FALL MIGRATION AND WEATHER, A RADAR STUDY

SYLVIA SUE HASSLER, RICHARD R. GRABER, AND FRANK C. BELLROSE

MANY ornithologists have found evidence of a relationship between changing weather and the timing and volume of bird migration. Recently, Lack (1960*b*) reviewed much of this work on the weather factors which appear to affect flights of nocturnal migrants. His review represents a real contribution and a service to students of migration, but certain of his generalizations and conclusions are so at variance with findings from our own studies that we feel called upon to discuss the subject further in detail.

Behavior patterns of migrants vary not only from species to species, but probably also from place to place. Lack's conclusion (p. 185) that low temperature in autumn is the dominant factor in stimulating flights of migrants may be true of migrants in some areas of North America and the old world, but this relationship, i.e., temperature change and migration, does not generally hold for nocturnal migrants in the Great Lakes area of the United States, at least in early and mid-fall. It is the purpose of this paper to consider the factors that do influence migration in this area.

Our data were acquired with the use of a 3-cm (APS-31) radar installed at the University of Illinois Airport south of Champaign, Illinois, specifically for the purpose of observing migration (see Graber and Hassler, 1962). In 1961–62, radar observations of migration were made by Graber across a three-state area (Iowa, Illinois, and Indiana) and we believe that the data presented here are generally representative of a large section of the midwest, not merely of our local area. The study, initiated in the spring of 1960, was supported by the National Science Foundation and the Illinois Natural History Survey.

METHODS

Drury, Nisbet, and Richardson (1961) presented an excellent review of the radar studies of migration. The equipment used in this investigation and the methods of collecting and recording data were described by Graber and Hassler (op. cit.).

We have utilized the relative flight densities and flight altitudes taken from our radar film record for the period 2 August 1960 through 30 October 1960. The number of bird targets detected by the radar during each 2-minute period of film exposure was counted. To determine whether flight densities of migrants varied from hour to hour during the night, we computed hourly densities for each night, and constructed a curve (Fig. 1) representing the typical hourly trend of the migration activity. This curve includes data (averaged) from 10 nights of migration between 5 August and 11 September. The

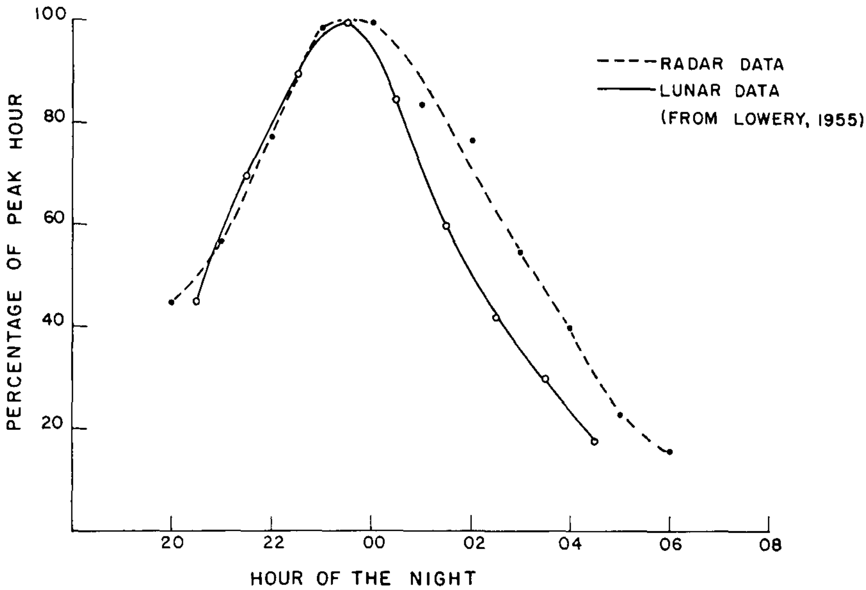


FIG. 1. Comparison of average temporal patterns of nocturnal migration obtained from lunar and radar data. Solid line is Lowery's curve "A" (1955:259). Broken line was plotted from radar data (averaged) for ten nights in autumn 1960. Nights included were clear, and without change in surface wind direction. Curves are based on hourly data plotted as percentage of the peak value.

seasonal variation in flight density was graphed (Figs. 2, 3, 4) from the average volume of flight per hour for each night, obtained by dividing the total nightly count by the number of hours of operation (usually sunset to 0500 CST). No attempt has been made to equate these relative densities to the true number of birds in flight. Because of technical trouble, radar data for the nights of 9 August, 2, 7, and 8 September, and 18 October are missing.

Meteorological information which we examined in order to obtain an accurate picture of the weather conditions during this 3-month period include the U.S. Weather Bureau daily surface maps; microfilm copies of the hourly surface observation made at Chanute Air Force Base, Rantoul, Illinois (about 25 miles north of the radar station); thermograph, barograph, and recording anemometer records supplied by Illinois State Water Survey stations in Champaign; and winds-aloft data from the nearest radiosonde station (Peoria, Illinois).

