escala es en función de poder minimizar el tiempo (hipótesis de selección temporal) y la otra que el tiempo de escala es determinado sobre la base de maximizar la ganancia de energía (hipótesis de selección energética). Durante la primavera de 1993 pusimos a prueba estas hipótesis durante un estudio sobre captura-recaptura del playero *Calidris alba* en la Isla de Portsmouth, Carolina del Norte. Marcamos individualmente 204 playeros y usamos el método de captura-recaptura para estimar las tasas de residencia durante 10 intervalos de 5 días entre finales de abril y mediados de junio. Los modelos que mejor explicaron las tasas de residencia revelaron una tendencia cuadrática decreciente. Los datos no apoyaron modelos de tendencia lineal ni tasas de residencia período-específicas. No encontramos evidencia de que el peso corporal ni un índice simple de condición física contribuyesen a explicar mejor las tasas de residencia. Nuestras estimaciones de las tasas de residencia a 5-días para *C. alba* en la Isla de Portsmouth permanecieron relativamente altas ($\phi_i > 0.80$) durante la segunda mitad de mayo, y disminuyeron rápidamente hasta que los playeros partieron del área. La probabilidad condicional de recuperación visual período-específica fue de 0.39 (EE = 0.03). Nuestros resultados no demostraron evidencia concluyente a favor de ninguna de las dos hipótesis (selección temporal, selección energética). Sugerimos que esta información resalta la necesidad de llevar a cabo estudios detallados a través de regiones geográficamente más amplias para poder entender qué factores explican mejor el comportamiento migratorio.

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INTRODUCTION

Many shorebirds undergo lengthy annual migrations from their Arctic breeding grounds to wintering areas in temperate and tropical regions (Myers et al. 1987). How shorebirds invest time and energy during migration is of critical importance to their fitness. Regardless of the distance traveled, south- and northbound migrants are under different time constraints. Southbound migrants must reach a migratory terminus that maximizes overwinter survival, but constraints are not particularly tight (Gudmundsson et al. 1991). Northbound migrants operate under a different scenario. Individuals must meet nutritional requirements for migration and reproduction under the constraints of reaching the breeding grounds on time to compete successfully for territories and mates (Morrison 1984, Johnson and Herter 1990).

Many migrating shorebirds stop at one or more stopover sites where they rest and refuel for the next leg of migration. Some authors distinguish staging areas (extended stopover for considerable fat deposition) from stopover sites (shorter stopover and less fat deposition; Skagen and Knopf 1994). Alerstam and Lindström (1990) and Gudmundsson et al. (1991) proposed two hypotheses to account for the selection of and time spent on migratory stopover sites. The time-selection hypothesis states that shorebirds minimize the time they spend on migration, bypassing poorer sites in favor of sites where potential energy gains are greater. Under this scenario, length of stay is lower for individuals that arrive in better body condition. The competing energy-selection hypothesis states that shorebirds migrate to the next stopover site as soon as their fat reserves allow them to cover the distance safely, regardless of the quality of the next site. In both cases, departure from an area is a function of body condition. Thus, regardless of the strategy followed by migratory shorebirds, birds in better body condition should depart from stopover sites faster than birds in poorer condition. Lyons and Haig (1995) later suggested that spring migrant shorebirds operated under time-selected migration while fall migrants exhibited an energy-selected strategy. The relationship between body condition and length of stay at stopover sites for shorebirds has been the focus of many studies (Gudmundsson et al. 1991, Holmgren et al. 1993, Skagen and Knopf 1994, Lyons and Haig 1995, Warnock and Bishop 1998, Pfister et al. 1998), but few have found a relationship between these variables.

