FAT DEPOSITION AND LENGTH OF STOPOVER OF MIGRANT WHITE-CROWNED SPARROWS

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ABSTRACT.—Ninety migrant White-crowned Sparrows (*Zonotrichia leucophrys leucophrys*) recaptured over a short term on stopover in Brunswick, Maine had a mean weight gain of 2.5 g, a mean minimum stopover length of 4.5 days, and a mean rate of weight gain of 0.6 g/day. The amount of fat deposited and length of stopover were both significantly related to the amount of fat upon arrival: lean birds gained more weight and stayed longer than fat birds. The pattern of weight gain was similar to that of *Z. l. gambelii* in a simulated stopover experiment, although the rate of gain was slower. The birds gained weight immediately after the first capture. This differs from the pattern of an initial weight loss followed by weight gain that has been observed for other species. The length of stopover and rate of weight gain did not differ between the spring and fall migrations, which suggests that the rate of migration is similar in the spring and fall. Comparative data for other species, however, show a slower fall migration rate. *Received 1 February 1982, accepted 11 April 1982.*

IT is thought that migrant birds use stopover periods to increase fat reserves that are depleted by migratory flight (Berthold 1975). Field measurements of amounts and rates of fat deposition have been difficult to obtain, however (Blem 1980, see Davis 1962, Nisbet et al. 1963, Mascher 1966, Mueller and Berger 1966, Dewolfe et al. 1973, Langslow 1976, and Rappole and Warner 1976 for specific examples). King (1961, 1963), King and Farner (1959, 1963), and King et al. (1963, 1965) have used captive or collected White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) in studies of migratory fattening. Here, I present field measurements of amounts and rates of fat deposition of White-crowned Sparrows (*Z. l. leucophrys*) and compare them with the results of King's work and with field results for other species. In addition, I examine the relationship of stopover length and amount of fat deposited with the amount of fat upon arrival and discuss the results in relation to migration behavior of the species.

METHODS

The study was conducted at the Coleman Farm Banding Station, which is located 5.5 km south of Brunswick, Maine (43°50'N, 69°50'W) on the properties of Bowdoin College and E. C. Livesay. Mist-nets and traps were set in two habitats: mixed deciduous/coniferous woods and an open field with a hedgerow, which is a 10-m-wide strip of small trees and shrubs, mostly American elm (*Ulmus americana*) and highbush cranberry (*Viburnum trilobum*). A pasture and a lawn with two large gardens and several large trees flank the hedgerow. All White-crowned Sparrows were caught in the hedgerow area.

David Mehlman and I collected data on migrants during the autumns of 1976, 1977, 1978 and the springs of 1977 and 1978. Capture effort and net locations were fairly uniform between migrations, except that in fall 1976 netting began in the hedgerow area on 17 October, about one month later than in other fall migrations. Also, baited traps were not used in fall 1976. Banding was conducted on a daily basis, usually for a portion of the day. The time of banding varied but can be generalized as mostly in the afternoons in the fall and in mornings during the spring migrations.

Birds were captured in 36-mm-mesh, 12-m-length mist-nets and in single-cell treadle traps baited with mixed seed. Nets and traps were checked at least every half-hour. The following data were taken for each capture: age, sex, wing chord, weight, date, time, fat class, and degree of skull ossification. During fall 1976 birds were weighed in plastic mesh bags with a Pesola 100-g spring balance to the nearest 0.5 g. During spring and fall 1977 and 1978 birds were weighed on an Ohaus triple-beam balance to the nearest 0.1 g. We used the fat classifications of Manomet Bird Observatory, which are based on the amount of fat in the interclavicular fossa (often called the furculum or furcular cavity). The classes are: (0) no fat, (0.5) trace of fat, (1) solid sheet of fat decurved down into the fossa, (2) fat filling fossa, (3) fat bulging out of fossa but not meeting layer of fat from

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TABLE 1. White-crowned Sparrow passage dates and handlings totals for each migration.

