AUTUMN MIGRATION OF THE BLACKPOLL WARBLER: EVIDENCE FOR LONG FLIGHT PROVIDED BY REGIONAL SURVEY*

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The long migrations of the Blackpoll Warbler (*Dendroica striata*) have been discussed extensively. The species breeds farther to the north and west and winters farther to the south and east than most other North American warblers (Fig. 3); on autumn migration it is found in large numbers along the Atlantic seaboard of North America. Cooke (1904, 1915) suggested that all birds of the species migrate SSW down the Atlantic Coast to the southeastern United States, before turning southeast towards their winter range. This hypothesis has been restated and mapped by Murray (1965, 1966a). On the other hand, Nisbet *et al.* (1963) suggested that many birds which stop over in southern New England migrate SSE from there across the Atlantic Ocean towards their wintering range. If confirmed, their long flight is of considerable importance for physiological, aerodynamic and navigational theories (Nisbet *et al.* 1963, Nisbet 1967, Griffin 1969). This paper attempts to resolve the question by surveying the abundance of Blackpoll Warblers on autumn migration throughout North America south of the breeding range.

Quantitative comparisons between regions in this paper are based mainly on two sources of numerical data: (a) collections of birds killed in accidents during nocturnal migration, and (b) systematic sampling by mist-nets at banding stations. For the critical area of the southeastern United States, I have also made a detailed survey of published and unpublished data on local occurrence of grounded migrants. The relative merits of these sources of data will be discussed at the end of the paper.

Data collected for this paper are for autumn migration only and are as complete as possible through the 1968 season. With one exception (the Virginia banding data included in Tables 3 and 4) I have not attempted to incorporate data for 1969.

NOCTURNAL ACCIDENTS

A large number of descriptions have been published of accidents in which large or small numbers of birds have been killed while migrating at night (see the Special Bibliography, where references are numbered for citation in this section). In North America most such accidents took place at lighthouses before 1930, at tall buildings or bridges between 1930 and 1948, at airport ceilometers between 1948 and 1956, and at television towers since 1956. Nowadays television towers cause the most mortality, which is in-

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creasing as more and higher towers are being built. Mortality at ceilometers decreased abruptly after the general installation of optical filters during the 1950's; mortality at lighthouses and tall buildings continues to be reported from some areas (166,187): its apparent decline in the last 50 years is probably real, but must also reflect in part a decline in the attention paid to it.

Ornithologists have long recognized the unique opportunities provided by these incidents to obtain and study large samples of migrants "snatched from the sky." A large number of these incidents have been thoroughly investigated; many detailed lists of species and numbers have been published, and others have been kept in unpublished form. This paper is one of the first to use this material in a quantitative survey.

An index of relative abundance.

The numbers of birds killed and reported vary greatly from place to place, and from state to state. These variations, however, are due primarily to local conditions such as the height of television towers and the presence of ornithologists: they do not necessarily indicate variations in the density of migration. In order to make comparisons between regions, I use as an index of abundance the *proportion of Blackpoll Warblers among the total number of warblers* (Parulidae) killed and identified in each region. In so doing, I assume that inter-regional differences in the index are primarily due to inter-regional differences in the abundance of migrating Blackpoll Warblers.

For this assumption to be valid, inter-regional differences in the abundance of other warblers (considered together) must be relatively small. In fact, observations by radar (Nisbet and Drury 1967, Graber 1968) and moon-watching (Lowery and Newman 1966) have consistently indicated that migration of small passerines takes place rather uniformly over a broad front throughout eastern North America, except over projecting parts of the Atlantic Coast. These observations presumably apply *pari passu* to warblers, which comprise a large fraction of the passerines which migrate at the season concerned (Nisbet 1963, Mueller and Berger 1967). The most extensive observations are those of Newman and Lowery (1964) which, despite large fluctuations in migration traffic rates from night to night, indicated similar average densities in different regions. The most general regional trend in migration density is expected to be an increase from north to south, as locally breeding birds join the southward flights. However, the data discussed in the Appendix indicate that this increase is not large, and is at least partly offset by east-west movements of northern species.

Other biases in the index.

The index of abundance is subject to several other types of bias:

1. Some warbler species may be more susceptible to the factors which lead to the accidents than others: this would lead to bias if

the susceptible species were unequally distributed. However, Graber (1968) demonstrated a good correlation between the frequencies of different warbler species in television tower samples and in counts of grounded migrants, especially when allowance was made for interspecific differences in conspicuousness. Data collected in this study further show a good correlation ($0.5 < r < 0.7$) between the relative frequencies of various warblers in television tower samples and in samples of banded birds in Wisconsin, Ontario and Maryland. The only conspicuous exception in all these comparisons is the under-representation of the Myrtle Warbler (*D. coronata*) in the television tower samples; this may be associated with its late migration (see next paragraph). The relative proportions of different species of warblers in samples from lighthouses, television towers and ceilometers are similar where sufficiently large samples are available from the same regions (12, 13, 187; 44; 66, 67; Buskirk 1968).

2. The great majority of reported accidents for all species fall into limited periods of the autumn: late August to mid-September in western Canada, throughout September in the Great Lakes area, mid-September to mid-October in the northeastern United States, late September to late October in the southeastern United States. Earlier and later migrants appear to be under-represented, except perhaps at places where they are systematically searched for (137, 138, 187). However, these periods coincide exactly with the migration period of the Blackpoll Warbler (Table 4), so that little bias is likely in this survey.

3. In a few cases collectors faced with large numbers of dead birds have selected a small sample of each species, or have searched for rarities. However, these cases have been too infrequent to bias significantly the regional averages used in this paper: nearly all published lists have been based on either complete collections or random samples.

4. Errors in identification are known or suspected in a number of cases, especially among the older records. Prior to 1934 there appears to have been confusion between the Blackpoll and the Bay-breasted Warbler (*D. castanea*) in the southeastern states (see later); in other areas (notably Maine and Bermuda) there appears formerly to have been confusion between the Blackpoll and the Pine Warbler (*D. pinus*). Two cases in which doubtful records comprise a significant proportion of the state totals (Georgia and Florida) will be discussed later. Otherwise errors in identification are unlikely to have had a significant effect on regional averages: in particular, most recent records of Blackpoll Warblers in areas where the species is rare have been confirmed by reliable ornithologists.

Sampling errors.

The overall effect of the biases considered above is believed to be small: the most important limitation of the data is probably

TABLE 1. OCCURRENCE OF BLACKPOLL WARBLERS (*Dendroica striata*) AMONG WARBLERS (PARULIDAE) KILLED AT NIGHT WHILE MIGRATING IN AUTUMN

State/Province	No. of Sites[1]	No. of Years	Range	Total Warblers[2]	Blackpolls	%	References
Plains							
Saskatchewan	5	5	1959-65	1,487	100	7%	15, 47, 77, 78, 79, 100, 178.
Manitoba	3	2	1956-68	258*	34	13%	54, 132.
South Dakota	1	1	1965	50	2	(4%)	118.
Kansas	1	1	1954	534	0	0%	142.
Missouri	2	6	1954-66	3,050*	0	0%	5, 33, 35, 46, 57.
Great Lakes							
Minnesota[3]	6	4	1961-64	1,903*	28	1.5%[4]	38, 49, 50, 51, 64, 69, 72, 73, 130, 140, 185.
Wisconsin	3	11	1887-1968	56,112	2,388	4%	58, 69, 70, 71, 72, 73, 75, 122, 177.
Illinois	13	14	1886-1967	2,972	51	1.4%	18, 45, 48, 115-117, 155, 170, 181.
Indiana	2	6	1959-67	321	62	19%[5]	96, 99, 156, 181.
Michigan	8	6	1884-1964	5,006	1,238	24%	21, 22, 98.
Ohio	2	5	1964-68	535	57	11%	181, 184.
Pennsylvania	3	7	1899-1965	1,142*	39	3.5%	11, 74, 165, 186.
New York (upstate)	10	7	1962-68	1,846*	144	8%	2, 34, 36, 59, 97, 124, 143, 144, 164, 167, 174, 183.
Ontario	13	10	1929-68	7,233[6]	738[6]	10%	2, 12, 13, 62, 63, 95, 125, 149, 152, 153, 187.
Eastern Inland							
West Virginia	2	3	1965-67	(c. 500)	(c. 150)	(c .30%)[7]	53, 176.
Kentucky	2	3	1951-65	152	0[8]	0%	1, 23, 43, 44, 94
Tennessee	7	17	1948-68	18,590*	24	0.13%	30, 41-44, 55, 56, 60, 76, 80-92, 109, 126, 127, 135, 136, 141, 148, 154.
Alabama	1	3	1954-68	846*	0	0%	101, 161, 175.
Mississippi	1	1	1957	600*	0	0%	102.
Atlantic Coast							
Nova Scotia	1	1	1966	123	115	(93%)[9]	29, 146, 166.
New Brunswick	1	1	1885	75*	15	(20%)	19.
Maine	4	10	1893-1959	610*	c. 270	c .45%	10, 16, 39, 40, 114, 121, 133, 134.
New Hampshire	2	2	1959-60	74	16	22%	128, 129.
Massachusetts	4	5	1957-68	324	57	18%	9, 158, 159, 160, 173.