An essential requirement to test either the time- or energy-selection hypothesis is that body condition be a factor influencing stopover duration. In previous studies of the stopover ecology of shorebirds, radio-telemetry has been used to examine this relationship (see Warnock and Bishop 1998). Radio-telemetry increases detection probability to near 1, but raises concern for possible negative effects on survival resulting from the attachment of the radio-transmitter. We chose a different analytical approach that utilized capture-recapture theory and the flexibility to model the effects of body condition on local apparent survival. The underlying theoretical basis, assumptions, and robustness of our analytical approach are well developed and tested (Pollock et al. 1990, Lebreton et al. 1992, White and Burnham 1999). In this study, we estimated local apparent survival as a function of body condition for migratory Sanderlings (*Calidris alba*) using a segment of North Carolina's Outer Banks in spring 1993. This information is necessary to (1) better understand the mechanisms influencing migration and stopover use by shorebirds, (2) aid in the understanding of the dynamics of migrant shorebirds on the Outer Banks, (3) provide a basis to assess the importance of the Outer Banks as a staging area for Atlantic Flyway Sanderlings, and (4) help improve sampling designs to monitor migratory shorebirds.

METHODS

STUDY AREA

We studied Sanderlings along the Outer Banks on the central coast of North Carolina (Fig. 1). This area is a series of narrow barrier islands approximately 228 km in length, stretching from just south of Nags Head in Dare County to Beaufort Inlet in Carteret County. Much of this area is part of Cape Hatteras and Cape Lookout National Seashores. On the basis of a pilot study in 1992, we restricted our work to Portsmouth Island (34°57′N, 76°11′W), a 36-km barrier island at the north end of Cape Lookout National Seashore; other areas of the seashore had insufficient numbers of Sanderlings during the study period. The topography was typical of barrier islands, with a low elevation and flat relief. Outer beach habitat occupied by Sanderlings was

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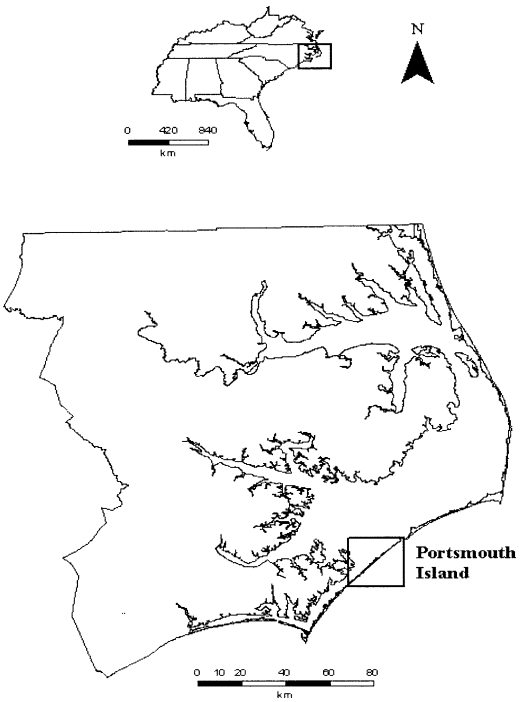

FIGURE 1. Map of coastal North Carolina showing the Outer Banks and Portsmouth Island.

devoid of vegetation. Mean tidal amplitude was approximately 1 m.

CAPTURE AND MARKING

Sanderlings were captured at communal roosts with an 18 × 9 m rocket net. All birds were fitted with an aluminum U.S. Geological Survey numbered leg band and a series of three colored, UV-stable PVC leg bands (A.C. Hughes, London) arranged in a unique combination. Color-band combinations were derived from 10 possible colors, which were picked to minimize reading errors. Color-band seams were fused to reduce band loss. Before release, each bird was weighed to the nearest 0.5 g and measures of natural wing chord and exposed culmen were taken (both to nearest 0.1 mm). We did not attempt to age birds (see Prater et al. 1977), so all our analyses pertain to a single age class (birds >9 months of age). Most shorebirds, including Sanderlings (Prater et al. 1977, Summers et al. 1987, Soloviev and Tomkovich 1995), are sexually dimorphic with females typically having longer bills. Sanderlings exhibit this general pattern of sexual dimorphism, but because of considerable overlap and our inability to sex birds using laparotomies (Maron and Myers 1984), we did not determine sex of the birds in our sample. Sanderlings were released at the capture site within 1 hr of capture.