Migration		First seen or captured	Last seen or captured	Median date of capture	Total banded	Total individuals repeating	Percentage of individuals repeating	Total repeats handled
Fall	1976	09/19	11/07	10/22	36	16	44	18
Spring	1977	05/03	05/29	05/12	31	17	54	30
Fall	1977	09/24	10/28	10/08	32	17	53	30
Spring	1978	05/11	05/20	05/11	4	0	0	0
Fall	1978	09/23	11/03	10/11	65	40	61	147
Totals					168	90	54	225

abdomen, and (4) fat bulging out of fossa and meeting layer of fat from abdomen. We tried to hold the birds in the same position when examining for fat, because stretching or shortening the neck causes the size of the fossa to change. The banding procedure took from 1 to 5 min, and the elapsed time from capture to release was usually less than 30 min.

Measurements of fat deposition were based on repeat records of individuals. A repeat is defined as a bird that was recaptured within 90 days of the last capture at the same site as the last capture (North American Bird Banding Manual). This study deals only with repeats. Two methods to assess fat deposition were used: change in fat class, which is not a precise measurement, and change in body weight. Connell et al. (1960) have shown that variations in weights of migrant birds are almost entirely caused by variations in amounts of stored fat.

Migrant bird weights vary through the daily cycle, because birds feed during the day and metabolize fat and gut contents overnight (Baldwin and Kendeigh 1938). Morton (1967) found that migrant *Z. l. gambelii* fed at a constant rate throughout the day. To make valid comparisons of weights from one capture to the next, one must take weights at the same time of day (Rappole and Warner 1976) or correct weights to the same time using the rate of weight gain for the daylight hours. I determined the rate of weight gain during the daylight hours by computing the mean rate of weight gain of the 14 birds that were captured twice in the same day. The mean was 0.24 ± 0.09 g/h. This rate was used to correct all the weights to 1200 before making further calculations.

The weight change of an individual bird was computed by subtracting the weight on first capture from the weight on last capture after correcting the weights to 1200. The minimum stopover length was computed by subtracting the date of first capture from the date of last capture. The rate of weight change was computed by dividing the weight change by the minimum length of stopover. For example, a bird captured first on 16 October with a corrected weight of 28 g and last on 20 October with a corrected weight of 30 g would have a 2-g weight change, a 4-day stopover, and weight gain of 0.5 g/day. My method of computing minimum stopover differs from that of Borror (1948) and others in that they counted each day a bird was present as a day of stopover. This would give a minimum stopover of 5 days in the example above. I used my method, because the Borror method would have given erroneous results when calculating the rate of weight change. For the example above, dividing the weight change by a stopover of 5 days does not make sense, because the weight change was measured from 1200 on the first to 1200 on the last capture, which is a 96-h or 4-day period. It is necessary to add 1 to my stopover figures in order to make them comparable with figures computed by the Borror method.

RESULTS

Of the 168 White-crowned Sparrows banded, 90 individuals repeated at least once. The passage periods and numbers of birds handled for each migration are given in Table 1. Many birds repeated more than once, as shown by the "total repeats handled" column. The large number of repeats handled in fall 1978 was caused by an increased use of baited traps. The late start of netting in the hedgerow area in fall 1976 caused the total handled to be lower and the median date of capture to be later than would have occurred if we had started earlier. The mean passage period for spring was 18 days and for fall was 42 days.

A frequency histogram of fat class for the first and last captures of birds that repeated is shown in Fig. 1. The mode for first captures was class 1, with 51 occurrences, and for the last captures was class 3, with 38 occurrences. This shows that the birds gained fat and that high fat classes were usually attained before departure.

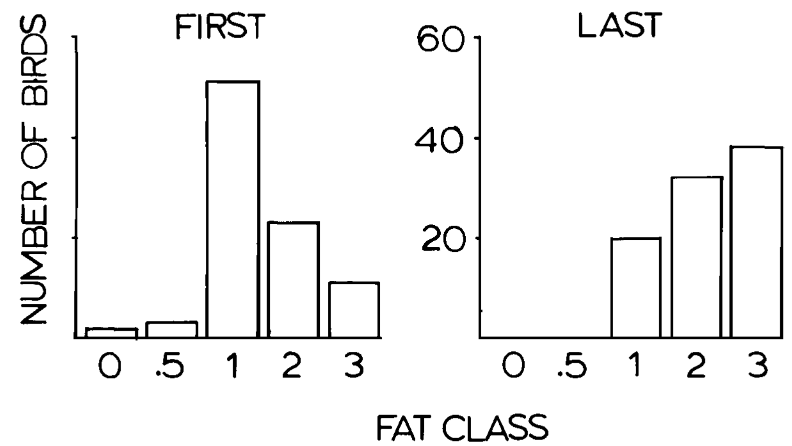

Fig. 1. Frequency distribution of fat classes for first and last captures of repeating White-crowned Sparrows.

