A RADAR AND DIRECT VISUAL STUDY OF PASSERINE SPRING MIGRATION IN SOUTHERN LOUISIANA

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RADAR studies of bird migration have been restricted to latitudes north of 32° N. These studies have contributed greatly to our knowledge of migration, but have examined only a portion of the long-distance migrations made by many bird species. No radar studies of migration have been published for regions nearer the equator where environmental conditions are more constant. This paper reports on a radar and telescopic study of spring migration on the Louisiana coast of the Gulf of Mexico between 29° and 31° N, one of the first landfalls that migrants reach after leaving the tropics and crossing the Gulf (Figure 1).

MATERIALS AND METHODS

In 1962 I began using the WSR-57 radar at the United States Weather Bureau in New Orleans, Louisiana, to study bird migration. During the spring of 1965 at Lake Charles, Louisiana, I completed an evaluation of the WSR-57 as a research tool for migration studies (Gauthreaux, 1965). I gathered additional radar and telescopic data at these stations during the spring seasons of 1966 and 1967, and data from the three spring seasons of principal investigation (1965–1967) represent nearly 1,100 hours of combined radar and telescopic observation on 113 days.

The characteristics of the WSR-57 radar are given elsewhere (Gauthreaux, 1968, 1970). To quantify the migration displayed on the radar screen, I used an attenuation method (Gauthreaux, 1970) and a thinning technique similar to that described by Nisbet (1963). All the radar data collected in the spring of 1967 were analyzed by the attenuation method; the radar data from the spring seasons of 1965 and 1966 were analyzed by a thinning technique derived from the results obtained with the attenuation method. Ian Nisbet (pers. comm.) pointed out that doubling the range of a radar target reduces the reflected power by a factor of 16. In principle this is the same as keeping the range of the target constant and attenuating the received signal by a factor of 16 (12 decibels). Thus a given density pattern of bird echoes represents 16 times the number of birds at 20 nautical mile range as it does at 10 nautical mile range, provided most of the migration stratum aloft is within the spread of the radar beam in both instances. I used this relationship to analyze quantitatively the 16-mm and the 35-mm cinematic records of the Lake Charles and New Orleans radar stations for the spring seasons of 1965 and 1966. Both quantification techniques yielded similar results.

For all direct visual observations of migration aloft, I most often used a Bausch and Lomb BALscope, Sr., with a 60-mm objective and changeable 20-power and 30-power oculars, but some observations were made with hand-held 10 × 50 binoculars. Telescopic watches on moonless nights were made with the aid of a portable ceilometer that projects a narrow vertical beam of light (Gauthreaux, 1969).

The methods followed for telescopic observations are essentially those described by Lowery and Newman (1963). During the day the telescope was mounted vertically and a small portion of the sky directly overhead was sampled. At night the telescope was

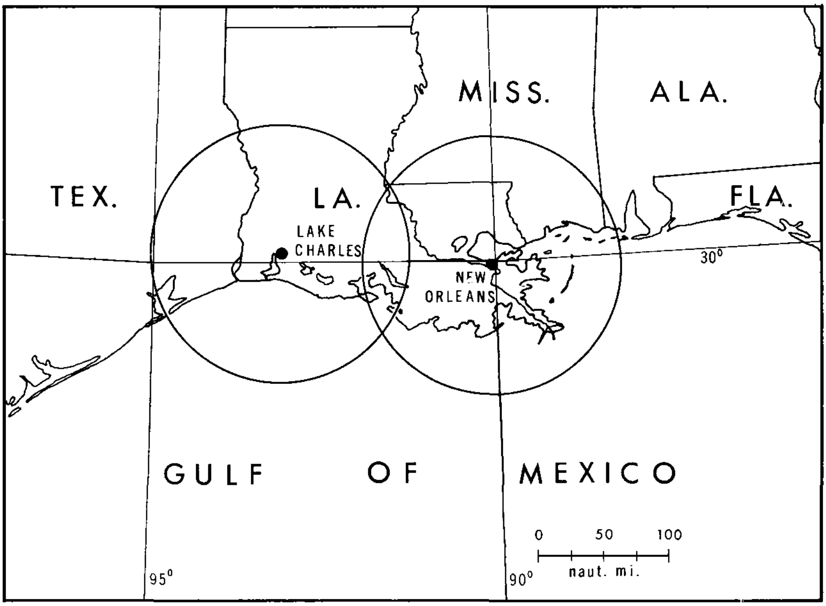

Figure 1. Map of the central, northern coast of the Gulf of Mexico showing the radar surveillance areas for Lake Charles and New Orleans Weather Bureau WSR-57 radars. The circles represent 100 nautical mile range.

trained on the moon when it was visible (Lowery, 1951) and directed up the ceilometer beam when its was not.

I conducted field censuses in woodlands near the radar stations to gather information on the numbers and species of grounded migrants in the radar surveillance areas. All weather data collected by the United States Weather Bureau stations during the study were available to me at the Lake Charles and New Orleans stations. Winds aloft information were at hand from weather stations in Central America, around the Gulf of Mexico, and in the Caribbean Sea. The New Orleans station received directly weather satellite photographs of the Gulf of Mexico, and I used these telemetered photographs to determine weather patterns over the Gulf.

RESULTS

Arrival of trans-Gulf migration on the Louisiana coast.—The "Summary of seasonal occurrences" in "Louisiana birds" (Lowery, 1960) gives the status of the passerine migrants that frequent Louisiana during spring migration. Most of the species normally migrate at night and must therefore leave the land areas south of the Gulf of Mexico under the cover of darkness. Lowery (1946, 1951) presents evidence that in spring large numbers of land birds do embark on nocturnal migrations that take them northward over the waters of the Gulf. The distance across the Gulf is such

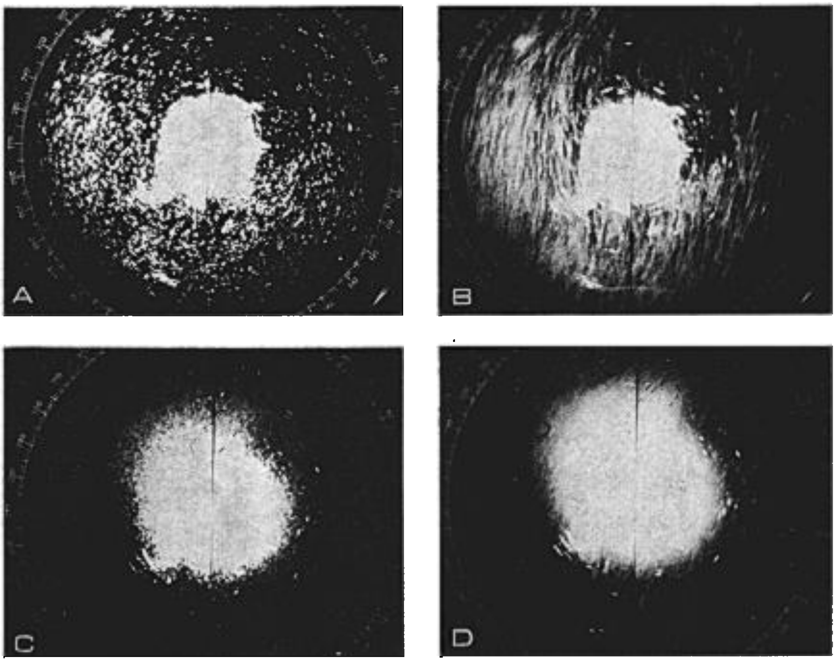

Figure 2. Radar photographs of daytime and nocturnal migration. All photographs were taken with 3° antenna elevation on 25 nautical mile range at the Lake Charles Weather Bureau on 14 May 1965. A, 13:47 c.s.t.; B, 13:48–13:53; C, 20:10; D, 20:10–20:15.

