The Condor 90:824–835

LENGTH OF STAY AND FAT CONTENT OF MIGRANT SEMIPALMATED SANDPIPERS IN EASTERN MAINE[1]

PETER O. DUNN,[2] TERRY A. MAY,[3] MARK A. MCCOLLOUGH
Department of Wildlife Resources, College of Forest Resources, University of Maine, Orono, ME 04469

MARSHALL A. HOWE
United States Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD 20708

Abstract. Semipalmated Sandpipers (*Calidris pusilla*) stop at coastal staging areas in the Canadian maritime provinces and northeastern United States to replenish fat reserves before initiating a nonstop transoceanic flight of at least 3,200 km to wintering areas in South America. The relationship between estimated fat content at capture and length of stay (days between marking and last observation) of Semipalmated Sandpipers at one of these staging areas in eastern Maine was studied during 1980–1982. Total body mass and wing chord length were used to estimate fat content. When data were analyzed by week of initial capture, mean length of stay of both adults and juveniles decreased with increasing fat content. This supports the assumption that resumption of migration is affected by fat content at staging areas for long-distance nonstop flights. However, fat content at capture was a poor predictor of length of stay, which suggests that other factors are more important in determining length of stay.

Key words: Semipalmated Sandpiper; Calidris pusilla; *migration; Maine; fat content; length of stay; shorebirds; staging areas; Bay of Fundy; flight range.*

INTRODUCTION

Large reserves of body fat are common in birds before and during long-distance migrations (Odum and Connell 1956). Because fat is catabolized during migratory flight, the amount of body fat is one factor limiting flight range, and, therefore, adequate fat reserves should be accumulated before long-distance flight is initiated (Raveling and LeFebvre 1967, reviewed in Blem 1980). Body mass has been measured frequently as an index to fat changes before and periodically during migrations (e.g., Nisbet et al. 1963, Murray and Jehl 1964, Mascher 1966, Johnson and Morton 1975, Pienkowski et al. 1979, Mercier 1985), but only a few studies have used recaptures or resightings of marked individuals to examine length of migratory pause in relation to fat content (Page and Middleton 1972, Post and Browne 1976, Cherry 1982, Lank 1983, Morrison 1984).

Many species of shorebirds (Charadrii) migrate long distances between breeding and wintering areas (Matthiessen and Stout 1967). Semipalmated Sandpipers (*Calidris pusilla*), which breed in the Canadian arctic, stop at estuaries in the Canadian maritime provinces and the northeastern United States before they initiate a nonstop transoceanic flight of >3,200 km to wintering areas in South America (McNeil and Burton 1973, 1977; Morrison 1984; Hicklin 1987). On the Magdalen Islands, Quebec, estimated flight-range capabilities of captured Semipalmated Sandpipers averaged 2,420 km, and those of some birds exceeded 3,225 km (McNeil and Cadieux 1972). Individuals with longer flight-range capabilities could fly directly to South America (McNeil and Cadieux 1972), but others would presumably need to remain longer to accumulate greater fat reserves before such a flight. If Semipalmated Sandpipers arrive at a staging area, gain fat to a threshold value determined by the minimum length of the next flight and continue their migration soon afterwards, then length of migratory pause should be inversely related to fat content (depending on the influence of other factors).

Most published studies of the relationship between fat content and migratory pause in shorebirds were conducted at inland staging areas where birds presumably do not have to accumulate as

[1] Received 10 February 1988. Final acceptance 7 July 1988.
[2] Present address: Department of Zoology, University of Alberta, Edmonton, Alberta T6G 2E9, Canada.
[3] Present address: College of Marine Studies, 118 Robinson Hall, University of Delaware, Newark, DE 19716.

much fat to reach another stopover site as at coastal staging areas. Length of stay of Semipalmated Sandpipers at Long Point, Ontario was not related to fat level (Page and Middleton 1972), nor was fat accumulation related to length of stay of shorebirds at two reservoirs near Raleigh, North Carolina (Post and Browne 1976). At inland sites, migrating birds might be able to complete subsequent flights successfully, regardless of fat content. At coastal staging areas, however, where sandpipers have to accumulate large fat stores before initiating long-distance flights, one might expect length of stay to be related to fat content. However, a brief review of unpublished data on Semipalmated Sandpiper length of stay (Morrison 1984, see also Lank 1983) suggests that fat content may be a poor predictor of length of stay even before nonstop flights >2,000 km. In this paper we examine the relationship between estimated fat content at time of capture and length of migratory pause of Semipalmated Sandpipers in eastern Maine.

STUDY AREA AND METHODS

Sandpipers were counted and captured during 1980–1982 along the Maine coast from the town of Perry (44°58′N, 67°04′W) to West Quoddy Head (44°49′N, 66°58′W). The coastline consists of tidal (5.5 m mean amplitude) mud flats used by sandpipers for feeding, and rocky shorelines and gravel bars used for roosting. Sandpipers were counted at all major roost sites about every 10 days. Birds were captured with mist nets at roosts and along flight paths 2–3 hr before high tide. Banding began on 8, 16, 13 July in 1980–1982, respectively, although birds were present on the study area by the first week of July in all years. Trapping ended on 27 August in 1981 and 1982, and on 5 September in 1980. After the end of trapping, observations of marked birds continued on weekends until 18–19 September each year. Captured sandpipers were marked on the breast with Rhodamine B red dye or blue or green fluorescent paint, and on the leg with a numbered yellow vinyl leg flag (about 1.3 cm by 0.7 cm), affixed over a USFWS band (after Gerstenberg and Harris 1976). Juveniles were differentiated from adults by plumage characteristics (Prater et al. 1977). After banding, individually marked birds were relocated and identified at roosts and feeding areas during almost daily observations. Length of stay in the study area was defined as the number of days from initial capture to last observation. Length of stay represents a minimum number of days resident on the study area because birds probably arrived before the day of capture and they may have stayed after the last day that they were observed.

