ON THE AUTUMN MIGRATION OF THE BLACKPOLL WARBLER

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nonstop, trans-Atlantic flight from New England to the Lesser Antilles and South America has been proposed for the Blackpoll Warbler (Dendroica striata) and, perhaps, other passerine species migrating in autumn (Drury and Keith, 1962; Nisbet, Drury, and Baird, 1963; Drury and Nisbet, 1964). The hypothesis is based on radar observations of southward movements of small migrants off the Massachusetts coast and the occurrence of warblers at Bermuda. Previously, Cooke (1904, 1915) proposed that Blackpoll Warblers converge toward the southeastern United States, and from there proceed southeastward toward the winter range in South America.

Information from the Island Beach Operation Recovery Station in New Jersey, as well as already published data, causes me to favor the hypothesis of Cooke, rather than that of Drury, Keith, Nisbet, and Baird, and to hypothesize further that the occurrences of Blackpoll Warblers at Bermuda are a result of wind drift.

The following discussion is restricted to the overwater flight of the Black-poll Warbler from the United States mainland to Bermuda.

WIND DRIFT OF BLACKPOLL WARBLERS

Blackpoll Warblers occur most often at Bermuda during October (Nisbet et al., 1963). Of the 141 birds captured in 1962, 107 (76 per cent) occurred during the period 7 to 15 October. Another 17 occurred later, and only 17 occurred earlier (Table 1). Nisbet et al. (1963:132-133) suggested that the arrivals of 7 and 11 October "left North America south of New England. The latter suggestion seems more probable [than their leaving New England], 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." Most of the Blackpoll Warblers that reach Bermuda, then, leave North America from south of New England. In fact, Nisbet et al. (1963) report only one departure from New England that could account for arrivals at Bermuda—that on the night of 1-2 October. That departure was noted at Bermuda on 3 October by the arrival of 14 Blackpoll Warblers, which were captured by a lighthouse keeper during a sudden rainshower. Nisbet et al. (1963:133) concluded that the few Blackpoll Warblers at Bermuda in September and early October indicate "that the birds which migrate southwards from New England do not stop at Bermuda unless seriously delayed by the weather, although they pass overhead " It is with this last interpretation that I disagree. These 14 birds, as well as the others, can be considered

		August-						October	
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31	0	0	2	_	1	7	13	30	0
1	0	0	0		2	5	16	18	1
2	2	1	2	_	3		8	6	14
3	1	1	0	_	4	-	15	47	1
4	5	0	0	_	5	3	1	10	0
5	1	0	0		6	6	152	3	0
6	13	3	0	_	7	5	37	1	12
7	0	10	3		8	6	9	1	9
8	0	0	6	_	9	1	1	7	13
9	2	1	4	_	10	2	11	9	3
10	13	7	2 6	_	11	0	3	4	19
11	6	17	12	_	12	4	11	5	14
12	1	5	0	_	13	2	0	2	29
13	11	8	6	_	14	4	7	4	0
14	5	0	0		15	0	3	2	8
15	0	18	1	_	16	0	0	0	0
16	19	48	_	0	17	0	2	4	0
17	4	5	5	0	18	0	0	2	0
18	0	9	0	0	19	1	0	1	0
19	0	9	77	0	20	2	0	0	0
20	_	3	27	0	21	0	0	0	0
21	0	35	31	0	22	_	2	_	10
22	73	15	65	0	23	-	1	2	0
23	20	1	78	0	24		1	2	0
24	15	18	28	0	25	-	3	1	0
25	16	6	17	0	26	-		0	0
26	22	15	11	1	27	_	0	0	0
27	21	24	42	0	28	0	0		7
28	4	8	48	0	29	0	1	_	0
29	11	8	2	0	30	_	1		0
30	18	62	62	0	31	_	3	_	0

¹ Data from Nisbet et al. (1963:131).

vagrants, having been drifted offshore from the mainland by northwesterly and westerly winds. The following evidence and arguments seem relevant:

(a) The strongest evidence for the wind-drift hypothesis is the association of occurrences of Blackpoll Warblers at Bermuda and offshore winds (Tables 2 and 3). The wind on the night of 1–2 October, when the birds departed from New England, was westerly and northwesterly in New England and New York. The period 7–15 October, when 76 per cent of the Blackpoll

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¹Data taken from the Daily Series, Synoptic Weather Maps, Part II, Northern Hemisphere Data Tabulations, published by the U.S. Weather Bureau.
²Blackpoll Warblers were captured at Bermuda on dates in bold face.

