Anim. Behav., 1983, **31**, 173–180

COMPUTER SIMULATION OF AUTUMNAL BIRD MIGRATION OVER THE WESTERN NORTH ATLANTIC

By PHILIP K. STODDARD,* J. ELLEN MARSDEN† & TIMOTHY C. WILLIAMS‡§

**Animal Behavior Program, Department of Psychology, NI-25, University of Washington, Seattle, WA* 98195

†*Section of Neurobiology and Behavior, Mudd Hall* 3, *Cornell University, Ithaca, NY* 14850

‡*Department of Biology, Swarthmore College, Swarthmore, PA* 19081

Abstract. Two hypotheses for the orientation of autumnal migration over the western North Atlantic Ocean, proposed by Williams and Richardson, were tested by simulating the flight of birds from North to South America through calculated wind fields in the western North Atlantic Ocean. Use of a constant compass heading proved to be a tenable strategy for birds departing from the North American coast as far north as Nova Scotia. The range of successful headings, however, became increasingly restricted at northern latitudes. Airspeed, heading, altitude, and point of departure all had major effects on migratory success. Time required for successful non-stop migration was found to lie between 70 and 100 h for passerines and 40 to 60 h for shorebirds.

The shortest route between the northeastern coast of North America and the neotropical wintering grounds of many North American migrants lies over the western North Atlantic Ocean. This route is one half shorter than the overland route through Mexico or a third shorter than the island-hopping route along the chain of Antilles in the Caribbean. While it is energetically the most efficient route, this non-stop overwater flight approaches or exceeds the estimated limits of passerine flight (Tucker 1974; Greenewalt 1975; Hussel & Lambert 1980).

This paper examines two proposed mechanisms explaining how birds navigate over the Atlantic during autumn migration. (1) Williams & Williams (1978) proposed that passerines and shorebirds make such flights by maintaining a constant compass heading, and allowing natural deflection by the wind to guide their course. Their observations show that migrants arrive at the North American coast and wait until the passage of a cold front moving off the coast, and then depart to the south or southeast, obtaining beneficial tailwinds in the wake of the frontal system for 10 to 20 h (Drury & Keith 1962; Drury & Nisbet 1964; Richardson 1972, 1979, 1980; Williams et al. 1977). The birds then overtake the front and continue with variable winds until they reach the northeast trade winds south of Bermuda. The model predicts that these trade winds will then deflect the birds' tracks to the southwest, accounting for the westerly component in the movement of many migrants seen with Caribbean radars (Richardson 1976; Williams et al. 1977). (2) Richardson (1979) recorded shorebirds departing from Nova Scotia on headings too far east to reach South America, and he suggests that at least some of these birds redirect their flight en route. Both Richardson (1976) and Williams et al. (1977) noted, from radar observations, that birds migrating across the western North Atlantic tend to increase their altitudes during migration; some shorebirds, however, have been observed at very high altitudes as they leave the North American coast (Nisbet et al. 1963; Richardson 1979).

We investigated these hypotheses by simulating the movement of birds through an averaged wind field over the North Atlantic Ocean, and by examining how migrant tracks are affected by their airspeed, heading, altitude, and point of departure. Our primary intention was to test the duration and distance limitations on passerine migration, because these birds are the most restricted in terms of endurance and flight speed during overwater migration. Larger birds such as some shorebirds are thought to make much longer non-stop flights, e.g. from James Bay, Canada, to at least the north coast of South America (Richardson 1979), or possibly as far as Patagonia (Hagar 1966). We simulated the flights of shorebirds to determine if there is an advantage to reorienting en route as opposed to maintaining a constant heading.

§Reprint requests should be sent to T.C.W.

To test these hypotheses, we used the following parameters:

Altitude. 1500 m, 3000 m, and 5800 m. These altitudes correspond to the meteorological constant pressure charts that are closest to the minimum, average, and maximum altitudes of flight for Atlantic migrants as reported by Williams et al. (1977) and Richardson (1976, 1979).