Sandpipers were weighed in the field using either a triple-beam balance (to the nearest 0.1 g in 1980) or a Pesola spring balance (to the nearest 1 g in 1981 and 1982). We did not directly compare the precision of the two scales; however, the variances of total body mass of sandpipers in 1980 vs. 1981 or 1982 differed ($P < 0.05$, F-tests); therefore, we analyzed each year separately. Total body mass and wing chord length (nearest 1 mm) were used to estimate percent body fat using the regression equation (fat-free mass = $-9.0513 + 0.3134$[wing length]) of Page and Middleton (1972) for Semipalmated Sandpipers at Long Point, Ontario. The validity of our use of this equation was evaluated by determining the relationship between wing length and fat-free mass of nine carcasses obtained in 1980. These carcasses were shaved, cut into pieces no longer than 1 cm and dried in a vacuum to constant mass. Fat was extracted from the dried remains using a Soxhlet apparatus for 24 hr. Page and Middleton (1972) extracted fat from the entire carcass, but otherwise our procedures were the same. Fat-free mass was total body mass minus extracted fat.

Unless stated otherwise, our analysis of length of stay used data only from sandpipers that were reobserved at least once after banding. Length of stay and estimated fat were analyzed: (1) across the entire season for general patterns, and (2) with individuals caught in the same weekly period, to reduce the confounding effects of combining data from birds arriving throughout the season. There are two reasons for factoring out the effect of date: (1) there may be differences in environmental factors that vary seasonally and affect length of stay and fat deposition (e.g., relative prey abundance) and (2) cohorts of birds caught during different capture periods have potentially different probabilities of being reobserved (even though observational effort is constant throughout the season). Reobservation probabilities may differ because birds caught early in the season could potentially be seen for a period of over 2 months, while birds caught later in the season could only be seen for less than 1 month (almost all birds leave by mid-September).

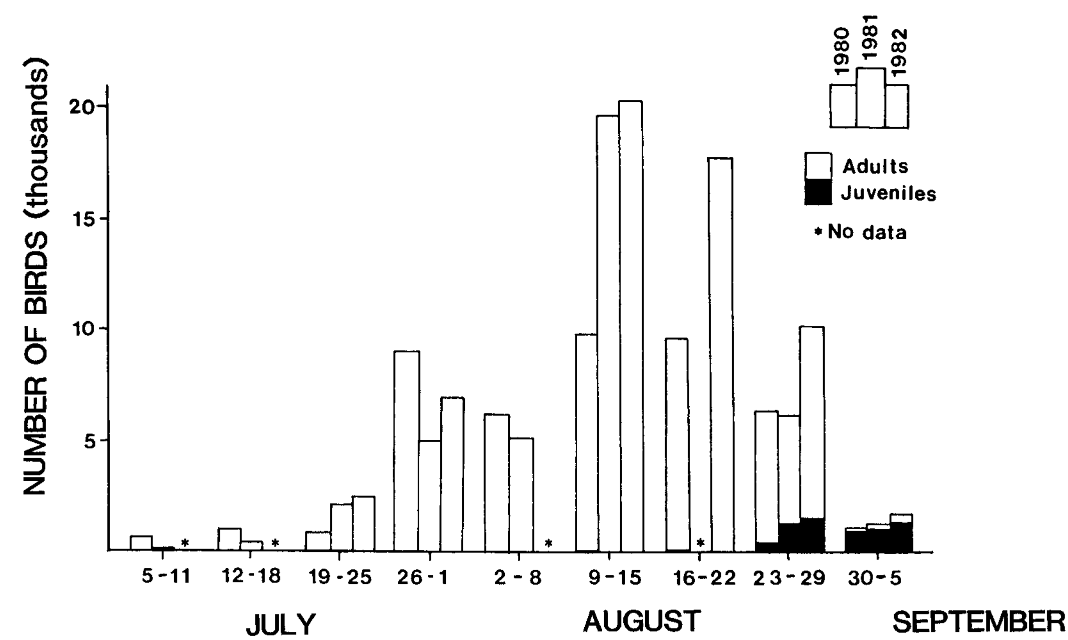

FIGURE 1. Weekly maximum counts of Semipalmated Sandpipers on roosts near Eastport and Lubec, Maine, 1980–1982. The number of birds should be read from the length of each open (adults) or closed (juveniles) bar.

RESULTS

ABUNDANCE

In 1980, 513 (80.7% adults and 19.3% juveniles) Semipalmated Sandpipers were captured during 20 attempts (25.7 birds/attempt), and 404 adults and 98 juveniles were color-marked. In 1981, 1,727 (79.0% adults and 21.0% juveniles) sandpipers were caught during 29 attempts (59.6 birds/attempt), and 1,340 adults and 313 juveniles were color-marked. In 1982, 860 (86% adults and 14% juveniles) sandpipers were caught during 48 attempts (17.9 birds/attempt), and 738 adults and 99 juveniles were color-marked.