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	TABLE	4			
OCCURRENCES OF BLACKPOLL	WARBLERS	AND	PRECIPITATION	ат Р	SERMUDA ¹

September	Precipitation (inches)	Blackpoll Warblers	October	Precipitation (inches)	Blackpoll Warblers
15	0.0	0	1	0.16	0
16	0.12	0	2	0.05	1
17	0.28	0	3	0.67	14
18	0.12	0	4	0.01	1
19	0.01	0	5	0.08	0
20	0.0	0	6	0.26	0
21	1.56	0	7	0.15	12
22	0.59	0	8	0.0	9
23	0.0	0	9	Trace	13
24	0.14	0	10	Trace	3
25	1.42	0	11	0.0	19
26	0.19	1	12	0.0	14
27	1.47	0	13	0.0	29
28	0.94	0	14	0.0	0
29	0.55	0	15	0.0	8
30	0.21	0			

¹ Captures of Blackpoll Warblers from Nisbet et al. (1963:131); precipitation from Surface Weather Observations, Kindley Air Force Base, Bermuda.

Warblers occurred at Bermuda, was characterized by persistent westerly winds along the eastern coast of the United States, as well as at Bermuda. The arrivals of 22 and 28 October also occurred when the winds were westerly.

That the mid- and late-October birds reach Bermuda by wind drift is not surprising. There seems to be no reasonable, alternative explanation of why birds departing from southeastern United States in a southeastward direction toward South America should occur on Bermuda.

- (b) Nisbet et al. (1963) suggest that Blackpoll Warblers "do not stop at Bermuda unless seriously delayed by the weather, . . ." because of the 14 Blackpoll Warblers caught in the rain by a lighthouse keeper. However, most of the Blackpoll Warblers at Bermuda were captured by mist nets on days without rain (Table 4). Blackpoll Warblers seem to land at Bermuda whether it is raining or not.
- (c) Blackpoll Warblers arrive at Island Beach from over the ocean (Murray, MS.; Murray and Jehl, 1964). Although a few are fat, most are light (Fig. 1; Murray and Jehl, 1964) and could not continue a long-distance flight. Assuming that Blackpoll Warblers are nocturnal migrants, the arrivals at Island Beach have flown between 10 and 14 hours. Blackpoll Warblers passing Bermuda would have flown over 30 hours (Nisbet et al., 1963). Some of the Blackpoll Warblers passing Bermuda would weigh about the same as Island Beach arrivals, and they could not continue a long-distance flight.

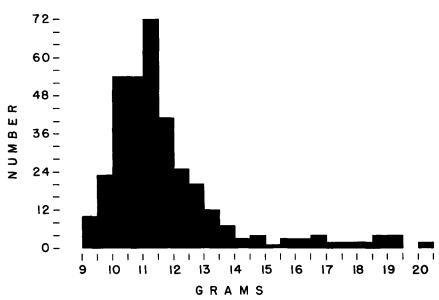


Fig. 1. Frequency distribution of weights of 352 Blackpoll Warblers captured at Island Beach, New Jersey, in September and October 1962. The weights are grouped in half-gram intervals—for example, the column to the left of "10" represents birds weighing 9.5 to 9.9 grams, and the column to the right of "10" represents birds weighing 10.0 to 10.4 grams. The mean of the sample is 11.7 grams.

Thus, Blackpoll Warblers should occur at Bermuda as frequently as they are flying near Bermuda.

- (d) Blackpoll Warblers are captured almost every day at Island Beach during the migration from early September to mid-October (Table 1). Presumably, Blackpoll Warblers are regularly flying over or near New Jersey during this period. If Blackpoll Warblers are flying over or near Bermuda as regularly, I should expect them to occur more frequently than they do.
- (e) Perhaps the most interesting anomaly reported by Nisbet et al. (1963) was the average weight of Blackpoll Warblers at Bermuda, which quite unexpectedly was higher than average weights from the mainland. Although Nisbet et al. (1963) state that light, as well as heavy, Blackpoll Warblers apparently depart on migration, they suggest the "normal departure weight" was between 19.7 and 23.2 grams. Such an hypothesis seems necessary if one were to account for the high average weight of Bermuda birds and for a 1,600 mile nonstop, overwater flight. However, only 46 birds, of their sample of over 2,000 from New England, weighed over 19.6 grams. That the weights of the extreme two per cent of the population represent the "normal departure weight" seems to me to be a tenuous hypothesis.

