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CONSTANT COMPASS ORIENTATION FOR NORTH AMERICAN AUTUMNAL MIGRANTS

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Abstract.—Autumnal migrant flights were simulated from central North America to the Atlantic coast. Synoptic weather conditions associated with major S and SE bird migrations observed with radar were used to create a wind matrix for the simulation. Constant compass orientation was found to be a tenable strategy for the continental as well as the transatlantic portion of migration from North to South America via the western North Atlantic. Selection of wind conditions and heading were found to be more important than airspeed for trajectory of simulated tracks. Winds at 1500 m altitude offered shorter transit times than winds at 300 m and increased accuracy of orientation compared to winds at 5800 m. Although the simulation was restricted to S and SE migrants in eastern North America, it demonstrated the general importance of wind selection (as opposed to compensation for wind drift) for migratory strategy.

USO CONSTANTE DE LA BRÚJULA PARA LA ORIENTACIÓN POR PARTE DE MIGRATORIOS OTOÑALES DE NORTE AMÉRICA

Sinopsis.—Vuelos migratorios otoñales fueron simulados desde la parte central de Norte América hacia la costa del Atlántico. Condiciones climatológicas sinópticas observadas a través del radar y asociadas a migraciones mayores de aves al sur y al sureste, fueron utilizadas para establecer una matriz del viento para las simulaciones. Se encontró la utilización constante de la brújula como la posible estrategia para la orientación tanto de migratorios continentales como de individuos que se mueven de Norte a Sur América utilizando la ruta al oeste del Atlántico Norte. La selección de las condiciones del viento y su trayectoria resultaron ser más importantes que la velocidad del vuelo para determinar el movimiento de las aves en las simulaciones. El viento a 1500 m de altura ofreció un tiempo menor de tránsito que éste a 300 m, y una mayor precisión en la orientación que vientos a 5800 m. Aunque las simulaciones fueron restringidas a migrantes del este de Norte América, en sus movimientos hacia el sur y el sureste, éstas, demostraron la importancia de la selección del viento (en oposición a la compensación por la deriva del viento) para establecer estrategias de migración.

Stoddard et al. (1983) simulated constant compass orientation during autumnal migration from North America to South America over the western North Atlantic Ocean. Departures of transatlantic migrants from the North American coast were simulated from as far north as Nova Scotia. An iterative computer program moved birds with constant headings of 130–180° and airspeeds of 35–60 km/h through a matrix of wind velocities. These winds were derived by averaging wind conditions over the ocean during the period of three heavy migrations (as observed by radar). Stoddard et al. (1983) found constant compass orientation to be a tenable strategy for the transoceanic migrants, although heading was constrained at northern latitudes. Observed headings of migrants in the Caribbean corresponded to simulated headings. Flight times were within the estimated maximum durations of flight for several species, and drift by northwest trade winds was sufficient to account for the observed change in track direction from SE over Bermuda to S or SSW over the Caribbean. (Track and ground speed refer to the velocity of a bird relative to the ground. Heading and airspeed refer to the velocity of a bird relative to the air mass in which it flies.)

Information from experimental and observational studies now indicates that constant compass orientation may be used by continental as well as transoceanic migrants, especially for first-year flights (Berthold 1988, Gwinner 1990). Radiotelemetry has shown that individual migrants maintain constant headings during flights of 200–700 km even under shifting wind conditions (Cochran and Kjos 1985). Thus, transatlantic migrants might use constant compass orientation to move from breeding grounds to the coast as well as to cross the ocean to South America. To investigate the feasibility of North American migrants using a single compass heading for their entire flight, I simulated flights backward in time from heavy migrations observed with radar on the Atlantic coast and forward from heavy migrations observed with radar near the center of the continent.

SIMULATION MODEL

The simulation of North American migration used the following model. A bird on the ground at sunset would first assess the synoptic weather situation and then the wind direction before deciding to fly. If the bird were between a cold front and the center of the high west of the front, and if the wind direction were in the sector blowing toward 90–270°, the bird would fly at a specified airspeed and heading for 12 h (equivalent to one night). Reducing the flight time to less than 12 h did not affect the results. These criteria for departure were based on radar observations of bird migration. Transatlantic migration (Williams et al. 1977) and autumnal North American migration in general (Richardson 1978) were most likely to be triggered by sunset and these weather and wind conditions. For birds simulated to fly at altitudes of 1500 m and 5800 m, I first applied the criterion of synoptic weather at ground level, then wind direction at ground level, then wind direction at 1500 m, and then, if necessary, wind direction at 5800 m. This model follows the behavior of individual, radio-tracked migrant thrushes (*Catharus* spp.) reported by Cochran and Kjos (1985).

I used an improved version of the Stoddard et al. (1983) computer program, which computed the latitude and longitude of a simulated migrant at 1-h intervals. The program corrects for the curvature of the earth and computes a weighted average wind velocity (direction and speed) for each hour of flight.