that most of the migrants should arrive on the northern coast during the daylight hours. The radar and telescopic data I collected during this study confirm a daytime arrival, and it appears that the timing of the arrivals is influenced by weather conditions encountered over the Gulf.

Figure 2A shows the type of echoes that appear on the WSR-57 radar screens when migrants arrive from over the Gulf of Mexico during the daytime. The echoes are strong and persistent and can be tracked on the radar screen for distances of 2 to 6 nautical miles. Their density seldom caused saturation of the radar screen, and separate echoes could usually be distinguished and counted. Figure 2B is a time exposure and shows the direction of movement. With a 20× or 30× telescope or 10 × 50 binoculars I could see that flocks of passerines produced most of the dot echoes on radar, but flocks of shorebirds and nonpasserine land birds contributed a few of the echoes. Individual migrants caused the scattered, fine echoes in the daytime radar patterns. The flocks of passerines ranged from 2 or 3 to more

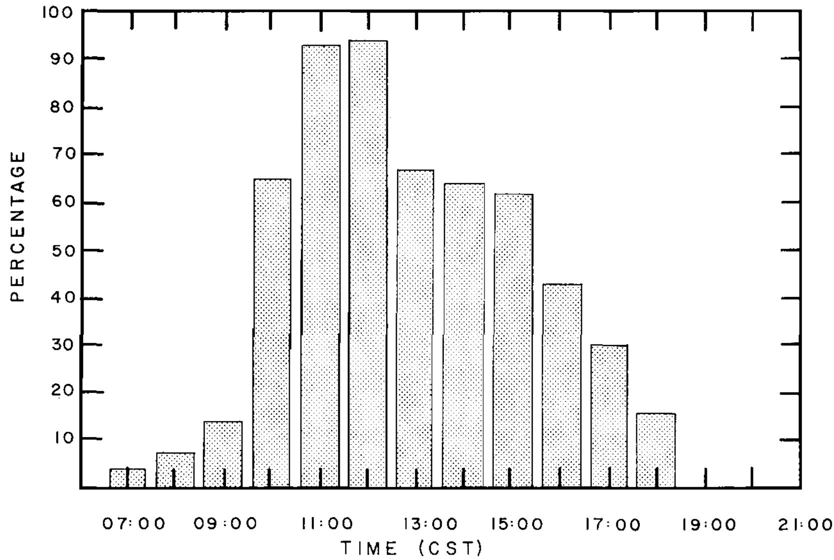

Figure 3. The average hour to-hour change in the quantity of daytime migration arriving from over the Gulf when peak densities occurred before 13:00. The data from 11 dates are plotted as percentages of peak densities.

than 100 individuals; the average was 20 birds. I estimated the largest flock seen during daytime telescopic and binocular watches as 175 birds.

Migrating passerines arrived on the Louisiana coast from over the Gulf on 95 of the 113 days I examined during the three springs of study. Radar occasionally showed echoes from the migrants when they were still 130 nautical miles offshore, but usually did not record them until the birds came within 50 to 75 nautical miles of the coast. The time of day the first echoes from trans-Gulf migrants appeared off the coast depended on the winds and weather over the Gulf. On 20 days when the 06:00 winds-aloft data from coastal weather stations showed southerly winds of 30 to 35 knots between 2,000 and 5,000 feet, the migrants appeared offshore between 04:15 and 06:00 c.s.t. The echoes appeared offshore between 06:00 and 10:00 on 61 days when the winds aloft were generally from the south at velocities from 10 to 30 knots. On 14 days the trans-Gulf flights were delayed, and the migrants did not appear 50 to 75 nautical miles offshore until 10:00 or later.

Figure 3 illustrates the daytime changes in the numbers of flock echoes aloft when the trans-Gulf migrants arrived early. On these days the migrants started flying over the radar stations between 06:30 and 08:30, and the echoes reached peak densities between 10:00 and 12:00. By 18:00 the number of migrants still passing over the stations was greatly reduced—on

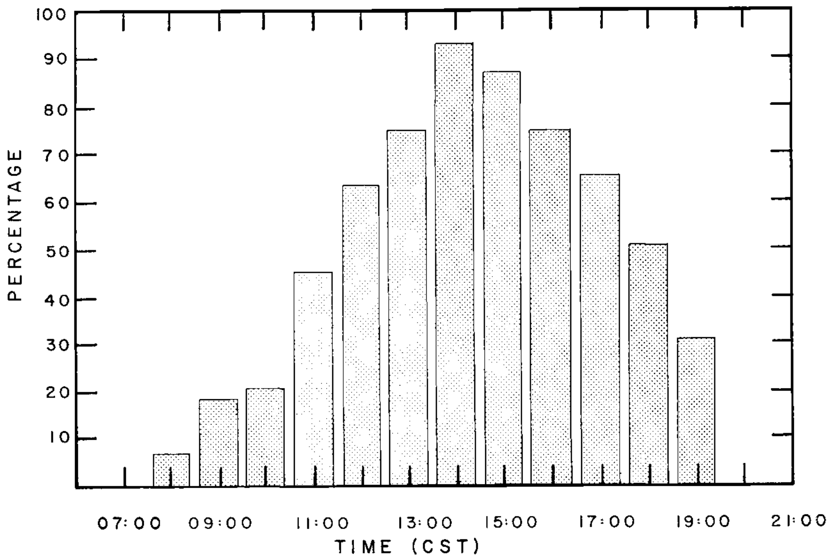

Figure 4. The average hour-to-hour change in the quantity of daytime migration arriving from over the Gulf when peak densities occurred between 13:00 and 17:00. The data from 18 dates are plotted as percentages of peak densities.

the average only 16 per cent of the maximum number recorded earlier in the day.

Figure 4 shows the variation in the migration over the radar stations during what I considered normal timing of arrivals; 64 per cent of the trans-Gulf flights during the study conform to this pattern. The first migrants started passing over the stations between 08:00 and 11:00, and radar echoes reached peak concentrations between 13:00 and 16:30. By sunset the amount of migration still passing over was reduced by two-thirds.

