FALL MIGRATION IN COASTAL LOUISIANA AND THE EVOLUTION OF MIGRATION PATTERNS IN THE GULF REGION

KENNETH P. ABLE

MANY passerine birds make long overwater flights during the course of their seasonal migrations; it is obvious that natural selection has favored these flights in spite of the risks and energetic demands involved. The Gulf of Mexico is one region where the arrival and departure of overwater migrations can be observed to advantage.

Even at the height of the exchange between Lowery (1945) and Williams (1945) concerning the occurrence of spring trans-Gulf migration, it was generally assumed that autumn migrants regularly cross the Gulf in large numbers (e.g., Williams, 1947). In the years following the controversy, spring migration in the Gulf region has been extensively studied, but there have been few concentrated investigations of fall migration. More or less anecdotal observations of birds crossing the Gulf in fall were made by Griscom (1945), Paynter (1951, 1953) and Siebenaler (1954). Buskirk (1968) studied the arrival of migrants on the north coast of Yucatán.

The extensive investigations of vernal trans-Gulf migration have shown that the pattern of air flow around the Bermuda high-pressure system characteristic of that season is conducive to overwater flights (Lowery, 1951; Gauthreaux, 1971). Indeed, Gauthreaux has shown that trans-Gulf migrations early in spring, when the Bermuda high is not a consistent feature, occur in spurts which are dependent upon the establishment of southerly air flow over the Gulf. After the beginning of April, moist tropical air moves northward across the Gulf, interrupted only by the infrequent penetration of powerful cold fronts. The consistency of this favorable flow pattern has probably been a strong selective force in the evolution of vernal trans-Gulf migration. If this is true, one would predict the development of a different pattern in fall because wind patterns are not favorable for regular, large-scale Gulf crossings.

During the fall of 1969 I obtained data on the direction and magnitude of bird flow in southwestern Louisiana while I was conducting field studies on the orientation of nocturnal migrants. These observations shed light on three questions: What is the general flow pattern of autumn migration on the northwestern Gulf coast?; How is this pattern related to major weather systems?; and What evolutionary strategy has led to the broad-front migration patterns we see today?

METHODS

I conducted this study on 34 nights in August, September, and October at Lake Charles, Louisiana, about 23 nautical miles north of the Gulf coast. The nights were not selected in any way, except that no data were used from nights with several hours of rain. I used the WSR-57 radar at the U. S. Weather Bureau station to determine the traffic rates (in birds per mile of front per hour) of nocturnal passerine migration as described by Gauthreaux (1970). I determined the direction of passerine movement (tracks) on the same nights using two portable ceilometers and a 20 × 60 telescope (see Gauthreaux, 1969).

For comparative purposes in the following discussion, I have used the maximum hourly traffic rate recorded on each night as the magnitude of migration on that night. The flight direction parameters of the birds observed with the portable ceilometer (half-hour samples taken 19:00–20:00 or 20:00–21:00 CST) were determined according to Batschelet (1965).

GULF WEATHER PATTERNS IN AUTUMN

The typical low-altitude air flow across the Gulf of Mexico in fall is similar to that in late spring and summer. The southeasterly flow characteristic of these seasons is produced by the clockwise circulation of air around the strong Atlantic subtropical high-pressure system (Bermuda high) and the cyclonic circulation around a low-pressure area over the Mexican Plateau. As autumn progresses, the Gulf area comes under the increasing influence of a continental high-pressure system over central North America. This cold air mass is separated from the Atlantic high by a cold front. Wind conditions over the Gulf in autumn depend upon the juxtaposition of these two pressure systems and the polar front (Petterssen, 1958). When the front passes into the Gulf, as it does infrequently in fall, northerly winds conducive to trans-Gulf flights occur. These conditions occur most regularly later in fall, after the bulk of passerine migrants has passed. During the longer periods between invasions by the continental high, the predominantly southeasterly winds are generally opposed to direct flights from the northern Gulf coast to Yucatán.

