

# REORIENTATION OF NOCTURNAL LANDBIRD MIGRANTS OVER THE ATLANTIC OCEAN NEAR NOVA SCOTIA IN AUTUMN

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**ABSTRACT.**—The behavior of landbirds involved in the predominating SSW-W migration over and near Nova Scotia during autumn nights was studied by radar. Takeoff began  $28 \pm 5$  min after sunset. Many landbirds flew from Newfoundland across Cabot Strait to Nova Scotia and from western Nova Scotia across the Gulf of Maine toward New England. Contrary to most previous night observations, some changed course to reach land or to avoid moving offshore. However, many crossed coasts at right or acute angles without hesitation or turning. Landbirds moved offshore on nights with offshore, alongshore, and even onshore winds. Landbirds flying SSW-W over the sea late in the night sometimes ascended and/or reoriented WNW-NNE toward land, especially when winds were unfavorable for continued SW flight and/or favorable for flight to the NW. Reoriented birds usually continued to arrive at the coast until noon, but the density of arrival declined steadily through the morning. Indirect but strong evidence indicates that directional cues additional to sight of land were often used for reorientation. No evidence of dawn reorientation by landbirds flying SE-SSW toward the West Indies was found. *Received 15 November 1977, accepted 9 April 1978.*

LANDBIRDS that normally migrate at night often occur over the western Atlantic Ocean during autumn days (Scholander 1955). Three groups are distinguishable. First, many migrants that fly SW or WSW from near-coastal areas move offshore (Fig. 1) and are 200+ km from land at dawn. Second, some landbirds migrate south from New England and Nova Scotia to the West Indies and South America (Drury and Keith 1962; Drury and Nisbet 1964; Richardson 1972a, 1976; Ireland and Williams 1974; Williams et al. 1977). The Blackpoll Warbler (*Dendroica striata*) is the only species of landbird convincingly shown to follow this route (Nisbet et al. 1963, Nisbet 1970, Ralph 1975), but it cannot be the only species involved (Murray 1965). Third, landbirds of species that rarely migrate successfully over the ocean are often found far at sea, at Bermuda (Wingate 1973) and even in Europe (Alexander and Fitter 1955, Sharrock 1974)—often after periods of offshore winds. These birds may be windblown vagrants and/or individuals with maladaptive orientation systems (Ralph 1975).

Landbirds considered to be nocturnal migrants are often seen on autumn mornings flying NW and N toward land and up to 160 km inland (Bagg and Emery 1960, Baird and Nisbet 1960, Able 1977), usually with NW headwinds. It has been suggested that migrants are often drifted offshore by NW crosswinds at night, change direction ('reorient') at dawn, and then fly NW or N toward land (Stone 1937, Bagg and Emery 1960, Baird and Nisbet 1960).

Dawn reorientation also appears to occur in autumn over the Pacific Ocean off California (DeSante 1973) and over the northern Gulf of Mexico (Hebrard 1972), and is well known east and north of Britain (Lack 1963, Lee 1963, Myres 1964, Wilcock 1965). These British birds may also ascend at dawn, and ascent sometimes occurs without reorientation (Lee 1963).

Dawn reorientation was not found during radar studies at Cape Cod (Drury and Keith 1962), but was evident on Nova Scotian radars (Richardson 1972a). This

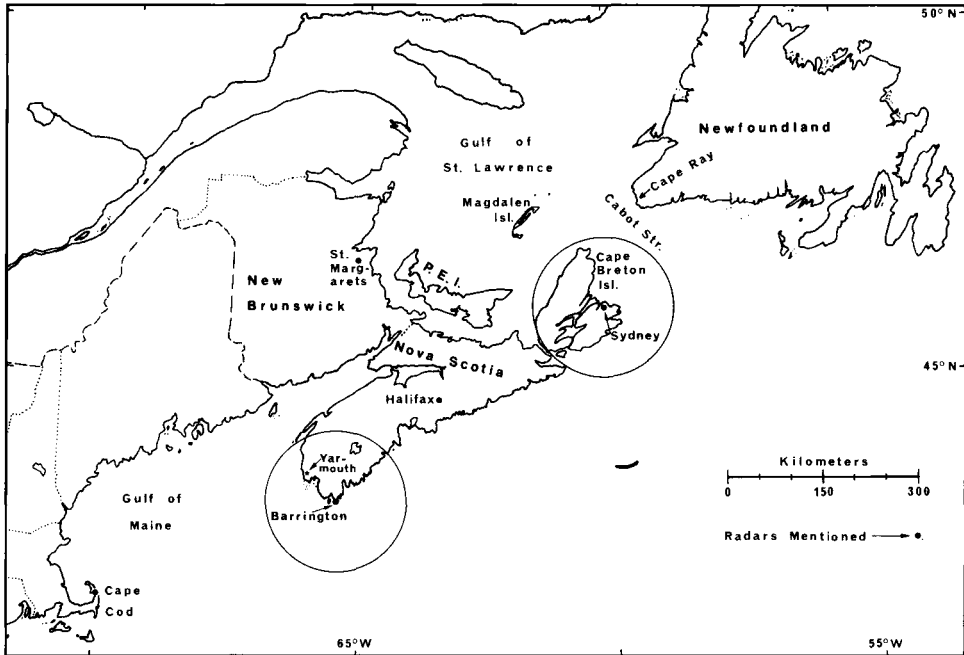


Fig. 1. Study areas and areas mentioned in text. Circles demark the approximate coverage areas of the radars used (radius 60 nautical miles = 111 km).

paper analyzes the Nova Scotia data, with emphasis on characteristics of the nocturnal movements preceding reorientation, timing of onset and duration of reoriented flight, weather accompanying reorientation, and occurrence of dawn ascent.

#### METHODS

Military surveillance radars near Sydney ( $46^{\circ}10'N$ ,  $60^{\circ}10'W$ ) and Barrington ( $43^{\circ}27'N$ ,  $65^{\circ}28'W$ ), Nova Scotia, were used (Fig. 1); specifications and performance cannot be published. Continuous 16 mm time-lapse films of PPI displays were obtained with display radius 110–130 km (210 km in 1970 at Sydney). Data were obtained from Sydney on 60 nights between 1 September and 10 November 1965 and on 17 nights between 13 August and 27 September 1970; from Barrington on 54 nights between 1 September and 19 November 1970 and 81 nights between 20 August and 16 November 1971. Data from Sydney in 1970 and from Barrington in October 1970 were of limited value because specialized circuitry severely suppressed bird echoes. At other times 'raw video' (Richardson 1972b) was used. With raw video, overwater movements were reliably recorded but overland movements were partially obscured by ground echoes, especially at Sydney. Figure 2 shows representative frames, but bird echoes were much more distinct on time-lapse film, where their motion was evident.