On the 14 occasions when the trans-Gulf flights were delayed so the first migrants did not reach the radar stations until 11:00 or later (Figure 5), peak numbers occurred on the radar screen after 17:00, and at nightfall large numbers of migrants were still arriving from over the Gulf.

Landing areas in southern Louisiana.—The field censuses of grounded migrants that I conducted in small, isolated woodlands south of the radar stations showed that some of the arriving migrants regularly alighted in the scattered woodlands that lie in the coastal belt of marsh and prairie south of treeline. The numbers of birds that landed before reaching the large, inland forests depended on the weather conditions over the Gulf and over southern Louisiana. By comparing the density of radar echoes where the migrants appeared to be landing (disappearing from the PPI) with the density of

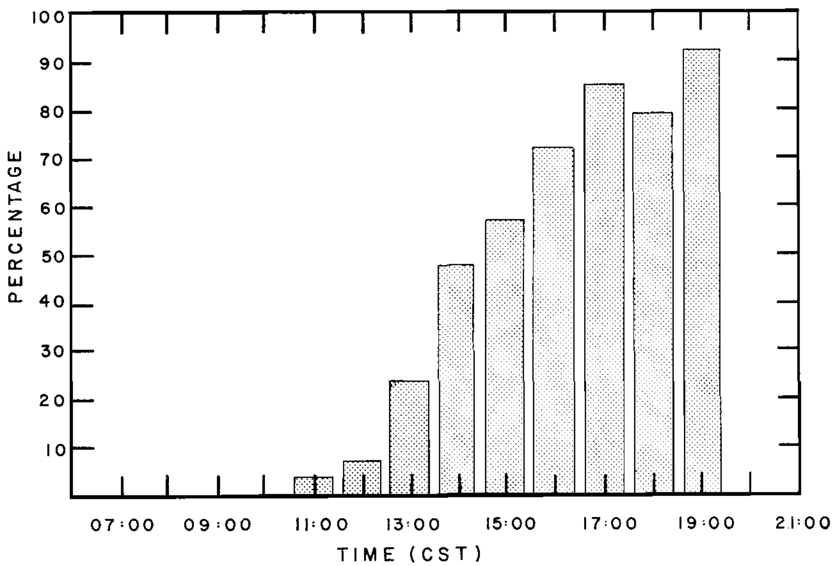

Figure 5. The average hour-to-hour change in the quantity of daytime migration arriving from over the Gulf when peak densities occurred after 17:00. The data from five dates are plotted as percentages of peak densities.

echoes where the migrants did not appear to be landing, I estimated the proportion of migrants that alighted in the coastal belt south of the radar stations.

When meteorological grounding factors (hard rain, unfavorable winds, or both) were absent over the Gulf and along the Louisiana coast, radar showed that most of the arriving migrants flew over the 20 to 30 nautical miles of marsh, prairie, and scattered woodlands and lit in the extensive inland forests. On 78 of 95 occasions, 70 to 90 per cent of the trans-Gulf migrants alighted in forests 25 to 75 nautical miles north of the coastline. Only on 8 of 95 occasions did some migrants (25 per cent) land as far inland as 100 to 130 nautical miles, and on each of these days the weather was fair and the winds aloft were southerly and blowing at 20 to 35 knots.

The first extensive forests in southwestern Louisiana lie 30 nautical miles north of the coastline, or approximately 8 nautical miles north of the Lake Charles station, but in southeastern Louisiana the first large woodlands are 25 nautical miles north of the coastline, or approximately 10 nautical miles south of the New Orleans radar station. Accordingly the number of migrants that landed south of Lake Charles in fair weather was usually less than the number that landed south of New Orleans. During favorable weather an average of 10 per cent of the migrants alighted south of Lake Charles, against an average of 32 per cent that landed south of New Orleans.

When the trans-Gulf migrants encountered bad weather over the Gulf or along the Louisiana coast, the proportion of migrants that alighted in the isolated woodlands south of treeline increased. The measure of increase was usually dependent on the severity and duration of the meteorological grounding factors. On 9 occasions during 95 arrivals, from 60 to 80 per cent of the migrants that encountered thunderstorms over the Louisiana coast appeared to land in the small woodlands scattered throughout the coastal belt. I could not tell from the radar displays whether the migrants came down and flew close to the ground or actually landed, but on visiting the woodlands shortly after recording "landings" on the radar I found spectacular concentrations of grounded migrants and flocks of passerines still plummeting into the trees from extreme heights. But even in very hard rain, some migrants continued to fly until they passed beyond the squally weather. The storm systems never lasted longer than 3 hours, and once the rain slacked or stopped, most of the birds moving inland from over the Gulf continued to treeline as they had done before the rain. When isolated showers occurred over the coastal belt, I saw on the radar screen that some of the bird echoes that moved into rain echoes did not emerge from them, and undoubtedly even these light rain showers grounded some of the migrants.

Rain and adverse winds over the Gulf were probably responsible for the delayed arrivals of 14 trans-Gulf flights during the study. On four of these occasions as migrants continued to arrive on the Louisiana coast after dark, the radar showed many of the birds were landing south of the radar stations. Unlike the usual radar patterns of nocturnal migration where the density of the echoes thins with distance from the antenna, on these nights the bird echoes were very dense over the Gulf waters, but over the coast the density dropped sharply; only a few echoes continued to move inland past the radar stations.

The beginning of nocturnal migration.—On 89 of 95 dates, the field censuses I conducted in the isolated woodlands of the coastal belt showed nearly all the trans-Gulf migrants that had alighted before darkness were gone by the next morning. Only on six mornings did I find appreciable numbers of grounded migrants in the census areas, and on these mornings the species composition and relative numbers of individuals showed either an increase or little change from the previous afternoon.

Weather conditions permitting, the nocturnal migration from southern Louisiana started 30 to 45 minutes after sunset, between the end of civil

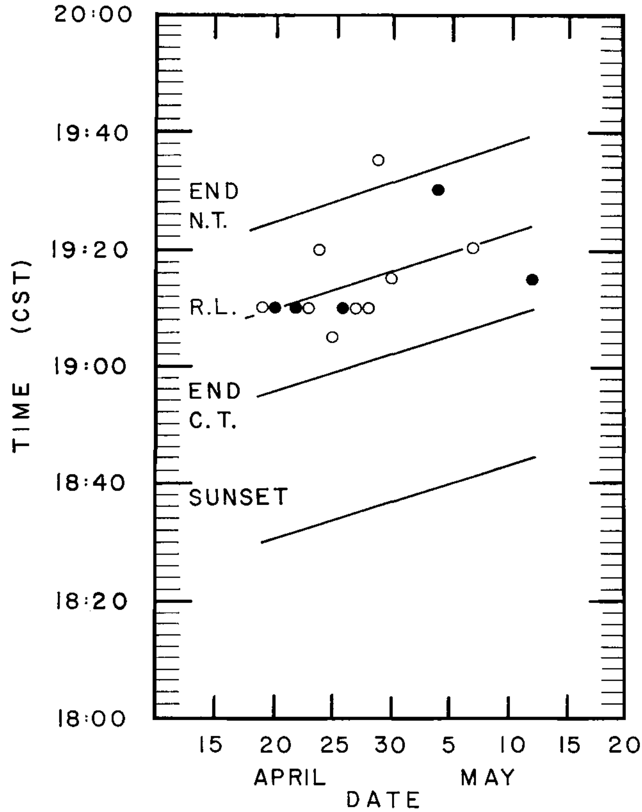

Figure 6. Starting times of nocturnal migration from the Louisiana coast for the spring of 1966, New Orleans, Louisiana. Solid dots mean overcast at sunset; open circles mean clear to partly cloudy at sunset (RL = regression line, NT = nautical twilight, CT = civil twilight).

