MIGRATION: MECHANISMS AND ADAPTIVE SIGNIFICANCE

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THE INFLUENCE OF WEATHER ON ORIENTATION AND NUMBERS OF AVIAN MIGRANTS OVER EASTERN CANADA: A REVIEW

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ABSTRACT

This paper reviews the effects of weather on numbers of birds aloft, and on bird orientation and flight routes over southeastern Canada. New data concerning responses of different types of avian migrants to weather are given.

Each category of migrants tended to fly on occasions when winds were more or less following relative to its own direction of travel. However, many birds flew under calm conditions and some in cross or even opposing winds. Numbers aloft tended to be reduced under cloudy skies, but flight directions under overcast seemed little different from those under clear skies. There was no greater tendency for downwind flight under overcast than under clear skies.

Routes of migrants can be affected by proximate responses to weather, such as dawn reorientation when winds are unfavorable for continued flight in the original direction. Also, routes of some migrants are adapted to prevailing winds. For example, in autumn many birds fly over water, with following winds, from SE Canada to the West Indies. In spring they apparently return along a more westerly route where winds are more favorable.

INTRODUCTION

Weather can influence migrating birds in various ways. Average wind speeds are a substantial fraction of a bird's airspeed, such that a bird will make faster progress over the ground and use less energy to travel a given distance if it flies with following rather than opposing winds. A moderate crosswind will strongly influence track over the ground unless the bird makes a corresponding major adjustment in its heading through the air. In areas where there is a prevailing wind direction, wind patterns may influence migration routes; it will be easier to fly in some directions than in others. The occurrence of fog, cloud or precipitation has major implications for visual orientation mechanisms that use either celestial cues or landmarks.

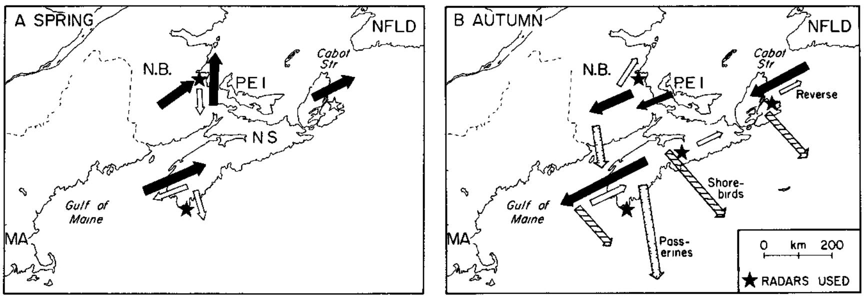

Figure 1
The main groups of migrants over SE Canada in (A) spring and (B) autumn.

This paper examines the effects of weather on numbers, orientation and routes of avian migrants by reviewing data from Nova Scotia and New Brunswick, Canada. I emphasize comparisons of the ways in which the various groups of migrants respond to weather. The detailed characteristics of migration in this area have been described elsewhere and are only summarized here.

Most spring data were obtained from two long-range surveillance radars, one in southwest Nova Scotia and one in New Brunswick (Fig 1A). In spring the predominant directions of migration are to the northeast, parallel to the coast, and to a lesser degree to the north (Richardson 1971). Reverse migration to the south and southwest involves far fewer birds, but occurs intermittently throughout the spring (Richardson, in preparation). During spring, birds are not seen arriving from the south, the direction of the West Indies.

Most autumn data were from three surveillance radars in Nova Scotia and one in New Brunswick (Fig 1B). More birds go SW, parallel to the coast, than in any other direction (Richardson 1972). However, small reverse movements to the NE occur intermittently throughout autumn (Richardson 1982a). In addition, there are SE flights of shorebirds and southward flights of passerines on certain dates; these birds are beginning nonstop flights to the West Indies or South America (Richardson 1979, 1980).

NUMBERS ALOFT VS. WEATHER

Numbers of migrants aloft over eastern Canada, as elsewhere, can differ by a factor of 100× or even 1000× from one day to the next and are strongly correlated with weather. A detailed review appears in Richardson (1978a); this section summarizes the main relationships in SE Canada.