Densities and tracks were abstracted from films as in Richardson (1976). In brief, density was recorded on a 0 to 8 ordinal scale eight times every 24 h—at  $1\frac{1}{2}$  h before and 1, 4, and 7 h after sunset and sunrise. Tracks of individual echoes were traced six times every 24 h—at  $1\frac{1}{2}$  h before and 1 and 7 h after sunset and sunrise (8–86 echoes at each time; mean  $n = 36$ ). Henceforth such times are abbreviated SS -  $1\frac{1}{2}$ , SR + 7, etc. Densities and tracks were recorded separately for four movement types: SE shorebird; NE reverse; SW and S landbird. A minority of landbird echoes sometimes moved SSW, so the last two types were sometimes not totally separable.

A nodding height finder radar was used at Sydney on one night (17–18 September 1970) when SW movement and reorientation occurred. The altitude span of the mass of unresolved echoes from landbirds was determined directly from the RHI display.

Landbirds were recognized on all radars by their weak, slow-moving echoes and high density. Only

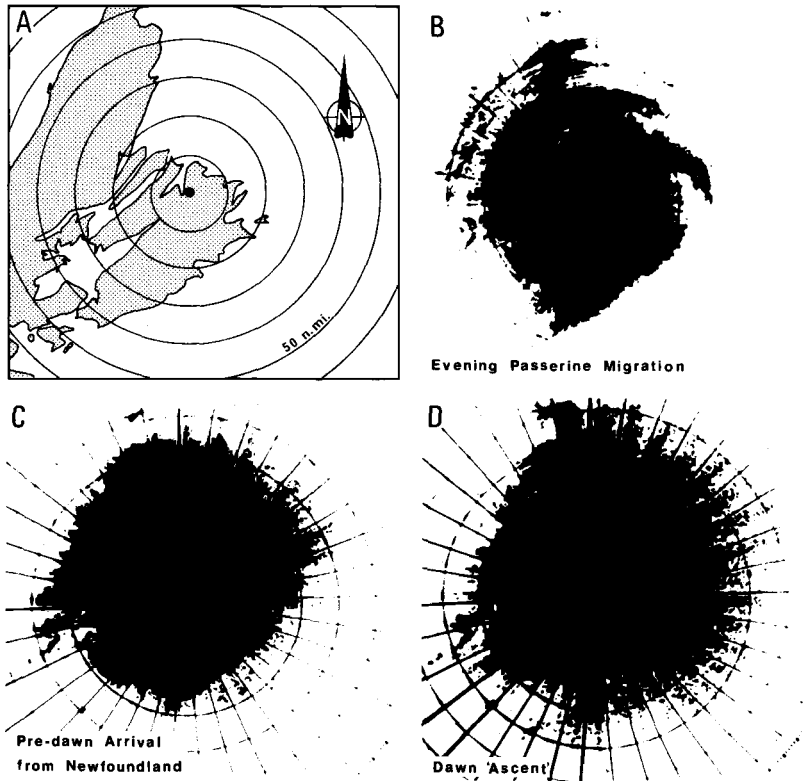


Fig. 2. Sydney, N.S. radar display. Negative film was used so echoes are dark on light background. Range rings at 10 n. mi. (18.5 km) intervals. **A.** Map of radar coverage area. **B.** Evening departure of landbirds to SW, 1 h after sunset on 19 September 1965. **C, D.** Landbirds from Newfoundland moving WSW over ocean NE of radar,  $\frac{3}{4}$  h before sunrise (C) and at sunrise (D) on 14 September 1965. Note increased echo prominence and range of detectability in D.

movements with peak density  $\geq 5$  are considered. The data presented undoubtedly include some waterbirds flying SW, but waterbirds rarely reached density 5 and when they did were conspicuous by their intense and usually fast-moving echoes. Shorebirds flying SE were readily identified by their echo characteristics (Richardson 1979). Thus almost all birds within all movements considered were small landbirds.

Surface weather data were from official records for Sydney and Yarmouth. No radiosonde data were available, so geostrophic winds were used as indicators of winds aloft. K indices of magnetic disturbance (0 to 9 scale; 3 h intervals) were obtained from stations in Ontario—Agincourt in 1965 and Ottawa in 1969–71.

## RESULTS

Both radars commonly recorded dense SW migration of landbirds at night, their presence over the sea at dawn, and occasional increases in echo prominence and/or reorientation to the NW before dawn. The behavior at dawn of different birds flying SW was, on most days, more consistent near Sydney than near Barrington. Only at Sydney were reoriented flights sufficiently distinct from non-reoriented flights to warrant detailed analysis. SW movement of landbirds continued at reduced density into November, but during November was sometimes difficult to distinguish from waterbird movements. Hence only the data collected before 1 November are considered.

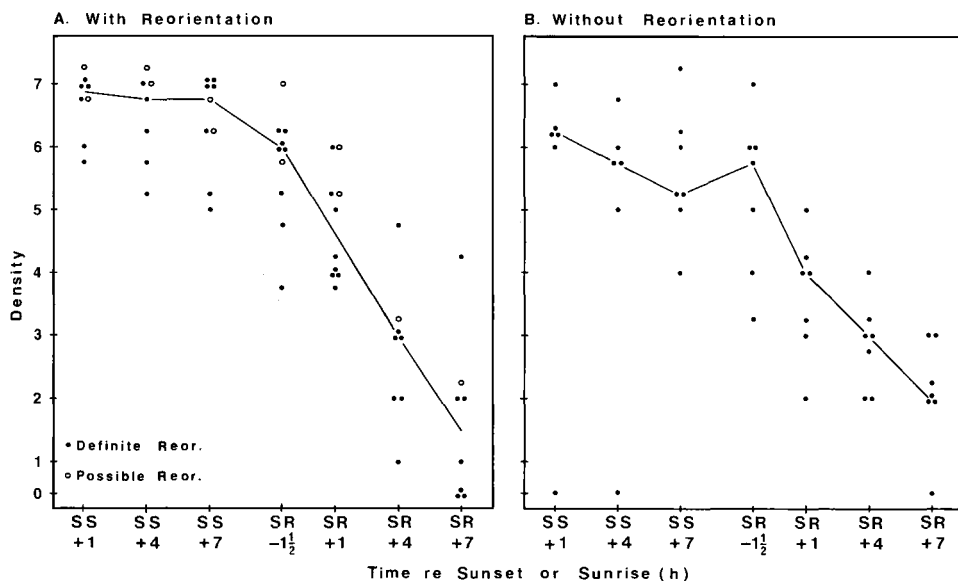


Fig. 3. Hour-to-hour variation in the density of SSW-W and reoriented NW migration near Sydney, N.S. on autumn nights. Each point represents the density on the 0-8 ordinal scale (see Methods) at one time on one date. The line shows the median density at the various times. Nights with no movement or no radar record around sunrise are omitted.

