BIRD-BANDING

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WEIGHT-LOSS DURING MIGRATION

PART I: DEPOSITION AND CONSUMPTION OF FAT BY THE BLACKPOLL WARBLER *Dendroica striata.*

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Drury and Keith (1962) have given circumstantial evidence that large numbers of wood warblers (Parulidae) migrate in autumn from New England and Nova Scotia directly across the western North Atlantic to the West Indies, a non-stop flight of at least 1,600 miles. Their evidence was of four kinds:

1. Radar observations have shown large numbers of birds, whose echoes are of the type and speed characteristic of small passerines, moving southwards out to sea in September and October. These southward movements are additional to movements southwest: indeed the two types of movement often take place simultaneously.

2. About 13 species of wood warblers occur in autumn and winter in the Lesser Antilles, an area difficult for them to reach from the southeastern U. S. A. because of the strong prevailing winds (Northeast Trades).

3. The same 13 species of wood warblers occur commonly in autumn on Bermuda.

4. Blackpoll Warblers (*Dendroica striata*) are still extremely fat when they arrive at the Bermuda lighthouse (observation by D. B. Wingate).

One of the most important problems raised by these observations is whether the birds' reserves of energy are sufficient for the long flight which is hypothesized. The usual flight-speed of a small bird is 20-25 knots, so that even in normal weather conditions a warbler would take some 60-70 hours to fly from New England to the West Indies, and it would take considerably longer if it were to meet unfavorable winds. Before it can be definitely concluded that the southward movements observed by radar reflect a successful over-water migration, it must be shown that the birds involved consume

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energy sufficiently slowly to fly non-stop for at least 70 hours. In a preliminary discussion of this problem, Drury and Keith (1962) showed that many warblers became extremely fat before leaving New England, but that the rate at which they consume their fat must nevertheless be less than that predicted by current theories, if they are to fly for even 60 hours.

In September and October 1962 we attempted to measure the rate at which warblers consume fat, by catching and weighing them in New England and in Bermuda. The Blackpoll Warbler was chosen for special attention because of its abundance, and its extreme fatness, in both places. Netting stations were established inland in Massachusetts, because it is known that migrants observed on the New England coast are in some ways abnormal (Baird and Nisbet 1960), but weights obtained on the coast in earlier years are also discussed. Radar was used to observe nocturnal departures from the region, and to relate them to the ground observations.

Part I of this paper describes our observations of Blackpoll Warblers, and sets out an estimate of their rate of weight-loss during migration. Part II compares this estimate with published estimates of the rate of weight-loss in other species, and with physiological and aerodynamic theories of flight.

Range of the Blackpoll Warbler

The breeding range of the Blackpoll Warbler extends from Alaska across Canada to the Atlantic coast, where it breeds north to northern Labrador and south to Newfoundland, Nova Scotia and the mountains of northern New England. It winters in northern South America, west to eastern Ecuador and northeastern Peru, and east to Venezuela and French Guiana (A. O. U. Check-List, 1957). On autumn migration it is abundant in the Atlantic coastal region from Nova Scotia at least as far south as Virginia, and has been recorded in numbers as far south as Florida, but it is rare on the coast of the Gulf of Mexico. Birds which breed east of Hudson Bay have to fly no more than 1,000 miles to reach the New England coast, scarcely one-third of the distance to their winter-quarters; for birds from Alaska, however, the Atlantic coast is nearly two-thirds of the way to the winter quarters.

Other species

During our field-work in 1962 we observed and weighed many other species of wood warblers, but none of them showed all the peculiar features which we found in the migration of the Blackpoll Warbler. Although the evidence quoted by Drury and Keith (1962) suggests that some other species make long flights over the western North Atlantic, our observations in 1962 suggest that none of them makes such a long flight, or migrates so far east, as the Blackpoll Warbler. Hence we have reserved discussion of these species until more evidence is collected, and in Part I we have confined our attention to the Blackpoll Warbler. Unless otherwise stated, all references to "birds" in Part I refer to that species.

METHODS

Netting, weighing and measuring

Birds were caught in Japanese mist-nets of ½-inch mesh specially designed for wood warblers. The nets were cleared about once per hour, and the birds were transferred to multiple holding-cages. On average, the birds were detained for about 1½ hours after striking the nets until they were weighed; most of them defecated at least once during this period. The birds were weighed on a spring balance purchased from the British Trust for Ornithology: this was accurate to within 0.1 gm. and was calibrated at intervals during the season. Netting was stopped in wet weather.

Wing-lengths of birds caught in Massachusetts were measured with the wing flattened. Wings of birds caught by Baird in Bermuda and in Rhode Island, however, were measured unflattened, and 1½ mm. have been added to his measurements for the few occasions when they are compared with these from Massachusetts.

Visible deposits of subcutaneous fat were assessed on an arbitrary scale, from 0 to 4, as defined by Helms and Drury (1960: Table IV). The weights of birds in different fat-classes overlap considerably (Table 1), so these data have not been used in this paper, except to group the data for analysis of weight and wing-length (Tables 1 and 2).

Age criteria

The age of the birds was determined by two methods:

1. The technique described by Baird in Norris (1961). The feathers on the side of the crown are moistened and separated, and the skull is examined through the skin under bright light, preferably with a hand-lens. In adult birds the secondary ossification of the skull shows through the skin as a speckling of white dots on a whitish ground. In immature birds at least part of the skull is unossified, appearing pale pink without white speckling.

2. A modification of a European technique, suggested by F. Vuilleumier. In immature birds the dark sooty secondary greater coverts and alula contrast with the brownish primary coverts; in adult birds the primary coverts are sooty also.

In a few cases where these two methods disagreed, method (2) was discarded. Hence a few precocious immature birds in which the unossified area was confined to the fore-part of the skull may have been recorded as "adults". It is unlikely that any appreciable number of adults were recorded as "immatures".

According to these criteria, 61 percent of the 1,832* birds examined at our main netting-station at Round Hill, Massachusetts, in 1962 were identified as adults, and 39 percent as immatures. At our other inland netting-station, Drumlin Farm, adults comprised 64 percent of 54 birds caught in 1962, and 42 percent of 123 birds

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*Totals given at various places in this paper differ because some birds were not aged, some were not sexed, some were not measured and some were not weighed.

TABLE 1. WING-LENGTHS AND WEIGHTS OF BLACKPOLL WARBLERS CAUGHT IN MASSACHUSETTS, AUTUMN 1962

Sex and age group	Wing-lengths (mm.)	Weights (in grams) of birds of fat-class: 0	1	2	3	4
Adult "males"	**73.53 ± 0.10** R 66-81 S.d. 2.59 N = 671	**11.81 ± 0.09** R 9.9-14.0 S.d. 0.84 N = 90	**12.02 ± 0.07** R 10.4-14.8 S.d. 0.92 N = 193	**12.83 ± 0.07** R 10.4-15.7 S.d. 0.97 N = 182	**13.64 ± 0.12** R 10.4-16.0 S.d. 1.22 N = 109	**15.99 ± 0.22** R 12.3-21.0 S.d. 2.06 N = 86
Adult "females"	**71.58 ± 0.11** R 64-79 S.d 2.32 N = 450	**11.31 ± 0.11** R 9.6-13.0 S.d. 0.73 N = 47	**11.68 ± 0.07** R 9.6-14.2 S.d. 0.76 N = 118	**12.35 ± 0.07** R 10.2-15.2 S.d. 0.76 N = 134	**13.41 ± 0.13** R 11.0-17.7 S.d. 1.22 N = 92	**16.19 ± 0.27** R 11.8-21.1 S.d. 2.02 N = 58
Immature "males"	**71.52 ± 0.17** R 65-78 S.d 2.57 N = 233	**11.32 ± 0.10** R 9.8-13.3 S.d. 0.78 N = 64	**11.64 ± 0.11** R 9.8-14.7 S.d. 0.87 N = 64	**12.38 ± 0.12** R 10.7-14.7 S.d. 0.95 N = 60	**12.90 ± 0.19** R 10.9-15.0 S.d. 1.01 N = 29	**16.37 ± 0.53** R 13.5-19.0 S.d. 1.83 N = 12
Immature "females"	**70.70 ± 0.13** R 65-78 S.d. 2.92 N = 482	**11.20 ± 0.08** R 9.3-13.0 S.d. 0.75 N = 89	**11.54 ± 0.06** R 9.7-13.5 S.d. 0.79 N = 171	**12.04 ± 0.09** R 10.3-14.3 S.d. 0.95 N = 123	**12.96 ± 0.13** R 10.8-15.5 S.d. 1.04 N = 67	**15.12 ± 0.32** R 12.2-21.5 S.d. 1.68 N = 28

Notes. The figures given are the **mean** and **standard error**, the observed range (R), the standard deviation (S.d.) and the sample size (N).

caught in 1961. The proportion of adults inland in 1962 is surprisingly high, but since more immatures were caught in 1961, it is possible that there was a genuine shortage of immatures in 1962, reflecting a poor breeding season. There is also evidence that immatures greatly outnumber adults near the Atlantic coast. Among 55 birds examined by Baird during 1959-61 at Middletown and Block Island, Rhode Island, and Wellfleet, Massachusetts, only 18 percent were adults, and among 78 birds examined at Island Beach, New Jersey in 1962, only 19 percent were adults. However, the excess of immatures on the coast is much greater in other species (Baird's data, partly published in Drury and Keith 1962).

