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Autumn Landbird Migration over the Western Atlantic Ocean as Evident from Radar

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Introduction

Most landbirds in easternmost North America migrate southwest parallel to the coast during autumn, but some move SE-SSW offshore (Drury & Nisbet, 1964; Richardson, 1972). Some of the latter change course and return NW to land (Baird & Nisbet, 1960; Murray, 1976; Richardson, in press), and others become exhausted and apparently perish at sea (Scholander, 1955). However, some are still aloft 2000 km from shore (Penard, 1926; Williams et al., 1977b), and some fly to Bermuda (Wingate, 1973) or even Europe (Sharrock, 1974). Radars on Bermuda, the West Indies and ships have recently shown that many landbirds fly non-stop from SE Canada and NE U.S.A. to the West Indies (2550–3300 km), and perhaps even South America (a further 800 km). The Blackpoll Warbler *Dendroica striata* seems to be a major user of this route (Nisbet, 1970).

I present here new data about offshore departures from Nova Scotia, Canada, and then summarize evidence concerning landbirds over the western Atlantic in fall. Spring migration and autumn shorebird migration in this area are reviewed in Richardson (1974, 1979), and southeast flights from Florida along the West Indies are described by Richardson (1976) and Williams et al. (1977a, b).

Southward departure from Nova Scotia

One or more of three surveillance radar sites in Nova Scotia and one in New Brunswick were used in 1965 and 1969–71 (Fig. 1; for methods, see Richardson, 1972, 1979, in press). The most reliable data were from Barrington, N.S., in 1971 and Sydney, N.S., in 1965, but landbird flights were always difficult to study. Available data are usually incomplete and/or qualitative because of (1) limited abilities of the radars for resolving echoes from passerines, (2) occasional equipment malfunctions, and (3) the fact that landbirds often flew in all directions between SE and WSW, but with modes SSE-S and SSW-WSW. Because of (3), I often could estimate modal directions, but could not assign all individual echoes to one or the other group, and so could not calculate the mean or dispersion of directions of the SSE-S group.

Unequivocal southward landbird departures of at least moderately high density (5 on a 0–8 ordinal scale) were recorded from Barrington as early as 29 and 31 Aug. (1971) and as late as 27 and 29 Oct. (also 1971). Relative frequencies and densities in various parts of this period are uncertain, but the 31 Aug. 1971 flight was a major migration (density 7 on the 0–8 scale), and density 5 or 6 flights were frequent from mid-Sept. to late Oct. The densest SSE-S and SW flights appeared similar in density, but dense SW flights were much more common (Richardson, 1971).

Broad-front SSE-S departures were recorded by all three Nova Scotian radars, but high densities (6 or 7) were not recorded over eastern Nova Scotia. Migrants appeared 20–30

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min after sunset over all land areas of Nova Scotia within radar range-not just from coastal areas. All of western Nova Scotia was sometimes outlined on the Barrington radar display just after these birds took off. Sometimes birds from southern New Brunswick and eastern Maine also departed SSE-S. For example, on 31 Aug. and 30 Sept. 1971, the density over western Nova Scotia declined briefly about 1–$^{1}/_{2}$ h after sunset as birds from Nova Scotia moved offshore, but then increased as others from north of the Bay of Fundy moved into range over western Nova Scotia and the Gulf of Maine. The density of southward flight over western Nova Scotia usually decreased markedly by midnight. This, together with the measured mean ground speed of 51.6 km/h (n=126 echoes on 9 nights), indicates that few landbirds initiated SSE-S trans-oceanic flights more than 150 km inland from the coast of New Brunswick or Maine. Data from the St. Margarets, N.B., radar corroborate this; it commonly detected some southbound passerines, but no major southward flights were noted.