Surveys of Portsmouth Island for marked Sanderlings were done by four-wheel-drive vehicle; we did not search other areas. Surveys always lasted a single day and occurred at 5-day intervals from 22 April to 11 June 1993. These surveys are hereafter referred to as resighting periods. All recaptures occurred by live resightings; we did not physically recapture any birds. Very large concentrations of Sanderlings (>500 birds) were rare, which increased the ease of examining birds for color bands. Sanderlings foraged in the intertidal zone where wave action kept the legs mud-free and provided a light background against which the birds were viewed; this improved accuracy in reading color band combinations.

Although we occasionally captured Sanderlings during the resighting periods, it was more common to capture birds 1 to 2 days either side of a resighting period. For purposes of this study, we assigned each bird to a cohort, defined by the previous resighting period, even though some Sanderlings were captured outside these periods. In this manner, all birds were assigned to 1 of 4 cohorts (actual banding dates are in parentheses) as follows: cohort 1: 22 April (22 and 24 April), cohort 2: 27 April (30 April), cohort 3: 17 May (18 May), and cohort 4: 22 May (22 and 23 May).

A PRIORI MODELS

We hypothesized that three specific sources of variation affected the local apparent survival and conditional capture probability of Sanderlings, and then used predictions about these variables to develop a concise list of models for consideration. Our predictions for the 3 sources of variation we included in our models were:

Temporal variation in local apparent survival. In coastal North Carolina, spring migrant Sanderlings arrived in mid-April (augmenting small numbers that overwintered), reached peak abundance in May, and departed by mid-June (Dinsmore et al. 1998). To explain this pattern, we modeled local apparent survival as a function of both linear and quadratic time trends and as period-specific. In each case, we anticipated a general negative trend in local apparent survival

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across time as birds inevitably departed the study area, although we had no other information to suggest which of these patterns best fit our data.

Effect of body condition on local apparent survival. Of primary interest to us was the influence of body condition on residency patterns of Sanderlings. Body condition can be measured several ways, but we chose only two measures for this study. First, we used a simple measure of body mass at capture as a measure of body condition. However, because of individual heterogeneity and sexual dimorphism, an individual's mass alone may not be the best measure of body condition. To account for some sexual variation, we calculated a simple body condition index (BCI) as body mass divided by the length of the exposed culmen and used this as a second measure of body condition. We further assumed that every bird was capable of gaining weight to a threshold permitting departure to the next destination, regardless of the weight at capture. Because we did not know the values of these two variables after the bird was released, the effects of body mass and body condition index were modeled only on the first local apparent survival rate following release and were not used in subsequent intervals.

Variation in conditional capture probability. We always modeled the conditional capture probability (p) as a single parameter because we had no *a priori* reason to believe this varied within the spring 1993 season. Complete coverage of the study area during each resighting period, the use of the same observers, and the narrow, linear nature of the habitat used by Sanderlings suggested this was a reasonable assumption.

STATISTICAL ANALYSES

MODELING LOCAL APPARENT SURVIVAL

We modeled the local apparent survival of Sanderlings during spring (10 five-day intervals from 22 April to 11 June) using the Jolly-Seber models for open populations (Pollock et al. 1990) and generated parameter estimates using the recaptures-only model in program MARK (White and Burnham 1999). Pollock et al. (1990) reviewed the assumptions and robustness of this approach. This approach permits estimation of both local apparent survival (ϕ_i) and conditional capture probability (p_i). Local apparent survival is the probability that a bird remained in the study area from resighting period i to period $i + 1$ (an interval of 5 days), conditional on the bird being alive and available for resighting. Parameter estimates in MARK are maximum-likelihood estimates with 95% confidence intervals based on a logit or log transformation (White and Burnham 1999).

