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ANALYSES OF WEIGHT AND FAT VARIATIONS IN TRANSIENT SWAINSON'S THRUSHES

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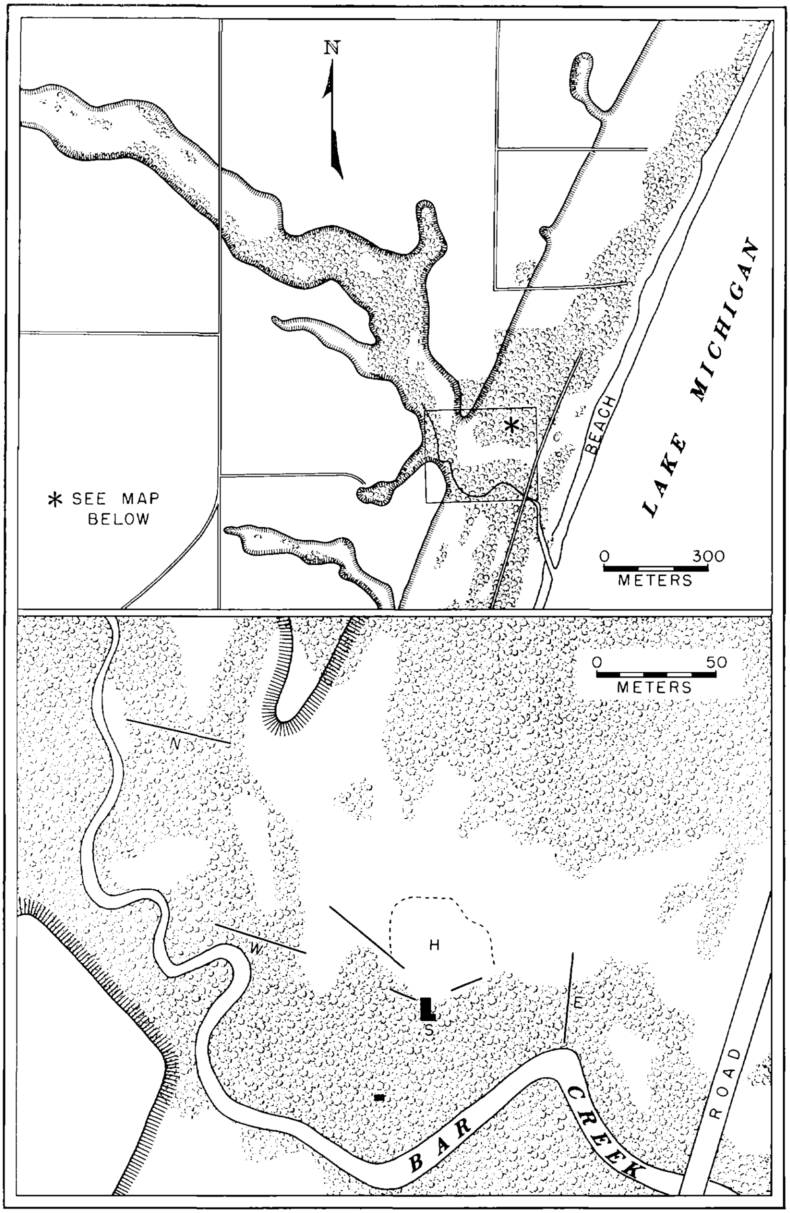
This paper represents an attempt to derive useful information from data collected in the process of banding and recapturing migrant birds. The Swainson's Thrush (*Hylocichla ustulata*) was selected for this study because it is a long distance, nocturnal migrant and because it is the most common bird in our area in autumn. The paper is a series of analyses of weight and fat variations, occurrence, and fluctuations of both recaptures and previously unhandled birds. A number of hypotheses concerning various aspects of migration are presented and compared with the data. Some of the hypotheses are not entirely consistent with others; several interpretations are possible for some aspects of the data. The data for this study are derived from 5,580 handlings of 4,328 Swainson's Thrushes taken in a standardized mist-netting scheme at the Cedar Grove Ornithological Station in the autumns of 1959 through 1962.

The Swainson's Thrush breeds from California, Colorado, the northern Great Lakes, and West Virginia north to central Alaska and central Canada. The winter range extends from southern Mexico to Peru and northwestern Argentina (abridged from the A. O. U. Checklist, 1957). The breeding range of the Swainson's Thrush in Wisconsin is apparently confined to the northern tier of counties (Gromme, 1963). We have received four recoveries on Swainson's Thrushes banded in autumn at Cedar Grove: (1) at Montgomery, Alabama, in early May one and one-half years after banding, (2) at Winnipeg, Manitoba, in early May of the year following banding, (3) at Vernon, British Columbia, in early August 23 months after banding, and (4) near Caparrapi, Columbia, South America, in January four months after banding.

The Cedar Grove Ornithological Station is located on the west shore of Lake Michigan some 64 km north of Milwaukee, Wisconsin. A 400 m wide strip of beaches abandoned by ancient recessions of the lake separates the intensively farmed red-clay-glacial till from the lake at this point (Figure 1). The thin soils covering the abandoned beaches support a fairly dense stand of second growth forest (*Populus*, *Betula papyrifera*, *Prunus serotina*, *Fraxinus*) in some areas. Much of the area, however, is covered only by a brushy growth (*Cornus stolonifera*, *Salix*, *Rubus*, *Alnus rugosa*) or with grasses and *Juncus balticus*, and occasional blowouts of sand occur. Agricultural use of this land is usually limited to pasturing. The

Fig. 1. (lower) Map of the Cedar Grove Ornithological Station. Key: S, banding laboratory; E, W, and N, positions of nets used in this study; fringed line, edge of bluff; shading, areas largely covered by trees or brush. The area shown in the lower map is an enlargement of the rectangle marked with an asterisk in the upper map.



abandoned beaches do not exceed 6 m in elevation above the lake level. The glacial till of the hinterland terminates abruptly in a bluff which rises some 9 to 12 m above the abandoned beaches. A small stream wanders through the station area. The valley cut into the glacial drift by this stream has considerable brush and tree cover. The proximity of the lake, the lack of cover in the immediate surroundings except in the strip along the lake, and the abundance of *Prunus serotina* undoubtedly all aid in concentrating Swainson's Thrushes in the vicinity of the station.

Observation and occasional netting in July and August have shown that the main fall migration of the Swainson's Thrush at Cedar Grove begins in the last few days of August. An occasional Swainson's Thrush can be found in the area in early August, and catches of 5 to 10 birds can occur as early as 20 August. We began full time netting on 10 August in 1959, 27 August in 1960 and 1961, and 1 September in 1962. Nets were left up day and night until at least 20 October in all four years except for 10 days when flooding, severe weather, or other emergencies prevailed. Few Swainson's Thrushes remain in the area as late as 20 October (Table 9). The nets were up for 286 full days during the four autumns, and Swainson's Thrushes were taken on 191 of these days.

TECHNIQUES

Eighteen 36 mm mesh, 12 m long mist-nets were used in this study. Nets were set in the same manner in the same locations each year. The nets were placed two high and three lengthwise in three lanes cut through dense cover 2 to 4.5 m high. The bottom of each net was about 15 to 30 cm off the ground, and the top was about 3.1 m from the ground. The total area of the nets was about 313 m^2. The locations of the three nets(E, W, and N) are shown in Figure 1.

Mist-nets were inspected about every 40 minutes. The birds were removed as rapidly as possible and transported to the banding laboratory in an opaque container. The birds usually were processed and released within 20 minutes, although in exceptional cases as much as an hour and a half elapsed between removal from the net and release. Weights were taken to the nearest 0.1 g on an Ohaus triple-beam balance calibrated to 0.1 g. The birds were weighed in upright cylinders made of sheet aluminum 115 mm high and 40 mm or 55 mm in diameter. Weights of the cylinders were equalized to each other and to a tare beam on the balance. The furculum, abdomen, and axilla were inspected for subcutaneous fat deposits, and the amount of fat was evaluated as belonging to one of four classes: none, light, moderate, or heavy (compare Wolfson, 1945). All birds were banded with U. S. Fish and Wildlife Service bands. The band numbers of all recaptured birds were noted, and the birds were again weighed and checked for fat.

To permit the calculation of mean fat, the fat classes were assigned numerical values of 0 (none) through 3 (heavy). The mean weights of, and differences between, birds in the four fat classes are given in Table 1. Mean fat class calculations are presented in this paper as

TABLE 1. MEAN WEIGHTS OF EACH FAT CLASS

Fat class	No. of birds	Weight (g) Min.	Max.	Mean	Difference
None	702	23.5	36.2	28.37	
					1.41
Light	2194	23.2	39.8	29.78	
					1.86
Moderate	1007	25.5	39.3	31.64	
					2.18
Heavy	211	26.0	43.5	33.82	

correct to two decimals. This was done for convenience and no such accuracy is implied. The visual determination of fat class is qualitative and cannot be very accurate. Bljumental and Dolnik (1962) give confidence limits for various methods of measuring fat; no such attempt was made in the present study. The reader is warned to pay close attention to sample size wherever visual fat estimates are used.