Sex criteria

The sex of the birds was determined by a method tentatively proposed by Baird, using the markings on the rump and upper tail-coverts. Birds identified as "males" had dark centers to most of these feathers, forming streaks which were wider and sharper than those on the lower back. Birds identified as "females" had unstreaked rumps, and no more than six blurred or hair-like streaks on the upper tail-coverts. Marginal birds, with eight to ten thin streaks scattered over the rump and upper tail-coverts, were recorded as "males".

Figure 1. Frequency distributions of wing-lengths among Blackpoll Warblers caught in Massachusetts in autumn 1962, grouped by age and sex. Wing-lengths were measured with the wing flattened.

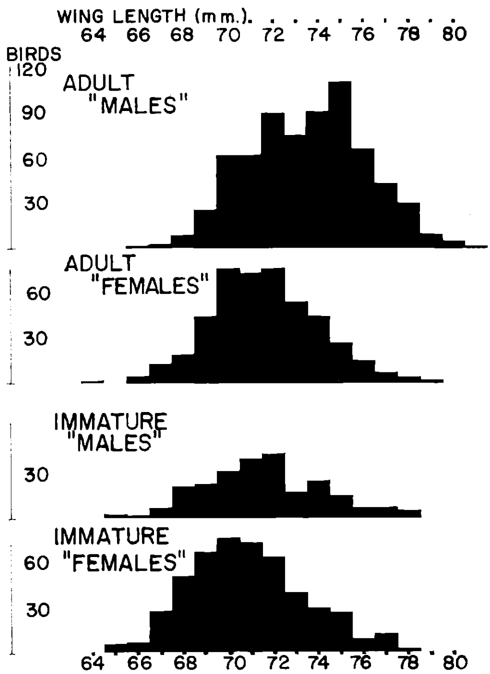


Table 1 shows that these criteria resulted in a disproportionately large number of birds identified as adult males, and a disproportionately small number of birds identified as immature males. Figure 1 shows that the frequency distribution of wing-lengths of "adult males" was noticeably bimodal, and that of "immature females" was skewed: both distributions suggest the presence of a discrete group of birds with wing-lengths grouped around 71-72 mm., in addition to the main groups centered about 74.5 mm. and 69.5 mm. respectively. Hence it seems likely that about 20 percent of the adult females were recorded as adult males, and about 20 percent of the immature males were recorded as immature females. If a correction based on this deduction is applied to the total figures, the sex ratio is about equal in both adults and immatures. Subsequent dissection of birds killed at television towers in autumn 1962 has confirmed that some adult females have the characters attributed above to males, and that some immature males have the characters attributed above to females.

Age- and sex-differences in size

Table 1 summarizes the wing-lengths and weights of 1,842 Blackpoll Warblers caught in 1962. The average wing-length of adults was about 1.4 mm. greater than that of immatures, and comparing birds of the same fat-class, the average weight of adults was about 0.4 gm. greater than that of immatures. It is difficult to compare the sizes of males and females, because there is evidence that about 10 percent of the birds were wrongly sexed (see previous paragraph). However, if approximate allowance is made for this, adult males were larger than adult females by about 2.3 mm. in wing-length and about 0.5 gm. in weight, and immature males were larger than immature females by about 1 mm. in wing-length and about 0.15 gm. in weight. Thus the size-difference between the sexes appears to have been larger in adults than in immatures.

Fat-free weights

Odum (*in litt.*) has supplied eight measurements of fat-free weights of Blackpoll Warblers, killed at a television tower in Michigan on 25 September 1961, and extracted by the method of Odum (1960). Four males (not aged) weighed between 11.45 and 12.57 gm. without fat; four females (not aged) weighed between 9.92 and 11.71 gm. without fat. The average fat-free weight was 11.21 and the standard deviation 0.94, which agrees reasonably well with our weights of birds of fat-class 0 (Table 1). In fact, we caught a number of immatures and even a few adults weighing less then 10 gm. (Figure 2), but these may have lost water, or have started to consume muscle tissue. Baird netted one emaciated (but active) adult on Bermuda whose weight was only 7.9 gm., and Voous (1953) reported birds arriving in the Lesser Antilles weighing only 8 to 9 gm. However, the minimum weights for Blackpoll Warblers in good condition are probably in the range 9.5-11.5 gm.

TABLE 2. VARIATION OF WEIGHT WITH WING-LENGTH IN THE BLACKPOLL WARBLER

	Wing-length (mm.)										
Age Group	67	68	69	70	71	72	73	74	75	76	77
Adults: Mean weight			11.47	11.52	11.47	11.74	11.85	12.00	12.26	12.31	12.38
Standard error			0.13	0.09	0.08	0.10	0.10	0.09	0.11	0.19	0.22
Immatures: Mean weight	11.12	11.28	11.35	11.38	11.54	11.55	11.52	11.64	12.00		
Standard error	0.13	0.12	0.12	0.10	0.09	0.11	0.13	0.14	0.18		

Notes. The figures used are based on a sample of 411 adults and 356 immatures, chosen so that in each age-group 33 percent of the birds were of fat-class 0 and 67 percent of fat-class 1. In order to obtain large enough samples, weights of males and females, and of fat-classes 0 and 1, have been lumped together, but this lumping was responsible for only about one-third of the variance of the lumped sample. Among samples of the same age, sex, wing-length and fat-class, the standard deviation of the weights was usually about 0.7-0.8.

Variation of weight with wing-length

Table 2 summarizes the average weights of 767 birds of fat-class 0 and 1, grouped according to wing-length. On average, the weight increased by 0.10 $\pm$ 0.024* gm. per mm. increase in wing-length. Since each group had, on average, about the same amount of fat, this increase probably reflects primarily the relation between fat-free weight and wing-length. Our figure of 0.10 is however much less than the figure of 0.30 gm. increase in fat-free weight per mm. increase in wing-length, quoted by Connell, Odum and Stoddard (1960) for "small and medium-sized birds", but Connell *et al.* did not in fact give any measurements of birds as small as the Blackpoll Warbler. Table 2 also shows that, among birds of the same fat-class and wing-length, adults were heavier by about 0.18 gm. than immatures, but this difference is barely significant statistically.

Age- and sex-differences in migration period

Table 3 summarizes the relative numbers of birds of the four age- and sex-classes during four periods in the autumn season of 1962. Except for a slight increase in the ratio of adult males to adult

TABLE 3. PERCENTAGE FREQUENCIES OF DIFFERENT AGE- AND SEX-CLASSES AMONG BLACKPOLL WARBLERS CAUGHT AT ROUND HILL, MASSACHUSETTS, DURING AUTUMN 1962.

	Date of first capture			
	3-11 Sept.	12-19 Sept.	20-28 Sept.	after 29 Sept.
Adult males	38%	31%	27%	30%
Adult females	15%	25%	19%	23%
Immature males	15%	13%	10%	10%
Immature females	17%	22%	21%	22%
Not examined or doubtful	15%	9%	10%	15%
Number of birds	294	707	665	359

females in the first week of observation, there was no evidence of significant changes in the proportions of the four classes during the period of observation.

Combination of observations

In this paper we use the weights of birds primarily as measures of the amount of fat they carry. The total weight of a bird, however, depends also on its fat-free weight, and Tables 1 and 2 show that this depends on its age, sex and wing-length, in addition to the expected individual variations. Since there is no evidence that the proportions of the sexes, or the average wing-length, changed significantly from day to day during the season, we have grouped

*Here and elsewhere in the paper the symbol $\pm$ is used to denote the standard error of the mean; standard deviations are referred to by name.

together weights of males and females, and of birds of different wing-lengths, whenever we compile averages. However, we often compare the weights of fat carried by immatures and by adults, and it is then necessary to take into account the average difference of about 0.4 gm. between the fat-free weights of adults and immatures. In order to facilitate such comparisons, we have added 0.2 gm. to each observed weight of an immature bird, and subtracted 0.2 gm. from each observed weight of an adult, before compiling averages. The effect of this modification is that the difference between the average weight of a group of adult birds and that of a group of immatures is (within the limitations of statistical variation) an estimate of the average difference in the weights of fat they carry. Unless otherwise stated, all weights quoted later in this paper have been modified in this way.

BIRDS CAUGHT IN NEW ENGLAND

Netting at Round Hill

Our main netting-site was at Round Hill, Sudbury, Massachusetts, which is an isolated, rounded hill rising about 100 feet above the valley of the Sudbury river, whose marshes almost surround it. The commonest trees on the hill, and in the adjoining lowlands, are White Pines (*Pinus strobus*) and oaks (*Quercus* spp.), but there is also an area of Gray Birches (*Betula populifolia*), about 20 feet high, on the west and north sides of the hill. Nets were set in, and on the edge of, the stand of birches. Nine nets were operated throughout the daylight hours (except for periods of rain) from 3 September through 14 October 1962, comprising a total of about 3,500 net-hours; altogether 2,025 Blackpoll Warblers were caught and banded. The average netting rate, over 500 birds per 1,000 net-hours, compares favorably with that for any species at coastal netting-stations (Baird *et al.* 1959). In fact, the Blackpoll Warbler was the commonest species on the hill until early October, when its place was taken by the Myrtle Warbler (*D. coronata*); at this time the birch leaves began to fall and the supply of insect food presumably declined.

Table 4 summarizes the results of trapping at Round Hill day by day through the autumn. The largest numbers of birds were caught between 15 September and 1 October. Between 4 and 25 September the birds' average weight remained almost constant at about 12 gm. each day. After 25 September the birds were much heavier, and the average weight fluctuated greatly from day to day. For reasons which will appear later, we interpret the first period as that in which the birds were arriving in this area from the north, and the second period as that in which they became fat and departed southwards.