Our approach to modeling survival rates and conditional capture probability of Sanderlings in MARK was as follows. We began by running three initial models in an attempt to explain time variation in local apparent survival. Next, we took the best time variation on local apparent survival (in this case, ϕ_{TT}) and added the effects of body mass and a simple body condition index. We modeled each of these effects in two ways: as a single parameter (no cohort effect) and then as cohort-specific parameters. Finally, in order to assess possible cohort-specific differences in local apparent survival, we included two additional models, one with only cohort effects and a second with time-specific cohort effects. This resulted in a list of nine candidate models for our analyses (Table 1).

MODEL SELECTION

We assessed the fit of the global model (a model with full cohort and temporal variation in apparent survival and capture probability) to these data by examining the results of tests 2 and 3 in Program RELEASE (Burnham et al. 1987). After examining overall fit, an appropriate model was selected using the methodology of Burnham and Anderson (1998). We used Akaike's Information Criterion, corrected for small sample sizes (AIC_c; Akaike 1973), as a means of objectively ranking our set of candidate models and to select a best-approximating model or models for inference (Burnham and Anderson 1998). To properly account for possible extrabinomial variation in our data, we used quasi-likelihood theory ($QAIC_c$; Burnham and Anderson 1998) to adjust the AIC_c values. We estimated overdispersion, denoted, as the goodness-of-fit test statistic for the global model divided by its degrees of freedom, and this was later used to correct the variances of parameter estimates.

Once $QAIC_c$ values were computed for each model, we ranked the nine models relative to the model with the lowest $QAIC_c$ value and compared models using $\Delta QAIC_c$ values. Generally, models with $\Delta QAIC_c$ values ≤ 2 have strong

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TABLE 1. Model selection results for Sanderlings on the Outer Banks of North Carolina, spring 1993. Models are ranked by ascending $\Delta QAIC_c$ (the difference between a given model and the model with the lowest $QAIC_c$ score); w_i is the model weight (weights sum to 1 and indicate the relative strength of evidence for a given model); and k is the number of parameters. Local apparent survival rate (ϕ) and capture probability (p) included full time effects (t; survival rate varied across each of the 10 intervals), a linear time trend (T), a quadratic time trend (TT), and a constant rate with no time variation (.). Deviance is computed as $-2[\ln(L(\hat{\theta})) - 2\ln(L_s(\hat{\theta}))]$ where $\hat{\theta}$ represents a maximum likelihood estimate whose log-likelihood is evaluated for the model in question $[L(\hat{\theta})]$ and for the saturated model $[L_s(\hat{\theta})]$. The estimate of overdispersion used in our analyses was $\hat{c} = 2.26$.

Model	$QAIC_c$	$\Delta QAIC_c$	w_i	k	QDeviance
ϕ_{TT}, $p(.)$	651.97	0.00	0.49	4	643.72
$\phi_{TT+BCI\ common}$, $p(.)$	653.53	1.73	0.21	5	643.42
$\phi_{TT+Mass\ common}$, $p(.)$	653.80	2.00	0.18	5	643.69
$\phi_{TT+BCI\ by\ cohort}$, $p(.)$	656.31	4.51	0.05	8	640.03
$\phi_{TT+Mass\ by\ cohort}$, $p(.)$	656.42	4.62	0.05	8	640.14
ϕ_T, $p(.)$	658.64	6.85	0.02	3	652.60
ϕ_t, $p(.)$	660.78	8.99	0.01	11	638.27
$\phi_{cohort*t}$, $p(.)$	662.97	11.17	0.00	14	634.16
ϕ_{cohort}, $p(.)$	677.81	26.01	0.00	5	667.70

support while those with $\Delta QAIC_c$ values >10 have little support (Burnham and Anderson 1998). We also computed normalized Akaike weights (w_i) for each model. These weights provided another means of directly evaluating the strength of evidence for each model and were useful for computing parameter estimates that reflected model-selection uncertainty (Burnham and Anderson 1998). When building models, we used two link functions in MARK (White and Burnham 1999). Models incorporating an individual covariate such as body mass used a logit link function; all other models used a sine link function.