The mean difference in weight between successive fat classes (adjusted for differences in sample size) is 1.74 g. Later in this paper we use this mean difference of 1.74 g as the weight of the total body fat represented by one of our fat classes. Since the difference between successive fat classes varies from 1.41 to 2.18 (Table 1), as much as 25% error could be involved in the estimate of weight of fat if all of the birds in a given sample were in the heavy fat class. The error of estimate becomes negligible as the distribution of fat classes in a given sample approaches that of the total sample presented in Table 1. In the analyses utilizing the weight difference between successive fat classes the fat class distributions are essentially random and, in samples of reasonable size, not markedly different from the distribution in Table 1.

The difference in weight between successive fat classes is an estimate of the difference in total body fat, not merely subcutaneous fat. Odum and Perkinson (1951) have shown that the amount of subcutaneous fat is proportional to the total fat in a migratory bird. Odum *et al.* (1964) have shown that (aside from gut content) fat is responsible for essentially all of the weight change in migrants. Connell *et al.* (1960) extracted the fat from the carcasses of 10 female Swainson's Thrushes and found that the birds had a mean fat free weight of 26.22 g; 2.15 g lighter than our mean for birds of fat class "none". This suggests that birds which we have visually estimated as having a fat content of "none" actually may be carrying as much as 2 g of fat. The mean fat content of birds of our "heavy" fat class thus probably approaches 8 g.

No attempt was made to determine the age or sex of the thrushes used in this study. Annan (1962) presents data which suggest that thrushes of the genus *Hylocichla* are not segregated temporally as to age or sex during the fall migration in northeastern Illinois.

ANNUAL VARIATIONS IN WEIGHT AND FAT

In the majority of phenomena investigated in this study we found little difference between data for the years 1959 and 1960 and, similarly, between 1961 and 1962. However, many differences were found when the combined data for 1959-60 were compared with the combined data for 1961-62.

The mean weight and fat of all thrushes taken during a given autumn did not differ significantly from those data from other autumns (Table 2). The median stay of recaptured birds (counting birds taken on the day of banding as having stayed one day, see Borror, 1948; Blake, 1950) was two days in 1959-60 and three days in 1961-62. The median date of the annual catch (the day on which 50 per cent of the total catch of thrushes for the season was attained) varied considerably but with no consistent pattern. In 1959 the median date of catch was 22 September; in 1960, 11 September; in 1961, 15 September; and in 1962, 11 September.

More birds were taken in 1961-62 than in 1959-60, and the percentage of birds recaptured in 1961-62 was twice that of 1959-60 (Table 2). There were also fewer multiple recaptures in 1959-60 than in 1961-62 (Table 3).

The record of recaptures given in Table 3 differs markedly from a comparable tabulation for the White-throated Sparrow (*Zonotrichia albicollis*) published by Borror (1948). Borror had proportionally more recaptures several to many days after banding, and he also found proportionally more multiple recaptures. Aside from possible species characteristics this difference may be due largely to differences in trapping technique. Borror used baited traps which probably acted in part as feeding stations for the sparrows, considerably increasing the probability of recapture and perhaps also the length of stay of the birds. The probability of a bird being recaptured in a mist-net may be biased in the opposite way since birds may learn to avoid nets. However, our observations on species that breed in the station area indicate that it generally takes several encounters with a net before a bird learns to avoid the net in that location. Each net location must apparently be learned quite apart from prior experience.

TABLE 2. ANNUAL VARIATIONS IN OCCURRENCE, WEIGHT, AND FAT

Year	No. banded	Per cent recaptured	Mean weight (g)	Mean fat	Median stay (days)
1959-60	1687	12.1	30.14	1.19	2
1961-62	2641	24.3	30.18	1.15	3
All	4328	19.6	30.17	1.17	

TABLE 3. TEMPORAL DISTRIBUTION OF RECAPTURED BIRDS*

Days since banding	1959-60					1961-62							
	1	2	3	4	5	1	2	3	4	5	6	7	8
0	80	4				218	14						
1	44	7				148	25	3					
2	25	4	1			88	23	6	2	2	1		
3	15	5	2			61	29	9	2				
4	15	4		1		44	23	7	4				
5	8	3	2			26	16	16	5				
6	4	1	1	1		17	24	9	1	1			
7		2	1			13	14	5	4	1			
8	2	1	2			6	6	5	3	4	1		
9	3	2				6	4	3	4		1		
10	3	1	1	1			5	2		2	1		
11	2	2				4	5	1		1		1	1
12	2	1	1		1	1	1	1		1		1	
13			1			2		1					
14				1		2		1			1		
15	1							1			1		
16		1		1			1	1				1	
17									1				
18						1	1						
20						2							
21						1							
22						1							
23							3						1
25								1					
27						1							
28								1					
29									1				
31									1				
34													
Total	204	38	12	5	1	642	194	73	28	13	6	3	2

*This table is best explained by recourse to example:

In 1959-60, 25 birds were recaptured for the first time 2 days after they were banded. Four birds were recaptured for the second time 2 days after banding. These latter birds could have been recaptured for the first time on the day of banding, or 1, or 2 days after banding.

WEIGHT AND FAT CHANGES IN RECAPTURED BIRDS

Recaptured Swainson's Thrushes in all four years showed little change in weight on the day of banding, a decrease on the day after banding, and an increase on the second day after banding which brought the birds back to approximately their weight at the time of banding (Table 4). After the second day the thrushes increased in weight rather steadily until the sixth or seventh day after banding. The mean weight and fat class differences given in Table 4 for more than seven days after banding are not reliable because of restricted sample size. The extreme variation shown by the few birds that did remain in the area for more than seven days suggests, however, that the factors which govern extended stay are unrelated to fat deposition. Birds recaptured for the first time on the sixth day after band-

TABLE 4. CHANGES IN WEIGHT AND FAT BETWEEN BANDING AND FIRST RECAPTURE

Days since banding	No. of birds	Mean fat difference	Mean wt. difference
0	298	0	−0.08
1	192	−0.16	−0.67
2	113	−0.01	+0.27
3	76	+0.20	+0.94
4	59	+0.30	+0.97
5	34	+0.21	+1.42
6	21	+0.76	+2.61
7	13	+0.31	+2.81
8	8	+0.25	+3.21
9	9	+0.33	+1.64
10	3	0	−0.53
11	6	+0.50	−0.27
12	3	−0.66	−0.57
13	2	0	+1.15
14	2	+0.50	+2.60
15	1	+1.00	+0.10
18	1	0	−0.50
20	2	+0.50	+2.30
21	1	0	+2.70
22	1	−1.00	−2.10
27	1	−1.00	−2.30

ing averaged 2.61 g and 0.76 fat classes heavier than at the time of banding. This can be interpreted as an average daily gain of 0.44 g and 0.13 fat classes.

The decrease in weight on the day following capture has been noted in other migrant species (Davis, 1962; Browne and Browne, 1956; Nisbet *et al.*, 1963), but no satisfactory explanation has been advanced for it. Browne and Browne (1956) rejected handling as a cause of this lack of weight gain primarily because the lack of correlation between the weight of migrants and the time of day suggested that unbanded, unhandled birds were not gaining weight during the day. They hypothesized that newly arrived birds were spending less time feeding and that the feeding was of a desultory nature. In the present study we find both a considerable correlation between bird weight and time of day (Figure 3) and a pronounced decrease in weight on the day following banding (Table 4). Baldwin and Kendeigh (1938) analyzed recapture data on resident Chipping Sparrows (*Spizella passerina*) taken in baited traps and found no handling effect. Apparently no one since then has examined a sufficiently large sample of trapping data for handling effect, although the probable effects of handling on the weights of occasional individual birds has been recognized (e. g. Lees, 1949).