Airspeed. Very few measurements of airspeeds of birds have been made under conditions approaching sustained migratory flight (see Williams & Williams 1980). Aerodynamic calculations (Greenewalt 1975; Pennycuick 1969) and observations of identified migrants tracked with radar (Bruderer & Steidinger 1972) suggest migratory airspeeds of 30 to 50 km/h for small songbirds and 60 to 100 km/h for shorebirds. To investigate limiting conditions, we used 35 km/h for passerines and 60 km/h for shorebirds. Higher values were used for typical passerine tracks: the average airspeed of presumed passerines detected over Antigua in October was 47 km/h (Williams, in preparation). Because optimal airspeed changes with weight and thus fat consumption during migration (Nisbet et al. 1963), the speeds used are assumed to be averages of airspeed over the entire flight.

Heading. The daily mean heading of birds' flight over Antigua ranged from 128° to 166° (Williams, unpublished data). Mean headings of birds departing the North American coast varied much more widely, due, at least in part, to the inclusion of many birds not adapted to the overwater flight (see Williams & Williams 1978). We used headings of 130° to 180°.

Flight time. We chose 100 h as the maximum limit for the simulated flights; this is an average value between the conservative estimate of 80 h and the upper limit of 115 h cited by Nisbet et al. (1963).

Methods

The simulations were performed on an IBM 5100 microcomputer with a program written in APL. The speed, heading, altitude, and point of origin of a 'bird' were entered; the program then referred to the appropriate wind field (see below) and calculated the vector sum of the velocities of the bird and the wind, multiplied by a time increment of 5 h. Shorter time increments, while they greatly extended the running time of the program, were not found to significantly alter the precision of the resulting tracks. The bird's new longitude and latitude were then determined, including correction for a spherical earth. The program ran until the bird reached South America (south of 10° N), became an unsuccessful migrant by exceeding 100 h flying time, or flew east of 50° W or west of 80° W (see Fig. 1a), thereby missing the South American coast entirely.

To obtain average wind conditions for Atlantic migrants we first used data from Williams et al. (1977) to select time periods during which major migrations of landbirds successfully crossed the western North Atlantic Ocean. Our criteria were: (1) Caribbean radar had to indicate large numbers of birds arriving from the north or northeast, (2) there had to be an absence of tropical storms in the area, and (3) the Caribbean arrivals had to precede by 72 to 90 h the passage of a major cold front over the eastern coast of North America (see Williams et al. 1978). Three dates met these criteria, with cold fronts passing the coast on 3 October 1971, 2 October 1972, and 3 October 1973. North of 30° N, we calculated the geostrophic winds over 5° quadrangles (indicated in Figs 1 and 2) at 12-h intervals for 5 days after each of these dates, using 850 millibars (mb), 700 mb, and 500 mb NOAA (National Oceanic and Atmospheric Administration) constant pressure charts corresponding to altitudes of approximately 1500 m, 3000 m, and 5800 m, respectively. The matrices were then averaged, by taking the angular mean of each set of vectors, to produce one 5-day wind map for each altitude. South of 30° N winds cannot be predicted by the same techniques used for analysing mid-latitude weather maps (see Barry & Chorley 1970, pp. 218–219); consequently, winds below this latitude were estimated from winds aloft recorded at Miami, Puerto Rico, Antigua, Barbados, and Trinidad over the periods of 20 September to 20 October, 1971, 1972, and 1973, and from 10-year average wind profiles supplied by the Woods Hole Oceanographic Institution for September and October. Wind data began at 2000 Eastern Standard Time (EST) the night after a cold front passed over the coast, and the wind matrix was updated every 12 h (approximately the shortest time a bird could fly through a 5° quadrangle). The averaging technique described above obscured several small scale features of weather systems, such as the strong southwest winds encountered just in advance of a cold front. Because they are of limited geographical extent, such features had minor (less than 10%) effects on simulated flight time.

Results

1. Simulation of Williams & Williams' Hypothesis

The simulated tracks in Figs 1a and 1b indicate that lateral wind drift from a constant compass heading, as proposed by Williams & Williams (1978), could produce the curved tracks of Atlantic migrants inferred from radar data. Maintenance of constant flight to the south, or in some cases southeast, resulted in successful flights over the western North Atlantic of less than 100 h for the three departure points tested. Table I gives the results of multiple simulation runs in terms of elapsed time for successful migrants and final destination of unsuccessful migrants. Table II shows the simulated flight of birds that increase in altitude during migration as reported by Richardson (1976, 1980) and Williams et al. (1977) from their radar observations. These results will be discussed in relation to each of the flight variables.