Using the Akaike weight and estimate of local apparent survival from each model, we computed a model-averaged estimate of local apparent survival as

$$\bar{\hat{\phi}}_i = \sum_{r=1}^{R} w_i(\hat{\phi}_i)$$

with sampling variance

$$\widehat{\text{var}}(\bar{\hat{\phi}}_i) = \left[\sum_{r=1}^{R} w_i\sqrt{\widehat{\text{var}}(\hat{\phi}_i|M_i) + (\hat{\phi}_i - \bar{\hat{\phi}}_i)^2}\right]^2$$

where M_i was the ith model in the candidate set (Burnham and Anderson 1998). The 95% confidence intervals for the model-averaged estimate of local apparent survival were

$$95\%\ \text{CI} = \bar{\hat{\phi}}_i \pm 1.96\left[\widehat{\text{SE}}(\bar{\hat{\phi}}_i)\right]$$

where

$$\widehat{\text{SE}}(\bar{\hat{\phi}}_i) = \sqrt{\widehat{\text{var}}(\bar{\hat{\phi}}_i)}.$$

RESULTS

We individually color banded 204 Sanderlings at Portsmouth Island during spring 1993 (Table 2). The total number of releases (newly marked Sanderlings plus all live resightings) was 534. Mean weights and culmen lengths of birds in the four cohorts did not differ (Fig. 2), although there was a slight tendency for birds to be heavier late in the season. No band loss was detected among the 330 resightings.

The fit of the global model to the spring 1993 Sanderling data was poor ($\chi^2_{24} = 41.9$, $P = 0.01$); most of the lack of fit was due to fewer-than-expected resightings for birds banded in late April (cohort 2). There was good evidence of overdispersion in these data: we computed $\hat{c} = 2.26$ and adjusted this in MARK.

Among the set of models we considered, we found strong evidence for a quadratic time trend in the spring local apparent survival of Sanderlings; this model had almost half of the model weight and received much better support than the second-best model (Table 1). A model with a linear time trend received substantially less support ($\Delta QAIC_c = 6.85$), and a model with time-specific local apparent survival received almost no support. There was no evidence that local apparent survival differed among the four cohorts. When mass and body condition were added to the best model, the results indicated that each of these effects was best supported

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TABLE 2. Resighting data for four cohorts of Sanderlings banded on the Outer Banks of North Carolina, spring 1993. Cohorts were released on 22 April (cohort 1), 27 April (cohort 2), 17 May (cohort 3), and 22 May (cohort 4). The m_j row gives the number of Sanderlings resighted in resighting period j, and z_j is the number of Sanderlings resighted in a resighting period other than period j.

Resight period (i)	No. of releases (R_i)	No. of resightings in resight period ($m_{i,j}$)								Sum of resights (r_i)
		2	3	4	5	6	7	8	9	
Cohort 1										
1	99	30	18	11	7	0	6	2	1	75
2	30		16	3	1	2	2	1	0	26
3	34			18	1	2	2	2	0	25
4	32				10	11	2	1	0	24
5	19					4	7	2	1	14
6	20						7	3	1	12
7	26							11	1	13
8	22								4	5
m_j		30	34	32	19	19	26	22	8	
z_j		45	37	30	35	30	16	7	4	
Cohort 2										
2	55		21	7	2	4	3	1	0	38
3	21			11	0	1	1	1	0	14
4	18				8	7	1	0	0	16
5	10					3	4	1	0	8
6	15						8	1	1	10
7	17							8	0	8
8	12								1	1
m_j		0	21	18	10	15	17	12	2	
z_j		0	17	13	19	12	5	1	0	
Cohort 3										
6	34						11	7	4	22
7	11							3	2	7
8	10								3	3
m_j		0	0	0	0	0	11	10	9	
z_j		0	0	0	0	0	11	8	2	
Cohort 4										
7	16							2	1	4
8	2								0	0
m_j		0	0	0	0	0	0	2	1	
z_j		0	0	0	0	0	0	2	1	

when modeled as a single parameter; there was poor support for cohort-specific effects of mass and body condition. Neither mass nor body condition was a good predictor of Sanderling local apparent survival. Although models containing each of these variables had moderate weight (0.21 and 0.18) and $\Delta QAIC_c$ values ≤ 2, the slope coefficients for both effects ($\beta_{Mass} = -0.16$; 95% CI: -1.74 to 1.42; $\beta_{BCI} = 0.45$; 95% CI: -0.98 to 1.89) did not differ from zero.