*Nocturnal SW movement at Sydney.*—Substantial SW movements of landbirds (density 5+) were detected near Sydney during 27 nights. Birds first appeared over Cape Breton Island 20-37 min after sunset ( $\bar{x} = 28$ ,  $SD = 5$ ,  $n = 16$ ). By 1 h after sunset (SS + 1) their density had usually reached the peak achieved all night (Fig. 3).

Between SS + 2 and SS + 3 birds from SW Newfoundland became visible over Cabot Strait N-NE of Sydney. Such birds approached Cape Breton Island on a broad front, reached land, and continued SW-WSW overland toward mainland Nova Scotia. Late in the night, however, some flew SW parallel to and 0-35 km offshore from the SE coast of the island. Most of these birds approached from the direction of south-central Newfoundland, but some may have come from SE Newfoundland.

After midnight during several nights (e.g. 1, 12, 22, 23 October 1965) there was dense movement of landbirds from Newfoundland over southern Cape Breton Island and virtually none a few km to the SE over the sea. Since these birds had flown over water from Newfoundland and since there was always considerable variance among tracks of different individuals over the sea (see below), the sharp edge of the dense movement at the coast could only have resulted if some birds changed course in order to congregate and/or to remain overland.

On the nights of 21-22 and 24-25 September 1965, dense SW-WSW landbird movements were detected over the Gulf of St. Lawrence west of Cape Ray—up to 185 km north of Sydney (Fig. 1). Most of these birds were flying toward the Magdalen Islands and Prince Edward Island, not toward Cape Breton Island. A radar at St. Margarets, N.B. often shows birds approaching from the direction of the Magdalens and Newfoundland in autumn (Richardson 1975). Thus some landbirds

TABLE 1. Tracks of landbirds involved in dense SW movements near Sydney, N.S.

| Parameter                            | SS + 1 <sup>a</sup> | SS + 7  | SR - 1½ | SR + 1  |
|--------------------------------------|---------------------|---------|---------|---------|
| <b>A. Nightly mean tracks</b>        |                     |         |         |         |
| Vector mean                          | 228.7°              | 236.0°  | 244.9°  | 260.7°  |
| Angular deviation                    | 12.7                | 11.4    | 21.9    | 35.2    |
| Range                                | 203-261             | 215-254 | 221-309 | 215-331 |
| Pairwise comparison <sup>b</sup>     | *                   |         | *       | **      |
| <b>B. Nightly angular deviations</b> |                     |         |         |         |
| Mean                                 | 15.4°               | 13.4°   | 14.6°   | 22.8°   |
| Standard deviation                   | 3.6                 | 4.3     | 5.0     | 4.8     |
| Range                                | 10-24               | 6-22    | 7-25    | 16-33   |
| Pairwise comparison <sup>b</sup>     | **                  |         | ns      | **      |
| No. dates with measurable tracks     | 20                  | 20      | 17      | 16      |

<sup>a</sup> Times are given in hours before (-) or after (+) sunrise (SR) or sunset (SS)  
<sup>b</sup> Pairwise comparison of successive means (i.e. SS + 1 vs SS + 7, SS + 7 vs SR - 1½, SR - 1½ vs SR + 1) using Student's *t*-test. In this and other tables ns means  $P > 0.1$ , (\*) means  $0.1 \geq P > 0.05$ , \* means  $0.05 \geq P > 0.01$ , \*\* means  $0.01 \geq P > 0.001$ , and \*\*\* means  $P \leq 0.001$

from Newfoundland do not use the relatively short water crossing from SW Newfoundland to Cape Breton Island.

On the 16 nights when high-density SW-WSW movement was known to occur throughout the night, densities of arrival from Newfoundland at SS + 7 and especially at SR - 1½ were significantly ( $P < 0.05$ ) lower than densities of departure from Cape Breton Island at SS + 1 (Wilcoxon matched-pairs tests). The SW-WSW movement disappeared before sunrise on five other nights. On 21-22 October 1965 the SW movement did not begin until a cold front passed around midnight and the wind shifted from SW to NW.

The mean of the nightly mean tracks was 229° at SS + 1 and 236° at SS + 7 (Table 1A). These values represent birds that had taken off from Cape Breton Island and

TABLE 2. Dates and times of reorientation and 'ascent' near Sydney, N.S.

| Date   | Reorientation began <sup>a</sup> |            | Ascent began <sup>a</sup> |                     |
|--|----------------------------------|------------|---------------------------|---------------------|
|  | AST                              | re Sunrise | AST                       | re Sunrise          |
| <b>A. Mornings without reorientation<sup>b</sup></b> |                                  |            |                           |                     |
| 4 September 1965                                     | -                                | -          | 0510                      | SR - ¼ <sup>c</sup> |
| 5 September 1965                                     | -                                | -          | 0430                      | SR - 1 <sup>c</sup> |
| 6 September 1965                                     | -                                | -          | -                         | -                   |
| 9 September 1965                                     | -                                | -          | 0510                      | SR - ¼ <sup>c</sup> |
| 19 September 1965                                    | -                                | -          | Time uncertain            |                     |
| 20 October 1965                                      | -                                | -          | -                         | -                   |
| 22 October 1965                                      | -                                | -          | -                         | -                   |
| <b>B. Mornings with reorientation</b>                |                                  |            |                           |                     |
| 10 September 1965                                    | 0515                             | SR - ¼     | 0510                      | SR - ¼              |
| 15 September 1965                                    | 0330                             | SR - 2     | 0505                      | SR - ½              |
| 1 October 1965                                       | by 0515                          | SR - ¾     | 0520                      | SR - ¾ <sup>c</sup> |
| 12 October 1965                                      | by 0530                          | SR - ¾     | 0545                      | SR - ½              |
| 19 October 1965                                      | by 0600                          | SR - ½     | Occurrence uncertain      |                     |
| 21 October 1965                                      | 0230                             | SR - 4     | 0545                      | SR - ¾              |
| 23 October 1965                                      | 0330                             | SR - 3     | -                         | -                   |
| 18 September 1970                                    | 0400                             | SR - 1¾    | 0515                      | SR - ½              |
| <b>C. Possible reorientation</b>                     |                                  |            |                           |                     |
| 14 September 1965                                    | Partial and gradual              |            | 0500                      | SR - ½              |
| 18 October 1965                                      | Occurrence uncertain             |            | Occurrence uncertain      |                     |