Effects of Flight Variables

Heading. Figure 1a illustrates the effect of different headings on simulated bird tracks from Cape Cod. All of the simulated 45 km/h migrants with constant headings greater than 150° reached South America in less than 90 h. As illustrated by these simulated tracks, birds with headings less than 150° cannot make a successful landfall because the coast of South America angles sharply southward east of 60°W, increasing the flight distance and time beyond the presumed endurance of passerine migrants. This restricts low-airspeed, constant-heading migrants departing from more northerly points to headings greater than 150°. As may be seen from Fig. 1a, many simulated migrations from Nova Scotia failed because they were shifted too far east.

Departure point. Because of the northeast–southwest orientation of the North American coast, northern departures begin to the east of southern departures. As illustrated in Fig. 1b and Table I, this eastward displacement causes the landfall in South America to be farther south, thus lengthening the flight distance at both ends. While it might seem that birds departing from farther north should take longer to reach South America, the simulation indicates that flight times actually do not vary much, because of the compensating effect of favourable wind velocities at higher latitudes.

Altitude. Winds vary both in speed and direction with altitude. North of Bermuda, the primary difference is in the strength of north and west winds behind a cold front. These are generally most favourable at 1500 m and 3000 m, with the 5800 m weather systems lagging 12 to 24 h behind the 1500 m weather systems. In the Caribbean, average winds decreased in velocity from 1500 m to 5800 m (see Richardson 1976; Williams et al. 1977). Lower altitude birds over the Carribbean are thus deflected westward to a greater extent than birds at 5800 m (see Fig. 1c).

Wind conditions, and thus altitude of flight, are most important for slow flying birds (35 to 45 km/h); the faster fliers (60 to 75 km/h) are little affected by winds, as may be seen in Fig. 1d. The best flight strategy for the faster birds, such as shorebirds, would be to head for their destination along a great circle route with little regard for wind conditions or altitude. The slower fliers (e.g. passerines, which appear to make up the bulk of the Atlantic migrants in late September and early October (Richardson 1976; Williams et al. 1977)), would be more affected by wind conditions and would require a flight strategy accounting for wind drift.

Table II shows the results for simulated birds increasing their altitude during migration while maintaining a constant heading throughout the flight. The flight times are similar, but as illustrated in Fig. 1c, increasing altitude over the Caribbean results in progressively greater eastward displacement of the final destination. This displacement is undesirable for birds departing from the more northern (and thus more eastern) areas of the North American coast and therefore limits this migratory strategy to birds with headings greater than 160°. Increasing altitude might, however, be beneficial to birds departing from the North American coast south of Cape Cod with destinations in eastern South America. Such migrants could greatly reduce the length of west-to-east flights over the South American continent without greatly increasing the total time spent in overwater flight (see also Richardson 1976; Pennycuick 1978).

2. Simulation of Richardson's Hypothesis: Shorebird Strategies

Richardson's (1979) data showed shorebirds departing from Nova Scotia with an average ground speed of 74 km/h and a range in daily mean tracks of 110° to 170° (average 134°). Richardson (personal communication) estimates average airspeed at 60 km/h. The simulation, in agreement with Richardson's interpretation, indicated that the majority of the shorebirds had

