

# BIRD-BANDING

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## ORIENTATION OF SPRING MIGRANTS STUDIED BY RADAR\*

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In a previous paper (Drury and Nisbet, 1964) we analyzed in detail the orientation of songbirds on autumn migration, using a moving picture film record of a radar screen on Cape Cod, Massachusetts. In this paper we report an analysis of the orientation of spring migrants, studied in the same way. Movements of birds near Cape Cod are less complex in spring than in autumn, so that a more detailed analysis of some aspects of orientation is possible.

### *The film record.*

The radar station is at South Truro, Massachusetts (Figure 1): its technical characteristics and its performance in detecting birds have been described by Richardson, *et al.* (1959) and by Nisbet (1963a); its use to analyze orientation has been described in detail by Drury and Nisbet (1964). Briefly, echoes from birds are displayed on a screen in the form of bright dots on a circular map (the "PPI") which is photographed on 35-mm. movie film: each frame of the film records a single sweep of the beam, lasting 12 seconds. By projecting the film on a cinematic viewer, the slow motion of the echoes on the screen can be speeded up sufficiently to give a clear, but qualitative, impression of the flight directions and spatial distributions of the birds. For accurate measurements of orientation, it is necessary to employ an electronic device (the "MTI") which eliminates from the PPI echoes from all targets with no radial motion relative to the radar station. Thus, if all the birds are moving in the same direction, the MTI removes from the screen all echoes in a wedge-shaped sector on each side of the center of the screen, the axis of the wedge being perpendicular to the direction of movement. In practice, the MTI-wedges are diffuse (Figure 2), because birds do not all fly in the same direction, but the center-line of the wedge is exactly perpendicular to the mean direction of the birds, which can thereby be measured within limits of error of only two or three degrees. MTI-wedges are visible only where the movements of the targets are (locally) reasonably uniform; they are obscured when the directions of flight of individual birds are random (as in "disoriented movements"), widely dispersed (as with a strong headwind), or poly-modal (as when several discrete movements overlap).

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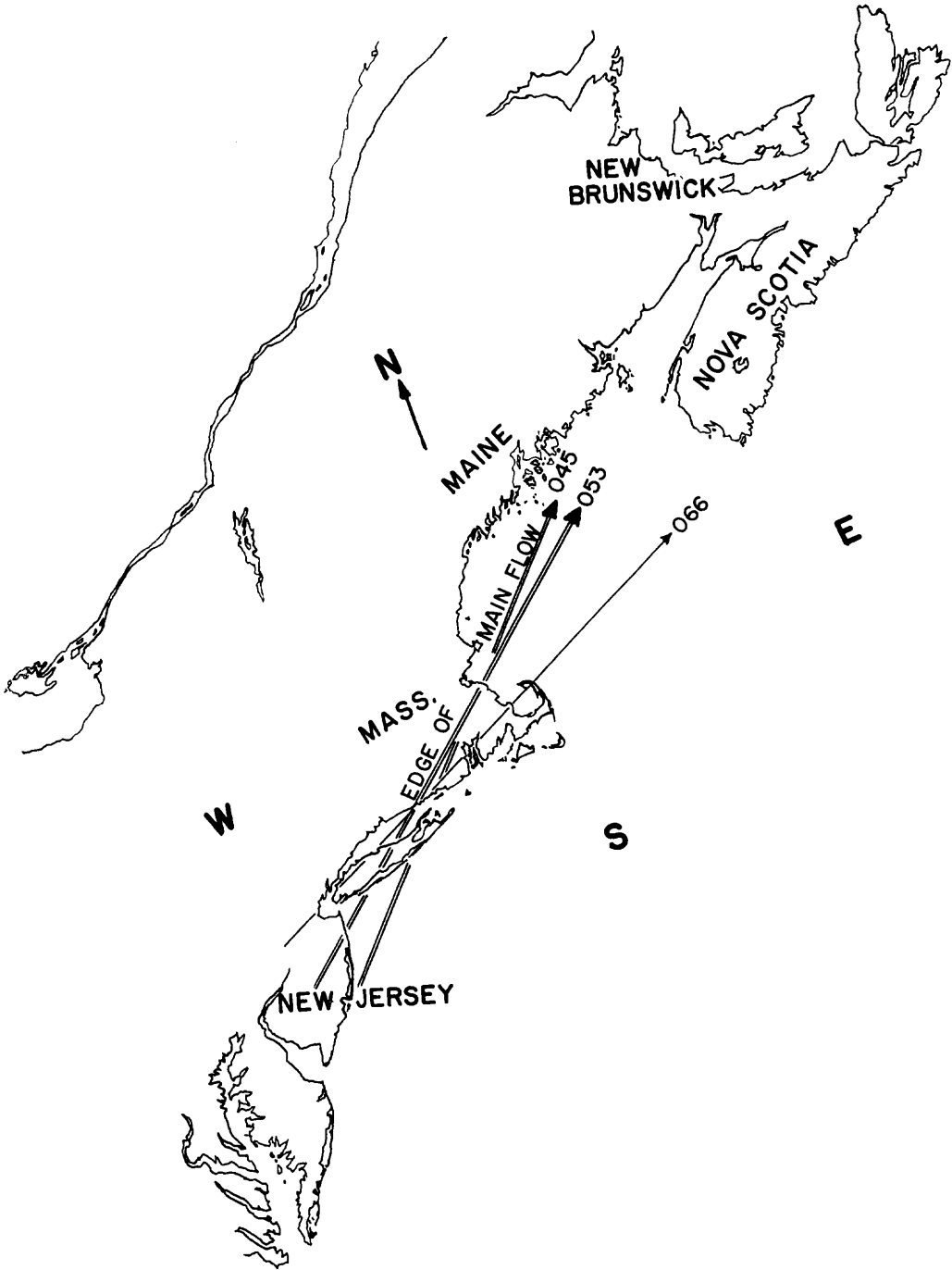