<sup>a</sup> Times in Atlantic Standard Time (AST) and in hours before sunrise (SR)  
<sup>b</sup> Only days when SW-W landbird movement over the sea continued until dawn are considered  
<sup>c</sup> Only a slight increase in prominence on this date

TABLE 3. Tracks of landbirds migrating generally SW near Sydney, N.S., on occasions with and without reorientation

| Parameter                        | SS + 7 | SR - 1½ | SR + 1 | SR + 7             |
|----------------------------------|--------|---------|--------|--------------------|
| A. Without reorientation         | n = 6  | n = 7   | n = 7  | n = 4 <sup>b</sup> |
| 1. Daily mean track              |        |         |        |                    |
| Vector mean                      | 222.7  | 226.9   | 226.1  | 226.5              |
| Angular deviation                | 5.0    | 3.8     | 7.4    | 6.5                |
| Pairwise comparison <sup>a</sup> |        | (*)     | ns     | ns                 |
| 2. Daily angular deviation       |        |         |        |                    |
| Mean                             | 12.7   | 13.4    | 21.6   | 22.3               |
| Standard deviation               | 5.3    | 4.5     | 3.3    | 3.9                |
| Pairwise comparison <sup>a</sup> |        | ns      | **     | ns                 |
| B. With reorientation            | n = 7  | n = 8   | n = 8  | n = 1 <sup>b</sup> |
| 1. Daily mean track              |        |         |        |                    |
| Vector mean                      | 245.6  | 263.5   | 294.7  | 308.0              |
| Angular deviation                | 7.4    | 19.4    | 18.0   | —                  |
| Pairwise comparison <sup>a</sup> |        | *       | ***    | —                  |
| 2. Daily angular deviation       |        |         |        |                    |
| Mean                             | 13.6   | 15.3    | 24.3   | 13.0               |
| Standard deviation               | 4.4    | 6.0     | 6.0    | —                  |
| Pairwise comparison <sup>a</sup> |        | ns      | (*)    | —                  |

<sup>a</sup> Pairwise comparison of successive means, as in Table 1

<sup>b</sup> Tracks not measurable on other days

Newfoundland, respectively. Mean tracks varied considerably from night to night (Table 1A) and were strongly correlated with the crosswind component of the surface wind both at SS + 1 ( $r = 0.582$ ,  $n = 20$ , one-sided  $P < 0.01$ ) and at SS + 7 ( $r = 0.712$ ,  $n = 20$ ,  $P < 0.001$ ). The mean track was usually ~WSW with a strong SE component and SSW-SW with a strong NW component. Similarly, the mean track at SS + 7 averaged  $228.4 \pm 9.0^\circ$  (vector mean  $\pm$  angular deviation,  $n = 7$ ) when the geostrophic wind was from the birds' right and  $243.3 \pm 8.5^\circ$  ( $n = 7$ ) when it was opposing or from the birds' left. These values are significantly different ( $F$ -test of Batschelet 1965,  $P < 0.025$ ). The modest size of this difference suggests at least partial compensation for lateral wind drift. Partial compensation and 'pseudodrift' were indistinguishable, however, because of inadequate data on winds aloft. Most of the birds considered were over the sea, so partial compensation might be expected (Alerstam and Pettersson 1976).

I found no relationship between mean track and magnetic disturbance. Their partial correlation was only 0.043 at SS + 1 and 0.055 at SS + 7 ( $n = 20$  and  $P \gg 0.1$  at each time) after I accounted for the confounding effects of crosswinds and (at SS + 1) date.

Tracks of birds aloft simultaneously were significantly less variable at SS + 7 than at SS + 1 (Table 1B), probably for geographical reasons (Fig. 1). However, at SS + 7 as well as SS + 1 variation among tracks of birds participating in the dense 'SW' movements was considerable; angular deviations ranged from  $6^\circ$  to  $24^\circ$  and a few individual echoes flew on tracks as extreme as S and WNW (but not concurrently).

*Reorientation at Sydney.*—On 17 nights at Sydney, substantial SW-W landbird movement continued until dawn. Birds over water E and SE of Cape Breton Island on these occasions remained aloft after dawn.

On seven mornings (Table 2A) mean tracks over the sea at SR + 1 were little changed from SS + 7 and SR - 1½ (Table 3A). The variance among individual

tracks was, however, higher at SR + 1. As at night, many birds reached Cape Breton Island and others continued SW parallel to and offshore from the SE coast. On 6 of 7 days, small numbers of birds still flew SW over the sea at SR + 7 (Fig. 3B). Birds flying SW offshore at SR + 1 were clearly nocturnal landbird migrants that had been offshore at dawn, since they were  $>1\frac{1}{2}$  flight-hours from Newfoundland. Most of those detected at and after SR + 4 had presumably left Newfoundland after sunrise and may have been typical diurnal migrants that took off around sunrise.

On eight dates (Table 2B) most or all landbirds over the sea late in the night changed direction and flew on new straight tracks toward the W, NW, and N on a broad front. For mean tracks, see Table 3B. Reorientation was usually rapid and simultaneous over all offshore areas within range. On six of eight mornings mean tracks changed little from SS + 7 to SR - 2, but by SR and particularly by SR + 1 had changed markedly. On the other two occasions reorientation began earlier: (i) on 20–21 October 1965 the mean track was  $\sim$ WSW after midnight—by 0230 (SR - 4) a few birds flew WNW, and by SR -  $1\frac{1}{2}$  the mean track was  $309 \pm 25^\circ$ ; and (ii) on 22–23 October 1965 a few birds flew WNW as early as 0330 (SR - 3) but most flew WSW-W as late as SR -  $1\frac{1}{2}$ , and reoriented to  $290 \pm 20^\circ$  by SR + 1. These two nights with early reorientation were also the two nights with the strongest SE component in the surface wind.

Many reoriented birds reached the E or SE coasts of Cape Breton Island—some before but most after sunrise. Ground echoes hid most birds once they reached the coast, but at least a few continued inland on reoriented courses for at least a few km. Other reoriented birds flew NW from the Atlantic Ocean into Cabot Strait and toward the Gulf of St. Lawrence. These birds would not have reached either Cape Breton Island or SW Newfoundland without a further course change. It was rarely possible to follow them past northern Cape Breton Island, and some may have changed course to the W or SW toward land after they were beyond radar range.

