Flight Directions of Passerine Migrants in Daylight and Darkness: A Radar and Direct Visual Study

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ON ALMOST EVERY NIGHT IN SPRING, migrant songbirds depart from regions south of the Gulf of Mexico, fly over the Gulf, and arrive on the northern Gulf coast during the daylight hours (refs. 1 and 2). The migrants contained in these flights encounter a night/day transition while over the Gulf, and some of the migrants also encounter a subsequent day/night change before making a landfall on the northern Gulf coast. Still others alight on the northern coast during the day and, after a few hours, continue their journey after nightfall. These events present one with a unique opportunity to study the orientation of nocturnal migrants in daylight and in darkness.

MATERIALS AND METHODS

I collected radar and simultaneous telescopic data on 140 dates during the spring seasons of 1965 to 1967 and 1969 at the Lake Charles and New Orleans weather bureaus in southern Louisiana (fig. 1). These stations are equipped with the new WSR-57 radars. These sets are 10-cm radars of 500-kW power and have 2° beam widths. A pulse length of $4 \mu$sec was used during the study; the set

FIGURE 1. Map of WSR-57 radar surveillance areas at Lake Charles (left) and New Orleans (right) with circles delimiting 25- and 50-n. mi. ranges.


also has a 0.5-$\mu$s pulse length. I collected most of the radar data on a 25-n.mi. range, but some data were gathered on 50- and 100-n. mi. ranges. I determined the altitude of the echoes from the range and elevation of the radar beam and from the range-height indicator (RHI). Additional characteristics of the WSR-57 radar appear elsewhere (ref. 3).

The methods for telescopic observations are essentially those described by Lowery and Newman (ref. 4). During the day the telescope was mounted vertically and a small portion of the sky above the observer was sampled. The 20-power ocular was normally used (field of 112 ft at 1000 yd), but a 30-power eyepiece (field of 78 ft at 1000 yd) was used when birds were flying very high. Occasionally I made brief vertical observations with 10 $\times$ 50 binoculars to supplement the telescopic watches. At night the telescope was trained on the Moon when the latter was visible and directed up a narrow beam of intense light (ref. 5) when it was not. Telescopic watches were normally made near the radar stations, but a few were made 19 to 24 km (12 to 15 mi) from the stations.
Before and after a period of telescopic observation, a single 35-mm exposure was made of the radar screen for one revolution of the antenna (20 seconds) followed by another photograph continuously exposed for 9 to 15 revolutions of the antenna (3 to 5 min). The short exposure was used to estimate the density of radar echoes; the long exposure was used to obtain information on the direction and speed of echo movement. Most of the photographs were taken with a 35-mm single lens reflex camera mounted on a tripod in front of the main radar screen. Kodak Plus X film (ASA 125) was used for most of the photography, but several Polaroid transparencies (46-L film) were taken of the remote radar screen.

I recorded all the available winds-aloft data from the weather stations surrounding the Gulf of Mexico. Radiosonde winds-aloft data (radar-tracked balloon) were gathered each day at 0600 and 1800 hr at these stations; pibal winds-aloft data (visually tracked balloon) were collected at 1200 and 2400 hr when cloud cover was above 1500 m (5000 ft). Local surface weather data for Lake Charles and New Orleans are available each day of the study.

RESULTS

Early in the study after examining the first few radar photographs, I realized that the echoes on radar from passerine migrants arriving from over the Gulf appeared to move with the wind at the various altitudes where the migrants were flying. Figure 2 illustrates this point. Figure 2A is an exposure for one revolution of the antenna; the dot echoes on this photograph are produced by flocks of passerine migrants. Simultaneous telescopic observations indicated that the flocks ranged in size from two or three to 175 birds, and the average flock size was 20 birds. Some of the dot echoes are contributed by flocks of shorebirds. The change in track directions with change in altitude (and wind direction) is illustrated in figure 2B.