Figure 1. Map of New England, showing the main directions of spring migration observed near Cape Cod. The double lines show the southeastward fringe of the dense mass of migrating songbirds: it closely coincides with the northeast-southwest trend of the Atlantic Coast.

Films were available for 85 nights in the periods 1 May-5 June during 1959, 1960 and 1961. Some migration in directions between north and east was observed on 74 of these nights; the remaining 11 films either showed reversed movements only, or were obscured by echoes from rain. Films were also available for a number of nights during March and April in 1960 and 1961, but are not analyzed here. MTI-wedges were visible during part or all of 52 nights.

Since MTI-wedges are sometimes difficult to measure exactly, we preserved objectivity by extracting all the data before starting to analyze them, and we did not refer back to the films after analyzing the data.

#### DESCRIPTIVE SURVEY

On most nights the main direction of migration over Massachusetts Bay is to the northeast or east-northeast; but the movements of individual birds show a wide spread, sometimes as far to the north as  $020^\circ$  and sometimes as far to the east as  $085^\circ$  (but it is rare for both these directions to be observed on the same night). We cannot measure quantitatively the spread in flight directions, but

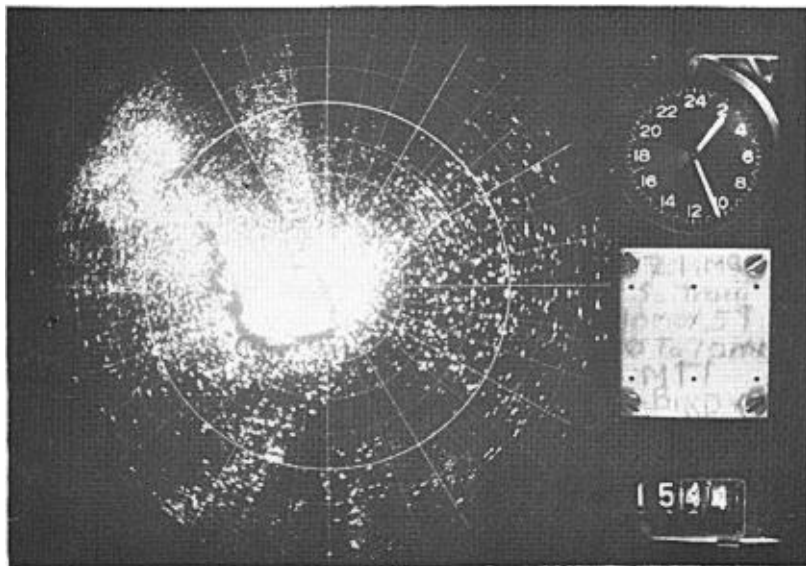


Figure 2. PPI screen at South Truro, Mass., photographed at 0225 Greenwich Time (2125 Eastern Daylight Savings Time) on 10 May 1959. The axis of the dark wedge extending northwest from the center of the screen is perpendicular to the local mean track of the migrating birds.

we estimate that on typical nights the standard deviation is about  $10^\circ$ . For obvious geographical reasons (Figure 1) the more easterly directions are more apparent in the eastern half of the radar screen, so that the birds appear to be fanning out from a center to the left of the radar screen. This paper is concerned primarily with this widely-spread northeastward movement.

Other directions of movement which are frequently observed on the films are the following:

(a) Northwestward movements of bright, fast-moving echoes; these have been attributed to shorebirds arriving from South America (Nisbet, 1963b).

(b) Southeastward movements of bright, fast-moving echoes; perhaps reversed movements of shorebirds.

(c) Southwestward or southward movements of weak, slow-moving echoes; these have been attributed to reversed movements of songbirds (Drury and Keith, 1962).