The mean minimum stopover length, weight change, and rate of weight change for each migration are presented in Table 2. The mean minimum stopover for the entire sample was 4.5 ± 3.4 days (n = 90), ranging from 1 to 20 days. The mean minimum stopover lengths varied little between migrations (Table 2). The mean weight change for the entire sample was 2.6 ± 2.5 g (n = 89), ranging from −2.8 to 9.4 g. The mean weight changes for the migrations were similar, except that fall 1977 was lower, although not significantly so ($P > 0.05$, Table 2). The mean rate of weight change for the entire sample was 0.60 ± 0.64 g/day (n = 89), ranging from −1.9 to 2.0 g/day. The mean rates of weight change for the migrations were similar, except that fall 1977 was lower, although not significantly so ($P > 0.05$, Table 2).

The weight changes of individual birds in the fall of 1978 are shown in Fig. 2. The patterns were similar for the other migrations. Most birds gained weight immediately after the first capture. There was variability in the weight changes of birds from capture to capture. Environmental factors and the internal migratory state of a bird might influence the rate of fat deposition. The data indicate some periods during which all birds captured on two consecutive days had similar weight changes. For example, from 28 to 29 September all five birds lost weight at a similar rate (Fig. 2), which suggests that the same external factors affected all these birds. There were other day-to-day periods during which the weight changes were not similar, which suggests that other factors also affect the rate of fat deposition. There were

TABLE 2. Mean minimum stopover length, mean weight change, and mean rate of weight gain of White-crowned Sparrows for each migration.

Migration	Sample size	Mean stopover[a]	Mean weight change[a]	Mean rate of gain[a]
Fall 1976	16	4.5 ± 3.2	2.8 ± 2.7[b]	0.69 ± 0.70[b]
Spring 1977	17	4.0 ± 3.6	3.2 ± 3.4	0.64 ± 0.91
Fall 1977	17	4.7 ± 3.5	1.3 ± 1.9	0.24 ± 0.44
Fall 1978	40	4.7 ± 2.9	2.9 ± 2.2	0.69 ± 0.53
One-way ANOVA				
Degrees of freedom		3, 86	3, 85	3, 85
F statistic		0.145	2.066	2.211
P		0.93[c]	0.11[c]	0.09[c]

[a] Means are given with ± 1 SD. See methods section for methods of computing minimum stopover, weight change, and rate of weight change.
[b] Sample size for mean weight change and rate of gain in fall 1976 was 15: weight not taken on recapture of one bird.
[c] No significant difference between means for migrations, $P > 0.05$.