TABLE 1. OCCURRENCE OF BLACKPOLL WARBLERS (*Dendroica striata*) AMONG WARBLERS (PARULIDAE) KILLED AT NIGHT WHILE MIGRATING IN AUTUMN

State/Province	No. of Sites[1]	No. of Years	Range	Total Warblers[2]	Blackpolls	%	References
Rhode Island	1	1	1960	2	1	(50%)	159.
New York (N.Y.C. & L.I.)	5	8	1882-1955	2,280*	857	38%	6-8, 16, 20, 31, 32, 36, 103, 104, 120, 136.
New Jersey	2	2	1889-1957	48	1	(2%)	147, 162.
Maryland	1	3	1964-66	2,424	19	0.8%	163.
Washington, D.C.	1	3	1935-37	1,234	14	1.1%	16, 110-113.
Virginia	1	1	1960	31	0	(0%)	37.
N. Carolina	7	8	1952-66	1,895*	4	0.2%	3, 24, 93, 106, 108, 131, 139, 145, 172, 179.
S. Carolina	4	14	1929-68	4,989*	5	0.1%	3, 4, 24, 66, 67, 107, 119, 131, 139, 145, 182.
Georgia	6	5	1884-1957	4,615*	38	0.8%	14, 52, 66, 67, 105.
Florida	7	30	1884-1967	18,348*	764	4%	16, 26, 27, 98, 102, 123, 137, 138, 150, 151, 156, 157, 168, 169, 171, 180.
Bahamas	4	3	1900-66	137	29	21%	17, 68.
TOTAL	135	50	1884-1968	140,342	7,310	5.2%	

NOTES. *includes estimate of a small proportion of the total, based on the assumption that the proportion of warblers among the birds killed was similar to the regional average.
[1]Places within the same city, or less than 10 km apart, are usually treated as a single 'site', but the exact locations are not always clear from the published accounts.
[2]Total numbers of Parulidae identified.
[3]including birds on ship in W. Lake Superior.
[4]7% in three kills in northeast, 0.3% elsewhere.
[5]36% in three kills in north, 0.8% in two kills in south.
[6]including 1,339 warblers (139 Blackpolls) caught alive at Long Point lighthouse, 1960-68.
[7]The commonest warbler in at least two kills, not fully recorded.
[8]Two listed as not certainly identified.
[9]Present but less common in two other kills, not fully recorded.

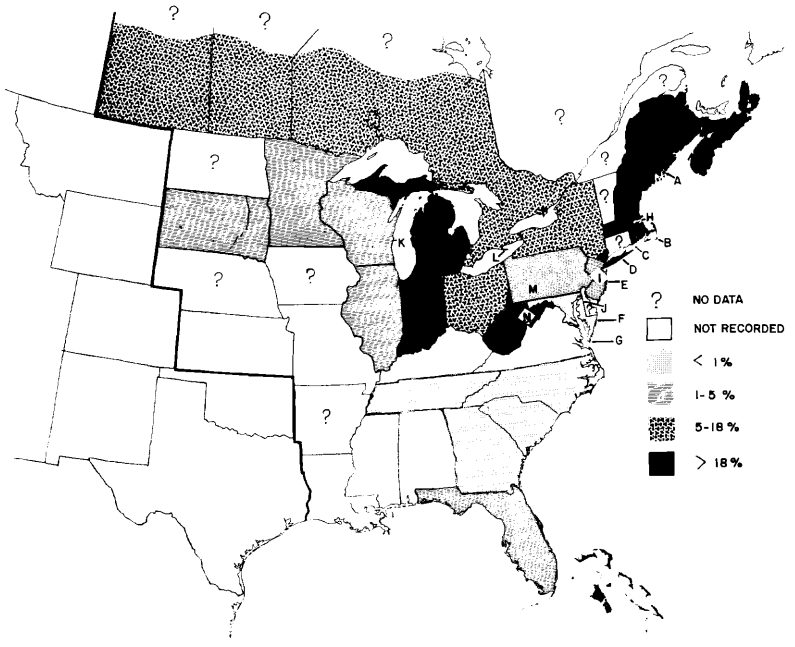

Fig. 1. Percentage frequency of Blackpoll Warblers among warblers killed in nocturnal accidents.

For sample sizes and other information see Table 1.

Data were not collected for states and provinces west of the heavy line.

Letters denote the banding stations listed in Table 3.

sampling error, arising from small samples in many areas and year-to-year variations in numbers of the species. If sampling errors were an overwhelming limitation of the data, they would obscure altogether any spatial patterns in the occurrence of the species. In fact, however, very marked spatial patterns can be observed (Table 1). The consistency of these patterns suggests that any regional average based on a collection of 20 or more Blackpoll Warblers is statistically reliable within a factor of 2 or 3; such errors would be much smaller than the regional differences in the relative abundance of the Blackpoll Warbler, which are of the order of 10 to 1000, or even 10,000 (Table 1).

Regional differences in abundance.

Data have been obtained from about 135 different places in 33 states and provinces from Saskatchewan, the Dakotas, Kansas and Mississippi eastwards. The total number of birds killed in the reported incidents is not known, but well over 200,000 have been

examined and identified; of these about 140,000 were warblers and 7,310 (5.2%) were Blackpoll Warblers. Table 1 summarizes the data by states and provinces; a complete tabulation has been deposited at the Patuxent Wildlife Research Center.

The records fall into very marked patterns of regional abundance (see Fig. 1). In Saskatchewan, Manitoba, and throughout the Great Lakes states, the Blackpoll Warbler is relatively common, comprising some 5-13% of the warblers in most samples. It is more common towards the east, in Michigan (24%), northern Indiana (36% of a small sample) and West Virginia (the commonest warbler in several samples, not all fully reported), but not outstandingly common in Ontario or up-state New York (10% in a large sample). To the south and west it becomes abruptly rare, comprising only 1.5% of a varied sample in Illinois, 0.3% in western Minnesota, and 0.8% in southern Indiana, completely lacking in Kansas, Kentucky, Mississippi, and Alabama, and extremely rare in Tennessee (0.13%) and northwest Florida (0.02%). The transition between abundance and rarity occurs in less than 150 km, the boundary line passing between Dayton, Ohio, and Louisville, Kentucky (156,184), and between Eau Claire, Wisconsin, and Lewisville, Minnesota (72,73).

On the Atlantic seaboard the Blackpoll Warbler is by far the most common warbler in large samples from Long Island and Maine, and is consistently the most numerous species in smaller samples from Massachusetts, New Hampshire, New Brunswick, and Nova Scotia. In the area from Long Island to Nova Scotia it comprises, on average, about 40% of all warblers, the highest ratio of any region on the continent. Southwards the proportion of Blackpoll Warblers decreases rapidly: 6% of 622 warblers in New York City and Newark, 4% of 604 in Philadelphia, 0.8% of 2424 in Baltimore, 1.1% of 1234 in Washington, 0.21% of 1895 in North Carolina and 0.10% of 4989 in South Carolina. The proportion increases again in Georgia (0.82% of 4615), and in Florida (4.2% of 18,348) where most of the birds were killed in two incidents (to be discussed later).

