BIRD-BANDING

A JOURNAL OF ORNITHOLOGICAL INVESTIGATION

VOL. XXXV | APRIL, 1964 | NO. 2

RADAR STUDIES OF ORIENTATION OF SONGBIRD MIGRANTS IN SOUTHEASTERN NEW ENGLAND*

By W. H. DRURY, JR. & I. C. T. NISBET

INTRODUCTION

This paper summarizes the results of studies of the orientation of songbirds on autumn night-migration, made at a radar station on Cape Cod, Massachusetts. In a general survey of the migration observed by radar in this area, Drury & Keith (1962) discussed primarily the effects of weather on the start of migration, and did not analyze the observed directions of flight. As found by Lack (1959-63) in Europe, migration over Cape Cod is made up of a number of discrete broad-front movements characterized by uniformity and consistency of direction.

In this paper we describe the main autumn migration movements, paying special attention to the way in which directions of flight vary from hour to hour and from place to place, and to the effects of wind, clouds, rain, and fog upon the flight directions. We confine our attention, so far as practicable, to passerines and other small landbirds, and do not discuss in detail observations of "reversed" migrations, i.e., movements in direction between NNE and ESE. However, for completeness, we list all the well-defined movements, including those attributed to non-passerines.

Except in phrases of qualitative description, we express all directions in degrees from True North (East = 90°, South = 180°, West = 270°). By convention, the direction of a bird's flight is the direction towards which it is flying, but the direction of the wind is that away from which it is blowing. Speeds are quoted in knots. Times are Eastern Standard Time.

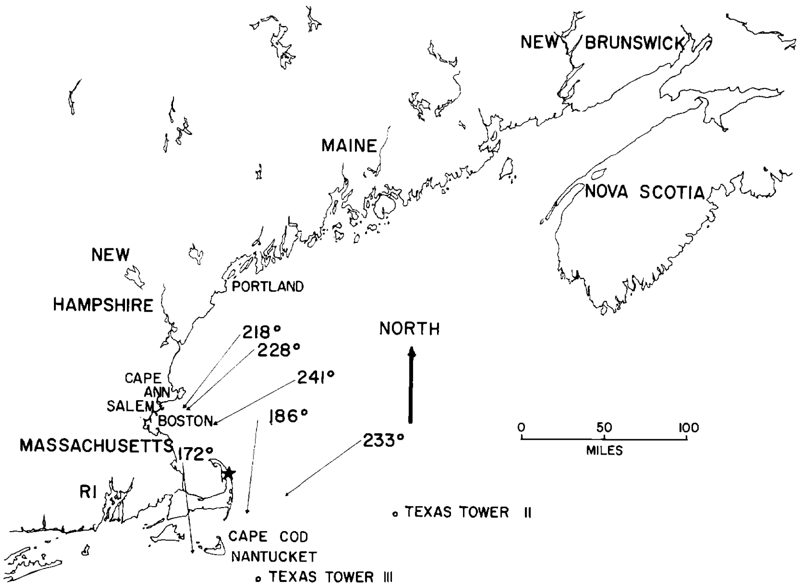
Radar

The radar station is at South Truro, on Cape Cod, Massachusetts (Figure 1); its technical characteristics and its suitability for detecting bird migration have been described by Richardson *et al.* (1959) and by Nisbet (1963b). We based this study on observations of a continuous 35 mm. movie film record of the Plan/Position Indicator (PPI) screen. Figures 2-8 show some typical frames from the film. Echoes from birds appear as white spots on a circular map, centered

*Contribution No. 48 from the Hatheway School of Conservation Education, Massachusetts Audubon Society, Lincoln, Massachusetts.

Figure 1: MAP OF NEW ENGLAND AND MARITIME CANADA.

The map shows the area covered by the radar and the regions from which migrants come on autumn migration. Arrows trace the track and give the compass direction, True, of the major movements. The South Truro radar site is at the star on outer Cape Cod.



on the radar station. Small birds typically give echoes at ranges up to about 40 nautical miles, and on nights of dense migration their echoes appear up to 70 or even 80 miles, although at such ranges low-flying birds are usually missed because they are below the visual horizon of the radar. Directions and ranges may be measured by means of a 10-mile/10-degree grid displayed on the screen.

Each frame of the film corresponds to one complete revolution of the radar beam, lasting 12 seconds. When the film is projected on a cinematic viewer at, say, 15 frames per second, the motion of the echoes is speeded up by a factor of 180, and the direction and speed of moving echoes become apparent. This procedure allows one to see an impression of the main flight directions and spatial distributions of the birds, but it is not, however, suitable for detailed studies of orientation. Although the echoes from some large birds and large flocks (e.g., gulls and shorebirds) are persistent and can be traced for some distance across the screen, the echoes from small birds are ephemeral and each usually disappears from the screen after 1-5 revolutions of the radar beam (Nisbet 1963b). Because of the characteristics of the radarscope, we cannot use the direction of afterglow tails to measure orientation, as did Lack (1959). Although the general direction of movement of a mass of echoes from small birds can be determined from the cine-film (much as the direction of the wind during a blizzard can be determined without following any individual snowflake for more than a split-second), it is usually impossible to measure directly the exact speed or direction of movement of an individual target.

The MTI-wedge method.

The *average* track of a mass of birds, however, can easily be determined by means of a circuit in use at the South Truro radar station, known as a Moving Target Indicator (MTI). This removes from the radar screen the echoes of all targets whose velocity has a component of less than one or two knots towards or away from the radar station. The chief function of the MTI is to remove echoes from stationary targets (e.g., hills), so that aircraft can be observed continuously (birds usually give echoes too weak to be detected above such stationary targets). An advantage of the MTI circuit for our use of this radar is that it removes echoes from all targets which are moving perpendicularly to the line joining them to the radar station (i.e., tangentially to the range-rings on the radar screen). Hence, if all the targets are moving in the same direction, the MTI removes echoes from a wedge-shaped sector on each side of the radar station (like two slices cut on opposite sides of a pie—Figures 2-8), the center line of each wedge being perpendicular to the direction of movement. If (as is the case in practice) the directions of movement of the targets are not all identical, but are spread around a mean, the MTI wedges are diffuse, but the center-lines are perpendicular to the mean.

The clarity of the MTI-wedges depends on the quality of orientation of the birds and their speed. The more closely the birds' tracks are grouped about the mean, and the higher their average ground-speed, the narrower and more sharply-defined are the wedges. Hence, other things being equal, MTI-wedges are much sharper when the birds have a tail-wind than when they have a head-wind. Usually, however, if an MTI-wedge is visible at all, it is possible to estimate the position of its center-line within 2°, or at worst, 3°; we have excluded from this study all observations which are more uncertain than this. Examples of MTI-wedges of varying degrees of clarity are shown in the photographs (Figures 2-8). When the film is run through a cinematic viewer, the movement of targets and their disappearance when they pass into the MTI-wedge usually makes that wedge much more clearly visible than it appears on any of the single frames reproduced.

Unfortunately, it is rare at South Truro for migration to show only one mean direction: on most nights there are at least two, and often more. If two groups of echoes from songbirds with different mean tracks are superimposed in roughly equal densities, each obscures the other's MTI-wedge, so that it is impossible to measure the mean track of either by this means. However, if one group of echoes is several times more dense than the other, it is often possible to observe its MTI-wedge clearly; at South Truro most of the major movements of birds do not take place uniformly but are usually much denser on one side of Cape Cod than on the other. Hence it is often possible to measure the orientation of two movements on the same film, and in favorable circumstances we have even been able to measure three or four MTI-wedges, at different ranges from the radar station (for example, Figure 3). Errors are possible where the tracks of the two movements differ by 15° or less, because the MTI-wedges may overlap and appear as a single broad wedge; but experience has, we believe, allowed us to pick out such cases (see below, page 93).

In spite of its simplicity and accuracy, the MTI-wedge method has several limitations:

1. It gives accurate information only about the *average* direction of movement of a large mass of birds, and it gives only a very rough qualitative idea of the amount of scatter (i.e., the quality of orientation).

2. It applies only to birds in certain directions from the radar station, and cannot be used to study local variations in orientation.

3. It can only be used intermittently, because MTI-wedges are often obscured by echoes of birds moving in other directions, by lapses in adjustment and stability of the radar equipment, and by other factors which we do not understand.

4. It is biased, giving information mainly for those occasions when the birds are best-oriented (especially the occasions with more or less following wind). It gives little information about orientation against head-winds, or about movements on those occasions when orientation breaks down (although these can be studied independently).

5. It is not dependable on several azimuths (145°, 260°, and 335°) where the lower part of the radar beam is interrupted by low hills. These hills cast a wedge-shaped "shadow" in which comparatively few birds are detected, so that we can measure the MTI-wedges only when movements are dense and well-oriented.

In this paper we list and analyze *all* our records of clear MTI-wedges during autumn nocturnal migration of small landbirds, excluding records of shorebirds, waterfowl, etc., and of landbirds migrating by day; we also exclude "reversed" migration (between NNE and ESE) of nocturnally migrating passerines, which we intend to study in detail later. The reader should bear in mind: (i) that the records quoted are an incomplete record of migration near Cape Cod; (ii) that they refer to small and medium, as well as large densities of migration (very small movements do not give clear MTI-wedges); (iii) that they refer mostly to occasions of light or following winds.

Observations available.

Our radar observations covered both spring and autumn seasons in 1959, 1960 and 1961, and 29 days in the autumn of 1962. The record was reasonably complete for May, September and October during 1959-1961, but was severely limited for other months. Nominally, films were taken throughout each night; in fact, films for many nights were incomplete because of priority of other research operations at The Mitre Corporation site, and the problem of staffing in the hours after midnight for this gratuitous undertaking.

Definitions.

Track: The direction of a bird's flight relative to the ground.

Heading: The direction of a bird's flight relative to the air; i.e., the direction in which the bird is pointing.

Orientation: The process (sensory responses to external clues) by which a bird takes up its heading and/or follows its track (Type II of Griffin 1953).

Navigation: The process by which a bird moves consistently between two points on the earth's surface, by means other than the recognition of known landmarks. An essential feature of this process (Type III orientation of Griffin; "map" process of Kramer 1961 and Lack 1962b) is the reference to two predetermined points, a starting-point and a goal. Hence our definition excludes "dead-reckoning" or "direction-and-distance" orientation; but it includes inertial navigation which, although directly based only on reference to the starting-point, implicitly makes reference to the goal (see below).

Disoriented movement: A phenomenon in which a mass of birds appears to be moving at random. (This term is defined in more detail below).

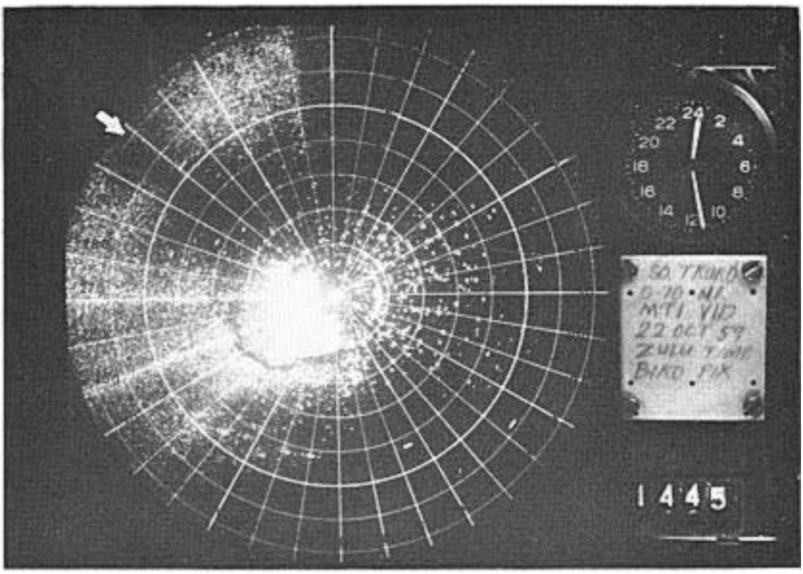
Tracks, headings and winds.

The MTI-wedges measure the average tracks, but to discuss orientation, it is also necessary to know the average headings, and this requires knowledge of the winds which affect the birds.

Cape Cod is an area where cold and warm air-masses, and cold and warm ocean currents meet, and the direction of the sea-level winds is a very unreliable indication of that of winds above the surface. Most landbirds in this area migrate between 600 and 5,000 feet above sea-level (Nisbet, 1963a), and actual measurements of winds in this range of heights are not available in complete form and are not made frequently enough to be useful for this study.

For our purposes, the most reliable measure of upper-air wind that is available is the "gradient" or "geostrophic" wind. This wind, usually a good approximation to the wind above the earth's boundary layer and within a few thousand feet of the ground, is parallel to the sea-level isobars and proportional to the sea-level pressure gradient, and can be measured directly from the sea-level weather maps. Suitable maps are available for every three hours, and the estimates of gradient winds which we have used are listed in Appendix Table 1. As estimates of the *average* wind in the Cape Cod area, these figures are probably reliable within about 10° in direction and 3 knots in speed, but, of course, they give no information about

Figure 2: PPI Scope Picture of Southwestward Movement over Mainland. 2029 on 21 October 1959. Coarse targets (seabirds) appear east of Cape Cod; a dense southwestward movement of songbirds appears west of the cape and over Cape Ann. MTI gap appears over Boston (see arrow). Aircraft appear at 4 and 5 o'clock in the bottom right corner. Notice that over the heavy permanent targets of Cape Cod (removed by MTI circuits) the small bird targets are lost also.



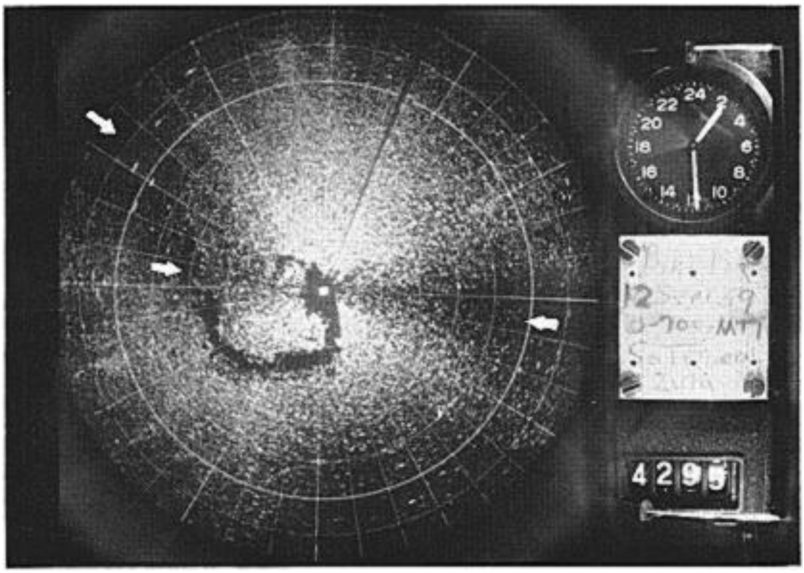
local variations within the 70-mile-radius circle covered by the radar station.

We determined headings from the observed tracks by means of the triangle of velocities (equation: **heading + wind velocity = track**), using a simple graphical method which was accurate within 1°, much more reliable than the estimates of wind velocity. For this purpose we assumed that the average air-speed of the birds was 22 knots. We were usually unable to estimate the air-speed of the birds directly, because most of the echoes could not be traced for a sufficiently long time; but in cases where we could measure the air-speed of small birds, the results were usually in the range 18-26 knots (Nisbet *et al.* 1963). We have found little variation in the average air-speed during the season, and there is no great variation in the average size of the birds (Nisbet 1963b).

Errors of 10° are probably frequent in the estimates of the birds' headings because of uncertainty in estimating the average upper-air winds, and a few estimates of headings are probably wrong by 20°, or even more. Errors are, of course, much more likely when the birds are drifted by the wind, and estimates should be treated with caution when they differ by more than 40° from the mean track. *The few such estimates included in the tables are marked with a dagger.*

Figure 3: PPI SCOPE PICTURE OF SOUTHWESTWARD AND SOUTHWARD MOVEMENTS.

2229 on 11 September 1959. Note MTI cap at 305° over Boston, indicating the track of the movement over the mainland; compare with Figure 4, three hours and fifteen minutes later. Compare the clarity of the wedges related to the southward departure (arrows at 096°-276°) with that in Figure 4.