(d) Eastward or east-southeastward movements of bright echoes; these are similar to the movements attributed to waterbirds in autumn (Drury and Nisbet, 1964).

These movements generally involve small numbers of birds on only a few nights and do not yield MTI-wedges; they will not be considered in detail in this paper.

Whereas in autumn at least four discrete types of movements were observed, each with its own orientation and spatial pattern (Drury and Nisbet, 1964), we could subdivide the spring movements into only two discrete types. To the northwest of Cape Cod, especially over Boston Bay and the adjacent mainland, most echoes are of the weak, flickering type attributed to dense movements of songbirds by Drury and Keith (1962) and Nisbet (1963a). According to published surveys (Griscom and Snyder, 1955; Bailey, 1955), the most numerous landbirds migrating by night through eastern Massachusetts in May and June are members of the families Parulidae, Emberizidae, Turdidae, Tyrannidae and Mimidae; according to breeding-bird censuses summarized by Nisbet (1963a), these five families account for 85-90 per cent of the migrant birds of the northern forests. Over Cape Cod itself, however, and the sea to the east and south, the density of these weak echoes is some 150 times smaller (Drury and Keith, 1962), and the most conspicuous movement is one of bright, faster-moving echoes which start to move several hours before sunset; the density of this movement declines steadily during May and it has hence been attributed mainly to ducks, geese, and gulls (Nisbet and Drury, in prep.).

Although these two movements diverge as they extend northeast over the Gulf of Maine, they overlap and intergrade in the area of Massachusetts Bay where we observe MTI-wedges. Hence we have not attempted to separate them in our analysis of orientation. Probably for this reason, the spread in observed directions on a given night appeared to be larger in spring than that in any of the four autumn movements; and the night-to-night variation in mean

directions (s.d. about  $12^\circ$ ) was larger than that in the most variable of the autumn movements. We therefore suggest that the variability in flight directions at both seasons was primarily due to the presence of a large number of species with different migratory behavior, the differences being greater in autumn than in spring. In particular, the birds which fly south in autumn must return by a more westerly route in spring. Bellrose and Graber (1963) found this "loop-migration" to be normal for all species in the Mid-west; both they and Drury and Keith (1962) independently explained it as an adaptation to the prevailing wind-systems.

#### DETAILED OBSERVATIONS

##### *MTI-wedges.*

MTI-wedges were visible on 65 per cent of the nights on which northeastward movements were detected. Comparison of Table 3 with Table 4 shows that most of the remaining nights were nights when the winds had northerly or easterly components. Such winds are partly opposed to the normal direction of migration and are usually associated with reversed movements (Drury and Keith, 1962). Thus we suggest that the major obstacle to observing MTI-wedges is the presence of birds moving in other directions. This is supported by the fact that in autumn, when directions of migration are more diverse, we observed MTI-wedges on only about 30 per cent of the nights of southward or westward migration (Drury and Nisbet, 1964).

##### *Directions at different ranges.*

Figure 2 shows a spring photograph of the radar screen. It will be seen that the density of echoes is much greater to the northwest of the radar station than to the southeast, and that the MTI-wedge is curved. Table 1 summarizes the mean tracks as observed by the MTI-wedge method at different ranges from the radar station: it will be seen that the birds (mainly waterbirds) over Cape Cod fly, on average, some  $20^\circ$ - $25^\circ$  more to the east than those (mainly song-

TABLE 1. MEAN DIRECTIONS OF MIGRATION, AS RECORDED BY THE MTI-WEDGE METHOD, AT DIFFERENT RANGES FROM SOUTH TRURO. RECORDS FROM ALL DATES AND ALL TIMES HAVE BEEN SUMMARIZED IN THE TABLE.

Range (nautical miles)	Number of records	Mean track $\pm$ s.e.m.
0-10	57	$066^\circ \pm 3.2^\circ$
5-15	83	$058^\circ \pm 1.5^\circ$
10-20	213	$057^\circ \pm 0.6^\circ$
20-30	180	$054^\circ \pm 0.9^\circ$
30-40	92	$048^\circ \pm 1.0^\circ$
40-50	24	$046^\circ \pm 1.1^\circ$
50-70	6	$042^\circ \pm 1.8^\circ$

birds) over the mainland of Massachusetts. Figure 1 shows that this difference can be related simply to the geography of the area: most birds which depart from the mainland of New England on tracks north of  $050^\circ$  do not pass close to the radar station.

*Directions at different times.*

Table 2 summarizes the mean tracks during each hour of the night. It will be seen that the mean tracks tended to turn towards the right by about  $7^\circ$  during the hours between 2000 and midnight, and to return to the left during the subsequent four hours. Both tendencies are apparent at each of the three ranges for which there were adequate data, and are statistically significant ( $p < 0.01$ ) when data for the three ranges are combined.