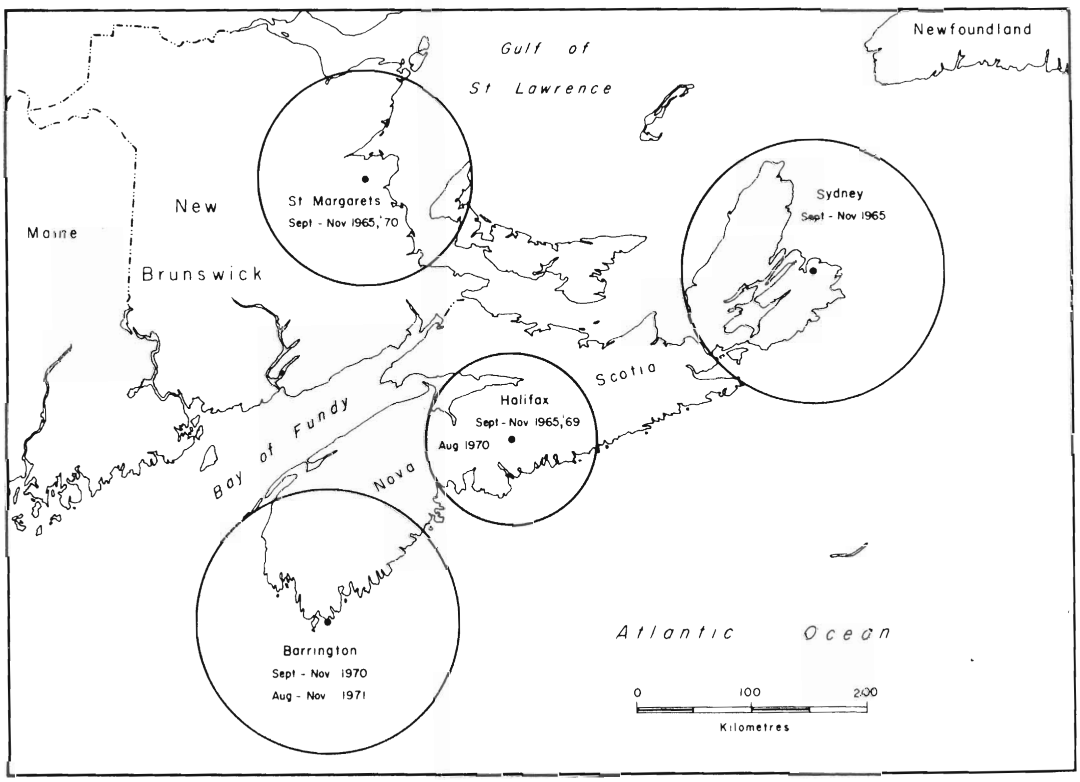

FIGURE 1. Radar locations, coverage areas and months of use during autumn.

A nodding height-finder radar at Barrington showed dense, unresolvable echoes from landbirds up to 0.6 km ASL on one evening with SSE-S but no SW landbird migration (21 Sept. 1971) and up to 1.8 km on another (31 Aug. 1971). On three evenings with both SSE-S and SW miqration (not distinguishable on the height finder) dense echoes extended up to 0.9, 1.5 and 1.8 km. In contrast, on 14 evenings with SW but no obvious SSE-S passerine migration, passerines were abundant only up to 0.6–1.2 km (mean 0.8 ± s.d. 0.2 km). These results are consistent with NISBET et al. (1963), who found that passerines moving south from Cape Cod on 4 nights were somewhat higher (typically at 0.6–1.2 km) than other passerines.

Tracks of individual echoes were measurable at Barrington on only three evenings when there was no overlap in track distributions of SSE-S and other types of movements: 22 Sept. 1971 – vector mean 170° ± angular deviation 11.9° (29 echoes measured); 24 Sept. 1971 – 167 ± 10.5°, n=49; 30 Sept. 1971 – 171 ± 15.8°, n=66. On other nights modal tracks of the SSE-S group around 1 h after sunset ranged from ~155° (8 Oct. 1971) to ~175° (25 Sept. 1971). Some birds moved S-SSW on most of these nights, and on at least one night at Sydney the mean track of passerines just after take off was intermediate between 'typical' SSE-S and SW-WSW departures: 19 Oct. 1965 – 203 ± 11.4° (n = 41). Directional data for the SSE-S departures of landbirds were too meagre and imprecise to warrant detailed analysis, but there was no evidence of a correlation between wind direction and nightly modal direction at Barrington, and little evidence of such a correlation for all Nova Scotian sites (Fig. 2). DRURY & NISBET (1964) also found no such correlation near Cape Cod, but my data do not support their conclusion that there are two distinct directional classes (~171° and ~186°) among landbirds moving offshore.

