

BODY-FAT LEVELS AND ANNUAL RETURN IN MIGRATING SEMIPALMATED SANDPIPERS

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ABSTRACT.—Rapid deposition of body fat in preparation for long-distance migration is assumed to be one of the crucial activities of shorebirds at migration staging areas. We tested the hypothesis that annual return rate of Semipalmated Sandpipers (*Calidris pusilla*) to a migration stopover site is related to fat levels at the time of migratory departure for a long flight over the Atlantic Ocean. Length of stay of color-marked individuals was used to estimate fat levels at departure based on a relationship established at the study site between length of stay and the increase in estimated levels of body fat. Our results support the hypothesis that fat levels at migratory departure are related to the annual return rate and also to annual survival. Individuals remaining long enough to accumulate excess body fat (i.e. the low-risk group) were nearly twice as likely to return as were those below theoretically sufficient fat levels (the high-risk group). Fat levels attained at departure may be an important factor in surviving a long migration flight. However, the fact that some individuals in the high-risk group returned (approximately 25% of individuals in two years) indicates that flight-range formulas may underestimate flight capabilities. In the first year of the study 45%, and in the second year 32%, of individuals remained longer than necessary to accumulate theoretically sufficient fat levels, suggesting that some individuals were not operating on a time-selected migration schedule. Disturbance of shorebirds at staging areas may increase the mortality of these birds. Received 8 August 1997, accepted 4 March 1998.

RAPID DEPOSITION OF BODY FAT is assumed to be a crucial activity of migratory shorebirds at staging areas (Morrison 1984, Senner and Howe 1984). Many shorebird species depend on key staging areas to build up levels of body fat (hereafter "fat levels") for long migratory passages (Myers et al. 1987). Because many shorebird staging areas are threatened by various human interventions (Senner and Howe 1984, Myers 1988, Pfister et al. 1992), it is of interest to determine if the amount of body fat acquired at staging areas is related to survival. Haramis et al. (1986) demonstrated a relationship between body mass of wintering American Black Ducks (*Anas rubripes*) and annual survival. Nisbet and Medway (1972) found a trend between body mass and annual return rate of Eastern Great Reed Warblers (*Acrocephalus orientalis*) departing northward from their nonbreeding grounds. To our knowledge,

the only study showing a relationship between body fat or mass and annual survival or return rate for a bird during migration was by Piersma and Jukema (1990), who found that five of six Bar-tailed Godwits (*Limosa lapponica*) recaptured at a spring staging area in the Dutch Wadden Sea were heavier than average for the time of year when they were first captured. We tested the hypothesis that fat levels acquired by Semipalmated Sandpipers (*Calidris pusilla*) before southbound departure from a coastal staging area are related to their annual return rate to the area.

The Semipalmated Sandpiper breeds at high latitudes across North America and winters in northeastern South America (Morrison 1984, Gratto-Trevor 1992). Because large numbers of yearlings remain in South America during the boreal summer (Spaans 1978), most southbound adults are probably at least two years old, although some yearlings breed (Gratto 1988). Semipalmated Sandpipers and other species of shorebirds make direct flights from the northeastern United States and Maritime Canada to South America or the West Indies (McNeil 1969, McNeil and Cadieux 1972). Radar studies show that large flocks of migrating

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shorebirds depart on headings consistent with a nonstop flight to South America (Richardson 1979, Stoddard et al. 1983). That southbound Semipalmated Sandpipers along the northeastern Atlantic coast depart on direct flights is also supported by: (1) the low rate of sightings of individuals passing through the northeastern United States and Maritime Canada along the lower Atlantic coast (Morrison 1984); (2) higher mass gain by individuals at staging areas in coastal northeastern North America compared with inland staging areas (Page and Middleton 1972, Lank 1983); and (3) an individual banded in Maine and killed in Guyana two days later (Dunn et al. 1988). The elliptical migration pattern of Semipalmated Sandpipers (Harrington and Morrison 1979) indicates that a southbound flight from the study area is likely the longest flight that an individual would make along its annual migration route. Thus, an autumn staging site in the northeastern United States may be the most likely point along the migration route to find a relationship between the amount of fat an individual deposits before departure and its ability to survive the migration flight.

Many shorebirds, including the Semipalmated Sandpiper, are highly faithful to specific sites at migration, wintering, and breeding areas (Pienkowski 1976, Evans and Pienkowski 1984, Oring and Lank 1984, Smith and Houghton 1984, Evans and Townshend 1988). For migrating species, survival may be equivalent or proportional to annual return rate (Haramis et al. 1986); however, factors other than survival may determine annual return rate. Southbound flocks of Semipalmated Sandpipers passing through northeastern North America are composed of individuals from different breeding areas (Harrington and Morrison 1979). Individuals from various breeding areas might show variation in site fidelity because of different migration timing and behavior. Seasonality of migration at the staging area could affect the ability of observers to detect the return of an individual (Dunn et al. 1988) and may affect return rates through association with the sex and breeding origin of an individual that might represent different migration patterns (Morrison 1984). Transient individuals (Lank 1983) or those affected by the capture and marking process (Henschel and Louw 1978, Davidson 1984) might depart a staging area with low levels of

TABLE 1. Flight-range estimates for southbound Semipalmated Sandpipers from Plymouth Beach, Massachusetts, based on Castro and Myers (1989).^a

Percent body fat	Body mass at departure (g)	Estimated flight range (km)
20	25.9	1,800
25	27.6	2,300
30	29.6	2,800
35	31.9	3,400
40	24.5	3,900

^a Calculations based on mean estimated fat-free mass of 20.7 g and wing chord length of 9.45 cm; assumes average flight speed of 75 km/h and all fat depleted during flight.

body fat, yet stage elsewhere before migration departure.