Recaptures at Round Hill

Only 61 birds (less than 3 percent of the total) were caught twice in the same day, and only two were caught three times in the same day. If it were assumed that the population at Round Hill was

TABLE 4. NETTING OF BLACKPOLL WARBLERS AT ROUND HILL, MASSACHUSETTS, IN AUTUMN 1962

Date	Birds caught			Over 14.7 gm.		Mean weight (gm.)	Recaptures		Weather at 1800				
	Adult	Imm.	Total	Adult	Imm.		Same day	Other	Rain	Rel. Hum.	Temp.	Wind	
Sept. 3	2	0	3	0	0	10.52	0	0	0	70	65 °	E	8
4	9	5	14	0	0	11.33	1	0	0	73	65	ESE	10
5	14	10	24	0	0	12.51	0	0	T	84	62	ESE	11
6	7	3	10	3	0	12.97	0	0	.07	51	63	NW	13
7	33	14	47	1	0	11.88	1	1	0	55	70	WSW	7
8	24	11	35	0	0	11.96	3	1	0	38	73	SW	12
9	33	17	51	1	0	11.58	2	0	0	63	69	S	14
10	37	31	68	1	0	12.17	2	2	T	63	78	SW	14
11	34	25	59	1	0	12.15	0	4	0	74	72	WNW	17
12	4	10	14	0	0	12.46	0	0	0	55	71	N	11
13	31	34	65	2	0	12.26	0	1	0	76	69	ESE	11
14	23	28	52	2	2	12.31	0	3	.15	90	71	WSW	10
15	96	66	162	1	0	11.58	1	2	0	39	71	W	14
16	40	32	72	1	0	11.63	1	2	0	73	64	E	9
17	68	41	112	0	1	11.92	4	1	.38	84	64	SE	11
18	107	45	156	4	0	11.80	2	7	.01	35	68	WSW	12
19	77	33	110	6	0	12.39	1	11	.06	47	64	SW	13
20	72	50	136	1	0	11.73	4	13	T	36	52	NNW	13
21	23	20	43	0	1	11.99	0	5	0	38	54	WNW	12
22	18	20	48	0	1	12.18	2	3	0	55	58	SSE	4
23	73	55	140	4	0	12.19	5	6	0	71	56	ENE	12
24	88	59	158	8	3	12.29	8	19	T	43	58	WNW	10
25	79	52	136	2	3	12.21	4	15	.18	48	65	S	15
26	59	36	99	16	1	13.20	1	10	.03	78	64	E	6
27	....	....	....	No netting due to rain	....	....	....	....	2.37	100	53	NNE	26

	28	No netting due to rain								.84	100	59	SSE	10
	29	43	30	80†	28	17	14.96	2	24	.02	93	57	E	11
Sept.	30	115	64	194	53	12	14.03	9	45*	0	41	64	W	9
Oct.	1	53	36	96	11	3	12.76	3	15	0	50	63	NNW	8
	2	16	21	39	6	3	13.19	1	6	0	69	62	ESE	8
	3	8	14	22	3	1	13.25	2	1	0	53	70	SSW	11
	4	12	14	27	4	4	13.72	5	7	T	75	64	E	8
	5	No netting due to rain								1.93	96	56	NE	25
	6	No netting due to rain								3.00	93	58	NNE	15
	7	No netting due to rain								2.08	71	53	WNW	19
	8	9	3	13	9	2	16.92	0	4	0	67	62	ESE	8
	9	2	4	6	2	2	16.22	0	1	.03	96	51	NE	20
	10	No netting due to rain								.03	89	51	NNW	6
	11	2	1	3	2	1	17.69	0	2	T	60	61	SW	9
	12	1	1	2	1	1	18.74	0	1	.01	59	76	WSW	28
	13	2	0	2	0	0	12.09	0	0	0	41	54	WNW	16
	14	1	2	3	0	1	13.69	0	0	0	38	55	W	12

Notes. The columns headed "birds caught" give the total numbers of captures per day, including recaptures and a few birds not aged or not weighed. All weights have been slightly modified to eliminate differences in mean fat-free weight between adults and immatures (see text). The fifth and sixth columns give the numbers of birds heavier than 14.7 gm. The seventh column gives the mean weight of all the birds caught, including recaptures. The eighth and ninth columns give the number of recaptures, divided into same-day repeats and repeats from an earlier day. The tenth column gives the precipitation (in inches) during the 24 hours starting at 0000. "T" indicates an amount too small to measure. The last four columns give the weather observed at Boston at 1800—relative humidity in %, temperature in °F., wind direction, and wind-speed in knots.

Rain prevented netting on 27, 28 September, 5, 6, 7 and 10 October. †Netting in afternoon only. *Many birds caught on 29 September were removed from Round Hill.

stationary throughout each day, these figures would suggest that it consisted of several thousand birds on most days during September. However, many more birds were recaptured on days after those on which they were first caught, and some birds which stayed for two or three weeks were caught every three or four days. This suggests that only a small number of birds stayed in the netting-area for more than a few hours, and that most left soon after being caught.

Records of birds caught twice in the same day suggested that most of the birds which stayed at Round Hill did not gain weight rapidly. Among 32 birds first weighed in the morning (0700 to 1200 hours), 21 recaptured in the afternoon (1200 to 1600) had gained an average of 0.34 ± .14 gm., and 11 recaught in the evening (1600 to 2130) had gained an average of 0.48 ± .10 gm. Among 30 birds caught in the afternoon, 15 recaptured later in the same afternoon had lost 0.27 ± .15 gm., and 15 recaught in the evening had lost 0.38 ± .26 gm. These figures suggest that the birds usually gained weight in the mornings, reached peak weight around 1200 and lost weight in the afternoons. In fact, the birds seem to have been most active in the late mornings, for more were caught between 0900 and 1200 than earlier or later.

Table 5 summarizes the records of birds caught on two or more days. As shown in Table 4, only 7 percent of these recaptures took place before 18 September, so Table 5 reflects primarily the changes in weight of the birds which stayed on Round Hill after that date. Most of these birds lost weight during the first day after they were banded, and did not regain their original weight until the third day. This phenomenon of loss in weight immediately after migratory flights has been recorded for the Robin (*Erithacus rubecula*) by Davis (1962), while Browne and Browne (1956) reported only very small gains in weight in European warblers during the first day after banding. (Similar observations have been reported to us, informally,

TABLE 5.
CHANGES IN WEIGHT IN BLACKPOLL WARBLERS CAUGHT ON TWO OR MORE DAYS AT ROUND HILL, MASSACHUSETTS

Days after first capture	Number of records	Change in weight (grams)	
		Mean	Standard deviation
1	65	−0.40	0.88
2	30	−0.17	0.84
3	35	0.01	1.07
4	23	0.81	1.46
5	26	0.99	1.60
6	20	1.39	1.58
7	11	1.41	2.63
8–11	14	2.35	2.08
12–23	10	3.08	3.45

The change in weight is the increase or decrease which took place after the bird was *first* captured. If birds were caught three or more times, the change in weight between the second and subsequent captures has not been taken into account. However, if birds were caught or recaught twice in one day, both pairs of weights have been used: hence the total number of records used is greater than the total number of recaptures.

by several operators of banding stations, which suggests that it may be a general phenomenon.) After the third day the average weight of the recaptured birds increased steadily until the tenth day: this agrees with the figures in Table 4, which show that most of the birds at Round Hill gained weight in late September and early October. However, after the tenth day the changes in weight became more irregular, and some birds actually lost weight. Some specific examples of these weight changes are provided by the following:

> 33-20579, immature: weight 13.2 gm. on 15 September, 18.7 gm. on 2 October, 17.5 gm. on 8 October.
>
> 102-36408, immature: 11.4 gm. on 18 September, 12.5 on 21 September, 11.4 on 23 September, 12.1 on 24 September, 12.3 on 25 September, 16.1 on 29 September, 16.0 on 30 September.
>
> 102-36413, immature: 11.1 gm. on 18 September, 10.7 on 30 September, 12.5 on 3 October.
>
> 102-36488, immature: 10.5 gm. on 19 September, 9.8 on 20 September, 10.8 on 22 September, 11.6 on 24 September, 11.3 on 30 September.
>
> 103-75083, immature: 10.0 gm. on 20 September, 10.2 gm. later on 20 September, 10.2 on 23 September, 12.2 on 30 September.

In fact, on most days the birds recaptured were lighter than those caught for the first time, the average difference being about 0.5 gm. This is partly because immatures predominated in the recaptured sample. Although immatures comprised only 40 percent of the total catch, they included 50 percent of the birds recaptured, and 67 percent of the birds recaptured after seven or more days. Table 4 shows that proportionately fewer immatures than adults weighing over 14.7 gm. were caught at Round Hill, that immatures became fat later than adults, and that proportionately more immatures remained after the last major exodus on 1 October.

All these facts suggest that Round Hill was not a good place for Blackpoll Warblers, at least in the period after 18 September when most of the recaptures took place. Most of the birds trapped there appear to have stayed for only a few hours, and the birds which did stay there for days or weeks (including a disproportionate number of immatures) did not become fat as quickly as those which moved through from other areas. It is therefore surprising that we were able to catch such a large number there. The most plausible explanation of its attractiveness is that it acts as a focal point for arriving and dispersing migrants, perhaps because of its position as an isolated eminence surrounded by marshes.