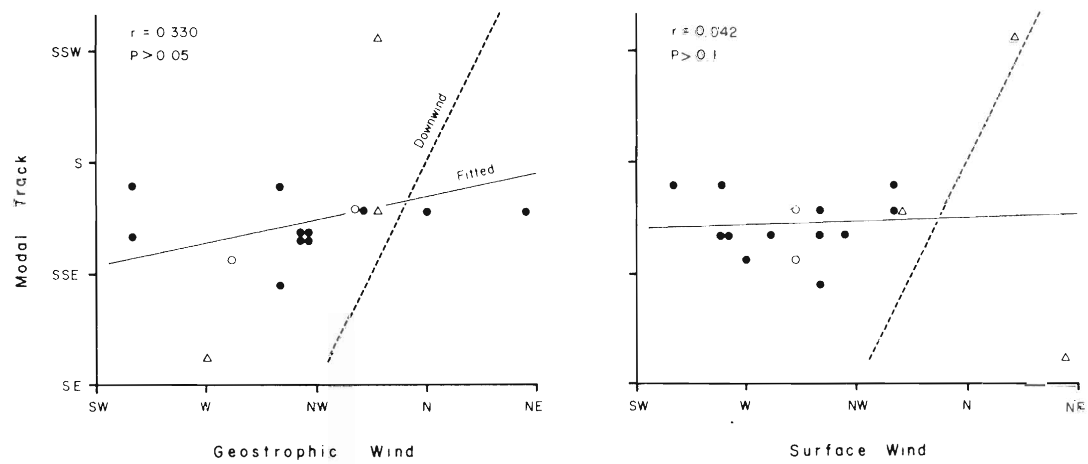

FIGURE 2. Modal track directions of landbirds departing seaward from Nova Scotia on various evenings vs wind direction. Tracks were measured about 1 h after sunset with the Barrington ●, Halifax ○ and Sydney Δ radars. One-sided probabilities are given.

On at least two evenings at Barrington the modal track shifted from 165 or 170° soon after take off to 195–205° around midnight (21 and 30 Sept. 1971). Whether individual echoes changed course is uncertain, since individuals couldn't be followed for more than ~30 minutes. On 21 Sept. the change in tracks coincided with clearing skies and a shift in surface wind from 280° at 13 km/h to 340° at 18 km/h; on 30 Sept. the wind was 300–310° at 16 km/h and the sky was at least partly clear all evening. These were also the only two occasions when an evening departure to the SSE-S was followed by a pre-dawn reorientation of birds over the sea from SW to NW.[1] It is unlikely that any of the individuals that departed SSE-S in the evening were moving SW within radar range of the

[1] Evening departures to the SW were often followed by such reorientation (RICHARDSON, in press).

coast late in the night. Thus there was no proof that landbirds departing SSE-S over the ocean ever turned back to land, and considerable evidence that few if any did so.

Most offshore departures occurred with west, northwest or north winds. Of 26 definite cases of density 4–7 SE-SSW landbirds departure from Nova Scotia. 4 were in WSW-NW winds close behind cold fronts, 1 was in a NW airflow SW of a low pressure area, 14 were in N, NW or N airflows north, east or near the centre of high pressure areas, 1 was in the NE airflow SE of a high, 2 were in the SW airflow NW of a high, and 4 were in unclassifiable circumstances having W, NW or N winds. Offshore departures of landbirds were more frequent with NW than NE winds, whereas SE departures parallel to the coast were more frequent with NE winds (Richardson, 1972, 1978). Thus offshore departures tended to begin sooner after cold front passage than peak SW departures. The 21 Sept. 1971 departure (see above) began under overcast during cold front passage.

Landbirds over the Atlantic

The Blackpoll Warbler is the only landbird whose main fall route has been shown to be from NE U.S.A. and SE Canada over the Atlantic to the West Indies and South America (Nisbet, 1970; Ralph, 1975). However, Blackpolls – like other species – sometimes return NW to land after dawn (Murray, 1965), and late Aug., early Sept. and late Oct. departures evident on radar must be other species (Nisbet et al., 1963). Few North American passerines reach the West Indies before mid-Sept. (McCandless, 1962; Richardson, 1976), so birds moving offshore earlier may be poor orienters that will perish at sea (Ralph, 1975). Other warbler species seen south of Bermuda (Penard, 1926; Williams & Williams, in press) and major SSE-SSW arrivals of landbirds at Puerto Rico in late Oct. (Richardson, 1976) may leave the coast south of New England, but specific evidence about their take-off locations is lacking. Offshore departures occur at least from eastern Nova Scotia to New Jersey (Drury & Keith, 1962; Swinebroad, 1964; this study), and probably to Virginia, where birds with low airspeeds depart east of 170° (Williams et al., 1977b).