STUDY AREA AND METHODS

The sand and mudflats of Plymouth and Duxbury bays (see Iwanowicz et al. 1974, Schneider and Harrington 1981) near Plymouth Beach, Massachusetts (41°55'N, 70°37'W), comprise an important staging area for southbound Semipalmated Sandpipers and other shorebirds (Harrington et al. 1989). Southbound migrants from Plymouth must fly at least 3,500 km to reach South America, although landfall is possible on the Antilles Islands after a flight of 3,000 km. Flight-range estimates (Castro and Myers 1989) predict that 35 to 40% body fat at departure would be adequate for a South American landfall (Table 1).

Most shorebirds at the Plymouth staging area roost at high tide on Plymouth Beach or Duxbury Beach, where they are easily observed. Adult Semipalmated Sandpipers begin arriving in mid-July, most leave during the first half of August, and virtually all are gone by the second week in September. Juveniles begin arriving about mid-August and depart by late September.

Despite extensive color banding and dyeing of Semipalmated Sandpipers for more than a decade, fewer than 10 United States Atlantic coast sightings south of the study area have been reported during fall migration. Semipalmated Sandpipers captured at Plymouth Beach also rarely appear at other staging areas along the Massachusetts coast (Manomet Center for Conservation Science unpubl. data), supporting the conclusion that most individuals undertake an overwater migration to northern South America.

Semipalmated Sandpipers were captured at Plymouth Beach in mist nets at nocturnal high tides on 11 dates between 16 July and 7 September 1985 and on 14 dates between 16 July and 10 September 1986. Individuals captured during two- to seven-day periods are referred to as capture groups 1 through 4 in 1985

TABLE 2. Mean capture dates of adult Semipalmated Sandpipers at Plymouth Beach, Massachusetts. Each capture group represents capture effort on one to three separate dates.

Capture group	Mean capture date	<i>n</i>
1985		
1	17 July	152
2	29 July	145
3	12 August	216
4	26 August	32
1986		
1	20 July	115
2	2 August	140
3	17 August	54
4	24 August	71
5	5 September	38

and 1 through 5 in 1986 (Table 2). Captured birds were transported approximately 10 km to Manomet, where age was determined by plumage (Hayman et al. 1986). Mass was measured to the nearest 0.1 g and culmen length (proximal nares to tip of bill) and wing chord length to the nearest 1 mm. Each bird received a unique combination of heat-sealed, ultraviolet-resistant color bands and picric acid on the breast before release the next morning at Plymouth Beach. Censuses were conducted at Plymouth Beach through 28 August at least five times per week in 1985, at least four times per week in 1986, and at least three times per week in both years through 18 September. The possibility of a seasonal effect of underestimating length of stay because of reduced census effort between 29 August and 18 September in both years was probably offset by a reduced probability of missing color-marked individuals present owing to a sharp reduction in the number of individuals during this period (see Results).

In 1985 and 1986, observers censused Plymouth Beach at high tides and recorded observations of color-banded sandpipers on each census. The minimum length of stay for each year was determined by the difference between the date of release after capture and the date of last sighting. Additional censuses were conducted in 1986 at Duxbury Beach and in 1987 at Plymouth Beach and Duxbury Beach in order to obtain annual return rates for individuals captured in 1985 and 1986. Censuses were conducted two or three times per week at Duxbury in 1986, except for the last week, when only one census was made. In 1987, censuses were conducted at least once per week at Plymouth and Duxbury, with the exception of the first four weeks at Plymouth and the first two at Duxbury, when two or three per week were conducted. No census was conducted at Duxbury in the last week. Because census efforts in 1987 were

lower than in 1986 at both sites, we did not compare return rates between years.

To remove age effects (Evans and Townshend 1988), juveniles were excluded from analyses. To reduce the effect of transients and the possible effects of the capture process, we excluded individuals with a length of stay of two days or less.