Daytime movements

We did not watch systematically for visible migration at Round Hill in 1962, but on 18 September 1961 Baird saw many warblers flying northeast over the hill, and others flying up from the trees and departing northeastwards against a light northeast wind; out of 134 warblers seen moving, all those identified were Blackpolls. Other observations of daytime movements of Blackpoll Warblers in September in New England mention the following flight directions: northeast at Hartford, Connecticut (Bagg 1950); north and northeast at New Haven, Connecticut (Bishop 1905); north in the White Mountains, New Hampshire (Allen 1903); north and northwest at Martha's Vineyard, Massachusetts (Bagg and Emery 1961); west-northwest at Nantucket, Massachusetts (Dennis and Whittles 1955); southwest at Belmont, Massachustts (C. S. Robbins *in litt.*). Although none of these movements was directed towards the Atlantic Ocean, collectively they differ considerably from daytime movements of other nocturnal migrants in this region which, according to records listed by Baird and Nisbet (1960*), are oriented much more consistently between west and north. Probably the function of the daytime movements of the Blackpoll Warbler is to disperse the birds after their arrival in New England and to enable them to find good feeding-areas.

Arrivals at Round Hill

During the period 4-25 September, the average weight of the birds caught at Round Hill varied little from day to day (Table 3). The only changes that were statistically significant were the decreases from 14 to 15 September and from 19 to 20 September. These two decreases, and similar decreases noted on 7 and 13 September, coincided with increases in the netting-rate, which suggests that they reflected fresh arrivals of light migrants. All four of these arrivals followed the passage of cold fronts through the area, either during the night (15 and 20 September) or during the previous day (7 and 13 September). The weather data listed in Table 3 show that behind these fronts the wind directions varied between west and north; in only one of the four cases was there a marked fall in temperature, but in all four cases there was a marked drop in relative humidity. In New England, the last change is probably the most reliable indication of the passage of a cold front.

Netting at Drumlin Farm

Drumlin Farm, South Lincoln, Massachusetts, is an area of mixed woodland and open fields on the low ridge between the Sudbury and Charles river drainage systems. It is three miles northeast of Round Hill, about 35 miles west of the east coast of Massachusetts and about 65 miles north of the south coast of New England. Mist-nets were set in a small vale lying between an area of Red Pine (*Pinus resinosa*) plantations and a Red Maple (*Acer rubrum*) swamp with mixed oak woodland on ridges. The netting area, kept damp by an artificial spring, has grown up with Willows, Barberry, Siberian Privet, *Euonymus*, *Spiraea* and brier patches, and is surrounded by tall trees (up to 80 feet high).

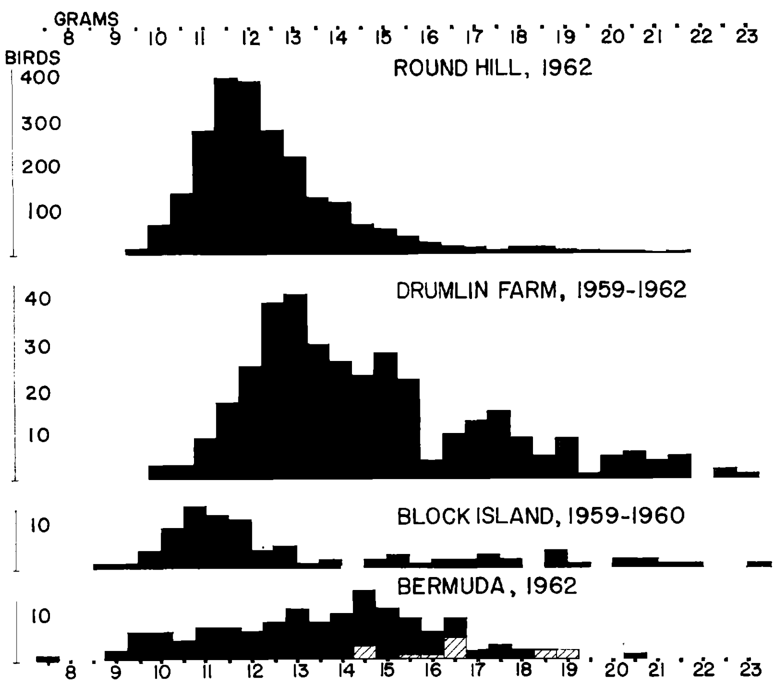
*Most of the exceptions mentioned in Baird and Nisbet's list in fact referred either to the Blackpoll Warbler or to unidentified warblers.

Up to eight mist-nets were set on most days in the periods 15 September-15 October 1959, 14 September-13 October 1960, 16 September-13 October 1961 and 22 September-13 October 1962. In a total of 5,000 net-hours, 335 Blackpoll Warblers were caught (including repeats). The average rate of trapping was thus only about one-tenth of that at Round Hill in 1962, but this is partly because the birds at Round Hill were concentrated in low trees. The Blackpoll Warbler is an abundant autumn migrant throughout the coastal region of New England, and those caught at Drumlin Farm are probably typical of those throughout many thousands of square miles.

Weights at Drumlin Farm

Figure 2b summarizes the weights of the birds trapped at Drumlin Farm in the four years 1959-62. Comparison with Figure 2a, which gives a similar summary of the weights at Round Hill in 1962, shows two major differences:

Figure 2. Frequency distributions of weights among Blackpoll Warblers caught in September and October at four different places: (a) Round Hill, Sudbury, Massachusetts, 1962; (b) Drumlin Farm, S. Lincoln, Massachusetts, 1959-1962; (c) Block Island, Rhode Island, 1959-1960; (d) Bermuda, 1962. The weights of the birds caught at the Bermuda lighthouse on 3 October 1962 are hatched. Note that the vertical scale for Round Hill is ten times smaller than that for the other three places.



1. The main group of light birds at Drumlin Farm, grouped around 13.2 gm., is significantly heavier than that at Round Hill, grouped around 11.9 gm. This suggests that the light birds at Round Hill consisted mainly of new arrivals which quickly dispersed into surrounding areas more suitable for intensive feeding.

2. The long "tails" on the histograms show that heavy birds (over 16 gm.) were numerically much more important (26 percent of the total catch) at Drumlin Farm than at Round Hill (4 percent of the total catch); most of these heavy birds were trapped after 25 September. This suggests that in suitable areas (such as Drumlin Farm), Blackpoll Warblers remain until the end of September, when they become very fat.

In at least two years (1959 and 1961) the records of heavy birds at Drumlin Farm fell into two well-marked groups—roughly 16.1-19.1 and 19.9-23.1 gm.; in 1960 and 1962 the patterns were similar, but too few birds were trapped for definite conclusions. We suggest the hypothesis that 19.9-23.1 gm. is the range of weights within which the Blackpoll Warbler usually departs southwards. Assuming that all the birds reach this range of weights before departure, and that the heavy birds are not markedly different in activity from the light birds, the Drumlin Farm records suggest that, on average, the birds spend about 18 days in the 11-15 gm. range, four or five days in the 16-19 gm. range, and only one or two days in the 20-23 gm. range.

Departures from Round Hill

Before 26 September: Since there was evidence for continuous local movements of Blackpoll Warblers to and from Round Hill throughout September, it was difficult to detect departures of heavy birds on long-distance migration. The only evidence for such departures before 26 September was obtained on the nights of 19/20 and 24/25 September, when there were decreases in the numbers of heavy birds trapped, and on 20/21 September, when there was a decrease in the rate of recaptures. However, these departures seem to have been small.

After 26 September: As noted above, the main period of departures (26 September onwards) was characterized by large day-to-day fluctuations in the average weights of the birds caught at Round Hill. Table 3 shows that during this period recaptures comprised 23 percent of the total catch, whereas before 24 September the proportion of recaptures was only 6 percent. This suggests that the local movements which took place during the arrival period largely stopped about 25 September; this supports the idea that their function is to enable the birds to find suitable places in which to become fat at the end of September.

27-29 September: Steady rain prevented netting on 27 and 28 September and on the morning of the 29th. When netting was resumed in the afternoon of the 29th, it was evident that many birds had stayed at Round Hill during the storm and had gained much

TABLE 6. NUMBERS OF BLACKPOLL WARBLERS OF VARIOUS WEIGHTS TRAPPED AT ROUND HILL, MASSACHUSETTS, 29 SEPTEMBER TO 3 OCTOBER 1962.

	Weight (grams)													
Date	9-9.9	10-10.9	11-11.9	12-12.9	13-13.9	14-14.9	15-15.9	16-16.9	17-17.9	18 18.9	19-19.9	20-20.9	21-21.9	TOTAL
29 Sept	1	0	4	11	9	21	13	6	6	4	3	1	1	79
30 Sept	0	7	25	35	40	26	23	15	10	11	1	1	0	194
1 Oct	2	9	28	24	12	9	4	3	2	3	0	0	0	96
2 Oct	0	0	14	8	6	4	5	0	0	2	0	0	0	39
3 Oct	0	0	6	7	2	3	2	1	1	0	0	0	0	22

Both recaptured and newly banded birds are included in this table. The figures illustrate: (1) the progressive departure of the heavier birds on the nights of 30 September/1 October, 1/2 and probably 2/3 October, coinciding with southward departures seen by radar; (2) the progressive loss of weight by the remaining birds from 29 September through 2 October, confirmed by records of recaptures. On 29 September nets were set in the afternoon only.

weight: the recapture rate was over 30 percent, the average weight was 2.14 gm. higher than that on the 26th, 45 birds weighed over 14.7 gm. and two weighed over 20 gm. Six birds were weighed on both the 26th and the 29th: three lost a little weight, but the other three put on an average of 2.3 gm. Many other birds recaptured on the 29th or 30th had put on substantial amounts of fat about this time: the largest individual gain recorded was 3.8 gm. between the 25th and 29th.