twilight and the end of nautical twilight (Figures 6 and 7). Civil twilight ends when the sun is 6° below the horizon. At this time terrestrial objects can be distinguished easily and the brightest stars are just visible. The duration of civil twilight during spring migration at this latitude is 24 to 25 minutes. Nautical twilight ends when the sun is 12° below the horizon. At the end of nautical twilight the general outlines of ground objects are visible, the horizon is indistinct, and all the stars that mariners use for navigation can be discerned. From 19 March to 19 May at 30° N the duration of nautical twilight is 52 to 58 minutes. As spring twilight bears an almost constant relationship to the time of sunset at this latitude, I have used the

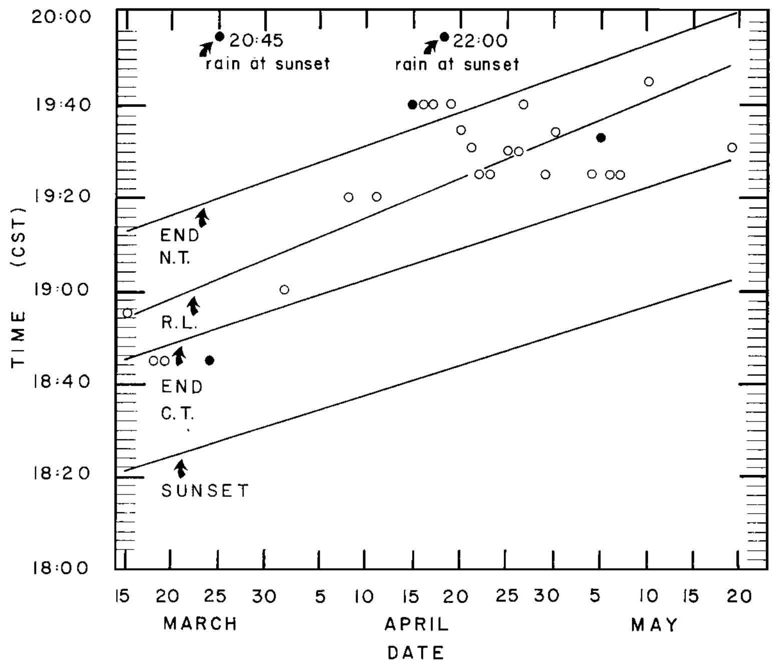

Figure 7. Starting times of nocturnal migration from the Louisiana coast for the spring of 1967, Lake Charles, Louisiana.

time of sunset as the reference base in discussing the time that nocturnal migration begins.

Often the start of nocturnal migration from southern Louisiana was almost eruptive in its suddenness. For a brief time the echo patterns on the radar screen approximated the locations of the woodlands the birds were leaving. Figures 6 and 7 are based on information I gathered from radar film records for the springs of 1966 and 1967 at the New Orleans and Lake Charles Weather Bureaus respectively. The plotted points give the approximate starting times of the nocturnal departures for various dates in March, April, and May. I could not determine the departure time from the coast when late-arriving trans-Gulf migrations obscured the exodus, and in certain instances when the film record was otherwise unsuitable. As the exposures making up the film records were taken only every 15 minutes when no precipitation echoes appeared in the area of radar surveillance, the true departure time may have been up to 15 minutes earlier than the recorded departure time.

From the middle of March to the middle of May 1967, the recorded starting time of nocturnal migration changed about 51 minutes; the change

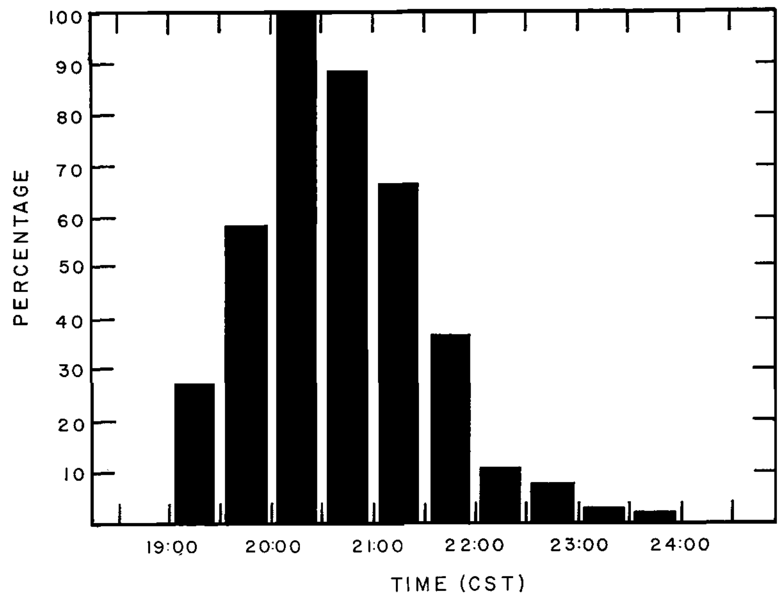

Figure 8. The average hour-to-hour change in the quantity of nocturnal migration plotted as the percentage of peak density. The data for 22 nights were gathered by the radar attenuation technique in New Orleans, Louisiana, during the spring of 1967.

in the time of sunset and in the end of nautical twilight for the same period was 41 and 43 minutes respectively. In spite of the crudeness of the starting time determinations from the film records, the time that nocturnal migration begins is clearly related to the time of sunset and the end of civil and nautical twilight. The computed regression lines that best fit the plotted points in Figures 6 and 7 are nearly parallel to the lines representing the end of nautical twilight. Although fewer data are available for the spring of 1966, the change in the time that nocturnal migration began from 19 April to 12 May is also related to the change in the time of sunset and the end of civil and nautical twilight.

The difference in the time of sunset between New Orleans and Lake Charles is 13 minutes. The average difference in the time of departure for nocturnal migrants from these two localities was about 15 minutes. As can be seen in Figures 6 and 7, rain at the normal time of departure delayed, but did not necessarily prevent, a departure on a given night. Although rain echoes obscure bird echoes on the radar screen, when rain either delayed the start of a migration or stopped a migration in progress, the areas immediately northward of the rain echoes on the screen were void of bird echoes.

Solid overcast at the time of departure did not consistently prevent or delay the exodus of migrants from the woodlands in southern Louisiana.