OCCURRENCE AT BANDING STATIONS

This section analyzes the occurrence of Blackpoll Warblers in samples of warblers caught at banding stations. Most of the regularly-manned stations are in the Great Lakes and northern Atlantic coastal states, where Table 1 indicates that the species is generally numerous. Accordingly, this section analyzes: (1) regional differences within these areas; (2) seasonal patterns of frequency; (3) differences between coastal and inland stations.

The analysis is based primarily on records gathered during the "Operation Recovery" program, launched in 1957 to study autumn migration along the Atlantic Coast. Reports on the first two years of the program have been published (Baird *et al.* 1958, 1959); results of subsequent years' work are filed at the Patuxent Wildlife Research Center. After 1958 participants were encouraged to

TABLE 2. ANNUAL AND SEASONAL OCCURRENCE OF BLACKPOLL WARBLERS AT OCEAN CITY, MARYLAND

Year:	1960	1961	1962	1963	1964	1965	1966	1967	1968	Total	Mean
Net hours (nh)	12,052	12,577	15,292	c.20,000	24,669	14,118	29,980	29,850	20,995	200,883*	
Blackpolls	83	34	84	101	185	152	203	241	150	1,291 *	
Blackpolls/1000 nh	6.9	2.7	5.5	5.0	7.5	9.3	6.8	8.1	7.2		6.4
Other warblers	673	890	1,258	1,255	1,264	1,295	1,844	2,333	2,195	14,450*	
% Blackpolls	10.9	3.7	6.5	7.4	12.8	10.5	9.9	9.4	6.4		8.9
% in 4 peaks	61	65	48	36	39	29	46	67	37		48
Seasonal occurrence:											
27-31 August	—	—	—	0	—	—	0	0	—		0
1-5 September	0	0	0	0	7	—	1	0	0		1
6-10	0	6	4	8	12	0	3	0	5		4
11-15	10	6	78	15	26	5	2	2	16		18
16-20	5	65	54	38	32	48	12	4	7		30
21-25	19	24	46	73	23	14	100	6	35		**38**
26-30	41	100	100	100	45	100	23	5	100		**68**
1-5 October	100	(0)	71	69	70	61	29	17	23		**55**
6-10	—	—	—	62	100	30	21	100	40		**59**
11-15	—	—	—	8	10	48	21	9	9		18
16-20	—	—	18	12	13	7	9	1	9		10
21-25	—	—	0	—	10	14	5	2	14		7
26-30	—	—	—	—	3	20	6	4	3		7
31-4 November	—	—	—	—	0	0	1	4	0		1
				1963	1964	1965	1966	1967	1968		Mean
First quartile											24 Sep.
Median date				28 Sep.	3 Oct.	1 Oct.	25 Sep.	8 Oct.	29 Sep.		30 Sep.
Third quartile											7 Oct.
Duration (5-95% of records) (days)				27	38	39	33	34	39		35
r.m.s. deviation of median dates (days)											4.6

*These figures include data from smaller samples in 1957-59, not otherwise used in the table.

—Data missing or inadequate.

TABLE 3. FREQUENCY OF BLACKPOLL WARBLERS AT BANDING STATIONS

Station		No. Years	Years	Net-hours	Blackpoll Warblers banded Total	per 1000 nh	% of warblers	% in 4 peak days
	Coastal							
A.	Mount Desert, Maine	6	1959-67	9,709	263	26.9	17.8	43
B.	Nantucket, Massachusetts	12	1957-68	29,701	864	29.1	13.3	61
C.	Block Island, Rhode Island	6	1959-68	20,641	389	18.9	7.6	50
D.	Tiana Beach, L. I., New York	9	1958-66	20,796	369	17.7	15.6	61
E.	Island Beach, New Jersey	9	1960-68	194,422	3,783	19.5	9.2	46
F.	Ocean City, Maryland	12	1957-68	200,883	1,291	6.4	8.9	48
G.	Kiptopeke Beach, Virginia	6	1964-69	78,508	612	7.8	4.0	62
	Subcoastal							
H.	Sudbury, Massachusetts	7	1962-68	18,740	6,084	325	84	40
I.	Jamesburg, New Jersey	6	1958-63	45,172	647	14.3	34	48
J.	Chestertown, Maryland	6	1961-68	54,079	154	2.8	6.2	64
	Far inland							
K	Cedar Grove, Wisconsin	7	1958-64	c.117,000	379	3.2	5.6	45
L.	Long Point, Ontario	9	1960-68	traps	1,029	117*	17.5	60
M.	Powdermill, Pennsylvania	8	1961-68	no data	319	no data	3.3	55
N.	Allegheny Front, W. Virginia	6	1963-68	17,269	1,363	79	21.4	65

*Based on a single year of mist-netting only.

set up permanent stations on the coast and to operate them daily for long periods. Less successful attempts were also made to encourage systematic banding at inland stations. In the 12 years of the program about 750,000 birds have been banded at 100 stations (C. S. Robbins *in litt.*); including some large independent stations inland, data are available for more than one million banded birds.

In a preliminary screening of the data I examined records from all stations operated on a daily or near-daily basis from mid-September to mid-October in one or more years. Because the pattern of occurrence varied markedly from year to year (Table 2) I selected only those stations manned during at least five different years. Among the coastal stations, I then selected the most fully manned in each state, discarding two from Maine, one from Rhode Island, two from Long Island, and one from New Jersey. I use data from seven coastal stations, three stations less than 150 km from the coast, and four far inland (Table 3).

Table 2 illustrates how the data were extracted for one typical station—Ocean City, Maryland. The first three lines list for each year the total number of net-hours, number of Blackpoll Warblers banded, and the average number banded per 1000 net-hours. Although there are several reasons why this average netting-rate is not an exact measure of abundance, it is probably the best index for comparison of abundances between years at the same station (Robbins 1968). It may not be a good index of differences in abundance between stations, because netting-rates are affected also by local factors such as the structure of vegetation and choice of net-sites.

The next two lines list the number of other warblers banded and the percentage of Blackpolls among the warblers (in making the calculation, Myrtle Warblers were excluded because many stations close before the peak passage-period of this late migrant). This percentage is probably the best index for comparison of abundances at different stations in the same year; it may not be a good index of differences between years, because the relative abundance of other species may vary also. The next line lists the percentage of the season's total banded in the four best days for the species: this provides an index of the degree of concentration of the banding records into "waves."

The remainder of the table analyzes variations in the seasonal pattern of occurrence. Data for 1957-59 were not used because the station closed before 3 October in those years (incomplete data from 1960-62 were admitted, but their exclusion yields statistically indistinguishable results). For the remaining seasons, the banding totals were grouped in five-day periods as shown, corrected for differences in netting-effort if the number of net-hours per five-day period differed by more than 20% from the mean for the year, and scaled so that the peak period in each year was assigned the figure 100. The average of the scaled totals then places equal weight on the records from each year and is listed in the last column. Inconsistency in pattern from year to year is

indicated by the occurrence of seasonal peaks in four different five-day periods (indicated in boldface in the last column), and by the fact that the largest weighted average for any five-day period was only 68. The next lines give the median date of the banded sample in each year, and the first and third quartiles of the weighted averages. The mean of the medians in the six fully covered years (1963-68) is in good agreement with the median of the weighted averages. The root-mean-square deviation of the annual medians (4.6 days) is a measure of year-to-year variation in passage period. The penultimate line gives the interval between the 5th and 95th percentile of the banded sample in each year, a measure of the duration of the migration period.

Tables 3 and 4 tabulate the same quantities for the other 13 regularly manned stations.

Differences between coastal and inland stations.

Tables 3 and 4 indicate some average differences between the records of Blackpoll Warblers at coastal and inland stations. On the average, at the inland stations:

(1) more Blackpolls are caught per 1000 net-hours;
(2) more Blackpolls are caught per 100 warblers;
(3) the peak period varies less from year to year;
(4) the median dates of passage vary less from year to year;
(5) the migration period (5th-95th percentile) is much shorter.

However, the first four of these differences are not very clear-cut, and only the fifth is statistically significant ($p = 0.001$, Mann-Whitney U-test). One reason for the lack of consistency is that both groups of stations are heterogeneous: that at Mount Desert, where the records resemble those of the inland group in the above respects, is about 12 km from the Atlantic Ocean; those at Chestertown, Cedar Grove and Long Point, where the records resemble those of the coastal group, are on the shores of Chesapeake Bay, Lake Michigan and Lake Erie respectively.

