

# THE ORIENTATION OF PASSERINE NOCTURNAL MIGRANTS FOLLOWING OFFSHORE DRIFT

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**ABSTRACT.**—Nocturnal autumn passerine migrants are frequently drifted by wind or carried by downwind flight from New England to offshore islands. Most individuals in these flights are immatures. Many recover the mainland via reoriented northward flights. During fall 1972, I made field observations and performed orientation cage tests on nocturnal migrants on Block Island, Rhode Island. Migrants reached the island during four southward movements in following winds. Migration was very light or absent on most other nights. Reoriented diurnal flights left from the island immediately after the arrival of a large nocturnal migration. Northward movements occurred on two nights following daytime reoriented flights. These nocturnal movements are tentatively interpreted as constituting reoriented flights. About 27% of the 79 individuals tested in orientation cages showed significantly directional nocturnal activity. About two-thirds of these oriented basically northwestward, corresponding to the reoriented flight of free-flying birds. These and similar reorientations of immature birds can be explained by a simple compass reorientation in response to wind drift over the ocean without invoking complicated navigation mechanisms. The remaining individuals oriented toward the southeast. Eleven birds exhibited a significant eastward orientation during the first few hours after dawn; this is interpreted as a positive phototaxis. Three of four Blackpoll Warblers oriented southward. No correlation existed between the quantity of *Zugunruhe* and the amount of subcutaneous fat, but fatter birds were significantly more likely to show oriented nocturnal activity.—*Department of Biological Sciences, State University of New York, Albany, New York 12222*. Accepted 3 November 1975.

NOCTURNAL passerine migrants face the risk of displacement from their normal routes of migration. At any time only a small fraction of the migratory population of a species may be involved, but natural selection should strongly favor individuals able to recognize and correct for these accidents. Evidence that migratory passerines have this ability comes primarily from two sources. Homing has been demonstrated in a few species (Mewaldt and Farner 1957; Perdeck 1958, 1967; Schwartz 1963; Mewaldt 1964a, 1964b), but these experiments were not designed to clarify the navigation mechanism. Field observations by Baird and Nisbet (1960), radar surveillance (Myres 1964, Richardson 1972), and banding recoveries (Evans 1968) indicated that nocturnal migrants drifted by wind reorient in a manner that compensates for the drift.

Studying this phenomenon in the field is confounded by practical problems. One can rarely be certain that migrants in flight are performing a compensatory movement of some type or that birds on the ground have been displaced from normal migration routes. As a result, most workers have resorted to artificial displacements and examined the subsequent cage orientation of the birds (Sauer and Sauer 1959; Hamilton 1962; Potapov 1966; Dolnik and Shumakov 1967; Rabøl 1969, 1970, 1972). Birds are usually transported unrealistically great distances to make the predicted shifts in orientation directions detectable and the results have been ambiguous.

A few localities exist where displaced migrants can be recognized with reasonable confidence and occur in considerable numbers, and the orientation directions of compensating birds can be predicted. Evans (1968) exploited a situation of this type in northeastern Britain where Scandinavian nocturnal migrants occasionally make a landfall when drifted by strong southeasterly winds over the North Sea.

More clear-cut cases of displacement and reorientation occur regularly in fall along the New England coast. Radar studies (Drury and Keith 1962, Drury and Nisbet

1964) have shown that passerine movements through this region occur in two main directions: (1) Large numbers of birds move southwestward on a broad front more or less parallel to the coast; (2) following the passage of cold fronts, large southward migrations of passerines depart from New England and the Maritime Provinces over the western Atlantic Ocean. This southward migration may be made up of a number of species, but only the Blackpoll Warbler (*Dendroica striata*) has been shown convincingly to make a transatlantic flight to northern South America (Nisbet et al. 1963, cf. Murray 1965, Nisbet 1970).