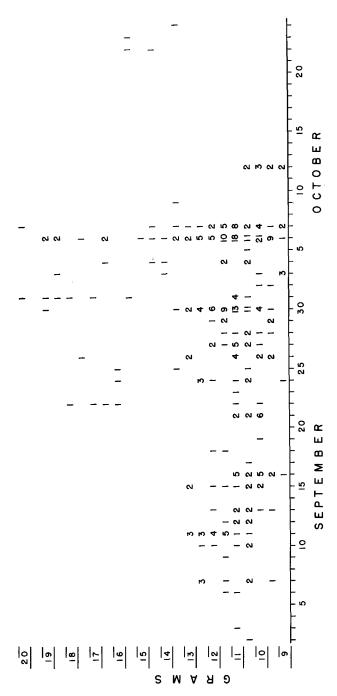


Fig. 2. Daily frequency distribution of weights of Blackpoll Warblers captured at Island Beach, New Jersey, in September and October 1962. The weights are grouped in half gram intervals-the row marked "10" contains weights from 10.0 to 10.4 grams, and the row above contains weights from 10.5 to 10.9 grams.

Alternatively, if the average departure weight were nearer the measured average weight (12–14 grams), the stored energy of the average bird would still be sufficient to sustain a night's flight. Birds of above average weight could fly longer, and birds below average weight could not fly as long. If a portion of the migrants were drifted over the ocean, only the fatter birds would have the potential of remaining airborne long enough to reach Bermuda. The distribution of weights of Blackpoll Warblers is skewed toward the heavy end (Fig. 1; Nisbet et al., 1963). If the preponderant lighter birds were to succumb, the average weight of the population that arrived at Bermuda could be higher than the average weight of the departing population.

The seasonal distribution of Blackpoll Warbler weights is of importance. During the first 3 weeks of September, there are no fat Blackpoll Warblers, either at Round Hill in Massachusetts (Nisbet et al., 1963) or at Island Beach (Fig. 2). Even though Blackpoll Warblers are migrating from the beginning of September (Table 1; Nisbet et al., 1963) on nights with offshore winds (Table 2), no Blackpoll Warblers reach Bermuda during this period, probably because too few (if any) Blackpoll Warblers have energy reserves sufficient to sustain the long overwater flight.

(f) The usual flight direction during the day of passerine migrants in autumn along the coast of the eastern United States is between west and north (Baird and Nisbet, 1960). These authors suggest that these northward-bound migrants are birds that had been drifted over the ocean and are returning to the mainland after reorienting. However, Drury and Keith (1962) and Nisbet et al. (1963) state that species involved in transoceanic migration were exceptions to this generalization, that is, transoceanic migrants do not reorient toward the mainland, while other species do reorient when drifted offshore.

At Island Beach the Blackpoll Warblers are common in autumn (Table 5), and they fly northward in company with other migrants. There is no evidence of a difference in orientation behavior between the Blackpoll Warbler and other species while over the ocean.

THE DRURY-KEITH ARGUMENT AGAINST WIND DRIFT

The possibility that wind drift may be the cause of occurrences of migrants at Bermuda was considered and rejected by Drury and Keith (1962) and was not further considered by Nisbet et al. (1963) or Drury and Nisbet (1964). The argument that led to the rejection of the wind-drift hypothesis is as follows:

"—those wood warblers which winter in Central America and northwestern South America, but not in the Antilles, do not turn up in Bermuda; whereas the wood warblers that winter chiefly in the Antilles and northern South America are numerous every autumn in Bermuda. This differential is inexplicable on the theory that Bermuda catches a

Table 5 Numbers of Warblers Captured at Three Coastal Netting Stations and RELATIVE ABUNDANCE AT BERMUDA^{1, 2}