Figure 1 shows that these changes can be simply explained by reference to the geography of the Atlantic coast. Early in the night the birds crossing Massachusetts Bay are those which have taken off in southeastern Massachusetts and Rhode Island; later in the night they are replaced by birds from the New York City region lying more to the west; still later, these are replaced by birds from

TABLE 2. MEAN DIRECTIONS OF MIGRATION DURING EACH HOUR OF THE NIGHT, AS RECORDED BY THE MTI-WEDGE METHOD.

Hours (E.S.T.)*	Range (nautical miles)			Mean track	Number of Records
	10-20	20-30	30-40		
2015	$053^\circ$	$050^\circ$	$047^\circ$	$051^\circ \pm 1.3^\circ$	54
2115	$055^\circ$	$055^\circ$	$048^\circ$	$054^\circ \pm 1.0^\circ$	88
2215	$057^\circ$	$057^\circ$	$050^\circ$	$056^\circ \pm 1.0^\circ$	84
2315	$059^\circ$	$058^\circ$	$053^\circ$	$057^\circ \pm 1.1^\circ$	70
0015	$061^\circ$	$057^\circ$	$047^\circ$	$056^\circ \pm 1.2^\circ$	58
0115	$057^\circ$	$055^\circ$	$045^\circ$	$053^\circ \pm 1.6^\circ$	42
0215	$060^\circ$	$057^\circ$	( $043^\circ$ )	$057^\circ \pm 1.5^\circ$	33
0315	$059^\circ$	$053^\circ$	( $040^\circ$ )	$054^\circ \pm 1.8^\circ$	31
0415	$051^\circ$	$052^\circ$	( $044^\circ$ )	$049^\circ \pm 2.7^\circ$	18

\*Data for 2000 and 2030 have been combined in the line labelled 2015, and so on.

more southern areas in New Jersey. Since the winds were generally favorable (Table 3) on the nights in question, the reversal of the trend in the mean tracks about 5 hours after the start of the migration is consistent with the expected time of passage of birds from the New York City area 180 miles away. However, it is possible that the changes in mean track may also reflect changes in the tracks of individual birds: Gehring (1963) observed similar changes in the tracks of diurnal migrants in Switzerland, where they are difficult to explain on geographical grounds, and he showed that they are to be expected on geometrical grounds if the birds use an uncorrected sun- or star-compass mechanism of orientation.

*Fluctuations in directions related to wind.*

Tables 1 and 2 describe the average pattern of orientation recorded by the MTI-wedge method, and can therefore be used to obtain the deviation of a single observation from the average pattern. For example, at a range of 10-20 nautical miles, the average pattern is for the mean track to change from about 055° at 2000 E.S.T. to 062° at 0000 E.S.T. Thus the observation of a wedge at 335° at 2000 E.S.T. represents a deviation of +10° from the average, the + sign indicating deviation to the birds' right.

In Table 3 the deviations of the mean tracks from the average pattern are related to the direction and speed of the geostrophic wind (which approximates the average wind at the birds' usual height above the earth's boundary layer). It will be seen that positive deviations are associated with winds from the birds' left, and *vice versa*.

*Subjective measurements of flight directions.*

Table 3 shows that most records of MTI-wedges were with following or partly-following winds. (As already noted, the main reason for this is probably that the wedges are obscured by movements in other directions when the winds are abeam or opposed.) In order to measure the effect of beam- or head-winds, it is necessary to use subjective measurements of flight directions, obtained from visual inspection of the films. This was not possible on the autumn films (Drury and Nisbet, 1964), because of the complex nature of the movements, but on the spring films we could classify movements under four directional groups, viz., 020°-035°, 040°-055°, 060°-070° and 075°-085°; usually two or three of these could be seen on each film. In Table 4 we have summarized the number of times each of

TABLE 3. DEVIATIONS OF MEAN TRACKS FROM THE AVERAGE PATTERN, RELATED TO THE GEOSTROPHIC WINDS

Notes: The geostrophic winds were obtained by standard graphical methods from the 3-hourly weather maps prepared by the U. S. Weather Bureau. Mean tracks were measured by the MTI-wedge method, usually once per hour, and were related to the nearest available wind measurement; for example, tracks measured at 0200, 0300 and 0400 were related to the wind at 0300 to yield three data for the table. The figures plotted are the means of all the deviations corresponding to the given ranges of wind speed and direction, ± the standard error of the mean, with the sample size in parentheses.