We suggest that handling a migrant bird acts as a trauma which affects the behavior or metabolism of the bird in such a way as to prevent normal weight gain and fat deposition for several days following the handling. Birds recaptured for the first time showed a loss in weight only on the first day after banding, whereas the birds

TABLE 5. MEAN CHANGE IN WEIGHT AND STANDARD ERROR* FROM TIME OF BANDING

Days since banding	No. of times recaptured 1		2		3		4	
0	−0.08	**0.06**	−0.40	**0.25**				
1	−0.67	**0.12**	−0.39	**0.28**	−0.20	**1.16**		
2	+0.25	**0.19**	+0.14	**0.33**	−0.38	**0.71**	−1.20	**1.50**
3	+0.94	**0.22**	+0.26	**0.36**	+1.36	**0.48**	−1.85	**0.96**
4	+0.97	**0.31**	+1.03	**0.46**	−0.24	**0.53**	−0.44	**0 50**
5	+1.42	**0.43**	+1.30	**0.56**	+1.32	**0.58**	+1.80	**0.77**

*Standard error of the mean is bold.

recaptured for the fourth time showed a loss in weight on the second, third, and fourth days (Table 5). On the fifth day all recaptures showed about the same gain in weight. The variability in weights is considerable, as evidenced by the large standard errors of the mean, but the trend in the data is obvious. (The mean weights of the fourth recaptures for days 3 and 4 are significantly different from those of the first recaptures.) Although there are irregularities in the data, for the most part the changes in fat correspond with those of weight (Table 6).

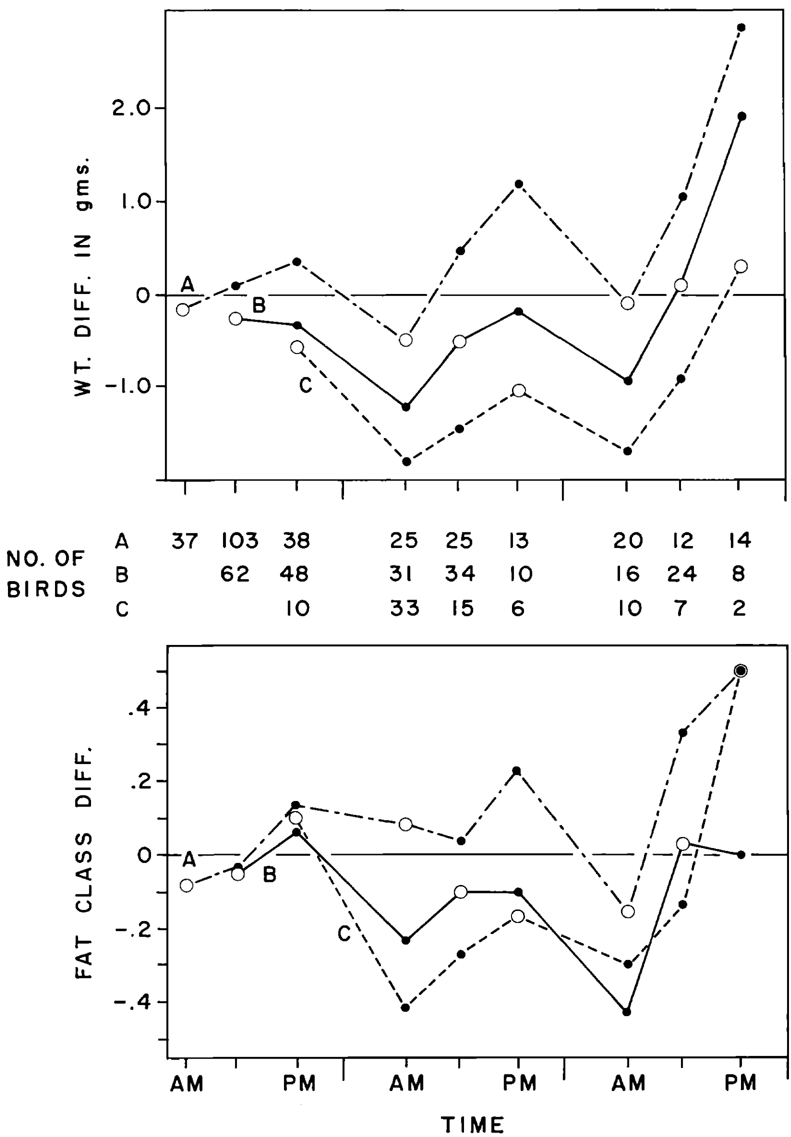
TABLE 6. MEAN FAT CLASS CHANGE FROM TIME OF BANDING

Days since banding	No. of times recaptured 1	2	3	4
0	0	+0.17		
1	−0.16	−0.34	−0.33	
2	−0.01	+0.11	+0.71	0
3	+0.20	+0.12	+0.15	−0.50
4	+0.30	+0.26	+0.57	−0.40
5	+0.21	+0.31	+0.72	+0.60

CHANGES DURING THE TWO DAYS FOLLOWING BANDING

The large sample permitted an examination, in somewhat greater detail, of the weight and fat changes in birds recaptured for the first time during the day of banding and the two subsequent days. The weights and fat classes of birds were grouped according to (a) time of banding and (b) time of recapture. The day was separated into three intervals: (1) before 0900 hours (morning), (2) between 0900 and 1600 hours (midday), and (3) after 1600 hours (evening). The resulting 24 groups of weight and of fat class data were plotted in terms of change since time of banding (Figure 2). In Figure 2 a line connects all recaptures of birds banded in the morning, another all birds banded during midday, etc. Open circles represent data from recaptures taken during the same time interval as that of banding or 24 or 48 hours later. Since birds are heavier (in weight and fat) in the evening than in the morning and since the position of the points

Fig. 2. Weight and fat class changes (from time of banding) of birds recaptured for the first time during morning, midday, or evening of the same day, or 1, or 2 days after banding. Key: curve A, birds banded in the morning; curve B, birds banded during midday; curve C, birds banded in the evening. Open circles indicate time of banding and corresponding points 24 and 48 hours later.



is determined by the change in weight or fat from that of the time of banding, the three lines tend to run parallel, with the distances between lines largely a function of the differences in weight or fat at the time of banding.

The curves in Figure 2 permit estimation of weight and fat fluctuation through the day of banding and the two days following banding with a minimum of handling bias on the data. Only the weights and fat estimates at the time of banding and at the first recapture are considered. The curves appear to increase in daily amplitude with increasing time lapse from the time of banding. The net decrease in weight and fat on the day following banding seems thus to be due largely to reduced weight and fat gain during the day rather than to increased overnight loss. This suggests that the birds are feeding less or are utilizing food with reduced efficiency.

HOURLY CHANGES IN WEIGHT AND FAT

We can get an estimate of the change in weight and fat through the day in previously unhandled Swainson's Thrushes by finding the mean weights of all unbanded thrushes taken during each one-hour interval through the day (Figure 3). These previously unhandled birds showed an increase of about 2 g in weight and 0.38 fat classes over the day. Recaptured birds did not show the same magnitude of daily weight and fat gain as previously unhandled birds until the second day after banding (Figure 2).

RATES OF FAT DEPOSITION AND UTILIZATION

We can estimate the diurnal gain in fat by Swainson's Thrushes in two ways:

(1) The difference in mean fat class of previously unhandled birds taken between 0500-0859 hours and of those taken at 1600-2000 hours was 0.38 (Figure 3). Since the mean weight difference between our fat classes is 1.74 g (Table 1), 0.38 fat classes may be considered approximately 0.66 g of fat.

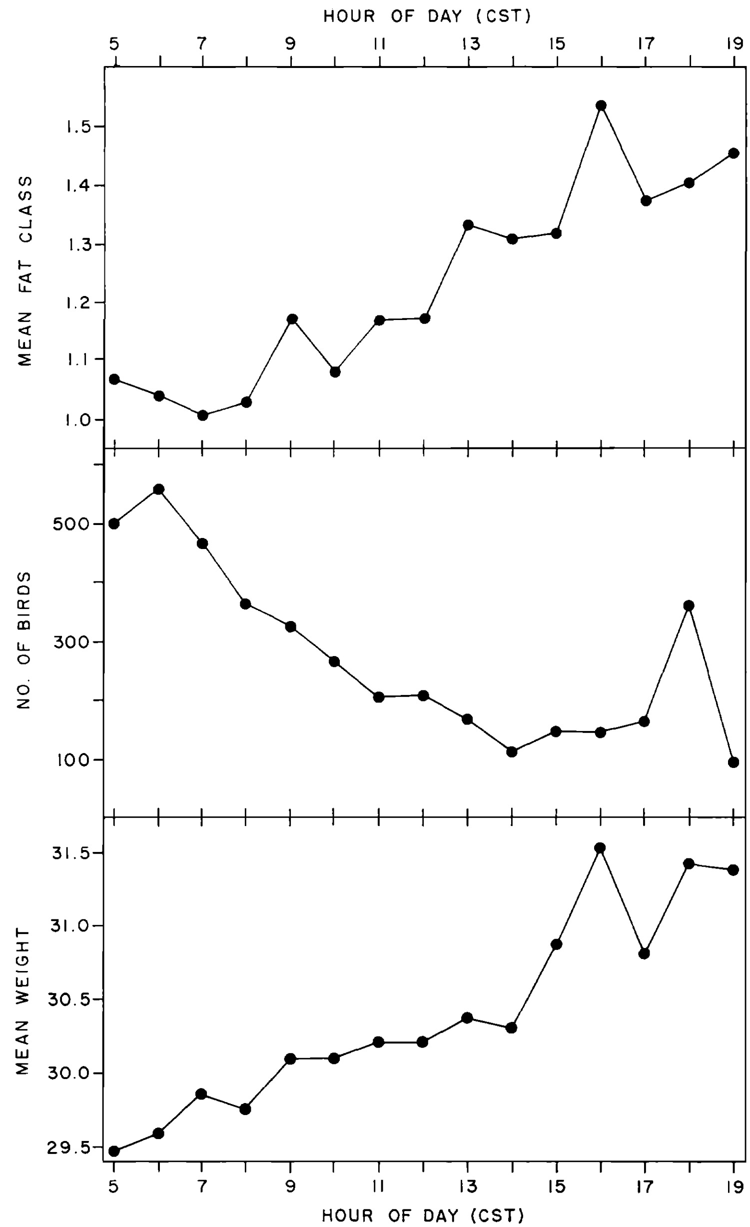
(2) The difference in mean fat class of birds recaptured for the first time in the morning of the second day after banding and of those birds taken that evening was 0.63 (Figure 2). This is equivalent to approximately 1.10 g of fat. This estimate is in part based on a sample of limited size.