29-30 September: On 30 September 140 birds were banded and 54 recaptured. This was the largest catch of the season, which suggests the possibility of an arrival of fresh migrants, but the recapture data suggest that any such arrival must have been small. The proportion of recaptures was unusually high, and would doubtless have been higher but for the fact that 45 of the 78 birds caught on the 29th were taken to Drumlin Farm for measurement of their overnight weight-loss (see below). Seven of the remaining 33 birds, however, were recaptured on the 30th and all had lost weight: the average loss was 0.96 gm., almost exactly the same as the overnight decrease in the average weight of all the birds trapped (Table 4). Table 6 shows that the frequency distribution of observed weights on the 30th was very similar to that on the 29th, shifted down by one gram. This suggests that few, if any, birds departed on the evening of the 29th—perhaps because low cloud and drizzle did not clear until midnight. The loss of 0.96 gm. in an average interval of 17 hours is very similar to the average loss of 0.062 gm./hour observed in the birds kept overnight (see below); this suggests that the birds fed very little in the afternoon of the 29th or the morning of the 30th.

1-3 October: The evening of 30 September was dry and clear for the first time since 24 September, and next day the trapping-rate and recapture-rate were down by more than 50 percent, indicating a large-scale departure. Thirteen birds caught on both 30 September and 1 October lost, on average, 0.32 gm. If it is assumed that all the birds which stayed at Round Hill lost about as much weight as this, the figures in Table 5 suggest that most of those which left weighed between 13.5 and 19 gm.

The trapping- and recapture-rates decreased further on 2 and 3 October, indicating continuing departures, but Table 6 shows that the trapping-rate decreased as much for light birds as for heavy birds. It is unlikely that birds weighing only 10-12 gm. would set out on long-distance migration, so it is possible that many birds merely moved from Round Hill to more favorable feeding-areas nearby. The few recaptures on 2 October showed further losses in weight, which again emphasizes the poor food supply in the birches in which the birds were caught.

5-8 October: The period from 5 to 8 October was similar to that from 27 to 29 September. Continuous heavy rain preventing netting on 5, 6 and 7 October, and on the 8th the recapture-rate was high and the average weight was 3.2 gm. higher than that on the 4th. Next day only five birds were banded and only one recaptured, which suggests an overnight departure, but too few birds were caught for further analysis. Most of the birds caught on and after the 8th were very heavy (16.5-21.5 gm.), as were all the birds caught at Drumlin Farm at the same period.

Two points may be emphasized in conclusion:

1. Although a few birds attained weights of around 21 gm. (which we suggested earlier to be the normal departure weight of the species) at the very end of the season, most left Round Hill at much lower weights. It is not known whether these birds actually set out on long-distance migration, but there is circumstantial evidence that some did so, at least on 30 September. It is likely that even at Drumlin Farm some immatures left at weights below 19 gm., since immatures comprised 40 percent of the birds trapped in the 16-19 gm. range, but only 25 percent of those in the 20-23 gm. range; however, this could merely mean that the immatures spent less time than the adults in the latter range before they departed.

2. The only two periods in which the birds at Round Hill gained weight rapidly were during rainstorms: then many birds were able to increase their weight by more than 0.8 gm. per day, even though most birds appear to have lost weight on the intervening dry days. Evidently rainstorms provide good conditions for the birds to deposit fat quickly; water itself probably accounts for only a little of the weight change. It is possible that rain, or some other factor connected with the storm, actually stimulates the birds to overeat, so that they are ready to depart as soon as the storm clears; this would have selective advantage, because the passage of storms is usually followed immediately by a flow of polar air from the northwest, which favors southward migration. However, in other years large departures of Blackpoll Warblers have taken place during dry periods.

Southwestward departures?

So far we have assumed that most of the birds we trapped eventually took part in the southward over-sea migration observed by radar. The evidence for this assumption is as follows:

1. During 3-20 September, a period when arrivals of light birds were detected at Round Hill in 1962, trapping at Drumlin Farm in 1959-62 has shown a progressive increase in the local population, the peak being reached in each year at the end of September, the period when large departures started in 1962.

2. Recaptures in 1962 show that at least some birds stay in Massachusetts for two or three weeks, and their increase in weight parallels the progressive increase during September in the average weight of all the birds caught.

3. Departures from Round Hill in 1962 coincided with southward departures observed by radar, but not with southwestward movements (see below).

None of this evidence, however, precludes the possibility that some of the Blackpoll Warblers observed in Massachusetts (e.g. some of the light birds caught early in September) later migrated southwest to areas farther down the Atlantic coast, as was assumed by Cooke (1915) and later writers. It is perhaps unlikely that two overlapping populations of this species should differ so much in their migratory behavior, but it is difficult to disprove this possibility.

Birds killed at a television tower

We have 13 weights of birds killed at a television tower in Needham, Massachusetts, collected by Baird and A. M. Bagg. Nine of these (7 adults, 2 immatures) were killed in September: seven on 20 September 1958, one on 27 September 1958 and one on 25 September 1959. The average weight of these birds was 12.3 $\pm$ 0.45 gm., which agrees with the weights of the birds arriving at Round Hill (Table 4), and confirms that arrivals of light birds in New England continue until late September. Of four birds killed in October, two on 3 October 1959 weighed 13.4 and 14.6 gm.: these were heavier than the earlier arrivals, but seem much too light for birds departing on long-distance migration. An immature killed on 3 October 1959 weighed 23.1 gm. (wing 73.5 mm.), and an adult killed on 8 October 1961 weighed 20.0 gm. (wing 77.0 mm.): these weights are within the range which we suggested was normal for departing birds.

General picture of migration in Massachusetts

The above observations suggest the following picture of the migration of the Blackpoll Warbler in Massachusetts. Most birds arrive from the north behind cold fronts between 3 and 20 September, weighing 10-13 gm. During the first few days they disperse, sometimes concentrating briefly at striking landmarks such as Round Hill, but soon settling in better feeding-grounds in forested areas, where they quickly increase their weight to 11-15 gm. After 10-20 days (i.e., in the last week of September) their weight increases to 16-19 gm., where it stays for a few days, then rapidly increases (often during rainstorms) to 20-23 gm.; the birds leave on the first cool dry evening after reaching the latter range of weights. Some birds, however (especially immatures), settle in unsuitable areas such as Round Hill, put on weight more slowly and may depart weighing only 13.5-19.5 gm.

Massachusetts as a fattening-area

Our observations thus suggest that one population of Blackpoll Warblers interrupts its migration for three to four weeks in the coastal region of New England, specifically for the purpose of putting on fat for a long non-stop flight. This "fat-stop" is not merely an interruption in the birds' migration, but probably also involves changes in their migratory behavior. For example, many of the birds must breed within 600 miles of New England, and since they arrive there with very little fat they must put on much less fat for their flight to New England than for their subsequent departure. Similar "fat-stops" are well-known among migratory waterfowl and shorebirds, but they have rarely been reported for passerines. However, it seems likely that more will be recognised now that it is becoming known that many passerines make very long flights as part of their normal migration (e. g. Moreau 1961).

Birds caught at Block Island, Rhode Island

Figure 2c summarizes the weights of 91 Blackpoll Warblers caught by Baird and Mr. and Mrs. S. S. Dickerson on Block Island, eight miles south of the mainland of New England, in the periods 21 September-12 October 1959 and 29 September-19 October 1960. They resemble the Massachusetts records in falling into two distinct groups, a light group (63 birds under 13.7 gm., unmodified weights) and a heavy group (28 birds over 14.5 gm., unmodified weights). Only about half the birds were aged by the banders, but the average wing-length of the light group was 1.3 mm. shorter than that of the heavy group, and the observations suggest that the heavy group consisted of adults and immatures in roughly equal numbers, while the light group consisted almost entirely of immatures. The average weight of the light group was slightly lower in 1960 (11.12 gm.) than in 1959 (11.60 gm.): both these figures are less than the average weight of any group trapped in Massachusetts, and both are close to the average fat-free weight of the species.

The weight-records from the heavy group fall into two clearly-marked subgroups, with a division about 19.0 gm., agreeing with the data from Massachusetts. The average weight of the nine birds in the heaviest subgroup was about 20.7, very close to that of the heaviest group at Drumlin Farm. In 1959 all the seven birds from this sub-group were trapped during a period of rain from 9-11 October; one of the two birds in 1960 was an adult killed at the lighthouse on 29 September (wing 76 mm.; weight 20.7 gm. after 1-2 hours' flying).

We interpret these results to show that most of the heavy birds which depart from inland Massachusetts do not stop at the coast, although they migrate directly across it (Drury and Keith 1962) and may stop if their migration is interrupted (e. g. by a lighthouse). The records of 9-11 October 1959, and similar records obtained by Baird at Middletown, Rhode Island, suggest that a few birds become fat in the coastal area before departing on long-distance migration. The light immature birds at Block Island present a puzzle, however. Most of them were caught after 28 September in 1959, and after 12 October in 1960. Thus they were much too late to be connected with the arrivals of light birds inland: indeed, arrivals of light birds at Block Island continued long after the departure of all but the last stragglers from inland New England (Table 4; Griscom and Snyder 1955). Without further research, it cannot be decided whether Block Island preferentially intercepts these late stragglers as they depart, or whether it preferentially attracts birds which have wandered from the south where the main migration is later—or both.

