1

several helpful comments on the manuscript. Mr. Clench also kindly prepared the figure.

LITERATURE CITED

HUSSELL, D. J. T., T. DAVIS and R. D. MONTGOMERIE. 1967. Differential fall migration of adult and immature Least Flycatchers. Bird-Banding 38: 61-66.

HUSSELL, D. J. T. and J. WOODFORD. 1961. The use of a Heligoland trap and mist-nets at Long Point, Ontario. *Bird-Banding* **32**: 115-125.

PHILLIPS, A. R., M. A. HOWE and W. E. LANYON. 1966. Identification of the flycatchers of eastern North America, with special emphasis on the genus *Empidonax. Bird-Banding* 37: 153-171.

PRESTON, F. W. 1966. The mathematical representation of migration. *Ecology* **47**: 375-392.

Carnegie Museum, Pittsburgh, Pennsylvania, 15213

Received August, 1968.

A MIGRATION WAVE OBSERVED BY MOON-WATCHING AND AT BANDING STATIONS*

By I. C. T. NISBET AND WILLIAM H. DRURY, JR.

INTRODUCTION

While studying a migration "wave" in eastern Massachusetts in 1968 we noted some striking discrepancies between migration as recorded by moonwatching and the changes in numbers of birds caught at netting stations. This sort of discrepancy has been reported before in general terms, but the events of 4th-6th October 1968 provided some unusually clear illustrations of the different types of information provided by the two techniques.

Baird *et al.* (1959) reported that in the autumn of 1958 banding stations on the Atlantic coast reported "waves" of arriving migrants immediately after the passage of cold fronts, but that a banding station 25 miles inland at Jamesburg, New Jersey, consistently reported waves one day later. They suggested that the records of the inland station may have reflected better the migration of birds overhead, and that the coastal waves may have resulted from smaller movements of birds, exaggerated by lateral drift of the birds to the coast in the strong NW winds which usually prevail

^{*}Contribution No. 72 from the Hatheway School of Conservation Education, Massachusetts Audubon Society, Lincoln, Massachusetts 01773.

behind cold fronts. Subsequently, working with radar in Massachusetts, we have confirmed that coastal waves usually result from comparatively small movements of birds (Nisbet and Drury, 1967a). However, the drift hypothesis has had to be modified, because, on the average, autumn migrants correct for drift (Drury and Nisbet, 1964). Most of the birds which comprise the waves at coastal stations appear to be those inexperienced individuals which undercompensate for drift (Drury and Nisbet, 1964). Some of these may stop or turn when they reach the coast; others appear to cross the coast during the night and return to land in the morning (Baird and Nisbet, 1960; Murray and Jehl, 1964).

WEATHER SEQUENCE

For much of September 1968 the eastern United States were under the influence of a stationary high pressure system, and with the exception of a weak cold front on 26th September, the cold front of 3rd/4th October was the first to affect the area since 11th September. The front passed through the Boston area about midnight on 3rd/4th October and moved rapidly offshore; on the evening of the 4th Boston was in the NE quadrant of a high centered in southern Indiana, and on the evening of the 5th it was in the northcentral part of the high centered in Virginia.

Table 1 tabulates measurements of weather variables observed at Portland, Maine, Burlington, Vermont, and Bedford, Massachusetts, at the time of take-off of nocturnal migrants on the evenings of 3rd, 4th and 5th October. Table 2 gives measurements of the winds affecting birds after take-off. On the evening of the 3rd, rain was ceasing in northern New England at sunset, but drizzle continued at Burlington until after 20:00 and rain continued at Portland and Bedford until 02:00 and midnight, respectively. The evenings of 4th and 5th were clear, dry and cool; northwest winds were still moderate in strength at dusk on the 5th, 44 hours after the cold front had passed, but had been stronger at dusk on the 4th.

MOON-WATCHING RESULTS

On each of the evenings 4th and 5th October we spent one hour (20:00-21:00) moon-watching at Lincoln, Massachusetts. Rain had prevented observation on the evening of 3rd October. The observations are summarized in Table 2.

On both evenings unusually large numbers of birds were seen, but the directions of flight were strikingly different. On 4th/5th October, 101 birds were seen flying in directions between southeast and south (mean track 171°) and only 21 birds between SSW and west (mean track 222°). On the 5th/6th October the observed tracks again fell into two groups, but the relative proportion was reversed: only 4 birds were seen flying SSE, but 233 between SSW and west (mean track 226°).