The weather conditions accompanying offshore flights are also associated with the arrival of large numbers of migrants on the coast and offshore islands. The grounded migrants probably consist of individuals from the southbound flight as well as birds drifted southeastward from the movement paralleling the coast. The number of migrants grounded in coastal regions under such circumstances may be impressively large (Baird and Nisbet 1960), although it probably constitutes only a small fraction of the total migration that occurred during the night (Drury and Nisbet 1964; C. J. Ralph, pers. comm.). Immediately after such flights, large numbers of nocturnal migrants move northward from coastal areas, especially from the offshore islands. This phenomenon and the evidence that it reflects reorientation following drift are detailed by Baird and Nisbet (1960). Briefly, the bulk of passerine migrants appears to avoid the immediate New England coast and offshore islands. Most individuals that do occur are immatures, presumably because they are inexperienced and less able to recognize or correct for such displacements (Baird and Nisbet 1960, Drury and Keith 1962, Nisbet et al. 1963, Drury and Nisbet 1964).

Because the main directions of movement of passerine migrants in southern New England are reasonably well-known and involve several distinct directions, it is an ideal place to conduct experiments on migratory orientation. This paper describes some preliminary experiments designed to examine the orientation of autumn nocturnal migrants on Block Island, a circa 3600-ha island 15.5 km off the coast of Rhode Island. Pertinent data on the simultaneous behavior of free-flying migrants are included for comparison.

#### METHODS

Between 23 September and 6 October 1972, I studied the orientation of nocturnal migrants on Block Island, Rhode Island. Observations of free-flying nocturnal migrants were made with portable ceilometers (Gauthreaux 1969, Able and Gauthreaux 1975) at the Block Island Airport. During the first several hours after dawn each day I made counts of birds leaving the north end of the island (Baird and Nisbet 1960).

Birds used in orientation cage tests were captured in mist nets on the property of F. David Lapham on the northeast side of the island. The birds were usually caught in the afternoon, and each was weighed, measured, aged by skull ossification, and banded. The birds were held in individual cells in a holding cage and were exposed to natural photoperiod, but were not allowed to see the sky. The individuals used in orientation cage tests were not a random sample of birds captured in the course of routine banding operations. Rather, when possible, I selected the fattest individuals of nonresident species.

The orientation cages were "Emlen funnels" (Emlen and Emlen 1966) placed on the ground on an open bluff along the northeast coast of Block Island. No terrain features or horizon glows should have been visible to the birds from this point. The cages were exposed to environmental sounds, including the ocean to the east. Birds were placed in the cages at night after all visible traces of light from the setting sun had disappeared. I checked the cages immediately before dawn, placed new funnels in the cages of individuals that showed an apparent directional tendency during the night, and returned these birds to the orientation cages for 3-4 additional hours. All birds were released at the end of the tests.

The blotter paper cones bearing the footprint records of the birds' activity were analyzed as described by Emlen and Emlen (1966). Each cone was divided into 16 sectors (22.5° each). From the quantified footprint densities in each sector I computed a mean vector, length of the mean vector ( $r$ ), and angular

TABLE 1  
SUMMARY OF VISUAL OBSERVATIONS OF MIGRATION

| Date    | Nocturnal migration    |           | Wind blowing toward | Reoriented diurnal flight |
|---------|------------------------|-----------|---------------------|---------------------------|
|         | Magnitude <sup>1</sup> | Direction |                     |                           |
| 22 Sep. | 3000                   | SE        | SE                  | No observations           |
| 23 Sep. | 800                    | NNW       | NNE                 | Small                     |
| 24 Sep. | None                   | —         | NE                  | None                      |
| 25 Sep. | Fog                    | —         | NE                  | None                      |
| 26 Sep. | None                   | —         | NNE                 | Small                     |
| 27 Sep. | Rain                   | —         | Variable            | None                      |
| 28 Sep. | 8400                   | SW        | SW                  | None                      |
| 29 Sep. | Fog                    | —         | NE                  | Very small                |
| 30 Sep. | 7000                   | SSE       | SE                  | None                      |
| 1 Oct.  | 9700                   | SSE       | S                   | None                      |
| 2 Oct.  | 300                    | NE        | N                   | Moderate                  |
| 3 Oct.  | 400                    | Mixed     | NE                  | Large                     |
| 4 Oct.  | None                   | —         | NW                  | Moderate-large            |
| 5 Oct.  | No obs.                | —         | —                   | None                      |