We estimated model-averaged local apparent survival rates for each 5-day interval between resighting periods from 22 April to 11 June (Fig. 3). Local apparent survival remained relatively high ($\phi_i > 0.80$) through late May and then declined rapidly thereafter.

DISCUSSION

The pattern for spring-migrant Sanderlings at Portsmouth Island was one of high local apparent survival through late May, after which departure was rapid until all birds had departed by mid-June. We hypothesized that body condition at capture was a good predictor of local apparent survival, but found no evidence to support this in our models. A critical assumption here is that fat deposition rates are the same for birds with different body conditions, although admittedly there is little information in the literature to support this contention (Morrison 1984, Skagen and Knopf 1994). Because body condition indices might reflect condition only at the time of cap-

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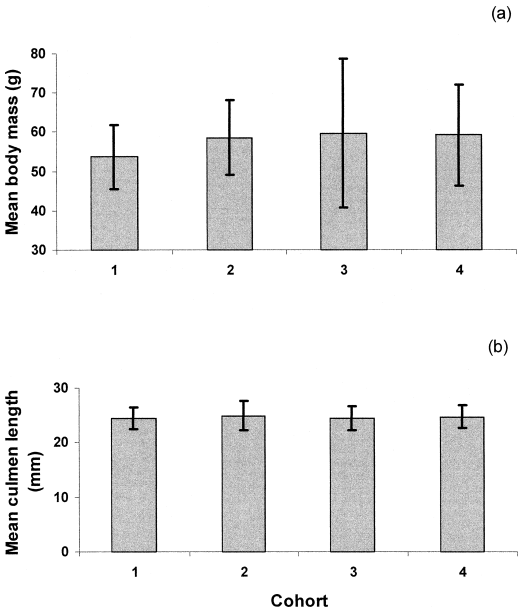

FIGURE 2. Mean ± 95% CI (a) body weights (g) and (b) culmen lengths (mm) of Sanderlings banded in spring 1993 on Portsmouth Island, North Carolina. The four cohorts included birds released on 22 April (n = 99), 27 April (n = 55), 17 May (n = 34), and 22 May (n = 16).

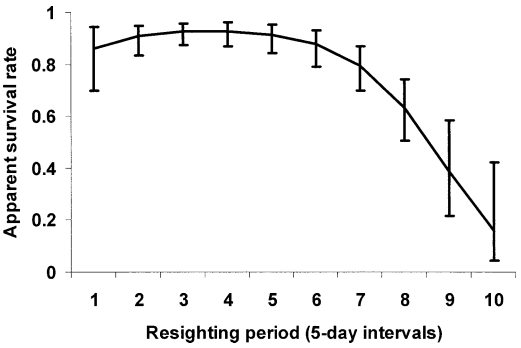

FIGURE 3. Period-specific local apparent survival rates (±95% CI) for Sanderlings on Portsmouth Island, North Carolina, spring 1993. Resighting periods (in 5-day intervals) spanned the period 22 April to 11 June 1993. Local apparent survival rate is the probability that a bird present at the beginning of one resighting period will still be present (survive) at the beginning of the next resighting period.

ture, we suggest that future work combine body condition indices with the use of plasma metabolites (Williams et al. 1999, Guglielmo et al. 2002) to better reflect previous activity (e.g., migration, forage quality, fat deposition rates). Plasma metabolites have the advantage of predicting the ensuing physiological state of birds in terms of fat deposition (e.g., 2–5 days postcapture). The ability to forecast fat deposition rates may be better suited for modeling local apparent survival than was our approach.