Wind direction	Wind Speed		
	0-8 knots	10-20 knots	Over 22 knots
190°-215°	-1.5 ± 2.4 (13)	-4.8 ± 1.1 (52)	-1.9 ± 3.0 (8)
220°-245°	(0)	-3.2 ± 0.9 (43)	+0.3 ± 1.2 (73)
250°-275°	ca. + 0.3 (4)	+2.3 ± 0.9 (53)	+4.3 ± 1.0 (33)
280°-325°	ca. + 3 (3)	+2.8 ± 1.7 (26)	+8.9 ± 2.2 (15)

these groups was recorded in relation to the direction of the surface wind observed at Boston at midnight. Regression analysis of the data in Table 4 indicated that on average, the birds' mean track deviated to the right by  $(0.041 \pm .010)$  groups, that is about  $(0.65 \pm 0.16)$  degrees, for each change of the wind by one compass point ( $11\frac{1}{4}^\circ$ ) towards the left. This is consistent with the corresponding figure of about  $(1.2 \pm 0.4)^\circ$  per compass point obtained from Table 3.

*Changes in flight pattern.*

These figures suggest that cross-winds did not cause much deviation of the mean tracks; but study of Figure 1 shows that, although deviations to the right should be observed easily, deviations to the left might not be conspicuous because any birds so deviated would pass further from the radar station. As an independent test for deviation by cross-winds, we attempted to correlate fluctuations in the position of the southeastward edge of the mass of echoes with the direction of the wind. It is difficult to locate the edge of the mass of echoes objectively, but an approximate measure of its

TABLE 4. OBSERVED DIRECTIONS OF FLIGHT OVER MASSACHUSETTS BAY RELATED TO THE WIND OBSERVED AT BOSTON  
Regression equation:  $y = 3.184 - 0.0824x$

Direction of flight		020°-035°	040°-055°	060°-070°	075°-085°
Variable y		1	2	3	4
Wind					
Direction	Variable x				
ENE	0	—	1	2	2
NE	1	—	—	1	1
NNE	2	—	1	1	—
N	3	—	2	1	1
NNW	4	—	1	4	1
NW	5	1	3	3	1
WNW	6	—	3	6	—
W	7	1	4	6	4
WSW	8	3	7	7	3
Calm	8 1/2	—	1	4	1
SW	9	5	13	14	2
SSW	10	2	9	5	2
S	11	—	1	1	—
SSE	12	—	—	—	—
SE	13	—	1	—	—
ESE	14	3	3	—	—
E	15	2	3	2	—



position is provided by the closest range at which an MTI-wedge was observable. Table 5 summarizes the relation between this measure and the geostrophic winds. It will be seen that the shift in the southeastward edge of the mass of echoes was only about 1/2 mile per compass point shift in the wind; since most of the birds had flown for 1-6 hours before being recorded (Table 2), this shift is no more (and probably less) than that expected from Tables 3 and 4.

*Migration under overcast skies.*

Of the 52 nights when orientation was good enough for us to observe MTI-wedges, 12 were overcast at Boston and a further 8 were very cloudy (average cloud cover eight-tenths or more). The orientation of the MTI-wedges appears to have been exactly similar on these nights to that on the remaining 32, and we have found no qualitative or statistical differences between the two sets of data. On at least one night (21/22 May 1961) the MTI-wedge shifted to the right by  $5^{\circ}$ - $10^{\circ}$  before midnight and back again after midnight in the normal way (Table 2), in spite of uniformly overcast skies. We conclude that, as in autumn (Drury and Nisbet, 1964), overcast skies do not significantly impair orientation.

TABLE 5. MINIMUM RANGES AT WHICH MTI-WEDGES WERE OBSERVED, RELATED TO THE GEOSTROPHIC WINDS.

THE FIGURES GIVEN ARE THE MEAN RANGE (IN NAUTICAL MILES)  $\pm$  STANDARD ERROR, WITH THE NUMBER OF RECORDS IN PARENTHESES.

Wind directions	Wind strength (knots)		
	0-8	10-20	Over 20
190°-210°	ca. 28 (5)	12 $\pm$ 1.4 (11)	17 $\pm$ 3.5 (3)
220°-245°	—	11 $\pm$ 0.8 (13)	11 $\pm$ 1.0 (24)
250°-275°	—	9 $\pm$ 1.0 (20)	11 $\pm$ 2.2 (10)
280°-320°	—	8 $\pm$ 1.8 (12)	13 $\pm$ 1.8 (7)

DISCUSSION: DRIFT?

Tables 3, 4 and 5 agree in indicating that cross-winds were associated with a shift in the observed mean tracks of the birds of  $0.5^{\circ}$ - $1^{\circ}$  for each compass point between the birds' normal mean track and the direction of the wind. This is much smaller than the deviation of about  $5^{\circ}$  for each compass point expected on the hypothesis that the birds' mean heading was the same on each night, so that they were drifted passively. Thus the birds must have compensated for most, if not all, of the drifting effect of cross-winds.