The daily surface map describes the location of surface weather phenomena (i.e., fronts, high and low pressure centers, areas of precipitation, etc.) at 0100 and 1300 EST, or 0000 and 1200 CST. The Rantoul surface data include

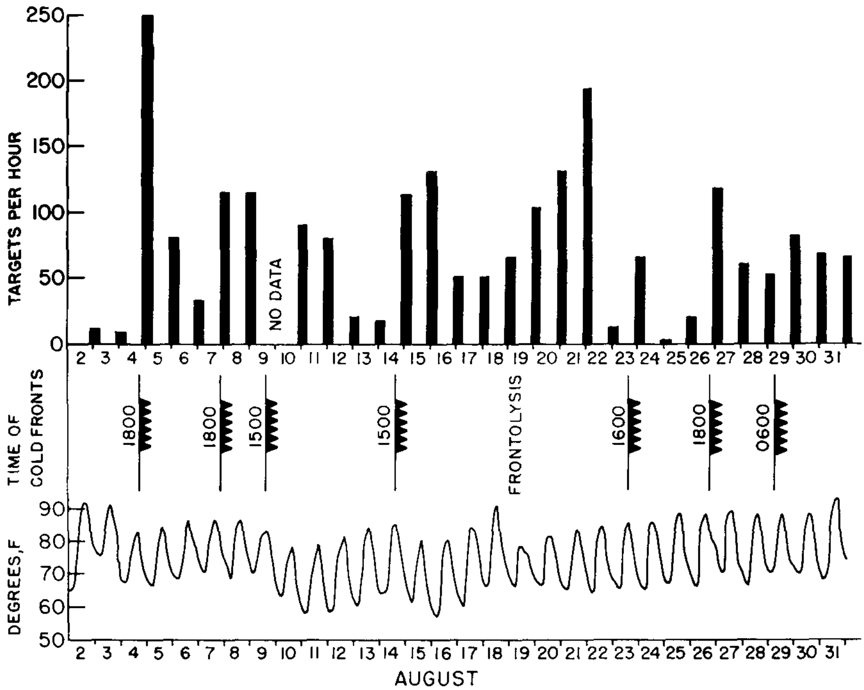


FIG. 2. Volume of nocturnal migration, cold front passages, and temperature at Champaign, Illinois, during August 1960. Bars represent the average number of bird targets per hour detected each night during the period from sunset until 0500 CST. Pips indicate midnight. Cold front symbols indicate to the nearest hour the time at which the pressure trough passed Champaign. The continuous daily temperature curve was constructed from thermograph charts, with values plotted for every three hours.

temperature, dew-point, barometric pressure, surface wind direction and velocity, sky cover and precipitation, recorded hourly, or more frequently when changing conditions warranted. The barograph, thermograph, and anemometer charts provided a continuous graphic picture of variations in pressure, temperature, and wind speed and direction.

Using the surface maps and the Rantoul observations, we determined the time of passage of each cold front through Champaign during August, September, and October 1960. Theoretically, a front is defined by the line of temperature discontinuity between the two air masses involved and this temperature discontinuity coincides with the pressure trough and wind-shift line. Actually, however, a frontal "line" is an area of considerable width in which the temperature, pressure, and wind may all be changing at different rates, locations, and intensities. The pressure trough is used to plot the position of the front on

TABLE 1
TEMPERATURE ON FIRST AND SUCCESSIVE NIGHTS OF MIGRATION WAVES, AUTUMN 1960

Temperature	Dates		
	August	September	October
Lower			
Initial night of wave	4, 10, 19	9, 19, 25, 30	6, 19
Successive nights of migration	15	16, 20, 28	3, 7, 15, 23
No change			
Initial night of wave	7, 14, 23	17, 27	2, 14
Successive nights of migration	8, 11, 20, 21	26	
Higher			
Initial night of wave	26, 29	3, 11, 22	9, 22
Successive nights of migration	30, 31	1, 4	8, 10, 11, 20

the surface map. Since it is also the easiest of the various elements to localize in time, we shall, for convenience, define the time of occurrence of the pressure trough to be the time of cold front passage, and will discusss temperature and wind changes in relation to it. The barograph records enabled us to locate the time of this pressure fall and rise within approximately one hour.

To determine specifically how the elements of weather might influence migration, it was necessary to study both the daily weather conditions under which the birds were living, and the nature and magnitude of the changes which occurred with the passing of fronts. In preparing Tables 1 and 2 from this analysis we defined the "first night of a wave" to be a night on which an increase in migration volume occurred following one or more nights of decrease. An increase of less than 30 targets per hour was not considered significant, as this represents an increase of only one target per film frame and is within the possibility of error in film analysis. Nights included in the tables as having significant continuing migration after the initial night of a wave are those on which the density was approximately two-thirds or more of the density on the first night or which showed migration of 200 targets per hour or more.