To further examine the relationship between track directions and wind directions, I compared the radar track directions of daytime migrants with simultaneous winds-aloft data for the spring seasons of 1965 to 1967 and 1969. Only track directions within 1 hour of the time of winds-aloft measurements are considered. Figure 3 shows the scatter diagram of daytime migration track directions and the corresponding wind directions. Each dot represents the track direction of migration on a particular date for a particular altitudinal stratum within an hour of a winds-aloft measurement. Eighty-six percent of the points fall within 40° of the wind direction. The remaining points indicate track directions that cannot be consid-
Figure 4. Scatter diagram of nocturnal migration track directions and corresponding wind directions. Dashed line represents perfect agreement between track direction and wind direction; thin continuous lines delimit a 40° sector on each side of dashed line. N equals 136.

Figure 5. Scatter diagram of resultant vectors of nocturnal migrations and corresponding wind directions. Migration data gathered on 28 nights by ceilometer observations at New Orleans, Louisiana, during spring 1967. Open circles represent wind speeds less than 6 knots; solid dots represent wind speeds greater than 6 knots.

ered downwind. These latter points represent, with only two exceptions either very weak winds (less than 6 knots in velocity) or shorebird movements. Dot echoes on radar identified as flocks of shorebirds always moved at air speeds in excess of 25 knots in directions that were the same as the flight directions of the shorebirds that passed through the field of the telescope.

Figure 2 (C and D) shows the characteristic presentation of nocturnal migration on the radar screen. Figure 2C is an exposure for one revolution of the antenna; Figure 2D is a time exposure showing movement of the fine, grainy echoes produced by songbirds flying individually in the night sky. The scattered dot echoes in the misty pattern yield distinct streaks on the time exposures, and simultaneous Moon-watching and ceilometer observations indicate that the dot echoes are contributed primarily by flocks of waterfowl and shorebirds. Figure 4 is also a scatter diagram of bird track directions and the corresponding wind directions, but these data are for nocturnal migration. Seventy-six percent of the points fall within 40° of the wind direction. The remaining points fall beyond this zone, and as during the day these points are the result of light winds (more prevalent after dark) and strong flying shorebirds and waterfowl (airspeeds from 25 to 35 knots).

The relationship between wind direction and migration direction at night is further documented in Figure 5, where the direction of migrations computed from ceilometer data and the corresponding wind data at 305 m (1000 ft) are plotted. Samples from 28 nights during the spring of 1967 at New Orleans, Louisiana, are represented. The migration directions are the resultant vectors computed
from individual bird directions for a particular night's movement. The ceilometer data were gathered during the first two hours of darkness, and the wind directions are those for 1800 hr. In figure 5 winds of less than 6 knots are plotted as open circles; winds above 6 knots are plotted as solid dots. Seventy-nine percent of the points in the figure are within 40° of the wind direction. Only two solid dots appear out of this zone, but four of the five open circles are out of the 40° sector.

The frequency of track, wind, and heading directions during the day are illustrated in figure 6. The specifics concerning wind and track directions are the same as those given earlier in the text for figure 3. There is a tendency for track directions to vary less than heading directions, and this implies some correction for wind drift by the migrants. I found that shorebirds exhibited this ability during the day, and the flocks of passerines also maintained their "preferred" flight direction when unfavorable winds were less than 6 knots. In southern Louisiana, the wind most frequently blew in a direction that was quite favorable for the movement of spring migrants. In fact, the vast majority of spring migrants during the study did fly in the correct seasonal direction by simply flying downwind.

Figure 7 gives the track, wind, and heading directions for nocturnal migration for 136 observations during the spring seasons of 1965 to 1967 and 1969. The data presented here are the same as those given in figure 4. The spread in the directions of spring nocturnal migration is greater than that recorded during the day. At night the NW component of the migrations is more pronounced and is found at lower altitudes below 760 meters (2500 ft). Both the NW and NE nocturnal movements are downwind at their respective altitudes. In contrast to the daytime migrations, reverse migrations or flights in an inappropriate direction for the season are present at night, and some of these occur under clear skies.

When trans-Gulf migrations continued to
arrive after dark, the flight directions did not change from the daytime flight directions independent of changes in wind direction. On 10 occasions trans-Gulf migrations moved inland in the afternoon to the northwest with strong winds from the southeast; the migrants that continued to arrive after dark did not change their direction at nightfall but continued flying to the northwest.