Presentation of results.

In order to analyze our results, we first grouped them into well-defined movements, basing the classification on (a) where each movement was seen on the PPI scope map, (b) time-variations in density, and (c) the mean tracks. An indication of the reliability of the classification is that only two cases remain unassigned: these will be discussed separately at the end.

In the tables we give hour-by-hour measurements of the mean track of the birds—perpendicular to observed MTI-wedges. Blanks in the tables mean that no wedge was visible, not that movements were not observed. Headings, as described above, are given for the times at which the wind data are available (1900, 2200, 0100, and 0400).

SOUTHWEST MOVEMENTS OVER THE MAINLAND

About 45 minutes after sunset a dense mass of echoes appears over the mainland in the northwest corner of the screen—Boston and Cape Ann. Usually birds also fly up from the mainland areas west and southwest of the radar station and from Cape Cod, but these birds do not contribute to the MTI-wedge. An MTI-wedge in the vicinity of Salem, Mass. (Figure 2) is often the only indication

TABLE 1. SOUTHWEST MOVEMENTS OVER MAINLAND

Date	Tracks at time: 19	20	21	22	23	24	01	02	03	04	05	Headings at: 19	22	01	04	Initial Track	Initial Heading	CLOUD COVER Portland 22	Portland 01	Boston 22	Boston 01	Nantucket 22	Nantucket 01
4/5 Sept. 59	—	214	—	—	—	—	—	—	—	—	—	—	—	—	—	214	(224)						
4/5 Sept. 61	—	220	220	225	225							—	225	—	—	220	(220)	2		0		10	
5/6 Sept. 61	—	—	222	225	226							—	243	—	—	(222)	(240)	3		0		4	
6/7 Sept. 61	—	219	214									—	—	—	—	219	(200)						
8/9 Sept. 61	—	220	219									—	—	—	—	220	(207)						
9/10 Sept. 61	—	220	222	227	225							—	237	—	—	220	(220)	0		0		4	
9/10 Sept. 59	—	—	—	220	212	217	218	220				—	205	205	—	—	—	1	0	0	10	10	10
11/12 Sept. 59	215	216	212	216	224	218	222	224	225	225	225	227	245	244	250	215	227	0	0	0	0	0	0
15/16 Sept. 61	217	218	214	215								235	237	—	—	217	235	7		10		5	
16/17 Sept. 61	—	218	218	220	220							—	199			218	(211)	0		1		0	
19/20 Sept. 61	—	—	217	221	220	220	222	226	225			—	182	195		(217)	(177)	10	9	10	8	10	10
21/22 Sept. 60	—	220	226	224	220	233	224	222					217	221		220	(220)	10	0	8	10	0	0
23/24 Sept. 61	222	225	221	228	228	228	229	223	225	226	—	215	225	207	209	222	215	10	10	10	10	10	10
26/27 Sept. 62	215	208	220	220								196	211			215	196	9		10		10	
29/30 Sept. 60	225											236				225	236						
2/3 Oct. 62	214	214	214									240				214	240						
2/3 Oct. 59	218	217	215	220	226	222	226	228	228	225	—	202	201	207	210	218	202	0	1	10	10	10	10
3/4 Oct. 62	221	219	217									240				221	240						
7/8 Oct. 61	224											217				224	217						
8/9 Oct. 60	—	—	—	—	222	222	223	220				—	—	256		—	—		5		7		1
15/16 Oct. 62	211											193				211	193						
16/17 Oct. 61	218	215	222	—								242				218	242						
17/18 Oct. 62	216	219	223	—								243				216	243						
18/19 Oct. 62	221	222	—	—								221				221	221						
20/21 Oct. 61	—	—	—	215	220	212	218	215				—	225	239	—	—	—	10	10	10	10	10	10
21/22 Oct. 59	219	218	223	225	225	228	230	238				199	206	212	—	219	199	0	0	0	0	3	7
23/24 Oct. 61	—	225	—	216	219	218	231	228				—	194	233	—	225	(190)	9	0	10	10	10	10
24/25 Oct. 61	225	225	—	231								218	250			225	218	10		10		10	

of the direction of movement, because the echoes are usually weak and flickering. After one to three hours the density of echoes decreases rapidly because (a) birds move out of the area, (b) birds fly lower, and (c) later in the night permanent land shadow seriously cuts down the visibility of this movement. After two to four hours, some targets come in over Massachusetts Bay from the direction of Maine to the northeast, but the density of echoes over the Boston area usually continues to decrease, while echoes do not become dense near Cape Cod and are not numerous enough to detect an MTI-wedge southeast of Cape Cod. The density of birds over the Boston area is typically at least 100 times that over Cape Cod (Nisbet 1963b).

This type of movement is probably the largest, in terms of numbers of birds, of all the autumn movements in the area, but our radar does not record it as regularly as some of the other movements which pass nearer to Cape Cod. This is because most of the birds involved pass more than 50 miles away from the radar station, where their detection is irregular and depends critically on their height and on atmospheric conditions, and because the movement appears on a part of the screen especially likely to be obscured by movements in other directions.

Probably a wide variety of species is involved, especially flycatchers, warblers (excluding those involved in the southerly movements discussed later), thrushes and buntings; in fact most of the passerine species which breed in New England and eastern Canada, as well as a few non-passerines. The movement is observed regularly on the cold side of high pressure systems from mid-August until well into November, but the August records are usually of small numbers of birds and do not give clear MTI-wedges.

The MTI-wedge measurements of tracks are summarized in Table 1. Most of the wedges appeared only at ranges of 40-70 miles (i.e., over Boston Harbor and the mainland to the northwest); on some occasions wedges were visible at ranges of 10-40 miles, but we were unable to detect any differences in direction between these and the outer parts of the wedges, and we have not listed them separately.

Initial directions.

The "initial track" listed in the tables is our first observation of the movement concerned early in the night—usually at 1900 or 2000. The "initial heading" is the calculated heading corresponding to the initial track. The initial track is included in parentheses if it was observed at 2100. The initial heading is placed in parentheses if it is based on the comparison of an observed track with the wind observed one hour earlier or later.

Perhaps the most striking feature of Table 1 is that all the initial tracks are closely grouped between 211° and 225°, the mean being 219.0° and the standard deviation 3.70°. In contrast, the initial headings are much more variable, ranging from 177° to 243°, the mean being 218° and the standard deviation 18.50°. The difference in the standard deviations is highly significant statistically (F =

TABLE 2. SOUTHWEST MOVEMENTS OVER MAINLAND: HOUR-TO-HOUR VARIATION IN MEAN TRACK

Time	19	20	21	22	23	24	01	02
No. of Records	15	20	18	16	15	10	10	10
Mean Track	218.7	218.7	218.8	221.7	221.8	221.8	224.3	224.4

25.0, $p < .001$*). Although some of the variation in the headings is due to errors in estimating the upper-air winds, these cannot account for much of the difference, because none of the calculated headings differs from the corresponding track by more than 39°. This suggests that the birds adjusted their headings so that their track was about the same each evening, regardless of the direction of the wind: in other words, these birds on departure corrected for the drifting effect of the wind. J. A. Keith first observed the greater scatter of headings as compared to the tracks, and Bellrose and Graber (1963) reported similar observations in Illinois but concluded that correction is never quite complete.

In order to avoid the dependence upon accurate knowledge of the wind, we divided the records of initial tracks into three broad categories: upper-air wind at 1900 clearly blowing from the birds' right (255°-005°), from the birds' left (070°-170°), and from behind the birds (006°-069°). The mean tracks of the birds in these three categories were 217.8°, 217.9° and 222° — which confirms that crosswinds,at least in the circumstances where the birds are well-oriented, did not alter the birds' tracks at all.

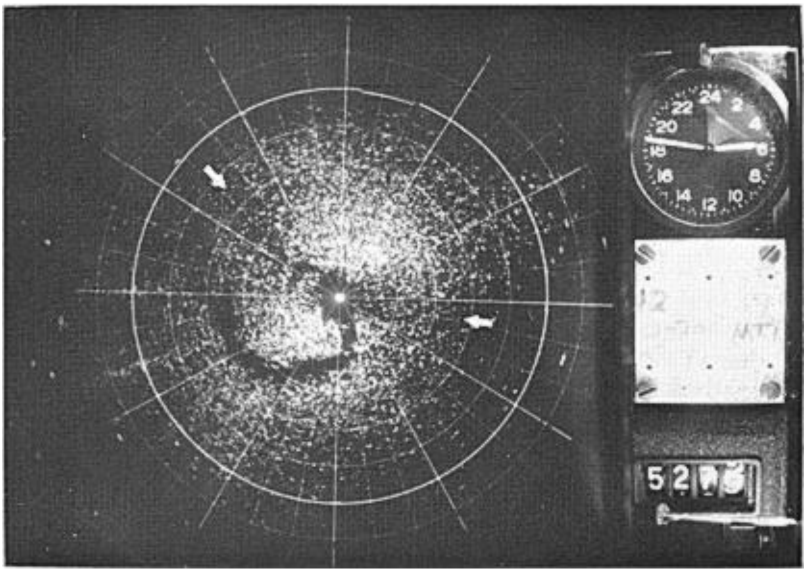
Table 1 shows that there were no detectable systematic changes in the initial tracks of the birds during the course of the season. This is surprising in view of the fact that the birds which migrate early in September winter largely in Central America, and those late in October winter largely in the southeastern United States.

Table 2 summarizes the average tracks of the birds in each hour between 1900 and 0200 (there are too few data for reliable averages later in the night). On average, the mean track turned towards the west by about 0.92° in each hour, the trend being highly significant statistically ($p < 0.001$). Thus, during the course of the night, the birds turned slightly but steadily to their right, so that the whole mass of birds slowly moved inland (Figures 3 and 4). This is one of the main reasons why the density of echoes decreased rapidly after 2100. In fact, for this reason the figures under-estimate the extent of the change in track, because on the nights when the birds turned

*The variance ratio F is the ratio of the variances of the two samples. For the tests used in this paper, with 15-30 degrees of freedom, a value of F greater than about 3.5 would be significant at the .001 level. Most of our tests give much larger values of F than 3.5, but published tables of the F-distribution do not extend to smaller probabilities. However, the exact level of "significance" is not meaningful since the values obtained for F are somewhat augmented by errors in estimating the mean winds.

Figure 4: PPI SCOPE OF SOUTHWESTWARD AND SOUTHWARD MOVEMENTS AFTER MIDNIGHT.

11/12 September 1959. Note that the southwestward movement has shifted to the birds' right by 7° (to 312°) at 0147. Note, too, that the MTI wedges are very much less clear, having been partly filled by scattered, rather coarse targets. This phenomenon occurs nearly every night.



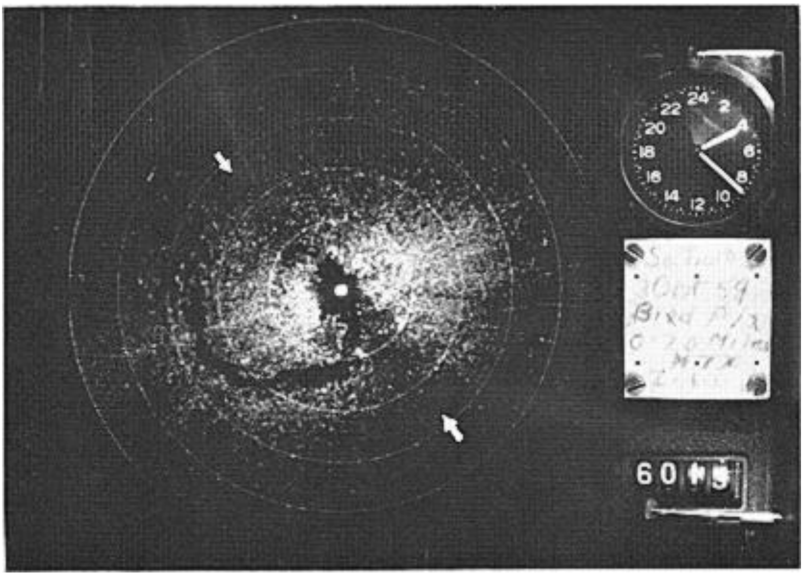
faster than average, the edge of the mass of echoes moved away more quickly, so that observations ceased; most of the observations later than 2100 perforce refer to nights when the change in tracks was slower than usual. Probably the average change in tracks was actually at least 1.5° per hour, representing a change of about 15° during the night.

Table 1 includes 19 cases where the mean heading of the birds was estimated twice, spanning a three-hour interval. The average change during these three-hour periods was $+8.3 \pm 2.64$, the change being statistically significant ($p < 0.01$). This shows that the change in mean tracks was due to a definite change in mean headings, not to a chance change in the mean winds. The nights of 23/24 September 1961 and 24/25 October 1961, in which the birds' tracks turned only slightly in spite of a significant change in the wind, show this especially clearly (see Table 10).

Because we obtained the figures in Table 1 from observations in the area near Salem and Boston Harbor, the mean tracks observed during different hours of the night are those of different groups of birds which moved successively through this area: presumably those observed at 1900 and 2000 took off in eastern Massachusetts, while those observed later in the night took off progressively farther northeast along the Maine coast. Hence it is not immediately clear

Figure 5: PPI Scope Picture of Southwestward Movement from Nova Scotia.

0022 on 3 October 1959. The wedge of southwestward movement from Nova Scotia (136°) appears partly obscured by the permanent shadow zone southeast of Cape Cod. The wedge northwest of Cape Cod is just visible, but is too diffuse to locate precisely.

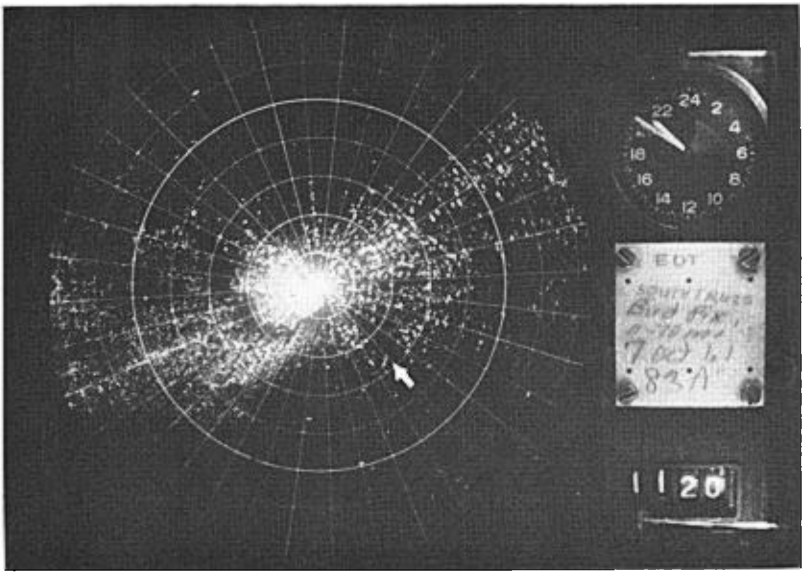


whether (a) all the birds progressively change direction during the night, or (b) the birds from Massachusetts depart on a slightly more southerly track than those from Maine, all maintaining the same track during the night. Our reason for rejecting the latter hypothesis is that birds which might leave the coast of Maine, flying on a track of 225°, would not come into the area of Boston Harbor at all, but would pass well inland of Salem and would not be recorded on our radar (Figure 1).

Hence, we conclude that most of the birds which depart from eastern Massachusetts and southern Maine start with a track of about 218°, and gradually turn to their right until by dawn they have a track of about 233°. This change in direction, and its resulting effect of shifting the birds over the land and away from the sea, are reminiscent of the changes in the flight directions of Chaffinches (*Fringilla coelebs*) migrating through The Netherlands during daylight hours (Van Dobben 1953, Mook *et al.* 1957). Possibly, therefore, one of the functions of this behavior is to lead the birds away from the sea and the dangers of offshore drift, but it is hard to see why the birds could not achieve this result more simply by flying straight on a more westerly track. It is noteworthy that all the birds observed late in the night must have flown for some hours over

Figure 6: PPI Scope Picture of Southwestward Movement from Nova Scotia.

1952 on 6 October 1961. Notice the songbird targets southwest of Cape Cod and the coarse targets to the northeast. The wedge at 241° is difficult to see in this still picture with few echoes, but is much easier to see on the cine-viewer.