The amount of fat utilized overnight by a sleeping Swainson's Thrush can be estimated in the following ways:

(1) Eight birds held overnight in opaque containers showed a mean loss of 0.38 fat classes (0.66 g of fat). This estimate may be excessive because of handling effect (compare Helms and Drury, 1960; Nisbet *et al.*, 1963).

(2) The difference in mean fat class of birds recaptured for the first time in the evening of the first day after banding and of those taken the morning of the second day after banding is 0.28 (Figure 2). This represents a loss of approximately 0.49 g of fat.

Fig. 3. Mean weight, fat class, and number of previously unhandled Swainson's Thrushes taken during one-hour intervals through the day.



(3) The mean of nine series of measurements of standard metabolism taken at night in seven species of passerines with a body weight range 23.5 to 31.1 g is 0.0142 kcal/g/hr at thermoneutrality (King and Farner, 1961, Tables 2 and 3). The mean temperature coefficient for three species (body weight 22.0 to 26.4) is 3.9, and the lower limits of the thermoneutral range for these three species ranges from 25 to 32° C (*op. cit*). On the basis of the above measurements, we would expect the nocturnal, resting metabolic rate of Swainson's Thrushes to be about 0.0236 kcal/g/hr at an ambient temperature of 10-12° C. Our thrushes had a mean weight of 30.17 g (Table 2), and standard metabolic rate per bird would thus be about 0.712 kcal/hr.

Small passerines void the last remnants of a meal or complete food absorption about one and one-half to three hours after a meal (Stevenson, 1933; Kendeigh, 1944; Wallgren, 1954). Sources of energy other than fat contribute to the resting metabolism of small birds for four to six hours after fasting begins (Baldwin and Kendeigh, 1932; Benedict and Fox, 1933). Stored fat may begin to contribute to the metabolism as early as one and one-half hours after a meal (Kendeigh, 1944). Glycogen stores may be sufficient to maintain metabolism for 40 minutes to an hour (Lapicque, 1911; Kendeigh, 1944).

The above data lead us to assume that nonfat energy sources are sufficient to provide for the equivalent of at least two hours resting metabolism in thrushes. In the remaining eight nocturnal hours the birds would require about 5.7 kcal. Nisbet *et al.* (1963) give the caloric equivalent of bird fat as 9.5 kcal/g (compare Rogers and Odum, 1964). The thrushes would thus require about 0.60 g of fat or 0.34 of one fat class overnight.

The net daily gain of fat in migrant Swainson's Thrushes can be estimated in several ways. The mean increase in fat class per day for birds recaptured for the first time over the interval of two to six days after banding is 0.19 (Table 4). This is equivalent to a net gain of 0.33 g of fat per day. Other estimates of net daily fat increase can be obtained by combining the various estimates for diurnal gain with those for overnight loss given above. The resulting estimates for net daily increase in fat by thrushes range from 0 to 0.35 fat classes (0 to 0.61 g of fat), with a mean of 0.18 fat classes (0.32 g of fat). A reasonable estimate of the net rate of fat gain in Swainson's Thrushes in autumn at Cedar Grove would probably be 0.20 fat classes per day (0.34 g of fat).

The above estimated rate of fat deposition suggests that a Swainson's Thrush would require three days to deposit one gram of fat and three weeks to acquire a heavy fat deposit. Estimates of the time required for fat deposition based on laboratory studies are much lower, e. g. White-crowned Sparrows (*Zonotrichia leucophrys gambelli*) increased their weight to a maximum in three to five days after fasting (King, 1961); Ortolans (*Emberiza hortulana*) showed a 30 per cent increase in weight in ten days (Wallgren, 1954); White-throated Sparrows (*Zonotrichia albicollis*) can acquire heavy fat deposits in four to six days (Wolfson, 1954).

In the field White-throated Sparrows require about seven to ten days to acquire 2 g of fat (Odum, 1949), a rate of fat deposition similar to that which we observe in Swainson's Thrushes. It would thus appear that rates of weight and fat gain in migratory birds based on laboratory results are much higher than those actually occurring in nature. Wallgren (1954: 70) anticipated this conclusion in his laboratory study of two species of *Emberiza:* "Such a great increase in weight presumably does not occur in the wild state, but seems to be in some way connected with captivity. When the bird is in a state to accumulate fat, captivity apparently offers suitable conditions for a marked gain in weight. Food abounds but activity is limited, and stores are not as readily depleted as in nature."

A comparison of Table 9 of this paper with Table 2 of Galindo *et al.* (1963) indicates that the peak of the Swainson's Thrush migration in Panama occurs some 6 to 7 weeks after the peak at Cedar Grove. At a rate of 0.34 g per day Swainson's Thrushes could acquire about 17 g of fat during this interval. Nisbet *et al.* (1963) estimate the in-flight power consumption of a small bird at 0.076 kcal/g total wt/hr (compare Le Febvre, 1964). The 17 g of fat would provide a Swainson's Thrush with a possible flight time of about 71 hours. The bird would have to maintain a mean ground speed of 56 km/h during flight in order to cover the 4,000 km distance between Cedar Grove and Panama in 71 hours. This flight speed approximates those of nocturnal migrants observed on radar (Harper, 1958; Graber and Hassler, 1962). A net fat accumulation rate of 0.34 g/day is thus probably sufficient to enable the Swainson's Thrush to migrate to its winter range in the time available for migration.

Estimates of rates of change in body weight can be made by the methods used above to estimate rates of fat deposition and utilization. The diurnal gain in weight can be estimated in two ways:

(1) The difference in mean weight of previously unhandled birds taken between 0500-0859 hours and of those taken between 1600-2000 hours in 1961-62 was 1.95 g (Figure 3). We have previously shown that thrushes gain 0.38 fat classes or about 0.66 g of fat during this time interval. The gain of 1.95 g thus might be resolved into a fat gain of 0.66 g and a nonfat gain of 1.29 g.

(2) The difference in mean weight of birds recaptured for the first time in the morning of the second day after banding and of those taken that evening was 2.63 g (Figure 2). The gain in fat during this interval was 0.63 fat classes or 1.10 g. The nonfat gain is thus about 1.53 g.

The overnight loss in weight can be estimated as follows:

(1) Eight birds held overnight in opaque containers showed a mean loss of 2.38 g. Fat loss was 0.38 fat classes or 0.66 g. The nonfat loss is thus about 1.72 g.

(2) The difference in mean weight of birds recaptured for the first time in the evening of the first day after banding and of those taken

the following morning was 0.91 g (Figure 2). Fat loss during this interval was about 0.28 fat classes or 0.49 g of fat. The nonfat weight loss is thus about 0.42 g.

The approximate net daily change in weight of migrant Swainson's Thrushes can be found by combining the various estimates for diurnal gain with those for overnight loss. These combinations yield estimates ranging from −0.43 to +1.72 g, of which −0.43 to +1.11 g can be considered as the nonfat change in weight.