<sup>1</sup> Traffic rate in units of birds per mile of front per hour.

deviation (s) for each bird as described by Batschelet (1965). To determine whether the activity of the birds was concentrated in any compass direction, I applied a Rayleigh test to each distribution (Batschelet 1965, 1972), using sample sizes corrected as described by Emlen (1969). Emlen's corrections were derived only from observations of Indigo Buntings, but they appear to be sufficiently conservative to be applied to other species as well. Other statistical tests will be described as appropriate.

## RESULTS

*The origin of migrants on Block Island.*—Table 1 summarizes the magnitudes and directions of nocturnal migration over Block Island during the study. These data agree in general with the radar picture of migration in southern New England (Drury and Keith 1962, Drury and Nisbet 1964). Moderate or large movements occurred on only four nights. In each case, the flights were moving toward between southeast and southwest in following winds. On a number of nights no detectable migration occurred. Two nights, 23 September and 2 October, saw very slight northward movements. Both these flights were in light southerly winds on nights following a large southward migration. Their directions and the fact that the birds were seen within 2 hours after darkness suggest that they initiated migration on the island.

Northward reoriented flights left the island on one or more mornings following the arrival of a large nocturnal migration (Table 1). Departures failed to materialize when no nocturnal migration occurred over the island for several days. On the first morning after a large migration, the reoriented flights left into a head wind as described by Baird and Nisbet (1960), but on subsequent days departures also occurred with following winds.

Based on these observations and the species composition of the netted birds, it is virtually certain that most of the individuals tested in the orientation cages arrived on the island during one of the four southward migrations and thus originated north of the island. Of course the exact dates of the netted birds' arrival or their length of stay on the island could not be determined.

*Cage orientation.*—I tested 79 individuals of 23 species in orientation cages on 11 nights. The compilation in Table 2 shows that only 21 (26.5%) of the birds showed significant orientation at night. As expected at this locality, immatures overwhelmingly predominated in the netted samples of almost all species, the Blackpoll Warbler being the outstanding exception.

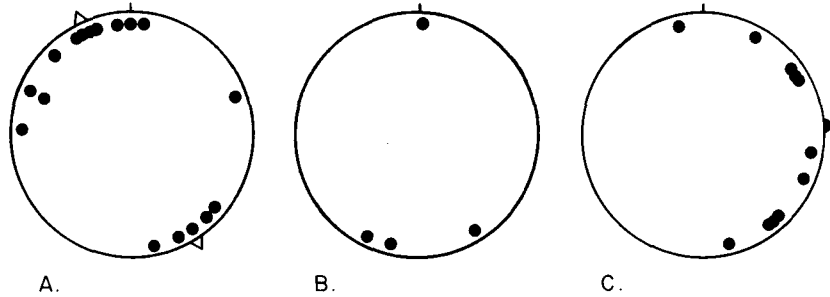


Fig. 1. Distribution of mean orientation vectors of individual birds. A, mean vectors of all individuals that showed statistically significant cage orientation at night (excluding data from Blackpoll Warblers). B, mean vectors of nocturnal orientation of four Blackpoll Warblers. C, mean vectors of orientation during the first hours after dawn.

Some species and species groups were consistently better orientation cage subjects than others. Gray Catbirds (*Dumetella carolinensis*) were notoriously poor, but some of the individuals may have been from the island's breeding population. As a group the warblers (Parulidae) performed well, and Blackpoll Warblers had an especially high proportion of orienters. Vireos (Vireonidae) were poorly suited to the orientation cages. They fluttered a great deal and marred the blotter cones with slashing wing marks. Also all vireos characteristically clung to the hardware cloth tops of the cages and hung upside down for long periods.

Solid overcast prevailed through only one night. None of nine birds tested on this night was oriented.