The "average" temporal curve.—Lowery (1951) showed that the flight density of migrants was not constant but varied with the hour of the night. He pointed out several patterns of variation but found one particular pattern which occurred most frequently. In this pattern the flight density of migrants increased sharply after sundown, reached a peak around midnight, and fell off steeply thereafter. In fall at Champaign the common temporal pattern shown by our radar observations was very similar to that presented by Lowery based on lunar data (Fig. 1). Lowery also discussed various factors which could

TABLE 2
SURFACE WIND DIRECTION ON EACH NIGHT OF AUTUMN 1960

	Wind direction				
	NW–NE (310–060)	Calm	E (070–110)	SE–SW (120–240)	W (250–290)
Initial night of wave					
August	4, 10, 14, 23, 26	29 (360°)		19	7
September	9, 11, 17, 19, 22, 25, 27, 30			3	
October	2, 6, 9, 14, 19			22	
Successive nights of migration					
August	11, 15, 21			8, 20, 30, 31	
September	26, 28	1 (360°)		20	4
October	3, 7, 8, 10, 15, 23	11 (090°)			16, 20
Nights of little or no migration					
August	22	3 (variable) 12 (180°)	5, 16	2, 6, 13, 17, 18, 24, 25, 27, 28	
September	12, 29	14 (220°)	5, 10, 13, 15	6, 16, 18, 21, 23, 24	
October	17		24	1, 4, 5, 12, 13, 21, 25	

affect the pattern including the method of observation itself, species differences among the migrants, and topography of the land.

In our entire fall record (85 nights) we found few exceptions to the "average" temporal pattern, but these exceptions are important in showing the influence of weather on the flight density of migrants. In the ensuing discussions it will be necessary to refer to the average temporal pattern and the exceptions.

TIMING OF FALL MIGRATION WITH COLD FRONTS

Many investigators have observed that waves of migration followed the passing of a front. Graber and Cochran (1960) presented information on the precise time relationship between migration and fronts, but their audio data were subject to special behavioral interpretation, and the radar data presented here are superior for analyzing the timing of migration with various environmental factors. Some migration was detected by radar at Champaign on every night recorded but one (21 October) between 1 August and 25 October 1960. It is nonetheless true that migrants pass through this area in definite waves or rushes (Figs. 2, 3, 4) of which there were eight in August, nine in September, and six in October. Marked increase in migration followed 19 of the 20 frontal

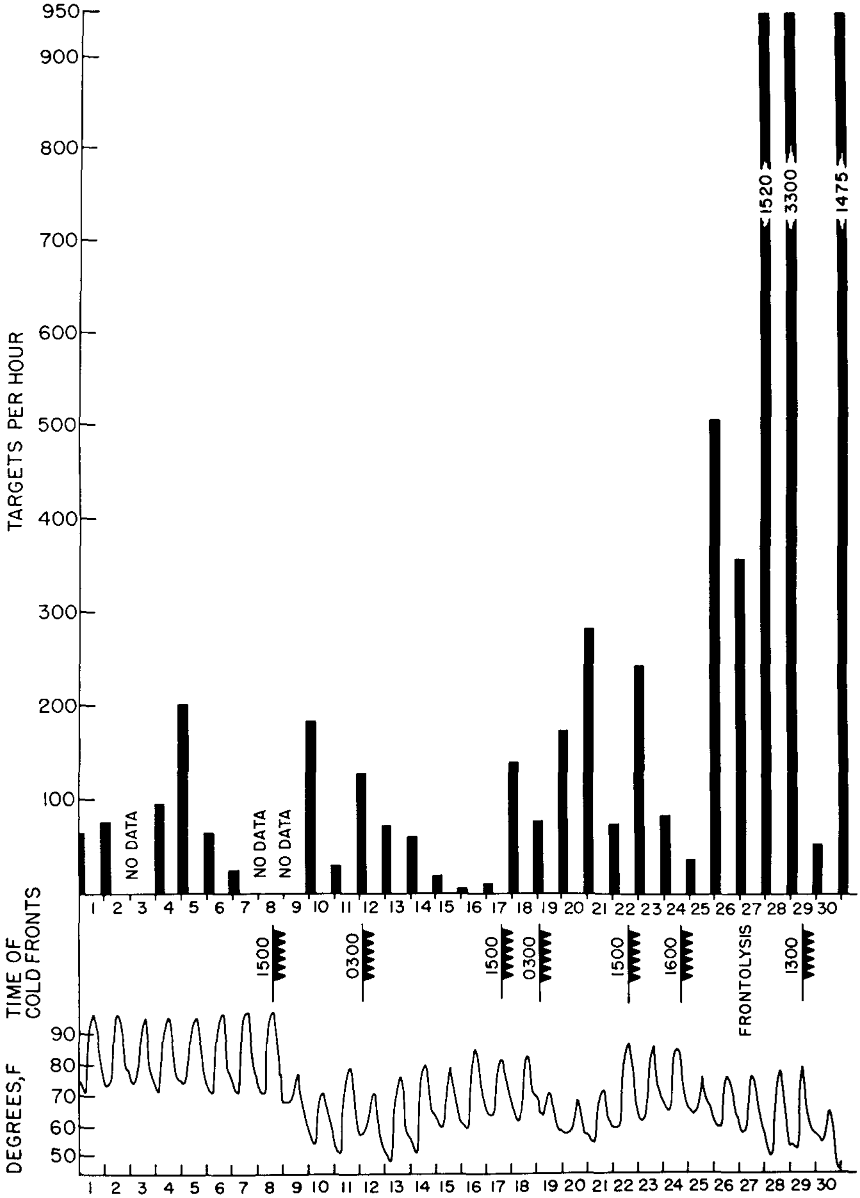


FIG. 3. Volume of nocturnal migration, cold front passages, and temperature at Champaign, Illinois, during September 1960. Bars represent the average number of bird targets per hour detected each night during the period from sunset until 0500 CST. Pips indicate midnight. Cold front symbols indicate to the nearest hour the time at which the pressure trough passed Champaign. The continuous daily temperature curve was constructed from thermograph charts, with values plotted for every three hours.