Each year, adult sandpiper numbers on counted roosts reached a seasonal peak in mid-August (Fig. 1). Juveniles were first seen in early August and their numbers peaked in late August to early September. After 5 September each year, sandpiper numbers declined to <800 birds.

FAT CONTENT

We evaluated the validity of our use of the Page and Middleton (1972) equation to estimate fat-free mass of Maine birds by measuring body fat of nine carcasses in 1980. Analysis of covariance revealed that the regression line derived from Maine sandpipers was parallel with the regression of Page and Middleton (data taken from fig. 2 in Page and Middleton 1972); however, there was a barely nonsignificant treatment (location) effect ($F = 5.18$, $P = 0.054$, df $= 1, 58$). Fat-free mass averaged 2.5 g greater for any given wing length in Maine than in Page and Middleton's study in Ontario. Although this difference does not affect any of the conclusions for our study area, it precludes direct comparisons of our fat content data with Page and Middleton's results. Page and Middleton (1972, p. 87) also found that fat-free mass did not differ between adults (n = 23) and immatures (n = 30); there was only one juvenile in our sample of nine carcasses. There were also nearly identical regressions between actual (extracted) fat and predicted fat (r^2 = 0.9163), and actual fat and total body mass (r^2 = 0.9167) in our sample. All of our analyses using estimated fat content (in grams) were repeated with total body mass with no qualitative difference in the results. Therefore, correcting for fat-free mass with Page and Middleton's equation or using total body mass made no difference in our results because fat content varied much more than fat-free mass. We have used grams of fat instead of total body mass because fat is the main energy source for migratory flights.

TABLE 1. Total body mass (g), estimated fat (g), and wing length (mm) of all captured Semipalmated Sandpipers, and length of stay (days) of reobserved sandpipers.

	1980				1981				1982			
	$\bar{x}$	SE	n	P[a]	$\bar{x}$	SE	n	P[a]	$\bar{x}$	SE	n	P[a]
Total body mass												
Adults	32.0	0.25	402	0.001	31.3	0.15	1,364	0.001	29.7	0.20	736	0.001
Juveniles	28.7	0.63	98		28.0	0.23	362		27.2	0.38	99	
Estimated fat												
Adults	10.9	0.20	402	0.001	9.2	0.20	1,364	0.001	8.5	0.20	736	0.001
Juveniles	7.8	0.60	98		6.3	0.02	362		6.1	0.40	99	
Wing length												
Adults	96.2	0.14	404	0.86	99.4	0.08	1,364	0.001	96.5	0.10	738	0.43
Juveniles	96.3	0.26	98		98.1	0.13	362		96.3	0.24	99	
Length of stay												
Adults	11.2	0.61	135	>0.05	11.0	0.36	442	>0.05	13.7	0.42	459	>0.05
Juveniles	9.9	1.30	22		11.6	0.86	64		11.5	0.67	62	

[a] Probability of no difference between adults and juveniles; Mann-Whitney U-tests.

Total body mass and fat content were greater in adults than juveniles in all years (Table 1). Although this could have been due to the larger structural size (fat-free mass) of adults, adult wing lengths were significantly longer only in 1982 (Table 1). The significant difference in mean wing lengths (1.3 mm) between adults and juveniles in 1981 translated into such a small difference in fat-free mass (0.41 g) that its potential effect on estimated fat was unimportant compared with the greater difference in total body mass (3.3 g, Table 1). Estimated fat increased throughout the autumn migration for adults in all years and for juveniles in 1981 and 1982 (Tables 2, 3). There was no increase in estimated fat of juveniles in 1980, probably because the sample size was small.

Recaptures of banded birds support the hypothesis that sandpipers gain body fat while on the study area (Fig. 2). There were two recaptures in 1980, 18 in 1981, and five in 1982. Linear regression indicated that estimated body fat increased with time from initial capture to last recapture (change in fat [g]= $-1.03 + 0.379$[days from initial capture to recapture]; $r^2 = 0.34$, $P < 0.005$). A quadratic function explained slightly more variation ($r^2 = 0.36$) than the linear equation probably because sandpipers tend to lose body mass for several days after capture before gaining body mass (Morrison 1984). Five of the nine birds that lost fat were recaptured within 5 days of initial capture.

LENGTH OF STAY

Of the sandpipers marked individually and released, 157 (31.3%) were reobserved in 1980, 506 (30.6%) in 1981, and 521 (62.2%) in 1982. The high resighting probability for both age classes in 1982 resulted from an intensified resighting effort. Adults were reobserved more frequently (33%) than juveniles (22–20%) in 1980–

TABLE 2. Pearson's product-moment correlations between estimated fat (g) at capture or total body mass (g) and date of capture.

Age	1980			1981			1982		
	r	P[a]	n	r	P[a]	n	r	P[a]	n
Estimated fat									
Adults	0.46	0.001	400	0.55	0.001	1,364	0.68	0.001	736
Juveniles	0.01	0.96	98	0.36	0.001	362	0.46	0.001	99
Total body mass									
Adults	0.41	0.001	400	0.51	0.001	1,364	0.65	0.001	736
Juveniles	0.01	0.97	98	0.37	0.001	362	0.42	0.001	99

[a] Probability of no correlation between fat or body mass and date of capture.

TABLE 3. Minimum length of stay (LOS, in days), estimated fat at capture (FAT, in g)[a], estimated fat (g) that must be accumulated in addition to fat at capture to fly 3,200 km (FATACCUM, in g)[b] and observed length of stay minus estimated length of stay (in days) based on estimates of fat deposition rate from Hicklin (OBES-H) and Lank (OBES-L)[c] for Semipalmated Sandpipers. FAT, FATACCUM, OBES-H, and OBES-L were calculated individually for each bird.