The data from all individuals showing statistically significant nocturnal orientation (Rayleigh  $P \leq 0.05$ ) are presented in Table 3. The mean directions of nocturnal

TABLE 2  
SPECIES AND AGE COMPOSITION OF BIRDS TESTED IN ORIENTATION CAGES

| Species   | Number tested |        |           | No. of orienters |
|---|---------------|--------|-----------|------------------|
|   | Total no.     | Adults | Immatures |                  |
| Gray Catbird, <i>Dumetella carolinensis</i>           | 18            | 0      | 18        | 0                |
| Swainson's Thrush, <i>Catharus ustulatus</i>          | 2             | 0      | 2         | 0                |
| Gray-cheeked Thrush, <i>C. minimus</i>                | 2             | 0      | 2         | 0                |
| Veery, <i>C. fuscescens</i>                           | 1             | 0      | 1         | 1                |
| White-eyed Vireo, <i>Vireo griseus</i>                | 2             | 0      | 2         | 1                |
| Solitary Vireo, <i>V. solitarius</i>                  | 1             | 0      | 1         | 0                |
| Red-eyed Vireo, <i>V. olivaceus</i>                   | 17            | 0      | 17        | 6                |
| Philadelphia Vireo, <i>V. philadelphicus</i>          | 3             | 0      | 3         | 0                |
| Warbling Vireo, <i>V. gilvus</i>                      | 1             | 0      | 1         | 1                |
| Black and White Warbler, <i>Mniotilta varia</i>       | 1             | 0      | 1         | 1                |
| Magnolia Warbler, <i>Dendroica magnolia</i>           | 1             | 1      | 0         | 1                |
| Yellow-rumped Warbler, <i>D. coronata</i>             | 2             | 0      | 2         | 0                |
| Blackpoll Warbler, <i>D. striata</i>                  | 6             | 4      | 2         | 5                |
| Ovenbird, <i>Seiurus aurocapillus</i>                 | 1             | 0      | 1         | 1                |
| Northern Waterthrush, <i>S. noveboracensis</i>        | 4             | 0      | 4         | 2                |
| Common Yellowthroat, <i>Geothlypis trichas</i>        | 2             | 0      | 2         | 1                |
| Wilson's Warbler, <i>Wilsonia pusilla</i>             | 2             | 0      | 2         | 1                |
| American Redstart, <i>Setophaga ruticilla</i>         | 2             | 0      | 2         | 2                |
| Indigo Bunting, <i>Passerina cyanea</i>               | 1             | 0      | 1         | 0                |
| Dark-eyed Junco, <i>Junco hyemalis</i>                | 3             | 0      | 3         | 1                |
| White-throated Sparrow, <i>Zonotrichia albicollis</i> | 5             | 0      | 5         | 2                |
| White-crowned Sparrow, <i>Z. leucophrys</i>           | 1             | 0      | 1         | 0                |
| Lincoln's Sparrow, <i>Melospiza lincolnii</i>         | 1             | 0      | 1         | 0                |

TABLE 3  
PARAMETERS OF NOCTURNAL AND DIURNAL CAGE ORIENTATION FOR INDIVIDUALS THAT SHOWED  
STATISTICALLY SIGNIFICANT DIRECTIONALITY