In contrast with its abundance inland, the Blackpoll Warbler is not strikingly common on the Atlantic coast. For example, it was only the sixth commonest warbler banded at coastal stations during August-October 1958 (Baird *et al.* 1959), and at Nantucket, Massachusetts, it comprises only about 7 percent of the warblers netted during September (unpublished data from 'Operation Recovery'). Yet inland in Massachusetts only the Myrtle Warbler occurs in comparable numbers, and at Round Hill in September 1962 the Blackpoll Warbler was ten times commoner than all other species of warblers put together.

SOUTHWARD DEPARTURES FROM NEW ENGLAND

Films of radar echoes from migrating birds, of the type described by Drury and Keith (1962), were available for 29 nights between 10 September and 19 October 1962 from the radar station at South Truro on Cape Cod, Massachusetts (65 miles ESE of Drumlin Farm). On most nights the films were confined to the period 1800 to 2400 E. D. T.; films in earlier years have shown that there is little southward migration over the sea after midnight.

Observations of southward departures* of passerine-type echoes are summarized in Table 7. Large departures were observed throughout the period covered: in other years they have been observed before the end of August (Drury and Keith 1962), but these early departures, and those on 17 and 18 October 1962, must have consisted of species other than the Blackpoll Warbler. In 1962 the birds moving in early October appear to have been heading slightly more to the west than those earlier or later, but in previous years this situation has been reversed: the birds' orientation will be discussed fully in a separate paper (Nisbet and Drury in prep.). In 1962 all six departures detected at Round Hill (19/20, 20/21, 24/25 September, 30 September/1 October, 1/2 and 2/3 October) coincided with southward departures seen by radar, and only on the last two of these nights was there evidence of southwestward movements as well. Moreover, at least three of the four marked arrivals of light birds at Round Hill (12/13, 14/15 and 19/20 September) coincided with southward movements seen by radar, and in two cases there was no evidence of a simultaneous southwestward movement (although, for technical reasons, southwest movements are often obscured on the South Truro radar). Hence, although the radar observations were incomplete and included movements of other species, they strongly support the hypothesis that Blackpoll Warblers arrive in Massachusetts from northwest and north and depart over the sea east of south.

Height and speed of migration

No radar observations were available of the height of migration in 1962, but in 1961 height measurements were made on four nights (22/23, 26/27, 27/28 September and 5/6 October) when there was a large southward movement during the departure season of the Blackpoll Warbler. The heights of radar echoes on these nights have been summarized by Nisbet (1963a). On average, the echoes were considerably higher than those observed on most of the other nights studied by Nisbet; among the echoes higher than 600 feet,

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*"Southward departures" are movements in which the birds head between SSW and SSE. In 1962 most of the observed tracks were slightly east of south, but in other years movements west of south have been equally frequent (Nisbet and Drury in prep.).

TABLE 7. SOUTHWARD NOCTURNAL DEPARTURES FROM NEW ENGLAND OBSERVED BY RADAR IN AUTUMN 1962

	Density Scale	Tracks	Wind 1900	Wind 2200	Headings
Sept 10/11	0	—	—	—	—
11/12	5	150°-160°	325°/26	315°/30	155°-195°
12/13	5	170°-175°	340°/18	005°/19	165°-180°
13/14	0	—	—	—	—
14/15	2	170°	—	335°/24	175°
17/18	0	—	—	—	—
18/19	0	—	—	—	—
19/20	1	140°	235°/12	—	185°
20/21	4	170°-174°	035°/15	020°/15	140°-175°
21/22	3	170°-185°	340°/10	340°/10	175°-200°
24/25	4	160°	340°/30	320°/30	160°-235°
25/26	0	—	—	—	—
26/27	0	—	—	—	—
27/28	0	—	—	—	—
28/29	0	—	—	—	—
Oct 1/2	5	170°-173°	320°/9	340°/10	180°
2/3	5	168°-172°	—	295°/13	185°-190°
3/4	3	172°-174°	255°/13	250°/10	195°-205°
4/5	0	—	—	—	—
5/6	0	—	—	—	—
9/10	0	—	—	—	—
10/11	1-2	173°	355°/13	—	170°
11/12	0	—	—	—	—
15/16	0	—	—	—	—
16/17	0	—	—	—	—
17/18	5	170°-173°	005°/19	350°/14	165°-170°
18/19	2	175°	—	250°/5	185°
19/20	0	—	—	—	—

Notes. The list is confined to observations of passerine migration in a south or southeast direction. The film for 8 October was defective; no films were available for the other ten days omitted from the list.

'Density' of migration is assessed on a logarithmic scale. Scales 1, 2, 3, 4, 5 correspond roughly to 2, 10, 50, 200 and 1,000 birds per square nautical mile (see Nisbet 1963b for method of calibration), but records of scales 1 and 2 are unreliable because of simultaneous movements in other directions.

'Tracks' are the observed directions of the birds relative to the ground; the average direction is given, but this sometimes varies during the evening (Nisbet and Drury in prep.).

'Winds' are the 'gradient' or 'geostrophic' winds, calculated from the direction and spacing of the isobars on the surface weather maps for 1900 and 2200 hours; the figures listed are the direction in degrees and the speed in knots. 'Headings' are calculated from the tabulated tracks and winds, assuming the birds' average air-speed to be 22 knots. Wind records are listed only for times when observations of tracks were available.

69 percent were in the range 2,000-4,000 feet above sea-level. This suggests that the Blackpoll Warbler migrates higher than many other common species in eastern Massachusetts: its average height of migration in 1961 was probably about 3,500 feet during the hours of darkness. On the morning of 27 September 1961 (and probably on those of 28 September and 6 October also) the average height of the observed echoes rose considerably in the hours after dawn (Nisbet 1963a). Although this increase in the average height was at least partly due to the dropping out of the lower birds (Nisbet 1963a), it also indicates that Blackpoll Warblers fly at least as high by day as by night.

During the nights of heavy southward migration in 1962, the average air temperature at 3,500 feet over eastern Massachusetts was about 8° C. at 1900 hours and about 6° C. at 0700 hours. It is not known at what height the birds flew between Massachusetts and Bermuda, but it is unlikely that the average air-temperature they experienced could have been much higher than 13° C.

It is difficult to measure the air-speed of small birds by means of radar, because their echoes usually flicker on and off the screen (Nisbet 1963b, Nisbet and Drury in prep.). However, on some occasions of southward migration we have been able to track echoes from individual groups of birds for some distance, and on other occasions we have been able to track the sharp edge of a mass of echoes moving away from the coast in the evening. After subtracting the velocity of the winds 2,000 to 6,000 feet above sea-level, the air-speeds estimated by these means are usually in the range 18-26 knots. We have adopted 22 knots as the most likely average air-speed of the Blackpoll Warbler.

Time of take-off

Radar observations in 1962 (and in earlier years) suggest that nearly all the birds involved in the southward movements take off at the same time, between 35 and 45 minutes after sunset. On 1 October 1962, for example, the first echoes appeared about 1908 (E. D. T.), and the density of echoes reached its maximum value within 10 minutes, remaining approximately constant for four or five hours. Records from earlier years show that southward migration declines greatly after midnight; hence most of the birds which pass out to sea must start their migration within 100 miles of the coast, and any which may take off farther inland must stop before they reach the coast.

Density of migration

The largest southward migrations (Density scale 5 in Table 6) are too large for their density to be estimated with any accuracy by means of radar (see Nisbet 1963b), but they are certainly denser than 250 birds per square mile, and are probably of the order of 1,000 birds per square mile. Two of these large movements have also been sampled by moon-watching, the estimated densities being about 500 and about 1,500 birds per square mile (Nisbet 1963b). Assuming 1,000 birds per square mile to be a typical density, and using the observed values of about 30 knots for the average ground-speed and about four hours for the average duration of the densest movements, we estimate that on a typical night something like 10 million migrate southwards across the 80-mile stretch from Narragansett Bay to Cape Cod alone. Since the movements are known to take place across a front of at least 225 miles, as shown on radar (Drury and Keith 1962), the number of birds which leave New England each year in the period 25 September-10 October probably exceeds 100 million. The average density of the birds involved in such a flight must be roughly 5 per acre throughout the region from which departures are observed. It is not known whether the Blackpoll Warbler is as common as this in the coastal region of New England, but our observations in Massachusetts suggest that it probably is.

BIRDS CAUGHT IN BERMUDA

Baird and D. B. Wingate operated mist-nets and looked for birds in various parts of Bermuda from 16 September to 15 October, 1962. Wingate continued observations until the end of October, but his netting was severely hampered by cats.

Figure 2d summarizes the weights of the 138 Blackpoll Warblers weighed, and Table 8 summarizes the banding records day by day. Although 25 percent of them were very light (less than 12.2 gm.), the majority of the birds weighed between 13.0 and 16.8 gm.—heavier than most of the birds trapped on the mainland!