	July						August								
	12–18		19–25		26–1		2–8		9–15		16–22		23–29		
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	P[d]
Adults															
1980															
LOS	16.3	5.0	11.0	7.0	15.5	2.1	16.7	2.6	11.1	0.8	7.7	1.0	6.5	2.7	0.002
FAT	5.0	1.4	9.0	2.7	9.3	0.5	13.3	1.2	10.2	0.5	13.4	0.7	16.7	1.7	0.0001
FATACCUM	5.8	1.1	3.2	2.0	2.9	0.4	−0.1	0.9	2.1	0.3	−0.3	0.5	−2.5	1.1	0.0001
OBES-H	12.7	4.4	9.0	7.0	13.7	2.1	16.7	2.6	9.9	0.8	7.9	0.9	8.0	2.0	0.03
OBES-L	13.8	4.6	9.7	7.0	14.3	2.1	16.7	2.6	10.3	0.8	7.8	0.9	7.6	2.0	0.013
	(n = 4)		(n = 3)		(n = 16)		(n = 9)		(n = 67)		(n = 30)		(n = 6)		
1981															
LOS	11.8	1.7	14.7	0.7	13.6	0.8	9.3	0.7	7.2	0.6	6.5	0.8	10.0	0.0	0.0001
FAT	5.0	0.5	5.2	0.4	7.8	0.5	7.8	0.5	9.9	0.5	13.7	0.5	4.8	2.5	0.0001
FATACCUM	5.8	0.3	6.0	0.3	4.3	0.3	4.1	0.3	2.7	0.4	−0.3	0.4	6.1	1.8	0.0001
OBES-H	8.3	1.7	11.0	0.8	11.0	0.8	6.8	0.7	5.6	0.6	6.6	0.7	6.3	1.1	0.0001
OBES-L	9.4	1.7	12.1	0.8	11.8	0.8	7.6	0.7	6.1	0.6	6.6	0.8	7.5	0.7	0.0001
	(n = 22)		(n = 100)		(n = 105)		(n = 95)		(n = 68)		(n = 50)		(n = 2)		
1982															
LOS	21.5	2.0	20.5	1.1	16.7	0.8	13.5	0.8	8.0	0.9	7.9	0.5	6.8	0.5	0.0001
FAT	3.4	0.4	5.3	0.4	6.1	0.3	8.9	0.6	11.1	0.9	11.8	0.4	13.0	0.5	0.0001
FATACCUM	7.1	0.3	5.6	0.3	5.0	0.2	3.0	0.4	1.6	0.7	1.0	0.3	0.1	0.4	0.0001
OBES-H	17.4	2.1	17.1	1.1	13.7	0.7	11.6	0.8	7.0	0.9	7.3	0.4	6.7	0.5	0.0001
OBES-L	18.7	2.0	18.2	1.1	14.6	0.7	12.2	0.8	7.3	0.9	7.5	0.4	6.8	0.5	0.0001
	(n = 25)		(n = 83)		(n = 110)		(n = 68)		(n = 26)		(n = 86)		(n = 61)		

TABLE 3. Continued.

	July						August								
	12–18		19–25		26–1		2–8		9–15		16–22		23–29		
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	P^{d}
Juveniles															
1980															
LOS													9.5	1.4	
FAT													8.7	1.2	
FATACCUM													3.1	0.8	
OBES-H													7.6	1.2	
OBES-L													8.1	1.2	
													(n = 20)		
1981															
LOS											11.7	1.0	11.5	1.4	0.90
FAT											5.1	0.5	8.8	1.7	0.03
FATACCUM											5.8	0.3	3.2	1.2	0.02
OBES-H											8.2	1.0	9.5	1.2	0.47
OBES-L											9.3	1.0	10.1	1.2	0.72
											(n = 51)		(n = 11)		
1982															
LOS											5.9	2.1	12.3	0.6	0.003
FAT											4.2	1.4	6.6	0.5	0.04
FATACCUM											6.3	1.0	4.6	0.3	0.04
OBES-H											2.1	2.3	9.5	0.6	0.005
OBES-L											3.3	2.2	10.4	0.6	0.004
											(n = 8)		(n = 54)		

[a] Estimated from the equation of Page and Middleton (1972).
[b] FATACCUM = fat required to fly 3,200 km (g) − estimated fat at capture (g). Fat required to fly 3,200 km calculated using the flight-range formula of McNeil and Cadieux (1972) and a flight speed of 80.5 km/hr.
[c] Rates of fat accumulation came from Lank (1983, p. 100–101). Weight gain (which was probably mostly fat accumulation) was 1.65 g/day in the upper Bay of Fundy (Hicklin), and rate of fat gain on Kent Island, New Brunswick was 2.4–2.5 g/day (we used 2.4 g/day).
[d] Probability of no difference among capture periods for the particular variable; Kruskal-Wallis and Mann-Whitney U-tests.