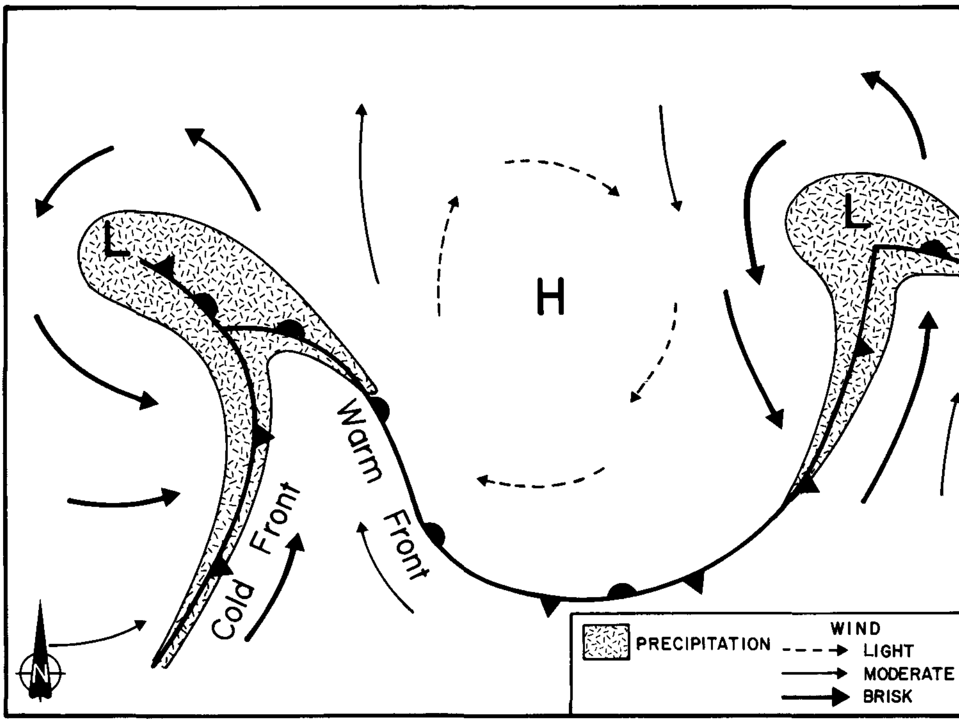

Figure 2
Typical configuration of high (H) and low (L) pressure systems, fronts, precipitation and winds at north temperate latitudes.

Pressure Systems, Fronts, and Wind

Weather patterns in eastern Canada are similar to those at any north temperate latitude (Fig 2). Low and high pressure areas move generally west to east. Winds are clockwise around highs and counterclockwise around lows. Thus winds are southerly when there is a high to the east, a low to the west, or both. Winds are northerly when there is a low to the east, a high to the west, or both. Winds are near calm near the center of a high. Precipitation and thick cloud are most likely when a low is near or when a front between air masses passes overhead.

Many studies in North America and Europe have shown that most bird species tend to migrate when winds are more or less following, relative to the preferred direction of those particular birds (Richardson 1978a). This is true in eastern Canada as well.

Far more birds fly N and NE over eastern Canada in spring on nights and days when there are following winds from the S or SW than on dates when winds are opposing. The association with following S and SW winds is even closer for the small number of birds that engage in NE reverse migration in autumn (Fig 3).