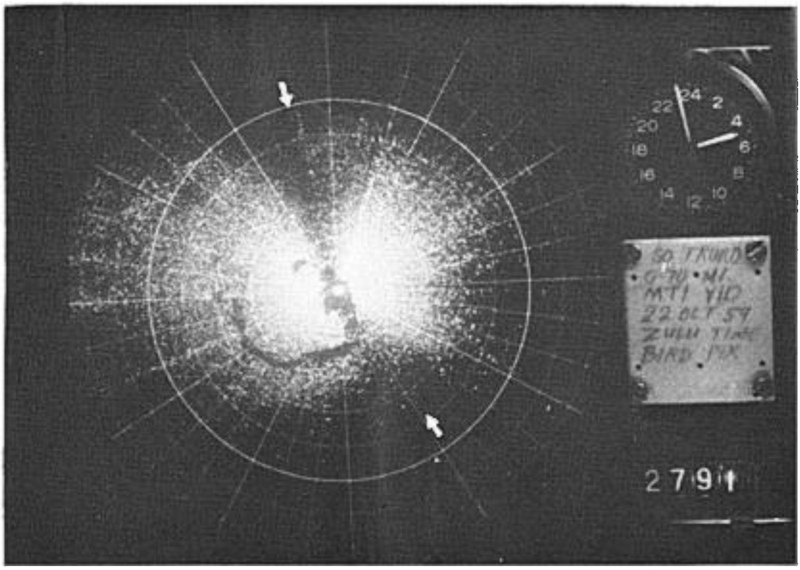


the sea, and it is therefore possible that the change in direction might be a response to the presence of the sea beneath the birds. This suggestion needs to be investigated by observations of birds which migrate over the land throughout the night.

Finally, we should like to point out that, although radar shows that the majority of birds compensate for drift, and that only a meagre fringe of the movement passes over Cape Cod and Nantucket, many of the species concerned are abundant migrants on the coast in this region, occurring regularly during periods of northwest winds after cold fronts (for discussion see Baird & Nisbet 1960). The explanation of this apparent contradiction is probably that the MTI-wedge method only measures the average direction of the main mass of birds; those which scatter on either side of the main direction have no effect except to reduce the clarity of the wedges. Thus radar shows that, in spite of their abundance, the migrants grounded at the coast are numerically a small fraction of the total migration over the mainland. Further, radar shows that they are exceptional individuals, in that they do not behave in the same way as the bulk of the population: specifically, they do not compensate sufficiently for the drifting effect of northwest winds. This is consistent with the fact that nearly all are immature individuals (Drury & Keith, 1962).

Figure 7: PPI SCOPE PICTURE OF DISPLACED SOUTHWESTWARD MOVEMENT FROM NOVA SCOTIA.

0058 on 23 October 1959. Compare the dense movement of songbirds arriving from the northeast with the scattered coarse targets a few hours after dusk in Figure 2. The arrows at 348° and 148° (partially obscured by the permanent shadow) in this case show a movement shifted to the west associated with moderate easterly winds. This night was followed by a widespread arrival of juncos.



SOUTHWEST MOVEMENTS FROM NOVA SCOTIA

We apply this name to autumn movements which approach Cape Cod from the northeast; they are usually equally conspicuous northwest and southeast of the Cape, although the birds which pass to the northwest are often obscured by birds moving in other directions, and the MTI-wedge of those to the southeast is often hard to observe on the South Truro radar because of the permanent shadow-zone to the southeast (see Figures 5 and 7). Typically, the earliest birds pass the Cape some four to five hours after sunset (presumably birds which left Nova Scotia around dusk) and birds continue to pass for all or most of the night. Occasionally, movement has already started at sunset and the birds involved must have started migrating from Nova Scotia during the afternoon (Figures 2 and 6), but in most such cases the birds involved give coarse echoes and fly fast, and are probably mainly ducks (e.g., eiders, *Somateria mollissima*) or shorebirds. We have included in the tables records of such movements adequate to give an MTI-wedge, but have not used observations earlier than 2200 in the analysis.

Southwest movements from Nova Scotia occur intermittently from mid-September to November, but are rare earlier than 17 September. This suggests that the main species involved are thrushes and sparrows. We have no evidence whether the early

TABLE 4: SOUTHWEST MOVEMENTS OBSERVED SOUTHEAST OF CAPE COD: HOUR-TO-HOUR VARIATION IN MEAN TRACK

Time	22	23	24	01	02	03	04
No. of Records	12	11	12	13	15	11	10
Mean Track	233.2	233.2	231.2	232.8	229.4	232.0	233.0

migrants (such as flycatchers and the earlier warblers) which breed in Nova Scotia migrate too far west to be detected from Cape Cod, or whether they migrate southwest but are too sparse to be conspicuous on radar. These movements are usually much less dense than those over the mainland, except for a few large movements in middle and late October, some of which have been correlated with arrivals of juncos (*Junco hyemalis*). They appear to be more strictly confined to nights of northeast and east winds than those over the mainland (which frequently occur with northwest winds), and hence they are more intermittent, but this point has not been studied systematically.

Southeast of Cape Cod.

Table 3 summarizes the records of MTI-wedges in the area southeast of the Cape. Table 4 shows that there was no systematic change in the tracks during the night, and analysis of the figures in Table 3 shows that there was no systematic tendency for headings to change during the night; hence we have grouped all the records from 2200 onwards in the following analysis.

The average value of the tracks was 231.9° and the standard deviation 8.57°, while the average of the headings was 229.9° and the standard deviation 22.16°. The difference in the standard deviations was statistically highly significant ($F = 6.68$, $p < .001$): this suggests that these birds were compensating for the drifting effect of the wind, although the scatter in their tracks was in fact more than twice as great as in those of the southwest migrants over the mainland. In order to test the effect of drift more directly, we divided the records into three categories according to the direction of the wind: from the birds' right (300°-010°), from the birds' left (063°-130°), and from behind the birds (048°-055°). The corresponding average tracks were 229°, 235°, and 232°. This suggests that the wind does have a slight effect on the tracks, although the difference between the averages for winds from the birds' right and the left is not statistically significant. In fact, however, most of the difference is due to two nights, 19/20 October 1961 (cloud cover 8-10/10ths), and 21/22 October 1959 (Figure 7; cloud cover 0-7/10ths): these were the only nights in this series with moderate (10-15 knot) winds from the east or southeast, and were the only nights when the observed mean tracks were farther west than 245°. If these nights are excluded from the analysis, the tracks are almost as closely grouped as those of the southwest migration over the mainland. This suggests that the birds compensate for the drifting effect of northwest winds, but only partly compensate for that of southeast winds. This would have obvious value for birds migrating, as these birds do, offshore from the Atlantic coast, but more evidence is needed.

TABLE 3. SOUTHWEST AUTUMN MOVEMENTS FROM NOVA SCOTIA OBSERVED SOUTHEAST OF CAPE COD

Date	Tracks at time: 19	20	21	22	23	24	01	02	03	04	05	06	Headings at: 19	22	01	04	Cloud cover: Portland 22	Portland 01	Boston 22	Boston 01	Nantucket 22	Nantucket 01
6/7 Sept. 61	—	—	—	—	240																	
16/17 Sept. 60	226	230	230	229	223	221	220	217	215	216	212	—	216	225	206	198	0	0	0	0	0	0
17/18 Sept. 61	—	—	230	230	235	232	234	228	238	242	—	—	—	215	219	226	0	0	0	8	2	0
19/20 Sept. 61	—	—	—	—	—	—	—	225	229	232	—	—	—	—	—	204						
23/24 Sept. 61	—	235	232	230	—	230	235	230	234	—	—	—	—	229	225		10	10	10	10	10	10
29/30 Sept. 61	—	—	—	—	—	—	228	230	232	225			—	—	242	225		0		0		0
1/2 Oct. 60	—	—	—	—	—	227	231	229		230			—	—	232			0		0		1
2/3 Oct. 59	225	—	—	230	232	226	232	227	230	231			213	218	217	219	0	1	10	10	10	10
3/4 Oct. 60	—	—	—	—	—	—	—	230	228													
4/5 Oct. 59	226	228	—	224	—	227	226	227	234	238	231		249	251	247	247	3	10	0	7	7	4
7/8 Oct. 61	227	225	231	231	233	231	231	240	243	242	245	235	221	230	223	249	4	5	10	10	10	10
8/9 Oct. 60	—	—	—	—	226	228	230	227					—	—	262			5		7		1
10/11 Oct. 59	—	—	—	228	227	227	228	233	—	231			—	238	225	223	9	10	9	10	10	8
10/11 Oct. 61	—	—	—	—	—	240																
14/15 Oct. 59	—	—	220	227	231	225	—	227	227				—	213			0		10		10	
19/20 Oct. 61	—	—	—	260									—	240			10		8		10	
21/22 Oct. 59	—	—	—	254	255	255	255						—	248	247		0	0	0	0	3	7
21/22 Oct. 61	—	—	—	—	228	—	238	239	245				—	—	207			10		10		10
22/23 Oct. 61	—	—	—	230	—	—	—	—	—	243			—	197	—	239	8		10		10	
23/24 Oct. 61	—	230	227	226	235	232	243	230	—				—	220	266	—	9	0	10	10	10	10

Northwest of Cape Cod.

Table 5 summarizes the records of MTI-wedges in the area within 10-40 miles northwest of Cape Cod (excluding cases in which the density of the movement increased very rapidly towards the mainland, which have been included in Table 1). These records are very similar to those in Table 3, except that they are consistently oriented more towards the west, the average track (excluding records before 2200) being 240.5°. In fact, on seven nights marked with an asterisk in Table 5, we made observations simultaneously on both sides of the Cape, and the average track to the northwest was 7° nearer to due west than that to the southeast (see Figure 7). This suggests that both sets of data refer to the same movement, which departs from Nova Scotia and fans out slightly over the Gulf of Maine — the birds which head more to the west than average passing north of Cape Cod, and those which head more to the south passing south of Cape Cod (see Figure 1).

All the observations in the area northwest of Cape Cod fall clearly into one of two categories: (a) the "mainland" movements, whose track usually increases from 218° to 227° during the night and which are concentrated near the mainland coast; (b) the "Nova Scotia" movements, whose track is usually between 230° and 250° and which pass Cape Cod on a broad front. There is no evidence whatsoever of intermediate types of movement, which suggests that the "Nova Scotia" birds belong to a discrete population with different migratory behavior from that of the "mainland" birds. We do not know whether this difference is due to genetic differences in populations of the same species, or to different proportions of different species in the two movements.

SOUTHWARD MOVEMENTS

"Southward movements" are those in which the mean track lies between 155° and 205°. The birds usually fly up about 45 minutes after sunset from Cape Cod, the mainland to the west of Cape Cod, and the islands to the south, and migration remains dense to the west of the Cape for two to four hours, declining later in the night. Over the Cape itself, and to the east, however, the migration usually appears several hours later; this is because birds from New Hampshire and Maine have to fly for 100-200 miles before they pass the Cape.

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 & Keith (1962) gave evidence that about 12 species of wood warblers might be involved, but subsequent study (Nisbet *et al.* 1963) has definitely identified only the Blackpoll Warbler (*Dendroica striata*) in these movements, and has suggested that most warbler species do not migrate east of south as does the Blackpoll Warbler (although some of them may migrate a little west of south). We suspect that other species of landbirds which winter in South America and occur on migration in the eastern West

TABLE 5. SOUTHWEST AUTUMN MOVEMENTS FROM NOVA SCOTIA OBSERVED NORTHWEST OF CAPE COD

	Tracks at time:											Headings at:				CLOUD COVER					
																Portland		Boston		Nantucket	
Date	19	20	21	22	23	24	01	02	03	04	05	19	22	01	04	22	01	22	01	22	01
16/17 Aug. 61	—	—	—	232								—	240			0		0		0	
6/7 Sept. 61*	—	—	—	—	248							—	—	—	—						
9/10 Sept. 59	228	228	226	242	244	237	228	236	247			217	228	213		1	0	0	10	10	10
17/18 Sept. 61*	—	—	230	232	240	238	243	238	247	248		—	219	235	239	0	0	0	8	2	0
9/10 Oct. 62	235											224									
10/11 Oct. 62	233	235										263									
14/15 Oct. 59*	243	240	237	235	231	230	241					228	226	249		0	0	10	8	10	10
19/20 Oct. 61*	—	—	—	260								—	240			10		8		10	
21/22 Oct. 59*	—	—	—	242	254	255	258	261	265	262	268	—	230	251	254	0	0	0	0	3	7
21/22 Oct. 61*	240	241	—	229	231	235	230	240	243			190†	188†	187†		10	10	10	10	10	10
22/23 Oct. 61*	—	—	228	227	230	227	—	239	224	242		—	205	—	236	8		10		10	
1/2 Nov. 61	—	—	—	—	—	—	—	—	—	233	230	—	—	—	268						

Indies may take part — especially the Yellow-billed Cuckoo (*Coccyzus americanus*), the Bobolink (*Dolichonyx oryzivorus*), the Barn Swallow (*Hirundo rustica*), the Bank Swallow (*Riparia riparia*), and the Connecticut Warbler (*Oporornis agilis*). The west of south departure direction is suitable for birds migrating to or through the Bahamas and Greater Antilles and may therefore include many thrushes (Turdidae). In late October and early November, when the radar echoes are usually much brighter and more "granular," the most likely species are ducks, especially the Blue-winged Teal (*Anas discors*). However, we have no direct evidence to connect any of these species with the observed southward movements.

Our records of southward movements are summarized in Tables 6 to 8. The observed tracks during these movements are much more variable than those in the southwestward movements, ranging from 153° to 202°, with most between 168° and 192°. However, much of this variation appears to be due to the overlapping of several different movements, each with its proper direction of flight. In fact, on at least four nights (20/21 and 21/22 September 1962, 6/7 September 1961, and 9/10 October 1961) our records show that there were two distinct directions of flight in different parts of the area covered by the radar station, one averaging about 171° and the other about 186°. On at least four other nights (summarized in Table 8) the records show that a movement towards 165° or 175° was replaced later in the night by one towards 180° or 190°. Hence we suggest that there were two main groups of directions involved in the southward movements (Figures 3 and 7), and we have separated them as far as possible in Tables 6 and 7. Cases in which the flight directions were intermediate or mixed are listed in Table 8.

Tables 6 and 7 show that, with the exception of the November movements which were probably not of passerines, our observations of the movements east of south (Figure 8) were usually made only in the first three or four hours of the night, while those west of south (Figure 3) were often not made until 2100 or 2200 and continued much later. Table 8 shows that on most nights when we observed both directions, we could follow movements during most of the night. This gives independent evidence for the validity of the distinction between the movements east and west of south.

We conclude that there are three distinct types of southward movement through the South Truro area: (a) the movements with tracks between 165° and 176° (Table 6) are usually confined to the early part of the night, probably because the birds involved are concentrated within 100 miles of the coast before take-off (Nisbet *et al.* 1963); (b) the movements with tracks between 179° and 200° (Table 7) usually occur later in the night, probably because most of the birds observed at South Truro take off farther northeast, in New Hampshire and Maine, and take several hours to reach Cape Cod (see Figure 1); (c) the movements in late October and November are tentatively attributed to waterfowl and are therefore not discussed further in this paper.