Our results for autumn were similar (Drury and Nisbet, 1964): in two movements we observed no deviation at all; in the other two movements we observed slight deviations, but they were not statistically significant and were much smaller than those expected on the hypothesis of passive lateral drift.

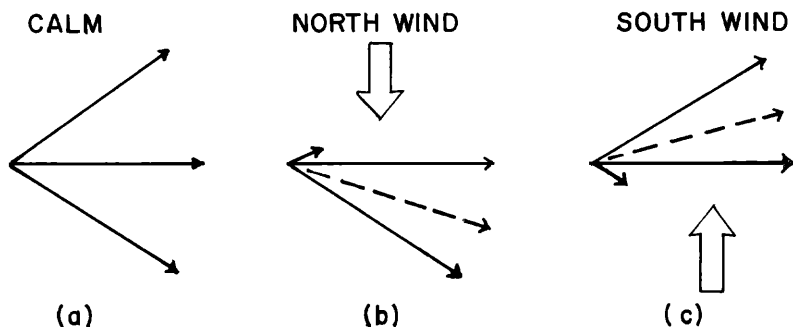


Figure 3. Effect of a cross-wind on a widely-spread bird movement. Diagram (a) shows the directional tendencies of the birds in calm weather. With a cross-wind from the left (diagram (b)), the birds which would otherwise fly to the left of average do not migrate, so that the mean track (dashed arrow) is deviated to the right. Similarly, a cross-wind from the right (diagram (c)) deviates the mean track to the left, thus simulating drift. If the birds do not compensate for drift, the deviations will be even larger.

It is usually taken for granted that wind-correlated deviations of the kind shown on Tables 3-5 are evidence for "lateral drift", even though the small size of the deviations indicates partial compensation for drift. This interpretation, however, requires the dubious assumption that the birds flying on each night have the same directional preferences, independent of the wind. An alternative explanation of the observed deviations (Drury and Nisbet, 1964: 92) is that the birds which normally fly on a track to the right of the average avoid migrating in winds from the right (which to them are partially opposed), but preferentially migrate in winds from the left (which to them are partially following). This mechanism is illustrated in Figure 3.

For a quantitative evaluation, consider a hypothetical bird population whose members fly on tracks between a minimum of  $-\Psi$  and a maximum of  $+\Psi$ , the density between these extremes being  $A d\theta$  within the range of tracks  $\theta$  to  $\theta + d\theta$ , where  $A$  is a constant. The total density of migration is then  $2A\Psi$ . Suppose that each bird's track is unaffected by a cross-wind, but that the density in each direction is augmented by partly following winds, and suppressed by partly opposed winds, by the multiplicative factor  $(1 - a \cos \alpha)$ , where  $\alpha$  is the angle between the wind and the direction concerned. This factor can become negative when  $\alpha$  is small (i.e., for headwinds) so we will apply the model only to tail- and crosswinds. A more realistic model would include the effect of varying wind strength, and would avoid the over-simplifying assumptions that  $A$  and  $a$  are constants; however, this simple model preserves the essential features of the mechanism illustrated in Figure 3.

In the simplest case, where the wind is at right angles to the undisturbed direction,  $\alpha = \frac{1}{2} \pi - \theta$ ; it can then be shown that the

mean direction of the birds which fly is given by

$$\bar{\theta} = a(\Psi^{-1} \sin \Psi - \cos \Psi),$$

or, if  $c$  is not very large ( $\Psi^2 \ll 10$ ),

$$\bar{\theta} = \frac{a\Psi^2}{3}.$$

This represents the deviation of the mean observed direction due, not to drift, but to modification of the *composition* of the flying population by the cross-wind. This deviation is proportional to  $a$  and to the square of  $\Psi$ , which measure respectively the suppressive effects of head-winds, and the spread of directions within the population.  $(1+a)$  is the ratio of the mean density of migration with tail-winds to that with cross-winds and is easily measured.

In the case of our spring migration,  $\Psi$  is about 0.6 radians ( $= 34^\circ$ ) and  $a$  is about 0.6 (Nisbet and Drury, in prep.), so the above model predicts a deviation of about .072 radians ( $= 4.1^\circ$ ) for a wind at right angles to the normal mean track, which is in reasonable agreement with our observed deviation of  $5.1^\circ$  from Table 4. We therefore suggest that this effect is the major, and probably the only, cause of the observed deviation. Our data are thus consistent with the hypothesis that, on average, the birds compensated exactly for the drifting effect of cross-winds.\*

The above model also explains why the observed deviations in autumn were smaller than those in spring, because the values of  $\Psi$  for the discrete autumn movements were much smaller (0.15-0.4) than those for the diffuse spring movement. Indeed the two autumn movements with the larger values of  $\Psi$  were the two in which we recorded small deviations (Drury and Nisbet, 1964).