To model the process of fat accumulation for migration, we assumed that most of the increase in body mass of staging birds consisted of fat. This assumption ignores the fact that increases in body mass may consist of an amount of nonfat tissue that approaches that of fat tissue (van der Meer and Piersma 1994). However, for our study, the simplification is justified because most evidence of nonfat tissue stores comes from large shorebirds, and in a study of migrating birds, individual variation in the timing of fattening should not be present to confound interpretations of mass changes (Lindström and Piersma 1993). Moreover, the composition of the fuel stores would not affect our study unless the ratio of fat mass to nonfat mass increase varied significantly with body mass. Page and Middleton (1972) found that 80% of the mass variation between individual migrating Semipalmated Sandpipers resulted from the mass of fat deposits. Our use of the term "body fat" for nutrient stores does not rule out the possibility that nonfat components may be accumulated as nutrient stores for migration (Gundmundsson et al. 1991).

We used the formula derived by Page and Middleton (1972) to estimate fat-free mass (g) and percent fat (EPF) at capture:

$$\text{fat-free mass} = -9.0513 + 0.3135(\text{wing chord}), \quad (1)$$

where wing chord length is in mm. Dunn et al. (1988) found that the formula could be used to estimate percent body fat for Semipalmated Sandpipers staging on the northeastern coast of the United States; however, fat-free mass in Dunn et al.'s study area averaged 2.5 g more for a given wing length than for individuals at Long Point, Ontario (Page and Middleton 1972). Although the use of such techniques to quantify levels of body fat are strictly speaking "predictions" of body fat for individuals not subject to fat extraction (van der Meer and Piersma 1994), we use the term "estimated body fat" after Page and Middleton (1972) and Dunn et al. (1988).

To quantify increases in body fat based on observed length of stay, data from Semipalmated Sandpipers banded and recaptured the same year at Plymouth Beach (1971 to 1985, $n = 73$) were used to derive a relationship between length of stay and estimated fat deposition. Although it has been asserted that changes in mean capture-group mass provide a better indication of population mass increase than data on recaptured individuals because of the capture effect (Gundmundsson et al. 1991), in our study all individuals have been captured; thus, any cap-

TABLE 3. Characteristics of fat levels and body mass of Semipalmated Sandpipers based on recapture data.^a EPF = estimated percent body fat at capture.

EPF	Daily EPF increase (% body fat per day)	Daily mass increase (g per day)
0	2.39	0.50
10	1.70	0.35
20	1.01	0.21
30	0.32	0.07

^a Calculations based on equation 2 (see text) and assume fat-free mass of 20.7 g and length of stay of 10 days.

ture effect would be common to all individuals. The use of capture-group averages also may fail to account for the decreasing rate of fat deposition by heavier individuals (see below). Although recaptured Semipalmated Sandpipers may show a wide variation in rate of mass change, our data show that the rate of increase of individuals with similar initial mass has been relatively consistent over many years (see also Dunn et al. 1988: figure 2). That a population average may provide a reasonable estimate of the rate of mass gain of an individual is supported by Piersma and Jukema (1990), who found that the rate of mass gain of staging Bar-tailed Godwit individuals closely followed the population average. The following linear regression model was derived from the sample to estimate the increase in body fat based on length of stay:

$$\Delta\text{EPF} = 15.10 - 0.69(\text{EPF}) + 0.88(\text{length of stay}), \quad (2)$$

where EPF is estimated percent body fat at capture and ΔEPF is the estimated increase in body fat at the last sighting. Data from individuals whose EPF exceeded 35% were not used in the model (reducing the sample size to 46), because some recaptured individuals with EPF higher than 35% showed significant mass decreases (Morrison 1984, Kasprzyk 1991), which significantly reduced the fit of the model. This result is probably due to the fact that individuals with EPF higher than 35% are near mean fat levels attained by departing migrants. We also excluded individuals whose length of stay was less than or equal to two days, because these would not be used in the analysis. The model ($R^2 = 0.64$, $P = 0.0001$) and all parameters were significant ($P < 0.001$). Equation 2 indicates that average daily fat deposition decreases with higher initial fat levels (Table 3).

The percent body fat of an individual at departure (EPFD) was estimated by adding EPF and ΔEPF . EPFD values higher than 50% were assigned a value of 50% because fat levels of Semipalmated Sandpipers exceeding 50% are rarely found in nature (observed EPF maximum was 48.6% in 1985 and 51.5% in 1986).

We used methods similar to those of Haramis et al. (1986) to test the hypothesis that annual return rate was related to EPFD. A logistic regression model was used to relate the dependent variable of return (1 = yes, 0 = no) to EPFD. The logistic regression model also included the dependent variables capture date, culmen length, and the ratio of culmen length to wing chord to test whether factors other than EPFD affected return rate. The latter two variables may be associated with sex or breeding origin (Harrington and Morrison 1979). Our results were unaffected when we used date of last sighting instead of capture date; thus, we report capture date in the Results. EPF was included in the model to test whether our estimation of fat level at departure (EPFD) provides different explanatory power than EPF, an estimate of body fat at capture. The appropriateness of alternative models with different combinations of dependent variables may be determined by a χ^2 test of a statistic based on the ratio of maximum-likelihood estimates of the full model and a reduced model with one or more variables removed (Agresti 1996). We used the fast-backward elimination procedure in PROC LOGISTIC (SAS Institute 1990, Agresti 1996) to remove variables that did not contribute to the model ($\alpha = 0.05$). We also used a Wilcoxon rank-sum test with return (yes or no) as a classification variable of the ranks of EPFD.