Examination of the figures in Table 6 shows that the average track of the east-of-south movements often increased by a few degrees in

TABLE 6. SOUTHWARD MOVEMENTS DEPARTING EAST OF DUE SOUTH

Date	Tracks at time: 19	20	21	22	23	24	01	02	03	04	05	Headings at: 19	22	01	04	CLOUD COVER Portland 22	Portland 01	Boston 22	Boston 01	Nantucket 22	Nantucket 01
28/29 Aug. 61	—	160	165	165								—	175			1		8		10	
31 Aug./1 Sept. 61	—	170	172	175	173							—	191			0		0		8	
6/7 Sept. 61	—	170	170	170								—	155			10		1		10	
7/8 Sept. 61	—	170	170	170								—	170			10		6		8	
8/9 Sept. 61	—	175	173									—	—								
12/13 Sept. 62	—	172	175									—	—								
14/15 Sept. 62	—	—	—	170								—	187			0		5		10	
20/21 Sept. 62	170	171	173	174								140	156			2		3		10	
21/22 Sept. 62	—	173																			
1/2 Oct. 62	170	170	173									183									
2/3 Oct. 62	—	168	172																		
3/4 Oct. 60	—	—	180	178	179	170	172	172				—	180	169	—	0	0	0	0	2	1
3/4 Oct. 60	—	—	177	174	173	172	171	174				—	174	167		0	0	0	0	2	1
3/4 Oct. 62	173	174	172									209									
9/10 Oct. 61	—	164	—	—	170																
10/11 Oct. 62	173											170									
14/15 Oct. 59	172	174	—	177	175	175	—	170				131†		140		0		10		10	
16/17 Oct. 61	—	—	—	—	—	—	175	170	174	170		—	—	195	193		0		0		2
17/18 Oct. 62	173	170	170									162									

TABLE 7. SOUTHWARD MOVEMENTS DEPARTING WEST OF DUE SOUTH

Date	Tracks at time: 19	20	21	22	23	24	01	02	03	04	05	Headings at: 19	22	01	04	CLOUD COVER Portland 22	Portland 01	Boston 22	Boston 01	Nantucket 22	Nantucket 01
16/17 Aug. 61	—	184	—	181								—	166			0		0		0	
4/5 Sept. 59	—	—	188	183	187	191	193	187	186			—	201	197		1	1	3	0	0	10
5/6 Sept. 61	—	—	—	182	186							—	185			3		0		4	
9/10 Sept. 61	—	183	182	178	181							—	200			0		0		4	
11/12 Sept. 59	181	181	181	187	191	192	196	202	202	202	199	153	179	186	209	0	0	0	0	0	0
15/16 Sept. 61	—	—	184	184								—	192			7		10		5	
16/17 Sept. 61	—	—	—	184	181							—	139†			0		1		0	
19/20 Sept. 61	—	—	180	185								—	141†			10		10		10	
20/21 Sept. 62	190	—	192	192								173	186			2		3		10	
21/22 Sept. 62	—	185	182	190								—	204			0		0		0	
23/24 Sept. 61	—	—	185	—	—	184	180	179				—	—	146			10		10		10
1/2 Oct. 60	176	177	181	182	183	186	189					169	170	162		0	0	0	0	0	1
1/2 Oct. 60	—	—	184	182	184	186	187	186	187			—	170	159		0	0	0	0	0	1
2/3 Oct. 59	187	—	—	190	—	—	—	184	186			161	154			0		10		10	
2/3 Oct. 59	197	196	190	200	—	—	195					173	169	157		0	1	10	10	10	10
7/8 Oct. 60	—	179	178	181	182							—	211			0		0		0	
8/9 Oct. 60	—	—	181	183	186	187	188	189				—	211	217		0	5	7	7	0	1
9/10 Oct. 61	—	—	—	—	—	—	—	186				—	—								
10/11 Oct. 59	—	—	—	175	180	189	186	188	188	180	183	—	181	177	166	9	10	9	10	10	8
18/19 Oct. 62	—	—	175									—	—								
8/9 Nov. 61	—	—	—	—	181	175	172	174	167	167	168	—	—	166	173		0		5		10
9/10 Nov. 61	160	165	170	171	175	174	171	174	168	176	175	158	173	168	185	10	10	8	10	1	0
10/11 Nov. 61	175	177	177	177	174	175	179	176	174	175	175	171	173	171	174	0	0	0	0	8	0
11/12 Nov. 61	175											187									

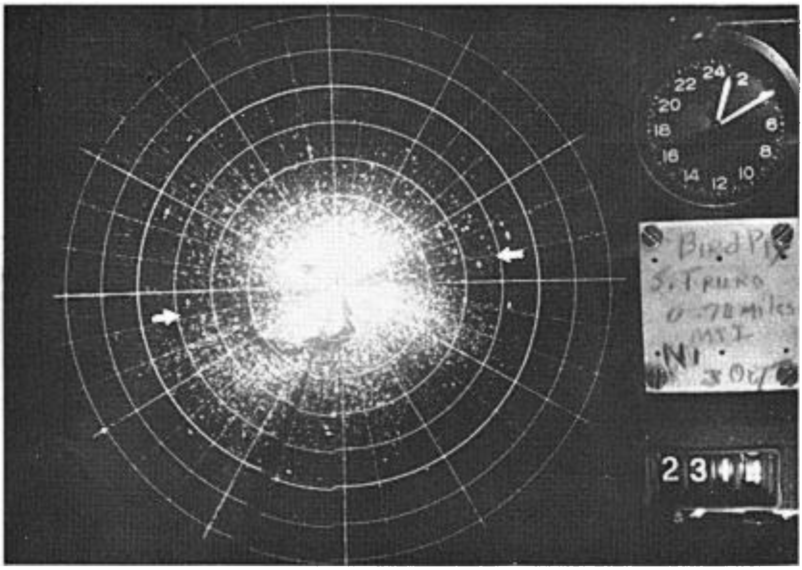
Note: On dates listed twice, wedges were seen on both sides of South Truro.

TABLE 8. OTHER SOUTHWARD MOVEMENTS

Date	Tracks at time: 19	20	21	22	23	24	01	02	03	04	05	Headings at: 19	22	01	24	CLOUD COVER Portland 22	Portland 01	Boston 22	Boston 01	Nantucket 22	Nantucket 01
28/29 Sept. 61	153	153	160	163	172	178	182	184	180	184		156	165	198	194	0	0	0	0	3	7
29/30 Sept. 61	168	163	159	168	181	183	189	190	192	175	177	168	168	189	175	0	0	0	0	0	0
15/16 Oct. 61	—	—	—	—	160	168	173	179	188	188	184	—	—	206	217	0	0	0	3	0	10
27/28 Oct. 61	192	—	181	179	176	174	165	164	174	171	179	198	184	161	180	0	0	0	0	2	0
1/2 Nov. 61	—	178	176	177	177	172	174	183	185	195		—	193	189	215	0	0	0	0	0	0

Figure 8: PPI Scope Picture of Departure East of South.

2110 on 2 October 1962. This moderate volume departure on a track 172° is suitable in date and direction for the migration of Blackpoll Warblers. This picture was taken about three hours after the birds had flown up.



the first two or three hours of the night (see Table 9). This is probably because the trend of the Massachusetts coast is such that the birds which reach Cape Cod earlier in the night head farther to their left than the main mass of birds from the mainland (see Figures 1 and 8). Hence in compiling averages we have used only the records from 2100 onwards. The average track of the birds was 172.3° and the standard deviation 3.18°; this shows that the tracks during the east-of-south movement were more closely grouped than in any other analyzed in this paper, perhaps because fewer species are involved. The average heading was 173.2° and the standard deviation 16.4°, the difference in the scatter from that of the tracks being statistically highly significant ($F = 26.47$, $p < .001$). Grouping the tracks according to the direction of the wind, the average track when the wind was from the birds' right (250°-335°) was 171.0°, whereas that when the wind was from the birds' left (005°-100°) was 173.2°. This confirms that these birds corrected for the drifting effect of the wind and flew on the same track every night. Indeed, they were able to maintain their mean track about as accurately as we could measure it. Table 9 shows that, except for the tendency already mentioned for the mean track to increase between sunset and 2100, there was no significant tendency for the birds' tracks to change during the night.

Table 9 shows that there was a tendency for the tracks of the west-of-south movement (Figure 3) to average a few degrees farther west after midnight than before, but the tendency is not statistically

TABLE 9: MEAN TRACKS OF SOUTHWARD MOVEMENTS HOUR-BY-HOUR

Time	19	20	21	22	23	24	01	02	03	04
East of South	171.8	170.2	172.6	172.6	——	173.4	——	172.0	——	
West of South	188.2	186.4	183.7	184.6	184.1	187.9	189.2	187.6	190.1	

significant, and in any case is probably due to the northeastward trend of the Maine coast, which means that the birds which take off farther east pass Cape Cod later in the night. Hence we have grouped all the data together in compiling averages. The average track of the birds in Table 7 was 186.0° and the standard deviation 5.94°, while the average heading was 177° and the standard deviation 21.4°, the difference in the standard deviations being statistically highly significant ($F = 12.94$, $p < .001$). Grouping the tracks according to the direction of the wind, the mean track was 183.7° when the wind was from the bird's right (170°-355°), and 187.5° when the wind was from the birds' left (013°-073°). This suggests that the birds did not fully compensate for the drifting effect of the wind, but the difference is small compared to the night-to-night variation in the tracks, and is not statistically significant. In any case the largest deviation from the average track, that observed late in the night of 11/12 September 1959, occurred when the wind was almost directly behind the birds, and hence cannot be attributed to drift. An alternative interpretation of our data is that the species whose preferred direction is slightly west of 186° are more likely to take off when the wind is east of north than those whose preferred direction is slightly east of 186°. The larger standard deviations found for this movement may reflect a larger number of species involved than in that leaving on a track east of south.

OTHER MOVEMENTS

In addition to the movements described above, we regularly observed four other types of nocturnal movement through the Cape Cod region in autumn:

1. Southeastward movements (130°-140°) of bright echoes moving at high speeds, which are densest in August but occur throughout the autumn. These movements start in late afternoon, several hours before sunset, and are attributed to shorebirds on direct migration towards eastern South America (Drury & Keith 1962). They are rarely dense enough to give clear MTI-wedges in the presence of echoes from other species, but occasionally they become confused with small departures of passerines towards 170° (we have omitted from our analysis a few cases where such confusion appears to have occurred).

2. Eastward movements (70°-110°) of bright echoes, most dense and regular in October. These echoes are attributed to species which winter off the New England coast, especially scoters *Melanitta* spp., Red-throated Loons (*Gavia stellata*), scaup *Aythya* spp., and Herring Gulls (*Larus argentatus*); and ten or more miles to the east, Gannets (*Sula bassana*) and Kittiwakes (*Rissa tridactyla*).

3. Eastward movements (75°-100°) of weak, flickering echoes, occurring throughout the season, especially on the warm side of high pressure systems. We attribute these to landbirds on "reversed migration."

We have not yet studied movements (2) and (3) carefully enough to make a reliable distinction between them. However, the small eastward movements are observed more frequently in autumn at South Truro than any other type of movement, except perhaps the SE movements of shorebirds!

4. Northeastward movements (40°-60°) of weak, flickering echoes, occurring throughout the season, especially on the warm side of high pressure systems. These are attributed to landbirds on "reversed migration". Like the northeastward movements in spring, these are usually densest over and near the mainland, and are often hard to observe from South Truro.

So far, we have classified the various movements mainly by means of the observed tracks. This has been justified in two ways:

1. The movements defined in this way show consistent differences in the geographical, seasonal, and temporal pattern of occurrence.

2. In each movement defined in this way, the tracks are consistent from night to night, and do not vary in a regular fashion with the wind direction.

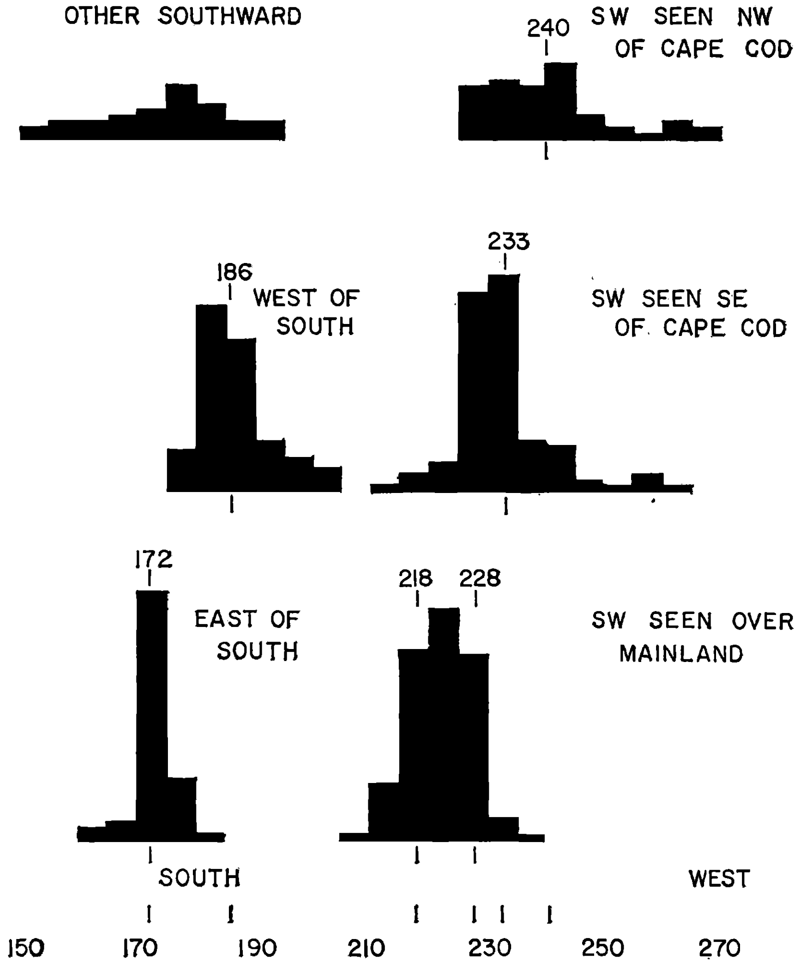
The best evidence, however, for classifying the movements by means of their tracks is that they then fall into clearly marked groups, and that intermediate cases are rare. Figure 9 summarizes the number of times we observed various tracks by means of the MTI method, and shows how the records fall into four clear peaks corresponding to the four mean tracks: 172°, 186°, 218°-228° and 233°-240° (arrows on Figure 9). In fact, only two cases observed by the MTI method were genuinely difficult to classify:

1. 22/23 September 1961. Movements in directions varying between 194° and 211° both east and west of Cape Cod between 1900 and midnight. Winds were northeast, 15-18 knots: birds were heading between 180° and 190°.

2. 8/9 November 1961. Birds near the mainland at 2000 and 2100 were tracking 203° and 198°, while a normal southerly movement occurred over Massachusetts Bay, closer to Cape Cod. Winds were north to northwest, 10-15 knots: birds heading about 225°.

Figure 9: Block Diagrams Showing Frequency of Recorded Tracks.

The tracks are grouped by five degrees and are based on observations of orientation using MTI wedge method; data are shown in Tables 1, 3, 5, 6, and 7. Mean compass directions of the major movements are shown.



Both of these cases were associated with movements in other directions, and in the first example the tracks fluctuated to an unusual extent from hour to hour. This suggests that there may have been confusion between two or more different movements, the MTI-wedge measuring the overall mean track, which was different from the mean track of either of the individual movements. However, it is also possible that these observations reflected mass movements of species whose preferred direction is between 194° and 211°, and which are usually too sparse to be detected in the main movements of other species in other directions. Species which might have such aberrant migration directions include Red-breasted Nuthatch (*Sitta canadensis*) and Bank Swallow (*Riparia riparia*), to name only two. It should be mentioned that small numbers of bright echoes often move in directions different from those indicated in Figure 9, but these are probably mainly non-passerines and do not come within the scope of this paper.

DIFFUSE ORIENTATION LATE IN THE NIGHT

A phenomenon which occurs on many, if not most, of the radar films from South Truro is a progressive filling-in of the MTI-wedge during the night. Sometimes a movement which starts apparently well-oriented will deteriorate so much during the night that there is little or no obvious direction of movement by 0300. On other occasions the direction of movement remains clear and unaltered, but the MTI-wedge gradually becomes more diffuse (for example, see Figures 3 and 4). This phenomenon means that the scatter in the birds' tracks progressively increases during the night. However, since we are unable to measure the scatter, we have not been able to study the phenomenon systematically, and it is tantalizing to watch it happening on the films because the orientation slowly deteriorates without any other noticeable change in the movements. One reason for it is that on many occasions the migration early in the night consists of only one main movement, but later on birds migrating in another direction spread into the area of observation. This effect should be at least partly balanced, however, by the fact that on other nights migration is multi-directional at first and becomes simpler as birds from one or two movements spread out of the area. Hence, we believe that there is a genuine tendency for the scatter in the tracks among birds of a single type of movement to increase progressively during the night. This might be caused either (a) by a tendency for individual birds to orient progressively less accurately, or (b) by a tendency for different species to change their orientations to a different extent during the night, or to react in a different way to changes in the wind. Since we can only measure the average orientation, we cannot distinguish these possibilities.