|                         | Nocturnal orientation |      |                | Diurnal orientation |      |                |
|-------------------------|-----------------------|------|----------------|---------------------|------|----------------|
|                         | Mean dir.             | s    | Rayleigh $P^1$ | Mean dir.           | s    | Rayleigh $P^1$ |
| Veery                   | 337.5                 | 66.6 | 0.001          | 347.1               | 70.8 | 0.025          |
| White-eyed Vireo        | 330.5                 | 71.1 | 0.025          |                     |      |                |
| Red-eyed Vireo          | 352.9                 | 66.9 | 0.001          | 54.4                | 72.4 | 0.100          |
|                         | 136.9                 | 72.8 | 0.025          |                     |      |                |
|                         | 146.2                 | 73.6 | 0.050          |                     |      |                |
|                         | 312.7                 | 72.8 | 0.010          |                     |      |                |
|                         | 339.9                 | 72.0 | 0.050          |                     |      |                |
| Warbling Vireo          |                       |      |                | 60.7                | 62.7 | 0.001          |
| Black and White Warbler |                       |      |                | 28.9                | 65.6 | 0.010          |
| Magnolia Warbler        |                       |      |                | 58.2                | 71.7 | 0.100          |
| Blackpoll Warbler       |                       |      |                | 112.7               | 67.0 | 0.010          |
|                         | 0.6                   | 73.8 | 0.025          |                     |      |                |
|                         | 194.1                 | 67.2 | 0.050          |                     |      |                |
|                         | 3.4                   | 65.6 | 0.050          |                     |      |                |
|                         | 147.7                 | 55.2 | 0.001          |                     |      |                |
|                         | 207.4                 | 58.0 | 0.010          |                     |      |                |
| Ovenbird                | 168.7                 | 67.4 | 0.010          | 142.3               | 69.2 | 0.010          |
| Northern Waterthrush    | 292.9                 | 70.2 | 0.050          | 165.9               | 36.2 | 0.001          |
|                         | 293.4                 | 75.5 | 0.050          | 99.3                | 60.6 | 0.001          |
| Common Yellowthroat     | 71.9                  | 70.8 | 0.001          | 140.3               | 69.4 | 0.001          |
| Wilson's Warbler        |                       |      |                | 137.3               | 70.3 | 0.100          |
| American Redstart       | 272.4                 | 63.6 | 0.050          |                     |      |                |
|                         | 6.6                   | 69.7 | 0.001          |                     |      |                |
| Dark-eyed Junco         | 155.2                 | 67.9 | 0.010          |                     |      |                |
| White-throated Sparrow  | 332.9                 | 71.4 | 0.010          |                     |      |                |
|                         | 130.2                 | 73.6 | 0.050          |                     |      |                |

<sup>1</sup> Rayleigh statistic probability based on sample size corrected according to Emlen (1969). See Methods.

activity for each individual are plotted in Figure 1A. Excluding Blackpoll Warbler points, the distribution of mean activity vectors appears to be bimodal, with points concentrated in the northwest and southeast sectors. I tested the null hypothesis that this sample was drawn from a uniform distribution using Rao's test (Batschelet 1972), which is powerful when applied to multimodal cases. The distribution of mean orientation directions of the 17 birds differed significantly from uniform ( $U = 169.4$ ,  $P < 0.05$ ). The five points in the southeast quadrant are closely clustered around their mean direction of  $147.4^\circ$  ( $s = 13.6^\circ$ ,  $Z = 4.7$ ,  $P < 0.01$ ). More scatter existed among the 12 points in the north half of the circle, but if treated as a separate population, they are significantly oriented about their mean (mean =  $333.0^\circ$ ,  $s = 37.3^\circ$ ,  $Z = 7.5$ ,  $P < 0.001$ ). There is reason to hypothesize that two populations (in a statistical sense) exist based on their nocturnal orientation directions. Making this assumption, application of the Mardia-Watson-Wheeler two sample test (Batschelet 1972) shows that a significant difference exists between these two groups of sample points ( $P < 0.001$ ).

About twice as many individuals oriented toward the northwest as toward the southeast. Nonetheless the group of birds oriented southeastward consisted of five species tested on several nights and it seems unlikely that the observed distribution is an artifact. Apparently two nocturnal directional preferences exist among grounded fall migrants on Block Island.

Because Blackpoll Warblers are believed to embark on a southward transatlantic flight to South America (Nisbet 1970), I analyzed separately the small amount of data obtained from this species. Four of six Blackpolls tested showed significant nocturnal

TABLE 4  
RELATIONSHIP OF CAGE ORIENTATION TO AMOUNT OF SUBCUTANEOUS FAT DEPOSITS

|                        | Fat class |       |       |       |       |
|------------------------|-----------|-------|-------|-------|-------|
|                        | 0         | 1     | 2     | 3     | 4     |
| Number of nonorienters | 10        | 15    | 16    | 10    | 3     |
| Number of orienters    | 2         | 5     | 6     | 6     | 2     |
| Total individuals      | 12        | 20    | 22    | 16    | 5     |
| Proportion orienting   | 0.165     | 0.250 | 0.273 | 0.375 | 0.400 |

orientation (Fig. 1B). Three of these birds (two adults, one immature) oriented southward, while the fourth (an adult) showed a weak northward orientation. Although no conclusions can be drawn from such a small sample, most Blackpoll Warblers tested showed the predicted orientation direction, which differed from that of most of the other individuals tested.