The prevailing weather situations during autumn, 1969, were typical for the region and fall rather neatly into five categories as follows:

I. This condition is dominated by the continental high pressure system when it is situated in the central or eastern United States. Figure 1 shows this pattern, which occurs after the passage of a cold front into the southeastern states. The degree of penetration of the front and the exact position of the high-pressure area will determine the orientation of isobars and winds, but the air flow is generally from the northeast or east. This was the most frequent of the five weather conditions, occurring on 11 (35.5 per cent) days during the study (9–10, 10–11, 11–12, 12–13, 18–19, 19–20, 20–21, 21–22 September, 8–9, 22–23, 23–24 October).

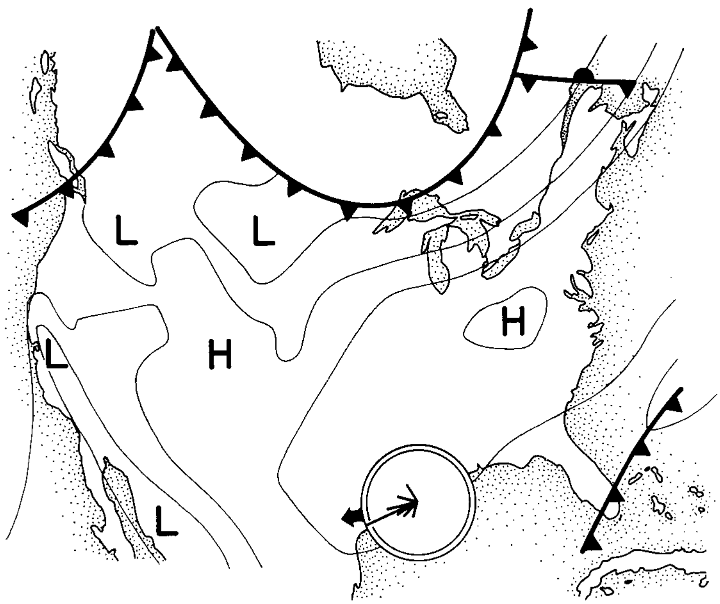


FIG. 1. The flight directions of birds in Weather Pattern I. The vector diagram is plotted so that the radius equals the greatest number of birds in any 7.5° sector. The arrowhead denotes the mean flight direction. See text for a discussion of the weather patterns. The weather map shown is that for 12 September 1969.

II. High pressure over the southeastern United States generates southeasterly winds over most of the Gulf. This condition occurred on 8 (25.8 per cent) days during my study and was particularly characteristic in August. A typical example is shown in Figure 2. (5–6, 6–7, 7–8, 25–26, 26–27, 27–28, 28–29 August, 3–4 October).

III. This pattern is characterized by a well-developed southerly air flow on the back side of a high-pressure system just ahead of a cold front. Winds tend to be strong and thundershowers are frequent. This weather pattern occurred on 5 (16.1 per cent) days during my observations and is shown in Figure 3 (17–18, 22–23 September, 10–11, 11–12, 12–13 October).

IV. Pattern IV is more or less intermediate between II and III. It is dominated by southerly winds in the central and western Gulf produced by the northward flow of moist tropical air in the warm sector of a high-pressure ridge over the eastern United States. This condition usually occurs as a cold front approaches from the west, but the air is more stable than that closer to the front. This pattern occurred on 4 (12.9 per cent) days and is illustrated in Figure 4 (1–2, 2–3, 4–5, 9–10 October).

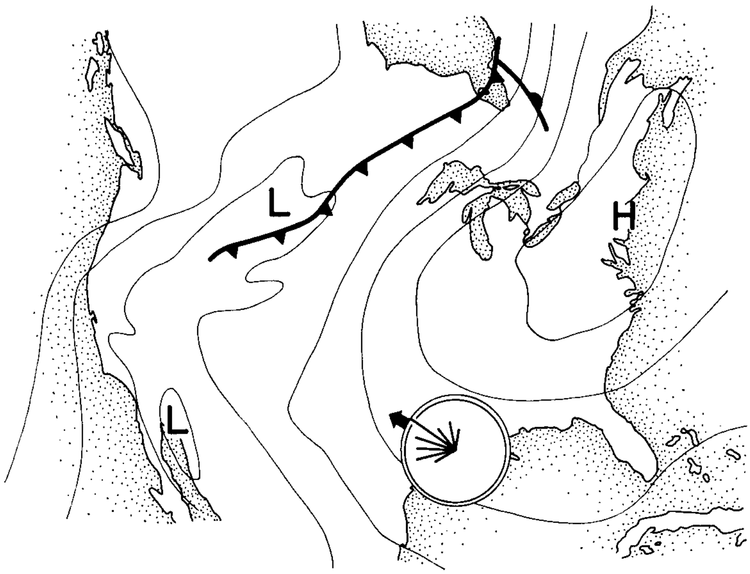


FIG. 2. The flight directions of birds in Weather Pattern II, plotted as in Figure 1. The weather map shown is that for 28 August 1969.