	Bermuda Rela-	. Na	antuck	et, Ma	ass.	Isl	and E	each,	N.J.	C	Ocean	City,	Md.
	tive abun- dance	1958	1959	1960	Rank	1958	1959	1960	Rank	1958	1959	1960	Rank
Black-and-white	3	46	53	9	5	118	81	53	8	38	54	22	8
Prothonotary	3	0	0	0	_	0	1	0	_	0	1	0	_
Worm-eating	4	0	1	0	_	0	0	1	_	2	0	1	_
Golden-winged	6	0	0	0	_	0	0	0	_	1	1	0	_
Blue-winged	4	0	1	0	_	3	3	1	_	0	0	0	_
Tennessee	5	5	2	2		18	22	18	_	0	3	8	
Orange-crowned	7	0	0	0	_	0	0	0	_	0	1	0	_
Nashville	6	11	0	6	17	23	30	41	16	2	4.	13	17
Parula	3	3	7	4	19	14	25	33	19	1	6	7	19
Yellow	3	12	4	6	15	39	54	22	13	1	5	0	_
Magnolia	4	22	13	22	9	86	109	43	9	21	59	37	7
Cape May	2	49	25	70	3	102	123	91	6	9	57	32	10
Black-throated Blue	4	6	22	14	12	32	84	83	12	11	78	85	3
Myrtle	2	1	19	51	8	9	36	48	17	0	16	23	12
Black-throated Green	3	7	11	5	14	45	44	24	14	5	7	5	18
Cerulean	6	0	0	0	_	0	0	0	_	0	0	0	_
Blackburnian	4	3	3	2	_	13	13	6	_	0	3	3	_
Yellow-throated	4	0	0	1		0	0	0	_	0	0	1	_
Chestnut-sided	4	2	3	1		17	17	7	_	0	2	1	
Bay-breasted	4	31	10	44	7	17	26	17	20	3	2	7	20
Blackpoll	1	15	39	49	6	127	141	212	3	13	31	79	6
Pine	8	0	0	3	_	1	0	0	_	0	0	1	_
Prairie	4	1	4	4	_	15	24	17	_	4	9	13	14
Palm	2	0	19	29	11	51	100	93	10	9	24	15	11
Ovenbird	2	18	24	14	10	95	64	55	11	43	43	40	5
Northern Waterthrus	h 2	69	67	41	2	161	205	58	5	51	54	41	4
Louisiana Waterthrus	h 4	0	0	0		0	0	0	_	0	0	0	_
Kentucky	4	0	1	0	_	0	0	0	-	0	0	0	
Connecticut	6	4	2	1	_	22	58	29	15	3	16	17	13
Mourning	6	9	1	2	20	7	8	6	_	3	0	4	_
Yellowthroat	2	58	44	23	4	242	153	172	2	24	34	49	2
Yellow-breasted Chat	6	13	8	10	13	117	88	72	7	45	61	82	2
Hooded	3	0	2	2	_	3	1	1	_	1	0	3	_
Wilson's	6	11	3	4	16	18	20	14	_	5	13	5	16
Canada	6	8	4	5	17	39	30	16	18	13	13	11	15
American Redstart	2	122	122	78	1	533	452	241	1	136	179	162	1

¹ Relative abundance at Bermuda from Drury and Keith (1962:481): 1. Regular—abundant throughout; 2. Regular—common in suitable places; 3. Regular—several records per season; 4. Regular—single or a few records per season; 5. Frequent—common in suitable places; 6. Frequent—single or a few records per season; 7. Occasional—single or a few records per season; 8. Very rare.

² The period of operation of each Operation Recovery station differed. In order to facilitate comparisons, the number of birds captured during the period when all three stations were in operation are reported here. Dates (all stations in operation): 1958, 6–21 September; 1959, 5–27 September; 1960, 3 September–2 October.

random sample of drifted migrants from a broad-front southwestward migration . . ." (Drury and Keith, 1962:481).

and

"[Those species that migrate or winter commonly in the Antilles] Myrtle, Blackpoll, Palm, Ovenbird, Northern Waterthrush, Yellowthroat, and American Redstart are our commonest wood warblers and would be expected to predominate even if Bermuda records were of storm waifs and a non-selective sample. However, [those species that winter commonly in Central America] Tennessee, Nashville, Blackburnian, Chestnut-sided, Baybreasted, Mourning, Hooded, Wilson's, and Canada Warblers are sufficiently common [in New England] to be expected to be represented on Bermuda in comparable numbers, if the arrivals there were simply drifted" (Drury and Keith, 1962:482).