Figures 2C and 2D show the typical display of nocturnal migration on the PPI of the WSR-57. Figure 2C is an exposure made for a single revolution of the antenna; Figure 2D is a photograph exposed continuously for several revolutions of the antenna. Moon-watching and ceilometer observations revealed that passerine birds flying individually in the night sky produced the abundant, finely granulated echoes, but flocks of waterfowl and shorebirds made the scattered dot echoes.

Changing density of nocturnal migration.—Figure 8, based on data I collected by the radar attenuation technique, shows the hour-to-hour variation in the amount of nocturnal migration passing over New Orleans on 22 nights during the spring of 1967. Although nocturnal migrations from the woodlands south and southwest of New Orleans occurred on 52 nights during the spring of 1967, only on 22 of these nights did I gather enough radar data for temporal pattern analysis. The migrations from southern Louisiana were short in duration. The movements peaked at the latitude of the radar station between 20:00 and 20:30, or about 1 to 1½ hours after I recorded the first nocturnal departures on the radar screen. By 22:00 the density of the migrations decreased by a factor of 10, and by 23:00 the movements were essentially finished. After 23:00 only a few isolated bird echoes remained over coastal Louisiana, and these echoes, moving in various directions, probably represented nocturnally active nonmigrants (e.g. *Nycticorax*, *Nyctanassa*, *Chordeiles*).

The moon and ceilometer watches I made during the study yielded similar results to those obtained with radar. On the 11 nights when enough moonwatch data were collected, the migrations reached peak densities over the radar stations between 19:30 and 21:30, with peaks occurring between 20:00 and 20:30 on seven of these nights. By 22:00 the movements were essentially finished. On 32 of the 36 nights I made ceilometer observations in New Orleans during the spring of 1967, the number of birds flying through the beam increased sharply after dark and peaked between 20:00 and 21:00. By 22:00 the number of birds passing over was usually only 10 to 15 per cent of the peak amount recorded earlier in the evening. Only four times did I observe peak numbers of migrants in the ceilometer after 22:00, and these instances were associated with delayed trans-Gulf flights.

From the second week in March to the second week in April, the highest migration traffic rates at night were less than 500 birds on 20 of 27 dates and less than 2,000 birds on the remaining 7 nights. From the second week in April to the second week in May, the maximum nocturnal migration rates averaged 15,000 birds. During the second week of May the amount

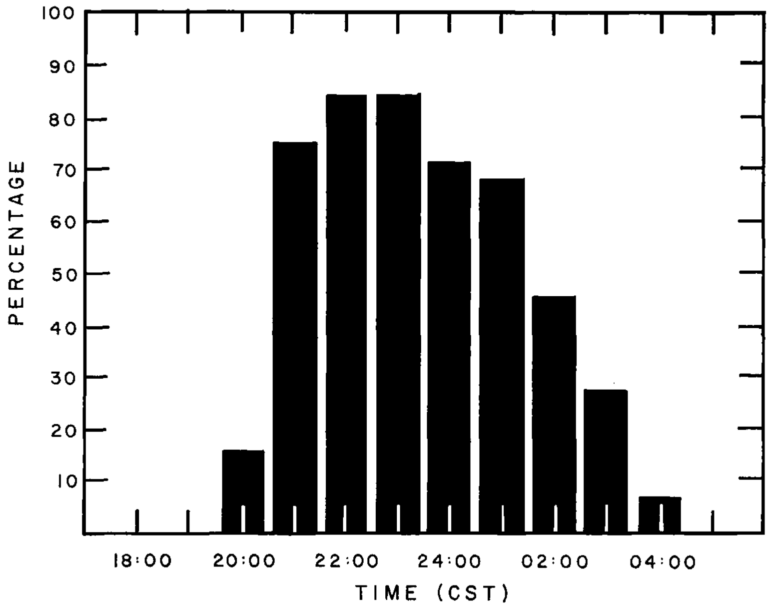

Figure 9. The average hour-to-hour change in the quantity of nocturnal migration plotted as the percentage of peak density. The data for 8 nights were gathered by the radar range-thinning technique at Lake Charles, Louisiana, during the spring of 1965.

of migration entering Louisiana from over the Gulf decreased, and by the middle of May the night migration rates were less than 500 birds.

The quantity of nocturnal passerine migration in southern Louisiana in spring depends largely on two factors: 1) the number of migrants on the ground ready to migrate by nightfall, and 2) the number of birds still arriving from over the Gulf at the time of darkness. In late April and in early May the maximum nocturnal traffic rate was lowered by as much as 80 per cent on those dates when very few of the incoming migrants alighted around and south of the radar stations. Likewise on those dates when no trans-Gulf migrations arrived on the coast and very few migrants were in the coastal woodlands, the magnitude of the nocturnal departures was reduced by as much as 85 per cent.

When large numbers of migrants alighted near the coast in the late afternoon, the migration traffic rates at night were often higher than normal. On 8 May 1967 the trans-Gulf flight was delayed by adverse winds, and many migrants landed south and southwest of New Orleans late in the afternoon. After dark when birds were still moving inland from over the Gulf, the grounded migrants started their nocturnal migration. That night a peak radar density equivalent to a migration traffic rate of 50,000 birds occurred at 21:12. This is the highest density I recorded during the study and is probably representative of the magnitude of an entire trans-Gulf flight (in terms of birds crossing a mile of front) for a given date in late April and in early May.

After the nocturnal migration from southern Louisiana moved northeastward and could not longer be monitored by the Lake Charles and New Orleans radars, a nocturnal migration moving east-northeast (50° to 60°) could be seen on the north and northwest sectors of the Lake Charles radar screen on 25 and 50 nautical mile range. The echoes produced by this movement were characteristic of passerine migrants, and I was able to confirm this by listening to call notes and by moon-watching on the few occasions when the southern edge of the migration passed over the Lake Charles station. These migrations from the coastal regions of Texas reached peak densities between 23:00 and 01:00. Around 03:00 the density of the migrations was usually reduced by two-thirds, and near dawn the migrations, much reduced in magnitude, ended (Figure 9). These migrations were underway on each of the 83 nights I checked for them, but only on 8 of the nights did I obtain a complete record of the movements from start to finish. The peak traffic rates for these eight flights ranged from 1,300 to 12,000 birds, and the average maximum on these nights was 4,800 birds per mile of front per hour (SD = 3,780 birds). These movements probably contained a mixture of trans-Gulf migrants that had landed on the Texas coast earlier in the afternoon and overland migrants from northeastern Mexico.