Variations in gut content contribute materially to weight variation in birds. Baldwin and Kendeigh (1938) estimate the gut capacity of small birds at about 4.5 per cent of body weight. Weights of the gut contents of three Swainson's Thrushes accidentally killed in the present study were 0.9, 1.1, and 1.3 g (3.1, 3.4, and 4.4 per cent of body weight). The daily gains and overnight losses, after subtraction of the calculated weight of the changes in fat, approach these figures for gut content. Slight discrepancies probably can be attributed to error in making the various estimates.

INITIAL WEIGHTS OF RECAPTURED BIRDS

Since weight and fat deposits seem to show some correlation with migration, we might expect birds which remain in an area (as evidenced by recapture) to be lighter in weight and fat at the time of banding than birds which leave the area (are not recaptured). This expectation is fulfilled by our data, but the difference between the two groups is slight, amounting to about 0.5 to 0.7 g in weight and to 0.18 to 0.19 fat classes (Table 7). Birds which were recaptured several to many days later were not consistently lighter or heavier at the time of banding than birds which were recaptured only a day or a few days later (Table 8).

DAILY VARIATIONS

The mean weight and fat class of Swainson's Thrushes varied considerably from day to day. Several different ways of examining this variation are presented below:

In relation to time of year.—The mean weight and fat of all previously unbanded birds caught in each five-calendar-day interval

TABLE 7. INITIAL WEIGHTS OF RECAPTURED VS NON-RECAPTURED BIRDS

	Weight in g			Fat class			Sample size	
	Rec.	Not	Diff.	Rec.	Not	Diff.	Rec.	Not
1959-60	29.64	30.38	0.74	1.04	1.22	0.18	204	1483
1961-62	29.76	30.32	0.56	1.01	1.20	0.19	639	2002
Difference	0.12	0.06	0.18	0.03	0.02	0.01		

Key: Rec., birds that were recaptured; Not, birds that were not recaptured; Diff., difference.

TABLE 8. INITIAL MEAN WEIGHT AND FAT OF RECAPTURED BIRDS

Days since banding	No. birds	Weight (g)	Fat class	Days since banding	No. birds	Weight (g)	Fat class
0	243	29.7	1.07	13	3	28.6	1.00
1	151	29.6	1.06	14	5	29.0	0.80
2	95	29.5	1.09	15	2	30.6	1.00
3	80	29.5	0.88	16	3	31.6	0.66
4	68	29.7	0.99	17	1	31.6	1.00
5	55	29.8	0.96	18	1	30.3	2.00
6	41	29.4	0.83	20	1	28.2	1.00
7	27	29.7	0.93	21	1	26.5	1.00
8	23	30.1	1.00	22	1	31.3	1.00
9	14	29.4	0.79	23	2	28.0	1.00
10	10	29.0	0.70	27	1	29.2	1.00
11	10	31.6	1.20	29	1	29.7	1.00
12	6	28.2	1.17	34	1	28.5	0

through the autumn is given in Table 9. No consistent pattern of variation is evident.

In relation to the number of birds captured per day.—The data were divided according to the number of previously unhandled birds taken per day. The first division combined data for days on which 10 or fewer birds were caught; the second, days on which 11 to 20 birds were caught; etc. The mean weight and fat for each division are presented in Table 10. With a few anomalies, greater mean weight and fat is directly correlated with a greater number of birds caught per day in 1959-60, whereas in 1961-62 there is an inverse relationship between daily catch and mean weight and fat. This phenomenon is explored further in the following section.

TABLE 9. WEIGHT AND FAT CHANGES THROUGH THE AUTUMN

Inclusive dates	Sample size Days	Birds	Mean Weight (g)	Mean fat
27-31 Aug.	15	256	30.30	1.35
1-5 Sep.	20	597	30.80	1.40
6-10 Sep.	20	799	30.40	1.24
11-15 Sep.	20	646	30.04	1.07
16-20 Sep.	18	623	29.81	1.01
21-25 Sep.	19	612	30.21	1.18
26-30 Sep.	17	353	29.98	1.06
1-5 Oct.	20	131	30.13	1.20
6-10 Oct.	19	82	30.65	1.24
11-15 Oct.	10	17	28.33	0.76
16-20 Oct.	4	6	29.76	0.83

"WAVES" OF MIGRATION

If one graphs the number of previously unbanded birds caught per day throughout the autumn at Cedar Grove, the picture is generally one of sharp increases to a peak or "wave" followed by a

Table 10. Weight and Fat in Relation to Numbers of Birds Caught

No. of birds/day	1959-60 Sample size Days	Birds	Mean wt. (g)	Mean fat	1961-62 Sample size Days	Birds	Mean wt. (g)	Mean fat
1-10	46	170	29.89	1.08	25	100	30.92	1.31
11-20	16	246	30.38	1.24	12	183	30.70	1.19
21-30	11	270	30.51	1.18	12	287	30.14	1.19
31-40	6	213	30.45	1.13	14	503	30.48	1.25
41-50	6	271	30.27	1.25	9	405	30.03	1.13
51-60	2	110	30.30	1.40	6	310	30.23	1.31
61-70	1	64	31.61	1.67	3	185	30.26	1.12
71-80					2	144	29.79	0.92
81-90					1	90	31.76	1.50
101-110					2	208	29.33	0.94
121-130					1	125	29.29	0.91

gradual decline until the next wave is encountered. The magnitudes of waves vary as does the period between waves, and the resulting pattern is often complex. However, it would appear that the pattern is one of a wave influx with emigration prolonged over several days. The following analysis is based on the above assumption.

The trapping days were sorted into 9 categories: (1) Waves. Days on which the catch of previously unbanded Swainson's Thrushes exceeded the mean of the catches of the day preceding and the day following by at least 10 birds. (2) Increases. Any non-wave day on which the catch exceeded that of the day preceding by at least 5 birds. (3 - 8) Days following waves (W + 1, W + 2, etc.) The consecutive series of days following a wave terminated by the sixth day (W + 6), or by another wave, or by an increase. (9) Other days. Days which did not fit into any of the above categories. Generally these were days early and late in the season and were characterized by low catches of Swainson's Thrushes.

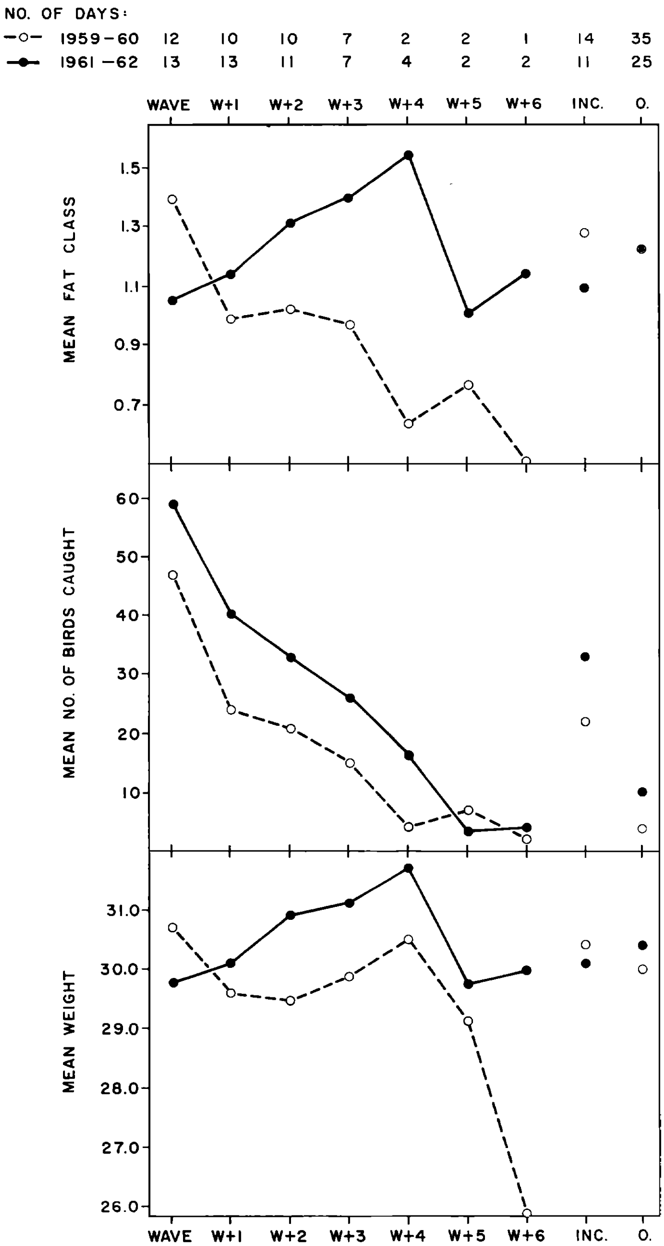
Figure 4 presents the mean numbers of Swainson's Thrushes caught per day in each of the data categories and the mean weights and fat classes in each category for the years 1959-60 and 1961-62. In the four years combined, 69 per cent of all birds caught were taken on waves or on succeeding days (W + 1, etc.)