Although EPFD provided the best estimate of fat levels at departure, because we excluded individuals with EPF higher than 35% from the analysis, the sample was potentially biased with respect to seasonality (i.e. more individuals of higher EPF should be captured later in the season). Thus, an alternate method was used to test the hypothesis that return is associated with fat levels. We defined relative length of stay (RLOS) as the difference between length of stay and the time in days that would have been required to attain 40% EPF, a fat level often found in long-distance migrant shorebirds at coastal Atlantic staging areas (McNeil and Cadieux 1972). RLOS is similar to OBES-H and OBES-L in Dunn et al. (1988). We interpret RLOS as indicating the likelihood of an individual having accumulated 40% EPF before migratory departure. We used RLOS to classify individuals into three "risk groups." High-risk individuals (RLOS less than -5) probably did not attain 40% body fat; medium-risk individuals (RLOS between -5 and 5) were probably near 40% body fat levels; and low-risk individuals (RLOS higher than 5) probably exceeded 40% body fat. "Risk" refers to the risk of mortality on an overwater flight because of low levels of body fat. In order to calculate RLOS, the following assumptions were made about the rate of fat increase. For individuals with EPF lower than 35%, fat increase was calculated according to equation 2. For individuals with EPF higher than 35%, we assumed daily fat level increases of 0.50%. Although we were not able to quantify rates of mass increase

for individuals with EPF higher than 35%, it is clear that many of those individuals continued to gain mass, because EPF values between 40 and 50% were common. We selected the 0.50% fat per day figure as a rough extrapolation based on equation 2 (Table 3). The rate of 0.50% is not so much a value to predict fat levels as a "yardstick" to estimate length of stay beyond a certain date associated with attaining EPF of 40% for individuals that continued to gain mass. Uncertainty regarding this rate may affect individuals near the classification boundaries for each risk group but was shown in a sensitivity analysis not be critical to the results (Pfister et al. unpubl. data). For individuals with EPF higher than 35%, two days were added to RLOS to account for the observed phenomenon of individuals initially losing mass after capture. This effect is implicitly accounted for in equation 2 for individuals whose EPF was less than 35%. A logistic regression identical to that above was used to determine whether risk group was related to return rate, except that risk group, a categorical dependent variable (Agresti 1996), was substituted for EPFD. A χ^2 test was also used to determine whether RLOS was related to annual return rate.

RESULTS

Adult Semipalmated Sandpipers began arriving in mid-July in 1985 and 1986 and reached a peak of 2,800 in the first week of August in 1985 and a peak of 1,700 in the last week of July in 1986. We captured and color marked 545 adults between 16 July and 7 September 1985 and 418 adults between 16 July and 19 August 1986. After eliminating individuals whose length of stay was less than two days, 372 and 295 individuals remained for analysis in 1985 and 1986, respectively. Based on 75 individuals whose length of stay was longer than seven days in each year, the probability of observing an individual known to be at the study site on a given census was 59.4% in 1985 and 65.9% in 1986.

Mean EPF increased through the course of the season in both years as staging individuals accumulated body fat, and as expected, mean length of stay decreased for individuals captured nearer to normal departure dates at the end of the season (Fig. 1). EPFD could be calculated for 255 individuals with EPF <35% in 1985 and 184 in 1986 (Fig. 2). The median EPFD was 40.9% in 1985 and 37.1% in 1986. The estimated mean annual return rate was 40.1% (149/372) in 1985 and 31.3% (93/295) in 1986 (Table 4).