The wind matrix through which I simulated bird flight was not an average of all winds but an average of only those wind and weather conditions known to have supported major bird migrations moving to the S and SE as observed by radar. The dates of major migrations departing the eastern coast of North America during late September and October 1971, 1972, and 1973 were determined from radar observations at Halifax, Nova Scotia, Chatham, Massachusetts, and Wallops Island, Virginia as reported by Williams et al. (1977). The dates of major migrations in the interior were determined from observations with a mobile ornithological radar at Clam Lake, Wisconsin (46°10'N, 90°50'W) during late September and October 1975 and October 1977. This radar is described in Sielman et al. (1981) and Williams et al. (1981). The direction and timing of these migrations were strongly related to season of the year and synoptic weather conditions (Williams and Williams 1979) and were similar to radar observations of migration at other sites in central North America (Richardson 1978).

The synoptic weather systems that were associated with bird migrations observed on radar were then followed in time as they crossed eastern North America. Average wind velocity was determined for each 5° by 5° matrix square for those areas that met the criteria for simulated departures. Wind velocities were determined from surface maps, from 850-mb constant-pressure charts (about 1500 m altitude), and from 500-mb constant-pressure charts (about 5800 m altitude). Radar observations of the altitude of bird flight indicate that the winds at 1500 m will be closest to the average altitude of migrant birds over continental areas (Eastwood 1967, Williams et al. 1977). Surface winds are critical not only for the initiation of migration but also for birds flying at altitudes of less than 300 m. Flight at altitudes greater than 5000 m is rare but has been observed for shorebirds (Richardson 1979, Williams et al. 1977).

RESULTS

The wind velocities used for the simulation are shown in Figure 1a. Average direction at 1500 m was NNW, toward 158° ± 35° (SD), N = 595, and average speed 19.7 ± 7.5 km/h (5.5 ± 2.1 m/s). Average winds at the surface were in a similar direction, toward 155° ± 35°, N = 500, but weaker, average speed 8.4 ± 4.1 km/h (2.4 ± 1.1 m/s). Average winds at 5800 m were much stronger: 35 ± 16 km/h (9.7 ± 4.4 m/s), N = 450, and northwesterly, toward 131° ± 28°. The effects of the jet stream can be seen in the band of strong westerly winds between 35° and 50°N at 5800 m in Figure 1a.

Simulated flights using winds measured at the earth's surface are shown in Figure 1b. These data are generally considered to be a good estimate of wind conditions up to 300 m when combined with geostrophic information (Neiburger et al. 1973). Simulations are shown for two starting points, one 45°N, 90°E near the western Great Lakes in Wisconsin, and the other at 51°N, 80°E just south of James Bay. Figure 1c shows simulations at 1500 m and Figure 1d shows simulations at 5800 m. Simulated tracks are shown for airspeeds of 35 km/h (10 m/s), probably a lower limit even for passerine migrants, and 60 km/h (17 m/s), a value typical for rapidly flying birds such as shorebirds or waterfowl (Stoddard et al. 1983). In addition to the simulated tracks using the average winds for each matrix square, I also ran simulations using wind speeds 1 SD above the mean calculated separately for each matrix square, and directions 1