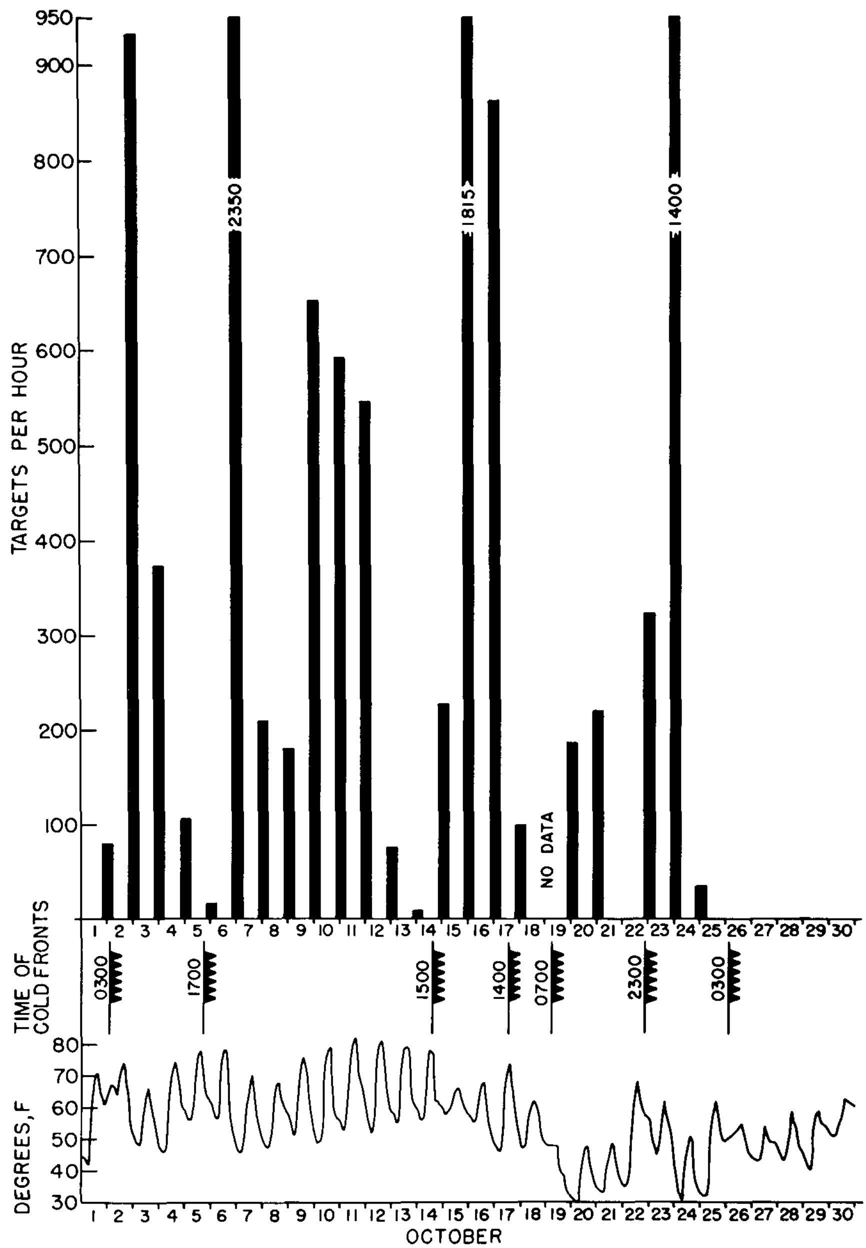


FIG. 4. Volume of nocturnal migration, cold front passages, and temperature at Champaign, Illinois, during October 1960. Bars represent the average number of bird targets per hour detected each night during the period from sunset until 0500 CST. Pips indicate

passages before 24 October. The exception (night of 17 October) will be discussed later. In addition, migration volume increased following the frontolyses (dissipating frontal systems) which took place during 19 August and 27 September, and on two occasions (3 September and 9 October) without the presence of any notable meteorological activity. The precise timing of fall migration with cold fronts is shown by the following examples.

On 4, 7, and 27 August, fronts passed through Champaign about 1800 CST, less than two hours before sunset (Fig. 2). On each of these nights a wave of migration began, with numerous echoes appearing on the radar indicator immediately after dark, by migrants which must have departed from near the radar station. On 14 and 23 August, 17 and 22 September, and 14 October (Figs. 2, 3, 4), frontal passages occurred a little earlier, about 1500 CST. Still only three to five hours had elapsed between the time of these frontal passages and darkness, when the first migrants of the waves were detected by the radar.

These examples indicate that migrants located very close to Champaign were responding directly and immediately to some element(s) of the weather situation which had developed with the recent passage of a front across the Champaign area on which they were situated. During the entire fall, migration waves initiated **prior** to cold front passage on only two nights, 11 September and 22 October. These exceptions to the general rule will be discussed later.