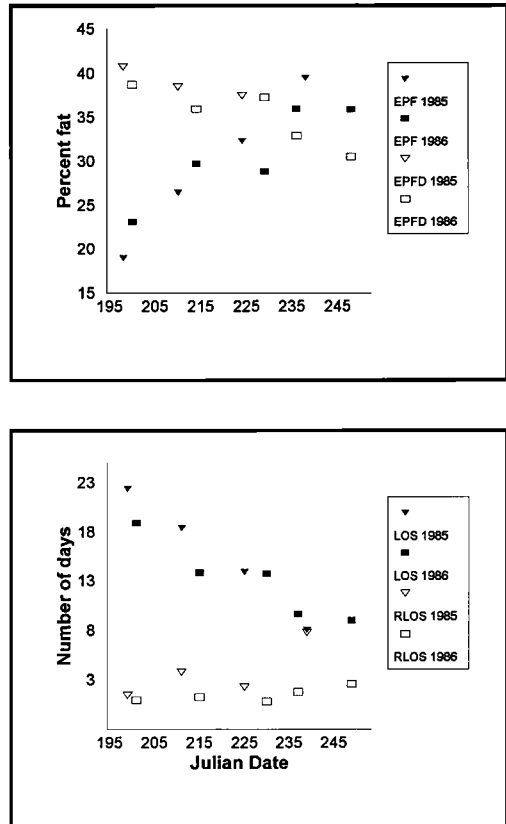


FIG. 1. Upper panel: Estimated percent body fat (EPF) and estimated percent body fat at departure (EPFD) by mean date of capture group of Semipalmated Sandpipers, 1985 and 1986. EPF sample sizes are given by capture group in Table 2; EPFD sample sizes are 111, 74, 70, and 1 (not shown) for capture groups 1 to 4, respectively, in 1985 and 76, 59, 27, 16, and 6 for capture groups 1 to 5, respectively, in 1986. Lower panel: Mean minimum length of stay (LOS) and relative length of stay (RLOS) for the same capture groups of sandpipers. LOS and RLOS sample sizes are 118, 115, 124, and 18 for capture groups 1 to 4, respectively, in 1985 and 92, 99, 40, 48, and 16 for capture groups 1 to 5, respectively, in 1986.

Mean EPFD was relatively consistent among capture groups, although a seasonal decline was suggested (Fig. 1). However, this decline is probably due to the exclusion of heavier individuals captured late in the season. For example, in 1985, mean EPFD could not be calculated for capture group 4 because the EPF of all but 1 of 18 individuals was >35%. Mean RLOS (Fig. 1) probably presents a more accurate account of average fat levels attained by depart-

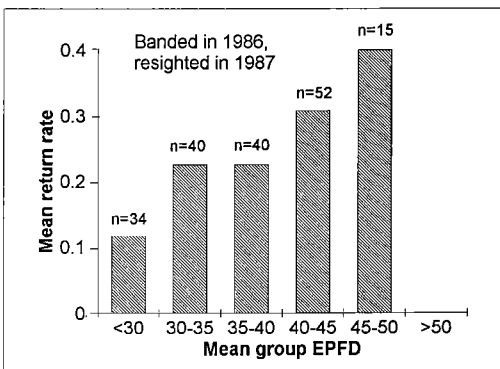
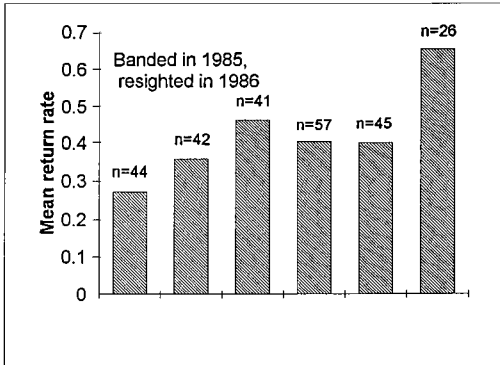


FIG. 2. Mean annual return rates for estimated percent body fat at departure (EPFD) in Semipalmated Sandpipers in 1985 and 1986. Values for EPFD >50% in 1986 not shown ($n = 3$).

ing individuals. Except for one outlying point (capture group 4 in 1985), mean RLOS for every capture group was shorter than four days. Although differences in censusing methods confound direct comparison of our data with a similar study of migrating Semipalmated Sandpipers in northeastern North America (Dunn et al. 1988), it appears that our data are similar relative to seasonal mean length of stay and estimated levels of body fat (Dunn et al. 1988: table 3).

Groups of marked individuals began disappearing from the study area after 8 August in both 1985 and 1986. Daily counts declined in the second week of August and showed sharp declines between 20 and 29 August 1985, during which time census totals dropped from 1,100 to less than 200, and most remaining marked individuals departed the study area. A similar decline occurred between 13 and 26 August in 1986. By the first week of September in

TABLE 4. Annual return rate by relative length of stay (RLOS) and risk group of Semipalmated Sandpipers captured at Plymouth Beach, Massachusetts, 1985 and 1986.

Risk group	n	No. returned next year	Return rate
Captured in 1985			
High (RLOS < -5)	97	24	0.25
Medium (-5 < RLOS < 5)	109	43	0.39
Low (RLOS > 5)	166	82	0.49
Totals	372	149	—
Captured in 1986			
High (RLOS < -5)	81	17	0.21
Medium (-5 < RLOS < 5)	120	39	0.33
Low (RLOS > 5)	94	37	0.39
Totals	295	93	—

1985 and 1986, fewer than 200 adult Semipalmated Sandpipers occurred on censuses.

In the first step of fast-backward elimination, four explanatory variables (EPF, capture date, culmen length, and culmen/wing ratio) were removed from the first logistic regression model in both years ($0.54 > P > 0.22$ in 1985; $0.83 > P > 0.27$ in 1986), and the coefficient of EPFD was significant in the final model ($P < 0.01$ in both years; Table 5). Individuals with higher EPFD returned more frequently in both 1985 (Wilcoxon test, $Z = 3.15, P < 0.002$) and 1986 ($Z = 2.68, P < 0.008$). In the second logistic regression, the same four explanatory variables were removed in the first step of backward elimination ($0.91 > P > 0.30$ in 1985; $0.80 > P > 0.17$ in 1986), and the coefficient of risk group, a categorical variable for fat level at departure, was significant in the final model ($P < 0.0001$ in 1985, $P < 0.01$ in 1986; Table 5). Individuals in the lower risk groups tended to return more frequently ($\chi^2 = 15.52, df = 2, P < 0.001$ in 1985; $\chi^2 = 6.89, df = 2, P < 0.03$ in 1986; Table 4). Thus, in both regression models, the variable of fat level at departure was the only explanatory variable with a statistically significant association with return rate.