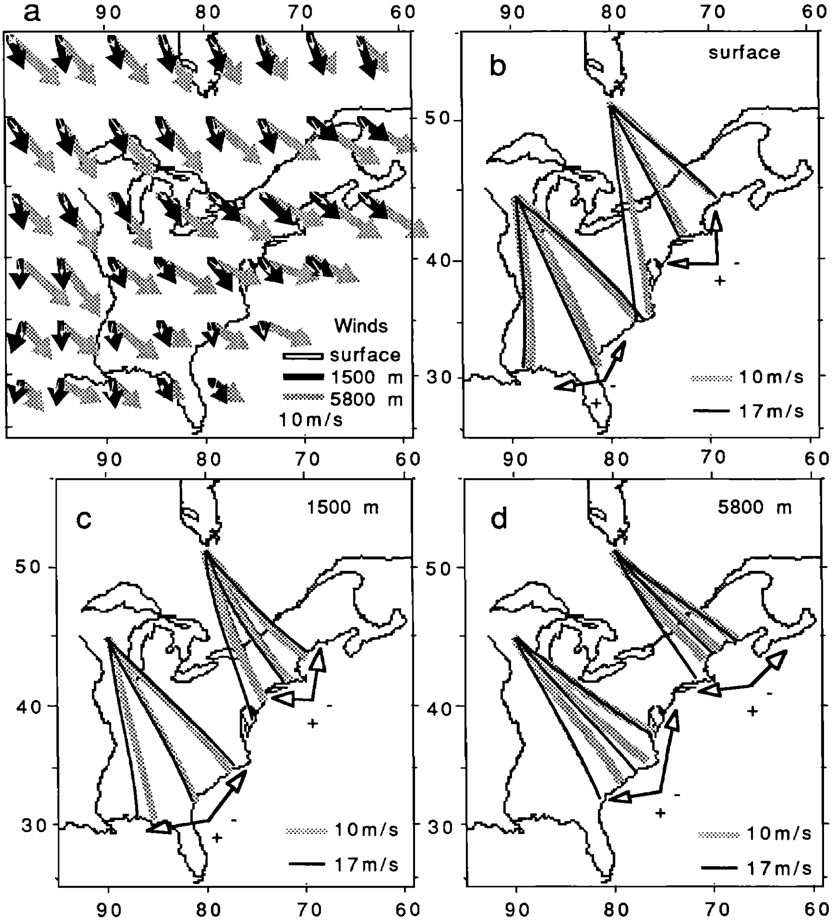

FIGURE 1. Wind velocities and tracks for simulated constant compass orientation over eastern North America. Degrees north latitude and west longitude are given at margins. 1a. Wind velocities used for simulation at three altitudes. Winds are the average of those dates which showed heavy bird migration to the south or southeast on radar at the coast or in northern Wisconsin. Vectors for surface winds may be offset slightly to the right in some cases for clarity. 1b. Simulated tracks in surface winds. At each of two departure points flights are simulated at headings of 130°, 155° and 180° clockwise from true north. Grey lines indicate tracks at a simulated airspeed of 35 km/h (10 m/s) and solid lines indicate tracks at 60 km/h (17 m/s). Open arrows indicate displacement east and west along coast for flights at 155° heading, 35 km/h airspeed, in winds 1 SD above the mean and 1 SD east (−) or 1 SD west (+) of the average wind direction for each matrix square. 1c. Simulated tracks with winds at 1500 m altitude, notation as in 1b. 1d. Simulated tracks with winds at 5800 m altitude, notation as in 1b.

TABLE 1. Time (h) for simulated autumnal migrants to reach North American coast.

Departure point	Surface 130°	Surface 155°	Surface 180°	1500 m 130°	1500 m 155°	1500 m 180°	5800 m 130°	5800 m 155°	5800 m 180°
	Airspeed = 35 km/h (10 m/s)								
Wisconsin	32	36	33	24	25	26	14	17	18
James Bay	22	24	36	16	16	18	10	10	10
	Airspeed = 60 km/h (17 m/s)								
Wisconsin	22	24	23	18	18	17	12	13	16
James Bay	15	17	25	11	12	15	9	9	10

SD above and below the mean for each square. These represented worst-case scenarios since winds would normally vary around a mean direction and speed during a flight. The displacements from a heading of 155° under these conditions are shown in Figures 1b, c and d.

All simulations showed birds moving rapidly and directly to the coast. Flight times to reach the coast are given in Table 1. Times varied from 36 h for flights in surface winds at an airspeed of 35 km/h to 9 h for flights in 5800 m winds at an airspeed of 60 km/h. I found that both passerines and shorebirds should be able to make the 900–1400 km flights shown in Figure 1 in two nights of flying. The average time for birds flying at a simulated airspeed of 35 km/h was 21.5 h. At 60 km/h the average flight time was 15.8 h. The short flight times reflect the strong, favorable winds used by autumnal migrants in North America. The small difference in transit times for the two airspeeds suggests that choice of wind conditions may be as important as airspeed for migrants. Flights in winds one SD greater than the mean wind speed shortened the flight by a few hours but had little effect on the trajectory of simulated tracks.

Each increase in flight altitude brought the birds under greater influence of wind conditions. At higher altitudes flight times were shorter (Table 1), tracks at different headings were more tightly clustered and overall displacement was shifted eastward (Fig. 1). Even birds with a SSE heading (155°) and an airspeed of 60 km/h were drifted far to the east if they flew high enough to encounter winds affected by the jet stream.

In the simulated flights, heading had a much greater effect than airspeed. Differences in the location of arrival at the coast were greatest in the relatively light winds near the surface (Fig. 1b). A difference of 25° in heading resulted in a displacement of 300–800 km along the coast. For comparison, a difference between airspeeds of 35 km/h and 60 km/h usually resulted in a displacement of less than 100 km.

The effect of heading on lateral displacement decreased at greater altitudes due to stronger winds (Figs. 1c, 1d). Flight at these higher elevations would not necessarily increase overall accuracy of orientation since variability in wind direction at altitudes of 1500 m and 5800 m becomes a major factor in track direction. This is illustrated by the worst-case scenario simulations shown by arrows in Figures 1b, c and d. At the surface, winds 1 SD above or below the mean resulted in much smaller lateral displacements than did a 25° change in heading (Fig. 1b). At 1500 m a 1 SD change in wind direction and speed produced about the same displacement as a 25° difference in heading (Fig. 1c), and at 5800 m the effect was considerably greater than a 25° difference in heading (Fig. 1d).