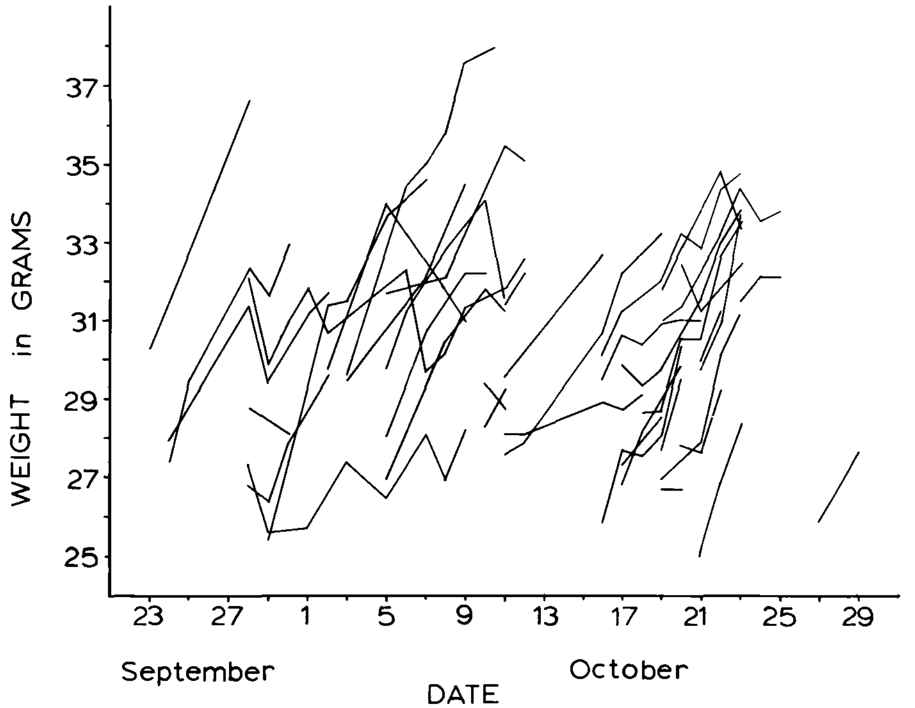

Fig. 2. Weight changes of individual White-crowned Sparrows by date in fall 1978.

five birds whose pattern of weight gain was different from the others'. These birds stayed from 11 to 20 days and either gained little weight or gained only several grams in the last few days of their stopover. Possibly, the internal migratory states of these birds differed from the others'.

The repeating birds usually attained a high fat class before departure (Fig. 1). It could then be predicted that a bird that arrived with a small amount of fat would have to deposit more fat and so stop over longer than a bird that arrived with a larger amount of fat. This could account for the variability of stopover lengths and amounts of weight gain. To test for a relationship between initial fat class and amount of weight gained, I constructed a 4 by 2 contingency table of initial fat class (classes 0 and 0.5 were grouped) against whether or not the bird repeated. I assumed that a bird arriving with a low fat class was more likely to repeat, because it would take longer to attain a high fat class. A larger percentage of the birds arriving with low fat classes repeated than of those with high fat classes ($\chi^2 = 15.38$, df $= 3$, $n = 166$, $P < 0.005$). To test this relationship further, I computed the mean stopover and weight change for each initial fat class, excluding the five birds mentioned above (Fig. 3). A one-way analysis of variance shows that there is a significant ($P < 0.05$) relationship in both cases.

Discussion

King (1961, 1963), King and Farner (1959, 1963), and King et al. (1963, 1965) have used captive and collected *Z. l. gambelii* to illustrate the timing and cycle of fat deposition through the annual cycle. In their work they have said that fat deposition in captive birds reflects what occurs in the wild, based on comparisons with collected birds. Meier and Fivizzani (1980) stated that the rate of fat deposition in captives is probably twice that of wild birds. The present study deals with the period of fat deposition between migratory flights and allows a comparison with one of King's experiments. King (1963) said that active hyperphagia persists through the migratory period and this assures that fat reserves will be regained quickly during stopover periods. King (1961) repeated an experiment performed by Wolfson (1954) on captives during the migratory period. Each allowed birds to fatten to maximum levels, then simulated migratory flight by starving the birds to low weights, and then allowed them to fatten again. Each found that the birds had weight increases of up to 8 g in 3 days, with a mean of 1.7 g/day [computed from Fig. 4 in King (1961)]. The pattern of weight gain following starvation reflects the pattern following migratory flight found in the present study. The main difference was in rate. The wild birds deposited fat at about 0.6 g/day, which was less than half the rate of the captives. Wild birds are not protected from weather changes or disturbances, and their food is not as concentrated as that of captives, all of which would probably slow their rate of weight gain.