ORIENTATION UNDER OVERCAST SKIES

Appendix Table 2 lists the observations of cloud cover, height of cloud ceiling, and visibility at Boston and Nantucket, Mass., and at Portland, Maine, on all the nights when we recorded good orientation by means of the MTI-wedge method. Special interest attached to the occasions of widespread fully overcast skies from Portland to Nantucket (10/10 cloud cover), because there is evidence that wild migrants in experimental situations, and trained homing pigeons, lose their orientation under overcast skies (for review, see Lack 1962b). Table 10 and Appendix Table 3 give further details of weather observations on these occasions.

It is immediately obvious from Appendix Table 3 that we regularly observed well-oriented migration when all three weather stations

TABLE 10. CLOUDS AND WINDS RELATED TO ORIENTATION UNDER OVERCAST

	19	22	01	04	Wind Shift
14/15 Oct. 59					
Cloud	3/10/10	0/10/10	0/8/10	7/10/10	
Wind	083/16	069/14	050/18	050/17	−33°
Track - [Heading]					
Table 3	(220)	227 [213]	(227)	(227)	
Table 5	243 [228]	235 [226]	241 [249]		
Table 6	172 [131]	177 [140]	(175-170)		
19/20 Sept. 61					
Cloud	8/10/10	10/10/10	9/8/10	6/10/10	
Wind	095/17	107/15	140/10	109/12	+45° −31°
Track - [Heading]					
Table 1		221 [182]	222 [195]		
Table 3			(225)	232 [204]	
23/24 Sept. 61					
Cloud	10/10/10	10/10/10	10/10/110	10/10/10	
Wind	052/15	052/15	071/13	070/10	
Track - [Heading]					
Table 1	222 [215]	228 [225]	229 [207]	226 [209]	
Table 3	(235)	230 [229]	235 [225]	(234)	
Table 7		(185)	180 [146]	+19°	
7/8 Oct. 61					
Cloud	8/10/10	4/10/10	5/10/10	7/10/10	
Wind	070/6	055/7	063/14	048/11	−22°
Track - [Heading]					
Table 3	227 [221]	231 [230]	231 [223]	242 [249]	
21/22 Oct. 61					
Cloud	10/10/10	10/10/10	10/10/10		
Wind	090/33	084/25	079/31		−11°
Track - [Heading]					
Table 3		(228)	238 [207]	(245)	
Table 5		229 [188]	230 [187]	(243)	
24/25 Oct. 61					
Cloud	10/10/10	10/10/10			
Wind	050/26	034/24			−16°
Track - [Heading]					
Table 1	225 [218]	231 [250]			

NOTE: — Cloud and wind data are taken from Appendix Tables 1 and 2. Cloud data are listed in sequence: Portland/Boston/Nantucket. Winds are listed: direction/knots.

recorded fully overcast skies. The average cloud cover (in tenths) on the occasions listed in Appendix Table 2 was 4.0 at Portland, 4.6 at Boston, and 5.4 at Nantucket, only slightly less than the overall averages for the months concerned, 5.9 at Portland, 5.8 at Boston, and 6.2 at Nantucket. Even these small differences should probably be attributed, not to a tendency for orientation to be better in clearer weather, but to the tendency (Drury & Keith 1962) for autumn migration to be denser in polar air, which is usually clear. In spring the largest migrations usually take place in warm air-masses which are usually very cloudy, yet they are almost always well-oriented (Drury & Keith 1962).

It should be recognized that occasions when the cloud cover is recorded as 10/10 include not only occasions of high clouds, but also occasions of low-lying coastal fog, when the cloud-ceiling is only a few hundred feet above sea-level (Appendix Table 3). Observations with a radar height-finder (Nisbet 1963a) suggest that birds usually fly above low-lying fog banks, but do not fly through or above clouds whose base is 2,500 feet or higher: Hassler *et al.* (1963) reported similar observations in Illinois.

Bellrose and Graber (1963) reported that in Illinois birds flew higher under overcast conditions, suggesting that migrants try to rise through clouds and fly above them unless clouds are too high. If so, they concentrate just below the clouds. Nisbet (1963a) described five cases in which migrants observed on the height-finder to be below the level of 10/10 clouds were observed on the PPI screen to be well-oriented. Appendix Table 2 includes at least 32 more cases (48% of the total number of nights listed) in which migration was observed to be well-oriented when one or all of the weather stations reported 10/10 cloud cover at 2,000 feet or higher. These examples include at least six (20/21 Oct. 1961, 21/22, Oct. 1961, 24/25 Oct. 1961, 26/27 Sept. 1962, 1/2 Oct. 1962, and 10/11 Oct. 1962) when birds took off in the evening over a wide area in spite of widespread overcast skies; at least 14 cases when birds were seen to be well-oriented for several hours in the immediate neighborhood of a weather station which reported fully overcast skies each hour; at least five cases (2/3 Oct. 1959, 14/15 Oct. 1959, 15/16 Sept. 1961, 7/8 Oct. 1961, and 23/24 Oct. 1961) in which birds which took off under clear skies remained well-oriented although they moved into an area of widespread overcast; at least four cases (2/3 Oct. 1959, 23/24 Oct. 1961, 24/25 Oct. 1961, and 26/27 Sept. 1962) in which the mean track of the southwesterly migrants over the mainland changed towards the birds' right during the night in the normal way in spite of persistent overcast; and several other cases (especially in the period 20-25 Oct. 1961) when migration remained well-oriented throughout the night over a large area in spite of persistent, widespread overcast.

Bellrose and Graber (1963) report a few observations of well-oriented autumn movements under widespread overcast. Their data are less directly applicable, however, because on the night of their clearest evidence (5 August 1960) they concluded that Upland Plovers (*Bartramia longicauda*) were the most numerous migrants. Our other observations indicate that shorebirds are able to orient with outstanding accuracy under a great variety of unfavorable circumstances, including patches of heavy rain.

Table 10 summarizes the observations of orientation during six nights when there was a marked change of wind in combination with

10/10 cloud cover (in five cases the clouds were high and in the sixth there was fog). Out of twelve separate movements observed during these nights, at least eight maintained their tracks without significant change, or shifted their tracks to the right in the normal way, in spite of the shift in wind. The remaining four cases all concern southwestward movements from Nova Scotia in backing winds: in each case the tracks shifted slightly to the birds' right, which is the opposite change from that expected if the birds were drifted by the backing wind. Hence Table 10 suggests that the birds were able to compensate (eight cases) or over-compensate (four cases) for changes in wind, in spite of 10/10 cloud cover.

It may be objected that the records of cloud cover at two or three weather stations are not representative of those over the whole area which we observed on the radar screen. However, 10/10 cloud cover is a common phenomenon in eastern New England, occurring in 39.7% of the hours of observation at Boston (U. S. Weather Bureau Local Climatological Data, Sept.-Oct. 1959 and 1960; 15 Aug.-15 Nov. 1961; and 15 Sept.-15 Oct. 1962), and more than half of these records are associated with continuous, unbroken cloud cover over thousands or tens of thousands of square miles (R. Fay, *in litt*). Yet oriented migration can be seen on our radar films on almost every night, and disorientation is a rare phenomenon (see below). Moreover, on most nights, including those with widespread overcast, we can see that at least the brighter radar echoes are clearly oriented throughout the 15,000 square miles covered by the South Truro radar. Thus, although it is not possible to state with absolute certainty that any individual group of birds observed by radar could not see the stars through a small gap in the clouds not observed at any weather station, the statistical evidence is overwhelming that large numbers of birds regularly migrate on their normal tracks without seeing the sky at all. The most crucial evidence is that of Nisbet (1963a) who on three occasions saw well-oriented migration on the radar height-finder directly below radar echoes from clouds which extended for several thousand feet above the highest echoes from birds.

Bellrose and Graber (1963) report similar observations. They summarize their conclusions as follows: "We are inclined to believe that some birds can initiate migration under overcast skies and can maintain proper directional flight lines without resorting to the use of the sun or the stars for cues. However, most species show better navigation under clear than under overcast skies. Some species of birds show better directional orientation when they view the nocturnal sky before the onset of an overcast than individuals of the same species that have no view of the sky." Lack (pers. comm.) has written to us that his data also suggest that birds readily orient accurately under total overcast.

We conclude that *small birds regularly migrate at night under extensive overcast in the South Truro area; there is no evidence that overcast skies per se impair their orientation in any way, and so far we have only slight evidence that overcast skies significantly deter birds from starting to migrate.*

DISORIENTED MOVEMENTS

"Disoriented movement" is a term used by Lack (1959, 1962, etc.) for a rare phenomenon in which birds lose their orientation and fly in directions which vary at random and change irregularly from time to time. Lack of orientation does not necessarily imply inability to orient, but we have nevertheless adopted the same term, although for practical reasons we define it in a slightly different way than does Lack.

The radar station at South Truro is less suitable for identifying random movements than that used by Lack, because the echoes it receives from small birds are much less persistent. As mentioned at the beginning of this paper, few echoes from small birds can be tracked on the screen uninterruptedly for more than one minute (5 revolutions of the radar beam). Hence we were unable to use one of Lack's most important criteria of disorientation: that the tracks of the birds should vary from minute to minute, so that the birds fly in circles or zig-zags. Instead, we used the following criteria to identify random flight on the radar screen:

1. Individual echoes should be tracked in many different directions, including directions such as north, northwest and west, which are not normally observed at South Truro during well-oriented movements.

2. Directions of flight should appear to be random in several different parts of the radar screen, where only one of the main directions of migration is usually important.

3. The mass of birds should be observed to drift slowly in the direction of the wind.

Because of criteria (2) and (3), we were not able to identify reliably cases in which movements were disoriented only within a small part of the area covered by the radar observations. All we could do was to pick out a few cases in which movements were obviously disoriented over a wide area. Also, we may well have missed cases in which birds were actually flying at random, but were carried along by a wind so strong that their tracks gave an illusory appearance of orientation in the downwind direction. Hence we are unable to estimate the frequency of disoriented movements near Cape Cod, except that we agree with Lack that the phenomena is rare.

In an attempt to find examples of disoriented movements, we first listed all the films (including those of spring migration) which showed no obvious direction of movement. After excluding cases in which the radar display was badly adjusted or unstable, we obtained several dozen examples which satisfied criteria (1) above. However, most of these examples fell into the following three categories which did not satisfy criteria (2) and (3):

1. Random movements of targets over the sea during the first hour after sunset: these usually gave displays of bright echoes and were probably dispersal movements of seabirds.

2. Random movements of echoes near the mainland coast in the last two hours before dawn. A few of these may have been movements of early-rising gulls or waterfowl, but most of them were of

weak echoes: we suggest that they may have been passerine migrants circling over the lights in the coastal towns. In one case (8/9 April 1961) one such random movement was observed over the mainland coast during most of the night (2300 onwards) although normal movements were observed elsewhere on the radar screen.

3. Random movements, sometimes over a large area, in which the mass of birds remained stationary or moved slowly *upwind*. We suggest that this phenomenon arises when birds are well-oriented, but their average heading is exactly opposite to a 15-25 knot wind, so that slight variations in wind or heading cause large variations in track. It is striking that, of ten cases in which this phenomenon (flying upwind) was identified, most were with northeast winds in autumn (5 cases), or with southwest winds in spring (3 cases): in other words, it was observed mainly during "reversed" movements and rarely during movements in the "normal" direction. This suggests that reversed movements occur less rarely against the wind than normal movements, but this conclusion (which is opposite to that of Lack, 1963b) should be regarded as tentative until we have studied reversed movements systematically.

After excluding the above types of movement, we were left with only five conclusive cases of large-scale disoriented movements which satisfied all three of our criteria:

11/12 May 1959. In the area of Massachusetts Bay, near Boston, especially 0100-0200 EST. Disoriented movements were observed after the clearance of rain, in the areas where echoes from rain had been seen. Birds moved in many directions and the whole mass drifted slowly northeast and east. Bright targets (apparently gulls) moved south-southeast through the confused area. Orientation was re-established (towards the northeast) by 0500. Migration density was low, but ground observers reported an arrival of many species in coastal Massachusetts.

Following an evening especially favorable for migration (temperature 9°-15° above seasonal normal, associated with the previous day's circulation around a Bermuda high), a cold front moved across Massachusetts preceded by rain squalls. Winds were dropping 12-6 knots and shifted from WSW to WNW at Boston about 2200; cloud cover was 8/10 to 10/10; visibility 7-15 miles.

23/24 May 1959. In the area of Massachusetts Bay, including the north tip of Cape Cod. Echoes seemed to come from the Cape, move slowly to the north and return on various tracks. Rain was visible on the screen and disorientation (birds moving in many directions and drifting downwind) appeared near the patches of rain. The birds on the rest of the screen seemed well oriented. Oriented shorebird arrivals appeared south and southeast of Cape Cod. Density was very low. Ground observers did not report any noteworthy arrivals or departures of migrants.

A cold front had moved eastward across New England and stalled on a line running east from southern New Jersey. There was a high over Nova Scotia and the west end of the front moved north to the border of New York and New England during 24 May. Rain was associated with the area of the stalled front; winds were variable 4-10 knots, SSE to ESE; cloud cover was 10/10, visibility 10-15 miles. Temperature on 22 May was 20° above the seasonal normal.

29/30 May 1959. Disorientation occurred in a large area over the outer Cape and the sea east, west and north of it. Echoes from small birds appeared about 1915 and by 2230 movement had become random. Flow to the northeast started again later, including directions 070° and 100°, but by 0315 general movement was again confused and a very slow north and northwest creep appeared. Echoes from small birds disappeared about 0200. Density was that of a large movement for spring, but ground observers did not report any noteworthy events.

A stationary front lay across the area of Massachusetts Bay; cloud cover was 10/10 and visibility was reduced to 2/10 of a mile in fog. Disorientation coincided with widespread and much reduced visibility (ceiling 100-200 feet). Temperature on 28/29 May was 17° above the seasonal normal. Winds were ESE at Boston and SE at Nantucket. There was no rain at Boston or Nantucket on 28, 29, or 30 May.

29/30 August 1959. Disorientation in the area of Cape Cod Bay was first observed as rain passed over the Cape, and was closely associated with rain visible on the screen. Birds in an area around the northern tip of the Cape moved slowly west into Cape Cod Bay. Shorebirds, however, maintained orientation and continued to move southeastward and south-southeastward throughout.

Density was low. Ground observers in New Hampshire reported the arrival of large flocks of northern migrants on 28/29 August — Veeries (*Hylocichla fuscescens*), Bobolinks (*Dolichonyx oryzivorus*), Gray-cheeked Thrushes (*Hylocichla minima*), and especially warblers (Parulidae); but these birds were not seen south of the stationary front at Cape Ann. In the Boston and Nantucket areas, there was fog but no arrival of birds was reported.

Winds were light, 5-7 knots, ENE to ESE; cloud cover was 10/10; visibility one mile to 4/10 of a mile. Temperature in New Hampshire dropped markedly on 29 Aug. but in the Boston-Nantucket area was 13 degrees above the seasonal normal.

10/11 October 1959. Birds observed by radar on Texas Tower III (40 miles south by east of Cape Cod) arrived from the north during the night, and stayed in the area, flying at random, until mid-day 11 October when they moved off. Meanwhile, some targets moved east and northeast, apparently well oriented.

Density was high and South Truro films showed good southward and eastward orientation. Ground observers on Nantucket reported large arrivals of Flickers (*Colaptes auratus*), Brown Creepers (*Certhia familiaris*), Robins (*Turdus migratorius*), Water Pipits (*Anthus spinoletta*), kinglets (*Regulus* sp.), Myrtle and Blackpoll Warblers (*Dendroica coronata, Dendroica striata*), White-throated Sparrows (*Zonotrichia albicollis*), Juncos (*Junco hyemalis*), and Song Sparrows (*Melospiza melodia*).