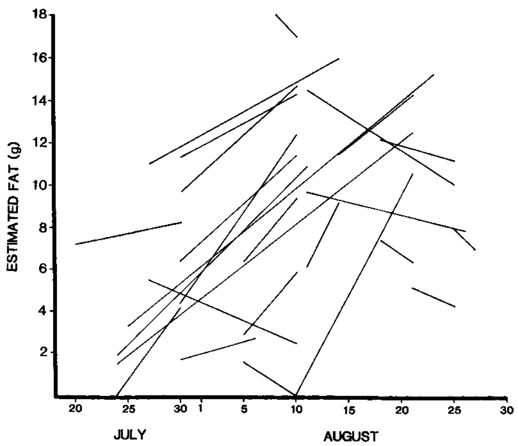

FIGURE 2. Change in estimated fat content (g) of 25 individual Semipalmated Sandpipers from initial capture to recapture during July–August 1980–1982.

1981, but both age classes were reobserved with equal frequency in 1982 (62–63%). We analyzed length of stay data from each year separately, so differences in sampling among years would not affect our results.

If birds that were never reobserved after marking and release differed in fat content or other characteristics from birds that were reobserved, then our estimates of minimum length of stay may differ from the true values. Estimated fat, body mass, and wing and culmen lengths generally did not differ between reobserved and non-reobserved sandpipers (Mann-Whitney U-tests, $P > 0.05$). A difference in wing lengths (0.6 mm) of reobserved and non-reobserved adults in 1980 did not affect estimated fat levels. In contrast, the shorter wings and greater body mass (1.6 g difference) of adult sandpipers not reobserved in 1981 yielded greater estimated fat levels in these birds than in sandpipers that were reobserved (1.8 g difference; Mann-Whitney U-tests, $P < 0.01$). Therefore, our estimates of length of stay may not be representative of the whole population of adult sandpipers in 1981.

There was no difference in estimates of mean minimum lengths of stay between adults and juveniles in any year (Table 1). In all years, lengths of stay of adults decreased over the season when analyzed according to weekly capture periods ($P < 0.001$, Kruskal-Wallis and Mann-Whitney U-tests; Table 3). When analyzed by weekly capture periods, length of stay of juveniles declined across the season in 1982, but not in 1981 (Table 3; there were not enough data in 1980 for this test). At the start of migration adult sandpipers were staying in eastern Maine for at least 11.8–21.5 days, on average. This range was 8.3–18.7 days longer than would be expected if these birds were departing as soon as they deposited enough fat (at rates estimated by Hicklin and Lank; both rates in Lank 1983, p. 100–101) to fly 3,200 km (Table 3). This "extra time" beyond what was required for fat accumulation decreased across the season each year (Table 3). By the last capture period, adults were staying 6.3–8.0 days beyond the minimum for fat deposition. Juveniles, which were caught only toward the end of the season, stayed 2.1–10.4 days longer than the estimated minimum required period (Table 3).

To evaluate the relative contributions of fat

TABLE 4. Simple and multiple regression models of Semipalmated Sandpiper length of stay (days) with estimated fat (g) and date of capture.

Year Age	n	r^2 (P^a)		Improvement in r^2 and (P^b) for model after inclusion of second variable	
		Fat	Date	Fat, date	Date, fat
1980					
Adults	135	0.08 (<0.01)	0.13 (<0.01)	0.07 (<0.01)	0.02 (0.08)
Juveniles	22	0.37 (<0.01)	0.00 (0.99)	0.01 (0.66)	0.37 (<0.01)
1981					
Adults	442	0.11 (<0.01)	0.16 (<0.01)	0.08 (<0.01)	0.03 (<0.01)
Juveniles	64	0.12 (<0.01)	0.00 (0.86)	0.01 (0.31)	0.14 (<0.01)
1982					
Adults	459	0.25 (<0.01)	0.34 (<0.01)	0.12 (<0.01)	0.03 (<0.01)
Juveniles	62	0.02 (0.26)	0.12 (<0.01)	0.17 (<0.01)	0.07 (0.03)

[a] Probability of no relation with length of stay; simple regression.
[b] Probability of no increase in the amount of variance explained following addition of the second variable; partial F-tests.

content and Julian date to length of stay estimates, r^2 was calculated for simple and multiple regression models using data from the entire season (Table 4). Because estimated fat content and date of capture were correlated (Table 2), we examined their partial effects with partial F-tests (Table 4). For all years, length of stay of adults showed a significant inverse correlation with both fat and date of capture in simple regressions (Table 4). However, the r^2 values were small (0.08 to 0.25). Using multiple regressions, in all years date of capture explained more of the variance in length of stay of adults than estimated fat content (Table 4). In 1981 and 1982, a significant amount of the variance in length of stay of adults was explained by fat level after controlling for date of capture (Table 4). In 1980 there was only a trend ($P = 0.08$) between length of stay and estimated fat after controlling for date of capture; this may have been due to the smaller sample size in 1980 (Table 4). Length of stay of juveniles was also related to fat level each year after controlling for the effect of date (Table 4). Because most juveniles were caught in a limited time period in late August, lack of a significant relationship with date of capture in two of the years was not surprising.

We tried to minimize the influence of covariance of fat level and date by partitioning capture data into 1-week periods. Within each capture period, we examined fat level and length of stay for nonlinear trends by comparing the amount of variance (r^2) explained by simple linear regression with analysis of variance (using 5-g fat classes). Nonlinear relationships would be expected if length of stay reached an asymptote at some high level of fat. We found four time periods with nonlinear relationships between length of stay and estimated fat (Table 5). In these cases a visual inspection of the plotted data revealed no consistent relationship between fat level and length of stay of adults during 9–15 August 1980 and 19–25 July 1981; however, for adults during 26 July–1 August 1982 and for juveniles during 16–22 August 1982 there was a general inverse relationship, although no threshold occurred. For these time periods with nonlinear trends we present the results of ANOVAs, rather than linear regressions (Table 5). Each year, for both adults and juveniles, there were more significant relationships between length of stay and estimated fat than would be expected by chance (Table 5). Therefore, length of stay was dependent on fat level; however, the low r^2 values for adults (mean r^2 of significant regressions = 0.19) and juveniles (mean r^2 = 0.23) indicated that fat was a poor predictor of length of stay.