Our model also appears to explain the results of Bellrose and Graber (1963), who observed small deviations in cross-winds and interpreted them as due to partially-compensated drift. For their autumn migration,  $a$  can be estimated as roughly 0.9 radians (Hassler, *et al.*, 1963: Figures 4 and 5), and  $\Psi$  as 1.2 (Bellrose and Graber, 1963: Table 2), so that our model predicts  $\theta = 0.43$  radians ( $= 25^\circ$ ), in good agreement with the observed value (Bellrose and Graber, 1963: Figure 4) of about  $21^\circ$ . Thus we suggest that they observed larger deviations in autumn in Illinois than we did in Massachusetts, mainly because the spread in flight-directions was greater in Illinois. In spring, the spread in their flight-directions was at least as large as in autumn (their Table 1), but they have published no data from which a could be estimated: their Figure 5 would be consistent with our model if  $a$  is less than 0.2. Bellrose (pers. comm.) has concluded that his data show that the birds he observed do compensate for drift.

\*After we had submitted this paper, Peter Evans, at the International Ornithological Congress at Oxford, reported an identical explanation which he had developed independently for pseudo-drift. This has now been published (Evans, 1966).

Our model may likewise explain the deviations observed by Bergman and Donner (1964), which they interpreted as due to passive drift by the wind. For their birds (Oldsquaws *Clangula hyemalis*, and Common Scoters *Melanitta nigra*),  $\Psi$  was about 0.50 radians ( $= 29^\circ$ ), (their Figure 7), and  $\alpha$  was at least as large as 3 (pp. 9, 45-47), so that our model predicts  $\theta = 0.25$  radians ( $= 14^\circ$ ), in good agreement with the value of  $15^\circ$  estimated by inspection of Figure 7.

Our model does not, however, fully account for the observations of Lack (1958), 1960, 1963b), who reported that birds flying east over the North Sea in spring appeared to be passively drifted. For these birds,  $\Psi$  was at least as large as 1.2 (Lack, 1960: Table 7), and  $\alpha$  at least as large as 1.0 (Lack, 1963b: 475; Lack, 1962: 75; Tedd and Lack, 1958). Hence, on our model,  $\theta$  would be expected to be as large as  $0.48$  ( $= 27^\circ$ ), but this still seems significantly smaller than the value of  $(38^\circ \pm 1.6^\circ)$  obtained by a linear regression analysis of the data in Lack's (1960) Table 10. Thus we suggest that the mechanism shown in our Figure 3 explains a substantial part of the wind-correlated deviation described by Lack, but that the remaining part must be attributed to drift. (This conclusion needs to be checked, because it is difficult to estimate  $\theta$  precisely from Tedd and Lack's numerical scale.)

However, it should be emphasized that our mechanism must be *additional* to any effect of drift. If Lack's birds had been passively drifted, he should have observed a much larger deviation than he did—of the order of  $60^\circ$  for a beam wind, instead of the  $40^\circ$ - $50^\circ$  predicted by the hypothesis of passive drift without taking account of our mechanism. Therefore, we suggest that his birds must have compensated, but did not fully compensate for the effect of drift.

Other European radar studies (Sutter, 1961; Parslow, 1962; Lack, 1962a, 1963a; Gehring, 1963; Lee, 1963; Myres, 1964; Wilcock, 1965) have all followed Lack (1960) in concluding that migrants in Europe are passively drifted by the wind. However, none of these papers included enough data for us to test critically how far the observed deviations can be explained by means of our mechanism.

If it is accepted that migrants in Europe do not fully compensate for drift, it is necessary to consider why their behavior differs so markedly from that of migrants in North America. One possible explanation is that the species studied in North America are mainly long-distance migrants with limited wintering areas, whereas most of those studied in Europe (Parslow's (1962) warblers being an exception) have been short-distance migrants, many of which are nomadic in winter (Lack, 1963a; Ashmole, 1962). Moreover, north-west Europe is stormy: it must often be impossible, and it may frequently be undesirable, for migrants there to attempt to preserve a constant track (cf. Nisbet, 1957; Lee, 1963).

Lack (1962b) has pointed out the theoretical importance of drift: if birds are drifted off-course by the wind, they need a navigational mechanism to reach their destination. As far as our birds are concerned, we would repeat our earlier conclusion (Drury and Nisbet, 1964) that they appear to preserve their tracks so precisely that it is unnecessary to suppose that they use any form of bi-co-ordinate navigation.

SUMMARY

Orientation of northeastward migration was studied using radar on Cape Cod during 85 nights in May and early June, 1959-1961.

Directions of migration were less diverse in spring than in autumn. The species which migrate south over New England in autumn must return by a more westerly route in spring.

The mean direction of migration was about 7° further to the right in the middle of the night than earlier or later.