In general, the volume of migration fluctuates according to a fairly typical pattern, increasing sharply on the night following frontal passage, then decreasing each successive night until conditions again occur which stimulate flight. Typical of this pattern are the nights of 11 through 16 September (Fig. 3).

When conditions suitable for migration develop much after midnight, birds do not usually depart until the following evening. Thus, the passage of a front late in the night (0300) on (18)–19 September and (1)–2 October brought no migration wave until the subsequent evening (Figs. 3, 4). Under certain circumstances, to be discussed, migration waves will develop after midnight.

Accompanying the passage of a cold front are changes in pressure, temperature, and surface wind. Although these meteorological elements are generally interrelated (all parts of the same phenomenon—the boundary between adjacent air masses) we found that we could study the effects of each individual factor upon the observed hourly and daily changes in the migration pattern.

Pressure.—We first examined the possibility that the migrants might be responding to the decreasing barometric pressure which invariably accompanies

---

midnight. Cold front symbols indicate to the nearest hour the time at which the pressure trough passed Champaign. The continuous daily temperature curve was constructed from thermograph charts, with values plotted for every three hours.

cold fronts. That this falling pressure might be a factor in stimulating migration was suggested to us by the work of Bagg, et al. (1950), a study of the relationship between spring migration and northern hemisphere pressure patterns. An examination of several barograph traces has caused us to believe that pressure change alone as a positive "trigger" of migration is improbable.

For example: During the period from 23 to 30 September, three distinct waves of migration were recorded; one on 25 September following a cold front, another on 27 September following a frontolysis, and a third on 30 September following a front. During these seven days the total variation in pressure from highest to lowest was 0.32 inch of mercury. Pressure change with the front of 24 September was 0.10 inch, with the frontolysis was negligible, and with the front of 30 September was 0.06 inch. It is easy, when looking at the barograph trace, to see the pressure trends, but it is also evident that pressure fluctuations unrelated to frontal activity are present. Diurnal variations in pressure (0.04–0.10 inch) which are related to the daily rise and fall of temperature also occur.

It is difficult to attribute to an animal the possession of an internal barometer sensitive enough to detect a 0.10-inch change in pressure such as that produced by the front of 24 September, and the discrimination to know which pressure change is due to a cold front and which is not. Convective showers, for example, although they may cause pressure fluctuations of 0.05–0.08 inch, apparently do not induce migration.

Temperature.—In considering a possible relation between the prevailing temperatures and migration activity, we had to decide what sort of temperature change the birds might respond to. Abruptly decreasing temperature (8–12 degress within an hour or two) would be a likely cue. Such a change occurred at Champaign only six times during the 3-month period of our study, usually as a result of thundershower activity. These changes showed no correlation in timing with the migration.

Another possibility would be for the birds to react to temperatures (during the day of departure) which were noticeably lower than those of the day before. How large a decrease would be required before a bird would respond is problematical. Weise (1956), in a study of the activity of caged migratory sparrows, considered a decrease of less than 5 F in the temperature at civil twilight to be no significant change.

Referring to Figs. 2, 3, and 4, one can compare changes in migration activity with temperature changes. In August there were eight mass flights. For two of these (4–5 and 19–20 August) one can see a possible correlation in timing between the flight and a notable temperature change. The flight of 4–5 August followed a drop in both maximum and minimum daily temperature of about 8 F during the preceding 24 hours. In the period 18–21 August, there was no change in the minimum temperature but the maximum dropped 10° coinciding with frontolysis and mass migration. Temperature declines **followed** mass flights on 10 and 14 August. As for the other August flights (7, 23, 27, and 30 August) there was either no change in temperature or a slight temperature increase in these periods. Temperature could not have been the primary stimulus in initiating these early fall mass flights of nocturnal migrants.

In September there were nine known mass flights (data for three nights missing). Sharp drops (10–20°) in maximum and minimum daily temperature preceded flights on 19, 25, and 30 September, but no temperature change accompanied the flights of 3, 17, and 27 September. Slight temperature increase was noted on 11 and 22 September. In October there were six mass flights. Sharp temperature declines preceded the mass flight on 19 October and **followed** flights on 2, 6, and 14 October, while the flights of 9 and 22 October occurred in a period of warming temperatures.

In further analyzing the temperature pattern at Champaign (Table 1) we made hour by hour comparisons of the temperatures of the first day of a migration wave with the temperatures of the day before the wave. For purposes of analysis, in Table 1 we have defined as being "cooler" any day on which temperatures were 2 F (or more) lower than the previous day (the same hours) for four or more hours. The same comparison was made for successive nights of migration following the initial night of a wave. In summary, we found that migration occurred on nights that were cooler, warmer, or without change in temperature in nearly equal proportion (Table 1). Of the 44 days (nights) on which significant migration was recorded, 17 (39 per cent) had cooler temperatures than the previous day, 12 (27 per cent) showed no temperature change, and 15 (34 per cent) were warmer.

We are dealing in this kind of study with a large number of species, and it is probable that some species respond to temperature change and others do not. It is also possible that changing temperature may be a secondary factor in stimulating flights and affects migration only when coupled with one or more other factors.