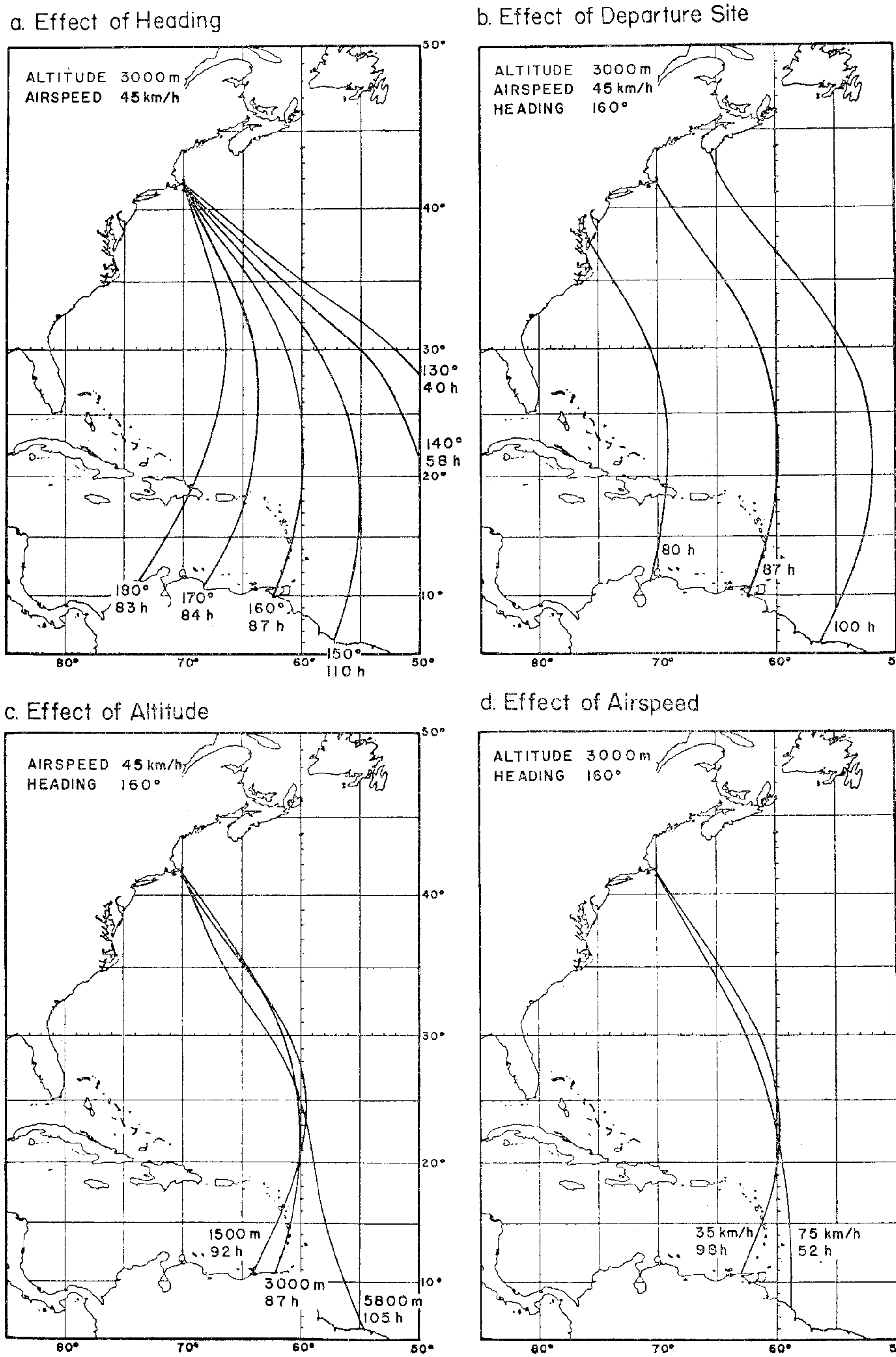

Fig. 1. Simulated tracks of North American land birds crossing the western North Atlantic Ocean using constant compass orientation. (a) Altitude and airspeed constant: effect of heading on birds departing Cape Cod. Heading and flight time indicated at the end of each track. (b) Altitude, airspeed, and heading constant: effect of departure point. (c) Airspeed and heading constant: altitude and simulated flight time indicated for each track. (d) Altitude and heading constant: airspeed indicated at end of each track. Tracks which exceed the 100 h limitation (see text, page 174) in mid-ocean were extrapolated until they reached their probable destination on the South American coast. Longitude/latitude lines correspond to the 5° quadrangles used for the weather matrices (see Methods section).

