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FAT CONTENT AND STOPOVER ECOLOGY OF SPRING MIGRANT SEMIPALMATED SANDPIPERS IN SOUTH CAROLINA[1]

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Abstract. Semipalmated Sandpipers (*Calidris pusilla*) stop at staging areas during migration to replenish fat reserves that fuel long distance flights. We hypothesize that if sandpipers are minimizing time spent en route between wintering areas and breeding grounds, a negative correlation should exist between fat content upon arrival at a staging area and length of stay. We examined the relationship between these two variables at a spring staging area in coastal South Carolina using simple and multiple regression models. Length of stay was independent of estimated fat content at capture after controlling for date in the season. Birds with sufficient energy reserves for long distance flights were as likely to remain on the study area as lean birds. Date in the season showed more influence on stopover time than estimated fat mass at capture. Stopover time decreased with later date, suggesting an increase in the speed of migration as the season progressed. These results show that date is a critical variable influencing Semipalmated Sandpiper migration stopover strategy. Migrants appear to shift their migration priorities with respect to fat stores and stopover time as the season progresses.

Key words: Fat mass; stopover; migration; Semipalmated Sandpiper; Calidris pusilla.

INTRODUCTION

Many Nearctic shorebirds complete long distance migrations from arctic breeding grounds to tropical wintering areas (Matthiessen and Stout 1967, Burger and Olla 1984, Morrison 1984). Routes and timing of movements have evolved to exploit seasonally abundant resources, both in the arctic and along the migratory path (Harrington and Morrison 1979, Myers et al. 1987, Hicklin 1987).

Subcutaneous fat is the primary fuel for long distance migrations (Odum and Connell 1956, Blem 1980, Piersma and Jukema 1990, Evans and Davidson 1990). Shorebirds often concentrate at staging areas before leaving the wintering grounds and at critical locations along the migratory path, where rapid deposition of body fat is possible (Myers 1983, Myers et al. 1987). During these stopovers, individuals are often in unfamiliar areas and face varying levels of prey, inter- and intraspecific competition, fluctuating environmental conditions, and predation pressure. Length of stay at staging areas, habitat selection, foraging behavior, rate of body mass gain, and arrival/departure body condition are aspects of stopover ecology that have been examined for passerines and shorebirds (Page and Middleton 1972, Cherry 1982, Lank 1983, Dunn et al. 1988, Gudmundsson et al. 1991, Moore et al. 1990, Lavee et al. 1991, Kuenzi et al. 1991, Winker et al. 1992, Lindstrom and Alerstam 1992, Holmgren et al. 1993).

The Semipalmated Sandpiper (*Calidris pusilla*) is a monogamous, territorial shorebird that breeds in the lower Nearctic. Males arrive on breeding areas in the last week of May and early June, and almost immediately establish territories (Gratto-Trevor 1992). Males defend territories against conspecific males with flight displays and chases. Females arrive several days after males (Gratto-Trevor 1992). Females are larger than males and the species exhibits clinal size variation with smallest birds breeding in the west and largest birds breeding in the east (Harrington and Morrison 1979).

The breeding range extends from the Alaskan coast across Canada to northern Quebec, Baffin Island and northern Labrador (AOU 1983; Gratto-Trevor 1991, 1992). The primary winter range is along the north and central coasts of South America (Harrington and Morrison 1979, AOU

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1983, Morrison and Ross 1989, Gratto-Trevor 1991). The following migration routes have been proposed based on banding and morphometric studies throughout the species' range. In spring, birds headed toward eastern Canadian arctic breeding grounds migrate north along the Atlantic coast. Central and western breeders migrate north primarily through the interior of North America. In fall, western and some central arctic breeders return south through the North American prairie. The remaining central and eastern birds migrate southeast to the northeast Atlantic coast, possibly east of the spring route. After staging in southeastern Canada and New England, most birds undertake nonstop transoceanic flights to wintering grounds on the north coast of South America (McNeil and Burton 1973, Harrington and Morrison 1979, Lank 1983, Morrison 1984, Hicklin 1987, Dunn et al. 1988, Gratto-Trevor 1994). On migration, Semipalmated Sandpipers concentrate at key staging areas, including coastal Surinam, Cheyenne Bottoms (Kansas), Delaware Bay (New Jersey), Quill Lakes (Saskatchewan), and the Bay of Fundy (New Brunswick), where local populations reach up to 350,000 (Gratto-Trevor 1992).