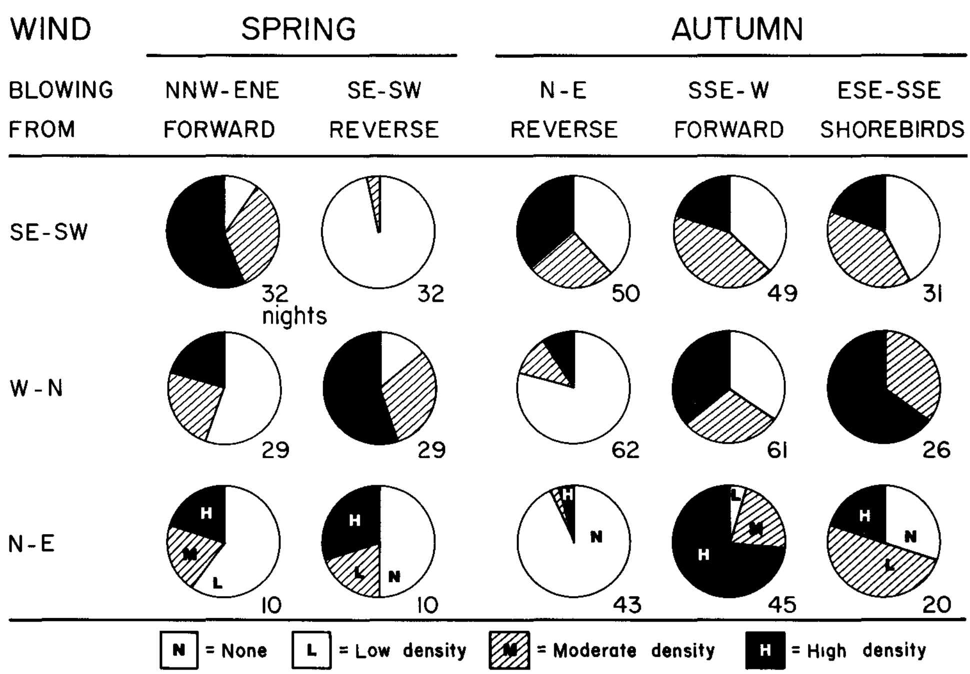

Figure 3
Amount of nocturnal migration of five types of birds detected over SE Canada with three categories of winds. Each circle shows the proportion of evenings when amount of migration was none or low, intermediate, and high.

In contrast, far more birds fly SW and S in autumn when there are following N and NE winds than with opposing southerly winds. Similarly, S and SW reverse migration in spring is strongly associated with following northerly winds.

In eastern Canada, as elsewhere (Richardson 1978a), groups of birds that travel in slightly different directions tend to fly with slightly differing weather. Shorebirds initiating SE flights toward the West Indies are significantly more likely to take off with NW following winds than with NE crosswinds (Fig 3; Richardson 1979). The predominantly SW flights of passerines, in contrast, tend to be denser on nights with NE following winds than with NW crosswinds (Fig 3). Furthermore, passerines that depart S toward the West Indies are more likely to fly with NW winds than are passerines that travel SW along the coast (Table 1). Thus, even excluding the extreme case of reverse migration, each group of migrants apparently prefers following winds relative to its own direction of travel.

Winds tend to be northwesterly soon after a cold front passes but often change to N or NE a day or so later as a high pressure area approaches. Thus, in both eastern Canada and elsewhere, SE migration often peaks immediately after a cold front passes, and SW migration peaks a day or so later (Richardson 1978a, p. 237).

Table 1
Occurrence of SW and SSE passerine migration over SW Nova Scotia in relation to broad-scale wind direction, autumn 1971.

Wind Direction	Number of nights when predominant migration direction was	
	SW	SSE
NW	7	8
NE	18	1

$\chi^2 = 9.95$, df = 1, $p < 0.005$

The association with following winds is by no means complete. Many birds fly under calm conditions, and some birds fly in cross and even opposing winds (Fig 3). Some categories and species of migrants show stronger preferences for following winds than do others (e.g., Alerstam 1978). Possible reasons for this variation in selectivity are discussed by Alerstam (1979a). Following winds will be especially important for birds that fly nonstop over inhospitable habitat, e.g., over the Atlantic Ocean from Nova Scotia to the West Indies in autumn. Without following winds, small landbirds probably could not complete this flight (Tucker 1975). Following winds may be less important for migrants flying short distances over habitat where they can land at any time.

Temperature and Pressure

Southerly winds tend to be accompanied by falling pressure and rising temperature as a high pressure area moves away to the east, a low approaches from the west, or both. It is not surprising that N and NE migrations, which are associated with southerly winds in both spring and autumn, tend to occur with falling pressure and rising temperature (Table 2). Conversely, northerly winds tend to be accompanied by rising pressure and falling temperature as a low moves away to the east, a high approaches from the west, or both. South and SW migrations also tend to occur with rising pressure and falling temperature.

Because of the close correlations among wind, temperature trend, and pressure trend, it is difficult to determine from uncontrolled field observations whether birds respond directly to pressure or temperature. Multivariate analyses sometimes indicate that numbers aloft are related to these variables even after the dominating correlations with wind have been taken into account (Richardson 1978a). This does not prove that birds respond to temperature and pressure, but it is suggestive. Direct responses to these variables might occur because they can be indicators of future food supply (e.g., insect availability), habitat suitability (e.g., freeze/thaw cycles), or winds aloft en route. Homing pigeons, at least, are remarkably sensitive to pressure change (Kreithen and Keeton 1974).