I also ran reversed flight simulations to determine the point of origin of transatlantic migrants passing over two well studied points on the Atlantic coast: Cape Cod, Massachusetts and Halifax, Nova Scotia. These more easterly departure points were chosen because the simulations by Stoddard et al. (1983) showed that constant compass orientation was severely restricted for such departure points. Specifically, birds departing Cape Cod with headings east of 150° or departing Nova Scotia with headings east of 160° would be unlikely to reach South America in less than 100 h. Simulations were run from the coast north to 55°N and showed that at 1500 m, birds reaching Cape Cod or Halifax on headings of 155° or greater must have initiated their flights east of James Bay (80°W). Flight at 5800 m with an airspeed of 35 km/h allowed the most westerly continental departure point (88°W, 55°N) as birds at this altitude and airspeed had the greatest drift to the east.

I also simulated flights of birds heading SW in the wind conditions originally selected for S and SE flight. A track direction of 220° would take birds from New England and the Maritime Provinces to the southeastern U.S., but birds with a heading of 220° and airspeeds of 35 or 60 km/h were soon drifted offshore even under surface wind conditions. Headings of 220° became tenable west of 75° W. Departures from the eastern Great Lakes (80°W, 45°N) were simulated at 220° heading and 35 km/h airspeed. In surface winds birds took 41 h to reach the Mississippi coast (88°W, 30°N). At 1500 m they reached the Georgia coast (81°W, 31°N) after 24 h and at 5800 m, birds were blown E over the North Atlantic at New Jersey (74°W, 39°N). Additional simulations showed SW headings under these wind conditions to produce inefficient, low groundspeed tracks and to expose coastal migrants to drift over the Atlantic Ocean. The exceptions were simulated tracks departing west of the Mississippi River at 1500 m, which used favorable winds to move rapidly to southern Texas and Mexico (Fig. 1a).

CONCLUSIONS

I conclude that constant compass orientation is a tenable strategy for transatlantic migrants moving from central continental areas to coastal departure points as well as for the oceanic portion of the flight. Even under worst-case scenarios, constant compass orientation would bring birds reliably to the coast. Flight at an altitude of 1500 m represents a compromise between low velocity winds at lower altitudes and significant drift by variable winds at altitudes of 5800 m. At 1500 m a group of birds departing southern James Bay at airspeeds of 35–60 km/h and headings of 130–180° or which encountered winds a full standard deviation above or below the mean in every point of the wind matrix, would all be expected to reach the eastern U.S. coast within 400 km of Long Island, New York. Transatlantic migrants departing the coast east of Cape Cod would be restricted to breeding in eastern North America if they were to maintain a constant heading for the entire migration.

Almost all studies of autumnal bird migration in North America have shown that the great majority of autumnal migrants move under the synoptic weather conditions used here for simulations of S and SE migrations (Richardson 1978). By choosing to fly only under a narrow range of synoptic conditions, birds reduce both their total flight time and the dispersal of their tracks at different headings. The poor performance of birds with SW headings under the conditions selected by S and SE migrants suggests that there must be additional selection for wind conditions within the synoptic conditions that trigger take off. Cochran and Kjos (1985) have observed such wind selection directly and report it is based on the birds' net ground speed in the direction of their heading.

Although this simulation pertains to birds using constant heading orientation and to migrants moving S and SE, the findings are pertinent to migratory behavior in general. The choice of when to take off and at what altitude to fly can be more important than the direction and speed of the flight itself, even within the range of favorable winds used in this study. Birds that alter heading to correct for drift would incur major energetic penalties for poor choice of flight conditions. Gauthreaux (1980) gives resultant surface winds for September and October in eastern North America. Comparison of Figure 1a above and Gauthreaux's (1980) Figure 3 suggests that for passerines, which fly at 300-3000 m, behavioral mechanisms for selecting wind conditions shorten continental flights by half and reduce dispersal of tracks by 40–70% relative to flight in randomly selected winds. Shorebirds achieve similar improvements by flying at very great altitudes as in Figure 1d. In both cases favorable wind speeds equal or exceed the airspeeds of the migrant birds.

Selection mechanisms of migrants for certain synoptic weather conditions may also have played an important role in the evolution of migratory routes. Gauthreaux (1980) concluded that autumnal migratory directions are often in rough agreement with average geostrophic wind conditions during the period of migration. This relationship is much more striking when synoptically selected winds are used. The 1500 m winds in Figure 1a show remarkable agreement with Gauthreaux's (1980) Figure 4 showing average direction of autumnal migration, especially in the areas of the midwest and the western Gulf coast.

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