If there is an advantage to arrival on the breeding grounds before intraspecific competitors, migrant birds may be attempting to minimize time spent on migration (Myers 1981a, 1981b). Individuals establishing breeding territories may gain a competitive edge by arriving earlier than conspecifics and establishing a breeding territory in high quality habitat (Oring and Lank 1982, Francis and Cooke 1986, Reynolds et al. 1986). Alerstam and Lindstrom (1990) reviewed the costs of time minimization during migration and constructed testable hypotheses regarding minimization of time, energy and predation risk by migrating birds. During "time-selected" migration the decision to stop at a particular staging area and the decision when to leave a staging area are dependent on both the current fat status of the individual and the expected fat deposition rate at future stopovers. During "energy-selected" migration stopover decisions may be influenced by fat content but are independent of expected rates of fattening at future sites (Alerstam and Lindstrom 1990). If there is a reproductive premium for early arrival on the breeding grounds, the cost of being "late" may be greater in the spring than in the fall. Under this scenario, spring migrants are predicted to be "time-selected" whereas fall migrants are more likely to be "energy-selected."

If migrants are attempting to minimize time spent reaching winter or breeding sites, it would be advantageous to make a series of long flights with few stops between end points of the journey (Alerstam and Lindstrom 1990). Migrants should thus arrive at staging areas in a lean, fat-depleted condition, feed and gain body mass as quickly as possible, and depart as soon as a threshold level of energy (sufficient to carry the individual to the next suitable staging area or end point) has been reached. This simple model suggests a negative correlation between length of stay at a migratory stopover and body fat (energy) levels at time of arrival, regardless of weather conditions, date in season, wintering location, etc. Three investigators have examined this model for autumn migrant Semipalmated Sandpipers, but none during spring (Page and Middleton 1972, Lank 1983, Dunn et al. 1988). After partitioning the entire migration season into seven-day intervals, Dunn et al. (1988) showed that fat mass at capture ("arrival") explained a significant, albeit small, amount of the variation in stopover time within time intervals. However, other studies conclude that fat content is a poor predictor of stopover time (Page and Middleton 1972, Post and Browne 1976, Lank 1983, Morrison 1984).

Much of the research into migration of Semipalmated Sandpipers has been conducted during southward migration at points prior to transoceanic flight. The purpose of this paper is to review the stopover ecology of Semipalmated Sandpipers during spring migration in coastal South Carolina, particularly the relationship between body condition and length of stay, and changes in stopover time and fat mass at capture across the season.

METHODS

This study was conducted in the brackish water impoundments of the Tom Yawkey Wildlife Center on South Island, Georgetown, South Carolina (33°13'N, 79°14'W). The twelve impoundments (size range 15–99 ha) are mosaics of saltmarsh grasses and extensive mudflat habitats. Water levels are manipulated primarily to provide food plants and foraging habitats for migratory waterfowl. Water levels are maintained at 25–40 cm during November–February, and then gradually reduced during March–June, exposing mudflat habitats for migratory shorebirds. Approximately 300 ha of mudflat habitats are available to shorebirds during migration. Primary invertebrate prey items found in mudflat substrates include chironomid larvae and polychaetes (Weber and Haig, unpubl. ms.).

All shorebirds were censused by direct count in all impoundments about every seven days from 10 January–5 June in 1992 and 1993. Semipalmated Sandpipers were captured (almost daily, 06:00–18:00 hr) over foraging areas using mist nets and wooden decoys, from mid-April to early June. Captured individuals were weighed (to nearest 0.5 g) using a spring balance, measured (natural wing chord, to nearest 1 mm; exposed culmen [0.1 mm]; tarsometatarsus [0.1 mm]), and aged. Aging criteria of Prater et al. (1977) were used to classify birds as second-year (i.e., hatched the previous year and in second calendar year) or after second-year (hatched before the previous calendar year). Individuals with very worn primaries or partial primary wing molt were classified as second-year. Birds with new primaries were classified as after second-year. If aging criteria were not clear, age was recorded as unknown.

Each bird received a United States Fish and Wildlife Service aluminum band, a plastic, colored leg flag (Myers et al. 1983), and an individual combination of three plastic, colored leg bands. All captured birds were also dyed with indelible ink on either the breast, flanks, or undertail coverts to help relocate marked sandpipers within flocks. However, only birds with individual color band combinations were used in the analysis of stopover time.

Daily searches were conducted to locate and identify color-marked individuals remaining on the study area. Stopover time (or estimated minimum length of stay) was defined as the number of days between capture and last resighting. This is an estimate of minimum length of stay, because captured birds could have arrived before the day of capture, and may have departed after the last day of observation.