The trans-Gulf migrants that alighted in the woodlands of southern Louisiana during the daytime arrival of a flight departed 30 to 45 min after dark. As the migrants left the woodlands, their flight directions were oriented to the NW, but as they gained altitude the directions changed to N and then NE. In southern Louisiana during the months of April and May the winds below an altitude of 450 m (1500 ft) usually blow to the NW; between 450 and 900 m they blow to the N and NNE; and above 900 m the winds usually move to the NE and ENE (National Summary of Climatological Data, United States Weather Bureau, 1965, 1966, 1967, and 1969).

Isobars are lines on a weather map connecting points of equal barometric pressure. The wind blows nearly along isobars at 600 to 900 m above the ground. On April 25, 1965, the isobars over the central, northern Gulf coast were oriented from 120° to 300° at 1200 hours, and the movement of birds in from over the Gulf at this time was directed to 300°. Between noon and midnight the orientation of the isobars changed 70°, and they were oriented from 190° to 10° at midnight. The arriving trans-Gulf migrants showed a corresponding change in their flight directions, and those that continued to arrive near midnight moved toward 10°.

During the study 19 percent of the 106 daytime observations were made with solid overcast skies, and 14 percent of the 136 nighttime observations were conducted with solid overcast skies. In no case were the directions of these migrations different from those under clear skies. The migrations that left the woodlands of southern Louisiana under overcast did so without delay and with no noticeable deviation from the regular departure direction under clear skies.

**DISCUSSION OF FINDINGS**

Lack (ref. 6) stated that radar observations fit best with the view that migrants in flight orient solely by a Sun compass or a star compass since they do not, so far as can be determined, allow for lateral displacement by the wind (unless flying very low). Bellrose and Graber (ref. 7) have reported that their radar data show that birds compensate only partially for drift. Evans (ref. 8) and Nisbet and Drury (ref. 9) have concluded from their observations with radar that birds compensate exactly and continuously for drift. These authors also point out that migrants tend to fly with favorable winds thereby reducing their chances of drift. Bellrose (ref. 10) has stated that migrants generally select winds that are favorable for their goal, but when forced to use unfavorable winds, they correct to a high degree for lateral drift. Lack (ref. 11) subsequently re-examined his wind-drift data and concluded that his findings also support the ideas that birds select favorable winds and that they can correct for wind drift.

Steidinger (ref. 12), working with radar in northern Switzerland, found that radar tracks of migrants were clearly deflected by strong crosswinds, and concluded that birds apparently do not compensate for the drifting effects of the wind or only to a small extent. My findings support the drift hypothesis for songbirds, but it appears that strong flying shorebirds and waterfowl can correct for lateral displacement by the wind provided
the wind velocity is not too great. I have recorded several cases of downwind flight under clear skies when the wind was blowing in a direction that was inappropriate for the seasonal advancement of the migrants.

Lowery (ref. 2) found a striking correlation between air currents and the directional flight trends of birds, suggesting that most night migrants travel by a system of pressure-pattern flying. Evidence that birds select winds blowing in a preferred direction has been obtained by Bellrose and Graber (ref. 7), Gauthreaux Jr., Evans (ref. 8), and Niabet and Drury (ref. 9).

Several authors on the basis of their radar studies of migration have reported that birds initiate migration under overcast and are able to pursue a flight in the normal direction of migration without reference to solar or stellar cues (e.g., refs. 7, 9, 13). My findings support the claims of these authors and suggest that wind direction is a possible alternative to solar and stellar cues when overcast skies prevail.

The correlation between wind direction and the direction of migration suggests that most passerine migrants fly with the wind or, to express the matter differently, the wind often blows in the same direction as the direction of their migration. Since the average monthly wind directions are frequently the same as the preferred direction of the migrants, the birds often fly with winds that require no compensation for wind drift. Occasionally some day migrants maintained preferred tracks, even though the winds varied considerably from tail winds. Why birds flew with the wind in certain cases and at various angles to the wind in other cases becomes explainable when one examines the types of winds-aloft information to support my stand, I do think it possible that the reorientation response by the migrants is probably influenced by a change in wind direction as the migrants gain altitude.

Basically the findings of this study support Pennyceck's (ref. 14) assertion that cross winds of moderate strength deflect slow birds
through a large angle, but have less effect on faster ones. In general, the slower (and hence smaller) the bird, the more it is affected by unfavorable winds. The influence of wind direction on the flight directions of migrants should be taken into consideration in future orientation studies of birds.