DISCUSSION

Although we did not attempt to include error estimates for our model, predictions of fat levels at departure (EPFD), comparisons of mean EPFD with other data inferring actual mean fat levels at departure indicate that our model lev-

TABLE 5. Logistic regression model final parameter estimates.^a Standard errors of model coefficients are in parentheses.

Year	<i>n</i>	<i>b</i> ₀	Wald χ^2	df	<i>P</i>	Body fat ^b	Wald χ^2	df	<i>P</i>
Estimated percent body fat at departure									
1985	255	-2.59 (0.69)	14.15	1	<0.001	0.05 (0.02)	9.45	1	<0.01
1986	184	-3.95 (1.10)	12.91	1	<0.001	0.07 (0.03)	7.04	1	<0.01
Risk group									
1985	372	-1.57 (0.33)	23.19	1	<0.0001	0.53 (0.14)	14.95	1	<0.0001
1986	295	-1.68 (0.40)	19.43	1	<0.0001	0.43 (0.17)	6.60	1	<0.01

^a Dependent variables removed in first step of fast-backward elimination (see text) were capture date, estimated percent body fat, ratio of culmen to wing length, and culmen length.

^b Body fat is a continuous variable, estimated percent body fat, in the first model, and a categorical variable, risk group, in the second model.

els are relatively accurate. Median EPFD (used instead of mean because of the difficulty of interpreting EPFD values >50%) corresponds closely with mean estimated EPF observed in individuals captured in the last capture groups when most individuals were on the brink of migratory departure (Fig. 1), with 40% body fat levels predicted by a flight-range formula (Table 1), and with levels commonly observed in migrating shorebirds (McNeil and Cadieux 1972, Zwarts et al. 1990, Skagen and Knopf 1994). That EPF itself was not associated with return rate supports the hypothesis that fat accumulation, as indicated by EPFD, is a crucial activity of individuals at our study area. Although EPFD seems to give a plausible indication of fat levels at departure, our results do not depend on the accuracy of EPFD. The alternative methods we used to classify individuals into risk groups by estimated fat levels at departure depended only on a relative ranking of body fat to evaluate the hypothesis. There is a high probability that the rankings were generally correct based on limits of rates of fat increase observed at the study area.

Our calculations of length of stay in relation to the time required to attain 40% body fat (RLOS) differed strikingly from a similar parameter (OBES) estimated by Dunn et al. (1988). Dunn et al. (1988) define OBES as the number of days an individual stays beyond that required to obtain sufficient body fat for migration according a flight-range formula. Dunn et al. (1988) report mean OBES of around two weeks in early capture cohorts and about one week in later capture cohorts. In this study, mean RLOS remained below four days, except for capture group 4 in 1985 (mean RLOS = 7.83, *n* = 18), which was one of the smallest capture groups. Dunn et al.'s results (1988) im-

ply that individuals are staying on average one to two weeks longer than necessary, whereas our results imply that average length of stay is close to that required to attain average predicted fat levels required for migration throughout the season. The comparatively high values of OBES appear to be due to assuming fat increases of 1.65 g per day (OBES-H) and 2.4 g per day (OBES-L) as found in other studies (Dunn et al. 1988:829). Such high rates of fat increase have not been found at our study site, where a regression model (equation 2) indicates that the population average rate of mass increase of lean individuals is between 0.50 and 0.35 g per day (Table 3). This range is similar to the value of 0.379 g per day based recaptured individuals (Dunn et al. 1988). If Dunn et al. (1988) had used lower estimates of fat increase, the values of OBES would probably have been closer to RLOS.

Our interpretation of the association between fat levels and annual return rate is that differences in return rate are due to mortality caused by fat depletion during overwater migration. The difference between return rates in our study of 40% in 1985 and average return rates of 60 to 70% in northern breeding areas (Gratto-Trevor 1992, Sandercock and Gratto-Trevor 1997) indicates that not all surviving individuals return to our study site. Return rates, however, may be an index of survival, although other possible explanations exist for the relationship between fat levels and return rate. Based on the available data on migrating shorebirds, the main alternative explanations to our proposed explanation are that: (1) departing individuals with low body fat do not actually leave on overwater migration, but make shorter flights to nearby staging areas for additional fat gains before actual overwater migration; or (2)

individuals with low levels of body fat tend to have low annual site fidelity. These alternatives are not mutually exclusive. The first alternative seems contrary to an overwhelming accumulation of data on shorebird migration detailed in the introduction. In addition, on days when we assume large numbers of marked individuals left the study site based on the last day of sighting—days probably associated with favorable meteorological conditions for migration departure (Lank 1983)—the wide range of fat levels of departing individuals indicated that members of the lean high-risk group were departing along with individuals in the low- and medium-risk groups. Thus, it is likely that high-risk individuals departed the study area under the same meteorological conditions and flock-behavior scenarios that have been associated with migration between the Atlantic Ocean and South America. We cannot rule out that some individuals have alternative destinations; yet, the lack of sightings in United States coastal Atlantic and Caribbean locations over the years indicates that few high-risk individuals visit intermediate sites en route to South American from the study area. Alternative 2 is more difficult to evaluate, because we have very limited information on individuals that did not return to the study area.