DISCUSSION

Semipalmated Sandpipers must have sufficient energy reserves to migrate at least 3,200 km from eastern Maine to the most northerly of the Antilles Islands, which provide the first possible rest site on a transoceanic flight to wintering areas. By substituting 38.1 kJ per gram of body fat (Johnston 1970) in the formulae presented by McNeil and Cadieux (1972), a sandpiper with an average wing length of 96 mm (21.0 g fat-free weight) would require 40% fat (14.0 g) to fly 3,200 km. We know that at least some of the birds we banded were migrating this distance because two banded birds were reobserved in Suriname (Spaans and Swennen 1982) and two band recoveries came from Guyana. When initially captured, many sandpipers apparently did not have sufficient fat reserves to fly 3,200 km; however, most birds remained on the study area long enough to accumulate these fat reserves (Table 3). Nevertheless, sandpipers may be able to complete long-distance nonstop flights with less than 40% fat if the flight-range formulae overestimate energy expenditure during flight.

The energy expenditure of shorebirds in flight may be lower than previously predicted if birds use tail winds or cooler ambient temperatures at higher altitudes (Torre-Bueno 1978) to reduce energy expenditure (see Davidson 1984 for a discussion of other factors). The evidence from our study to suggest this comes from a band recovery of a Semipalmated Sandpiper in Guyana. A bird we banded in Maine in 1980 (at banding it was 23% fat and total body mass was 27 g) was recovered 2 days later in Guyana (Band no. 1151-25849). This is the fastest documented flight record for a Semipalmated Sandpiper traveling from North to South America, and it coincides with the minimum estimate for the time required to fly this distance (40–60 hr; Stoddard et al. 1983). This apparent contradiction between observed ability to survive migration with only 23% fat and a theoretical estimate of 40% fat suggests that the flight-range formulae are incorrect by about a factor of two.

Sandpipers initiating a transoceanic migration are subjected to strong selective forces, as birds unable to reach land because of inadequate fat

TABLE 5. Simple regression models and ANOVAs of minimum length of stay (days) of Semipalmated Sandpipers with estimated fat (g) (5-g fat classes used for ANOVAs) for each capture period.[a]

Age Year	July									August		
	12–18			19–25			26–1			2–8		
	R	*P*	*n*	*R*	*P*	*n*	*R*	*P*	*n*	*R*	*P*	*n*
Adult												
1980	−0.96	0.04	4	−0.16	0.90	3	−0.03	0.92	16	−0.21	0.58	9
1981	0.03	0.89	22		<0.01	100[c]	−0.22	0.02	105	−0.33	<0.01	95
1982	0.27	0.20	24	−0.20	0.07	83		0.01	110[d]	−0.39	<0.01	68
Juvenile												
1980												
1981												
1982												

[a] Significant regressions or ANOVAs are underlined for ease of comparison.
[b] Probability of finding the observed number of significant relationships (each with a $P < 0.05$) by chance alone.
[c] Nonlinear relationship found. *P* values are for ANOVAs. 19–25 July was not used in calculating the overall *P* value (see far right column) because there was no consistent trend in the data when plotted. During 9–15 August there were no differences in length of stay among fat classes.
[d] Nonlinear relationship found. *P* values are for ANOVAs. These capture periods were used in calculating the overall *P* value (see far right column) because there was an overall negative relationship between length of stay and fat.

reserves or unfavorable weather conditions are certain to perish. One necessary, but not always sufficient, factor affecting length of migratory stopover is the time required to accumulate the minimum mass of fat required to complete successfully a long-distance flight. Assuming that fat content is the most important factor influencing length of stay, sandpipers passing through an interior staging area might only need to stop long enough to replenish sufficient fat to reach the next attainable, and presumably close, feeding site. Relatively lean birds might be able to depart from interior staging areas with a higher probability of survival than similar birds initiating transoceanic flights. On the coast, birds arriving with large fat reserves might continue nonstop flights to wintering areas, while birds with lesser fat reserves would have to stop and accumulate additional fat reserves before a transoceanic flight. Once fat levels reach some threshold level, birds will be able to continue migratory flights if weather is favorable.

Studies of Semipalmated Sandpipers migrating through eastern Maine (this study), Ontario (Page and Middleton 1972, Morrison 1984), and New Brunswick and North Dakota (Lank 1983) indicate that this model is too simple to describe length of stay of sandpipers during fall migration. Length of stay before a transoceanic flight was correlated with fat level in Maine and New Brunswick because relatively lean birds remained on the study area longer than fatter birds. However, other factors probably influenced length of stay more strongly because, after controlling for date, fat only explained an average of 11% of the variance in length of migratory pause (range = 2–37%, Table 4). In addition, length of stay of adults averaged 5.6–18.7 days longer than what would be expected if sandpipers continued migration soon after accumulating enough fat to fly 3,200 km (Table 3). At an inland staging area in southern Ontario, there was no relationship between length of stay and body fat of Semipalmated Sandpipers (Page and Middleton 1972). Similarly, after correcting for the effect of date, there was no correlation between body fat and length of stay of Semipalmated Sandpipers in North Dakota, although fatter birds had a higher probability of leaving on days favorable for migration (Lank 1983). Therefore, fat levels appear to influence length of stay at coastal staging areas, as predicted, but other factors such as weather and social behavior (see Lank 1983) delay departure after minimum fat deposits are attained.