There is probably also a tendency for occurrences at the inland stations to be less concentrated into peaks, but this tendency is obscured in Table 3 for two reasons. (1) For statistical reasons, the measure of this tendency used in Table 3 is biased upwards in small samples (e.g. Chestertown and Powdermill). (2) At several coastal stations it is customary to operate fewer nets on days of heavy falls of migrants, which de-emphasizes the numerical importance of the peaks.

Other differences between coastal and inland records of Blackpoll Warblers have been described. At coastal stations the proportions of immature birds are higher and the mean weights lower (Nisbet *et al.* 1963, Murray 1966a,b), and waves of migrants sometimes arrive one day earlier than those observed inland, in consistently different weather (Baird *et al.* 1959). In some years passage continues at coastal stations later than at corresponding inland stations (Nisbet *et al.* 1963). Table 3 provides further evidence for this

TABLE 4. MIGRATION DATES OF BLACKPOLL WARBLERS AT BANDING STATIONS

Station	Weighted mean frequencies (see text)													
	Aug.	September						October						Nov.
	27-31	1-5	6-10	11-15	16-20	21-25	26-30	1-5	6-10	11-15	16-20	21-25	26-30	31-4
Coastal														
Mount Desert, Maine	2	7	17	**58**	**51**	**42**	**58**	12	0	0	2	—	—	—
Nantucket, Massachusetts	0	+	**18**	**27**	21	**42**	**45**	**63**	**37**	**36**	20	4	4	0
Block Is., Rhode Island	0	1	7	41	**51**	57	**48**	**46**	**47**	**62**	12	0	0	0
Tiana Beach, L. I., New York	0	3	1	**14**	**41**	**58**	**50**	**43**	23	**41**	16	2	4	0
Island Beach, New Jersey	+	5	14	21	**46**	**65**	**55**	**59**	**39**	24	8	9	2	1
Ocean City, Maryland	0	1	4	18	30	**38**	**68**	**55**	**59**	18	10	7	7	1
Kiptopeke Beach, Virginia	0	0	1	6	6	17	34	**85**	**43**	**33**	**34**	10	2	—
Subcoastal														
Sudbury, Massachusetts	—	3	16	44	**63**	**88**	**79**	45	16	3	2	—	—	—
Jamesburg, New Jersey	0	0	0	33	23	**46**	**79**	**68**	28	13	2	+	0	1
Chestertown, Maryland	3	0	13	25	**46**	**53**	**37**	**59**	**56**	29	19	1	0	0
Far inland														
Cedar Grove, Wisconsin	19*	**69**	57	**62**	**54**	**55**	18	12	13	0	3	0	0	0
Long Point, Ontario‡	7†	**42**	**56**	**36**	21	**38**	**35**	17	6	4	+	+	0	0
Powdermill, Pennsylvania	2	0	**23**	39	**43**	**59**	**40**	**46**	36	17	1	+	1	0
Allegheny Front, W. Virginia	+	3	**30**	20	27	**57**	**56**	48	**47**	3	2	1	—	—

For full explanation see text. —, data inadequate or lacking. +, recorded but mean frequency less than 1. *, + in period 22-26 August. †, + in period 17-21 August. ‡, data not corrected for irregularity in trapping effort, but calculations based on daily censuses gave statistically indistinguishable results.

Table 4 (continued)

Station	First Quartile	Median Date	Third Quartile	r.m.s. deviation	Mean duration
Coastal					
Mount Desert, Maine	14 Sep.	19 Sep.	25 Sep.	5.3	30
Nantucket, Massachusetts	22 Sep.	1 Oct.	8 Oct.	5.4	35
Block Is., Rhode Island	20 Sep.	29 Sep.	9 Oct.	9.1	30
Tiana Beach, L. I., New York	22 Sep.	29 Sep.	8 Oct.	4.9	33
Island Beach, New Jersey	21 Sep.	28 Sep.	5 Oct.	4.1	37
Ocean City, Maryland	24 Sep.	30 Sep.	7 Oct.	4.6	35
Kiptopeke Beach, Virginia	1 Oct.	5 Oct.	13 Oct.	2.0	40
Subcoastal					
Sudbury, Massachusetts	18 Sep.	24 Sep.	28 Sep.	1.6	26
Jamesburg, New Jersey	22 Sep.	28 Sep.	3 Oct.	3.7	24
Chestertown, Maryland	20 Sep.	30 Sep.	7 Oct.	6.9	29
Far inland					
Cedar Grove, Wisconsin	6 Sep.	13 Sep.	21 Sep.	3.7	32
Long Point, Ontario	7 Sep.	14 Sep.	25 Sep.	6.7	29
Powdermill, Pennsylvania	18 Sep.	24 Sep.	3 Oct.	6.1	27
Allegheny Front, W. Virginia	20 Sep.	27 Sep.	3 Oct.	4.1	26

last difference in Massachusetts, New Jersey and Maryland; additionally, at Island Beach the passage period appears to extend several days earlier than at the inland station at Jamesburg.

Together these differences suggest three conclusions:

1) records on the coast (of both the Atlantic Ocean and the Great Lakes) consist to a substantial extent of waves of young birds;

2) these waves occur in weather different from that characteristic of migration overland;

3) they include a disproportionate number of birds which are out of season and perhaps out of range.

Because such birds may have wandered or drifted far out of their "correct" routes (Nisbet *et al.* 1963), caution should be exercised in using coastal records to infer the location of these routes. However, some of the biases are likely to be common to all coastal stations, so it should be permissible to compare their results.

Geographical and seasonal patterns.

On both measures of abundance used in Table 3, Blackpoll Warblers become progressively less numerous along the coast from Maine and Massachusetts south to Maryland and Virginia. The decrease is similar, but much more rapid, at the few stations inland on the coastal plain.

Within the limits of statistical errors in median dates, Table 4 shows that the passage of Blackpoll Warblers is essentially simultaneous at the coastal stations from Massachusetts to Maryland, and at the inland stations in New Jersey and Maryland. Passage is earlier at the inland station in Massachusetts and the station in Maine, later at the coastal station in Virginia, and progressively earlier at the stations far inland from West Virginia north and west to Wisconsin.

STATUS IN THE EASTERN AND SOUTHEASTERN UNITED STATES

Although the coastal states from Maryland southwards are the most important area for this survey, long-term daily sampling of migrant warblers with mist-nets has not been carried out south of Virginia. Accordingly, I have reviewed the status of the species in these states and in those adjoining them to the west, using unpublished sight- and banding-records as well as published data. Table 5 summarizes the results of the review: the remainder of this section lists sources and summarizes unpublished records. Numbered references refer to the Special Bibliography; OR indicates unpublished banding data supplied to "Operation Recovery."

Sources not used.

This review is based primarily on modern records. Burleigh (1934) reported widespread confusion prior to 1934 between the Blackpoll and Bay-breasted Warblers in Georgia and North

Carolina; according to Mengel (1965) and A. R. Laskey (*in litt.*) the same error was frequently made in Kentucky and Tennessee. Accordingly records published before 1934 are ignored unless individually vouched for by a subsequent author.

Undocumented general statements of status made in state bird-books by Sprunt and Chamberlain (1952), Sprunt (1954), Pearson, Brimley and Brimley (1942), and Burleigh (1958) have also been ignored: in each case these disagree with more recent, documented assessments cited below. The first two books repeated earlier, doubtful statements by Wayne (1910) and Howell (1932) respectively; Pearson *et al.* (1942) did not distinguish between spring and autumn records; Burleigh (1958) listed inland records but repeated an undocumented generalization from his 1934 paper about the coastal status.

Inland states. Ohio: abundant (Borror 1950, Trautman 1956, Table 1) except in the southwest where rare (Mengel 1965). Western Pennsylvania: common to abundant (Todd 1940, Leberman 1965, Leberman and Heimerdinger 1967, Tables 1 and 3). West Virginia: common to abundant (Hall 1964a,b, 1967, Tables 1 and 3, Mrs. C. Katholi). Kentucky: 3 certain records (Mengel 1965, K. P. Able); 2 doubtful records in Table 1 (ref. 23). Tennessee: 24 records (all in Table 1). Alabama: 6 records of 9 birds (Imhof 1962 and *in litt.*). Mississippi: no record traced. Louisiana: 2 records (K. P. Able).