Although nets were set on every day from 16 September through 2 October, only two Blackpoll Warblers were caught and no others were seen. At about 0300 on 3 October, during a sudden rainshower,

TABLE 8. BLACKPOLL WARBLERS CAUGHT ON BERMUDA IN AUTUMN 1962

	Birds caught			Weights (modified)	
	Adult	Immature	Total	Mean	Standard deviation
Sept 26	1	—	1	18.2	—
Oct 2	—	1	1	15.3	—
Oct 3	5	9	14	16.6	1.63
Oct 4	—	1	1	12.9	—
Oct 7	7	5	12	13.7	2.36
Oct 8	6	3	9	14.8	2.17
Oct 9	8	5	13	16.0*	0.98
Oct 10	2	1	3	14.1	—
Oct 11	7	7	19†	13.0‡	1.93
Oct 12	11	3	14	12.5	2.35
Oct 13	17	12	29	13.7	1.67
Oct 15	1	7	8	11.4	1.67
Oct 22	6	4	10	11.3	1.30
Oct 28	1	6	7	12.6	1.57
TOTAL	72	64	141†		

* Excluding birds weighing 7.7 and 9.4 gm.
† Including five birds not aged.
‡ Excluding bird weighing 20.5 gm.

at least 50 warblers were attracted to the Gibbs Hill Lighthouse; 14 birds caught by the lighthouse-keeper were all Blackpoll Warblers. When weighed 10-11 hours later their plumage was dry and their average weight was 16.64 $\pm$ 0.43 gm. However, although netting was continued throughout that day, and although a special search was made for Blackpoll Warblers, none was seen until a single light bird was caught on the afternoon of 4 October. It is evident that the flight sampled at the lighthouse *passed Bermuda without stopping, and would not have been detected at all if the rain had not brought the birds to the light.*

The next influx was on 7 October, when 11 birds were caught (average weight 13.7 gm.) and others seen. Some birds were then caught on every day until the 13th, but many of these may have been birds which had been on the island for one or more days. The only convincing evidence for a fresh arrival is the low average weight on the 11th, after few had been caught on the 10th. There was another influx of light birds about the 15th, and two of the birds banded on that day were recaptured on the 22nd, having gained 0.6-2.9 gm. Some Blackpoll Warblers were present on Bermuda throughout the second half of October; the few that were caught were much lighter than those in the first half of the month.

In summary, the birds weighed on Bermuda fall into three distinct groups:

1. Birds at the lower limit of weight for the species: recorded on six days.

2. Birds of moderate weight (11.5-16 gm.): influxes about 7, 11 and 15 October, and perhaps on other days.

3. Heavy birds (mean 16.6 gm.): attracted to the lighthouse on 3 October.

Earlier records by Wingate (*in litt.*) agree with categories (2) and (3). An immature netted on 10 October 1959 weighed 12.2 gm. Four immatures caught at the lighthouse weighed 16.8 gm. (4 October 1959), 18.2, 18.0 and 16.0 gm. (11 October 1960), mean 17.25 gm.

There can be little doubt that the heavy birds caught on 3 October 1962 were part of the flight, observed by radar in New England, which left the mainland of North America on the evening of the 1st, 32 hours earlier. The distance from Bermuda to New England is 720-820 miles, so that the time of arrival agrees exactly with the ground-speed of the birds (22 knots air-speed plus a favoring wind of a few knots), and cannot be reconciled with the hypothesis that they took off on the evening of 30 September (56 hours) or 2 October (8 hours). However, the lighter birds which arrived on 7 and 11 October could not have flown directly from New England, since there was rain there on the evening of 5 October and no southward departures were seen then or on the evening of the 9th. Hence these birds had either flown for some 60 hours, or had left North America south of New England. The latter suggestion seems more probable, since arrivals of light birds at Bermuda continued in 1962 (and in earlier years—Wingate *in litt.*) until the end of October, long after the last departures from New England. We conclude that the birds which migrate southwards from New England do not stop at Bermuda unless seriously delayed by the weather, although they pass overhead and are sometimes attracted to the lighthouse; the birds which do stop there are not representative of those which fly overhead.

"RESTING" POWER REQUIREMENTS

In order to estimate the Blackpoll Warbler's "resting" power requirement—that is, the power* required to maintain the body temperature with the minimum possible muscular activity—we caught 45 birds on the afternoon of 29 September and detained them overnight. To ensure that the birds' guts were empty, they were kept in a holding-cage, exposed to light, for 2-3 hours, before being weighed between 2000 and 2130. They were returned to the holding-cage and kept in complete darkness in a warm building (average temperature about 15° C.), then reweighed between 0630 and 0700 after an average interval of 10.0 hours. The average weight-loss was 0.62 ± .027 gm., or 0.062 ± .0027 gm./hr. The average weight-loss of heavy birds (14.6-21.5 gm. at first weighing) differed by only 0.02 gm. (not statistically significant) from that of light birds (9.7-14.4 gm.).

The experiments of Kendeigh (1944) suggest that after the preliminary holding period the birds should have been consuming fat, not carbohydrate, but it is not known whether they also lost water during the night. If we assume that the weight-loss consisted entirely of fat, the power consumption of the birds is estimated to be 0.59 ± .026 Kcal./hr., using the figure 9.5 Kcal./gm. for the calorific value of bird fat. Using the figure 11.2 ± 0.33 gm. for the average fat-free weight of the species (page 112), and assuming the fat deposits to be inert (see previous paragraph), the power consumption is estimated to be 0.053 ± .0029 Kcal./fat-free gm./hr. This is an upper limit, because some of the weight-loss of these resting birds probably consisted of water.

King and Farner (1961) have recently reviewed laboratory measurements of metabolic rates of birds. Their Tables 2 and 3 show that in a region of "thermo-neutrality", extending from about 31° to 35° C., the metabolic rates of small birds (10-20 gm. body-weight) remain constant at about 0.020 Kcal./gm. total weight/hr.; below 31° the metabolic rates increase by about 4.2-5.6 percent of this figure for each degree centigrade. Hence at 6°-12° C. the metabolic rates of most small birds probably lie in the range 0.036-0.048 Kcal./gm. total weight/hr. Unfortunately there are very few actual measurements of metabolic rates of small birds at this temperature, and none at all for insectivorous species; nor is it known how much

*Some authors use the word "energy" for the rate of utilization of energy, but we prefer to use the term "power". We use the term "power output" for the rate at which the flying bird does work in the air and "power consumption" for the total rate at which the bird consumes energy; the difference between the two usually represents production of heat. We quote figures for power in units of kilocalories per hour (1 Kcal./hr. = 1.14 watts = 1.52×10^{-3} horsepower).

of the experimental birds' body-weight consisted of fat. Pending a direct measurement, we have adopted 0.045 Kcal./gm. fat-free weight/hr. as the most likely average for the metabolic rate of a small bird resting at about 10° C. This figure is consistent with our measured maximum for the Blackpoll Warbler, and is a compromise between the figures of 0.040 and 0.050 assumed by Yapp (1956) and Odum (1960) respectively.

WEIGHT-LOSS DURING MIGRATION

The only records from which the Blackpoll Warbler's rate of loss in weight can be estimated are the weights of the birds caught at the Bermuda lighthouse on 3 October 1962. Using their average weight, 16.64 ± 0.41 gm. about 10.5 hours after capture, and our result that captive Blackpoll Warblers lose 0.062 ± .0027 gm./hr. at about the same temperature, we estimate their average weight at the time of capture to have been 17.29 ± 0.41 gm. This estimate may be slightly low, as the Bermuda birds were not kept in complete darkness, and are known to have been more active than those held overnight on the mainland. Since they are known to have taken off about 1910 E. D. T. on 1 October, and to have been caught soon after 0300 (Bermuda Time = E. D. T.) on 3 October, we estimate their average flight-time to have been 32 ± 0.4 hours.

Unfortunately we have no direct measurements of weights before departure on 1 October, since Table 5 shows that light birds as well as heavy birds left Round Hill on that evening. Hence we have assumed that the majority of the birds left New England at the normal departure weights for the species, 19.7 to 23.2 gm. (see above). Altogether we have 46 records of birds in this range of weights, 24 from Drumlin Farm, 8 from Round Hill, 6 from Block Island, 3 from Middletown, Rhode Island, in 1959; two from Nantucket, Massachusetts, in 1962; one from the Block Island lighthouse and two from television towers. The 43 netted birds had an average weight of 20.83 ± 0.13 gm. and an average wing-length of 72.0 mm., whereas the three birds killed while actually migrating had average weight 21.3 gm. and average wing-length 75.5 mm. Table 2 shows that most of the difference in average weight can be attributed to a difference in average fat-free weight, so it seems likely that most of the netted birds did not put on much more fat between the time they were weighed and their departure. Hence we will use 20.83 ± 0.13 gm. as the best available estimate of the mean departure weight of birds of wing-length 72mm.

The average wing-length of the Bermuda sample was 70.9 mm., so we estimate, using Table 2, that their departure weight was 20.72 ± 0.13 gm. Hence our estimate of their loss of weight during their 32-hour flight is 3.43 ± 0.43 gm. This represents an average rate of 0.107 ± .013 gm. per hour, or 0.56 ± .07 percent of the mean body-weight during flight per hour. This should be regarded as an upper limit, since we have adopted for the departure weight the mean weight of the heaviest group yet caught on the mainland. We are unable to give a lower limit for the rate of weight-loss, because there is evidence that some birds left Massachusetts in 1962 at weights much lower than this—some even at weights lower than the arrival weight at Bermuda (it seems a reasonable assumption that birds did not gain weight during their flight to Bermuda). The importance of this upper limit is that it is lower than any other estimate of the rate of weight-loss in migrating birds that has yet been published (see Part II).

Water-loss

Before these figures can be given much significance, however, it is necessary to know of what the weight-loss consists. It is unlikely to include gut-contents, since the birds were not feeding intensively when caught and were given time to defecate before being weighed. It may have included some carbohydrate (e. g. glycogen), but most of a bird's normal store of carbohydrate would have been consumed in the time for which the birds were held before being weighed, and in any case it would last less than an hour in flight (see Kendeigh 1944). No appreciable error is likely if it is assumed that the weight-loss consists only of fat and water.