Because a large portion of the northward exodus of nocturnal migrants from Block Island occurs during the early morning hours, I examined the behavior of orienting nocturnal migrants during the first hours of daylight. Of the 21 individuals that showed significant nocturnal orientation, 6 (32%) also exhibited a directional preference during the early morning. Five additional birds that failed to yield statistically significant nocturnal directionality did orient in daylight. The data on diurnal orientation are presented in Table 3, and the means are plotted in Figure 1C. With only one exception, the resultant vector of orientation for each of the 11 birds was in the eastward half of the circle. The distribution is significantly different from uniform ( $P < 0.025$ , Rayleigh test) and no difference exists between the directions chosen by individuals that showed significant orientation during the night and those that did not. A comparison of the nocturnal and diurnal orientation shows that most of the birds that showed oriented hopping both day and night shifted their orientation from northwestward to eastward or southeastward at dawn.

An eastward direction does not correspond with any observed diurnal migratory movement on Block Island, nor is it intuitively reasonable for numbers of birds to move eastward from New England. I think the most reasonable explanation for these results in orientation cages is that the activity of the birds was not the product of migratory motivation and that the observed direction was the result of a positive phototactic response to the sun. The results can be adequately explained as reflecting simple escape behavior.

*Zugunruhe, orientation, and subcutaneous fat.*—I tried to select the fattest available birds for orientation cage tests, but the limited numbers of birds available on some days forced me to use leaner individuals. I examined the relationship between the amount of migratory fat and the birds' cage behavior. I expected, *a priori*, that a positive relationship existed between the amount of subcutaneous fat and the intensity of migratory motivation of an individual bird. Thus it surprised me to find no correlation between the amount of nocturnal activity (based on the footprint records, quantified according to Emlen and Emlen 1966) and the visual fat classes of the migrants (Helms 1959). For the birds that showed significant orientation,  $r = -0.129$ ; for all birds combined,  $r = -0.088$ . Nor did the amount of nocturnal activity differ between orienters and nonorienters within a given fat class.

A significant relationship did exist between the amount of fat and the likelihood that a given individual would show oriented *Zugunruhe* during the night (Table 4).

The proportion of individuals that showed oriented *Zugunruhe* increased significantly with increases in subcutaneous fat deposits ( $\arcsin\sqrt{\text{proportion of orienters}} = 24.8 + 3.8 (\text{fat class})$ ,  $r = 0.979$ ,  $F = 68.3$ ,  $P < 0.001$ ). The proportion of orienters increased rather sharply between fat classes 2 and 3, suggesting a threshold of response in this relationship.

#### DISCUSSION

The absence of a correlation between *Zugunruhe* and the amount of depot fat in the birds I tested is contrary to prevailing theories on the relationship between energetics and migratory motivation (e.g. Dolnik and Blyumental 1967, Helms 1968, Evans 1968). Because my data were obtained from a number of species caught under special circumstances, other factors may have obscured the expected relationship. Some caution may be in order when quantitatively equating *Zugunruhe* with migratory motivation, even at the height of the migratory season. Oriented *Zugunruhe* has not generally been used, but may provide a much better indicator.

My field observations are in complete agreement with what is known of fall migration in southern New England (Baird and Nisbet 1960, Drury and Keith 1962, Drury and Nisbet 1964). Large migrations moved in southerly directions (between south-southeast and southwest) in generally following winds. During periods of opposing winds very little nocturnal migration occurred. Nearly all the migrants netted on Block Island thus originated on the mainland to the north. Although those birds arriving from the northwest may have experienced some southeastward drift, all the birds showed a basically southward orientation during the flight and brought them to the island.