Fat content and lean mass of live birds was estimated from an analysis of 15 individuals collected during 1–22 May 1992, as part of another study (Lyons and Haig, in press). These birds were processed (see above), euthanized by CO_2 inhalation, and frozen. Carcasses were freeze-dried for 48 hours and fats were extracted over 24–48 hr using petroleum ether in a Soxhlet apparatus. After extraction, fat mass (FM) and lean mass (LM) were measured to the nearest 0.1 g. Fat mass was estimated by subtracting a lean mass estimate from fresh body mass. A predictive equation for lean mass estimates was formulated using wing length, culmen and tarsus:

$$\begin{aligned} \text{LM} = 30.35 &- 0.14*\text{wing} \\ &+ 0.58*\text{culmen} + 0.83*\text{tarsus}. \end{aligned}$$

This equation explained 88% of variation in lean mass ($R^2 = 0.88$, $n = 20$, $P = 0.03$). Fat mass estimates, made by subtracting lean mass estimates from fresh body masses, were significantly correlated with actual fat mass values of this sample ($r = 0.94$, $n = 20$, $P < 0.01$). However, this sample was not large enough to formulate separate equations for each sex.

STATISTICAL ANALYSES

Comparisons among age classes for mean values of body mass, estimated fat mass at capture, estimated lean mass, wing length and stopover times were made using the Wilcoxon rank sum test. Correlations of fat mass at capture and stopover time with Julian date were evaluated (using data from the entire season) using Pearson product-moment correlations. Simple and multiple regression models were used to assess the amount of variation in stopover time (response variable) explained by estimated fat mass at capture and/or date. Birds that were not reobserved after banding ("transients") were not included in analyses of stopover time. Differences in body mass, estimated fat content and wing length between transients and reobserved birds ("residents") were made using the Wilcoxon rank sum test.

Migrants captured at different times of year may face different conditions at the same stopover area. Levels of prey abundance, amount of available foraging habitat, and other environmental factors affecting stopover decisions may vary seasonally. Therefore, we partitioned the migration season into three stages (early, middle and late) based on migration phenology. For each year, the mean Julian date of migration was determined from banding data. Birds captured within one SD of the mean Julian date were classified as middle migrants. Those captured prior to one SD from the mean Julian date were classified as early migrants, and those captured after one SD from the mean were classified as late migrants. The relationship between fat mass at capture and stopover time was analyzed within these migration periods using a simple regression

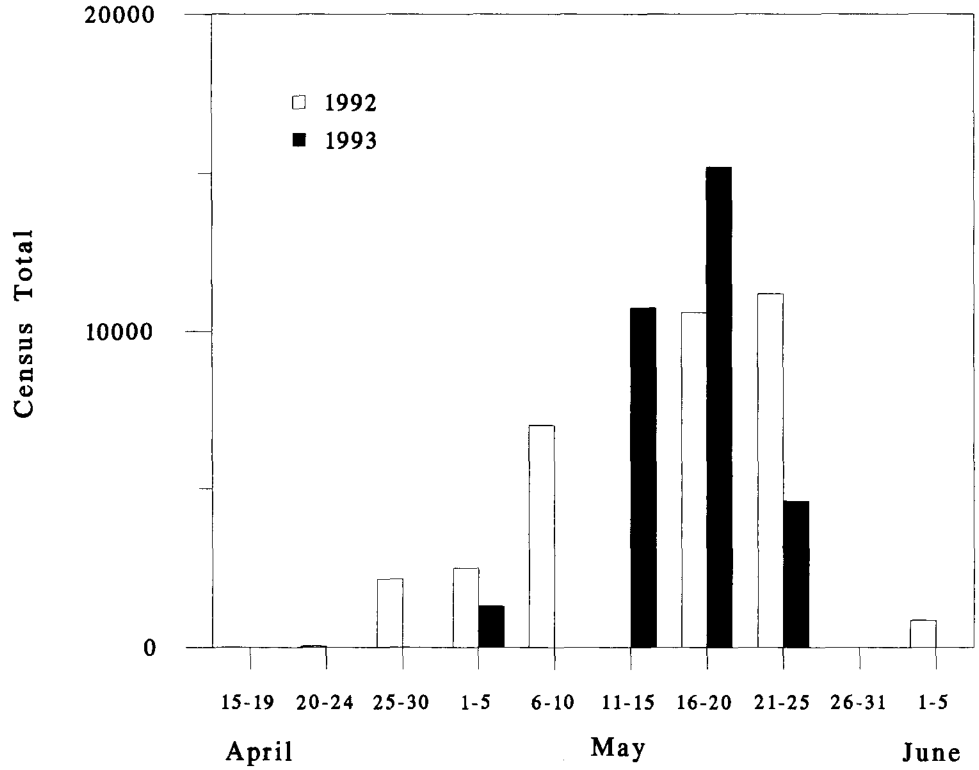

FIGURE 1. Total number of Semipalmated Sandpipers in impoundments of South Island, South Carolina during spring migration, 1992–1993.

model. Stopover time and estimated fat mass at capture were analyzed using the Kruskal-Wallis nonparametric one-way analysis of variance with migration period as the class variable. All calculations were made using SAS (1989). Results of hypothesis tests were considered statistically significant for P values ≤ 0.05.