Several writers have argued recently that water-loss may be significant in migratory flights:

1. Yapp (1956, 1962) quoted laboratory measurements of water-loss in resting birds at various temperatures, and pointed out that they exceed the rate of production of metabolic water predicted by his (1956) theory of flapping flight in birds of the same size. However, Yapp's predictions of power output (and hence rate of water production) are probably much too low (see Part II).

2. Salt and Zeuthen (1960) showed that if a bird expends a large amount of power in overcoming air-resistance at high speed, so much power is wasted in the muscles that it can only regulate its temperature by evaporating water. Using Zeuthen's (1942) estimates of air resistance, they calculated that a pigeon flying at various air-speeds should lose between 5.5 percent and 22 percent of its weight per hour, mainly in steam. However, Zeuthen's estimates of power consumption are probably too high (see Part II).

3. Eliassen and Hjelmtvedt (1958) claimed that birds they caught on ocean weather-ships had lost much more water during their flight than could have been replaced by oxidation of fat. However, their estimates of the rate of weight-loss are based on dubious assumptions and are much higher than other estimates for the same species (see Part II).

Against these arguments should be set the following observations:

1. E. P. Odum (*in litt.*) has found (in a preliminary analysis) that birds killed during nocturnal migration when very thin have no less water than birds of the same species killed when very fat.

2. Salt and Zeuthen (*op. cit.*) found that a Starling (*Sturnus vulgaris*) which died of exhaustion on a weather-ship contained relatively more water than a Starling of normal weight from the mainland.

3. Voous (1953, 1957) reported the arrival of numbers of exhausted Blackpoll Warblers in Curaçao, Netherlands, Lesser Antilles, in October 1951, whose average weight was only 8.8 gm., 2.4

gm. less than the average fat-free weight of the species. Wetmore (1939), who shot similar birds arriving in northern Venezuela in October 1938, stated that their breast muscles were "reduced to thin bands through which the angular ridges of the breast-bone projected". Thus, of the 2.4 gm. of lean body-weight which Voous's birds had lost, we may guess that more than half consisted of muscle tissue, and less than half of water. Our measurements of weight-loss suggest that Blackpoll Warblers must fly for at least 100 hours before their weight can be reduced as low as 8.8 gm. Hence Voous' observations place an upper limit of about 0.012 gm./hr. on the possible rate of water-loss in flight, less than one-ninth of our estimate of the total rate of weight-loss in the species. It is a commonplace observation among banders on remote islands that exhausted birds often arrive with eroded breast-muscles, and this implies that in many species fat-reserves are exhausted before flight can be stopped by shortage of water.

Kendeigh (1944) showed that House Sparrows exhale about 0.006 gm. of water per gm. of body-weight per hour at rest in the laboratory at about 10° C. Seibert (1949) quoted figures of 0.0044 gm./gm./hr. for Slate-colored Juncos (*Junco hyemalis*) and 0.0077 gm./gm./hr. for White-throated Sparrows (*Zonotrichia albicollis*). We know of no measurements of water-loss in insectivorous birds, but if we assume the rate of water-loss in the Blackpoll Warbler to be similar to those quoted above, the average loss per bird is about 0.07 gm. of water per hour, only about 60 percent of the rate of production of metabolic water by oxidation of 0.107 gm. of fat per hour. Hence there is no need to assume that a flying Blackpoll Warbler loses any water at all.

Yapp (1956) showed that if a bird's flight is very economical (power consumption less than about 1.2 times the resting value) it may lose water by normal respiratory evaporation. Salt and Zeuthen (1960) showed that if a bird works very hard in flight (e.g. to fly fast) it must evaporate water in excess of its metabolic production in order to regulate its temperature. In the previous paragraph we showed that there is an intermediate range of power outputs in which the bird need not lose water at all. Since birds can store large quantities of fat, but only small amounts of water, it is possible that selection has for this reason favored a moderate power output (i. e. moderate flight-speed) in long-distance migrants. This might explain why small birds fly at only about 20 knots, which *a priori* seems dangerously slow since it is similar to the average wind-speed at the average height at which they migrate.

In the rest of this paper we will assume that the net loss of water during migration is negligible compared with loss of fat; we have shown above that errors in this assumption are likely to be small for long-distance migrants. This assumption seems biologically reasonable, since natural selection could hardly have permitted the evolution of a long-distance migration route and a fat-store to fuel it, without favoring the simultaneous evolution of the water-conservation system without which the birds would not reach their wintering area.

Power consumption

Assuming that the observed weight-loss, 0.107 ± .013 gm./hr., consisted entirely of fat, of calorific value 9.5* Kcal./gm., we estimate that the average power consumption of the Blackpoll Warbler, in flight at temperatures of 6-12° C., was 1.02 ± .13 Kcal./hr., only 2.0 times the resting power consumption in spite of a load of 6-10 gm. of fat. Since the average weight of the birds during flight was 19.0 gm., this is about 0.054 ± .007 Kcal./gm. total weight/hr. This should be regarded as a maximum figure, since the estimate of weight-loss was itself a maximum, and may have included a little water.

Potential Flight-range

In order to estimate the time for which a Blackpoll Warbler can fly before it exhausts its fuel-reserves, we must first estimate the dependence of power consumption in flight on total body-weight. We have suggested elsewhere (in Moreau 1961, Odum *et al.* 1961 and Drury and Keith 1962) that in the relatively slow, flapping flight of a small bird the power required for flight (and hence the rate of weight-loss) decreases as the fat is consumed, roughly proportionally to the total weight. Let us apply this assumption to the birds which we weighed in Bermuda. During the first 32 hours of flight their average weight was 19.0 gm., and they lost weight at an average rate of about 0.107 gm. per hour, reducing their weight to 17.3 gm. During the next 32 hours of flight their average weight would be about 15.85 gm., so that we estimate their average rate of weight loss to be $0.107 \times 15.85/19.0 = 0.089$ gm. per hour, reducing their weight to $17.3 - (32 \times 0.089) = 14.4$ gm. During the next 16 hours of flight their average weight would be about 13.8 gm., so that we estimate their average rate of weight-loss to be $0.107 \times 13.8/19.0 = 0.078$ gm. per hour, reducing their weight to $14.4 - (16 \times 0.078) = 13.2$ gm. The average rate of weight loss is now only 0.074 gm. per hour, so that if we assume that the muscular efficiency is 20-25 percent, the power wasted in the flight muscles, about 0.051 Kcal./hr., is now only just enough to warm the body and to evaporate all the metabolic water. Hence the total power consumption cannot decrease much more, and we will therefore assume that the subsequent rate of weight-loss is about 0.07 gm. per hour. The fat-free weight of the birds is about 11.1 gm., so we therefore estimate that they can fly for another 30 hours before they use the last of their fat. The observations of Voous (1953) suggest that they can continue flying until their weight is reduced by a further 2.4 gm., but this loss must consist of muscle tissue and water, and might progress at a rate of 0.5 gm. per hour. Hence we estimate the potential flight time of these birds, which started with about 9.6 gm. of fat, to be

*This figure is appropriate to the oxidation of fat to CO_2 and liquid water. In this paper, however, we assume that the metabolic water is exhaled as vapor (whereas all the other water in the body is retained). The evaporation of the metabolic water requires about 0.6 Kcal. per gm. of fat oxidized, so that the bird's net gain of energy is about 8.9 Kcal. per gm. of fat.

about 115* hours. This may perhaps be an overestimate, since our figure of 0.07 gm. per hour for the minimum rate of weight-loss is barely sufficient for the birds to maintain their water-balance, but even if we assume a minimum rate of 0.08 gm./hr. the estimate of flight time is still 110 hours. Even if we were to assume that the rate of weight-loss remained the same throughout the flight, the estimate of flight-time would still be over 95 hours. Since our estimates of the initial rate of weight-loss may have been too high, these estimates of potential flight-time may be too low.

Drury and Keith (1962) assumed that the birds which they observed by radar heading southwards from New England would eventually stop in the Lesser Antilles, unless they were drifted westwards into the Greater Antilles. However, a flight from New England to the Lesser Antilles would take a Blackpoll Warbler only 60-70 hours in normal weather, and would only exceptionally take it as much as 90 hours. Hence Blackpoll Warblers departing from New England at their normal departure weights have ample fat-reserves for a non-stop flight to the mainland of South America (e. g. to their wintering area in northern Venezuela) unless they meet unusually unfavorable weather. Hence there is no need to assume that Blackpoll Warblers need to stop in the Lesser Antilles at all. Indeed, as Cooke (1915) pointed out, the entire area of the West Indies east of Puerto Rico is less than that of Rhode Island, and it is unlikely that such a small area could provide food for a sudden influx of 100,000,000 birds.

Conclusion

Drury and Keith (1962) showed that southward movements of small passerines out to sea from New England in autumn are regular and frequent. In this paper we have further shown:

1. That some of the southward movements coincide with departures of Blackpoll Warblers from inland Massachusetts;

2. That many Blackpoll Warblers stay in New England for some weeks and become very fat;

3. That Blackpoll Warblers pass Bermuda without stopping;

4. That Blackpoll Warblers have enough fat when they leave New England to fly non-stop for 105-120 hours.

No reasonable doubt can remain that a large group of Blackpoll Warblers regularly migrates southwards from New England in autumn, flying non-stop at least as far as the Lesser Antilles, probably as far as Venezuela.

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*These estimates supersede those of Drury and Keith (1962: 483-484), but it should be mentioned that their second calculation, which gave an estimate of 108 hours, was wrong since it twice took into account the effect of the assumed decrease in power consumption as the fat-reserves are consumed.