Reoriented movement continued beyond SR + 4 on 7 of 7 mornings with data and beyond SR + 7 on 4 of 7 mornings. However, the density declined steadily throughout this period (Fig. 3A). Birds detected at and after SR + 4 had moved into radar range after the time of reorientation, and in most cases after sunrise. Thus there was no direct evidence of reorientation by birds that approached land in late morning or early afternoon. Two facts indicate, however, that most of the birds approaching from the SE after as well as before SE + 4 were nocturnal migrants that had reoriented before sunrise while far from land. First, there is no land in the directions from which they were flying, so they were not diurnal landbird migrants that took off around sunrise. And second, the broad-front approach occurred continuously from the time of reorientation with no obvious change in echo characteristics between sunrise and SR + 4 or SR + 7. The decrease in density of arrival from the SE as the morning progressed is consistent with probable takeoff locations, observed flight directions, and ground speeds. Birds that flew SW from extreme eastern Newfoundland for 11 h at 45 km/h and then reoriented NW at SR -  $\frac{1}{2}$  would reach eastern Cape Breton Island at SR + 6.

On certain evenings large numbers of landbirds flew SE-SSW out over the ocean from Nova Scotia (Richardson in press). Few departed SE-SSW late in the night, so such birds were generally all far offshore and beyond radar range at dawn. I saw no evidence of a reoriented return to land during days following such departures.

TABLE 4. Conditions at sunrise with pronounced, minor, and no 'ascent' near Sydney, N.S.<sup>a</sup>

| Parameter (scale)                        | Pronounced<br>'ascent'<br>(n = 7) | Minor<br>'ascent'<br>(n = 4) | No<br>'ascent'<br>(n = 4) | P <sup>b</sup> |
|--|-----------------------------------|------------------------------|---------------------------|----------------|
| NE-SW wind component (km/h) <sup>c</sup> | -8.0 ± 13.1                       | 9.5 ± 11.2                   | 5.0 ± 5.2                 | *              |
| SE-NW wind component (km/h) <sup>d</sup> | 0.0 ± 7.9                         | -17.6 ± 11.7                 | -4.1 ± 17.1               | (*)            |
| Opacity (tenths)                         | 5.3 ± 3.7                         | 3.0 ± 2.9                    | 5.8 ± 4.9                 | ns             |
| K index at 0500-0800 (0-9)               | 1.1 ± 0.7                         | 1.3 ± 1.3                    | 2.0 ± 1.2                 | ns             |

<sup>a</sup> Values given are means ± SD. Only days when landbird movement over the sea continued until dawn are considered

<sup>b</sup> Kruskal-Wallis tests; \* means  $P \leq 0.05$ , (\*) means  $0.1 \geq P > 0.05$ , ns means  $P > 0.1$

<sup>c</sup> NE-SW component of surface wind at sunrise, NE +ve and SW -ve

<sup>d</sup> SE-NW component of surface wind at sunrise, SE +ve and NW -ve

These birds were presumably beginning non-stop flights to the West Indies or South America (Richardson 1976, Williams et al. 1977).

'Dawn ascent' at Sydney.—Landbird echoes over the sea near Sydney became more prominent on some but not all mornings. Increased prominence usually involved both increased intensity of typical echoes and an increase of 20–35 km in detection range (e.g. Fig. 2). Landbirds from Newfoundland were detectable late on 17 nights. Their prominence increased markedly on 7 mornings, slightly on 4, and nil on 4; on 2 mornings results were unclear. Increased prominence, if it occurred, began between SR - 1 and SR - ¼ (Table 2). When the increase was pronounced, maximum prominence was reached 20–45 min after the onset. Unlike results from the North Sea (cf. Myres 1964), on nights when landbirds over the sea disappeared late in the night they never reappeared around dawn.

Increased prominence of echoes at dawn might result either from ascent or from aggregation of birds into larger and/or more tightly-organized flocks. However, on one occasion with increased echo prominence (18 September 1970) heights were measured. Before midnight the densest concentration was below 750 m ASL, with many to 1,400 m and very few above 2,000 m. At 100, 70, and 40 min before sunrise, birds over the sea were low, with modal height ~150 m, few >750 m and none >1,400 m. By SR - 10 min the proportion at 750–1,800 m had increased, and by SR + 5 min there was a dense concentration at 0–600 m, many up to 1,800 m, and a few to 2,750 m. Many of the highest echoes moved SW-NNW. The increased proportion at moderate altitudes extended at least to 90 km offshore. On this same morning landbird prominence on the search radar display began to increase at SR - 25 min and reached a maximum at SR + 20 min. Thus increased prominence around dawn at least sometimes represented a real ascent. Whether aggregation also contributed to increased prominence could not be determined.

I attempted to identify behavioral and environmental parameters related to occurrence of ascent. Strong ascent was commoner on days with than on days lacking reorientation (Table 2). Ascent was significantly ( $P < 0.05$ ) associated with surface winds having an opposing SW component (Table 4). Similarly, geostrophic winds were opposing (SSW-WNW) on 4 of 7 days with but on only 1 of 8 days lacking strong ascent. Because occurrence of reorientation was related to wind direction (see below) and occurrence of ascent was related to that of reorientation, it is uncertain whether wind directly affected occurrence of ascent. The four dates with no ascent were all early (6 September 1965) or late (20, 22, 23 October 1965) in the migration season. Dates without reorientation also tended to be early or late, so it is also