Maryland and District of Columbia. "Common, occasionally abundant . . ." (Stewart and Robbins 1958, Table 3). 4.9% of 6162 warblers banded at six inland banding stations 1958-68 (Table 3, OR). Scarcer in nocturnal accidents (Table 1).

Virginia. Common at four localities in the northeast (Murray 1952, Table 3). Elsewhere "absent to fairly common" . . . "much more common in spring than in fall" (Murray 1952). Few recent data (Table 1, OR).

North Carolina. Northern coast: 35 of 682 warblers banded on Outer Banks, 1956-68 (Peacock 1964, Grey *et al.* 1964, Hailman and Hatch 1964, H. D. Haberyan, P. W. Sykes, Jr., OR). Southern coast: no records. Inland: 23 of 506 warblers banded at Chapel Hill, 1965-68 (R. P. Teulings); otherwise scarce to rare in the east and center (Wetmore 1941, Dawley 1954, Hauser 1967, Blake 1968, J. R. Norwood, Table 1, OR); only one record in the west (Burleigh 1934, R. Peake, T. M. Rial). Dates: most after 27 September; median of recorded dates 15 October.

South Carolina. Charleston: only one record among thousands of warblers in nocturnal accidents (Table 1); 6 of 1233 warblers banded 1963-68, but seen more commonly on the coast, scarcer inland (T. A. Beckett III); 32 of 91 warblers banded October 1959 (OR). Inland: about 2 of 150 warblers banded annually at Effingham in the northeast, and others seen (E. C. Clyde); elsewhere only 3 records traced (Norris 1963 and *in litt.*, T. M. Rial, R. Peake, Table 1).

Georgia: 37 listed among 2525 warblers killed 6-8 October 1954, at four localities within 250 km of the coast (ref. 66): of these 23 were in a sample with very unusual species proportions and should be regarded as doubtfully identified (D. W. Johnston). Otherwise very rare generally (Greene *et al.* 1945, Denton and Hopkins 1969, J. F. Denton, R. A. Norris, Table 1). Inland: 10 records published (Denton 1949, Burleigh 1958); 4 unpublished (T. M. Rial). Coast: 3 records published (Burleigh 1958, ref. 67); 1 unpublished (O. L. Austin, Jr., OR). I. R. Tomkins, the doyen of coastal observers (Tomkins 1958), first listed it as rare (in Greene *et al.* 1945), but recorded some in 1954 (in ref. 66, Tomkins 1960). Unrecorded from well-studied Sapelo Island (Teal 1959, Kale and Hyppio 1966).

Florida. Two well-documented records of large numbers will be discussed in the next section. Otherwise rare generally (Stevenson 1962, Cunningham 1965, Robertson and Ogden 1969); annual reports in *Audubon Field Notes* 1956-69 cite individual records, 25 in 1968 occasioning special comment (Robertson and Ogden 1969). Northwest: 2 among 9671 warblers killed in nocturnal accidents (refs. 137,138,150,180); no other records (Weston 1965, J. C. Ogden). Inland: two records (Robertson and Ogden 1969); otherwise negative statements (Nelson 1952, D. W. Johnston). West coast: two records (Stevenson 1960, Cunningham 1965). East coast: 9-10 among more than 1700 birds killed at Jacksonville, but only 2 sight records there (S. A. Grimes, R. O. Edwards); irregular in Brevard County, where up to 22 seen in some years, none in others (A. D. Cruickshank, W. F. White); rare at Vero Beach (H. W. Kale II); formerly rare at Miami (3 records in 349 field trips in 37 years: L. A. Stimson), more regular since 1960 with 10 in 1966 (L. A. Stimson) and 12 in 1968 (Robertson and Ogden 1969). Southern Peninsula: about one in 5000 warblers, on average (W. B. Robertson, Jr.). Florida Keys: 4 records (Greene 1946, Hundley 1962, Sprunt 1963, Robertson and Ogden 1969, A. Sprunt IV, Mrs. B. Fisk). Dates: extremes 12 September (Robertson and Ogden 1969) and 13 November (A. D. Cruickshank); about half 10-24 October; median 17 October.

Influxes into Florida. An influx in October 1964 contrasts strongly with the above picture of general rarity. At Jacksonville 273 Blackpoll Warblers (14% of the total of 1950 warblers) were killed at the television towers during three nights, 5-9 October (Cunningham 1965). In the Indian River area 322 Blackpoll Warblers (9% of the total of 3511 warblers) were killed at various places during the same nights (Case *et al.* 1965, W. F. White). "Moderate mortality" was also recorded at Daytona Beach and St. Augustine (Cunningham 1965—details untraced). Following the influx, unusual numbers were seen in other places: at least 27 at West Palm Beach (Cunningham 1965); 16 in two days at Merritt Island (Case *et al.* 1965, W. F. White); four at Coconut Grove, the highest count in 25 years (*per* L. A. Stimson). On 7 October the town of Franklin Park was "crawling with warblers," the Blackpoll being one of the four commonest among "hundreds" (Tucker 1965)—

TABLE 5. SUMMARY OF RECORDED STATUS OF THE BLACKPOLL WARBLER IN THE SOUTHEASTERN COASTAL STATES AND IN ADJOINING STATES TO THE WEST

West Virginia: Abundant
21% of netted warblers
c. 30% of warbler kills

Kentucky: Very rare
Two certain records
None in warbler kills

Tennessee: Very rare
No sight records
0.13% of warbler kills

N. Alabama: Very rare
Six records
None in warbler kills

S. Alabama: No record

N.W. Florida: Very rare
Two certain records
0.02% of warbler kills

Inland Maryland & D. C.: Common
5% of netted warblers
1% of warbler kills

Inland Virginia: Locally common
"absent to fairly common"
Very common in N and E

Inland N. Carolina: Scarce
1 record in west
0–5% of netted warblers in E
0.25% of warbler kills

N. Georgia & inland S. Carolina:
Scarce to rare
1.3% of netted warblers in NE
Elsewhere 14 records
0.2% of warbler kills

Inland S. Georgia: Very rare
One record

W. & inland Florida: Rare
Nine records, one of large numbers

Coastal Maryland: Very common
9% of netted warblers

Coastal Virginia: Common
5% of netted warblers

Coastal N. Carolina: Common
5% of netted warblers in N

Coastal S. Carolina: Fairly common
3% of netted warblers
0.1% of warbler kills

Coastal Georgia: Scarce or rare
Two records
0.5-1.2% of warbler kills

E. coastal Florida: Sporadic
Rare and not quite regular
1% of warbler kills
Influx in October 1964 — then
11% of warbler kills

apparently the first published record inland for the entire state! Two were seen at St. Marks on 17 October (R. O. Edwards) and 9 or 10 on the coast of Franklin County on 12 October (J. C. Ogden)—the only recent records from the northwest and Ogden's only record in 104 autumn field trips. The fact that the influx was noticed in so many places, being described as "amazing" or "astonishing," attests not only to its unusual character, but also to the thorough coverage of migration throughout the state, and hence to the reliability of the reports of rarity in earlier years.

Records of numbers at Sombrero Key Light, isolated in the Straits of Florida, south of Marathon in the Lower Keys, are less convincing, however (but have been included in Table 1). Cooke (1904) cited records from the lighthouse in each year from 1887 to 1891, including a total of about 150 Blackpoll Warblers (10% of about 1500 warblers killed there altogether), most of which were killed on the nights of 13-17 October 1887. These records have been cited by Howell (1932), Bent (1953) and others. It is less well known, however, that Merriam (ref. 98) had earlier published a report of Blackpoll Warblers at Sombrero Key, eight birds from among about 900 warblers killed in the autumn of 1884: these were dated between 14 August and 9 September, earlier than any other Florida records, and including five birds earlier than all but a handful of records in the northern United States (Bent 1953). Such improbable records cast doubt on all identifications at Sombrero Key, including those published by Cooke. Neither Cooke nor Merriam recorded either the Pine Warbler or the Bay-breasted Warbler: Merriam claimed to have identified every species himself, but examined only heads and wings, which are extremely similar in the three species.