Table 2

Direction and significance of association between four weather variables and various categories of migrants over SE Canada during night (N) and day (D). Pluses (or minuses) indicate that the variable tended to assume higher (or lower) values when the specified type of migration was present[1].

Type of Migration and Main Flight Directions	24-hour Temperature Trend		6-hour Pressure Trend		Amount Opaque Cloud		Precipitation	
	N	D	N	D	N	D	N	D
Spring								
Forward (NNW−ENE)	+++	ns	−−	ns	−−	ns	−−−	−−−
Reverse (SE−SW)	−−−	−−−	+++	+++	−	−−−	ns	−
Autumn								
Reverse (N−E)	+++	+++	−−−	−−−	+	ns	**[2].	ns
Forward (SSE−W)	−−−	−−−	+++	+++	−−−	−−−	−−	ns
Shorebirds (ESE−SSE)	ns	ns	+	++	−	ns	−−	(*)[2]

[1] ns if $p > 0.1$, (±) if $0.1 \geq p > 0.05$, ± if $0.05 \geq p > 0.01$, ±± if $0.01 \geq p > 0.001$, and ±±± if $p \leq 0.001$. Based on Kruskal-Wallis tests of weather when amount of migration was zero vs. low vs. high, or below- vs. near- vs. above-normal.

[2] Nonlinear

Cloud and Precipitation

In general, fewer birds migrate when it is cloudy or raining than when it is clear (Richardson 1978a). However, this relationship is more precise for some categories of migrants than others. In some cases, especially for the variety of species migrating by day, no significant relationship was evident in SE Canada (Table 2).

Avoidance of flight with cloud or rain is probably advantageous for several reasons. Cloud may impair orientation by obscuring celestial or terrestrial cues. Also, cloud often occurs with low pressure areas, fronts, precipitation, and changeable winds. These conditions may require increased energy expenditure during or after flight, or may increase the probability of being blown off course or forced to the ground.

Able (1982) found that reverse migrations in the northeastern U.S.A. occur when prolonged overcast coincides with winds blowing toward seasonally inappropriate directions. In eastern Canada, NE reverse migration in autumn was the one type of movement positively associated with cloudy conditions (Table 2; Richardson 1982a). However, the correlation was weak, and cases of reverse migration occurred with every sky condition from overcast to completely clear.

Southward reverse migration in spring, like most other types of migration, was slightly *less* frequent under overcast than under clear skies (Table 2; Richardson, in preparation). Thus, impairment of visual orientation mechanisms by cloud cannot account for many of the cases of reverse migration in eastern Canada.

ORIENTATION VS WEATHER

Flight Directions vs. Wind

Because most migrants in SE Canada tend to fly when winds are following relative to their usual flight directions, the overall distribution of tracks usually includes a large downwind component (Fig 4). This is so even when winds are blowing from the north in spring or the south in fall; reverse migration is a major component of total migration on those occasions. Some birds do move crosswind or even upwind, especially when winds are blowing in seasonally inappropriate directions. However, total numbers aloft in these latter situations are generally low (Fig 4).

The downwind tendency is not as strong in SE Canada (Fig 4) as in the SE U.S.A., where there is consistent downwind orientation by landbirds flying at night (Gauthreaux and Able 1970, Able 1974). In SE U.S.A. the few birds that take off when winds blow toward seemingly inappropriate directions orient downwind, as do the larger numbers flying with more favorable winds. In contrast, in SE Canada (Fig 4) and in the NE U.S.A. (Able 1982), some of the few birds taking off with seasonally inappropriate winds orient downwind, but many do not. Interpretation is hindered because there is little information about the species involved in the various types of flights detected by radar.

To further assess whether birds are actually orienting downwind using wind as a cue, I analyzed the tracks of various distinct categories of migrants over SE Canada (Richardson 1975, 1979, 1982a, in preparation). Daily mean tracks for each category of migration were significantly but usually weakly correlated with wind direction (e.g., Fig 5). Daily mean tracks usually were not precisely downwind, and tracks of individual birds were, of course, even more widely scattered. The slope of the regression of daily mean track vs. wind direction was always significantly less than 1.0 (Table 3). A slope of 1.0 would be expected if tracks were consistently downwind. Thus for each category of migrants, crosswinds seemed to deflect mean track from its average direction, but by only 36 to 66% of the deviation of the wind direction from following.