There are few comparative data on stopover length or fat deposition for transient White-crowned Sparrows. Dewolfe et al. (1973) found a mean minimum stopover of 2.5 days (Borror method) for *Z. l. gambelii* during spring in the Yukon Territory. No mean weight gain was given, but 38 of 46 repeats gained weight, with the weight changes ranging from −3.6 to 4.3 g. Fall transient *Z. l. gambelii* in California gained weight at 0.3 g/day (Morton et al. 1973). In both of these studies the birds did not deposit large fat reserves before departure. King and Mewaldt (1981) found that the mean minimum stopover of *Z. l. gambelii* in Oregon decreased from 5.6 days in the first week to 2.5 days in the last week of spring migration (Borror method). These data and the results of the present study show that there is variation in stopover time and pattern of fat deposition between different stopover sites. This variation may be caused by differences in the migration biology of populations, the stage of migration, and environmental conditions at the stopover site. Some difference between populations would be expected, as some populations migrate shorter distances than others. An obvious difference between populations is that nonmigratory *Z. l. nuttali* do not deposit fat during the migratory period of the other subspecies. It has been illustrated for other species that the amount of fat reserves varies with the stage of migration (Caldwell et al. 1964). This would involve changing stopover length and rates of fat deposition at different stages of the migration. Finally, local conditions at stopover sites, such as food availability and weather conditions, vary, and this would result in differences in stopover time and pattern of fat deposition. Further data are needed from several stopover sites in order to determine the relative contributions of each of these factors to variation in the pattern of fat deposition.

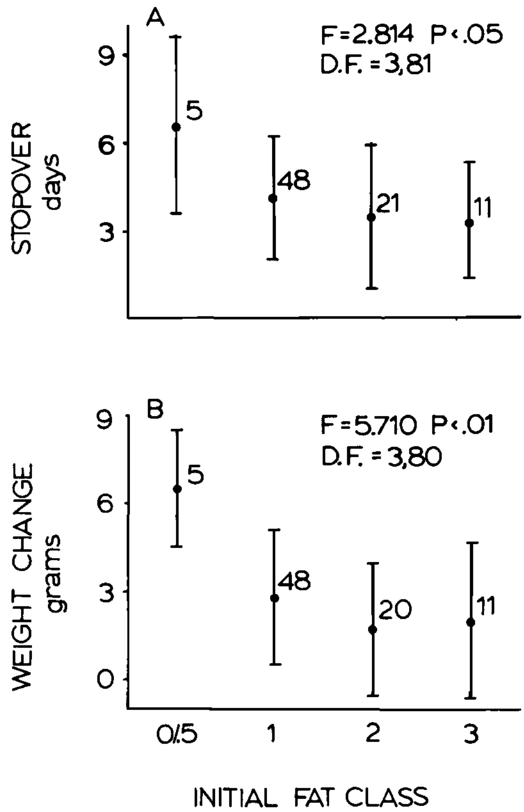

Fig. 3. Mean minimum stopover (A) and mean weight change (B) for initial fat classes. Sample sizes are given next to the means. Vertical bars indicate one standard deviation to either side of the mean.

Other studies of fat deposition of wild birds (Davis 1962, Nisbet et al. 1963, Mueller and Berger 1966, Langslow 1976, Rappole and Warner 1976) demonstrated a different pattern of weight gain than that of the present study (Fig. 2). In these studies, birds usually lost weight in the first few days after the first handling and then began to gain weight. Mueller and Berger thought that handling shock caused Swainson's Thrushes (*Catharus ustulatus*) initially to lose weight. Langslow, in his study of Blackcaps (*Sylvia atricapilla*), suggested that new arrivals are in a low state of *Zugdisposition* and are thus not hyperphagic for the first few days after arrival. Rappole and Warner found that Northern Waterthrushes (*Seiurus noveboracensis*) gained weight only after they had established territories, which usually took several days. The White-crowned Sparrows of the present study gained weight immediately after the first capture, which shows that handling does not affect weight gain in White-crowned Sparrows and that hyperphagia is not reduced just after a migratory flight. Incidental observations indicate that White-crowned Sparrows are not territorial on migration, so an initial weight loss would not be predicted for this species.