TABLE 11. WEATHER OBSERVED AT BOSTON AND NANTUCKET DURING NIGHTS OF WIDESPREAD DISORIENTATION

DATE	BOSTON 19	22	01	04	NANTUCKET 19	22	01	04
11/12 May 59								
Sky	10	10	10	8	8	9	8	7
Ceiling (100's ft.)	150	100	130	Unl.	Unl.	Unl.	CIR	Unl.
Visibility (Miles)	8	7	13	13	4	4	3	5
Wind Direction	WSW	WNW	W	W	WSW	WSW	WSW	W
Wind Velocity	14	16	10	10	16	13	12	11
Cloud Description		Double alto-cum.				Cirro-str. Frac.-str.		
Cloud Height			—			300-600'		
Sky Coverage		9/10				7-8/10		
23/24 May 59								
Sky	10	10	10	10	10	10	10	10
Ceiling (100's ft.)	150	50	55	45	140	60	60	40
Visibility (Miles)	15	12	15	15	15	15	15	10
Wind Direction	SSE	ESE	ESE	S	E	ESE	ESE	ESE
Wind Velocity	13	7	10	5	6	13	9	9
Could Description		Thick alto-str.				Strato-cumulus		
Cloud Height		5000-6500'				5000-6500'		
Sky Coverage		Total				Total		
29/30 May 59								
Sky	10	10	10	10	10	10	10	10
Ceiling (100's ft.)	2	2	1	1	1	1	1	1
Visibility (Miles)	1/16	1/2	1/8	1/8	1/16	1/8	1/8	1/16
Wind Direction	ESE	ESE	ESE	SE	ESE	SSE	SE	SW
Wind Velocity	6	6	6	3	7	6	7	3
Cloud Description		Sky Obscured				Sky Obscured		
Cloud Height		0				0		
Sky Coverage		Fog				Fog		
29/30 Aug. 59								
Sky	10	10	10	10	10	10	10	10
Ceiling (100's ft.)	4	2	1	2	30	35	100	1
Visibility (Miles)	1	1	1/4	3/4	1/2	3	1	1/16
Wind Direction	E	E	E	ENE	NW	ESE	NNE	ESE
Wind Velocity	6	7	5	7	10	8	2	2
Cloud Description		Stratus				Thick alto-cum.		
Cloud Height		0						
Sky Coverage		Total - fog.				1/10		
10/11 Oct. 59								
Sky	10	9	10	10	8	10	8	8
Ceiling (100's ft.)	Unl.	Unl.	CIR	CIR	CIR	Unl.	Unl.	CIR
Visibility (Miles)	10	8	9	1/2	10	7	7	10
Wind Direction	SSE	NNW	NNE	NNE	WNW	SSE	SE	WNW
Wind Velocity	6	4	3	5	4	6	3	5
Cloud Description		Cirro-stratus				Cirrus		
Cloud Height		—						
Sky Coverage		Total				8/10		

A cold front had moved across New England during 10 October and stalled, becoming a stationary front lying east-west to the south of Nantucket. The front was accompanied by rain which crossed the Texas Tower III area from the southwest and moved away to the north about mid-day on 11 October. Nantucket reported rain in the early morning of 10 October, fog during 10 and 11 October (only 3 hours of sunshine in both days), west and southwest winds averaging 10 knots; temperature 10° above seasonal normal.

Table 11 summarizes weather observation at Boston and Nantucket during the five nights when disoriented movements were observed. A feature common to all five nights was cloudiness — at times full overcast. Lack & Eastwood (1962) similarly reported that all the disoriented movements they observed in southeast England coincided with full overcast, rain or fog at a nearby weather station, "presumably because the sun or stars were obscured" (Lack 1962b). The latter explanation is unlikely to be valid for the birds we observed, however, since we often observed well-oriented migration under widespread overcast. Lack and Eastwood, moreover, recorded disoriented movements only for one to two percent of the hours of observation, although the frequency of full overcast in eastern England is about 40 percent (data from U. S. Weather Bureau). Hence their observations, like ours, suggest that overcast skies alone do not cause disoriented movements.

A feature common to four of our five examples is that echoes from rain appeared on the radar screen during part of the period of observation, and in three of our five examples the weather stations reported fog. Lack (1962) and Lack & Eastwood (1962) also placed emphasis on rain and fog in association with disoriented movements. Hence we suggest that the primary cause of disoriented movements is some factor, or combination of factors, which is correlated with the occurrence of rain, fog and clouds, but which is rarer than any of these three factors individually. Such factors might include limited visibility and darkness, both of which would interfere with visual orientation. They are unlikely to include other factors, such as contrasts between air-masses, which are characteristic of disturbed weather, since Lack and Eastwood also observed disoriented movements during fog associated with stable air-masses.

In all the cases of disorientation which we identified, there was an east-west occluded front or a stationary front with warm air overriding and rain moving over surface winds. This is a typical weather situation associated with mass bird mortality at TV towers in southern, mid-western, and northeastern United States, and with conspicuous calling of night migrants reported in Illinois (Graber & Cochran 1961) and in Massachusetts.

DISCUSSION

It is important to emphasize again the limitations of the MTI system of studying orientation. MTI wedges do not allow us to study those nights when orientation may be good but the flow of birds is not uniform. Secondary movements and poor radar adjustment may obscure the clarity of the wedges. The MTI system identifies only the average track and is not usable to study scatter or local variations in orientation. But because the method is biased toward recording chiefly those situations in which the birds are well oriented, our findings that orientation is good in unpromising conditions, with shifts in wind and with overcast, are especially meaningful.

In each movement which we studied, the birds were able to compensate for the drifting effect of the wind by adjusting their headings so their track was the same on every night.* Even more striking, the birds were able to adjust their headings *during* the night so that they flew on the same track in spite of changes in the wind (Table 10). Compensation for drift, in this sense, is such a commonplace observation in low-flying day migrants that it is hard even to find any published accounts of it; but we know of no previous observations which suggest that night migrants also show this behavior. Indeed, Lack (1958, 1959) gave strong evidence that both night and day migrants over the southern North Sea do *not* compensate for drift, but fly on the same heading irrespective of the wind; and later (Lack 1962b) he suggested that birds *cannot* compensate for drift at night. In fact, his observations of day migrants between County Devon and Ireland and east of Norfolk revealed as much drift in day-migrating Starlings as in nocturnal migrants (pers. comm.). The findings of Bellrose and Graber (1963) appear to be intermediate between ours and Lack's: "Although birds migrating over central Illinois were drifted by the wind, there is evidence that they correct to some extent for wind drift. Computed flight headings varied more in direction than did flight tracks. The degree of unintentional drift by migrants appeared to be related to altitude and wind velocity." The apparent disagreement of these observations with those of Lack may be a clue as to the mechanism involved in bird orientation. Until further evidence is available, we can only speculate that selection is much more severe on the species which we observed, whereas with birds like chaffinches, skylarks, starlings, etc., flying from the low countries to Britain, there is no "need" for pinpoint "navigation"; and granted their departure with following winds as Lack has shown, simply heading west and not worrying about the wind is good enough.

Conceptually, compensation for drift is a complicated process. It requires that the birds should (a) identify their preferred direction in the frame of reference (e.g., the co-ordinates provided by the sun or stars) which they use for their primary method of orientation; (b) project this direction into another frame of reference (e.g., the landscape) fixed in relation to the earth; (c) select a heading so that they move in the required direction in the second frame of reference. To describe the process in this way does not imply that the birds separate these operations, as a human navigator would, nor that they perform them in the stated order; however, compensation for

*This finding contradicts our earlier report (Drury, Nisbet & Richardson 1961), based on superficial analysis.

drift does require, in some sense, the comparison of two frames of reference and the assessment of their relative motion. It is, of course, well known that low-flying day migrants have this ability to assess relative motion; indeed, an analogous comparison must be made by every bird which lands on a perch in a cross-wind, for example — but it is worth emphasizing that the process is psychologically complex.

The orientation of free migrants can be divided into two distinct operations (which may or may not take place separately): (a) the selection of an initial heading before take-off; (b) the assumption and maintenance of the preferred heading during flight. Experiments on confined migrants (e.g., round-cage experiments) and most homing experiments are concerned with operation (a). However, because the bird is then fixed in relation to the earth, analysis of operation (a) is more complex than that of operation (b) — for example, a perched bird can in theory observe the direction and strength of the wind without reference to terrestrial features. Hence in this discussion we will be concerned primarily with operation (b), and we will not discuss how (nor whether) migrants select their heading before take-off.

Once the bird has established its correct track at the beginning of the night, it might maintain it in one of four ways:

(1) inertially, i.e., by keeping track of the small accelerations to which it is subjected at right angles to its track;

(2) by reference to a frame fixed in relation to the earth (e.g., the landscape);

(3) by reference to a frame not fixed in relation to the earth (e.g., the wind);

(4) by means of unknown physiological mechanisms which do not depend on external references.

Of these possibilities (4) is difficult to accept or reject until the observations of Merkel (1956), Precht and Lindenlaub (1956), Merkel and Fromme (1958) and Fromme (1961) that birds can sometimes orient in closed rooms are confirmed; but it is hard to understand how birds should ever become "disoriented" if they can orient without external references. As for (3), Vleugel (1954) and other papers) has suggested that nocturnal migrants establish their orientation at sunset and thereafter maintain a constant angle between their heading and the wind, but this is ruled out for our birds, because we repeatedly observed that they maintained a constant track in spite of changes in the wind.

Partly because of analogies with classical types of human navigation, most current theories of bird orientation belong to class (2), involving repeated reference to a frame of reference fixed (or moving predictably) in relation to the earth. It is usually assumed, for example, that low-flying diurnal migrants compensate for drift visually, by means of reference to features of the landscape below and ahead of them. Although this is certainly the simplest and most obvious method of compensation, it is by no means the only one theoretically possible. In theory, any frame of reference fixed in relation to the earth would suffice for maintaining a bird's track, provided that the bird has the faculties necessary for "measuring" its velocity relative to that frame without reference to other frames. This last condition, however, seems to rule out all the simpler methods of such orientation—*viz.*, reference to the earth's rotation, or to one component of its magnetic field, or to a single star — because these would require "knowledge" of the bird's ground-speed, which depends on the wind-velocity. For example, if a bird established its correct track at the beginning of the night, and then maintained the same heading by reference to the North Star, or arranged to cut magnetic lines at a constant rate, it would fly straight only if the wind velocity remained constant. Hence our observation that birds do fly straight in spite of changes in the wind requires a more complex method of compensation. One possibility is measurement of the direction of the e. m. f. induced by the bird's motion through the earth's magnetic field, but this would require an improbable degree of sensitivity to small voltages (Griffin, 1955). Another possibility is reference to the pattern formed by the stars after compensation for their secular motion — i.e., stellar navigation of the kind proposed by Sauer (1957), and Sauer and Sauer (1960), supposed to be accurate within about two miles. However, apart from the objections to stellar navigation put forward by Wallraff (1960), our own observations show that birds can compensate for changes in wind velocity without sight of the stars. Hence our observations make it difficult to entertain any theory belonging to class (2) which does not include visual observation of the landscape as the chief means by which the bird maintains its track. A theory of visual orientation would also help to explain why orientation sometimes breaks down in very thick weather, although overcast skies *per se* do not seem to impair orientation. King (1959) reported such an occasion.

Nevertheless, serious difficulties face any interpretation of our observations exclusively in terms of visual orientation. In the first place, our observations show that birds are able to fly straight on dark nights as well as on light nights: at new moon as well as at full moon, and under overcast skies as well as under clear skies. It would be surprising if birds are able to see the ground well enough from 4,000 feet on dark nights for the precise orientation which we observe, but further investigation of birds' eyesight is necessary before this can be argued seriously. In the second place, most of our observations were made of birds over the sea, where visual orientation would have to be based on the waves. "White-caps" are reasonably stationary features of the ocean's surface (and are presumably the features most easily seen from above at night), but they do move slowly with the winds and with ocean currents, and it would be surprising if birds can orient as accurately as they do with their aid alone. It is true that most of the birds were within 30 miles of land and hence were in sight of the lights of coastal towns, but some of the birds were 40-60 miles offshore, and at this range lights from ships and lighthouses would appear to be more hindrance than help. In any case, it is unlikely that compensation for drift has developed in all the species observed since the appearance of conspicuous coastal lights in the last 150 years. Finally, and most seriously, we observed well-oriented migration above low-lying coastal fog, and then orientation by means of landmarks seems totally impossible. It is possible that in these circumstances, birds might switch over temporarily to some other means of orientation; we do not have enough observations of birds above fog to test whether their orientation is then less precise than when the ground or the sea is visible. An important test would be to investigate whether birds can remain oriented *between* a layer of ground fog and a layer of high clouds, but ground-based weather stations do not record such situations.

Bellrose and Graber (1963) report well-oriented flight paths on 5 August 1960 in spite of ground fog and a high overcast. These birds had flown 200 miles under complete overcast, but included, primarily, Upland Plovers (identified by voice).

If only because no other type of orientation seems, by itself, adequate to explain all our observations, it is necessary finally to consider seriously theories belonging to class (1), involving orientation by inertial means. Barlow (1964) has recently examined the feasibility of inertial navigation by animals. In its conceptually simplest form, inertial navigation requires the accurate measurement of the accelerations to which the navigating system is subjected, and their repeated integration, first to obtain the system's velocity, and second to obtain its spatial position relative to its starting point. Barlow discussed the accuracy with which the accelerations must be measured for successful navigation, and suggested that the vestibular organs in vertebrates may well possess the required sensitivity (although there is no definite evidence that they do). For inertial *orientation,* the simpler process considered in this paper, it may suffice for the bird to determine its velocity, so that the second integration (which requires a higher degree of accuracy than the first) may be unnecessary.

The immediate objection (not discussed by Barlow) to inertial orientation is that the accelerations which must be measured are much smaller than those experienced in flapping flight. A wind-change of 6 knots in 9 hours, for example, represents an average acceleration of only about 10^{-5} times g, whereas a small bird experiences accelerations of the order of 0.2 - 0.4 times g during each wing-stroke and may flap its wings 50,000 times per hour. This direct comparison, however, overstates the objection to inertial orientation, for several reasons:

(i) the accelerations involved in flapping flight are almost entirely in the sagittal plane of the bird, whereas those of greatest importance for inertial navigation are lateral — i.e., perpendicular to this plane. As pointed out by Barlow, inertial control of motion which is restricted to a horizontal plane requires much less sensory discrimination than three-dimensional navigation. If birds maintain their vestibular organs in the horizontal plane (do not use these organs to maintain altitude) the vestibular organs could conceivably be extremely sensitive to small accelerations in the horizontal plane (Barlow, pers. comm.).

(ii) The random lateral accelerations due to atmospheric turbulence are usually much smaller than 0.2 g, and tend to upset the bird's lateral stability, so that they require conscious muscular reactions for controlled flight.

(iii) The accelerations due to flapping flight are directly related to activities of the bird itself. It is therefore not improbable that a proprioceptor system should develop to compensate for its effects.

(iv) It is already known that birds possess a well-developed inertial system which enables them to keep their heads in a fixed position in spite of movements of their bodies — e.g., by a captor, by wind moving their perch, or during aerial maneuvers (see photo, Lindström 1962). Moreover, birds are able to maintain control of their flight in the dark and in fog — conditions which would be hazardous to human aviators without an artificial horizon. In other words, inertial orientation is certainly used by birds to stabilize their flight for short periods (of the order of seconds and probably minutes), and this suggests the possibility that it may be used to stabilize orientation over longer periods. For long flights (once the time span of 84 minutes is passed), errors in navigation by inertial systems increase only as fast as the square root of the time (analysis quoted by Barlow 1964), so that for inertial control to be effective over many hours, it need not call for an enormous increase in sensitivity. It is preferable to explain the observed behavior of the birds as a refinement of a system already well-developed, rather then to invoke new senses.

(v) The accelerations due to both flapping flight and to atmospheric turbulence occur on a much shorter time-scale than those due to changes in the mean wind. Hence it is possible to envisage an inertial control system which operates in two frequency ranges — a high-frequency range imparting aerodynamic stability and a low-frequency range maintaining orientation.

For these reasons we suggest that the theoretical objections to inertial orientation, although numerous, are not overwhelming. At present, however, the only observational evidence is unfavorable to the hypothesis — Lack's (1960) observation that in disoriented movements birds do not fly straight. Since accurate knowledge of the local vertical is essential for inertial orientation in a horizontal plane (Barlow 1964), Lack's observation can be reconciled with the hypothesis of inertial orientation if it is supposed that birds become "disoriented" when they lose contact with the local vertical. This however, invokes the use of another sense — e.g., sight — as part of the inertial control system. Furthermore, Lack used the curving tracks of birds as one criterion of disorientation so that we may not be able to depend directly on this observation.