RESULTS

ABUNDANCE AND PHENOLOGY

Semipalmated Sandpipers first arrived at South Island in mid-April, and most had departed the study area by early June. Population levels on the study area peaked during 16–25 May in both 1992 and 1993 (Fig. 1). Maximum census counts were higher in 1993 and the peak ($n = 15,200$) occurred earlier (18 May 1993) than the peak count ($n = 11,200$) in 1992 (23 May 1992). By the first week of June, local population numbers declined to <900 in both years.

In 1992, 448 sandpipers were captured and marked during 24 banding attempts from 14 April–3 June; 78 (17%) individuals were subsequently resighted during their stopover. In 1993, 587 birds were marked during 18 banding attempts from 20 April–22 May, and 140 (24%) individuals were resighted. Of all birds resighted on the study area during the stopover period, 21 (27%) and 29 (21%) were recorded more than once during their stay in 1992 and 1993, respectively.

Mean date of migration in 1992 was 16 May (SD = 9 days). Early, middle and late stages for 1992 included 15 April to 8 May, 9–25 May, and 26 May to 4 June, respectively. Mean date of migration in 1993 was 11 May (SD = 6 days). Early, middle, and late stages for 1993 included 20 April to 6 May, 7–17 May, and 18 to 22 May. Adult Semipalmated Sandpipers tended to migrate earlier than second-year birds (Wilcoxon rank sum test on mean date of migration: 1992, $Z = 4.41$, $P = 0.0001$; 1993, $Z = 4.68$, $P = 0.0001$).

FAT CONTENT

Estimated fat mass at capture for all birds ranged from −5.14 to 20.17 g over both years. Negative values are a result of error associated with the

TABLE 1. Total body mass, estimated fat, estimated lean mass, wing length, and stopover time for resighted Semipalmated Sandpipers on spring migration in South Carolina (ASY = after second year, SY = second year, Unknown = age unknown).

	1992			1993		
	$\bar{x}$ ± SE	n	P[1]	$\bar{x}$ ± SE	n	P[1]
Total body mass (g)						
ASY	24.7 ± 0.18	369	0.07	25.6 ± 0.19	436	0.19
SY	25.4 ± 0.42	53		26.4 ± 0.46	85	
Unknown	24.8 ± 0.78	26		25.9 ± 0.46	66	
Estimated fat (g)						
ASY	3.6 ± 0.18	369	0.62	4.9 ± 0.20	436	0.37
SY	3.9 ± 0.53	53		5.3 ± 0.47	85	
Unknown	3.8 ± 0.77	26		5.5 ± 0.47	66	
Estimated lean mass (g)						
ASY	21.1 ± 0.06	369	0.02	20.7 ± 0.07	436	0.32
SY	21.5 ± 0.24	53		20.9 ± 0.17	85	
Unknown	20.9 ± 0.25	26		20.6 ± 0.17	66	
Wing length (mm)						
ASY	95.1 ± 0.13	369	0.21	95.1 ± 0.11	436	0.17
SY	94.7 ± 0.33	53		95.5 ± 0.26	85	
Unknown	95.0 ± 0.62	26		95.6 ± 0.30	66	
Stopover time (days)						
ASY	3.8 ± 0.3	69	0.12	5.7 ± 0.4	101	0.08
SY	5.5 ± 1.2	6		4.5 ± 1.1	19	
Unknown	7.3 ± 1.8	4		4.8 ± 0.8	20	

[1] Probability of no difference between ASY and SY; Wilcoxon rank sum test.

regression of fat content on body mass used to estimate fat stores. At the extreme low end of the range of body mass, some fat mass estimates occurred below the abscissa. Mean estimated fat mass (±SD) was 3.62 ± 3.56 g and 5.01 ± 4.16 g for 1992 and 1993, respectively. Total body mass and estimated fat content did not differ between second year and adult birds (Table 1); no comparisons were made with birds of unknown age.

Mean estimated fat reserves for adult birds ranged from 3.6–4.9 g, representing 14.5% and 19.1% of mean body mass in 1992 and 1993, respectively (Table 1). Estimated fat mass at capture increased across the spring migration period in both years (1992 Pearson correlation coefficient of fat mass and Julian date of capture, $r = 0.37$, $n = 448$, $P = 0.001$; 1993, $r = 0.32$, $n = 587$, $P = 0.001$). This increase could have been the result of: (1) longer residency at South Island prior to capture for late captures, (2) larger birds (i.e., able to carry more fat) arriving later in the season, or (3) birds arriving at South Island with larger fat loads as the season progressed.