Differences in body mass of sandpipers at coastal and inland staging areas appear to be due, in part, to the length of subsequent migratory flights. Body masses of Semipalmated Sandpipers at coastal staging areas were generally greater than those at inland areas (Morrison 1984), which suggests that sandpipers can successfully resume migration with less body fat at inland than coastal staging areas. However, at some inland areas, such as James Bay, Ontario, a substantial proportion of migrants may fly nonstop to South America (see table 3 in Morrison 1984). At inland sites where migrants are making long-distance nonstop flights, one might also find a re-

TABLE 5. Extended.

August									
9–15			16–22			23–29			
R	P	n	R	P	n	R	P	n	P[b]
	0.08	67[c]	−0.48	<0.01	30	0.09	0.87	6	0.041
−0.38	<0.01	68	−0.37	<0.01	50				<0.001
−0.09	0.66	26	−0.33	<0.01	86	−0.11	0.38	61	0.004
						−0.58	<0.01	20	0.050
				<0.01	51[d]	−0.49	0.13	11	0.010
			0.30	0.47	8	−0.38	<0.01	54	0.010

lationship between length of stay and fat content. However, it is not known what proportion of sandpipers at inland sites is making these long nonstop flights. The pattern of length of stay and body mass gain at a staging area is not simply a matter of whether it is on the coast or not, but also of the migration route traveled by birds using the site, food availability, number of competitors, date in the season, and weather (Lank 1983, Morrison 1984).

One question arising from the results of this study and others is why there are differences among sites in the temporal pattern of length of stay estimates. In both Maine and New Brunswick (this study, Lank 1983) length of stay was shorter toward the end of the season (after 20 July 1977 length of stay declined by about 0.33 days/day on Kent Island). However, in Ontario length of stay was longer toward the end of the season, and there was no obvious tendency for fat birds to depart more quickly than lean birds (Page and Middleton 1972). Semipalmated Sandpipers also appear to stay longer at the end of the migration season in the upper Bay of Fundy (Hicklin, pers. comm.). We do not think these geographic and seasonal trends in length of stay can be explained by the frequency of favorable weather because Lank (1983, p. 115) found that favorable weather occurred once every 4–5 days at Kent Island, and it is unlikely that there are major differences in weather patterns between eastern Maine and the upper Bay of Fundy (approximately 220 km away). Length of prior residency is also not believed to be an important factor. Although birds caught later in the season could have been on the staging area longer before capture than birds caught early in the season (and therefore could have gained larger fat reserves before capture and have been more likely to leave early), our analysis (Table 4) shows a significant seasonal decline in length of stay even after controlling for fat level.

Movements of birds from eastern Maine to other areas around the Bay of Fundy could also have led to differences among areas in length of stay. Our limited data on local movements suggest to us that this was not the cause of the seasonal decline in length of stay (and also not the reason for the poor performance of fat content as a predictor of length of stay). In 1981, Hicklin (pers. comm.) had 40 observations of marked sandpipers from eastern Maine around the Bay of Fundy (most were seen in Chignecto Bay, New Brunswick, 220 km away). Only one of these birds was individually identified, and a maximum of three color-marked birds was seen at once. This is a maximum of 2% of our marked birds (assuming no duplication); however, most of Hicklin's sightings involve one marked bird seen over several consecutive days, so it is more likely that fewer than 10 (out of 1,653 marked birds) were seen away from the Maine study area in 1981. It is possible that birds seen outside our study area were birds that were never seen after marking (38–68% of our marked birds) because of the trauma of banding or their inability to compete with resident birds (see Lank 1983, p. 79–84). These birds, however, were not included in the analysis of length of stay. On Kent Island, Lank (1983, p. 85) reported that 52% ($n = 25$) of birds reported off his study area were birds that disappeared after marking.

If relative food availability declines over the season (e.g., Schneider and Harrington 1981), then sandpipers might have to remain longer to finish their fattening. In the upper Bay of Fundy, sandpipers caught after the peak of migration may have remained longer to accumulate fat reserves because of a decline in biomass of the principal prey, *Corophium volutator* (Amphipoda; Hicklin, pers. comm.); however, we have no comparable data from eastern Maine. Differences in food availability and length of stay between eastern Maine and the upper Bay of Fundy may be important for understanding the cost and benefits of using various migration routes. These differences are especially relevant in light of recent concern for the sensitivity of shorebird populations to habitat destruction at major staging areas (Senner and Howe 1984, Myers et al. 1987).

ACKNOWLEDGMENTS

Financial support for this research was provided by the U.S. Fish and Wildlife Service (Contract Number 14-16-0009-80-018), the Maine Department of Inland Fisheries and Wildlife (MDIFW) through Federal Aid to Wildlife Restoration Project W-62-R-88, and the University of Maine Honors Program. The Maine Cooperative Fisheries and Wildlife Research Unit helped to administer funding from the MDIFW. We appreciate the courtesies extended to us by the faculty and staff of the R. S. Friedman Cobscook Bay Laboratory, and Mr. and Mrs. R. Goodrich. T. Chamberlain, J. Cofske, J. Kelly, and K. Murphy assisted in the field. We thank E. Snyder for her assistance in the field and laboratory throughout this study. N. Famous and S. Feffer provided useful advice and field equipment. G. Page critically reviewed an earlier version of this paper. S. Hannon, P. Hicklin, D. Krementz, D. Lank, M. Samuel, and several anonymous reviewers made valuable comments on the manuscript. P. Hicklin and D. Lank generously provided unpublished observations.