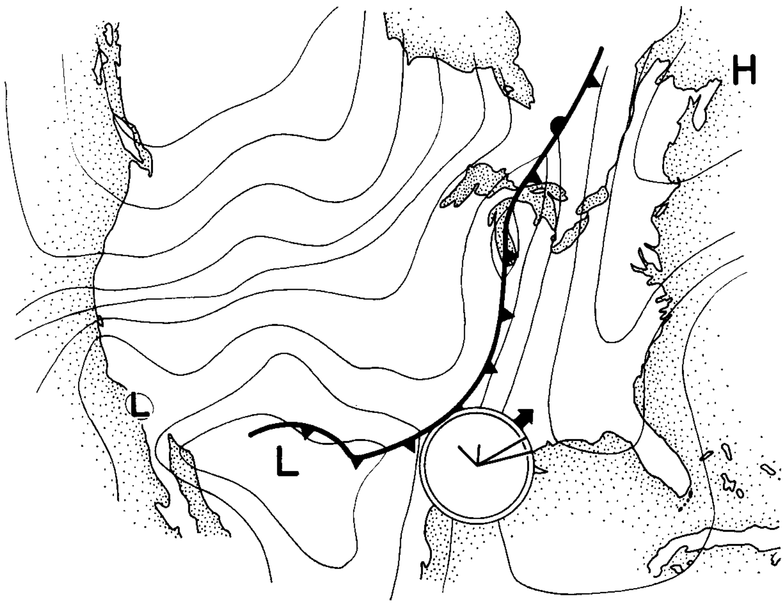


FIG. 3. The flight directions of birds in Weather Pattern III, plotted as in Figure 1. The weather map shown is that for 11 October 1969.

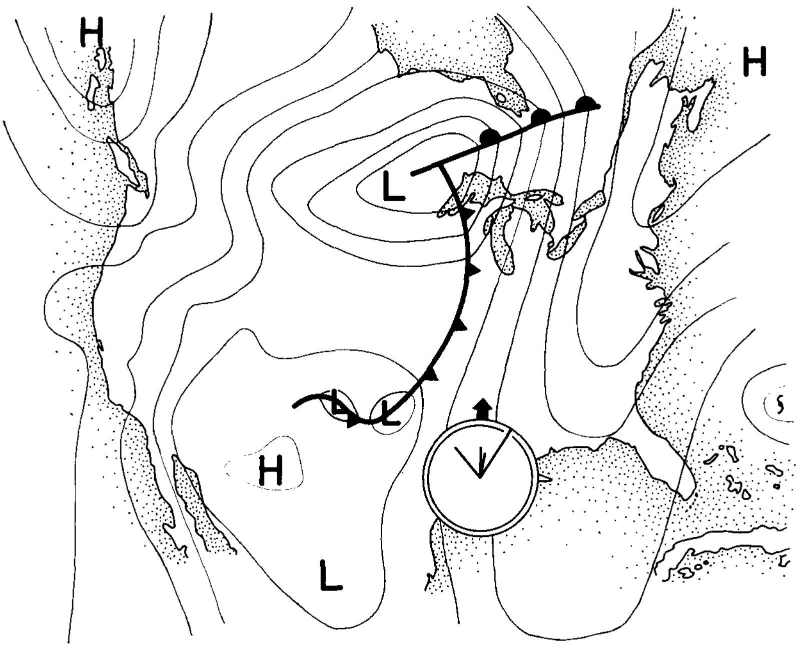


FIG. 4. The flight directions of birds in Weather Pattern IV, plotted as in Figure 1. The weather map shown is that for 10 October 1969.