After arriving from the mainland, migrants left by day from the northern end of the island, as described by Baird and Nisbet (1960). On two occasions nocturnal northward migrations occurred, both times on the night following a major southward flight and the arrival of numbers of migrants. The important question arises whether these reversed nocturnal flights represented the same type of reoriented movement seen during the day. I cannot be certain that they do. In both cases winds had shifted back to southerly during the day preceding the reversed flights, so the birds were not leaving for the mainland into a head wind as is often the case in the early morning flights. I believe it reasonable to hypothesize that these were reoriented flights on the following bases: (1) The flights occurred immediately following a large southward migration; (2) they occurred in very light and variable winds, rather than in a strong southerly air flow when broad front reversed migrations are most likely to occur (Drury and Keith 1962, Drury and Nisbet 1964, Nisbet and Drury 1968); (3) the temporal pattern of the movements indicated that the birds initiated migration on Block Island; (4) Baird and Nisbet (1960) described a northward nocturnal movement in opposing winds following a large southward flight on the previous night.

The majority of birds in orientation cages headed northwesterly at night, probably in a cage analog of the reoriented northward flights performed by free-flying birds. The birds are capable of selecting the reorientation direction on the basis of cues available in an orientation cage. This does not mean that the process of reorientation occurred in the cages or was based only on cues available to the birds while in the orientation cages. The integration of information leading to the reorientation may have occurred prior to the birds' capture, either during the flight that carried them

offshore or on the island itself. The results presented here support the conclusion that this information can at least be transferred to a cue system available to the birds in funnel cages. The failure of birds to orient under overcast skies suggests that stellar cues were of primary importance.

Some individuals oriented toward the south. This is the expected direction for Blackpoll Warblers based on Nisbet's (1970) hypothesis. The several other species that showed southward nocturnal orientation are not believed to make long overwater flights from New England. These birds may represent a portion of the migrant population that is unable to correct for displacement, although other explanations are possible.

Because most of the northward departure of migrants apparently occurs during the day, I predicted that birds showing nocturnal orientation might continue to show oriented hopping after dawn. The observed orientation after sunrise is not readily explicable in a migratory context. It is most suggestive of a phototactic response. In part this may be an artifact of the type of cage used. The funnel cages allow the birds to see the sun continuously once it is high enough in the sky. Wiltschko and Höck (1972) reported that the directions selected by European Robins (*Erithacus rubecula*) during early morning hours corresponded to the migratory direction, but only when the same individuals showed oriented restlessness during the previous night. Their cages precluded direct sight of the sun and birds in these cages do not orient consistently toward either the sun or moon even when these are directly visible to them (Wiltschko, pers. comm.).

Few other empirical data exist with which my results can be compared directly. Evans (1968) obtained orientation cage and band recovery data from Scandinavian migrants presumably drifted to the coast of northeastern Britain. The majority of birds (most were juveniles) oriented between southeast and south, eastward from their presumed normal migratory heading prior to drift. If the normal migratory heading was toward the south-southwest (cf. Nisbet 1969, Rabøl 1969), they seem to have reoriented in a direction that would intersect their normal migratory route north of the wintering area. The directions chosen by Evans' birds were very similar to the main reorientation direction noted on radars around the British Isles (data from a variety of places summarized by Myres 1964).

Based on several series of artificial displacement experiments with sylviid warblers, Rabøl (1969, 1970, 1972) proposed a migratory navigation system based on a hypothetical "goal area" that moves in space along the migratory route of the species in a time-programmed manner. Based on this hypothesis, the goal area (*sensu* Rabøl) of a bird drifted offshore from New England could conceivably lie to the northwest or north. Indeed Rabøl (1969) interpreted the observations of Baird and Nisbet (1960) in support of his hypothesis.