There are at least two possible explanations for such a pattern: uncorrected wind drift from fixed headings and "pseudodrift." The track over the ground is the vector sum of the bird's heading vector through the air plus the wind vector. Uncorrected drift occurs when birds fly on constant headings regardless of wind direction. Pseudodrift occurs when, even within a particular category of migrants, birds with slightly different preferred tracks fly selectively with winds that favor flight in their individual preferred directions.

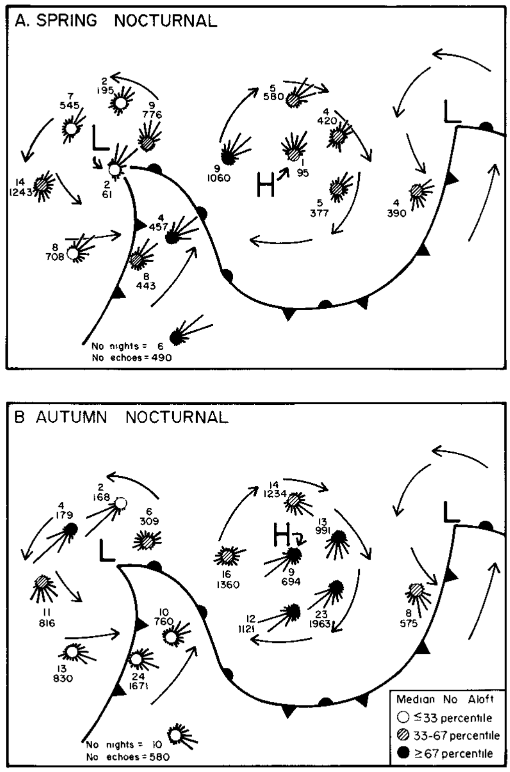

Figure 4

Directions of nocturnal migration over SE Canada with various types of synoptic weather. Each vector diagram is appropriately positioned with respect to pressure system and front locations and broad-scale wind patterns. Each vector diagram shows the percentage distribution of tracks of individual radar echoes. Total numbers aloft varied greatly among weather categories, as coded at the center of each vector diagram.

In the SE Canada study, there was insufficient information about winds aloft to distinguish between these two alternatives. In some studies, uncorrected wind drift has been found (e.g., Richardson 1976, 1982b) whereas in others the correlation between tracks and wind direction apparently represented pseudodrift (Alerstam 1976). Besides these two flight strategies and the "downwind flight" exhibited by many landbirds in the SE U.S.A., a fourth strategy has occasionally been found: maintenance of fixed tracks in a variety of winds through compensatory adjustments of heading (e.g., Drury and Nisbet 1964). Alerstam (1979a,b) has discussed the reasons why it may be advantageous for birds to drift in some situations and to correct for drift in others.

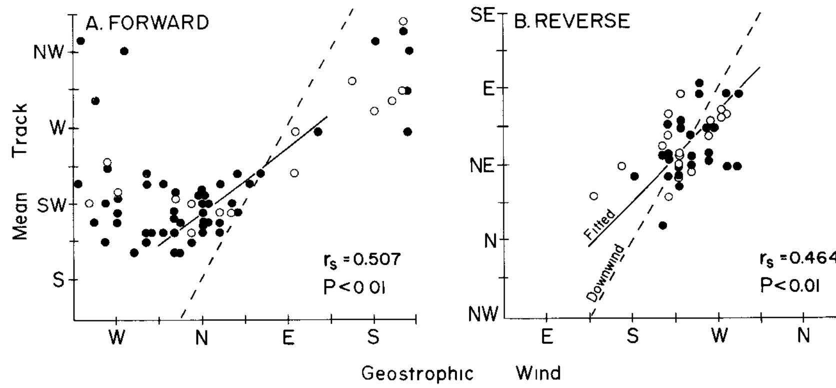

Figure 5

Mean tracks of migrants over Nova Scotia on autumn nights vs. geostrophic wind direction. Open symbols represent nights with 100% opaque cloud cover. Each symbol represents at least 10 radar echoes. Continuous lines were fitted by the geometric mean (GM) method (Ricker 1973). Only nights with winds in a 180° range were used in fitting the lines and in calculating Spearman rank correlations. The GM method is appropriate when the predictor variable is truncated (here to a 180° range) and subject to measurement error.