V. Conditions most conducive to autumnal trans-Gulf flights occur shortly after the passage of a massive cold front which penetrates far into the Gulf. The anticyclonic circulation around the continental high generates northerly winds, the persistence of which depends largely upon the strength of the frontal system. Only three cold fronts passed Lake Charles during fall, 1969, and Pattern V characterized 3 (9.7 per cent) days during this study. It was thus the most infrequent weather condition. A typical example of this pattern is shown in Figure 5. (7–8, 13–14, 14–15 October).

The five weather patterns encompass all but three days during the study. (30 September—1 October, 20–21, 21–22 October). These three days were each dominated by inconsistent, complex weather situations with low-pressure centers in the Gulf of Mexico. Migrations on each of the three nights were of low magnitude.

RESULTS

Flight directions of birds and weather patterns.—To obtain an overall view of the flow of autumn migration on the northern Gulf coast, I constructed a vector diagram of the direction and magnitude of nocturnal passerine mi-

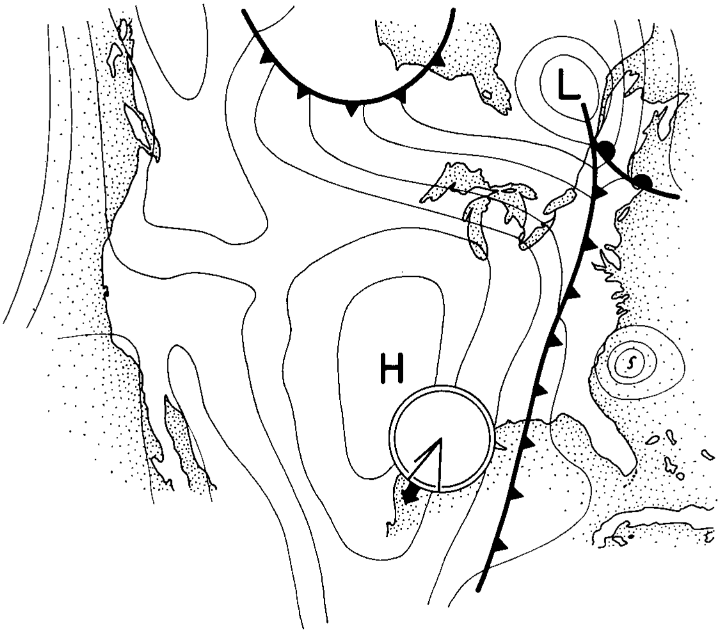
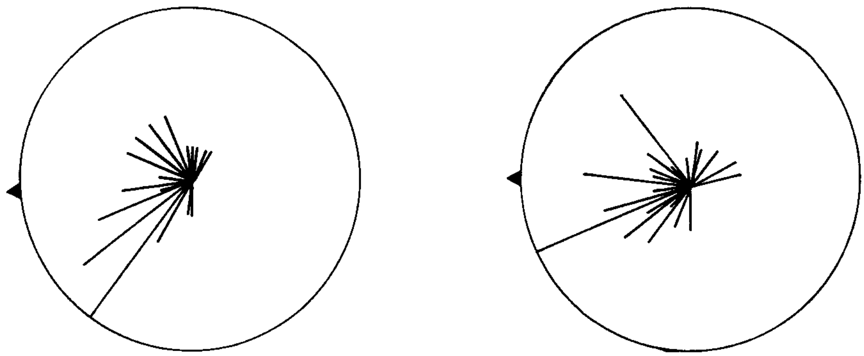


FIG. 5. The flight directions of birds in Weather Pattern V, plotted as in Figure 1. The weather map shown is that for 14 October 1969.

gration on all 34 nights of the study. For each night, the mean flight direction of landbirds was weighted by the $\log_{10}$ maximum traffic rate recorded during that night. The resulting distribution is shown in Figure 6*a*. The mean flight direction, and thus the net flow of birds, was toward the west (274°), but considerable dispersion in flight directions is indicated by the large angular deviation (s) of 55.7° and the resultant vector length (r) of 0.53. In Figure 6*b* are plotted the directions of surface winds on the 34 nights of the study. There is a remarkable similarity between the distribution of wind vectors and bird vectors and the mean wind direction (269°) and dispersion ($s = 54.9°$) do not differ significantly from the same parameters of the bird distribution (parametric two-sample F-test; Batschelet, 1965). If this relationship has sufficient generality, seasonal migration patterns in other geographic regions could be predicted from long-term wind direction data.