Three explanations are possible for the observations described in this paper, by Evans (1968) and by Rabøl (1969, 1970, 1972): (1) The birds may recognize the geographical displacement and employ navigation (Type III orientation) to recover the normal migration route or reach the migratory goal, as Evans proposed; (2) the birds may navigate toward an intermediate goal area as postulated by Rabøl; and (3) the birds may make an automatic response that will reorient them toward land should they find themselves over the ocean.

The classic studies of Perdeck (1958, 1967) indicated that juvenile birds making their first autumn migration employed only compass direction and distance components. In contrast to adults, they seemed unable to compensate for longitudinal



displacements. Similar results have been obtained with nonpasserine species (Bellrose 1958), but both Evans (1968) and Rabøl (1969, 1970, 1972) interpreted data from immature birds as supporting navigation at least back toward the normal route of migration.

Data from both free-flying migrants and birds tested in orientation cages show that some immature migrants reaching Block Island are capable of reorienting in a proper direction to correct for a departure from normal routes of migration. If a navigational response is involved, immature birds must be able to perform it in flight over the sea well out of sight of land (Baird and Nisbet 1960, Richardson 1972, Ferren pers. comm.). I believe all the currently available data on these migrants can be explained by a simple compass-based reorientation. It seems premature to attribute navigational ability to immature fall migrants, either in North America or in Europe.

A nocturnal migrant from an eastern North American breeding population finding itself over the ocean at dawn could most easily recover the coast by flying northwestward. Southwestward or westward flight would often be less reliable or involve greater distance because of the orientation of the coastline, especially south of New England. Substantial evidence summarized by Baird and Nisbet (1960) indicates that the migratory goals of the birds displaced to Block Island lie to the southwest. Birds could depart in that direction and reach Long Island, New York via an overwater flight of ca. 24.5 km, only ca. 9 km further than the distance to the mainland to the north. Both are visible from Block Island on clear days and a southwestward flight would often be accompanied by at least partially following winds, but neither free-flying birds nor orientation cage subjects oriented in that direction.

As offshore drift occurs frequently one would expect natural selection to have established a more or less automatic northwestward reorientation response. The occurrence of this kind of reorientation could be accomplished by simple compass orientation (see also Emlen 1975). It is probably not coincidental that a similar response occurs among unrelated species on the eastern side of the Atlantic and that the reorientation directions observed there are again such as to return the drifted migrants to a coast over the shortest possible distance (Myres 1964). Vagrant migrants pass over the Farallon Islands, California, in a northeasterly direction following morning reorientation over the sea southwest of the island. Immature Blackpoll Warblers captured on the island also tended to orient in that direction in funnel orientation cages (DeSante 1973). That a simple reorientation mechanism of this type may be of widespread occurrence is suggested by observations of migratory bats (probably *Lasiurus borealis*) and Monarch Butterflies (*Danaus plexippus*) flying northwest into the wind 90 km off the Rhode Island coast in autumn (Ferren pers. comm.).

The preponderance of immatures among grounded nocturnal migrants near the Atlantic and Pacific coasts has been well documented (Baird and Nisbet 1960, Nisbet et al. 1963, Murray 1966, Ralph 1971). Ralph (1971) summarized various hypotheses to account for this phenomenon and concluded that genetically induced navigational errors were the most likely explanation for it. As adult birds are rare near the coast, most of the immatures flying offshore must either perish or learn something that enables them to avoid the coastal belt during subsequent autumn migrations.

The distributions of adult and immature migrants clearly indicate some difference in the migration of these two age classes. Several causes are possible. Although most of the birds reaching the islands offshore from New England have flown on tracks from the north or northwest, they may be substantially drifted (Baird and Nisbet

1960, Able 1974). Thus the heading directions of adults and immatures could be the same, but immatures might be less able to recognize or to correct for lateral drift in flight. Alternatively, adults might be more selective of the weather conditions for starting migration and thereby avoid winds most likely to drift them offshore. No data now exist to distinguish between the several alternatives. The fact that migrants fly offshore does not necessarily imply that they have faulty basic orientation mechanisms. Evans' (1968) data and the results described here imply that at least some of these inexperienced birds recognize and correct for offshore drift.

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