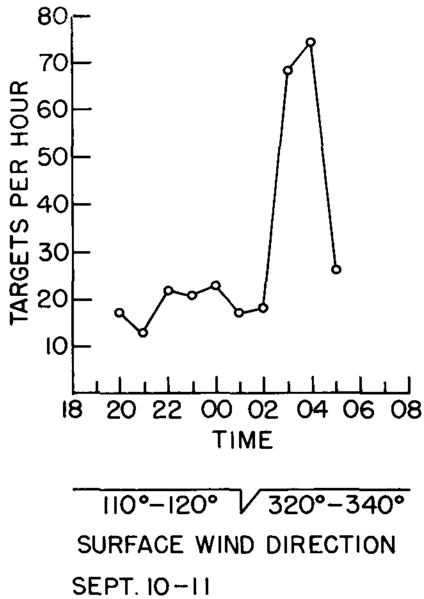
Surface wind.—We have already indicated that neither pressure nor temperature changes correlate well in time with the onset of nocturnal flights of migrants. Associated with the passage of a cold front there is a definite change in wind direction. This change is usually clockwise from a southerly direction to west, northwest, or northeast. It is possible that birds might recognize and respond to this wind shift.

From the Rantoul and Champaign, Illinois, weather records, we learned the surface wind directions for all of the nights of migration (Table 2). On 32 (73 per cent) of the 44 nights of significant migration, surface winds were northerly (300° to 60°), and on 12 (27 per cent) of the migration nights, winds were from other directions ranging from southeast (clockwise) to west-southwest.

It should be pointed out here that while in general migration waves are associated with cold fronts, and that in general cold fronts induce the wind shift described above, the method of analysis of wind direction versus migration (Table 2) did not presuppose the presence of a front. The analysis merely showed what surface wind prevailed on each night during the hours of flight without considering what affected the wind direction. Wind shifts may occur without frontal association, and wind shifts which are associated with frontal passage are not invariably of the classic type. For convenience, we have defined the time of frontal passage in terms of the passage of the trough. Related to this passing low pressure, the wind shift (to north) may come later or even, though rarely, earlier. The change in wind direction may also be erratic, shifting northward, backing and shifting again. In the case of a frontolysis, there is no distinct wind shift but northerly winds may develop over the area where the front dissipated.

We found that the wind shift associated with 14 of the 20 cold fronts of the fall of 1960 occurred within five hours after the passage of the trough. These were: 7 (2300) August, 9 (1900) August, 14 (1800) August, 26 (1800) August, 29 (0900) August, 8 (2000) September, 17 (1500) September, 19 (0700) September, 22 (1700) September, 29 (1400) September, 2 (0600) October, 14 (1600) October, 17 (1800) October, and 23 (0300) October. Of the remaining six cold fronts: on 4 August, wind shift preceded the front (trough) by about one hour; on 23 August, a distinct shift was not evident with the weak front; on 12 September, wind shift preceded the front by over 24 hours (if the two events can be truly associated); on 24 September, the wind shift was erratic, with the final shift occurring 10 hours after the frontal passage; on 9 October, the wind shift came nine hours after the front; and on 19 October, it preceded the front by about four hours.

How well did the migrations coincide with these wind-change patterns? Of the 21 migration waves for which we have complete data, 14 (4, 14, 26, 29 August; 11, 17, 19, 22, 25, 30 September; 2, 6, 14, 19 October) were initiated on nights following a wind change from southerly to northerly within the previous 12 hours. For three additional waves (23 August, 27 September, 9 October), winds were northerly but no wind shift (from the south) was involved. Two other flights (7 August, 22 October) actually *preceded* by several hours a wind shift (north), though the shift occurred on the same night as the migration. In two cases (19 August, 3 September), migration was initiated into *southerly* winds. We have already discussed the close relationship in timing between cold-front passage and migration. There were two instances (24



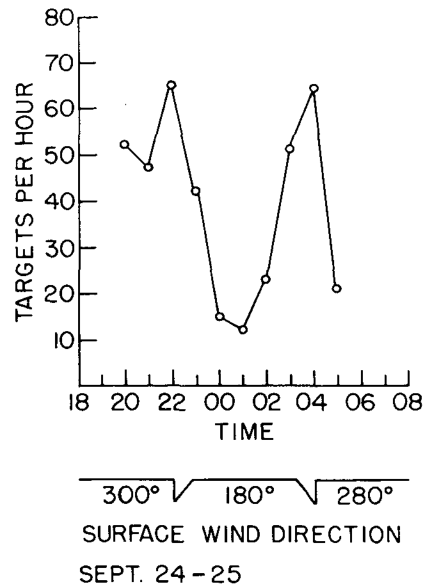


Fig. 5 (left). Hourly flight density and surface wind direction at Champaign, Illinois, on the night of 10–11 September 1960. Wind shift occurred at 0100 cst.

Fig. 6 (right). Hourly flight density and surface wind direction at Champaign, Illinois, on the night of 24–25 September 1960. Wind shifts occurred at 2200 and 0300 cst.

September, 6 October) during the fall when the frontal troughs passed Champaign in the evening but the wind shift lagged and did not occur until the following morning. In both cases, migration was initiated on the following evening; i.e., late in relation to the trough as though in response to the lagging wind change. Conversely, on 11 September, the wind shift to north preceded the trough and so did the migration—again as though migrants were responding to the wind shift.