In Table 5 are listed the numbers of warblers captured at the Operation Recovery Stations at Nantucket, Massachusetts; Island Beach, New Jersey; and Ocean City, Maryland, in 1958, 1959, and 1960, along with the relative abundance of warblers at Bermuda. The seven common species of Bermuda make up 57 per cent of the catch along the Atlantic coast. The nine species that Drury and Keith (1962) call "sufficiently common" along the coast make up only eight per cent of the catch. In fact, then, the common species along the Atlantic coast are common at Bermuda, and the relatively rarer species rare at Bermuda. Thus, the relative abundance of the species of warblers at Bermuda is exactly what one would expect, if a nonselective sample of the coastal migrants had been wind drifted over the ocean.

The Drury-Keith argument is further weakened by the fact that 83 per cent of the Blackpoll Warblers at Bermuda occur in mid- and late-October, when the birds almost certainly have been drifted from the southeastern United States (see paragraph (a) above).

THE SOUTHWARD MOVEMENTS ON RADAR

Perhaps the most interesting evidence in favor of the trans-Atlantic flight is the radar observations of southward movements of small migrants (Nisbet et al., 1963; Drury and Nisbet, 1964). "Southward movements occur regularly on the cold side of high pressure systems from late August until films stopped in early November, with the densest movements probably around the beginning of October" (Drury and Nisbet, 1964:85). Drury and Nisbet (1964) consider the late October and early November movements to be waterfowl, and Drury and Keith (1962), Nisbet et al. (1963), and Drury and Nisbet (1964) consider the earlier movements to be passerines. Specific identification of the landbirds is somewhat doubtful, the list of Drury and Keith (1962) being quite different from that of Drury and Nisbet (1964). Only the Blackpoll Warbler has been definitely assigned to the southward movements by Nisbet et al. (1963) and Drury and Nisbet (1964). However, the radar evi-

dence supporting trans-Atlantic migration of the Blackpoll Warbler is not entirely conclusive. Nisbet et al. (1963:115, 122, 126, 131) consistently state that Blackpoll Warblers do not depart from New England, at least in numbers, until after 25 September, much later than the onset of the southward movements observed on radar in late August. Even if Blackpoll Warblers were departing earlier, the peak numbers of mist-netted birds occur in Massachusetts in the last half of September (Table 4 in Nisbet et al., 1963) and in New Jersey in the last third of September (Table 1), whereas the densest southward movements observed on radar occur at the beginning of October. While the Blackpoll Warbler may form a part of the southward movements, other species are no doubt involved. What these are remains to be determined. The interpretation that the southward movements, which occur less than 70 miles offshore, are of passerines departing on a trans-Atlantic flight may be considerably altered when the species composition of the movements is known.

SUMMARY

The data and arguments supporting the trans-Atlantic flight of the Blackpoll Warbler are reviewed, and new evidence on Blackpoll Warbler migration from coastal banding stations is presented. The data, some of which were supposed to support the overwater flight, better support the hypotheses (1) that Blackpoll Warblers in the northeastern United States fly southwestward to the southeastern United States, before turning southeastward toward the winter range in South America and (2) that some Blackpoll Warblers reach Bermuda as a result of being drifted by offshore winds. The supporting evidence is (1) the association of occurrences of Blackpoll Warblers at Bermuda with westerly winds, (2) the low average weight of all mainland samples of Blackpoll Warblers, (3) the average weight of Blackpoll Warblers at Bermuda, which is higher than those from mainland populations, (4) the similarity in migratory behavior of Blackpoll Warblers and other species of passerines in coastal areas, and (5) the similarity in the relative abundance of warbler species in coastal populations and at Bermuda.

That the radar data on southward movements of small passerines are of Blackpoll Warblers departing on a trans-Atlantic flight is doubtful, because the radar data do not correlate well with the migration of the Blackpoll Warbler.

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