Swainson's Thrushes caught on wave dates averaged 0.95 g lighter in weight in 1961-62 than in 1959-60 (Figure 4). In 1961-62 the birds caught on "W + 1" through "W + 4" showed a steady increase in weight, averaging 1.9 g heavier on "W + 4" than on the wave date. In 1959-60 birds caught on "W + 1" and "W + 2" showed a decrease in weight as compared with the weight on the wave date. On "W + 3" and "W + 4" the birds showed an increase similar to that of 1961-62. The differences in weight of birds in 1959-60 compared with those in 1961-62 are all statistically significant from the wave dates through "W + 4". Between "W + 4" and "W + 6" both sets of years showed a decline in weight, although these results should be viewed with caution because of the limited sample size.

Swainson's Thrushes caught on wave dates in 1959-60 were 0.34 fat classes heavier than those of 1961-62 (Figure 4). In 1959-60 birds showed a general decline in fat from the wave through "W + 6". In 1961-62 the birds increased in fat through "W + 4" and then declined. The mean number of birds caught on a wave day in 1961-62 was 12 birds greater than in 1959-60 (Figure 4). The mean number of birds caught on the day following a wave (W + 1) in 1959-60 was only half that of the number caught on a wave. In 1961-62 "W + 1" produced two-thirds the number of birds taken on a wave. The rate of decline of birds caught from "W + 2" to "W + 6" was similar for all years although the absolute number taken was greater in 1961-62.

Thus 1961-62 differed from 1959-60 in the following ways: (1) more birds were trapped, (2) the birds were lower in weight and fat on wave days, and (3) the birds showed an increase in weight and fat through the four days following a wave. Before we go into

Fig. 4. Changes in mean number of birds caught, mean fat class, and mean weight for birds taken on "waves", days following waves, days of increase, and other days. Key: open circles and dotted line, 1959-60; closed circles and solid line, 1961-62.



possible causes of the differences between waves in 1959-60 and 1961-62, let us examine further the population structure and daily rate of emigration on waves and days following waves.

ESTIMATES OF POPULATION AND EMIGRATION

Another way of looking at the temporal distribution of recaptures (Table 3) is to reorganize the data into categories of days since the last time each bird was handled and to express the number of birds in each category as a percentage of the total number of birds that could possibly fall into that category (Table 11). Thus the total number of birds banded (or recaptured once, twice, etc.) is considered to be a population of known size from which we can take samples (by recapturing birds previously captured once, twice, etc.) each day following banding or previous recapture. If all banded birds remained in the area indefinitely and had equal and constant probability of being recaptured, all percentages in Table 11 would be identical.

TABLE 11. TEMPORAL DISTRIBUTION (IN PER CENT OF TOTAL POSSIBLE) OF RECAPTURED BIRDS*

Days since prior	1959-60 Recapture					1961-62 Recapture							
handling	1	2	3	4	5	1	2	3	4	5	6	7	8
0	5	8	8			8	7	7	6	7	8		33
1	3	5	11	25		6	6	13	15	12	8	17	
2	2	1	3		20	4	6	9	10	9	27	40	
3	1	2	3			3	4	5	8	14	13		
4	1	3	3			2	5	5	6	6			
5	1	1		11		1	4	3		12			
6		1	4	13		1	1	2	2				
7			4			1	1						50

*Examples: 5 per cent (80) of the 1687 birds banded in 1959 and 1960 were recaptured for the first time on the day they were banded. Of the remaining 1607 (1687-80) banded, but not recaptured, birds 3 per cent (44) were recaptured 1 day after banding. Of a total of 204 birds recaptured one or more times, 8 per cent were recaptured for the second time on the same day they were recaptured for the first time.

The percentages in Table 11 generally decline as one reads down a column, offering a crude index of emigration; and they increase to the right, showing that a bird once captured has a greater probability of being captured again. However, the recapture percentages on Day 0 are nearly constant at about 6 to 8 per cent. We believe that this indicates that our nets take approximately 8 per cent of the birds in the area on a given day. We also feel that the recapture percentages given in the first recapture column (Table 11) are fair estimates of the capture rates on Day 1 through Day 6 of the "population" existing on Day 0. The only outstanding exception to the 8 per cent recapture rate on Day 0 is the 5 per cent for the first recaptures in 1959-60. We feel that this is a result of large numbers of thrushes leaving the area during the day after the night of arrival in 1959-60.

If we assume that all thrushes at Cedar Grove on a wave day (Figure 4) arrived during the preceding night, we can use the recapture rate data (Table 11) to predict the number trapped on subsequent days. Thus:

$$\text{Expected catch on W} + 1 = \frac{(\text{Observed catch on W})\ (\text{Recapture rate on Day 1})}{\text{Recapture rate on Day 0}}$$

$$\text{Expected catch on W} + 2 = \frac{(\text{Expected catch on W} + 1)\ (\text{Recapture rate on Day 2})}{\text{Recapture rate on Day 1)}}$$

The actual catches and those expected by the above hypothesis are given in Table 12. The differences between the observed and the expected catches are not statistically significant. This suggests that our original assumptions have some validity, namely: (1) that most of the thrushes at Cedar Grove on a wave day arrived the previous night and (2) that recapture data can be used to estimate capture rates of unbanded birds.

Using our 8 per cent estimate of daily capture rate and the theoretical catches given in the above paragraph, we can estimate the (hypothetical) population of thrushes in the netting area on days "W" through "W + 6". These population estimates are presented in Column 3 of Table 12. Population estimates (1) and (2) are made by Borror's (1948) modifications of the Lincoln-Peterson index. The Lincoln-Peterson index assumes a constant population without emigration or immigration. Population estimates (1) and (2) are thus possibly not as good as (3) although they show much the same trends in population levels from the wave date through "W + 6".

If we subtract the number of birds banded on a given day from our population estimate (3) for that day and subtract from this result the population estimate of the following day, we have an estimate of the emigration from the area. The emigration, expressed as a percentage of the population of unbanded birds, is given in Table 12. Table 12 also gives the percentage of the original (wave day) unbanded population remaining in the area.

The "model" migratory Swainson's Thrush population shown in Table 12 indicates emigration was much heavier during the first few nights following a wave influx of birds in 1959-60 than in 1961-62. The emigration on the first night in 1959-60 was nearly double (relatively) that of 1961-62. A number of these birds probably left the area considerably before nightfall, resulting in a lower first re-

TABLE 12. MODEL MIGRATORY SWAINSON'S THRUSH POPULATION (SEE TEXT)

Day	Observed Catch	Expected Catch	Population Estimates 1	2	3	Per cent emigration	Per cent population remaining
			1959-60				
WAVE	47		698	90	588	38	57
W + 1	24	27	470	75	338	36	33
W + 2	21	16	284	60	200	32	20
W + 3	15	10	189	77	125	—	20
W + 4	4	10	60	17	125	45	9
W + 5	7	5	48	29	63	34	5
W + 6	2	3	29	9	38		
			1961-62				
WAVE	59		464	202	738	21	75
W + 1	40	43	384	136	538	32	47
W + 2	33	27	286	115	338	23	34
W + 3	26	19	203	108	238	20	26
W + 4	16	14	99	60	175	38	15
W + 5	3	8	46	25	100	32	10
W + 6	4	5	33	23	63		

capture rate on Day 0 in 1959-60 (Table 11). The model does not differentiate between diurnal emigration by relatively local movements and long-distance nocturnal emigration.

Ordinarily we would expect that diurnal movements of limited extent would result in a constant population level since as many birds would enter the area as were leaving. However, if (as seems to be the case) the influx of birds on a wave is greater in the immediate station area (along the lakeshore) than it is a short distance inland, dispersal would result in reduced populations of both banded and unbanded birds at the station. Our capture data for both banded and unbanded birds thus could support a hypothesis in which there is a wave influx of birds followed by dispersal into the surrounding area. In the following paragraphs we shall nevertheless assume that all, or most, emigration is nocturnal.

The model presented in Table 12 suggests that Swainson's Thrushes spend only a few days at Cedar Grove; indeed many seem to remain only one day or part of one day. It was previously shown in this paper that these thrushes gain (net) only 0.20 fat classes per day (0.34 g of fat). If we use 0.076 kcal/g of total weight/hr as an estimate of energy consumption during migratory flight (Nisbet *et al.*, 1963), then the net daily gain in fat by Swainson's Thrushes would be sufficient for a flight of only about one hour's duration. A stay of a few days would provide sufficient fat for several hours' flight. Lowery and Newman (1955), Graber and Hassler (1962) and others have shown that the volume of migration decreases markedly in the middle of the night, suggesting that birds normally migrate for only a few hours. All of the above evidence suggests that birds travel for short distances in a given night, rest for only a few days at the most, and continue on for short distances. Caldwell *et al.* (1963) came to similar conclusions in their analysis of birds killed at television towers in Michigan and Florida. Birds flying across the Gulf of Mexico would presumably "rest" for several weeks beforehand or accumulate fat at a more rapid rate to provide for prolonged flight.