The repeat percentage of 54% for White-crowned Sparrows (Table 1) is higher than that for other species at Coleman Farm. Ten percent of the 879 Song Sparrows (*Melospiza melodia*), 539 Savannah Sparrows (*Passerculus sandwichensis*), and 472 White-throated Sparrows (*Z. albicollis*) repeated, and less than 1% of all the warblers (*Parulidae*) repeated. This large repeat percentage for White-crowned Sparrows suggests that transient birds prefer habitat like the hedgerow at Coleman Farm and that they do not disperse much from appropriate habitat. This indicates that habitat selection can be important to migrants attempting to deposit fat and suggests that, in order to document fat deposition in migrants, banders must work in habitats where birds fatten and not in areas where birds concentrate just after a migratory flight (i.e. coastlines).

Cortopassi and Mewaldt (1965) observed a shorter passage period in the spring than in the fall for White-crowned Sparrows in northeastern North America. Vickery (1978) and Palmer (1949) give a spring passage period of about 1 month during May, with a 2-week peak in mid May. The fall passage is longer, from early September to mid-November, with a 4-week peak from mid-September to mid-October. Preston (1966) found that the distribution of captures of White-crowned Sparrows in Pennsylvania was wider and had a larger standard deviation in the fall than in the spring migration. At Coleman Farm a shorter passage in spring was also observed (Table 1). Cortopassi and Mewaldt suggested that the fall migration may be more leisurely than in the spring, that is, birds stop over longer and deposit fat more slowly or that the timing of the fall migration is not as precise as it is in the spring. The present data do not support the first hypothesis, because the mean rate of weight gain was not different from the spring to the fall and the mean minimum stopover length was not significantly shorter for the spring (Table 2). The timing of initiation of migratory behavior is very punctual in the spring compared to the fall (King 1963), and this might suggest that the passage period in the fall would be longer at a stopover site, but the longer passage observed in the fall might just be a function of the larger population in the fall. Longer passage periods in the fall than in the spring have been observed for other species (Preston 1966). This pattern has been well documented for the Dark-eyed Junco (*Junco hyemalis*) and White-throated Sparrow (Stack and Harned 1944, Borror 1948, Preston 1966). In these species the data do support the hypothesis that the fall migration is more leisurely, because the mean minimum stopovers were significantly longer in the fall than in the spring. White-throated Sparrows had mean minimum stopovers of 4.5 days for the spring and 10.7 days for the fall in Michigan and 5.3 days for the spring and 8.7 days for the fall in Ohio. These minimum stopover periods for White-throated Sparrows are similar to those found in the present study for the spring, but the fall stopover periods were twice that of the present study.

As shown by Fig. 3, a bird will stop over longer if its fat reserves are low. Some very fat birds repeated, and most of these birds lost weight or gained little weight. I suggest that weather conditions were probably not appropriate for a migratory flight on the nights that these birds had attained high fat levels, so they were forced to stay over despite having enough fat for a migratory flight. The present data cannot be used as a test, because the last date of capture was not necessarily the night of departure. Studies of weather conditions and nocturnal migration, however, show that heaviest migration occurs with favorable weather (Richardson 1978). Further, experimental nocturnal releases of White-throated Sparrows, followed with tracking radar, showed that birds were more likely to initiate a migratory flight if the weather was favorable and if they had larger fat reserves (Demong and Emlen 1978).

The events in a stopover period of a migrant White-crowned Sparrow can be summarized as follows. Upon making landfall after a migratory flight, the bird locates a suitable habitat for fattening. Fattening occurs at a certain rate through the daylight hours (0.24 g/h for the present study). In the evening, a choice of whether or not to make another flight is made depending on weather conditions and the amount of fat stored. If the bird flies, it metabolizes fat in flight and starts the stopover cycle again at the end of its flight. If the weather conditions are poor and/or the bird has insufficient fat to make a flight, the bird spends the night in the stopover area and metabolizes some of the fat it had gained. A bird arriving with no fat could not make another flight even if the weather were appropriate, whereas a bird with some fat could make a flight even if it had not attained maximum fat. Thus, if a bird did not utilize all its fat reserves in a night's flight, it could potentially make flights on sequential nights if weather conditions were appropriate. Gauthreaux (1971) has demonstrated that spring migrants that had just completed crossing the Gulf of Mexico often still had large fat reserves and that trans-Gulf migrants departed coastal Louisiana on the evening of the day of their arrival unless weather conditions were inappropriate.

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