Weather influences.—Major weather systems over the Gulf (Figure 10) directly influenced the timing of trans-Gulf migrations and indirectly affected the magnitude of the subsequent nocturnal migrations from southern Louisiana (Table 1). On 95 of the 113 dates that flights crossed the Gulf, 76 did so with no front over the Gulf (Figure 10A, 10C), 16 with a cold front over the northern Gulf (Figure 10D, 10E), and 3 with a weak cold front extending to the southern Gulf (Figure 10F). Rainy disturbances or cold fronts delayed 14 of the 95 flights, and on the 18 dates when trans-Gulf migrations did not reach the Louisiana coast, strong easterly winds or cold fronts were over the southern Gulf (Figure 10B, 10F). Only three of these 18 dates (30 April 1965, 1 May 1965, and 10 April 1966) fell within the period 8 April–15 May.

As the magnitude of the nocturnal departures from the woodlands around and south of the radar stations depended on the number of migrants in the woods ready to migrate at nightfall, the departures were either greatly reduced or absent when trans-Gulf migrations failed to arrive. Table 2 gives the relationship between the timing of the trans-Gulf flights, or their

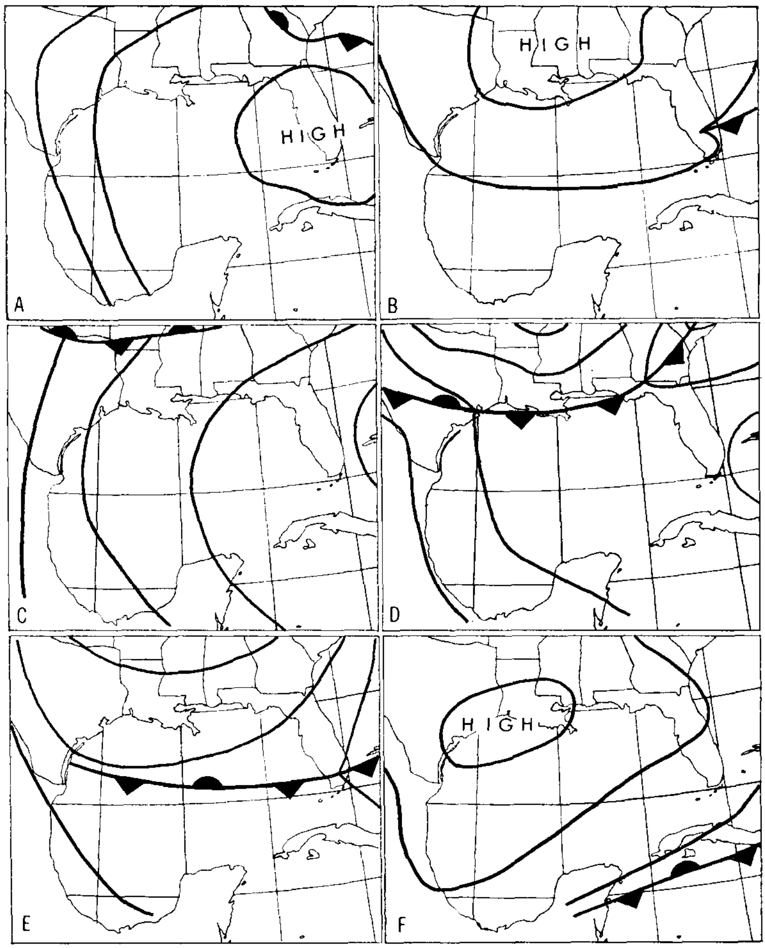

Figure 10. Weather maps for the Gulf region showing frontal systems and isobar orientation. A, 14 March 1967, 00:00 c.s.t.; B, 23 March 1967, 00:00; C, 23 April 1967, 00:00; D, 24 April 1967, 12:00; E, 28 April 1967, 00:00; F, 29 April 1965, 12:00.

absence, and the magnitude of the subsequent nocturnal migrations from southern Louisiana.

On four of the 14 occasions when trans-Gulf migrations were delayed, most of the migrants that alighted during the late afternoon did not resume their migration after dark, and those that continued to arrive at night landed near the coast. The trans-Gulf flights that departed from south of the Gulf on the nights of 27 and 28 April 1965 were expected to arrive on the Louisiana coast on 28 and 29 April, but they were delayed 15 to 20

TABLE 1

WEATHER PATTERNS ASSOCIATED WITH TRANS-GULF MIGRATIONS AND NOCTURNAL DEPARTURES FROM SOUTHERN LOUISIANA

Weather pattern[1]	Trans-Gulf flights			Nocturnal departures		
	On time	Delayed	None	Normal	Reduced	None
1	71	5	0	75	0	1
2	9	7	0	12	4	0
3	1	2	18	3	16	2

[1] Pattern 1, no cold front in Gulf but possible rain over Gulf (A and C in Figure 10). Pattern 2, cold front in northern Gulf (D and E in Figure 10). Pattern 3, cold front in southern Gulf or easterly circulation over Gulf (B and F in Figure 10).

hours by a powerful cold front and arrived on the Louisiana coast on 29 and 30 April. I saw from the radar displays that nearly all the migrants landed as they reached the coast. On 29 April the nocturnal migration that left the coastal woodlands was relatively low in magnitude, and on the night of 30 April, no nocturnal exodus occurred. The trans-Gulf flights that were destined to reach the coast on 30 April and 1 May did not materialize, but on the night of 1 May, the passerines that had been grounded on the coast for 1 or 2 days departed.

On 27 April 1967, a strong cold front was positioned approximately 100 nautical miles south of the Louisiana coast at 12:00. Radar showed that most of the migrants landed in the coastal woodlands that afternoon. That night the exodus of migrants from the coast was reduced, and the migrants that arrived after dark landed near the coast. During the day of 15 May 1967, a powerful cold front moved through coastal Louisiana and out over the Gulf. At nightfall no birds left the coastal areas where they had landed earlier in the day. At 21:00 some migrants were still arriving from over the Gulf and landing south of the radar stations.

Except for hard rain, the proximate weather conditions at the time of the initiation of nocturnal migration from southern Louisiana did not seem to influence the density of the movement. On 13 of the 90 nights when nearly all the grounded migrants around and south of the radar stations departed, anticyclonic conditions behind a cold front were present at the time of

TABLE 2

RELATIONSHIP BETWEEN THE TIMING OF TRANS-GULF FLIGHTS AND THE OCCURRENCE OF SUBSEQUENT NOCTURNAL DEPARTURES

Trans-Gulf flights	Subsequent nocturnal departures
81 on time	81 normal
14 delayed	8 normal, 4 reduced, 2 none[1]
18 none	1 normal, 16 reduced, 1 none

[1] Six instances with migrants remaining on coast overnight.

departure (e.g. increasing barometric pressure, falling temperature and relative humidity, and northwesterly to northeasterly winds). Of the 90 departures that I considered normal in timing and magnitude, 27 occurred under solid overcast, 30 took place on dates when the temperature at 18:00 was lower than that recorded at 18:00 the previous day, 34 occurred when the relative humidity at 18:00 was lower than that at 18:00 the day before, and 32 began with a higher barometric pressure at 18:00 than the previous day. As 29 per cent of the normal departures took place with adverse or crosswinds, almost one-third of the nocturnal departures from southern Louisiana began under weather conditions commonly considered unfavorable for migration.