It is more instructive to examine the flight directions of the birds under each of the five weather patterns. These data are plotted in Figures 1–5.

Pattern I is one of two (with Pattern V) weather situations which is generally favorable to fall migration, i.e., winds usually have a southward com-



A B

Fig. 6. A. Vector diagram of the mean flight directions of the birds (half-hour samples taken 19:00–20:00 or 20:00–21:00 CST) weighted by the $\log_{10}$ maximum traffic rate during the same night. B. Vector plot of the directions of surface winds, taken at the times of ceilometer samples, on the 34 nights of the study. The vectors are plotted as in Figure 1.

ponent. In general, air flow in this system parallels the Louisiana-Texas coast and large movements of birds were observed flying in this west-southwesterly direction. Under this general weather condition the mean flight direction was 255° and the relatively small amount of dispersion about the mean ($s = 28.8°$) shows that the flight directions of the birds are fairly consistent from night to night, reflecting the relative constancy of winds in this pattern.

Patterns II, III, and IV are characterized by winds blowing from the south, generally counter to the expected flow of autumn migration. One of these three patterns occurred on 54.8 per cent of the nights during this study. Migrations of landbirds occurred under all three conditions and in each case flight directions were toward the north. The mean flight direction under Pattern II was 300° ($s = 41.5°$; $r = 0.84$) as shown in Figure 2. The flight directions of passerines under Pattern III are shown in Figure 3. Here the mean flight direction was 47° ($s = 41.5°$; $r = 0.74$). Northward flights with a mean direction of 7° ($s = 28.3°$; $r = 0.88$) occurred in weather typical of Pattern IV. These data are plotted in Figure 4.

The optimum conditions for direct bird flow from the northern Gulf coast to the tropics occur when Pattern V prevails, i.e., following the passage of a cold front far into the Gulf. On the three nights when these conditions occurred, overwater flights departed from the Louisiana coast. Indeed, trans-Gulf departures took place only under these conditions. The flight directions

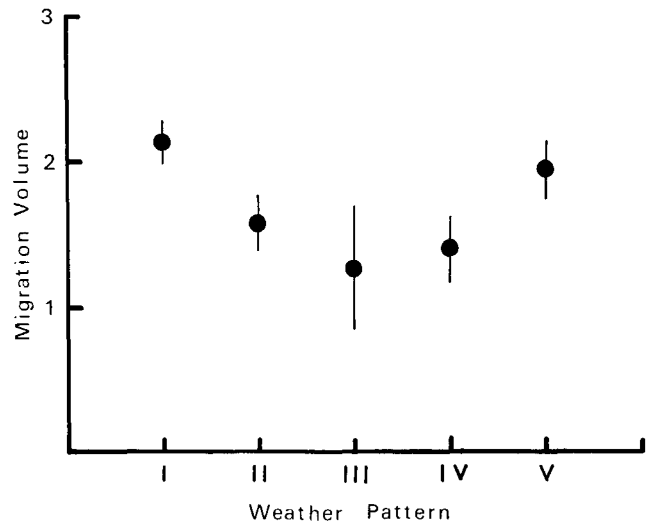


FIG. 7. The magnitude of migration under each of the five weather patterns. The dots and vertical lines show the mean nightly maximum traffic rate and its standard error under each condition.

of birds on these nights are plotted in Figure 5 where the mean direction is 207° (s = 19.2°; r = 0.94).

The relative magnitude of migration in different directions.—Among the diverse weather patterns which characterize the northern Gulf coast in fall, some are obviously more favorable for a direct movement to the wintering ground than others. We would expect, a priori, that passerine migrants would have evolved the ability to select optimum weather conditions in which to undertake long migrations. Most birds initiating a migratory flight from southwestern Louisiana in the fall will move in one of three general directions: 1) southwest on a circum-Gulf flight parallel to the coast; 2) southward directly across the Gulf to Yucatán; or 3) some direction generally counter to the normal flow of autumnal migration. The foregoing results and other data (Gauthreaux and Able, 1970, 1971; Able, 1971 and in prep.) show that passerine nocturnal migrants fly downwind even when this behavior carries them in apparent "nonsense" directions. It is, therefore, of considerable interest to know if migrations in seasonally appropriate directions are of disproportionately larger size.