To sum up, the most reasonable interpretation of our observations is that birds select their preferred heading at the start of the night (using some orientation process which we do not discuss in this paper, but which does not *always* require observation of the sun or the stars at the time of flying up), and maintain it during the night by various means which may include visual observation of the ground, and may perhaps include inertial orientation.

It is in this context that our observation of regular, well-oriented migration under overcast skies should be viewed. It is in fact exactly analogous to Tinbergen's (1956) observation of well-oriented migration under overcast skies by day, and it has the same significance. Neither observation is, in itself, inconsistent with any theory of orientation based on sun or stars, but both indicate that any such "celestial" (*sic*) theory is incomplete, and that birds must, for most of the time, use another means of orientation as well. In this paper, lacking critical evidence for or against inertial control, we suggest that the most important secondary means of orientation is visual observation of the landscape, but we wish to emphasize that we do not regard this suggestion as a satisfactory explanation of our observations, and that they do not completely exclude any of the current theories of orientation. In fact, our main conclusion is that orientation is a complex process achieved by several different means, and that if use of one reference system is prevented, the birds switch over to another; only when all possible means of orientation are interrupted does orientation break down. In this situation it is difficult to extract from field observations *any* critical evidence for or against the partial validity of any theory.

So far this discussion has been concerned exclusively with the problem of orientation, but we may consider briefly the relevance of our observations to theories of navigation. After reviewing various lines of evidence, Lack (1962b) supported the hypothesis (Perdeck 1958) that young birds may find their winter quarters by a "direction and distance" process — i.e., by "dead-reckoning" rather than by navigation. Since their subsequent migrations represent returns to known areas, Lack suggested that theories of innate navigational ability may be superfluous. Lack's suggestion is difficult to reconcile with his observation that autumn migrants in western Europe are drifted in a random way by cross-winds, but it seems more plausible for the birds which we observed, which almost always flew on the same track. Our birds may have had an innate ability to navigate, but our observations gave no evidence that they ever used it, nor that they ever needed to do so.

ACKNOWLEDGMENTS

We would like to thank again the private foundation, and the National Science Foundation of the United States which by its Grant #G-11571 has supported this research; the members of The Mitre Corporation of Lexington, Mass., Drs. Edward Reardon, Eugene Cormier, and Stephen Buchanan; Dr. Richard Fay of the U. S. Weather Bureau, Logan International Airport, Boston, Mass., for help and advice on weather data; and especially Dr. Robert E. Richardson of the Massachusetts Institute of Technology's Lincoln Laboratory, who saw the biological importance of a study of "angels" and made it possible.

APPENDIX TABLE 1. ESTIMATES OF WIND VELOCITIES OVER CAPE COD

Date	Wind direction and speed at: 19	22	01	04
4/5 Sept. 59	300/4	280/7	355/5	—
9/10 Sept. 59	170/5	120/6	160/6	—
11/12 Sept. 59	025/25	013/27	019/21	015/18
2/3 Oct. 59	070/11	068/15	073/16	069/14
4/5 Oct. 59	285/10	305/10	345/9	345/8
10/11 Oct. 59	—	320/4	065/4	130/7
14/15 Oct. 59	083/16	069/14	050/18	050/17
21/22 Oct. 59	076/12	084/12	093/10	092/16
16/17 Sept. 60	071/9	055/14	066/14	078/10
21/22 Sept. 60	054/12	059/10	049/13	—
29/30 Sept. 60	015/7	—	—	—
1/2 Oct. 60	014/21	024/10	050/15	—
3/4 Oct. 60	—	354/10	000/10	—
7/8 Oct. 60	—	313/15	—	—
8/9 Oct. 60	—	295/11	305/12	—
16/17 Aug. 61	—	035/10	—	—
28/29 Aug. 61	—	310/7	—	—
31 Aug./1 Sept. 61	—	275/6	—	—
4/5 Sept. 61 . .	Calm	Calm	—	—
5/6 Sept. 61	—	355/9	—	—
6/7 Sept. 61	130/7	100/6	—	—
7/8 Sept. 61	—	Calm	—	—
8/9 Sept. 61	130/5	—	—	—
9/10 Sept. 61	300/3	270/8	—	—
15/16 Sept. 61	348/9	348/11	—	—
15/17 Sept. 61	052/11	068/17	—	—
17/18 Sept. 61	—	070/16	072/18	076/23
19/20 Sept. 61	095/17	107/15	140/10	109/12
23/24 Sept. 61	052/15	052/15	071/13	070/10
28/29 Sept. 61	328/15	339/9	310/10	329/8
29/30 Sept. 61	351/4	350/5	010/7	Calm

Date	Wind direction and speed at: 19	22	01	04
7/8 Oct. 61	070/6	055/7	063/14	048/11
15/16 Oct. 61	—	—	315/20	316/13
16/17 Oct. 61	355/13	—	321/13	316/15
19/20 Oct. 61	—	110/15	—	—
20/21 Oct. 61	—	030/40	026/35	—
21/22 Oct. 61	090/33	084/25	079/31	—
22/23 Oct. 61	—	064/36	—	065/40
23/24 Oct. 61	—	050/32	050/40	—
24/25 Oct. 61	050/26	034/24	—	—
27/28 Oct. 61	347/14	351/13	350/12	336/12
1/2 Nov. 61	—	331/15	333/16	340/13
8/9 Nov. 61	—	345/14	000/15	—
9/10 Nov. 61	342/19	349/23	354/20	346/19
10/11 Nov. 61	359/21	002/16	008/18	356/17
11/12 Nov. 61	290/5	—	—	—
14/15 Sept. 62	—	335/24	—	—
20/21 Sept. 62	036/15	120/15	—	—
26/27 Sept. 62	135/7	135/3	—	—
1/2 Oct. 62	318/9	—	—	—
2/3 Oct. 62	320/8	—	—	—
3/4 Oct. 62	255/13	—	—	—
9/10 Oct. 62	074/12	—	—	—
10/11 Oct. 62	357/13	—	—	—
17/18 Oct. 62	005/19	—	—	—
18/19 Oct. 62	Calm	—	—	—

Note: The wind velocities listed (direction in degrees, speed in knots) are the "gradient" or "geostrophic" winds, estimated by standard methods from the direction and spacing of the isobars on the sea-level weather maps. The ways in which the maps are plotted and read tend to average out local variations in wind. Hence the figures probably underestimate the stronger winds and underestimate the extent of short-period changes. Only those wind velocities which are used to compute headings (Tables 1-8) are listed here.

APPENDIX TABLE 2.
CLOUD OBSERVATIONS AT THREE WEATHER STATIONS

Note: Cloud cover in tenths; visibility in miles; ceiling in 100's of feet.

	PORTLAND				BOSTON				NANTUCKET			
DATE	19	22	01	04	19	22	01	04	19	22	01	04
4/5 Sept. 59	3	1	1	0	6	3	0	0	8	0	10	10
	15	15	15	15	10	7	10	10	12	1	—	—
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	100	Unl.	1	2
9/10 Sept. 59	3	1	0	0	0	0	10	10	10	10	10	9
	15	15	15	15	15	10	5	—	—	1	7	10
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	5	1	12	3	11	35
11/12 Sept. 59	3	0	0	0	4	0	0	0	10	0	0	0
	15	15	15	15	15	15	15	15	15	15	15	15
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	80	Unl.	Unl.	Unl.
19/20 Sept. 59	0	0	0	0	0	0	0	0	0	0	7	3
	15	15	15	15	15	15	12	5	15	15	15	15
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
2/3 Oct. 59	4	0	1	0	10	10	10	7	10	10	10	10
	15	15	10	10	15	15	15	15	15	15	15	15
	Unl.	Unl.	Unl.	Unl.	17	20	25	26	18	15	15	21
4/5 Oct. 59	3	3	10	9	7	0	7	3	10	7	4	0
	7	10	10	15	10	12	15	15	1	3	3	3
	Unl.	Unl.	CIR	CIR	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
10/11 Oct. 59	8	9	10	3	10	9	10	10	8	10	8	8
	15	15	15	15	10	8	9	—	10	7	7	10
	Unl.	Unl.	CIR	Unl.	Unl.	Unl.	CIR	CIR	CIR	Unl.	Unl.	CIR
14/15 Oct. 59	3	0	0	7	10	10	8	10	10	10	10	10
	15	15	15	15	15	15	15	15	7	10	15	15
	Unl.	Unl.	Unl.	34	25	35	CIR	30	11	18	19	20
21/22 Oct. 59	0	0	0	0	0	0	0	0	0	3	7	8
	15	15	15	15	15	15	12	15	15	15	15	15
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	25
16/17 Sept. 60	0	0	0	0	0	0	0	0	2	0	0	0
	15	15	15	10	15	15	8	6	15	15	15	10
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
21/22 Sept. 60	10	10	0	7	0	8	10	10	4	0	0	0
	15	15	6	—	15	15	10	12	15	15	15	15
	50	46	Unl.	Unl.	Unl.	55	60	55	Unl.	Unl.	Unl.	Unl.
29/30 Sept. 60	10	10	10	10	10	10	10	10	8	10	10	10
	1	2	1	4	1	5	5	—	—	—	—	1
	2	5	2	0	3	6	14	3	Unl.	1	1	20
1/2 Oct. 60	0	0	0	0	0	0	0	2	0	0	1	3
	15	15	15	15	15	15	15	15	15	15	15	15
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
3/4 Oct. 60	0	0	0	3	0	0	0	0	7	2	1	0
	15	15	15	15	15	15	15	6	12	15	15	15
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	35	Unl.	Unl.	Unl.

Appendix Table 2 (Continued)

DATE	PORTLAND 19	22	01	04	BOSTON 19	22	01	04	NANTUCKET 19	22	01	04
7/8 Oct. 60	0	0	0	6	0	0	0	0	0	0	0	0
	15	15	15	15	15	15	15	15	15	15	15	15
	Unl.	Unl.	Unl.	60	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
8/9 Oct. 60	0	0	5	3	4	7	7	8	3	0	1	6
	15	15	15	15	15	15	12	13	15	15	15	15
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
16/17 Aug. 61	0	0	0	0	2	0	0	0	4	0	0	6
	15	15	15	15	15	15	15	15	2	8	15	10
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	70
28/29 Aug. 61	5	1	10	10	10	8	10	10	6	10	10	10
	7	7	7	7	8	12	6	6	1	—	—	—
	Unl.	Unl.	90	70	60	120	120	50	CIR	120	1	1
31 Aug./1 Sept. 61	0	0	5	5	4	0	2	3	8	8	2	0
	5	4	1	1	3	3	2	2	1	1	3	5
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
4/5 Sept. 61	8	2	3	4	0	0	4	4	10	10	10	10
	1	1	1	2	3	3	3	4	3	—	—	—
	6	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
5/6 Sept. 61	8	3	0	0	0	0	9	8	3	4	10	10
	10	10	10	15	7	5	8	8	2	—	—	—
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	60	65	Unl.	Unl.	2	1
6/7 Sept. 61	0	10	8	6	0	1	0	10	10	10	10	2
	15	12	15	15	15	8	7	1	—	—	—	7
	Unl.	60	65	60	Unl.	Unl.	Unl.	2	1	1	1	Unl.
7/8 Sept. 61	10	10	10	8	4	6	10	10	1	8	0	0
	15	15	12	12	15	13	12	12	15	1	12	12
	49	100	80	38	Unl.	100	70	65	Unl.	Unl.	Unl.	Unl.
8/9 Sept. 61	7	10	10	8	7	8	3	4	1	8	2	10
	5	3	1	1	8	8	6	4	10	10	10	12
	Unl.	80	55	42	CIR	50	Unl.	Unl.	Unl.	100	Unl.	60
9/10 Sept. 61	2	0	3	0	0	0	0	0	5	4	0	3
	5	4	6	8	6	3	5	5	1	1	2	1
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
15/16 Sept. 61	5	7	6	0	5	10	10	0	10	5	10	7
	15	15	15	15	15	15	15	15	7	15	15	15
	Unl.	55	150	Unl.	Unl.	75	70	Unl.	29	Unl.	50	60
16/17 Sept. 61	0	0	0	0	1	1	3	0	0	0	0	0
	15	15	15	15	15	15	15	15	15	15	15	15
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
17/18 Sept. 61	0	0	0	0	0	0	8	2	5	2	0	0
	15	15	15	15	15	15	15	15	15	15	15	15
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
19/20 Sept. 61	8	10	9	6	10	10	8	10	10	10	10	10
	7	4	8	4	10	8	7	7	15	15	10	—
	CIR	1	CIR	Unl.	Unl.	Unl.	Unl.	CIR	Unl.	35	9	1

Appendix Table 2 (Continued)

DATE	PORTLAND				BOSTON				NANTUCKET			
	19	22	01	04	19	22	01	04	19	22	01	04
22/23 Sept. 61	0	1	10	10	2	10	10	10	10	10	10	10
	15	8	4	3	12	1	—	1	—	2	—	—
	Unl.	Unl.	9	4	Unl.	2	2	5	1	2	1	1
23/24 Sept. 61	10	10	10	10	10	10	10	10	10	10	10	10
	4	4	4	2	—	1	—	—	—	—	—	—
	0	0	0	0	1	2	1	1	2	1	1	1
28/29 Sept. 61	0	0	0	0	3	0	0	0	1	3	7	7
	15	15	15	15	13	15	15	15	5	8	10	10
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	100	70
29/30 Sept. 61	0	0	0	0	0	0	0	0	0	0	0	0
	15	15	15	15	15	12	10	10	15	15	15	15
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
7/8 Oct. 61	8	4	5	7	10	10	10	10	10	10	10	10
	7	3	1	1	4	5	3	4	6	6	3	3
	Unl.	Unl.	Unl.	CIR	CIR	CIR	CIR	CIR	CIR	CIR	CIR	CIR
9/10 Oct. 61	0	2	0	0	3	6	3	0	3	0	0	0
	12	1	3	7	12	10	10	8	2	4	6	7
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
10/11 Oct. 61	8	10	10	3	0	0	9	10	0	0	0	0
	10	8	10	15	5	4	12	13	10	10	7	3
	50	55	50	Unl.	Unl.	Unl.	65	Unl.	Unl.	Unl.	Unl.	Unl.
15/16 Oct. 61	8	0	0	4	6	0	3	3	10	0	10	2
	15	15	15	15	15	15	15	15	15	15	15	15
	45	Unl.	Unl.	Unl.	55	Unl.	Unl.	Unl.	45	Unl.	29	Unl.
16/17 Oct. 61	6	10	0	0	3	3	0	0	2	6	2	0
	15	15	15	15	15	6	12	12	15	15	15	14
	60	65	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	35	Unl.	Unl.
19/20 Oct. 61	0	10	10	10	8	8	10	10	4	10	10	10
	1	—	—	—	10	7	4	3	8	7	7	7
	Unl.	0	0	1	Unl.	Unl.	Unl.	5	Unl.	Unl.	40	7
20/21 Oct. 61	10	10	10	10	10	10	10	10	10	10	10	10
	10	12	12	15	10	12	12	15	7	7	15	15
	55	44	55	210	38	65	80	80	12	16	14	20
21/22 Oct. 61	10	10	10	10	10	10	10	10	10	10	10	10
	15	15	15	12	15	12	12	5	7	3	4	2
	36	40	100	80	37	30	25	15	6	5	6	8
22/23 Oct. 61	8	8	2	0	10	10	10	10	10	10	10	10
	15	15	15	15	15	15	15	15	4	4	4	5
	Unl.	CIR	Unl.	Unl.	75	35	35	28	10	10	11	20
23/24 Oct. 61	5	9	0	7	10	10	10	10	10	10	10	10
	15	15	15	15	15	15	15	15	2	7	7	7
	Unl.	90	Unl.	85	36	50	25	20	6	20	12	15

Appendix Table 2 (Continued)