LITERATURE CITED

BLEM, C. R. 1980. The energetics of migration, p. 175–224. *In* S. A. Gauthreaux [ed.], Animal migration, orientation, and navigation. Academic Press, New York.

CHERRY, J. D. 1982. Fat deposition and length of stopover of migrant White-crowned Sparrows. Auk 99:725–732.

DAVIDSON, N. C. 1984. How valid are flight range estimates for waders? Ringing & Migr. 5:49–64.

GERSTENBERG, R. H., AND S. W. HARRIS. 1976. Trapping and marking shorebirds at Humboldt Bay, California. Bird-Banding 47:1–7.

HICKLIN, P. W. 1987. The migration of shorebirds in the Bay of Fundy. Wilson Bull. 99:540–570.

JOHNSON, O. W., AND M. L. MORTON. 1975. Fat content and flight range in shorebirds summering on Enewetak Atoll. Condor 78:144–145.

JOHNSTON, D. W. 1970. Caloric density of avian adipose tissue. Comp. Biochem. Physiol. 34:827–832.

LANK, D. B. 1983. Migratory behavior of Semipalmated Sandpipers at inland and coastal staging areas. Ph.D. diss. Cornell Univ., Ithaca, NY.

MASCHER, J. W. 1966. Weight variations in resting Dunlins (*Calidris a. alpina*) on autumn migration in Sweden. Bird-Banding 37:1–34.

MATTHIESSEN, P., AND G. D. STOUT [EDS.]. 1967. The shorebirds of North America. Viking Press, New York.

MCNEIL, R., AND J. BURTON. 1973. Dispersal of some southward migrating North American shorebirds away from the Magdalen Islands, Gulf of Saint Lawrence, and Sable Island, Nova Scotia. Caribb. J. Sci. 13:257–278.

MCNEIL, R., AND J. BURTON. 1977. Southbound migration of shorebirds from the Gulf of Saint Lawrence. Wilson Bull. 89:167–171.

MCNEIL, R., AND F. CADIEUX. 1972. Fat content and flight-range capabilities of some adult spring and fall migrant North American shorebirds in relation to migration routes on the Atlantic coast. Nat. Can. 99:589–606.

MERCIER, F. M. 1985. Fat reserves and migration of Red-necked Phalaropes (*Phalaropus lobatus*) in the Quoddy region, New Brunswick, Canada. Can. J. Zool. 63:2810–2816.

MORRISON, R.I.G. 1984. Migration systems of some New World shorebirds, p. 125–202. *In* J. Burger and B. L. Olla [eds.], Behavior of marine animals. Vol. 6. Shorebirds: migration and foraging behavior. Plenum Press, New York.

MURRAY, B. G., JR., AND J. R. JEHL, JR. 1964. Weights of autumn migrants from coastal New Jersey. Bird-Banding 35:253–263.

MYERS, J. P., R.I.G. MORRISON, P. Z. ANTAS, B. A. HARRINGTON, T. E. LOVEJOY, M. SALLABERRY, S. E. SENNER, AND A. TARAK. 1987. Conservation strategy for migratory species. Am. Sci. 75:19–26.

NISBET, I.C.T., W. H. DRURY, JR., AND J. BAIRD. 1963. Weight loss during migration. Bird-Banding 34: 107–159.

ODUM, E. P., AND C. E. CONNELL. 1956. Lipid levels in migrating birds. Science 123:892–894.

PAGE, G., AND A.L.A. MIDDLETON. 1972. Fat deposition during autumn migration in the Semipalmated Sandpiper. Bird-Banding 43:85–96.

PIENKOWSKI, M. W., C. S. LLOYD, AND C.D.T. MINTON. 1979. Seasonal and migrational weight changes in Dunlins. Bird Study 26:134–148.

POST, W., AND M. M. BROWNE. 1976. Length of stay and weights of inland migrating shorebirds. Bird-Banding 47:333–339.

PRATER, A. J., A. J. MARCHANT, AND J. VUORINEN. 1977. Guide to the identification and ageing of holarctic waders. British Trust for Ornithology Field Guide 17, Tring, Hertfordshire.

RAVELING, D. G., AND E. A. LEFEBVRE. 1967. Energy metabolism and theoretical flight range of birds. Bird-Banding 38:97–113.

SCHNEIDER, D. C., AND B. A. HARRINGTON. 1981. Timing of shorebird migration in relation to prey depletion. Auk 98:801–811.

SENNER, S., AND M. A. HOWE. 1984. Conservation of nearctic shorebirds, p. 379–421. *In* J. Burger and B. L. Olla [eds.], Behavior of marine animals. Vol. 5. Shorebirds: breeding behavior and populations. Plenum Press, New York.

SPAANS, A. L., AND C. SWENNEN. 1982. The 1980 Dutch mini-expedition to Suriname. Wader Study Group Bull. 34:32–34.

STODDARD, P. K., J. E. MARSDEN, AND T. C. WILLIAMS. 1983. Computer simulation of autumnal bird migration over the western north Atlantic. Anim. Behav. 31:173–180.

TORRE-BUENO, J. R. 1978. Evaporative cooling and water balance during flight in birds. J. Exp. Biol. 75:231–236.