LOCAL FOOD SUPPLIES

The relative abundance of food might affect rates of weight gain, fat deposition, and the length of stay in an area. Food preferences and nutritional requirements of the birds, and the availability of food items in its environment require considerable study. What little data we have are presented below.

Examination of gut contents and feces and observations of thrushes feeding indicate that thrushes at Cedar Grove feed primarily on the fruits of *Prunus serotina.* Fruits of *Vitis, Viburnum, Solanum, Cornus stolonifera,* and *Rhus radicans* are also taken. In 1959 and 1962 we judged the fruit crop of the above species to be "excellent". Many fruits remained unconsumed by birds in these two autumns. In 1960 and 1961 the fruit crop was estimated as "average". In these two autumns most of the fruits of *Prunus* appeared to be consumed by birds, and they probably expended more time and energy in finding fruits. The weight and fat data are similar for 1959 and 1960, years with dissimilar fruit crops; the same lack of correlation holds for 1961 and 1962. There is thus at least no obvious correlation between weight and fat variations and relative abundance of food.

WEATHER AND VARIATIONS IN WEIGHT AND FAT

We have previously shown that about 70 per cent of the 4,328 Swainson's Thrushes caught in this study probably arrived in the area on wave dates. For each wave date the Daily Weather Map for 0000 hrs (CST) was analyzed with regard to air mass and frontal positions and movements. The maps for the 25 wave dates were readily sorted into five groups, with all maps in a group being reasonably similar. The synoptic situation for each of the five groups is described below along with speculations about possible effects of weather conditions on migratory flight.

(1) Low pressure (27 September 1959). The weather map was very peculiar on this night. A cold front passed Cedar Grove at

about 1800 hours. A small low formed in southwestern Wisconsin, and another low center was located over western Lake Superior. Cyclonic flow around a deep low over Lake Winnipeg extended into Wisconsin. The clouds, rain, and variable winds existing in the Wisconsin area on this night probably offered poor conditions for migratory flight.

(2) Across front (7 and 23 September 1959; 1, 4, and 11 September 1960; 8 September 1961). These six nights were characterized by a front extending across Wisconsin in a generally E to W or NE to SW orientation. At 0000 hours Cedar Grove was 80 to 290 km ahead of this front. The birds migrating during these nights presumably crossed a dry, relatively inactive front into a head wind. Head winds can be presumed to be poor for migratory flight.

(3) High pressure (11 September and 4 October 1959; 14, 18, and 23 September 1960; 16 and 20 September 1961; 2, 6, 15, and 26 September and 6 October 1962). A high pressure cell was centered over or near Wisconsin on these 12 nights. The mostly clear skies and light winds predominating on these nights are generally considered to be optimal conditions for migratory flight (Lack, 1960).

(4) After front (29 August 1960; 29 August, 12 and 23 September 1961). The leading edge of a high pressure cell was located over Wisconsin on these four nights. A cold front was located a short distance south and east of the state. Skies were mostly cloudy to overcast and winds were of relatively high velocities. Except for the possibility that tail winds might aid migratory flight, these conditions would seem to be poor for migration.

(5) Cyclonic flow (11 and 18 September 1962). Wisconsin was in the strong air flow between a high pressure area to the southwest and a deep low to the northeast on these two days. Moderate to strong northerly winds and partly cloudy skies prevailed. If tail winds are really favorable for migration, these conditions might be considered optimal.

Birds caught after nights of "Low pressure" were significantly heavier than those in the other four weather situations (Table 13). The weights of birds taken following "Across front" and "High pressure" weather situations differed significantly from each other and from all other weather groups. The "After front" birds differed significantly in weight from all except those taken following "Cyclonic flow" conditions. With one exception the variance in weight decreases with decreasing mean weight. The high variance in weight (7.83) of birds taken following the "After front" situation is largely the result of an extraordinarily high variance in weight (11.60) on 23 September 1961, one of the four days which contributed data to this group. If we discard the data from 23 September 1961, the variance for the "After front" group is reduced to 5.83, leaving no significant differences between any of the variances in Table 13. Adjustment of the data by the deletion of 23 September 1961 does not appreciably change the mean weight (29.53) for the "After front" group.

TABLE 13. WEIGHT, FAT, AND SYNOPTIC WEATHER SITUATION (SEE TEXT)

Weather	No. of birds	Mean weight	Variance	Mean fat	No. of 59-60	days in 61-62
Low Pressure	64	31.61	6.28	1.67	1	0
Across Front	302	30.72	5.43	1.36	5	1
High Pressure	680	30.08	5.35	1.15	5	7
After Front	156	29.59	7.83	1.06	1	3
(adjusted)	102	29.53	5.83	1.18	1	2
Cyclonic Flow	119	29.48	4.91	0.87	0	2

The 54 thrush weights for 23 September 1961 fall rather nicely into two groups: (1) 43 birds with a mean weight of 28.13 g, a range of 24.3 to 30.7 g, and a variance of 3.18 and (2) 11 birds with a mean weight of 34.45 g, a range of 31.4 to 39.8 g, and a variance of 8.87. This peculiar bimodal distribution of weights has a possible explanation in the local weather existing on the night of 22-23 September 1961. A cold front passed at about 1810 hours, and within two hours the lower cloud layer had dissipated to scattered clouds and the upper cloud deck was broken. Shortly before midnight a low level overcast reappeared and light rain showers began. The after-frontal rain was confined to a band about 160 km long and 80 km wide. The showers lasted less than an hour, and the low overcast gave way to scattered clouds again. One of us (DB) heard great numbers of thrushes calling over Milwaukee (64 km south of Cedar Grove) immediately preceding the rain showers, indicating that many thrushes were flying at low altitudes at that time. Only a few thrushes were heard after the showers ended. We suggest that the local showers and low clouds caused some thrushes to end their flights prematurely before midnight while later birds, encountering no bad weather, ended their flights at Cedar Grove only after having flown greater distances. Two "grounded populations" resulted: one with relatively high weight, and one with low weight.

We propose that birds normally begin migratory flights only when conditions are propitious for flight, fly a reasonably constant distance, and arrive in an area at relatively low and uniform weight. Adverse local weather conditions occasionally act as a barrier to the flow of migrants, causing some birds to end their flights prematurely, yielding a grounded population with relatively high and variable weight. This hypothesis is reasonably consonant with the data as presented in Table 13, but let us look at weather-weight relationships in greater detail.

Analysis of weather maps seemed to indicate that wind direction and cloudiness might be important in determining the weight and fat levels of thrushes arriving at Cedar Grove. Accordingly, the hourly surface wind and sky cover recordings from the U. S. Weather Bureau at Milwaukee, Wisconsin, some 71 km south of Cedar Grove, were examined for the hours of 1800 through 0500 of the night preceding each wave day. The northerly component of each hourly wind record was calculated and the mean northerly component for the entire night was compared with the thrush data (Table 14).

TABLE 14. WEIGHT, FAT, AND NORTHERLY COMPONENT OF THE WIND*

Northerly component of wind (km/h)	No. of birds	Mean weight	Variance	Mean fat
+8 to +18	206	29.95	6.70	1.18
(adjusted)	152	30.33	4.96	1.31
0 to +8	161	29.78	5.60	0.95
0 to −8	650	29.61	5.06	1.16
−8 to −16	144	30.39	5.58	1.23
−16 to −23	168	31.51	6.85	1.48

*A mean of the 1800-0500 hr. surface recordings of the previous night for Milwaukee, Wisconsin.

September 23, 1961, again exerts peculiar influence on the data. Deletion of the data of this date reduces the variance of the "+8 to +18 km/h" northerly wind component group to 4.96 and increases the mean weight to 30.33 g. With this correction, all the mean weights given in Table 14 differ significantly from each other except for the "0 to −8" and "0 to +8 km/h" combinations. The variance in weight for the "−16 to −23 km/h" data group differs significantly from that of the "0 to −8" and "+8 to +18 km/h" groups.