DATE	PORTLAND 19	22	01	04	BOSTON 19	22	01	04	NANTUCKET 19	22	01	04
24/25 Oct. 61	10	10	0	7	10	10	10	10	10	10	10	10
	15	15	15	15	15	15	15	15	7	7	7	15
	27	44	Unl.	33	30	20	20	Unl.	10	20	12	15
27/28 Oct. 61	3	0	0	0	8	0	0	0	7	2	0	0
	15	15	15	15	15	15	15	15	15	15	15	15
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	50	Unl.	Unl.	Unl.
1/2 Nov. 61	4	0	0	0	5	0	0	0	0	0	0	0
	15	15	15	15	15	15	15	15	15	15	15	15
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
8/9 Nov. 61	10	10	0	0	7	2	5	0	8	10	10	10
	12	12	10	15	12	12	15	15	15	15	10	15
	50	80	Unl.	Unl.	100	Unl.	Unl.	Unl.	CIR	50	50	50
9/10 Nov. 61	10	10	10	0	4	8	10	1	3	1	0	1
	15	15	15	15	15	15	15	15	15	15	15	15
	90	27	80	Unl.	Unl.	Unl.	75	Unl.	Unl.	Unl.	Unl.	Unl.
10/11 Nov. 61	0	0	0	2	0	0	0	1	4	8	0	0
	15	15	15	15	15	15	15	15	15	15	15	14
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	35	Unl.	Unl.
12/13 Sept. 62	0	0	0	0	2	0	0	0	10	3	0	0
	15	15	15	15	15	15	12	12	10	10	10	10
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	50	Unl.	Unl.	Unl.
14/15 Sept. 62	3	0	0	0	10	5	0	0	10	10	10	0
	15	15	15	15	8	12	15	15	5	4	7	15
	Unl.	Unl.	Unl.	Unl.	90	Unl.	Unl.	Unl.	7	50	90	Unl.
20/21 Sept. 62	7	2	0	0	6	3	0	0	5	10	3	3
	15	15	15	15	15	15	15	15	15	15	15	15
	80	Unl.	Unl.	Unl.	100	Unl.	Unl.	Unl.	Unl.	50	Unl.	Unl.
21/22 Sept. 62	0	0	0	0	0	0	0	0	0	0	0	5
	15	15	15	15	15	15	15	6	15	12	15	15
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
26/27 Sept. 62	10	9	10	10	10	10	10	10	10	10	10	10
	3	0	3	3	8	5	4	3	3	3	1	4
	CIR	CIR	23	5	50	180	120	100	100	45	40	45
1/2 Oct. 62	10	0	0	2	10	0	2	0	0	0	0	0
	15	15	15	10	15	8	7	6	15	15	10	7
	65	Unl.	Unl.	Unl.	75	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
2/3 Oct. 62	0	0	0	0	0	0	2	0	0	0	0	0
	15	15	10	4	12	7	7	6	7	0	7	8
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.
3/4 Oct. 62	0	0	0	2	0	0	0	0	0	0	0	6
	8	5	7	1	8	7	6	5	7	10	10	7
	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	Unl.	CIR
9/10 Oct. 62	10	10	10	10	10	10	10	10	10	10	10	10
	15	15	7	10	7	12	10	6	5	3	4	4
	75	24	16	39	5	12	14	6	6	6	6	9

Appendix Table 2 (Continued)

DATE	PORTLAND 19	PORTLAND 22	PORTLAND 01	PORTLAND 04	BOSTON 19	BOSTON 22	BOSTON 01	BOSTON 04	NANTUCKET 19	NANTUCKET 22	NANTUCKET 01	NANTUCKET 04
10/11 Oct. 62	10 10 23	9 12 32	4 0 Unl.	0 7 Unl.	10 10 18	9 8 15	2 9 Unl.	0 9 Unl.	10 10 13	10 10 15	8 10 15	1 10 Unl.
15/16 Oct. 62	8 15 Unl.	3 15 Unl.	3 15 Unl.	8 15 Unl.	10 15 Unl.	7 15 Unl.	10 15 35	8 15 Unl.	0 15 Unl.	2 15 Unl.	7 15 40	10 15 40
17/18 Oct. 62	0 15 Unl.	0 15 Unl.	5 15 Unl.	1 15 Unl.	0 15 Unl.	0 15 Unl.	0 15 Unl.	0 12 Unl.	0 10 Unl.	0 15 Unl.	0 15 Unl.	0 15 Unl.
18/19 Oct. 62	3 15 Unl.	0 7 Unl.	7 5 Unl.	2 6 Unl.	0 15 Unl.	0 15 Unl.	0 8 Unl.	0 2 Unl.	6 15 Unl.	0 10 Unl.	0 15 Unl.	0 15 Unl.
19/20 Oct. 62	0 12 Unl.	0 12 Unl.	0 12 Unl.	0 12 Unl.	0 15 Unl.	0 15 Unl.	0 15 Unl.	0 8 Unl.	0 15 Unl.	0 15 Unl.	0 15 Unl.	0 15 Unl.

NOTE: — Cloud cover in tenths; visibility in miles; ceiling in 100's of feet; dashes indicate no observation listed in Weather Bureau data; Unl. indicates ceiling unlimited; CIR indicates cirrus clouds.

APPENDIX TABLE 3
CLOUD TYPES ON NIGHTS OF WELL ORIENTED MOVEMENTS WHEN COASTAL STATIONS REPORTED GENERAL OVERCAST

(Type of Clouds; Level of Base; Overcast)

N*ote*: Data from U. S. Weather Bureau Maps at 0100.

DATE	PORTLAND	BOSTON	NANTUCKET
28/29 Aug. 61	Thick alto-cumulus 600-1000 Total	Veil of cirro-stratus Thin alto-cumulus Total	Sky obscured 9/10 - low clouds
*9/10 Sept. 59	Clear	Stratus 300-600 Total	Strato-cumulus 1000-2000 Total
19/20 Sept. 61	Cirrus and Cirro-stratus — 9/10	Thick alto-cumulus — 7-8/10	Stratus 600-1000 Total
21/22 Sept. 60	Clear	Strato-cumulus 5000-6000 9/10	Clear

Appendix Table 2 (Continued)

DATE	PORTLAND	BOSTON	NANTUCKET
*23/24 Sept. 61	Sky obscured 0 9/10	Sky obscured 0 9/10	Sky obscured 0 9/10
26/27 Sept. 62	Strato-cumulus 2000-4000 Total	Strato-cumulus 5000-6000 Total	Strato-cumulus 3500-6000 7-8/10
29/30 Sept. 60	Sky obscured 0 9/10	Strato-cumulus 1000-2000 Total	Sky obscured 0 9/10
2/3 Oct. 59	Alto-stratus 2000-4000 < 1/10	Alto-stratus 2000-4000 9/10	Alto-stratus 1000-2000 Total
7/8 Oct. 61	Clear — —	Cirro-stratus — Total	Cirro-stratus — Total
10/11 Oct. 59	Double alto-cumulus — Total	Cirro-stratus — Total	Cirrus — 7/10
14/15 Oct. 59	Almost clear — < 1/10	Strato-cumulus 3500-5000 7/10	Strato-cumulus 1000-2000 Total
19/20 Oct. 61	Sky obscured 0 9/10	Cirro-stratus Alto-cumulus — 9/10	Double alto-cumulus Strato-cumulus 3500-5000 Total
20/21 Oct. 61	Strato-cumulus 5000-6500 Total	Double alto-cumulus — Total	Strato-cumulus 1000-2000 Total
21/22 Oct. 61	Double alto-cumulus — Total	Strato-cumulus 2000-4000 Total	Stratus 600-1000 Total
22/23 Oct. 61	Alto-cumulus — 2-3/10	Strato-cumulus 3500-5000 9/10	Stratus 1000-2000 Total
23/24 Oct. 61	Thin alto-cumulus — < 1/10	Strato-cumulus 2000-4000 Total	Strato-cumulus 1000-2000 Total
24/25 Oct. 61	Strato-cumulus — < 1/10	Strato-cumulus 2000-4000 Total	Strato-cumulus 1000-2000 Total

*N*ote*: 9/10 Sept. 59 and 23/24 Sept. 61 are not "overcast"; cloud too low for our definition.

SUMMARY

1. The orientation of night migrants was studied by means of a radar station on Cape Cod during four autumns, 1959-1962. The "Moving Target Indicator" circuit permits measurement of the average track of mass of birds accurately to within about 2°, but this technique can be used only intermittently. The records are biased towards occasions when migration was more or less unidirectional, and when orientation was good, especially when the wind was more or less behind the birds.

2. Four main types of passerine movement are described, with mean tracks about 220° (over the mainland of Massachusetts), 236° (immigrants from Nova Scotia), 172° and 186° (offshore departures of non-passerines and "reversed migration"). Intermediate directions of movement were very rare. Movements towards the southeast, east and northeast were observed regularly, but are not analyzed in this paper.

3. In each of the four movements, the birds compensated for wind-drift by adjusting their headings so that their mean track was about the same on every night. Cross-winds may have affected the mean tracks of two of the movements, but by no more than 3°. On some nights the mean track remained constant in spite of changes in the wind.

4. The birds migrating over and near the mainland turned towards their right by about 1.5° per hour during the night, thereby turning away from the sea.

5. The observed quality of orientation usually deteriorated steadily during the night, but this effect could not be studied quantitatively.

6. Well-oriented migration was regularly observed under fully overcast skies, and over low-lying fog.

7. "Disoriented migration" was rare, but a few cases were observed in which birds were flying at random over a large area: these cases were associated with overcast skies, rain, fog, stationary fronts and falls of migrants at the coast.

8. These observations are inconsistent with any *simple* theory of orientation. It is suggested that birds maintain their tracks primarily by visual observation of the landscape, but they must at times use other methods of orientation, perhaps including inertial orientation.

BIBLIOGRAPHY

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.

Barlow, J. S. 1964. Inertial navigation as a basis for animal navigation. *Journ. Theoret. Biol.,* **6**: 76-117.

Bellrose, F. C., and R. R. Graber. 1963. A radar study of the flight directions of nocturnal migrants. Proc. XIIIth Int. Orn. Cong., Vol. 1, pp. 362-389.

Drury, W. H., and J. A. Keith. 1962. Radar studies of songbird migration in coastal New England. *Ibis,* **104**(4): 449-498.

DRURY, W. H., I. C. T. NISBET, and R. E. RICHARDSON. 1961. The migration of "angels." *Natural History,* **70**(8): 10-17.

FROMME, H. G. 1961. Untersuchungen über das Orientierungsvermögen nächtlich ziehender Kleinvögel (*Erithacus rubecula, Sylvia communis*). *Zeits. Tierpsychol.,* **18**: 205-220.

GRABER, R. R., and W. W. COCHRAN. 1960. Evaluation of an aural record of nocturnal migration. *Wils. Bull.,* **72**: 253-273.

GRIFFIN, D. R. 1953. Sensory physiology and the orientation of animals. *Amer. Scientist,* **41**: 209-244, 281.

GRIFFIN, D. R. 1955. Bird navigation. *In* Recent Studies in Avian Biology, A. Wolfson, Ed. Univ. Ill. Press, Urbana, pp. 154-197.

HASSLER, S. S., R. R. GRABER, and F. C. BELLROSE. 1963. Fall migration and weather, a radar study. *Wils. Bull.,* **75**(1): 56-77.

KING, J. M. B. 1959. Orientation of migrants over sea in fog. *Brit. Birds,* **52**(4): 125-126.

KRAMER, G. 1961. Long distance orientation. Chap. XXII, *in* Biology and Comparative Physiology of Birds, A. J. Marshall, Ed., Vol. II. Academic Press, New York and London, pp. 341-371.

LACK, D. 1958. Migrational drift of birds plotted by radar. *Nature,* **182**(4630): 221-223.

LACK, D. 1959. Migration across the North Sea studied by radar. Part 1: Survey through the year. *Ibis,* **101**(2): 209-234.

LACK, D. 1960. Migration across the North Sea studied by radar. Part 2: The spring departure 1956-59. *Ibis,* **102**(1): 26-57.

LACK, D. 1962a. Migration across the southern North Sea studied by radar. Part 3: Movements in June and July. *Ibis,* **104**(1): 74-85.

LACK, D. 1962b. Radar evidence on migratory orientation. *Brit. Birds,* **55**(4): 139-158.

LACK, D. 1963a. Migration across the southern North Sea studied by radar. Part 4: Autumn. *Ibis,* **105**(1): 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**(4): 461-492.

LACK, D. and E. EASTWOOD. 1962. Radar films of migration over eastern England. *Brit. Birds,* **55** (9): 388-414.

LINDSTRÖM, U. 1962. Fotografiskt belägg för grågässens halsbrytande akrobatik vid landningskast. *Vår Fågelvärld,* **21**: 134-135.

MERKEL, F. W. 1956. Untersuchungen über tages- und jahresperiodische Aktivitätsanderungen bei gekäfigten Zugvögeln. *Zeits. Tierpsychol.,* **13**: 278-301.

MERKEL, F. W., and H. G. FROMME. 1958. Untersuchungen über Orientierungsvermögen nächtlich ziehender Rotkelchen (*Erithacus rubecula*). *Naturwiss.,* **45**: 499-500.

MOOK, J. H., J. ROOTH, and J. J. ZIJLSTRA. 1957. Stichting Vogeltrekstation Texel 1956: De Vogeltrekwaarnemingen op de Noord-Valuwe. *Limosa,* **30**: 76-83.

NISBET, I. C. T. 1963a. Measurements with radar of the height of nocturnal migration over Cape Cod, Massachusetts. *Bird-Banding,* **34**(2): 57-67.

NISBET, I. C. T. 1963b. Quantitative study of migration with 23-centimetre radar. *Ibis,* **105**(4): 435-460.

NISBET, I. C. T., W. H. DRURY, JR., and J. BAIRD. 1963. Weight-loss during migration. Part I: Deposition and consumption of fat by the Blackpoll Warbler *Dendroica striata*; Part II: Review of other estimates (I. C. T. Nisbet). *Bird-Banding,* **34**(3): 107-159.

PERDECK, A. C. 1958. Two types of orientation in migrating Starlings, *Sturnus vulgaris* L., and Chaffinches, *Fringilla coelebs* L., as revealed by displacement experiments. *Ardea,* **46**(1/2): 1-37.

PRECHT, H., u. MITARBEITER (=LINDENLAUB). 1956. Einige Versuche zum Heimfindevermögen von Vögeln. *Journ. für Ornith.,* **97**: 377-383.

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.

SAUER, F. 1957. Die Sternenorientierung nächtlicher ziehender Grasmücken (*Sylvia atricapilla, borin* und *curruca*). *Zeits. Tierpsychol.*, **14**(1): 29-70.

SAUER, E. G. F., and E. M. SAUER. 1960. Star navigation of nocturnal migrating birds: the 1958 planetarium experiments. *Cold Spring Harbor Symposia on Quantitative Biology*, **25**: 463-473.

TINBERGEN, L. 1956. Field observations of migration and their significance for the problems of migration. *Ardea*, 44: 231-235.

VAN DOBBEN, W. H. 1953. Migration in the Netherlands. *Ibis*, **95**(2): 212-234.

VLEUGEL, D. A. 1954. Waarnemingen over de nachttrek van lijsters (*Turdus*) en hun waarschijnlijke oriëntering. *Limosa*, **27**(1-2): 1-19.

WALLRAFF, H. G. 1960. Does celestial navigation exist in animals? *Cold Spring Harbor Symposia on Quantitative Biology*, **25**: 451-461.

Received February, 1964.

RENESTING AND SECOND NESTING OF INDIVIDUALLY MARKED RED-WINGED BLACKBIRDS

By DON P. FANKHAUSER

Renesting and second nesting of 26 color-marked female Red-winged Blackbirds (*Agelaius phoeniceus*) were studied during the spring and summer of 1962. Renesting was nesting that occurred after an unsuccessful attempt, and second nesting was nesting that occurred after a successful nesting (at least one young fledged).

PROCEDURES

The study was conducted on the Patuxent Wildlife Research Center, Laurel, Maryland, in habitats where the nesting population of Red-wings is large. The approximate nest density that prevails in this habitat is indicated by the results of an intensive search for nests in 1961, when 144 active nests were found in 150 acres of nesting habitat. More detailed nest studies were made in 1962: 26 nesting females were caught in nest traps and were individually marked with several layers of colored plastic tape wrapped around the tarsus of each leg. Previous testing of this type of color marker on captive and wild Red-wings had shown that such markers would remain for at least 3 months. Birds also were banded with Fish and Wildlife Service numbered bands. Each nest was identified by a numbered white tag 1 1/2" x 3" placed several feet from the nest. Twenty of the marked birds were in three adjacent upland hayfields totaling about 20 acres, and 6 were in a marsh of about 19 acres. Seven of the females were subadults in plumage and 19 were adults.