The explanation for the weak relationship between body condition and local apparent survival in this study likely stems from the strong selective pressures of spring migrants to reach the breeding grounds. It is possible that Sanderlings operate only under the time-selection hypothesis, at least prior to reaching major staging areas. Energy constraints and body condition may influence local apparent survival only during certain, probably brief, periods in a given migratory season, or only in staging but not stopover areas. This is consistent with findings reported by Farmer and Wiens (1999) for Pectoral Sandpipers, in which birds minimized time at stopovers on their way north to the breeding grounds. At such locales, Pectoral Sandpipers, particularly females, maximized energy intake and fat deposition to enhance reproductive output. Other studies (Lyons and Haig 1995, Warnock and Bishop 1998) have suggested that male shorebirds minimize time spent on migration while females minimize time and maximize energy. Our inability to look for sex-specific differences in local apparent survival may have contributed to our findings. Butler et al. (1997) demonstrated that frequency and duration of tailwinds were important variables explaining spring migration in Western Sandpipers. Tailwinds may permit birds to complete their migration without always having to store large amounts of fat. We did not explore this source of variation for Sanderlings, but acknowledge that it may have influenced the pattern of local apparent survival we detected.

POSSIBLE SOURCES OF BIAS

The Jolly-Seber model we used to estimate local apparent survival assumes emigration is permanent. Our nearly complete coverage of the study area and information about the site fidelity of Sanderlings (Dinsmore et al. 1998) suggests that temporary emigration was rare. Temporary emigration could have occurred when birds fed on tidal flats in nearby inlets; many of these sites were not regularly searched for marked birds. To counter this, we conducted resighting surveys during high tide to increase the probability that

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Sanderlings would be on outer beaches, where most communal roosts were located.

Temporary trap response, which results in either increased (''trap happy'') or decreased (''trap shy'') capture probability, can affect the precision of the estimates of local apparent survival (Pollock et al. 1990). It is possible that the handling and stress associated with capture altered the resighting or local apparent survival of newly marked Sanderlings, but we assumed such a response was negligible (see Schick 1983) and was not permanent. We concur with others (Warnock and Bishop 1998) that the effects of capture and handling on survival rates need to be rigorously investigated.

Our inability to sex Sanderlings may have affected our interpretation of seasonal patterns in local apparent survival. Sanderlings, as with many shorebird species, probably exhibit sex-specific migration patterns with females generally migrating later than males in spring (Lyons and Haig 1995), although we found no studies that examined this pattern in Sanderlings. However, mean culmen length did not differ among the four cohorts we marked, suggesting that later cohorts did not contain a disproportionate number of females. This in turn provides support that the strong seasonal change in local apparent survival was not the result of a sex-biased sample.

CONCLUSIONS

On the basis of Farmer and Wiens' (1999) conceptual framework, we believe that Sanderlings used the Outer Banks sparingly (or bypassed it entirely) during spring in favor of more suitable stopover sites elsewhere. From a regional perspective, the Outer Banks may then simply function as a stopover area and not as a major staging area (see Hands 1988). Under this strategy, the local apparent survival of Sanderlings of differing body conditions on the Outer Banks would not be expected to differ predictably. Sanderlings may depart to other sites, such as Delaware Bay, where they are known to add large amounts of fat reserves just prior to departure for the breeding grounds (Myers 1983). This pattern along the eastern seaboard would be consistent with observed patterns for Pectoral Sandpipers (Farmer and Wiens 1999) and match predictions of higher rate of energy gain at specific, northern locales during spring migration (Alerstam and Lindström 1990). Perhaps at such locales the possible influence of body condition on local apparent survival would be easier to detect.

This study underscores the need for detailed studies at multiple scales. We generated a series of competing models and used a sound analytical approach to investigate factors believed to influence site-specific shorebird migration behavior, an appealing analytical approach for future studies of this nature. Clearly, the interpretation of our findings would have been more straightforward if we had greater knowledge of within-season patterns of local apparent survival and body condition across a latitudinal gradient (Farmer and Wiens 1999). Such an approach is needed to carefully partition the number of factors influencing migrant shorebirds before explicit tests dealing with the evolution of migration are possible.

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