As seen against the moon, the two groups of birds differed in other ways, which were familiar to us from moon-watching in earlier years. The SSE migrants all appeared to be small birds, flying extremely high (most near to the limit of visibility) in direct flight

Weather Station	Portl	Portland, Maine	le	$\operatorname{Burlin}_{l}$	Burlington, Vermont	mont	Bedford, Massachusetts	Massachu	setts
Date (Oct. 1968)	3	4	л.	°°	4	ò	က	4	ΰ
Temperature (°F)	65	50	43	59	47	43	69	50	45
Relative humidity $(\%)$	84	66	58	87	68	56	81	59	57
Pressure (mb)	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	1008f	1011r	1020r
Sky cover (tenths)	10	0	0	10	6	x	10	1	7
Cloud ceiling (feet)	0002	UNL	UNL	3700	3600	0009	8000	0009	6000
Wind direction (°)	190	350	260	210	290	310	200	290	290
Wind speed (knots R)	14	9	9	8	×	7	13	10	4
Visibility (miles)	ŝ	15	15	15	25	30	Ð	15	30
Precipitation	HT	lin	lin	RW	lin	nil	Η	lin	liu

Vol. 40, No. 3

4

[245

Date	4 October	5 October
Upper-air wind: direction	300°	320°
speed (knots)	25	20
SSE-flying migrants: Number seen	101	4
Observed mean track	171 °	168°
Estimated mean heading	235°	193°
SW-flying migrants: Number seen	21	233
Observed mean track	222°	226°
Estimated mean heading	ca. 285°*	291°

TABLE 2. UPPER-AIR WINDS AND FLIGHT DIRECTIONS OF BIRDS OBSERVED BYMOON-WATCHING AT LINCOLN, MASSACHUSETTS, ON 4 AND 5 OCTOBER 1968

Note. Upper-air winds are the 'gradient' winds, estimated by standard methods from the direction and spacing of the isobars on the surface-level weather maps. Mean headings were estimated from the observed mean tracks and the upper-air winds, assuming a mean air-speed of 22 knots; that marked by an asterisk was estimated by direct observation, because only birds with air-speed greater than 25 knots could have maintained the observed tracks.

with scarcely perceptible undulations. The SW migrants were much lower (nearly all being easy to observe), of diverse sizes and shapes (those of flicker, catbird, robin, thrasher, heron and rail were tentatively identified, in addition to small passerines), sometimes undulating markedly and sometimes in loose groups (6 pairs and one trio were observed crossing the moon together). Because of the differences in height and direction, the 101 birds seen flying SSE on the 4th actually represent a migration two or three times denser than the 233 birds seen flying SW on the 5th. As calculated by the method of Nisbet (1963a, b), the former represent a migration traffic rate of about 50,000 birds per hour per mile, or a density of about 2,000 birds per square (nautical) mile. This is one of the densest migrations we have recorded, either by moon-watching or with radar, and is denser than all but a few of the North American samples listed by Newman and Lowery (1964) for the same October period in 1952.

The SSE and SW movements correspond exactly to movements in these directions observed by radar in earlier years (Drury and Nisbet, 1964). The SW movements are attributed to a variety of species which winter in the southern United States and in Central America; the SSE movements are attributed primarily to the Blackpoll Warbler, although other species appear to be involved, especially earlier and later in the season than early October (Nisbet *et al.*, 1963). Radar observation has shown that the mean tracks of these movements are always close to 172° and 219° respectively, whether the wind is from the birds' right or left; in other words that the birds, on average, adjust their headings to correct for drift (Drury and Nisbet, 1964). Our observations on 5th October are in accord with this conclusion, in that the mean headings of the two groups of species were about 193° (S by W) and 291° (WNW) respectively—headings which are inexplicable except in terms of correcting for the effect of wind-drift. Indeed the low flying birds on 5th October could be clearly seen to be "crabbing", heading about 60° to the right of their tracks. The behavior of some birds seen changing direction in flight will be described in another paper.