Thus, southerly or head winds yield grounded migrants with relatively high weights and variance in weight. Light winds yield grounded migrants with low weights and low variance in weight. It would be inefficient for a bird to continue migration into an appreciable head wind. Hassler *et al.* (1963) have presented evidence from radar observations which suggests that migrants respond quickly to a head wind by ceasing migration. The higher weights and reduced variance of migrants grounded following nights of moderate to strong northerly winds could be explained by assuming that less energy is required to fly in a tail wind. If the distance covered per night's flight is reasonably constant, less energy would be required to fly during nights on which tail winds predominate.

The mean weight of thrushes caught after nights with less than 15 per cent cloud cover is significantly lower than those of birds caught after nights of partly or mostly cloudy skies (Table 15). Adjustment of the data, by the deletion of 23 September 1961, changes the mean weight of the birds taken after nights with greater than 85 per cent cloud cover to 30.84. The variance is reduced to 5.38. With this adjustment there remains no significant difference among the variances in Table 15. Sauer (1957) has presented evidence which indicates that migratory European warblers are disoriented under overcast skies. Disoriented birds might end migratory flight prematurely, resulting in higher mean weights and greater variance in weight in grounded migrants. The data thus seem to support the idea that the primary influence of weather on thrush weights is in the local conditions permitting or halting migratory flight.

TABLE 15. WEIGHT, FAT, AND SKY COVER*

Mean nocturnal sky cover	No. of birds	Mean weight	Variance	Mean fat
≥85%	379	30.56	6.27	1.29
(adjusted)	325	30.84	5.38	1.37
16-84%	304	30.69	5.77	1.29
≤15%	646	29.73	5.27	1.09

*A mean of the 1800-0500 hr. recordings of the previous night for Milwaukee, Wisconsin.

If we assume that the birds arriving on each wave date had identical mean departure weights and fat levels, we can estimate the differences in flight time between birds which ended flight prematurely and those that continued flight until the "normal" landing time. Approximately ten hours of darkness (flying time) would be available to the birds during September when the observations were made. Nisbet *et al.* (1963) estimate the in-flight energy consumption of small passerines at 0.076 kcal/g total weight/hr and the caloric value of fat as 9.5 kcal/g. Two estimates of maximum difference in flight time are possible: one based on differences in mean weight and one based on differences in mean fat estimate. The difference in estimated flight time for birds of the "Low pressure" weather group from that of the "Cyclonic flow" weather group (Table 13) is 8.8 hours if based on weight differences and 5.7 hours if based on subcutaneous fat estimates. The difference in estimated flight time between birds flying on nights with a weak northerly or southerly component (less than 8 km/h) and that of birds flying on nights with a strong southerly component (16-23 km/h) is 7.9 hours if based on differences in mean weight and 3.8 hours if based on visual fat estimates (see Table 14). Birds flying on nights with largely clear skies (Table 15) flew an estimated 4.6 hours (based on weight) or 2.1 hours (based on visual fat estimates) longer than birds flying on nights with mostly overcast skies. The above estimates of differences in flight time based on differences in mean weight appear extreme while those based on estimates of subcutaneous fat seem reasonable, especially in view of the original assumptions.

The differences in estimated flight time between the birds which presumably ended their flight prematurely on the night of 22-23 September 1961 and that of the birds which were taken after continued flight is 26.2 hours if based on weight differences and 9.1 hours if based on estimates of subcutaneous fat. These estimated differences in flight time are incredible and are probably the result of small sample size.

Alternatively we can assume that the birds over the area at a given hour of the night come from a population which differs in departure weight from that of the population over the area at another hour of the night. This approach would fit the data nicely, voiding the speculations on differences in flight time and eliminating the need for explanation of some of the extreme estimates of flight time. If, on the other hand, the mean departure weights are uniform for all wave nights but the departure times vary, considerable bias would enter into estimates of differences in flight time.

Although we do not know from where the thrushes taken on wave dates departed on the previous night, we can determine the weather conditions at the point of departure with some certainty because similar weather conditions ordinarily extend over great areas. All of the thrushes taken on wave dates appear to have started migratory flight in a high pressure cell some distance behind the cold front. The speed and direction of movement of high pressure cells exhibit some degree of variability. Swainson's Thrushes migrate only by night. The timing of the inception of flight must be difficult. An early departure might result in the bird catching up with the front, a delayed departure might involve flying into the head winds prevailing on the trailing edge of the high pressure cell. If the timing of the passage of a given high pressure cell is unfavorable, the bird could wait several days for another, but passage cannot be delayed for long.

As a working hypothesis, it would seem reasonable to assume that Swainson's Thrushes begin migratory flight as soon as flight conditions become favorable after the passage of a cold front. About half of the time this results in the birds migrating largely through the center of a high pressure cell, about one-sixth of the time they migrate largely in the leading edge of the high pressure cell, and one-twelfth of the birds move in strong cyclonic flow (Table 13). "Mistakes" in timing of inception of flight occur frequently, for almost one-fourth of the birds catch up with and cross the front into a head wind (Table 13). Unusual circumstances occur occasionally to produce unfavorable flight conditions in the birds' path (Low pressure, Table 13).

The stimulus for the inception of a migratory flight is probably a summation of external factors (weather) and the internal state of the bird. If we assume that body weight or subcutaneous fat is an index of the internal disposition to migrate, an alternate hypothesis of weather-weight relationships is possible. Birds heavy in weight or fat might be disposed to fly under less than optimal weather conditions whereas relatively lean birds would migrate only on the best of conditions. The data of Tables 13, 14, and 15 are reasonably consonant with this hypothesis with the following notable exceptions: (1) the frequency distribution of wave influxes suggests that "High pressure" (Table 13) offers the best conditions for flight, yet "After front" and "Cyclonic flow" weather conditions yield lower thrush weights. (2) the "Across front" (Table 13) birds differ significantly in weight from the "After front" birds, yet it is impossible for us to conceive how the birds could differentiate between the two situations at the point of departure. The bimodal distribution of thrush weights on 23 September 1961 would also be difficult to explain by recourse to this hypothesis.

In 1959-60 more waves occurred following synoptic situations associated with high weight and fat. More 1961-62 waves occurred following synoptic situations associated with low weight and fat (Table 13). The major differences in thrush migration between 1959-60 and 1961-62 appear to be attributable to differences in weather patterns associated with wave influxes of thrushes. Since thrushes which remained in the area were lighter in weight and fat than those which left (Table 7), it is not surprising that the median length of stay was shorter in 1959-60 when the arriving birds were heavier (Figure 4). A lower recapture percentage (Tables 2 and 3), increased emigration soon after arrival (Tables 11 and 12), and a decrease in mean weight of thrushes for the two days following a wave (Figure 4) in 1959-60 can all be attributed to the fact that the weather conditions on the nights preceding waves were such that higher thrush weights prevailed on wave dates. In short, it would appear that local weather conditions which act to halt (or permit continuance of) migratory flight are possibly of the greatest importance in determining the weights and fat levels of newly immigrant thrushes. The length of time thrushes remain in an area and other related aspects of behavior appear to be at least partly dependent on weight and fat levels of the thrushes upon arrival in the area.

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SUMMARY

This paper presents a series of analyses based on field determinations of weight and fat of a long distance, nocturnal migrant. The data are derived from 5,580 handlings of 4,328 Swainson's Thrushes taken in a standardized mist-netting scheme in the autumns of 1959 through 1962 at the Cedar Grove Ornithological Station in southeastern Wisconsin. More thrushes were taken in 1961 and 1962 than in 1959 and 1960, and the recapture percentage was also higher in 1961-62. The percentage and temporal distribution of recaptures differs from similar studies on other species (Table 3). Recaptured thrushes showed a decline in weight and fat on the day after banding (Table 4, Figure 2). This decline was attributed to the effects of handling the bird. Birds handled several times remained at lower levels of weight and fat for several days (Table 5).

The diurnal gain, and overnight loss, in weight and fat were estimated in several ways. The mean net fat deposition for Swainson's Thrushes was estimated to be about 0.34 g of fat per day. This

rate of fat deposition appears to be adequate to permit Swainson's Thrushes to migrate to the winter range in the time available for the trip. The initial weights of the birds that were subsequently recaptured were lower than those of birds that were not recaptured (Tables 7 and 8). There was no consistent temporal variation in weight through the course of an autumn. Thrushes arriving in marked influxes or "waves" were relatively low in weight on arrival in 1961-62, and the transient population showed daily net increase in weight for several days following a wave influx. The opposite was true in 1959-60 (Figure 4).

A transient population model was constructed from the data of recaptures and wave influxes. The model suggests that thrushes remain in the area for only a few days (Table 12). No correlation was found between local food supplies and levels of thrush transient populations or the mean weight of these populations. Analysis of weather and wave influxes of thrushes suggests that the weight of recent arrivals is correlated with local weather conditions which act to permit or halt the flow of migrants over the area (Tables 13, 14, and 15).

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