Table I. Flight Times of Simulated Migrations Over the Western North Atlantic Ocean at Constant Altitude

Departure point	Altitude	130° 35	130° 45	130° 60	140° 35	140° 45	140° 60	150° 35	150° 45	150° 60	160° 35	160° 45	160° 60	170° 35	170° 45	170° 60	180° 35	180° 45	180° 60
Nova Scotia	5800 m	E	E	E	E	E	E	E	E	E	E	E	E	90	70	60	95	75	60
	3000 m	E	E	E	E	E	E	E	E	E	110	E	E	90	70	55	90	70	55
	1500 m	E	E	E	E	E	E	T	E	E	T	90	65	100	80	60	100	80	60
Cape Cod	5800 m	E	E	E	E	E	E	E	E	E	90	70	60	90	70	60	95	70	60
	3000 m	E	E	E	E	E	E	100	E	E	95	75	55	95	75	55	95	75	55
	1500 m	E	E	E	T	E	E	T	85	E	T	80	60	95	80	60	T	80	60
Wallops Island	5800 m	E	E	E	T	E	E	100	75	60	100	75	55	95	70	55	95	70	55
	3000 m	T	E	E	T	85	65	100	75	55	90	75	55	90	70	50	W	W	50
	1500 m	T	100	E	T	85	65	T	80	60	100	75	55	W	70	55	W	W	W

Heading: 130°–180°; Airspeed (km/h): 35, 45, 60.

E —track went east of 50°W longitude.
W—track went west of 80°W longitude.
T —flight time exceeded 100 h.

Table II. Flight Times of Simulated Atlantic Migrants Changing Altitude En Route: 0–20 h at 1500 m, 21–50 h at 3000 m, 51+ h at 5800 m

Departure point	130° 35	130° 45	130° 60	140° 35	140° 45	140° 60	150° 35	150° 45	150° 60	160° 35	160° 45	160° 60	170° 35	170° 45	170° 60	180° 35	180° 45	180° 60
Nova Scotia	E	E	E	E	E	E	E	E	E	E	E	E	95	75	60	95	75	60
Cape Cod	E	E	E	E	E	E	T	E	E	95	75	60	95	75	60	100	75	55
Wallops Island	T	E	E	T	85	65	100	75	55	90	70	50	90	70	50	90	65	45

Heading: 130°–180°; Airspeed (km/h): 35, 45, 60.

E —track went east of 50°W longitude.
W—track went west of 80°W longitude.
T —flight time exceeded 100 h.

headings too far east to accomplish a western Atlantic transit using a constant compass heading. He suggests that shorebirds reorient en route, turning from southeast to south after they depart from the coast. Figure 2 gives the results of simulated reorientations. The shortest route, in terms of distance, would be for birds to head due south along the meridian. Fast flying birds, such as shorebirds, with constant headings less than 150°, would fail to intersect the South American coast. For rapidly flying birds, the southeastward flight followed by southward reorientation has an effect similar to increasing altitude for slow fliers; it causes them to displace their landfall on the South American coast eastward without greatly increasing the over-ocean transit time. Shorebirds departing from Nova Scotia heading 134° for about 10 h and then turning to 170° for the remainder of their flight would reach Surinam or Guyana, major shorebird staging and wintering areas (McNeil & Burton 1973; Spaans 1978), after about 70 h.

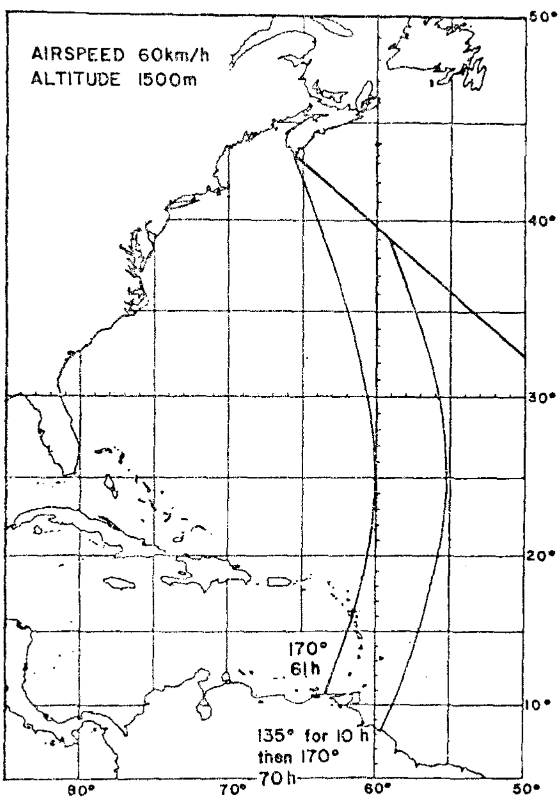

Fig. 2. Simulated tracks of shorebirds departing from Nova Scotia at constant altitude and airspeed, showing the effect of reorientation during transatlantic flight. Heading and flight time shown at the end of each track.