A remarkable feature of these observations is that the SSE and SW movements reached peaks on different nights, although all the birds experienced the same weather prior to take-off. Pending a detailed study, we cannot identify the difference in the birds' response to individual weather factors which was responsible for this difference. Whereas the upper-air winds on 4th/5th were favorable for the SSE-migrants, they were so strong that only the strongest fliers among the SW-migrants *could* have corrected for the lateral drift they produced. However, while this may have been the "ultimate" reason why most of the SW-migrants waited until the next night before migrating, it does not necessarily indicate that they were directly deterred from migrating on the 4th/5th by the strength of the surface winds. Other weather factors, such as low pressure and humidity, also provide information about the strength of upperair winds. Baird et al. (1959) first pointed out the danger to SWmigrants of migrating immediately after the passage of cold fronts, and suggested that migration may actually be denser on the second or third nights.

BANDING RESULTS

Tables 3 and 4 summarize the results of daily banding at Round Hill, Sudbury, Massachusetts, and at Manomet Bird Observatory, Manomet, Massachusetts, on 4th, 5th and 6th October; rain curtailed mist-netting at both stations on the 7th. The Round Hill site has been described by Nisbet *et al.* (1963): it lies some 15 miles west of Boston, some 25 miles southeast of a straight line between Portland, Maine, and New York City, and hence just within the southeastern fringe of the dense SW movements of landbirds through Massachusetts (Drury and Nisbet, 1964; Nisbet and Drury, 1967b). Manomet Bird Observatory is in an area of mixed trees and tall berry-bearing bushes on the cliff-tops some 40 miles SSE of Boston, and hence some 30-40 miles outside the fringe of the dense movements.

At Round Hill there was a small increase in the number of netted birds on 5th October, and a larger increase on 6th October. In contrast, Manomet recorded a major wave—the largest of the year on 5th October. Next day the banding totals were again high, but they were not significantly higher than on the 5th for any species, and the high proportion of recaptures indicates that many birds had stayed overnight.

Among the birds banded at Manomet, immatures outnumbered adults in the ratio of 18 to 1, and in only two species was the proportion of adults significantly greater than this. At Round Hill there was a marked excess of immatures in the three most numerous

, Massachusetts, During 4-6 ()ctober 1968.	D ON FARTER DAVE
TABLE 3. DAILY BANDING TOTALS FOR THE COMMONER SPECIES AT ROUND HILL, SUDBURY	FIGURES IN PARENTHESES DENOTE RECARTIRES OF BIRDS BANDED ON

October	4	5	9	% adults
Hermit Thrush Hylocichla guttata			6	0
Swainson's Thrush Hylocichla ustulata	1	2	2	67
Golden-crowned Kinglet Regulus satrapa	-	1	4	40
Ruby-crowned Kinglet Regulus calendula		1	3	50
Myrtle Warbler Dendroica coronata	10(1)	18	54(4)	12
Blackpoll Warbler Dendroica striata	3(1)	1(1)	τ÷	12^{*}
Other warblers	1	7	4	33
Slate-colored Junco Junco hyemalis	1	×	25(2)	6
White-throated Sparrow Zonotrichia albicollis	I	1	6	0
Other species	4(3)	5(3)	14(1)	29
TOTAL	20(5)	44(4)	123(7)	17.0
Net hours	120	120	114	

October	4	5	9	% adults
Black-capped Chickadee Parus atricapillus	37(3)	29(3)	36(2)	1
Cathird Dumetella carolinensis	15(25)	18(13)	13(18)	6
Robin $Turdus$ migratorius	10	7	ന	0
Swainson's Thrush Hylocichla ustulata	4(6)	22(7)	15(10)	15
Ruby-crowned Kinglet Regulus calendula	1(2)	9(1)	2(2)	25
Red-eyed Vireo Vireo olivaceus	3(10)	9(10)	5(8)	9
Nashville Warbler Vermivora ruficapilla		õ	7	0
Magnolia Warbler <i>Dendroica magnolia</i>	1	6(1)	1	14
Myrtle Warbler <i>Dendroica coronata</i>	13	13	15(1)	0
Black-throated Blue Warbler <i>Dendroica caerulescens</i>	[12(1)	3	0
Palm Warbler <i>Dendroica palmarum</i>	1	6	1	0
Yellowthroat Geothlypis trichas	1(1)	5(3)	3(2)	0
Other warblers	7	21(1)	7(1)	×
Slate-colored Junco Junco hyemalis	1	20(1)	ļ	0
White-throated Sparrow Zonotrichia albicollis	6(3)	61(10)	44(14)	4
Other species	24(8)	38(12)	28(10)	2
TOTAL	117(58)	278(62)	178(68)	5.3
Net hours	420	420	420	