It is difficult to determine if birds caught later in the season were at the study area longer before capture than birds caught early in the season. The probability of capturing a new arrival is relatively high early in the season and throughout the period of local population increase when thousands of new birds arrive each week (Fig. 1). In the later parts of the seasons, fewer new birds are arriving, but the local population size tended to decrease rapidly after the peak in late May. Therefore, the probability of catching a new arrival may have been similar across the season. Furthermore, if samples of captures from late in the season contained more individuals that had been at the study area longer, these samples should show a higher rate of transience (number of transients/number of birds banded) because presumably more birds in the sample are likely to depart. In 1992, the number of transients vs. residents was not independent of migration stage ($\chi^2 = 8.64$, $n = 448$, $P = 0.01$); the transient rate was similar in the early and late stages (88% and 90%, respectively) and lowest in the middle stage (78%). In 1993, the number of transients was independent of migration stage ($\chi^2 = 4.56$, $n = 587$, $P = 0.102$). This suggests that birds captured in the later stages of migration had not been at the study area for longer periods prior to capture.

Wing length in adult sandpipers was used as a measure of overall size to determine if larger

TABLE 2. Mean minimum stopover duration, estimated fat mass at capture and wing length of resighted Semipalmated Sandpipers captured during three stages of spring migration in South Carolina.

	Early $\bar{x} \pm$ SE	Middle $\bar{x} \pm$ SE	Late $\bar{x} \pm$ SE	P^1
1992	($n = 11$)	($n = 58$)	($n = 9$)	
Stopover (days)	4.82 ± 1.14	4.29 ± 0.36	2.44 ± 0.44	0.18
Estimated fat mass (g)	1.04 ± 0.69	4.34 ± 0.39	4.78 ± 1.39	<0.01
Wing length (mm)	95.00 ± 0.89	94.97 ± 0.36	95.77 ± 0.77	0.58
1993	($n = 27$)	($n = 82$)	($n = 31$)	
Stopover (days)	7.59 ± 1.06	5.05 ± 0.43	4.42 ± 0.43	0.06
Estimated fat mass (g)	2.92 ± 0.69	5.19 ± 0.39	9.27 ± 0.95	<0.01
Wing length (mm)	95.16 ± 0.58	94.33 ± 0.28	96.58 ± 0.49	<0.01

[1] Probability of no difference between stages; Kruskal-Wallis test.

birds arrived later in the season. The relationship between wing length and date was significant in both years (1992, $r = 0.11$, $n = 369$, $P = 0.03$; 1993, $r = 0.10$, $n = 436$, $P = 0.04$). After controlling for size, however, date still had a significant effect on estimated fat content of adults in both years (1992, partial correlation for date $F = 73.27$, $n = 369$, $P = 0.001$; 1993, partial correlation for date $F = 39.50$, $n = 436$, $P = 0.0001$). Thus, the increase in estimated fat level at capture does not appear to be caused by the migration of larger birds later in the season. It appears that birds are carrying greater fat stores as the season progresses.

STOPOVER TIME

Minimum length of stay ranged from 1 to 21 days, but most birds remained at South Island less than 11 days. Mean (±SD) stopover time was 4.2 ± 2.8 days and 5.4 ± 4.1 days for 1992 and 1993, respectively. Minimum length of stay did not differ between second-year and adult birds (Table 1); no comparisons were made with birds of unknown age.

In both years, stopover time decreased over the season (1992, Pearson correlation coefficient of stopover time and Julian date, $r = -0.32$, $P < 0.01$, $n = 78$; 1993, $r = -0.30$, $P < 0.001$, $n = 140$). Early in the season, sandpipers remained on the study area for an average of 4.82 and 7.59 days in 1992 and 1993, respectively (Table 2). At the end of season, mean stopover time had decreased to 2.44 and 4.42 days in 1992 and 1993, respectively (Table 2). Transient birds, which were excluded from stopover analyses, were examined for differences from resident birds. Body mass, wing length and estimated fat content of transients did not differ from residents in either year (Wilcoxon rank sum tests, $P > 0.05$).

Using data from the entire season, date alone explained a significant amount of variation (9–10%) in stopover time in both years (Table 3). Estimated fat level at capture, however, was not a good predictor of minimum length of stay (Table 3). The relationship between estimated fat content and minimum length of stay was significant in 1993, but the amount of variation explained was small (4%). Furthermore, fat level at capture and date were correlated; after controlling for date, fat did not explain a significant amount of variation in length of stay (Table 3). There was no relationship between estimated fat content and stopover time in 1992.