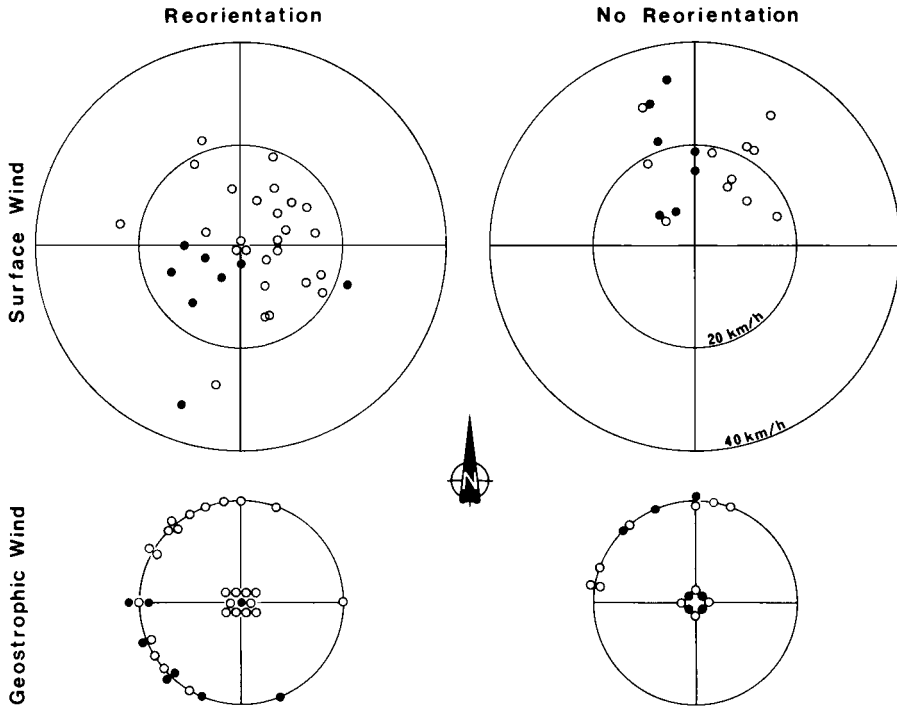


Fig. 4. Surface and geostrophic wind at sunrise on mornings when reorientation definitely did and definitely did not occur over the sea near Sydney (closed symbols) and Barrington (open symbols), Nova Scotia. Surface wind directions and speeds are plotted in polar co-ordinates. Geostrophic wind speeds were not estimated; symbols at centres of geostrophic diagrams represent indeterminate (generally light) winds aloft. Directions are those from which the wind blew.

uncertain whether date directly affected occurrence of ascent. The K index of *magnetic disturbance* and *cloudiness* were apparently unrelated to occurrence of ascent (Table 4). Precipitation, fog, low ceiling, and poor visibility were all too infrequent for effects on occurrence of ascent to be examined.

*Reorientation at Barrington.*—Many landbirds that took off from Nova Scotia about  $\frac{1}{2}$  h after sunset and flew SW-WSW crossed the coast at an acute angle during the night and were over water south of Nova Scotia at dawn. On 26 mornings in September–October of 1970–71 the Barrington radar showed definite reorientation by some or (rarely) all of these birds (dates in Richardson 1975: 649). On 11 other mornings they did not reorient. On other mornings with SW-W movement technical factors prevented me from determining whether reorientation occurred. Times and precise directions of reorientation, and also the occurrence of dawn ascent, often could not be determined reliably. When birds did reorient, they flew WNW-NNE and some continued inland on their reoriented tracks. The 26 definite cases of reorientation occurred from 2 September to 30 October. Probable cases were also noted in late August and until 7 November.

*Reorientation and weather.*—The occurrence of reorientation among landbirds migrating over the sea was significantly related to *wind* conditions. Reorientation to the NW or N was detected under a wide variety of surface and geostrophic wind directions. When the birds continued SW-W without reorienting, the winds were

TABLE 5. Conditions at sunrise on dates when reorientation definitely did and definitely did not occur near Sydney and Barrington, N.S.<sup>a</sup>

| Parameter (scale)                           | Area | Definite reorientation |       | No reorientation  |      | Significance          |                     |
|---|------|------------------------|-------|-------------------|------|-----------------------|---------------------|
|   |      | Mean                   | SD    | Mean              | SD   | One area <sup>b</sup> | Pooled <sup>c</sup> |
| NE-SW wind component <sup>d</sup><br>(km/h) | Syd. | -9.17                  | 11.28 | 9.39              | 6.82 | **                    | ***                 |
|   | Bar. | 3.39                   | 8.91  | 14.39             | 7.94 | **                    |                     |
| SE-NW wind component<br>(km/h)              | Syd. | 2.85                   | 9.73  | -16.32            | 8.42 | ***                   | ***                 |
|   | Bar. | 1.71                   | 10.75 | -7.36             | 9.03 | *                     |                     |
| Visibility (km; unlimited =<br>24.14 km)    | Syd. | 20.42                  | 7.80  | 24.14             | 0.00 | ns                    | ns                  |
|   | Bar. | 18.96                  | 9.30  | 18.68             | 9.34 | ns                    |                     |
| Opacity (tenths)                            | Syd. | 6.25                   | 4.27  | 3.71              | 3.50 | ns                    | ns                  |
|   | Bar. | 4.77                   | 4.29  | 6.27              | 3.80 | ns                    |                     |
| Ceiling (km)                                | Syd. | Median = 4.9 km        |       | Median = No ceil. |      | ns                    | ns                  |
|   | Bar. | Median = No ceil.      |       | Median = 3.0 km   |      | ns                    |                     |
| K index at 0500-0800 (0-9)                  | Syd. | 1.13                   | 0.99  | 1.71              | 0.95 | ns                    | ns                  |
|   | Bar. | 2.38                   | 1.39  | 2.00              | 1.34 | ns                    |                     |

<sup>a</sup> Sample sizes: at Sydney, 8 mornings with and 7 without reorientation; at Barrington 26 mornings with and 11 without reorientation. Only days when landbird movement over the sea continued until dawn are considered

<sup>b</sup> Mann-Whitney *U*-tests (two-sided). Significance coded as in Table 1

<sup>c</sup> Pooled probability from *U*-tests for the two separate areas (Sokal and Rohlf 1969: 621)

<sup>d</sup> Wind components derived as in Table 4

less variable; the surface wind always had a northerly component and the geostrophic wind was always either W-NNE or uncertain (Fig. 4). At Sydney, where information about birds and weather was most reliable, both surface and geostrophic winds were almost always S, SW or W (i.e. onshore or opposing) with reorientation and NW or N (offshore and side) without reorientation. At both sites, the surface wind had significantly stronger NE and NW components on mornings without than with reorientation (Table 5). Thus nocturnal migrants often, but not always, continued SW-W over the sea when winds favored (in an energetic sense) such a flight and/or opposed reoriented NW-N flight toward the closest land (i.e. WNW-N-ENE winds). However, reorientation to the NW-N always occurred when winds opposed continued SW-W flight and/or favored reoriented NW-N flight (i.e. E, SE, S, SW, and W winds).