A Migration Wave Observed

Bird-Banding July, 1969

species, but in all the other species the proportion of immatures was not unreasonable for a sample from a part of the species' population unsegregated as to age. A marked excess of immatures is normal in coastal samples (Baird *et al.*, 1959; Drury and Keith, 1962; Murray and Jehl, 1964), and is easily explained as reflecting a process of selection against poor navigators (Drury and Keith, 1962; Nisbet and Drury, 1967a). An excess of immatures at Round Hill, 20 miles inland, is more unexpected, but has been recorded in the Slatecolored Junco and White-throated Sparrow at Round Hill in earlier years (Howard, 1967): it is not known whether it reflects Round Hill's location near the fringe of the migration of good navigators (Nisbet and Drury, 1967a), or its situation as an ecological island which is associated with other ornithological anomalies (Nisbet *et al.*, 1963).

COMPARISON OF MOON-WATCHING WITH NETTING RESULTS

Because our moon-watching was undertaken primarily to record the SSE departures, we watched only in the evenings; hence the results are not fully comparable with the arrivals recorded at the netting stations (which were so large that simultaneous departures could not have been discerned). However, radar observations have indicated that in the absence of marked overnight weather changes, migration into our area in the early morning is highly correlated with emigration from the area on the previous night (Nisbet and Drury, 1968). On the evenings of 3rd, 4th and 5th October 1968. the weather on the Maine coast, NE of our area, was very similar to that recorded in Massachusetts (Table 1). Hence we assume that the density of SW immigration on the morning of 6th October was much greater than that on 5th October (though not necessarily exactly 11 times greater as suggested by Table 2). We therefore conclude that the netting at Round Hill gave a fairly good indication of the relative size of the immigrations on these mornings (perhaps exaggerating that on the 5th by a factor of 2 or 3), whereas the netting at Manomet gave a totally misleading indication. This accords with the conclusions quoted in the Introduction.

In earlier years massive SSE departures have been correlated with decreases in the netting-rate of Blackpoll Warblers at Round Hill (Nisbet *et al.*, 1963). However, in 1968 numbers of Blackpoll Warblers at Round Hill were unusually low (cf. Howard, 1967), so much so that a statistically significant fall in the netting-rate could not have been observed (Table 3). Nevertheless, our data indicate that heavy Blackpoll Warblers left Round Hill between 3rd and 5th October. Of six birds caught there on 3rd October, three weighed more than 20 g and hence were within the normal range of departure weights: no other Blackpoll Warbler heavier than 18.4 g was caught until netting ceased on 10th October. It is not known, however, whether these birds departed on the evening of the 4th or during the previous night (3rd/4th). Ordinarily we would not have expected a departure on the evening of the 3rd, because rain was starting at dusk and did not cease until around midnight; birds may have taken off after midnight, but radar observations have indicated that this is unusual (Nisbet et al., 1963).

It may be added that no other species which is known to winter SSE of Massachusetts was netted in significant numbers at this period, with the exception of the Magnolia Warbler which increased in numbers at the netting stations on the 5th. Likewise the massive SW departure on the 5th/6th was followed by a significant decrease in only a few species at Manomet, and in no species at Round Hill. Nisbet and Drury (1967a) reported that a small decrease in grounded migrants is often the best indication of a large-scale departure: in the case of 5th/6th October the decreases must have been largely obscured by arrivals.

CONCLUSIONS AND SUMMARY

- 1. Moon-watching indicated that the main SSE departure (presumed to be largely Blackpoll Warblers) took place on the first evening (4th/5th October) after the cold front of 3rd/4th October; the main SW movement (presumed to comprise most other species) took place on the second evening (5th/6th October). The behavioral responses to weather factors which resulted in this difference are not known, but it seems likely that the strength of the NW (offshore) wind is either a proximate or an ultimate factor.
- 2. As seen against the moon, both groups of species flew on the normal tracks observed by radar in earlier years (in spite of strong crosswinds for the SW migrants); hence they "corrected" for drift. The SSE-migrants flew much higher.
- 3. At the coastal station the wave of arriving SW-migrants took place on the second morning (5th October) after the cold front, following a small movement of birds. Immatures greatly predominated in all species.
- 4. At the inland station the wave of arriving SW-migrants took place on the third morning (6th October) after the cold front, following a large movement of birds; the arrival on the previous day had been smaller, agreeing at least qualitatively with the relative sizes of the movements detected by moon-watching. Immatures somewhat predominated in the three most numerous species.
- 5. The massive departure of SSE-migrants on the evening of the 4th was accompanied by a small (but not statistically significant) decrease in the netting rate of Blackpoll Warblers, and by no change in the numbers of any other likely species.