Landbirds tend to depart SSE-S with cool W, NW or N winds behind a cold front or in the eastern or central parts of a high pressure area (Drury & Nisbet, 1964; Richardson, 1972, this study; Williams et al., 1977b). Fronts often stall before reaching Bermuda. Some landbirds[2] that catch up with such fronts penetrate them and continue SE-SSW in the typically fair weather of the 'Bermuda High', but others apparently fail to penetrate to the High and may perish (Williams & Williams, in press). Species differences and factors affecting the probability of penetration are unstudied.

Few Blackpoll Warblers land at Bermuda (Nisbet et al., 1963; Ralph, 1975), and radar shows passerines and other birds passing overhead, usually SE (Ireland & Williams, 1974). Peak daytime passage (all species) is in the afternoon, ~18–22h after evening departure from coastal areas 1100–1550 km away (Williams et al., in press). However, nocturnal radar data from Bermuda are meagre, and many passerines may arrive at night >24 h after take-off (Nisbet et al., 1963). Ship radars show that SE-SSW migration, probably of landbirds[2], can extend 1000 km east and 800 km south of Bermuda (Williams et al., 1977b).

[2] My assumption, based on the low altitudes (the radars used couldn't detect birds above 500–1000 m), generally low airspeeds, and visual sightings reported by Williams & Williams (in press).

Radars at Puerto Rico and Antigua, West Indies (~1650 km S of Bermuda), often show birds approaching from the NW, N and even NE (HILDITCH et al., 1973; RICHARDSON, 1976; WILLIAMS et al., 1977b). Some are shorebirds, but low airspeeds at both sites, plus echo characteristics and abundance at Puerto Rico, indicate that many – including some at 4–6 km ASL – are passerines. Some (passerines?) pass Puerto Rico and most pass Antigua without stopping, apparently continuing ~800 km to South America. Imprecise relationships between times of known or suspected departure from NE U.S.A./SE Canada and arrival in the West Indies suggest a mean transit time (all species) of 60–70 h to the northern West Indies and 82–88 h to South America (RICHARDSON, 1976; WILLIAMS et al., in press).

NISBET et al. (1963) concluded that Blackpoll Warblers, based on weights at departure from New England and arrival at Bermuda, could fly for >95 h. GREENEWALT (1975) calculated a still-air range of 3465 km for Blackpolls. However, present theory indicates that these are overestimates (TUCKER, 1975, 1976). Since from Boston it is a minimum of 2700 km to Puerto Rico and 3400 km to Venezuela, the observed tendencies to take off with following NW winds and to approach the West Indies at high altitudes, where winds are often most favourable (RICHARDSON, 1976; WILLIAMS et al., 1977b), must have high adaptive value. High altitude flight may also conserve water (BERGER & HART, 1974) and increase airspeed (PENNYCUICK, 1975). Increased airspeed would decrease transit time, and thus reduce the risk of encountering a hurricane. Strip-like updrafts behind cold fronts might be useful in conserving energy early in the flight (GRIFFIN, 1969), but there is as yet no evidence that landbirds concentrate in the rising air.

Mean tracks of the landbirds are ~170° just after take off but ~190° near Puerto Rico. WILLIAMS & WILLIAMS (in press) suggest, considering shorebirds and landbirds together, that the entire flight is made with a constant SE heading, and that lateral wind drift causes the curved route. However, early in the flight most landbirds maintain SSE-S tracks by adjusting their headings around a mean of ~S to correct for wind drift (DRURY & NISBET, 1964; this study). At Puerto Rico, tracks (all species, but mainly passerines) are strongly correlated with wind, and result from uncorrected drift by the prevailing easterly trade winds from a mean heading of 174°.[3] In mid-ocean, headings of landbirds[2] average about 163° (WILLIAMS & WILLIAMS, in press). Thus, mean track, the relationship of headings to wind, and possibly mean heading change en route. The ultimate reason for the curved route is presumably a function of prevailing winds and energy conservation, but precise orientational processes and the energetic advantage over alternate routes are uncertain, and should be further examined for landbirds alone.

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[3] Calculated assuming that the birds are at the altitude with the most favourable wind (RICHARDSON, 1976). Other calculation procedures give means of 166–174°.

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