MIGRATION STAGE

In 1992, the early and late stages showed the predicted negative, but nonsignificant, correlation between stopover time and estimated fat mass at capture. In 1993, the early and middle stages showed the predicted negative relationship but neither was significant (Table 4).

Partitioning the data into migration stages may have biased the sex ratio within each sample if one sex migrates earlier than the other. Culmen lengths of adult birds pooled over the two years ($n = 805$) were significantly longer in the late stage than both the early and middle stages (Duncan Multiple Range test, $P < 0.001$). Based on the sexual size dimorphism in this species, this trend in culmen lengths (and the trend in wing lengths discussed above) suggests that females migrated later than males on average and that captures in the late stage were disproportionately female.

Estimated fat mass at capture and minimum length of stay were examined across the migration stages. In both 1992 and 1993, estimated fat mass at capture increased from the early to

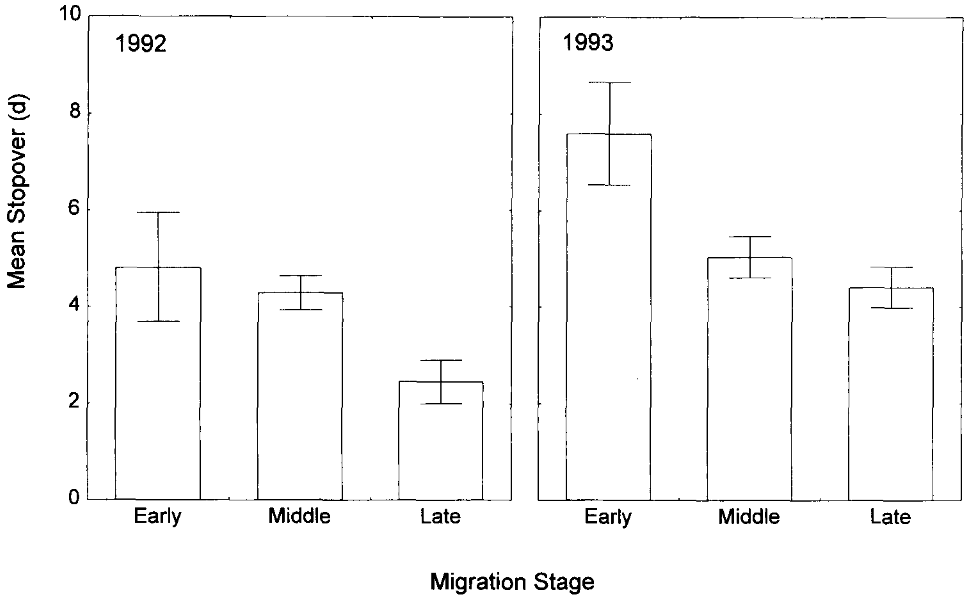

FIGURE 2. Mean fat content of Semipalmated Sandpipers in South Carolina for three stages of migration in spring 1992 and 1993. Error bars represent standard error of the mean.

late stages of migration, whereas minimum stopover time decreased (Table 2; Fig. 3). The decrease in minimum length of stay was not significant after the data were partitioned.

DISCUSSION

Estimated minimum stopover times for Semipalmated Sandpipers on spring migration in coastal South Carolina during 1992 and 1993 averaged four and five days, respectively (range = 20 days). There are no previous reports of stopover duration for this species during spring migration. The average minimum length of stay is considerably shorter than times reported for autumn migration in other parts of the species' range. These results are consistent with the idea

TABLE 3. Results of simple and multiple regression models of stopover time with fat mass at capture and date for Semipalmated Sandpipers on spring migration in South Carolina.

Predictor Variable(s)	R^2	F	P
1992 (n = 78)			
Fat	<0.001	0.02	0.889
Date	0.10	8.38	0.005
Fat and Date	0.11	4.49	0.014
Fat[1]		0.63	0.429
Date[1]		8.95	0.004
1993 (n = 140)			
Fat	0.04	5.45	0.021
Date	0.09	13.80	0.001
Fat and Date	0.10	7.16	0.001
Fat[1]		0.56	0.456
Date[1]		8.57	0.004

[1] Partial F-test.

TABLE 4. Correlation coefficients for stopover time and fat content at capture within three stages of spring migration for Semipalmated Sandpipers in South Carolina.

	1992	1993
Early migration		
r[1]	0.096	−0.145
P[2]	0.564	0.471
n[3]	11	27
Mid-migration		
r	0.127	−0.152
P	0.352	0.172
n	58	82
Late migration		
r	−0.403	0.002
P	0.282	0.991
n	9	31

[1] Pearson product-moment correlation coefficient.