The volume of migration under the five weather patterns is shown in Figure 7. The graph shows the mean maximum traffic rate recorded under each weather pattern. The means under Patterns II, III, and IV (those with

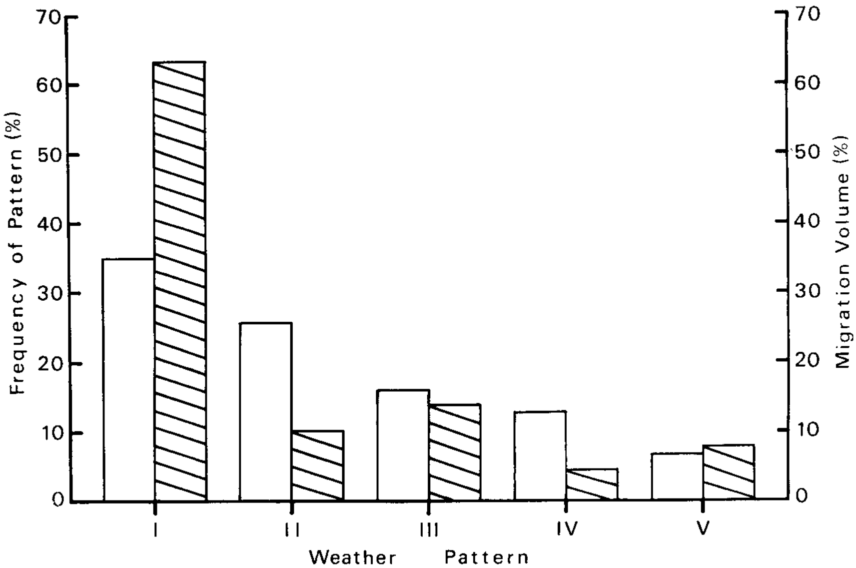


FIG. 8. The proportion of migration occurring under each of the five weather patterns. Open bars show the frequency of each weather pattern as a per cent of the total nights sampled. Hatched bars represent the per cent of the total migration volume (total nightly maximum traffic rates) observed under each condition.

generally southerly winds and "reverse" migrations) were significantly smaller than those under Patterns I and V (those generally favorable to fall migration) ($t_{29} = 14.42$; $P < 0.001$; two-tailed test). The histograms (Fig. 8) show the frequency of occurrence of each weather pattern and the proportion of the total migration volume (based on nightly maximum traffic rates) that took place under that Pattern. Only under Patterns I and V did more migration occur than would be expected on the basis of the frequency of occurrence of the condition. However, the differences were not great enough to yield a significant value of Chi Square. The volume of migration immediately following the passage of cold fronts (Pattern V) is surprisingly small, as this might be considered the optimum condition for migration. At least part of the reason for this anomaly is that the three cold fronts occurred late in the migration season after the bulk of birds had passed. Traffic rates in all weather conditions were considerably smaller toward the end of migration. In addition, October migrations contain a higher ratio of arriving winter residents to passage migrants than earlier flights and thus fewer birds would be likely to embark on trans-Gulf flights during post-frontal weather.

DISCUSSION

Trans-Gulf flights of considerable magnitude take place in fall, but in contrast to the spring migratory picture in the Gulf region, they are of irregular occurrence. The results of this study show that the direction of autumn passerine migration on the Louisiana coast conforms to the patterns of air flow in major weather systems. This was predicted by our finding that passerines at night fly downwind regardless of wind direction or speed (Gauthreaux and Able, 1970, 1971; Able, 1971). The correspondence of migratory flow to broad-scale weather patterns results in a fairly large net movement of birds on a circum-Gulf path.

Few other data are available with which my results may be compared. Lowery and Newman (1966) analyzed data from moon-watching on four consecutive nights. Trans-Gulf flights of considerable magnitude departed on two nights immediately following the passage of a cold front into the Gulf. Circum-Gulf flight directions were noticeable on the other two nights and at the eastern and western ends of the northern Gulf coast. Their data are thus in general agreement with mine.