Discussion

Our simulation of Williams & Williams' hypothesis indicates that constant compass orientation could be used successfully by passerine migrants departing from the North American coast as far north as Nova Scotia. However, the range of permissible headings for a successful transit in the simulation is in all cases much less than the range of headings of actual migrants observed with coastal radars (Drury & Keith 1962; Drury & Nisbet 1964; Richardson 1978, 1979, 1980; Williams & Williams 1978). As discussed by Williams et al. (1977) and Williams & Williams (1978), the majority of birds detected by coastal radars do not make successful Atlantic crossings. Thus those birds with headings beyond the permissible limits may reorient and return to land as reported by Baird & Nisbet (1960), Swinebroad (1964), Murray (1976) and Richardson (1978), or may be among the many lost at sea (Ralph 1975; McClintock et al. 1978).

The primary limiting factor in the constant compass hypothesis appears to be excessive eastward displacement. Both increasing altitude during migration, and an eastward flight from Nova Scotia followed by reorientation, serve to increase this eastward displacement of the landfall in South America. These strategies may be of importance to migrants with low flight speeds departing from southern or central U.S. coastal points, or for shorebirds departing from the Canadian Maritime Provinces, respectively.

The results of our simulations using Richardson's data indicate that successful migrants departing from Nova Scotia must either have headings greater than 150°, or must reorient their flight to the south en route, as Richardson hypothesized. However, at departure points farther south on the North American coast, Atlantic migrants may have increasingly easterly headings and still complete a successful transit with a constant compass heading orientation, as shown in Table I.

Finally, it is interesting to note that this simulation may also be used to infer the average point of origin of migrants detected passing over the Caribbean islands. Thus, passerines with a heading of 155° moving over Antigua or Barbados probably departed the North American coast somewhere between Cape Cod and New York, assuming they maintained their heading throughout the flight. Similarly, the migrants reported by Williams & Williams (1978), arriving over Antigua from the Atlantic at an average airspeed of 49 km/h and a heading of 163° probably departed from somewhere near New York; those moving along the Antilles (airspeed 45 km/h, heading 132°) probably departed from the vicinity of the Carolinas.

We emphasize that our simulation cannot provide evidence that the hypothetical routes shown are actually taken, but only that they could be used. The details of the daily wind patterns are surprisingly unimportant. To test our conclusions, we simulated tracks with the unaveraged wind patterns as well as the average values. Although the simulated tracks varied, the general conclusions did not.

Departure of birds at times other than shortly after the passage of a cold front would result in the loss of favourable wind conditions north of about 35°N. These northwest winds were essential for successful flights of low airspeed birds departing Cape Cod and Nova Scotia in our simulation. Thus a constant compass strategy within the limits outlined above should allow even passerine migrants to cross the western North Atlantic so long as they depart after the passage of a strong cold front (as they have been observed to do (Drury & Keith 1962; Drury & Nisbet 1964; Richardson 1972, 1979, 1980; Williams et al. 1977)), and do not encounter tropical storms en route.

Acknowledgments

We would like to thank D. Newitt, M. Wood, and the staff of the Swarthmore Computer Center for their assistance during the writing of the program. S. Gauthreaux, M. Hyatt, P. Kerlinger, M. Kreithen, R. Madden, I. Nisbet, W. Richardson and J. Williams made many helpful suggestions on drafts of the paper. This study was funded in part by Swarthmore College.

REFERENCES

Baird, J. & Nisbet, I. C. T. 1960. Northward fall migration on the Atlantic coast and its relation to offshore drift. *Auk*, **77**, 119–149.

Barry, R. G. & Chorley, R. J. 1970. *Atmosphere, Weather and Climate*. New York: Holt, Rhinehart and Winston.