[2] Probability of an r such as the one calculated given no relationship between stopover time and fat content at capture.

[3] Sample size.

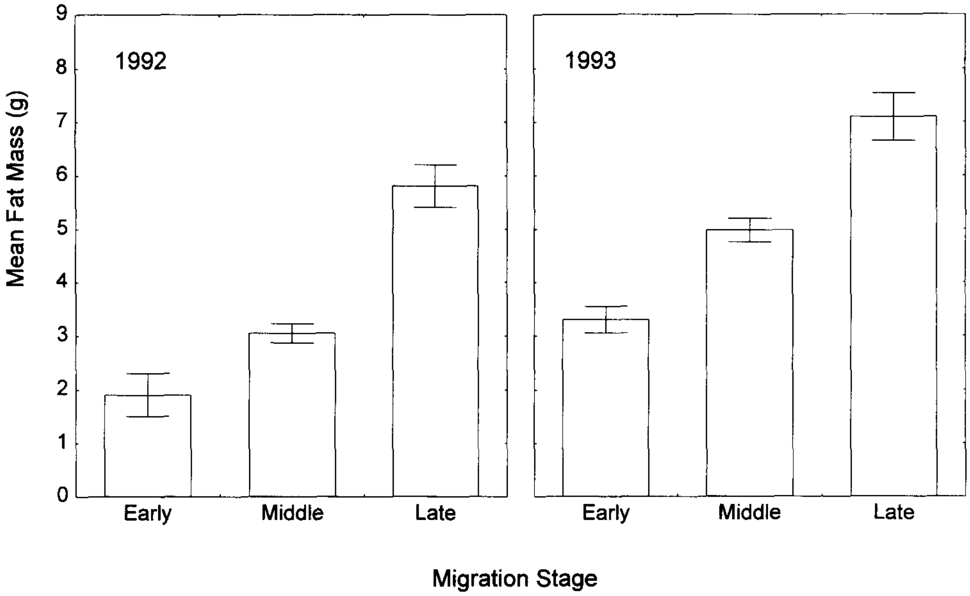

FIGURE 3. Mean minimum stopover time of Semipalmated Sandpipers in South Carolina for three stages of migration in spring 1992 and 1993. Error bars represent standard error of the mean.

that spring migrants are "time-selected" and fall migrants are "energy-selected."

Lank (1983) compared stopover times for autumn migrants in North Dakota, USA and New Brunswick, Canada. Mean length of stay in North Dakota was 15–20 days; in New Brunswick, the average was 21–24 days early in the season, but decreased to 10 days in the latter stages of migration (Lank 1983). Dunn et al. (1988) found autumn stopover time averaged 11–14 days in coastal Maine. In New Brunswick and Maine, birds were preparing for a transoceanic flight (ca. 3,500 km) to wintering grounds in northern South America, and longer mean stopover times might be expected. Shorter autumnal stopovers have been reported for other calidrid sandpipers. Using a probability model, Butler et al. (1987) estimated length of stay for Western Sandpipers to be 1–3 days during southward migration in southern British Columbia. Holmgren et al. (1993) used a mark-recapture model to estimate length of stay for adult Dunlin (*C. alpina*) in Sweden; mean stopover time was four days for adult birds.

Stopover time of sandpipers at South Island decreased throughout the spring migration season, suggesting an increasing speed of migration as the season progresses. Length of stay also decreased towards the end of autumn migration in eastern Maine (Dunn et al. 1988), North Dakota, and New Brunswick (Lank 1983). In Ontario (Page and Middleton 1972) and the upper Bay of Fundy (Hicklin *in* Dunn et al. 1988), however, length of stay increased with time during the southward migration. Dunn et al. (1988) claim that opposite trends in stopover time in eastern Maine and the upper Bay of Fundy (separated by about 220 km) cannot be explained by frequency of favorable weather, length of prior residence on the study area, or local movements, and suggest that prey depletion may have been the reason for increasing length of stay in the Bay of Fundy. It is not clear, however, what effect prey depletion will have on stopover times. Faced with reduced prey levels, birds may stay longer to deposit a certain amount of fat, or they may leave the area in search of better foraging conditions. If prey levels were depleted at South Island and this led to more departures, the number of transients should be greater in the late stage of migration. This was not the case at South Island; transient rates in the late stages were similar to other stages. Therefore it is unlikely that prey depletion caused decreases in stopover time at South Island.

"Time-selected" migrants base stopover decisions in part on the expected rate of fat deposition (Alerstam and Lindstrom 1990). Birds that migrated late in the season may have made shorter stopovers because the expected rate of fat deposition at future sites is greater at the end of the season than at the beginning. When migrants can expect greater fat deposition rates at future sites, stopover times will be decreased.