ACKNOWLEDGMENTS

Mrs. D. V. Howard performed most of the mist-netting work at Round Hill; data from Manomet Bird Observatory were supplied by the Director, Mrs. K. S. Anderson. Unpublished weather data were provided by the U. S. Air Force Sixth Weather Wing at Hanscom Field, Bedford, Massachusetts.

LITERATURE CITED

- BAIRD, J., A. M. BAGG, I. C. T. NISBET, and C. S. ROBBINS. 1959. Operation recovery—report on mist-netting along the Atlantic coast in 1958. Bird-Banding, 30(3): 143-171.
- BAIRD, J., and I. C. T. NISBET. 1960. Northward fall migration on the Atlantic coast and its relation to offshore drift. Auk, 77(2): 119-149.
- DRURY, W. H., and J. A. KEITH. 1962. Radar studies of songbird migration in coastal New England. *Ibis*, 104(4): 449-489.
- DRURY, W. H., and I. C. T. NISBET. 1964. Radar studies of orientation of songbird migrants in southeastern New England. *Bird-Banding*, **35**(2): 69-119.
- HOWARD, D. V. 1967. Five years of mist netting (1962-1966) at Round Hill, Sudbury, Massachusetts. *Records of New England Birds*, 23(2): iii-vi.
- MURRAY, B. G., JR., and J. R. JEHL, JR. 1964. Weights of autumn migrants from coastal New Jersey. *Bird-Banding*, **35**(4): 253-26.
- NEWMAN, R. J., and G. H. LOWERY, Jr. 1964. Selected quantitative data on night migration in autumn. Spec. Publ. Mus. Zool. Louisiana State Univ., 3: 1-39.
- NISBET, I. C. T. 1963a. Quantitative study of migration with 23-centimetre radar. *Ibis*, 105(4): 435-460.
- NISBET, I. C. T. 1963b. Estudio de la migracion sobre el disco lunar. Ardeola, 8: 1-17.
- NISBET, I. C. T., and W. H. DRURY. 1967a. Scanning the sky—Birds on radar (Part 1); Weather and migration (Part 2). Mass. Audubon, 51: 166-174; 52: 12-19.
- NISBET, I. C. T., and W. H. DRURY. 1967b. Orientation of spring migrants studied by radar. *Bird-Banding*, **38**(3): 173-186.
- NISBET, I. C. T., and W. H. DRURY. 1968. Short-term effects of weather on bird migration: A field study using multivariate statistics. Anim. Behaviour, 16(4): 496-530.
- NISBET, I. C. T., W. H. DRURY, and J. BAIRD. 1963. Weight-loss during migration. Bird-Banding, 34(3): 107-159.

Received February, 1969.

GENERAL NOTES

Nocturnal Migrants Changing Direction in Flight.—Moon-watching and radar observations in many parts of the world consistently indicate that nocturnal migrants usually maintain straight tracks. However, the section of a bird's track under scrutiny by a moon-watcher is usually shorter than 30 m., whereas radar echoes usually cannot be plotted in detail over distances less than about 1 km. The question remains whether birds' tracks would show zig-zags if plotted over distances of 100-500 m.

During our migration studies in Massachusetts, we have consistently observed that the scatter in tracks estimated by moon-watching is greater than that estimated by radar tracking (Nisbet, 1963a). The root mean square deviation of the former is typically $15^{\circ}-20^{\circ}$; the r.m.s. deviation of radar tracks is probably comparable for the bright echoes which attract most attention on the screen, but appears to be substantially smaller (often 10° or less) for the large masses of weaker echoes which correspond to the common species sampled by moon-watching.

Likely errors in observation by moon-watching are too small to account for the discrepancy (Nisbet, 1963b), and observed undulations by a small number of birds seen before the moon appear to involve changes in angles much smaller than