Bruderer, B. & Steidinger, P. 1972. Methods of quantitative and qualitative analysis of bird migration with a tracking radar. In: *Animal Orientation and Migration* (Ed. by K. Schmidt-Koenig and S. Galler), pp. 151–167. Washington, D.C.: NASA SP262.

Drury, W. H. & Keith, J. A. 1962. Radar studies of songbird migration in coastal New England. *Ibis*, **104**, 449–489.

Drury, W. H. & Nisbet, I. C. T. 1964. Radar studies of orientation of songbird migrants in southeastern New England. *Bird-Banding*, **35**, 69–119.

Greenewalt, C. H. 1925. The flight of birds. *Trans. Am. Phil. Soc.*, **65**, 1–67.

Hagar, J. 1966. Nesting of the Hudsonian Godwit at Churchill, Manitoba. *Living Bird*, **5**, 1–43.

Hussel, D. J. T. & Lambert, J. B. 1980. New estimates of weight loss in birds during nocturnal migration. *Auk*, **97**, 547–558.

McClintock, C., Williams, T. C. & Teal, J. M. 1978. Autumnal migration observed from ships in the western North Atlantic Ocean. *Bird-Banding*, **49**, 262–277.

McNeil, R. & Burton, J. 1973. Dispersal of some southbound migrating North American shorebirds away from the Magdalen Islands, the Gulf of St. Lawrence and Sable Island, Nova Scotia. *Carib. J. Sci.*, **13**, 257–278.

Murray, B. G. 1976. The return to the mainland of some nocturnal passerine migrants over the sea. *Bird-Banding*, **47**, 345–359.

Nisbet, I. C. T., Drury, W. H. & Baird, J. 1963. Weight loss during migration, Parts I and II. *Bird-Banding*, **34**, 107–159.

Pennycuick, C. J. 1969. The mechanics of bird migration. *Ibis*, **111**, 525–556.

Pennycuick, C. J. 1978. Fifteen testable predictions about bird flight. *Oikos*, **30**, 165–176.

Ralph, C. J. 1975. Age ratios, orientation, and routes of land bird migrants in the northeastern United States. Ph.D. thesis, Johns Hopkins University.

Richardson, W. J. 1972. Autumn migration and weather in Eastern Canada: a radar study. *Am. Birds*, **26**, 10–17.

Richardson, W. J. 1976. Autumn migration over Puerto Rico and the western Atlantic: a radar study. *Ibis*, **118**, 309–332.

Richardson, W. J. 1978. Reorientation of nocturnal landbird migrants over the Atlantic Ocean near Nova Scotia in autumn. *Auk*, **95**, 717–732.

Richardson, W. J. 1979. Southeastward shorebird migration over Nova Scotia and New Brunswick in autumn: a radar study. *Can. J. Zool.*, **57**, 107–124.

Richardson, W. J. 1980. Autumn landbird migration over the western Atlantic Ocean as evident from radar. *Proc. 17 Intern. Ornithol. Congr., Berlin*, **1978**, 501–506.

Spaans, A. L. 1978. Status and numerical fluctuations of some North American waders along the Surinam coast. *Wilson Bull.*, **90**, 60–83.

Swinebroad, J. 1964. The radar view of bird migration. *Living Bird*, **3**, 65–74.

Tucker, V. A. 1974. Energetics of natural avian flight. *Publ. Nuttal. Ornithol. Club*, No. **15**, 298–334.

Williams, T. C. & Williams, J. M. 1978. The orientation of transatlantic migrants. In: *Animal Migration, Orientation, and Homing* (Ed. by K. Schmidt-Koenig & W. Keeton), pp. 239–251. Berlin: Springer-Verlag.

Williams, T. C. & Williams, J. M. 1980. A Peterson's guide to radar ornithology? *Am. Birds*, **34**, 738–741.
Williams, T. C., Williams, J. M., Ireland, L. C. & Teal, J. M. 1977. Bird migration over the western North Atlantic Ocean. *Am. Birds*, **31**, 251–267.
Williams, T. C., Williams, J. M., Ireland, L. C. & Teal, J. M. 1978. Estimated flight time for transatlantic migrants. *Am. Birds*, **32**, 275–280.

(*Received* 24 *December* 1981; *revised* 27 *May* 1982; *MS. number:* A2769)