The occurrence of reorientation was unrelated to visibility, cloudiness or magnetic disturbance (Table 5). *Visibility* ranged from 0 to 24+ km on days with and from ½ to 24+ km on days without reorientation. Visibility was 24+ km on 25 of 34 days with and on 14 of 18 days without reorientation. *Fog* was present on 6 of 34 days with and on 2 of 18 days without reorientation. *Precipitation* (drizzle or rain showers) was present on 2 of 34 days with and 2 of 18 days without reorientation. *Opacity* ranged from 0 to 10 tenths both on days with and on days without reorientation. A *ceiling* was present (i.e. opacity > 5/10) on 17 of 34 days with and on 10 of 18 days without reorientation. When present, the ceiling ranged from 0 to 7,600 m on days with and from 30 to 6,100 m on days without reorientation. The K index of *magnetic disturbance* ranged from 0 to 5 on days with and from 0 to 4 on days without reorientation. Thus wind was the only parameter to which the occurrence of reorientation was found to be related.

## DISCUSSION

*Nocturnal SW movement.*—Several features of the nocturnal SW migration were of interest aside from the fact that such flights were often the prelude to reorientation.

Landbirds began to take off at  $28 \pm 5$  min after sunset. Because of the proximity of these birds to the radar and the hilltop location and high power of the radar, they would have been visible as low as tree-top height—even when aloft in small numbers. Alerstam (1976), who also used a high-power hilltop radar, reported a similar mean takeoff time but greater variance ( $32 \pm 23$  min after sunset). Other radar studies have demonstrated consistent initial takeoff times, but slightly later in relation to sunset: Drury and Nisbet (1964)—45 min after sunset; Casement (1966)—40 to 50 min; Parslow (1969)—29 to 49 min. Casement and Parslow observed radar displays directly and probably failed to detect the first birds to take off, which are less conspicuous in real time than on time-lapse film. The birds that Drury and Nisbet discuss were 85+ km from the radar and usually would be undetectable until many had climbed to  $\sim 350$  m ASL. Visual and aural studies (Hebrard 1971, Bolshakov and Rezvy 1975, Lindgren and Nilsson 1975) have also given initial takeoff times later than those at Sydney, probably because a long-range radar would be more likely than a short-range visual or aural method to detect the first individuals to take off in the general area. Thus nocturnal landbird migration apparently begins a few minutes earlier in relation to sunset than has been reported in most previous studies.

Landbirds flew without apparent hesitation and on a broad front across Cabot Strait and the Gulf of Maine. Some birds from Newfoundland missed Cape Breton Island completely and flew over the Gulf of St. Lawrence or the Atlantic on courses that, if maintained, would not reach land for 175–2,000 km. Comparable flights by landbirds across other bays and seas and parallel to other seacoasts are well known (Lack 1959, Schüz 1971), as are even longer flights over oceans and deserts (Bogert 1937, Fell 1947, Snow 1953, Nisbet 1970, Moreau 1972, Richardson 1976).

In this study, many landbirds crossed coasts at acute angles at night, but others changed course to concentrate overland or to avoid moving offshore from the SE coast of Cape Breton Island at an acute angle. Previous studies provide little systematic evidence that nocturnal landbird migrants follow coastlines or change course to avoid overwater flight (Lowery 1951, Lack 1962, Emlen 1975). However, coastlines are readily visible from low-flying aircraft at night (Bellrose 1971) and it would be very surprising if all landbirds ignored a detectable cue that could permit them to avoid moving offshore. There is, in fact, previous circumstantial evidence that landbirds occasionally parallel or concentrate over coasts at night (Lowery 1951, Vleugel 1954, Bagg and Emery 1960, Adams 1962, Lack 1963, Kiepenheuer and Linsenmair 1965, Lowery and Newman 1966, Bellrose 1967). Further study using a high-resolution radar or simultaneous ceilometer observations along and away from a coast could clarify the nature and frequency of responses to shorelines.

Drury and Nisbet (1964) found that mean tracks of landbirds migrating SW on autumn nights were unrelated to wind direction over eastern Massachusetts, and at most weakly related to wind direction over the adjacent sea after flights from Nova Scotia. In contrast, mean tracks at Sydney (this study) and elsewhere in Nova Scotia (Richardson 1975) were significantly related to wind direction. Whatever the orientational explanation for my results, landbirds were more likely to fly SSW-SW, and thus offshore, on nights with W, NW, and N offshore winds than on other nights.

*Reorientation over the western Atlantic as evident visually and on radar.*—Previous observations (visual) provide no definite information about tracks before reorientation. Most of the species involved are believed to migrate generally SW (Drury

and Keith 1962). However, many immatures caught near the New England coast orient SE (Ralph 1975, Able 1977). Furthermore, Blackpoll Warblers sometimes reorient (Bagg 1950, Murray 1965), and many of them migrate SE-SSW over the ocean toward the West Indies (Nisbet 1970). Thus reoriented flights might consist of individuals that had oriented SE or S during the night. However, most reorienting birds detected by Nova Scotia radars had flown SSW-W, not SE or S, during the night.

Visual and capture data from the coast indicate that reoriented flight occurs primarily in the morning (Baird and Nisbet 1960, Murray 1976). Radar data are consistent with this. Reoriented flight usually began 0–2 h before sunrise (occasionally earlier) and often continued at gradually declining density until noon.

Baird and Nisbet (1960) suggested that the wide range of directions of reoriented flight visible near the coast (WNW-NNE) is probably due to local topographic influences; at specific locations directions may be quite consistent (B. G. Murray pers. comm.). Radars show, however, that a wide range of directions also occurs far offshore—even among different birds aloft at one time in a particular area. Differences in individual responses to variable wind and wave directions and species differences in behavior may be responsible. Radar data confirm visual observations of continued NW-N flight overland, but fail to show how frequent or long such overland reoriented flights may be.

Field observers and radars apparently detect different (although overlapping) altitudinal components of the reoriented flights. Reoriented migrants seen are often flying very low and/or landing, but occasionally are reported as higher or climbing (Scholander 1955, Baird and Nisbet 1960, Murray 1976). Field observers would tend to see the lowest birds whereas radar would tend to detect the highest (Mascher et al. 1962, Axell et al. 1963, Gehring 1963, Wilcock 1964, Evans 1966, Rabøl and Hindsbo 1972). Some reoriented birds detected by my radars could have been very low, but those detected 90+ km from Sydney must have been 270+ m ASL. Reoriented flights are unlikely to be observed visually at such high altitudes.