We have some positive evidence that migrants respond very rapidly to the wind. The "average" temporal pattern of migration has already been discussed. On the nights of 10–11 and 24–25 September, the pattern varied considerably from this average (Figs. 5, 6). We examined our weather data for these nights to see if any meteorological factors could account for the irregularity of the temporal patterns. There was a remarkable correlation in timing between changes in flight densities and changes in direction of the surface wind, as though migrants were responding immediately to the wind shift. Frontal systems were associated with both these flights. On 24 September, the frontal trough passed Champaign at 1600 cst, a wind shift (to 300°) occurred about 1800, and, as might be expected, flight density of migrants rose sharply after sundown. On this night, as occasionally happens, there was vacillation in the frontal wind shift and at 2200 the wind swung back to south (180°). This change coincided with an abrupt reduction in the flight density. After midnight, flight density increased again, coincidentally with a wind shift back to WNW. On 10–11 September, a wind shift (to NW) occurred at about 0100, preceding the frontal trough by about 24 hours. Migrants appeared to respond to this shift and the flight density rose sharply after 0200 (Fig. 6).

Overcast.—The influence of an overcast sky upon the activity of the night migrants is pertinent both to the study of the timing of departure of mass flights and to the investigation of celestial orientation in birds. Here, study of the two problems overlaps, insofar as the ability of a bird to navigate satisfactorily will surely influence its "decision" to fly on a particular night. A forthcoming paper by Bellrose and Graber will discuss in detail navigation and orientation data obtained from the radar study. However, it is pertinent here to present briefly some observations which we have made on migration activity during conditions of overcast.

We found high cirrus overcasts present on several nights of no significant migration activity when southerly surface winds prevailed. On 14 August, 19 and 29 September, and 14 and 15 October, migration coincided with extensive overcasts that covered broad areas of the midwest. We have estimated that a bird which averaged 50 mph ground-speed or less (optimum for most passerines), and which arrived at Champaign near midnight on any of these nights must have departed under overcast conditions. On three of these nights, 14 August, 19 September, and 14 October, migration waves began. On 15 October, a considerable increase was recorded over the activity of 14 October. Only on 29 September did migration remain low, even in the presence of surface winds usually favored by the migrants.

We compared the flight altitudes of the migrants detected on nights of overcast with the height of the cloud bases, and could find no definite tendency on the part of the migrants for flying above or below a solid cloud layer. On 14 August, however, when the height of the overcast changed rapidly during the peak hours of migration, a definite change in the altitude distribution of the migrants occurred (Fig. 7). A 5,000-foot overcast was present on this night from well before sunset until after 2200 CST, when stratus clouds began to develop rapidly at 1,200 feet. This layer, which was probably about 500 feet thick, rose gradually to about 2,000 feet by 0600 CST. Our radar data show that virtually all of the migrants which were aloft prior to midnight were flying well below the overcast, with the maximum concentration at about 2,800 feet. After midnight, when the stratus layer had become established, the birds