Solid overcast did not delay a nocturnal departure, nor did it reduce the quantity of migrants in an exodus. Rain not only delayed two departures, it also stopped migrations in progress. On 1 May 1967 the migrants leaving the coastal belt moved into a row of severe thunderstorms about 80 nautical miles north of the coast. When the birds encountered the rain they apparently landed, for no bird echoes were visible north of the rain echoes on the radar screen. Where rain was not falling, the bird echoes continued moving through the dry portions of the squall line. During the day rain usually grounded some of the trans-Gulf migrants when they moved into rain storms over land.

DISCUSSION

Frazar (1881) was the first to present evidence that songbirds cross the Gulf of Mexico during spring migration. On the basis of reports of land bird migrants over the Gulf and observations of grounded migrants on the northern Gulf coast, Cooke (1904, 1915) proposed that many species of songbirds regularly cross the Gulf at night in spring and fall. This concept was later supported by Lowery (1945, 1946) but challenged by Williams (1945, 1947). Williams contended that nearly all the migrants that wintered south of the Gulf of Mexico returned to the United States along coastal routes east and west of the Gulf. Lowery (1946, 1951) established by moon-watching on the northern coast of Yucatan that considerable numbers of land birds migrate across the Gulf in spring. Stevenson (1957), after assembling data on the distribution of grounded migrants on the northern Gulf coast, also concluded that many spring migrants must reach the United States by trans-Gulf flights. My findings further document the almost daily occurrence of trans-Gulf migrations in spring.

The day-to-day frequency of trans-Gulf migrations and nocturnal departures from southern Louisiana in spring is in sharp contrast to the findings of Drury and Keith (1962) for vernal migration in New England. These authors reported that most migration (60 per cent or more) occurred on approximately 4–5 nights out of 90 in spring. The regularity of the flights entering the southern United States in spring is undoubtedly related to the stable, favorable weather that characterizes the tropical regions from which the migrations originate and the decreasing number of powerful cold fronts that move over the Gulf of Mexico after the first week in April. From 14 March to 7 April, trans-Gulf flights did not arrive on the northern coast when the winds over the southern Gulf were strong and blowing from northerly or easterly directions. After the first week in April when winds over the Gulf became favorable, the day-to-day constancy of flights across the Gulf was interrupted on only three dates during the study, and on each of these dates strong cold fronts were positioned over the southern Gulf.

If bird migration is triggered by certain weather stimuli, then my findings from the Gulf region suggest that these stimuli must nearly always be present during spring in the tropical regions from which trans-Gulf migrations originate. Monroe (1968: 390) has recently presented evidence that gives additional support to the daily frequency of migration from the tropics. He found by moon-watching that on every one of eight consecutive nights in early May a relatively large migration left northern Honduras (moon-watching traffic rates from 4,000 to 13,000) and moved to the north or northwest.

The first reference to the timetable of trans-Gulf migration was made by Cooke (1904) when he suggested that most migrants begin their flights across the Gulf at night. Lowery (1946, 1951) later confirmed this by lunar observations on the southern Gulf coast, and he deduced that most of the migrants should arrive on the northern coast during the following daylight hours. Many field observers working on the northern coast have subsequently confirmed this timetable (this subject and many other pertinent discussions of trans-Gulf migration can be found in the excellent accounts of spring migration for the Florida, Central Southern, and South Texas Regions of Audubon Field Notes, 1951–1968). The radar data accumulated during this study further clarify the timing of trans-Gulf migration. The flights generally first reached the Louisiana coast in the early daylight hours, and peak densities of arriving transients occurred around midday and early afternoon. The arrivals were delayed when rain, or adverse winds, or both were over the Gulf and were early when strong following winds helped the flights.

Lowery (1951) found that the duration of the nocturnal migrations over northern Yucatan was approximately 7 hours; I found the average duration of the arrivals on the Louisiana coast to be about 12 hours. The difference can best be explained by the varying air speeds of the species involved. A difference of a few knots in air speed between two species leaving Yucatan together can make a difference of several hours in their times of arrival on the northern coast.

Lowery (1945) confirmed Cooke's (1904) suggestion that many trans-Gulf migrants fly some distance inland before alighting, and he termed the coastal plain that was usually void of transients in fine weather the "coastal hiatus." Subsequently Lowery (1951) believed that the scarcity of records of transient migrants on the Gulf coastal plain in fair weather was largely the result of a wide dispersion of birds in the dense cover that characterizes the region. The radar data that I have collected support Lowery's more recent viewpoint regarding the landing areas of trans-Gulf migrants. On radar most of the echoes from migrants arriving from over the Gulf disappeared over the extensive forests 25 to 75 nautical miles north of the Louisiana coastline. Even in adverse weather some migrants continued flying inland until they reached the extensive inland forests.

The findings of this study generally support those of Lowery (1951) regarding the hour-to-hour variation in the number of nocturnal migrants aloft during the spring, but it appears that Lowery's postulate that "most migrants go to sleep for a period following twilight, thereby accounting for the low densities in the early part of the night" is erroneous. From radar studies of nocturnal passerine migration across the English Channel, Parslow (1962, 1969) reported that the first bird echoes appeared abruptly from 29 to 49 minutes after sunset, and once the initial departures had taken place, few or no other migrants started off the same evening. Casement (1966) commented that the bulk of passerines began their nocturnal migration about 45 minutes after sunset, and the increase in migratory activity was very rapid and dramatic. Similarly, in the United States, Nisbet and Drury (1968) found that songbirds began their nocturnal migration about 45 minutes after sunset. My data also suggest that most birds start their nocturnal migration in spring at the very beginning of the night between the end of civil twilight and the end of nautical twilight, or about 30 to 45 minutes after sunset.

Lowery (1951) found that the duration of nocturnal migration in spring in southern Louisiana was surprisingly short, and he used the phrase "Baton Rouge drop-off" to refer to the virtual cessation of migration near 22:00. My radar and telescopic data from New Orleans and Lake Charles show hour-to-hour patterns very similar to those Lowery (1951: 422) recorded for Baton Rouge. Unlike the nocturnal movements from the Louisiana coast, the migrations that originated from along the Texas coast and passed to the north and northwest of Lake Charles were sustained, and the hour-to-hour pattern of these movements agrees well with the average pattern found by Lowery (1951: 415).

The duration of the Texas flight is longer probably because the source areas along the Texas coast extend from the Louisiana border to Corpus Christi (Forsythe, 1967) and are in line with the direction of migration. Why the peak amplitude of the hour-to-hour curve is 3 to 4 hours later for the Texas flight than that for the flight from coastal Louisiana is best explained in terms of the distribution of migrants on the ground before the start of the nocturnal migration and the different airspeeds of the birds in the movement.

Most students of migration think of the initiation of a night's migration in terms of some external stimulus that releases migratory behavior. The frequency of trans-Gulf migrations and the subsequent nocturnal migrations from southern Louisiana under a wide variety of weather conditions suggests that the nightly initiation of migration in spring depends upon the absence of inhibitory factors rather than the presence of stimulatory ones.