Association with storms. Cunningham (1965) pointed out the coincidence of the influx of 6-8 October 1964 into Florida with the passage of a storm which represented the dissipating stages of hurricane 'Hilda.' The storm passed eastwards along the north shore of the Gulf of Mexico and across the north part of peninsular Florida, its center being near Jacksonville at mid-day on the 5th. At mid-night on 5/6 October, at the beginning of the three-night kill at Jacksonville, the storm was centered ENE of Jacksonville: strong northeast winds and heavy rain prevailed all along the coast as far as Cape Hatteras.

L. A. Stimson independently pointed out the association of a small influx (12 birds) at Miami and Key Biscayne on 4 October 1966 with hurricane 'Inez'. In this case the birds were seen just before the arrival of the hurricane, which approached from the east and was centered just to the south of Key Biscayne at mid-day on the 4th. A third influx involving 21 birds in the same area (Robertson and Ogden 1969) started on 17 October 1968 in strong SE winds ahead of hurricane 'Gladys', then approaching western Florida from the southwest. A fourth record of 12 on the Lower Keys on 25 October 1952 (only the second record there: Hundley 1962) coincided with the passage of hurricane 'Fox' from Cuba

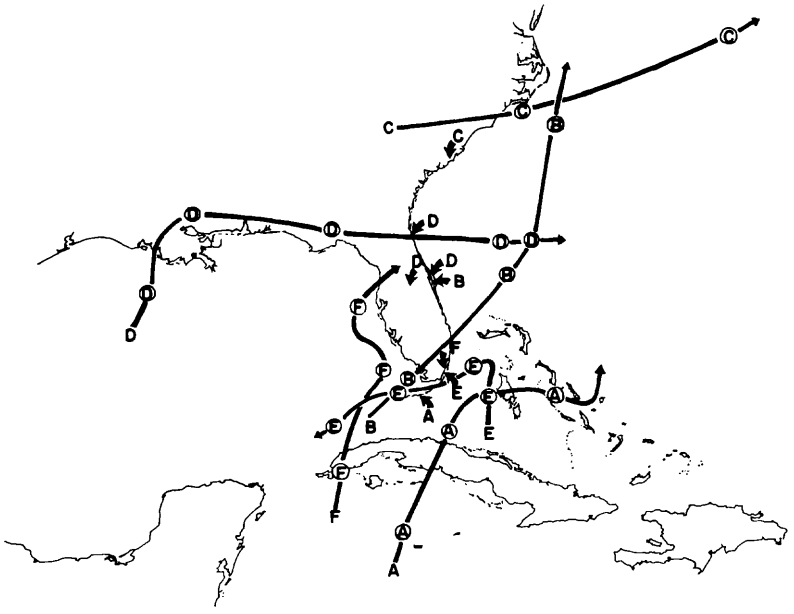

Fig. 2. Tracks of storm centers associated with falls of Blackpoll Warblers in Florida and South Carolina.

Circles denote the positions of the storm centers at 0100 on the corresponding date (data from Cry (1965) and U. S. Weather Bureau daily weather maps). Arrows denote falls of Blackpoll Warblers (details in the text).

A. Hurricane 'Fox', 24-26 October 1952.

B. Storm, 12-13 October 1955 (center ill-defined on 13 October).

C. Storm, 15-16 October 1959.

D. Hurricane 'Hilda', 3-4 October, and subsequent storm, 5-7 October 1964.

E. Hurricane 'Inez', 3-5 October 1966.

F. Hurricane 'Gladys', 16-18 October 1968.

northeast to Andros, its center passing 120 miles to the southeast of the Lower Keys during the morning. A fifth record of 22 in Brevard County on 12 October 1955 took place in "a wild easterly storm with wild gusty winds" (A. D. Cruickshank). Thus every dated record of more than four birds together in Florida coincided, within a few hours, with the passage of a hurricane or other severe storm. I have not traced any other published records of numbers

in the southeastern states in recent years, but one unpublished record—32 banded at Folly Beach, S. C., from 17 to 20 October 1959 (OR)—followed immediately after the passage on 15-16 October of a coastal low which brought strong NE wind to the coast.

Three older records in the southeastern states of numbers of Blackpoll Warblers, which have been treated in this paper as doubtfully identified, also coincided exactly with hurricanes. These were on the coast of South Carolina on 14 October 1885 and 26 September 1894 (Wayne 1910) and at Sombrero Key, Florida, from 13-17 October 1887 (Cooke 1904): the corresponding hurricanes were '1885/8', '1894/3' and '1887/11' (plotted by Cry 1965).

Figure 2 indicates the tracks of the three hurricanes and the three other storms clearly associated with influxes of Blackpoll Warblers. Hurricanes are so infrequent in the area concerned (averaging about 0.6 per year in the period 20 September-20 October between 1901 and 1963—Cry 1965) that this association could not have arisen by chance. The discovery of this association resolves some of the apparent contradictions in the published records for the area, because it indicates that the occurrence of the species is indeed sporadic. More important, it shows that in the absence of storms, the species is extremely rare throughout Florida.

It is perhaps significant that three of these six influxes were earlier in the season than the median date for other records of the species in Florida; only one small influx was later. The well-documented record of large numbers, on 5-8 October, was earlier than all but a small fraction (5%) of the Florida records in non-hurricane years.

OCCURRENCES IN THE WEST INDIES

According to J. Bond (*in litt.*), the Blackpoll Warbler is seldom seen on migration in the northernmost West Indies. Cooke (1904) stated that it was common in the northern Bahamas, scarce in the south; however, A. Patterson (*in litt.*) has not observed it on Andros and I have traced few other records of grounded migrants. Most of the birds listed in Table 1 were killed during a northeast storm (ref. 68), thus resembling the Florida records.

It is scarce in the Greater Antilles (Cooke 1904, Wetmore and Swales 1931, Bond *in litt.*); specifically, it is uncommon in Cuba (Barbour 1943) and Hispaniola (Wetmore and Swales 1931), and rare on Jamaica (Mrs. A. C. Downer and Prof. D. B. Stewart *in litt.*). It is common in Puerto Rico (Danforth 1936, McCandless 1961) and common, sometimes abundant, in the Virgin Islands (Beatty 1942, W. B. Robertson *in litt.*). Occurrence on any of the Lesser Antilles is more or less sporadic, but large numbers may appear on an island for a day or so (Bond 1956 and *in litt.*): such occurrences of large numbers have been described for Guadeloupe (Lawrence 1885), Trinidad (Junge and Mees 1958, Herklots 1961), Curaçao and Bonaire (Voous 1957).

Many of the West Indies records have been earlier in the season than the majority of arrivals in Florida. Voous (1957) records one on Curaçao on 11 September, earlier than any record in Florida 2000 km to the northwest. There are records in late September from at least three other islands, records of numbers from the first few days of October in Puerto Rico, Trinidad and Curaçao, and a record of large numbers on Guadeloupe on 10 October. The last date is the same as that of the first quartile of the Florida records (see above). De Schauensee (1964) cites a record in early September in Colombia.

In summary, the Blackpoll Warbler seems generally more frequent in the eastern than the western part of the West Indies, but appears irregular everywhere except perhaps in Puerto Rico and the Virgin Islands.

SYNTHESIS

The pattern of occurrence in Southern Canada and the northern United States, as recorded in Table 1, agrees exactly with the hypothesis of Cooke (1904), amplified by records in Bent (1953) and mapped by Murray (1966a), that the western populations of the Blackpoll Warbler fly ESE to the Atlantic Coast, and that the species as a whole is concentrated in late September between Virginia and Nova Scotia. The steady progression of arrival and median dates in the banded samples from Wisconsin, through Ontario and Pennsylvania, to Maryland and New Jersey (Table 4), further supports the hypothesis of a movement from WNW to ESE.