Improved flying conditions may also affect stopover times. Increasing temperatures and frequency of favorable winds may provide enhanced conditions for migration. If so, later migrants would use less fat during flights and require less time at staging areas to maintain adequate energy reserves. Among year variation in weather conditions may cause fat levels to vary. In 1993, sandpipers tended to carry greater fat stores than in 1992. Contrary to predictions relative to improved flying conditions, however, sandpipers tended to remain at South Island longer in 1993.

The decreasing trend in stopover times suggests that migrants may shift priorities with respect to current fat level and stopover times as the season progresses. Furthermore, this trend suggests differential strategies for male and female migrant Semipalmated Sandpipers.

Body mass and estimated fat mass at capture in this study were generally smaller than those reported for other migratory locations and other times of year. Mean body mass for spring migrants in coastal South Carolina was ca. 25 g. Gratto-Trevor (1992) reviewed body mass of adults from several spring and fall migration locations. Birds captured in Surinam on the north coast of South America in May were slightly heavier ($\bar{x} \pm$ SD, 27.6 ± 3.3 g) than those in South Carolina. Two spring staging areas in Ontario and one in Manitoba also showed slightly higher mean body masses (27–31 g) than South Carolina (Gratto-Trevor 1992). The only available estimates of Semipalmated Sandpiper fat loads in spring, from Surinam, averaged 75–100% of lean dry mass (McNeil and Cadieux 1972). These values are similar to, or greater than, ones found in this study. This suggests that Semipalmated Sandpipers weigh slightly more, and carry greater fat loads, both when they depart from the north coast of South America and when preparing for the final leg of northward migration from points north of South Carolina than when departing South Island.

Estimated fat mass at capture increased with later date. Dunn et al. (1988) found the same trend for adults during fall migration in Maine. Although the timing of sexes is reversed in fall, the conclusion is the same: migrants may shift priorities regarding optimal fat load with later date. Again, if this pattern is real, it suggests different migration strategies for male and female Semipalmated Sandpipers.

Estimated fat content at capture was not a good predictor of length of stay. Several shorebird studies have evaluated the relationship between these two variables in autumn (Page and Middleton 1972, Lank 1983, Dunn et al. 1988, Holmgren et al. 1993). Dunn et al. (1988) found fat content to influence length of stay in coastal Maine, but concluded that date in the season and weather were probably more important in determining stopover time. Lank (1983), using a different method, found a correlation between fat level and departure probability for New Brunswick and North Dakota sandpipers; lean birds were more likely to remain on the study areas than fat birds during favorable migration conditions. In this study, stopover time was independent of fat content, even when data were partitioned into early, middle, and late periods. Therefore, we fail to reject the null hypothesis that estimated fat content at capture does not influence length of stay.

Results of this study are consistent with other studies at other times of the year. Several reasons may account for the consistent failure to demonstrate a relationship between estimated fat mass and stopover time. First, extraneous variation and bias in estimates of minimum length of stay, and variation associated with estimation of fat mass at capture will decrease statistical power in this test and increase the probability of a Type II error. Second, local movements and risk-prone foraging may mask a true relationship. Alerstam and Lindstrom (1990) state that time-selected migrants will demonstrate risk-prone foraging during fat deposition. Semipalmated Sandpipers may make a series of local movements among areas with variable resources to maximize net energy gains. Third, birds staging at South Island may be able to use alternate sites along the coast and may not be maximizing flight distance between stopovers. For example, lean males early in the season may depart South Island whenever reasonably favorable weather permits with many options along the route should migratory conditions deteriorate or foraging at a particular site prove insufficient. The only within-season reports of color-marked birds at other migratory locations came from Cape Lookout, North Carolina, approximately 300 km north of South Island. A bird banded on 9 May 1992 was observed at Cape Lookout on 29 May 1992, and a bird band on 26 May 1992 was resident there from 6–10 June 1992 (S. Dinsmore, pers. comm.). These two birds were transients at South Island.

In summary, we found that our data on the stopover ecology of Semipalmated Sandpipers in South Carolina cannot be described by a simple model (e.g., arrive lean, fatten to a threshold level, and depart as soon as possible). The proximate mechanisms controlling stopover time probably include stage/date of the migration season, body condition, weather, available food resources, and social behavior (Lank 1983, Dunn et al. 1988). Spring migrant Semipalmated Sandpipers carried greater estimated fat stores and decreased stopover times later in the season. Males migrated before females, and adults preceeded second-year birds. These results suggest that date and differential migration strategies among age and sex classes should be considered in general models of migration.

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