After the first week in April only rarely was the day-to-day constancy of migrations across the Gulf interrupted. On every date that a trans-Gulf flight failed to arrive on the central, northern Gulf coast, unfavorable weather was over the southern Gulf. Whether these conditions prevented the start of migration south of the Gulf is not known, but the data I accumulated from the Louisiana coast show that unfavorable conditions did not consistently deter nocturnal migrations. Perhaps the migrants do start a trans-Gulf flight, and when they encounter bad weather early in the flight, they either return to the southern Gulf coast or continue the crossing. If they persevere in their attempt to cross the Gulf, several risks exist singly or in combination depending on the severity of the weather: 1) if strong crosswinds are blowing, the birds may be drifted; 2) if the birds are flying against adverse winds, their journey may be lengthened considerably; and 3) if rain is falling, the birds may get wet and increase their wing load. These possibilities are reasonably likely, and all influence the energy expenditure of the migrants.

While banding spring trans-Gulf migrants in fair weather on the Alabama coast Imhof (1965) found that many migrants had about one-third, or less, of their fat capacity, and a variable number of migrants were very lean. He further pointed out that some migrants must expend considerable energy combating cold fronts over the Gulf of Mexico, for in the wake of such fronts he has netted grounded migrants with concave abdomens and wasted pectoralis muscles. Great numbers of trans-Gulf migrants also alight on the oil rigs south of the Louisiana coast when bad weather is over the Gulf, and many of these birds, unable to find food, die of starvation. The dead migrants from the rigs that I have examined were extremely emaciated and had no traces of fat.

The trans-Gulf migrants that alight in coastal Louisiana in the afternoon have completed at least a 480 nautical mile flight over water, and most of these birds normally initiate a nocturnal migration a few hours later. Child (1966), Hicks (1968), and Johnson (1969) have shown that spring migrants netted on the Louisiana coast generally have moderate fat reserves (from 5 to 17 per cent of wet body weight) after crossing the Gulf. I have netted trans-Gulf migrants that were forced down by very hard rain as they reached the Louisiana coast, and 63 per cent of the 45 birds I examined had distinct abdominal fat pads and bulging fat deposits in the furcular region. Such birds can be assumed to be physiologically ready to migrate in terms of lipid reserves, and the recurring nocturnal departures of grounded transients from coastal Louisiana under every conceivable combination of weather factors attest to the validity of this assumption.

On every date that grounded trans-Gulf migrants in coastal Louisiana failed to start a nocturnal migration, either the birds had experienced bad weather over the Gulf earlier in the day, or intense rain was falling at the time of departure. Unfavorable weather probably *indirectly* influences the termination of a trans-Gulf flight and the inhibition of a subsequent departure. Fatigue, low energy reserves, or both probably *directly* cause large numbers of trans-Gulf migrants to alight on the first available land, and if these conditions are not corrected before nightfall, the migrants do not start a nocturnal migration.

During the arrival of most trans-Gulf flights, some migrants regularly landed in the coastal woodlands in fine weather. When cold fronts became stationary near the coast or over the northern Gulf, the percentage of migrants that came down in the first available woodlands increased. When strong cold fronts, extensive rain areas, or both were over the Gulf, the number of migrants that alighted in the small coastal woodlands increased greatly, and occasionally the magnitude of the subsequent nocturnal exodus of grounded transients was markedly lowered. In the latter cases, the population of grounded migrants present in the late afternoon was either increased or unchanged the following morning. Hebrard (1969) found grounded trans-Gulf migrants sleeping in trees when a nocturnal exodus from coastal Louisiana failed to materialize, and I have recorded similar instances on offshore oil rigs and in coastal woodlands.

Wolfson (1954) suggested that from an energetic standpoint birds must replenish exhausted fat reserves before initiating another long migration. The rate at which a bird can redeposit its lipid depots is known only poorly, but some investigators (e.g. Dolnik and Blyumental, 1964; Helms, 1968) have found that migrants accumulate about a gram of fat a day. Dolnik and Blyumental (1967) and Evans (1968) reported that depletion of fat stores can suppress *Zugunruhe* in caged migrants. It thus appears that adverse weather over the Gulf forces trans-Gulf migrants to terminate their flight on the first available land by necessitating increased or prolonged utilization of migratory lipid deposits while over the Gulf. These birds are often energetically incapable of resuming their migration after dark. When weather conditions are fine, nearly all the migrants that land on the northern Gulf coast during the day depart a few hours later at nightfall.

If results obtained from caged migrants can be related to the findings of this study, it seems that as long as migrants have the physiological capability to migrate, they will attempt to do so regardless of the local weather conditions. Such a hypothesis is in keeping with the numerous reports of migrations underway in bad weather, and it postulates that those spring migrants that fail to initiate a migration on a given night, once they have started their seasonal migration, are energetically (physiologically) incapable of doing so. McMillan (1969) and McMillan et al. (1970) present additional evidence in support of this idea. They report that spring *Zugunruhe* in caged White-throated Sparrows (*Zonotrichia albicollis*) persists for weeks in isolation chambers with constant dim light and shows a circadian periodicity.

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Summary

During the spring seasons of 1965, 1966, and 1967, 1,100 hours of combined WSR-57 radar and telescopic observations of migration were made at the Lake Charles and New Orleans Weather Bureaus in coastal Louisiana on 113 days. The radar displays of daytime and nocturnal migration were quantified with the aid of daytime telescopic and moon-watch information. Nearly all the passerine migrants that were detected passing through coastal Louisiana during the study arrived from over the Gulf of Mexico. From 8 April to 15 May trans-Gulf migrations arrived almost daily on the Louisiana coast. The total number of birds entering southern Louisiana from over the Gulf in early April was on the order of 20,000 to 25,000 birds per mile of front per day and increased to as high as 50,000 birds per mile of front per day near the end of April and the first week of May.

The nocturnal temporal pattern of migration in southern Louisiana was

normally of short duration near the coast and of long duration north and northwest of Lake Charles, where the nocturnal migration from coastal Texas continued through most of the night. Except for hard rain, no single local (proximate) weather condition nor combination of local weather conditions consistently prevented the start of a nocturnal migration from coastal Louisiana. The passerine migrants usually began their nocturnal migrations from southern Louisiana 30 to 45 minutes after sunset, and the departures were essentially finished an hour later. Overcast at the time of takeoff did not affect the time of exodus. Large numbers of trans-Gulf migrants landing on the coast and the subsequent inhibition of departures from the coastal woodlands was most noticeably related to the presence of powerful cold fronts over the Gulf. Fatigue and low energy reserves in the form of migratory lipids were probably the immediate causes of landing, and in such cases, the same causes were probably responsible when a nocturnal exodus of grounded migrants failed to take place. Thus the initiation of nocturnal migration in spring in the southern United States is probably dependent on internal factors rather than on environmental stimuli.

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