The mean direction of migration was deviated to the left by cross-winds from the right, and *vice versa*, but the deviations were much too small to be explained as drift from a constant heading. It is suggested that the birds compensated for drift, but that winds from the right suppressed the migration of the birds whose preferred direction was more to the right than average. The same mechanism can explain cases of apparent drift reported from North America, and can partly explain cases reported from Europe.

Orientation appeared to be unimpaired by overcast skies.

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LITERATURE CITED

- ASHMOLE, M. J. 1962. The migration of European thrushes: a comparative study based on ringing recoveries. *Ibis*, **104**: 314-346; 522-559.
- BAILEY, W. 1955. *Birds in Massachusetts—when and where to find them*. South Lancaster, Mass. 234 pp.
- BELLROSE, F. C. and R. R. GRABER. 1963. A radar study of the flight directions of nocturnal migrants. *Proc. XIIIth Int. Orn. Cong. (Ithaca, 1962)*, pp. 362-389.
- BERGMAN, G. and K. O. DONNER. 1964. An analysis of the spring migration of the Common Scoter and the Long-tailed Duck in Southern Finland. *Acta Zool. Fenn.*, **105**: 1-59.
- DRURY, W. H. and J. A. KEITH. 1962. Radar studies of songbird migration in coastal New England. *Ibis*, **104**: 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**: 69-119.
- EVANS, P. R. 1966. Migration and orientation of passerine night migrants in north-east England. *J. Zool., Lond.*, **150**(2): 319-370.
- GEHRING, W. 1963. Radar- und Felbeobachtungen über den Verlauf des Vogelzuges im Schweizerischen Mittelland: Der Tagzug im Herbst (1957-1961). *Der Ornith. Beob.*, **60**: 35-67.
- GRISCOM, L. and D. E. SNYDER. 1955. *The birds of Massachusetts: an annotated and revised check list*. Salem, Mass. xiii + 295 pp.
- HASSLER, S. R., R. R. GRABER, and F. C. BELLROSE. 1963. Fall migration and weather, a radar study. *Wils. Bull.*, **75**: 56-77.

- LACK, D. 1958. Migrational drift of birds plotted by radar. *Nature*, **182**: 221-223.
- LACK, D. 1960. Migration across the North Sea studied by radar. Part 2: The spring Departure 1956-59. *Ibis*, **102**: 26-57.
- LACK, D. 1962a. Migration across the southern North Sea studied by radar. Part 3: Movements in June and July. *Ibis*, **104**: 74-85.
- LACK, D. 1962b. Radar evidence on migratory orientation. *Brit. Birds*, **55**: 139-158.
- LACK, D. 1963a. Migration across the southern North Sea studied by radar. Part 4: Autumn. *Ibis*, **105**: 1-54.
- LACK, D. 1963b. Migration across the southern North Sea studied by radar. Part 5: Movements in August, Winter and Spring, and Conclusion. *Ibis*, **105**: 461-492.
- LEE, S. L. B. 1963. Migration in the Outer Hebrides studied by radar. (Ed. by D. Lack.) *Ibis*, **105**: 493-515.
- MYRES, M. T. 1964. Dawn ascent and re-orientation of Scandinavian thrushes (*Turdus spp.*) migrating at night over the northeastern Atlantic Ocean in autumn. *Ibis*, **106**: 7-51.
- NISBET, I. C. T. 1957. Passerine migration in south Scandinavia in the autumn of 1954. *Ibis*, **99**: 228-268.
- NISBET, I. C. T. 1963a. Quantitative study of migration with 23-centimetre radar. *Ibis*, **105**: 435-460.
- NISBET, I. C. T. 1963b. Measurements with radar of the height of nocturnal migration over Cape Cod, Massachusetts. *Bird-Banding*, **34**: 57-67.
- NISBET, I. C. T. and W. H. DRURY. In prep. Spring migration in New England in relation to weather.
- PARSLOW, J. L. F. 1962. Immigration of night-migrants into southern England in spring 1962. *Bird-Migration*, **2**: 160-175.
- RICHARDSON, R. E., J. M. STACEY, H. M. KOHLER, and F. R. NAKA. 1959. Radar returns from birds, and their elimination from radar outputs. Group Report 45-42, 22 December 1959, Mass. Inst. Tech., Lincoln Laboratory, Lexington, Mass.
- SUTTER, E. 1961. Einflüsse des Wetters auf die nächtliche Orientierung wandernder Vögel nach Beobachtungen am Radarschirm. Sonderbücherei der Funkortung, Diskussionstagung in Essen, 4-8 Jan. 1960, **1(8)**: 1-14.
- TEDD, J. G. and D. LACK. 1958. The detection of bird migration by high-powered radar. *Proc. Roy. Soc. B.*, **149**: 503-510.
- WILCOCK, J. 1965. Detection by radar of autumn migration in eastern Scotland. *Ibis*, **107**: 316-325.

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