Cooke (1904) and Murray (1966a) further proposed that all Blackpoll Warblers then fly SSW to Georgia and Florida, where they turn SE again to cross the Caribbean Sea. Neither author offered any evidence for the hypothesis, however, and six features of the survey reported in this paper oppose it:

1. Data from nocturnal accidents (Table 1), banded samples (Table 3) and sight records (Table 5) all indicate that the species becomes progressively less numerous southwards through the coastal states from Maine to Florida. This progression is most pronounced in inland areas (Tables 3 and 5), but is marked even at coastal stations (Tables 3 and 5) where out-of-range stragglers are expected to confuse the picture.

2. The species is rare everywhere south of a line from Cincinnati, Ohio, to Charleston, South Carolina. Despite good semi-quantitative reports on autumn migration from a network of observers in Florida, it is reported annually from only one area. Even in this area, in proportion to other migrant warblers, it is 25,000 times less frequent than, for example, in eastern Massachusetts. According to Cooke's hypothesis, however, it should be much more concentrated in Florida than in Massachusetts.

3. The dates of passage in Table 4 are essentially simultaneous from eastern Massachusetts to Maryland and West Virginia, contrary to the idea of a southwestward movement of the population.

4. An abrupt change of about 16 days in median dates occurs within 300 km between Maryland and northern North Carolina, thus coinciding with the steepest gradient in abundance.

5. Sporadic falls of small to moderate numbers (by northeastern standards) in Florida, the Bahamas and probably in South Carolina have coincided exactly with storms, suggesting disruption of migration.

6. Arrivals in the West Indies and even in South America have been recorded earlier than arrivals in Florida.

These data support an alternative interpretation: that most of the birds which are concentrated in the northeast in late September leave the North American continent without another stop (except perhaps for stragglers and storm-harried birds on the southeast coast). Nisbet *et al.* (1963) have already proposed this for part of the population which stops in New England. The results of this survey suggest that a major fraction of the population of the species makes a similar flight.

The data in Tables 1 and 3 indicate that the greatest concentrations of Blackpoll Warblers occur east of New York City, at least as far as southern Nova Scotia. Further observation in Nova Scotia and Newfoundland is required to determine the eastern limit. Table 5 suggests that the southwestern limit of large numbers is in the region of Cape Hatteras, but critical data are lacking for this area and it is likely that there is no sharp boundary.

The only evidence for the direction of departure is the repeated observation by moon-watching and radar in Massachusetts of mass flights with average track about 172° (Nisbet *et al.* 1963, Drury and Nisbet 1964, Nisbet and Drury 1969). The identification of these birds as Blackpoll Warblers is indirect, depending on views of silhouettes in front of the moon and on correlations of mass flights with observed decreases in numbers of that species; however, all other species appear less likely (Nisbet and Drury 1969).

On the western margin of the flights, some birds must pass within 100 miles of southern Florida, because the influence of the hurricanes plotted on Figure 2 extended no more than 200 miles; however, the numbers involved were extremely small. The influx in Florida in October 1964, and a kill on Grand Bahama in October 1966 (ref. 68), coincided with strong NE winds extending from Cape Hatteras and beyond; however, even these kills were small by comparison with records in Table 1 from Long Island and New England. Hence I tentatively place the western limit of large numbers as running SSE from Cape Hatteras to Hispaniola.

There is no evidence for the eastern limit of the flights, because there are no observations east of Sable Island, Bermuda, the Lesser Antilles and Trinidad. However, the irregular occurrence of grounded migrants in the West Indies suggests that most birds do not usually stop there.

Fig. 3. Distribution and migration of the Blackpoll Warbler.
(Oblique Mercator Projection: Pole 20°N, 25°E)
Vertical hatching: breeding range (from Bent, 1953, A.O.U. Checklist, 1957, and vegetation maps).
Diagonal hatching: winter range (little known).
Stippling: common to abundant on autumn migration (this survey).
Stars: sporadic falls associated with storms (Fig. 2).
? : too few recent records to assess status.
Short arrows: departures tracked by radar (probably this species).
Long arrows: Northeast Trade winds (zone of 50% persistence).

On the basis of the above evidence, the regional occurrence of the Blackpoll Warbler on autumn migration may be plotted as on Figure 3. Later papers in this series will report studies of the adaptations of the species to long-distance migration.

COMMENTS ON SOURCES OF DATA

This survey has been based largely on material collected during the last 10-15 years: data published earlier have proved to be almost as much hindrance as help. This is due in part to special problems raised by the Blackpoll Warbler: its similarity to other species, its unique distribution pattern and its fluctuating numbers in many places. However, it is due primarily to the paucity of quantitative information. To plot the migration route of a species from distributional data requires numerical comparisons of abundance in different regions: Moreau (1961) has pointed out the extreme difficulty of doing this from conventional published accounts. The most ambitious of previous attempts to plot migration routes quantitatively used systematically planned observations (Stevenson 1957).

Five sources of data have been used in this survey:

1. State handbooks and checklists. Few of these include quantitative estimates, and most attempt to generalize a mass of incomplete data into a single ill-defined adjective. The problem for the user is that words such as "common" are based on no absolute standard, and often appear to reflect the writer's idea of the species' total numbers, which in turn derives from his local experience. There are in fact a few hints in the literature that the Blackpoll Warbler is especially numerous in the north and northeast U.S.A. —e.g. "lavish abundance" (Griscom and Snyder 1955); ". . . during latter September may outnumber all other species combined" (Sutton 1928); ". . . certainly far more numerous than all the other warblers put together, excepting of course the Myrtle" (Griscom 1933); "outnumbers all other warblers combined" (Todd 1940). However, books on birds of the southeastern states also describe the Blackpoll as common in autumn: I have found in this survey (see Table 5) that these statements generally disagree with modern observations.

2. Local checklists and annual reports. There is a truly enormous literature under this heading, growing by dozens of titles each year. I did not attempt a comprehensive review, because I found that, at least for areas which I knew myself, this material was systematically and deliberately biased towards the unusual, especially early and late dates.

3. Unpublished notes of local ornithologists. These appear to be a rich source of qualitative data, incompletely tapped by the compilers of local and regional checklists. However, few ornithologists keep systematic notes on numbers of migrants, and there remains the problem of assessing adjectives such as "common" and "rare".

There is a notable exception in Florida, where many local ornithologists have kept long-term numerical records of birds encountered on regular field-trips. Such records are badly needed in other areas.

4. Banding stations. These appear to provide good quantitative samples of migration, the best available in some areas (Tables 3-5). However, this study has raised two problems. The first is that both the numbers and the seasonal pattern of occurrence of Blackpoll Warblers vary greatly from year to year at most stations, so that daily banding over a number of years is required to obtain self-consistent averages. The second is that data from the coast, where most of the permanent stations have been set up, appear to be systematically biased towards young, out-of-season, and out-of-range stragglers. Coastal sites were selected for these stations because of dense local concentrations of birds: it appears likely that in this way large samples have been obtained at the expense of representativeness.

I was surprised to find that the irregular peaks were nearly as prominent at many of the inland stations as on the coast. Some of the inland stations were set up on lake shores and mountain ridges where grounded migrants were locally concentrated: hence their data may be nearly as biased as those of the Atlantic coastal stations. Indeed, it seems possible that the irregular peaks occur everywhere, so that no single station can provide a representative sample.

5. Nocturnal accidents. The self-consistency of regional averages, and their agreement with long-term mist-netting averages where available, suggest that data from nocturnal accidents can provide good quantitative samples, at least for species which migrate at the period concerned. Night-to-night and year-to-year fluctuations in species composition appear, on the basis of limited data, to be smaller than those in banded samples. The main limitations of the data are the gaps in some areas where few birds have been collected (even in areas where both television towers and ornithologists are dense), and the irregularity of the kills in most places, so that a long period is required to obtain reasonable averages. However, this is potentially the best source of information on regional differences in relative abundances, and further collections to fill the gaps will be of great value.

SUMMARY

Occurrences of Blackpoll Warblers on autumn migration throughout eastern North America are reviewed, using quantitative data wherever available.

Records are analyzed of 140,000 warblers killed during nocturnal migration at 135 places. Expressed as a proportion of the total number of warblers, Blackpoll Warblers are relatively common around the Great Lakes, abundant on the Atlantic Coast from New York to Nova Scotia, and in West Virginia; they are rare in

southern and southeastern states except for one or two records of numbers in Florida.