Orientation vs. Overcast

Birds flying over SE Canada on overcast occasions were not disoriented, and there was little evidence of deterioration in orientation. These results were similar to those of many earlier studies (Emlen 1975). Even under overcast, most birds moved along straight lines, at least within the limits of resolution of the radars used.

For most categories of migrants, variance among tracks was no greater under overcast than clear skies. The one category for which variance was greater with overcast was shorebirds departing SE on autumn nights ($p < 0.01$, Richardson 1979). Many of these shorebirds were probably above the clouds, and thus terrestrial rather than celestial cues may have been obscured. On the other hand, in spring the tracks of both forward and reverse migrants tended to be *less* variable on overcast than on clear occasions (Richardson 1975 and in preparation).

Perhaps we should not be surprised by reduced variance in tracks under overcast. Reduced variance might indicate deterioration, not improvement, in orientation. For example, birds with a variety of preferred directions and orientation mechanisms might switch to a single mechanism, e.g., downwind flight, when flying under overcast.

Nocturnal landbird migrants over the NE U.S.A. apparently tend to orient downwind when under overcast (Able 1982). If so in SE Canada, one would expect the deviation of track from downwind to be reduced on overcast occasions. However, multiple regression analyses for each category of migrants showed no strong tendency for this (Richardson 1975). Instead, mean tracks were correlated with wind direction in a similar manner under cloudy and clear skies (e.g., Fig 5). Furthermore, reverse migration (RM) over SE Canada cannot be fully explained as downwind flight with overcast and seasonally inappropriate winds (see above). RM in both spring and

Table 3

Regression of mean tracks of various categories of migrants over SE Canada on geostrophic wind direction[1].

Type of Migration and Main Flight Directions	Wind Direction (from) Considered	Night Slope[1]	Night r_s[2]	Night *n*	Day Slope	Day r_s	Day *n*
Spring							
All Forward (NNW−ENE)	ESE−SSW−WNW	0.51	0.61	46	0.50	0.63	37
Passerines (NNE−ENE)	SE−SW−NW	0.36	0.45	27	–	–	–
Reverse (SE−SW)	W−N−E	0.66	0.51	29	0.57	0.61	31
Autumn							
Reverse (N−E)	SE−SW−NW	0.60	0.46	42	0.51	0.25	70
Forward (SSW−WNW)	NW−NE−SE	0.43	0.51	36	0.38	0.35	41
Shorebirds (ESE−SSE)	SW−NW−NE	0.44	0.42	47	0.40	0.57	43

[1] The geometric mean method (see Fig 5) was applied to occasions when winds were following or side. All slopes are significantly more than 0.0 but significantly less than 1.0 ($\alpha = 0.05$).

[2] Spearman rank correlation.

autumn occurred on both clear and overcast occasions.

Overcast had a more conspicuous effect on numbers aloft than on orientation. The reduced tendency to fly under overcast may be partly a result of the reduced range of orientation mechanisms usable when celestial or terrestrial cues are obscured. However, orientational problems are probably only one of several factors causing selection against individual birds that fly on cloudy occasions (see above).

ROUTES VS. WEATHER

Results from SE Canada illustrate (1) adjustments in routes of individual migrants in response to current weather, and (2) adaptation of large-scale migration patterns to prevailing wind patterns.

Dawn Reorientation of Landbirds

Landbirds that take off from Newfoundland and eastern Nova Scotia in the evening and fly SW may be over water east or south of Nova Scotia at dawn (Fig 1B). Around dawn, these birds sometimes turn to the NW, the direction likely to return them to land most quickly (Baird and Nisbet 1960, Murray 1976). However, on other mornings they continue SW (Richardson 1978b). Birds continuing SW, generally parallel to the coast, will not reach land for at least several hundred kilometers (no closer than Cape Cod, MA; possibly not until Cape Hatteras, NC).