We received eight reports of marked individuals that appeared to belong to alternative 1 or 2 above. Of these, two were low-risk group; four were medium-risk group; one was high-risk group; and one was transient (length of stay less than two days) and not included in the analysis. The reliability of the reports must be questioned, however, because three apparently reliable reports were received but were determined to be in error because the color combinations could not have been seen by the observer. Although the sample of individuals resighted off the study area is far too small to draw statistical conclusions, there does not appear to be an overwhelming trend for high-risk individuals to display different migration behavior or lower site fidelity than medium- or low-risk individuals. It is possible that individuals display different degrees of site fidelity and/or different migration strategies; however, there is no indication that such behavior would be related to fat levels attained at the study area.

Theoretical approaches to the ecology of bird

migration that depend on optimal foraging theory (Alerstam and Lindström 1990) predict that an individual's foraging success may determine the length of time spent at a staging area. Accordingly, it could be proposed that high-risk individuals in our study experienced low foraging success and departed to other staging areas. The above scenario might not apply to shorebirds, because oftentimes few alternative staging areas exist, and the risk of attempting to settle in an alternative area may be high. However, even if the theory applied, it is important to emphasize that differences in fat levels at departure were not determined by foraging success at our study site (which we could not measure and have assumed is equal for all individuals) but primarily to the decision of individuals to depart at a wide range of fat levels. Being "high risk" is associated with arrival at the study area with low levels of body fat (see below), although some individuals with low fat levels captured later in the season may have been unsuccessful in gaining body fat at the study area. Although relative foraging success may still be a factor in determining fat levels and subsequent survival, our results indicate that a large range of fat levels may result simply from an individual's decision to depart at a fat level differing greatly from the population average. A large range of fat levels at departure would be surprising if energetics were the only factor in determining survival during migration. However, large variation in fat levels at departure in Semipalmated Sandpipers is expected in light of the fact that body fat has been regarded as a poor predictor of length of stay at staging sites (Morrison 1984, Dunn et al. 1988).

In each year 26 to 27% of the individuals were in the high-risk group (Table 4) and probably did not attain fat levels sufficient for direct migration to South America. Nevertheless, many of these individuals returned, supporting the notion that flight-range formulas may underestimate flight-range capabilities (Dunn et al. 1988). It has been suggested that shorebirds depend on wind for long-distance, non-stop migration (Piersma and Jukema 1990, Marks and Redmond 1994, Butler et al. 1997). Our results are consistent with this view and with the interpretation of excessive fat levels as "risk insurance" against mortality during migration. In the first year of the study 45%, and in the second 32%, of the individuals were in

the low-risk group (Table 4) and probably remained longer than necessary to accumulate sufficient fat levels. Gudmundsson et al. (1991) also found that fat deposition beyond the theoretical minimum amount required may be common in three species of migrating shorebirds. Migrating Red Knots (*Calidris canutus*) had approximately 10% body fat upon arrival at a migration staging area and the breeding grounds (Evans and Davidson 1990). Extra body fat could act as a cushion against the possibility of unfavorable meteorological conditions and give a boost to survival probabilities at the next destination (Gudmundsson et al. 1991).

Alerstam and Lindström (1990) defined time-selected migration as a migration strategy that minimizes the time required to cover the distance of migration. The advantage of time-selected migration may include gaining a competitive advantage at staging or wintering areas. Individuals on a time-selected schedule might also be expected to depart before reaching the highest possible level of body fat, that is, to trade the advantage of an early arrival with the risk insurance of high fat levels. That we found some individuals staying days or weeks longer than necessary to obtain theoretically sufficient body fat may indicate that at least some individuals were not on time-selected migration. We found no indication that an early migration schedule was advantageous to individuals. Date of capture or last resighting was not a significant explanatory variable in the logistic regression models as would be expected if early arriving and departing individuals achieved a competitive advantage on the wintering grounds. Although shorebirds at our study area have been shown to deplete some prey resources during migration (Schneider and Harrington 1981), we found no indication that it is an advantage to move through the staging area on an earlier schedule. Gudmundsson et al. (1991) hypothesized that excess fat levels may also be explained according to time-selected migration if individuals experienced more advantageous conditions by lingering at the staging area compared with the next destination.

High levels of body fat have been associated with increased risk of predation because of a reduced ability to escape predators (Metcalf and Furness 1984, Houston and McNamara

1993). However, we found no indication that high fat levels were associated with any type of risk. For example, eight individuals captured early in the season in 1985 with estimated fat levels >40% remained at least three weeks after being captured; seven of these birds returned in 1986. It is possible that the disadvantages associated with carrying high fat loads are minimal at the jumping-off point for a long overwater flight. Escaping predators also may be of little importance at our study site, because avian predators are rarely present during the migration period of adult Semipalmated Sandpipers (Harrington pers. obs.).