Low-flying reoriented birds are commonly seen on mornings with offshore (NW) headwinds (Bagg and Emery 1960, Baird and Nisbet 1960). The radars showed, in contrast, that reorientation was most common with opposing or onshore (W or S) winds. This difference may represent the altitude biases of radar and visual observers. Birds flying upwind tend to fly low (Deelder and Tinbergen 1947, Mascher et al. 1962, Axell et al. 1963, Wilcock 1964, Rabøl and Hindsbo 1972). Thus radar probably underestimated low altitude NW flight with NW winds, whereas visual observations apparently underestimate high-altitude NW flight with winds other than NW. The latter bias may be more severe, since high-altitude landbird migrants are inconspicuous to casual observers (Deelder 1949, Lowery and Newman 1963) whereas both radars could detect birds at very low altitudes at least to 20 km offshore. This argument suggests that the radar-derived relationship between wind direction and probability of reorientation is real, not artifactual.

*Ascent and reorientation near Nova Scotia and Britain.*—In both these areas radar echoes often intensified and became visible to longer range around dawn. This phenomenon has been interpreted as dawn ascent but could, alternatively, have been due to aggregation of birds from the typical nocturnal pattern (singles and small loose groups—Lowery 1951, Bruderer 1971, Balcomb 1977) into the larger, more tightly-knit flocks characteristic of diurnal landbird migration (Gehring 1963, Gauthreaux 1972). However, Lack (1963), P. R. Evans (pers. comm.), and I each

obtained direct evidence from height-finding radars of dawn ascent on one day. Thus increased echo prominence at dawn was at least partly the result of actual ascent, but probably partly of aggregation.

Both near Britain and near Nova Scotia tracks after reorientation were often not those best suited to return the birds to land. Some Newfoundland birds that changed course from WSW to NW east of Cape Breton Island apparently flew through Cabot Strait into the Gulf of St. Lawrence (this study), whereas WSW-WNW flight would have brought them to land. Lack (1963), Myres (1964), and Wilcock (1965) all reported that only the birds close to land (within 16–24 km according to Lack) flew directly toward land after dawn. These results suggest that tracks of birds that reorient far from shore are chosen using cues other than sight of land.

Relationships between weather and the occurrence and directions of reorientation appeared to differ among areas. Near Nova Scotia, reorientation toward land was less common on days with offshore winds than on other days. Lack (1963) found, in contrast, that reorientation from SSW to SSE occurred primarily when there had been easterly (offshore) winds at night; reorienting birds thus tended to fly partially into the wind. Myres (1964) found no clear relationship between wind and either occurrence or directions of reorientation.

In both areas some birds landed at the coast whereas others continued inland. However, North American birds continuing inland apparently maintain their re-oriented tracks (Baird and Nisbet 1960, this study); European birds revert to pre-reorientation tracks (Lack 1963). Corroboration is needed, especially in Europe.

*Orientalional and adaptational significance.*—Birds that reorient over the western Atlantic at dawn may often be individuals drifted offshore by NW winds during the night (Stone 1937, Bagg and Emery 1960, Baird and Nisbet 1960). Others may be immatures with maladaptive preferred directions that lead them generally SE and offshore (Ralph 1975, Able 1977). These factors doubtless account for the presence of some landbirds offshore at dawn. However, Drury and Nisbet (1964) found that offshore wind drift is infrequent in New England, and I found that most birds reorienting off Nova Scotia had flown SSW-W, not SE, during the night. A larger proportion of the birds aloft near Nova Scotia moved SSW-SW, and thus offshore, when winds included an offshore (NW) than an onshore (SE) component. However, regardless of wind, whenever a SSW-W landbird movement continued all night, some migrants were over the sea at dawn.

The role of landmarks as cues for reorientation has been unclear. Murray (1976) concluded that the decline in rate of arrival from offshore as the morning progresses is evidence that only birds that can see land reorient. However, geographical considerations require, and radar observations confirm, that the density of SSW-W movement at dawn declines markedly with distance from shore. This decline alone could account for the temporal pattern of arrival at the coast regardless of whether reorienting birds oriented by landmarks or other cues. Furthermore, if reorientation far offshore—like that within radar range—occurs at or before dawn, then the prolonged arrival from offshore indicates that birds up to 250+ km SE of Nova Scotia reorient to the NW. While birds 2+ km aloft could, in theory, see the highlands on Cape Breton Island (500 m ASL) from this distance, haze, fog, cloud, and dim light would usually preclude sight of land. Thus many birds apparently reorient using cues other than landmarks. Nonetheless, landmarks do seem to be used when visible, as British studies indicate that birds near land at dawn reorient directly toward land. Also, the association between dawn reorientation and ascent, which

markedly increases the distance to which landmarks can be seen in clear weather, suggests that there has been selection for behavior enhancing the utility of landmarks.

Reoriented flight occurs in directions other than upwind (Fig. 4), so landbirds over the sea at dawn do not 'simply' fly upwind to counteract some assumed offshore wind drift. Neither do they 'simply' fly downwind. Although cloud data are too imprecise to be certain, the occurrence of reorientation near Nova Scotia with 10/10 opacity suggests that celestial cues may not be the only ones used.

Sufficient evidence is now available to permit speculation about the adaptive significance of the behavior of nocturnal landbird migrants in eastern North America in relation to overwater flight. More of these migrants fly SW with NNE-E along-shore following winds well behind cold fronts than with NW offshore crosswinds immediately behind cold fronts (Baird et al. 1959; Nisbet and Drury 1969; Richardson 1975, 1978). Most individuals of some species apparently migrate inland rather than near the coast (Drury and Keith 1962, Ralph 1975), and some individuals change course at night to avoid crossing the coast (this study). Additional adaptations to the proximity of the sea include compensation for lateral wind drift (Drury and Nisbet 1964) and ascent and reorientation toward land when the birds find themselves offshore at dawn in winds unsuitable for a long SW-W overwater flight. The occurrence of such flights in winds favorable to SW-W flight and/or unfavorable for NW reorientation, although previously unsuspected, is not inconsistent with lengths of flights by landbirds elsewhere. Even if many of these birds do not reach land, their numbers appear small enough to be expendable (Ralph 1975).

These generalizations doubtless do not apply to all nocturnal landbird migrants in eastern North America. Some birds that fly SE or S at night (e.g. some Blackpoll Warblers), as well as those that fly SSW-W, may reorient. Some species do appear to migrate predominantly near the coast (Ralph 1975), and many individuals do fly SW with NW rather than NE winds (Richardson 1972a). Some birds are drifted by the wind (Drury and Nisbet 1964), and the relationship between wind and occurrence of reorientation is far from precise. These factors, plus probable differences in orientation of adults and at least some immatures (Ralph 1975), may cause much of the variability in reorientation behavior among birds, areas, and dates.

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