On mornings when landbirds continue SW over the ocean, the wind is from the north or NE—favorable for continued SW flight and less favorable for NW flight back to land (Richardson 1978b). On mornings with other winds, especially opposing SW or W winds, the birds reorient from SW to NW and attempt to return to land. A bird's route will be quite different depending whether it continues SW or reorients NW at dawn. The route followed by these migrants seems largely determined by the winds encountered over the sea around dawn.

Migration from SE Canada to the West Indies

Some shorebirds and landbirds fly SE or S from Nova Scotia and New England toward the West Indies in autumn, but there is little or no reciprocal flight in spring. This is apparently an adaptation to prevailing wind patterns (Richardson 1974, 1976; Gauthreaux 1980). Weather over the western Atlantic is dominated by the so-called Bermuda high, which results in prevailing northerly winds east of Bermuda and southerly winds closer to the coast (Fig 6). Near the West Indies, the wind is almost always easterly.

Birds leave the coast in NW winds behind cold fronts (see above). Post-frontal following winds usually persist along the first 1/4−1/3 of the overwater route to the West Indies. Thereafter the birds are in the zone of prevailing following winds east of the Bermuda high, or in the light winds near the center of the high (Fig 6). South of Bermuda, mean tracks shift to S or SSW, and the birds usually arrive at the West Indies with side or partly following easterly winds (Richardson 1976, Williams and Williams 1978). Thus these birds usually encounter following or partly following winds throughout the nonstop flight to the West Indies. Flight altitudes range from low to extremely high ($>$ 6 km). Some birds may select altitudes with optimum winds (Richardson 1976, Alerstam 1981), although evidence on this point is inconclusive (Williams 1985).

Birds that fly SW down the coast to Florida and then SE along the West Indies avoid the long overwater flight but must travel much farther, largely against the prevailing winds (Fig 6). Many landbirds do fly SE along the West Indies (Richardson 1976). However, the disadvantages of this route apparently are sufficient to make it adaptively advantageous for many birds to fly along the "downwind" overwater route from SE Canada to the West Indies.

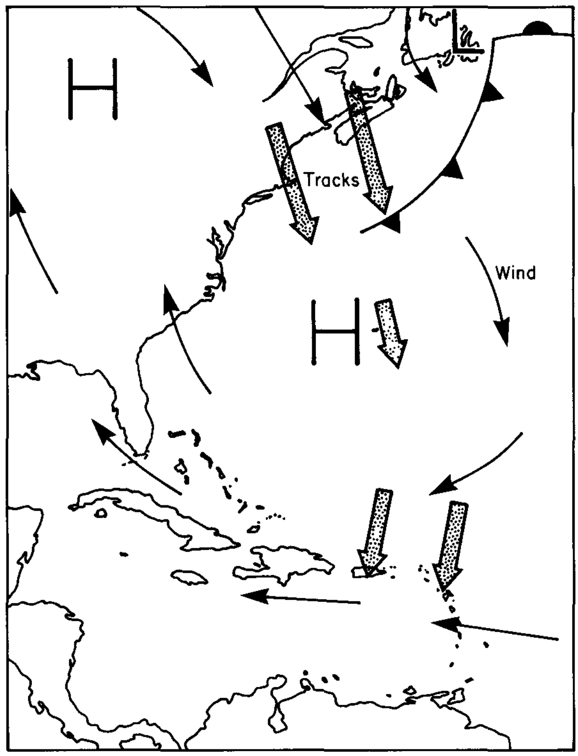

Figure 6
Typical weather over the western Atlantic when birds depart from SE Canada toward the West Indies in autumn.

Winds over the western Atlantic in spring are similar to those in autumn. These winds are favorable for NW flights from the West Indies toward Florida, and then for N and NE flights over the mainland and coast (Fig 6; Gauthreaux 1980). In contrast, winds do not favor northward flight over the ocean directly to eastern Canada. Radar observations in Puerto Rico show that spring migrants do indeed depart mainly to the NW; very few depart to the north (Richardson 1974).

This paper summarizes some but not all ways in which weather can affect the timing, orientation and routes of migration. Other influences not discussed here include the effects of weather in concentrating or dispersing birds at leading lines, the importance of updrafts to soaring birds, and weather-induced mortality during migration. I have also mentioned only a few of the important theoretical analyses and experimental studies that have been done. However, the data from eastern Canada do demonstrate that weather can influence avian migrants profoundly.

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