Arrival condition played an important role in determining the risk group of an individual. A wide range of fat levels was present in both 1985 and 1986 in capture group 1, in which most individuals had probably arrived within a few days, with fat levels ranging from 0 to amounts sufficient for immediate departure to South America. The study area is probably used by migrants to "top off" fuel stores before the long overwater flight and/or to await favorable weather for migration. It is possible that some benefit is associated with maintaining high levels of body fat during certain stages of migration and that individuals that deplete their fat reserves in reaching such a staging site are at risk. High-risk individuals may have departed with low fat reserves owing to their migration schedule or to proximate causes, such as favorable weather or social stimuli (Lank 1983, 1989; Safriel and Lavee 1988). Based on an optimal migration model, Alerstam and Lindström (1990) predict that time-selected dominant individuals will travel with higher fat levels than subdominant individuals because of greater foraging efficiency. Low-risk individuals in this study may represent a class of individuals that are able through some combination of foraging success and migration strategy to arrive at the study area—the jumping-off point for overwater migration—with relatively high levels of fat. Perhaps such individuals could adopt behavior patterns that allow them to be more selective in choosing a favorable departure date. Individuals arriving with low levels of fat may have to choose less-favorable departure dates because of exigencies of increasing mass to reduce mortality risk. Our recapture data (equation 2, Table 3) indicate that lean individuals on average gain body fat at a faster

rate than those with higher initial levels of fat. This phenomenon may be due to physiological limits on the efficiency of fat deposition as individuals gain mass, and/or to a lean individual's decision to increase fat levels at the expense of other activities, such as predator avoidance, resting, or social interaction.

If return rate is indeed an index of survival, our results suggest that although important benefits may be associated with long-distance migration, there are considerable risks as well. Fat levels attained by departing individuals at our study site appear to be strongly associated with the risk of mortality associated with a long migration flight. An individual's migration strategy and foraging success may be crucial factors in long-distance migration through their determination of fat levels at the jumping-off point for migration. However, other factors besides fat levels also may be important in long-distance migration. It appears that for individuals within the medium-risk range, fat levels may be a relatively minor factor in the probability of returning. The difference in return rates among EPFD groups was relatively small in the 35 to 45% range in 1985, and in one case was in the opposite direction predicted by the hypothesis (Fig. 2).

An intriguing possible insight into factors other than fat levels in determining return rate or survival appeared in examining return rates for cluster groups of individuals disappearing from the study area on the same dates in 1985. Several groups with relatively high mean fat levels had relatively low mean return rates. Although we do not know if the variation was statistically significant, the results suggest further research to determine whether factors associated with departing groups, such as meteorological conditions or departure headings, may affect return rates or survival. The elaborate behavior of shorebirds leading up to the formation of flocks departing on migration (Lank 1989, Alerstam et al. 1990, Piersma et al. 1990, Marks and Redmond 1994, Tulp et al. 1994) suggests that this phase is important in the annual cycle. It is possible that such behavior is associated with important individual or group decisions regarding migration strategies that could affect individual survival probabilities. In our study, observers noted color-marked individuals from the same capture cohorts in close proximity in roosting flocks on subse-

quent censuses. This observation suggests further research to determine whether social interaction is a significant factor in the behavior and survival of migrating shorebirds.

The results of our study should be interpreted in the context of the characteristics of the methods used and the study area. Captured individuals were held overnight and therefore may have experienced effects that influenced their migration behavior. These individuals may not represent the normal behavior of individuals passing through the study area, but such effects would not be a factor in testing our hypothesis. The migration strategy used by individuals at a coastal staging area, such as our study area, may differ from that at a winter stopover area or an inland staging area. Other specific characteristics of the study area may be different from other sites. The absence of aerial predators could cause optimal fat deposition rates to differ from other sites, where predator avoidance may be an important factor in survival. Finally, ecological factors may differ in relation to limiting the rate of fat increase compared with other sites. Ongoing studies comparing the rate of mass gain of Semipalmated Sandpipers at our study site with other areas indicate that individuals at Plymouth Beach may have relatively low rates of mass gain (Manomet Center for Conservation Science unpubl. data).

Our results support the conservation thesis that shorebird staging areas are important for migrating individuals to attain high fat levels for subsequent migration flights. Any type of disturbance at staging areas that reduces feeding efficiency may be hypothesized as leading to mortality of migrating shorebirds. We also find it important to consider that nonenergetic factors may be important during migration as part of the overall migration strategy. Conservation concerns should include the protection of undisturbed habitat to allow normal social interactions preparatory to migration departure. Because migration departures often occur from high tide resting areas or nearby mudflats (Lank 1989, Alterstam et al. 1990), disturbance in these areas (Pfister et al. 1992) may have the potential to threaten the migration process.

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