Systematic samples of migrant warblers over six or more years are available from seven coastal and seven inland banding stations north of Virginia and West Virginia. The Blackpoll Warbler becomes progressively less numerous along the coast from Maine and Massachusetts southwest to Maryland and Virginia. Median dates of passage become progressively later from Wisconsin ESE to Maryland, but not from Massachusetts SW to Maryland. Among other differences, records at coastal stations extend over much longer periods than at nearby inland stations.

Records of Blackpoll Warblers in the eastern and southeastern coastal states are reviewed. They become less numerous southwards, especially inland, and are generally rare south of Charleston. Sporadic falls of moderate numbers in Florida have coincided exactly with hurricanes and other storms.

Occurrences in the West Indies appear generally irregular except perhaps in Puerto Rico and the Virgin Islands.

No support is found for the Cooke-Murray hypothesis of concentrated passage through the southeastern United States. Most Blackpoll Warblers appear to fly directly from the northeastern U. S. towards their wintering grounds in northern South America.

Quantitative data on autumn migrants have only recently become available and are still insufficient for detailed analysis. Published summaries are too generalized and often unreliable. Present-day observing and recording of common species provides very little useful information. Systematic mist-netting can provide quantitative data, but most netting stations are now sited inappropriately. Television tower kills provide the best quantitative data, but there are still important gaps in coverage.

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SPECIAL BIBLIOGRAPHY: REFERENCES TO NOCTURNAL ACCIDENTS

For the sake of brevity, only the first author, journal, volume number and first page number are listed. Papers marked with an asterisk (*) contain useful information on causes of the accidents; otherwise only papers cited in the text are listed.

The most complete of several earlier bibliographies is that of Buskirk (1968), who also tabulated many published species lists. The remaining references were found by literature search, in complete sets of the *Auk*, *Wilson Bulletin*, *Condor* and *Bird-Banding*, and in those state and local journals available in local libraries (usually examined 1948-1969). Papers in all these journals were examined by title only: I did not read reports with titles such as "The Season", "Fall Migration Report", etc. The main sources of incompletely published information were the "Fall Migration" issues of Audubon Field Notes, 1947-1969. By correspondence I obtained details for most kills since 1960, but for few in earlier years. A circular letter was sent to regional recorders in states for which few records had been published, but it elicited very few additional records.

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TABLE 6. PERCENTAGE FREQUENCIES OF 37 SPECIES AMONG KILLS OF WARBLERS IN SELECTED STATES

State		Northern Tier			Middle Tier		Southern Tier	
		Wisconsin	Michigan	Ontario	Tennessee	Maryland	Florida	Georgia
No. of warblers		10,204	4,342	2,752	10,019	2,424	9,089	3,132*
References		71, 72	22	13	44	163	138	66, 67
Black-and-white	W	2.9	2.7	1.4	3.7	10.6	4.1	4.2
Prothonotary	S	0	0	0	0.03	0	1.0	0.03
Swainson's	S	0	0	0	0.04	0	0.66	0.03
Worm-eating	S	0	0	0	0.20	0.12	1.2	0.28
Golden-winged	W	0.29	0.07	0.04	0.10	0.04	0.57	0.22
Blue-winged	S	0	0	0	0.05	0.12	0.36	0
Tennessee	N	11.9	10.1	3.8	19.3	1.0	3.5	9.3
Orange-crowned	N	0.28	0.14	0.04	0.14	0	2.3	0.03
Nashville	N	1.6	7.3	3.1	0.58	0.58	0.01	0.19
Parula	W	0.11	0.14	0.22	0.11	2.4	7.5	1.1
Yellow	W	0.22	0.16	0.36	0.21	0.33	0.58	0.22
Magnolia	N	15.4	10.2	10.6	14.1	16.2	3.1	16.4
Cape May	N	2.5	3.2	0.72	0.11	0.33	0.04	0.19
Black-throated Blue	N	0.05	0.67	3.9	0.24	2.5	0.22	4.1
Myrtle	N	0.56	0.76	0.83	0.59	1.1	10.4	0.03
Black-throated Green	W	0.81	1.6	1.2	2.5	1.3	0.37	0.67
Cerulean	S	0	0	0	0.07	0	1.0	0
Blackburnian	N	1.0	1.1	4.2	2.6	3.1	2.1	4.5
Yellow-throated	S	0	0	0	0.08	0	1.1	0.03
Chestnut-sided	W	11.3	4.4	6.6	6.0	9.0	3.5	14.2

(Table 6 Continued)

TABLE 6. PERCENTAGE FREQUENCIES OF 37 SPECIES AMONG KILLS OF WARBLERS IN SELECTED STATES

State		Northern Tier			Middle Tier		Southern Tier	
		Wisconsin	Michigan	Ontario	Tennessee	Maryland	Florida	Georgia
Bay-breasted	N	12.6	3.7	10.4	6.9	3.1	1.6	1.6
Blackpoll	N	7.0	24.6	7.0	0.11	0.78	0.02	0.48
Pine	S	0	0.07	0	0.03	0	1.5	0.32
Prairie	S	0	0	0	0.09	0.08	5.1	0.22
Palm	N	3.9	2.4	0.58	2.5	0.17	15.7	3.7
Ovenbird	W	13.1	14.5	27.1	24.9	29.2	4.6	19.8
Northern Waterthrush	N	1.7	0.76	0.80	1.6	0.83	3.2	0.73
Louisiana Waterthrush	S	0.04	0	0	0	0	0.29	0
Kentucky	S	0	0	0	0.87	0	2.8	0.32
Connecticut	N	4.0	2.0	1.6	0	0.17	0	0.16
Mourning	N	0.22	0.67	0.89	0.20	0.08	0.02	0
Yellowthroat	W	0.76	2.2	10.6	5.0	5.0	8.4	7.3
Yellow-breasted Chat	S	0	0.05	0.07	1.8	0.83	0.60	0.80
Hooded	S	0	0	0	0.56	0.04	6.6	2.0
Wilson's	N	0.09	0.85	0.29	0.15	0.33	0.02	0.06
Canada	N	0.22	1.0	2.1	0.87	1.9	0.08	0.29
American Redstart	W	7.1	5.0	1.4	3.6	8.8	5.7	6.1

Notes. For references see Special Bibliography. The areas selected were those for which a large sample was summarized in one or two sources. All samples are based on a number of kills; except for Georgia all span the entire autumn season. S: southern species; N: northern species; W: wide-ranging species (see Appendix). *Omitting one doubtful sample discussed in the text.

APPENDIX

VARIATIONS IN ABUNDANCE AMONG OTHER WARBLERS

Table 6 lists the percentages of 37 species of warblers among seven large samples from television tower and lighthouse accidents. Species whose breeding range is largely north of latitude 43°N are labelled N; those whose breeding range is largely south of 43° are labelled S; wide-ranging species are labelled W. Table 7 summarizes the average proportions of the three groups of species in three tiers of stations. If the southward flow of migration were of uniform density from west to east, the simplest interpretation would be that the mean density of warbler migration is about 1.5 times larger over the southern tier than over the northern tier: for every 60N and 40W birds that pass the northern tier, about 60N, 70W and 20S birds pass the southern tier. I assume that this is a rough indication of the increase in the number of birds with decreasing latitude. However, this simple interpretation cannot be literally correct, because the data for most individual species in Table 6 show as marked differences from west to east as from north to south. These differences in many cases appear to indicate eastward or westward components to migration routes, and open up a large field for future research. Here I merely point out that the data for only five species in Table 6 present a pattern similar to that of the Blackpoll Warbler: these are the Cape May (*D. tigrina*) and Connecticut (*Oporornis agilis*) Warblers, which probably have an eastward component to their migration, and the Wilson's (*Wilsonia pusilla*), Nashville (*Vermivora ruficapilla*) and Mourning (*O. philadelphia*) Warblers, which probably have a westward component.

TABLE 7. THE DATA IN TABLE 6 AVERAGED BY GROUPS OF SPECIES AND BY LATITUDINAL TIERS OF STATIONS

	Northern tier (Wisconsin-Ontario)	Middle tier (Tennessee-Maryland)	Southern tier (Florida-Georgia)
Northern species	61.0%	41.2%	42.0%
Wide-ranging species	39.0%	56.3%	44.7%
Southern species	0.1%	2.5%	13.1%