ACKNOWLEDGMENTS

I wish to thank the personnel of the United States Weather Bureaus at Lake Charles and New Orleans, Louisiana, for their constant cooperation and assistance during the research. George H. Lowery, Jr., and Robert J. Newman kindly assisted me during the phase of this work that was used for a portion of my Ph.D. dissertation. I thank Kenneth P. Able for his help in the preparation of the manuscript. A portion of this work was completed under a grant (70-1879) from the Air Force Office of Scientific Research.

DISCUSSION

QUESTION: How do you correlate radar targets and visual identifications? You quite frequently distinguished between passerine and shorebird targets.

GAUTHREAUX: Moon-watching and ceilometer observations gave me information on the types of birds, their flight directions, approximate altitudes, and spatial distribution. I used these characteristics to identify the bird echoes on radar (e.g., intense dot echoes above 1500 m moving at an airspeed of 40 kt to the northeast corresponded to flocks of shorebirds and ducks at high altitudes flying to the northeast; smaller dust-like echoes below 700 m moving to the northwest corresponded to small and medium sized passerines flying to the northwest).

QUESTION: How high is your visual capability?

GAUTHREAUX: It varies during the day depending on atmospheric conditions. With a 30-power telescope I have seen birds when radar showed that the flight was entirely above 1200 m. These birds appeared very small and were near the limit of visibility.

WILLIAMS: I have done experimental work with a similar radar and also with a search radar at Otis Air Force Base in Cape Cod. My criticism is that you see a particular pattern of migration close to the radar and a different pattern of migration at some distance. Because of the elevation radar, you assume that the close pattern of migration is a low altitude one and the other is a high altitude one. I have also seen the same thing with a search radar. You mustn't forget that small targets will only be detected near the radar set itself. Search radar is presumably picking up all altitudes up to 3000 m (10 000 ft) including ducks and geese detected at great ranges and passerine birds moving in quite different directions at close range. Yet I wouldn't like to make any statement about altitude since I know that the small targets are detected at a closer range. Have you made any attempt to correct for that?

GAUTHREAUX: The small dust-like targets on the WSR-57 appear restricted to the center simply because of the antenna elevation and the low altitudinal distribution of the small and medium passerines at night. When I lower the antenna to 0°, the radar can detect these fine targets out to 50 to 60 n. mi. The pattern shrinks closer to the center of the screen as I raise the antenna. Thus, I am missing the small targets at 15 n. mi. because the 2° beam, when tilted 3°, starts to go above the bulk of the passerine migrants at that distance.

WILLIAMS: Another general question and perhaps criticism of all the work done on wind drift, the general tendency is to use the average heading of the birds using the M.T.I. wedge. Other people generally tend to take the average heading of the birds and compare that to the average track. In my work I have found that even with a good and clear M.T.I. wedge I can get a spread of 50° with the actual tracks.

Have you tried looking at your data when you actually plot the track for each individual bird? If you do take the average as shown on PPI's, do you actually have a number of birds going in a totally different direction?

GAUTHREAUX: It is nearly impossible to analyze individual tracks of the numerous fine, misty echoes on the WSR-57 radar at night, but the ceilometer data can be easily analyzed in that manner. The angular deviations in tracks during a night of observation are normally on the order of 30 to 40° for the ceilometer. True, it is often misleading to talk of migration directions in terms of resultant vectors. When a low altitude movement is going to the northwest and a high altitude flight is moving to the northeast, the resultant vector will indicate a northward migration. This is largely meaningless. There is an advantage to simply plotting the raw data and looking at the grouping and total dispersion of the tracks.
QUESTION: I wonder if the paradox on wind drift corrections might not be a reflection of the physical condition of the birds themselves? Could some of these drifting birds be just very tired birds?

GAUTHREAUX: That is certainly possible. Tired birds might fly slower, and if so, their track would be deflected more by an unfavorable wind of constant speed. However, if fatigue is responsible for drift in migrants flying over land, why don’t the birds land? I believe that the birds are in good health, are maintaining a constant preferred heading, and are being displaced by the unfavorable wind. Their track is the vector resultant of their heading and airspeed and the wind direction and its speed.

REFERENCES