On the north coast of Yucatán, Buskirk (1968) recorded at least small incoming flights of passerine migrants almost daily in fall. Heavy flights occurred only following the penetration of cold fronts into the Gulf. My observations at Lake Charles cannot account for the *regular* arrival of migrants in Yucatán in fall. However, predominant weather patterns often are favorable for flights from Florida or Cuba.

The major broad-front migration patterns can be explained on the basis of prevailing weather systems and the behavior of the birds. Large-scale wind patterns are probably strong selective forces in the evolution of passerine migration patterns, at least when these involve long overwater flights. The pattern of selective downwind flight described here assures that small landbirds will not embark on a hazardous overwater flight in unfavorable winds. On the other hand, the same behavior allows them to be opportunistic in taking advantage of northerly post-frontal winds when they occur in fall. In the Gulf region, birds embark on a water crossing in both spring and fall whenever winds are favorable. The major differences in the resultant seasonal patterns are due to the fact that the wind flow across the Gulf is roughly south to north during both seasons, while the main direction of bird flow is reversed. But, although southerly winds blow on a majority of days during the fall migratory period, a fairly strong net flow of birds in a southward direction results from downwind flight coupled with some behavioral selection of favorable synoptic weather situations.

All the data from the Gulf region show that passerine migrants will not depart on an overwater flight into head winds. However, the birds leaving Yucatán in spring or the northern Gulf coast in fall presumably cannot predict the presence of a cold front somewhere in the Gulf. We do not know specifically what happens when a mass of migrants flying in tail winds meets the front and its opposing winds over the water. However, when birds meet a cold front in the northern Gulf in spring, many abandon downwind flight and fight the head winds northward toward the coast. Since autumn cold fronts rarely reach Yucatán, the birds usually meet partially or completely opposing winds somewhere during the water crossing. Paynter (1953) and Buskirk (1968) observed birds arriving in head winds at Yucatán. On the contrary, Gauthreaux (pers. comm.) once observed the northward return of a fall migration which had departed from the Louisiana coast only to meet a retreating cold front not far offshore. These observations imply that the birds are employing some navigational ability ("map sense" of Kramer, 1953) and are somehow aware of their position in space relative to the geography of the Gulf. Once they have proceeded most of the way across the water barrier, they will abandon their customary downwind flight in order to reach the nearest shore if opposing winds are encountered.

SUMMARY

Passerine nocturnal migration was observed with radar and portable ceilometer on 34 nights during fall, 1969, at Lake Charles in southwestern Louisiana. Weather patterns over the Gulf in fall are generally similar to those of late spring and summer and are usually characterized by southerly winds. These conditions, which favor large-scale trans-Gulf migrations in spring, are opposed to such flights in fall. The daily weather patterns observed during this study were grouped into five basic types. Passerine migrants at Lake Charles flew with the wind, regardless of its direction. Because of the frequency of southerly winds, "reverse" migrations were common. However, a strong net flow of birds in a southwesterly direction resulted from prevailing northeasterly winds and the occurrence of disproportionately large migrations when air flow was favorable for movement toward wintering areas. Downwind flight assures that small landbirds will not embark on long overwater flights in unfavorable winds, but at the same time allows them to take advantage of northerly post-frontal winds when they occur.

ACKNOWLEDGMENTS

I am greatly indebted to the personnel of the U.S. Weather Bureau at Lake Charles, Louisiana. Without their technical assistance and hospitality, this work would not have been possible. Sidney A. Gauthreaux gave invaluable assistance during all phases of my work. During the preparation of this paper I was supported by a grant (70–1879) from the Air Force Office of Scientific Research to Dr. Gauthreaux and by a fellowship from the Institute of Ecology, University of Georgia. This paper was presented as a part of the Symposium on Bird Migration in the Region of the Gulf of Mexico held during the 1971 Meeting of the Wilson Ornithological Society under the chairmanship of George H. Lowery, Jr.

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DEPARTMENT OF ZOOLOGY AND INSTITUTE OF ECOLOGY, UNIVERSITY OF GEORGIA, ATHENS, GEORGIA. (PRESENT ADDRESS: DEPARTMENT OF BIOLOGICAL SCIENCES, STATE UNIVERSITY OF NEW YORK, ALBANY, NEW YORK 12203.) 1 NOVEMBER 1971.