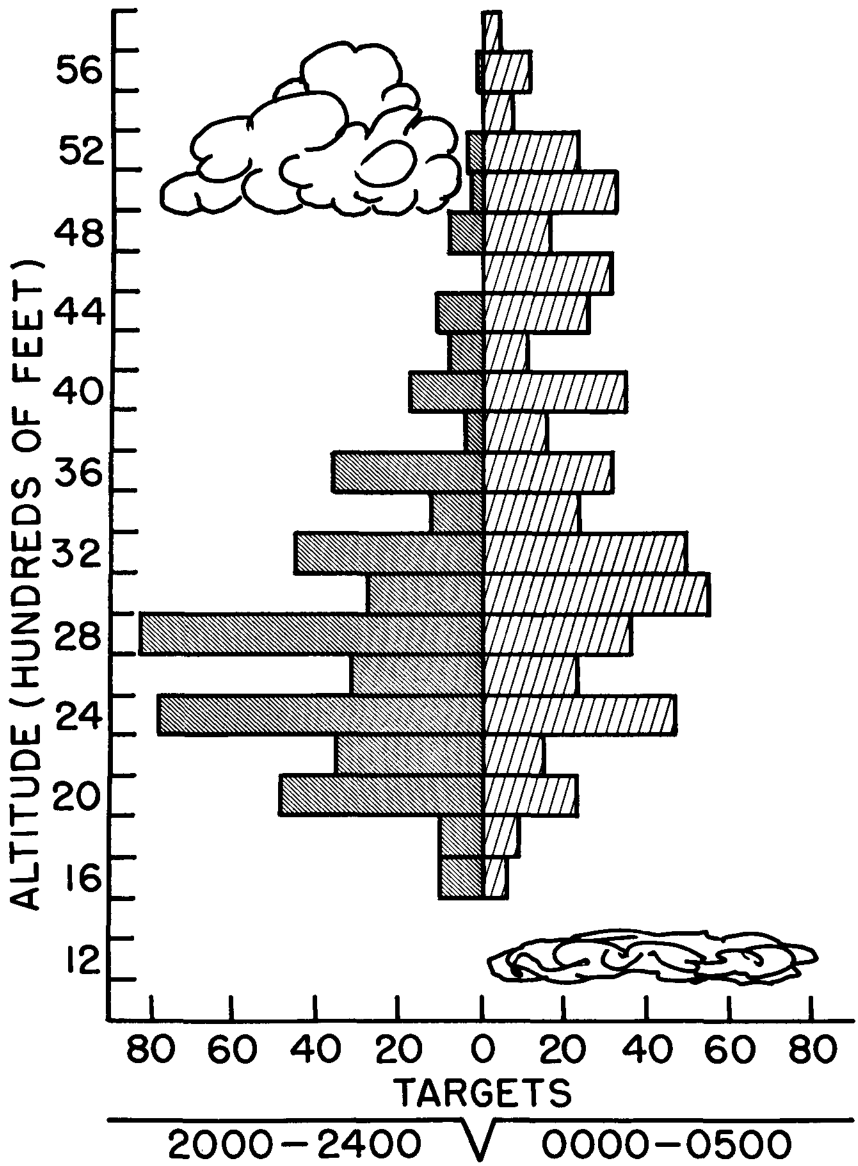


FIG. 7. Altitude distribution of nocturnal migrants on the overcast night of 14–15 August 1960. Cloud base was 5,000 feet until near midnight and about 1,200 feet thereafter.

were more numerous at about 3,200 feet and targets frequently appeared above 4,400 feet where few had been detected earlier.

A close examination of the migration record (Figs. 2, 3, 4) shows that while there was migration activity on the overcast nights, further increases occurred on the night following each of the first four dates. These observations suggest (1) some migration does occur on nights of complete overcast, (2) not all birds in the migratory state will depart under overcast skies, and (3) the radar may fail to detect some of the smaller or more distant targets present on the overcast nights because of attenuation of the radar energy by moisture particles in the clouds.

DISCUSSION

The relationship which exists between autumn departures of nocturnal migrants and weather is not a simple one. Investigations of this relationship by different methods have produced contradictory results, as have studies conducted in various localities, and many questions remain to be answered on what might be called the natural history of migration.

It is probable that different migratory behavior patterns have developed in different species, and in response to different environmental situations.

The migration of western Europe and that of the east coast of North America have certain features in common that do not apply to the migration through the continental interior of North America. This is to be expected, for the environmental characteristics of the first two areas, while certainly not identical, are nevertheless quite similar. These coastal situations have a distinctive topography and a marine-influenced climate. By contrast, the interior of North America is a flat, nearly featureless plain which experiences a distinctly continental climate. Clear nights prevail. Persistent overcast, fog, and precipitation are relatively rare. The pattern of the frontal systems which occurs is not complicated by orographic or marine influences which produce the rather complex weather systems typical of western Europe and the east coast of North America.

To illustrate the geographical influence upon migration, both Drury, et al. (op. cit.), in Massachusetts and Lack (1960*a*) in Norfolk, England, have in the course of their radar studies, examined the effect of coastlines on the direction of migratory movements, an effect which is, of course, absent in the midwest. Another migration problem which varies with geographical region is "reverse migration" (Baird and Nisbet, 1960). Drury (op. cit.) has witnessed this phenomenon on radar, and many field observations of this "wrong-way flight" have been recorded both in the eastern United States and in Europe. In contrast, observations of reverse flights in the midwestern United States during autumn are extremely rare, and in three seasons of radar observations we have seldom observed even a single target proceeding in a "wrong" direction.

As we have previously suggested, species differences in migratory behavior may also exist. For example, Baird, et al. (1959) showed that northward movements of Yellow-breasted Chats (*Icteria virens*) into New England in fall were associated with southwest winds. Again, the fall migration into southerly winds which we have found to be exceptional to the usual pattern may prove ultimately to represent the behavior of a few particular species.

Ironically, the lunar and radar techniques of migration study which provide the best direct quantitative record tell us little of the species involved, and there is a real need for detailed information on the migration habits of particular species such as that obtained from banding studies (Baird, et al., 1958, 1959).

Lacking species information it is still worthwhile to explore the subject in more general terms as we must when working with radar data. Because we are dealing with 200 or more species of migrants, the possibilities for different kinds of behavior patterns are numerous, and it is remarkable that the patterns of migration which we have observed on radar are as consistent as they are.

The variation in flight density of migrants from hour to hour during the night is a matter that requires further study. Our radar data on this temporal pattern coincide very closely (Fig. 1) with those obtained with the lunar technique of study (Lowery, op. cit.). From his radar data, obtained in Zurich, Switzerland, Sutter (1957) described a temporal pattern similar to our own, concluding that his data were in complete agreement with those of Lowery. Lack (1960*a*) also discussed the temporal variations in the volume of nocturnal migration. He found the pattern in Norfolk in spring to be essentially the same as that of Sutter, with peak density usually occurring from 2100 to 2200 (somewhat earlier than the peak hour in other locations).

The temporal pattern described from direct quantitative observation roughly parallels the hour-to-hour variation in nightly unrest of some captive migrants (Eyster, 1954; Farner, 1955). This suggests an internal timing of activity which may explain why mass flights are not usually released in central Illinois by cold fronts which pass much after midnight.

Audio records, however, indicate a very different pattern, in which maximum activity (i.e., flight calling) occurs in the pre-dawn hours (Graber and Cochran, 1959). The pattern has been observed so many times by both visual and aural methods that there can be no question about the validity of the observations, but their meaning is still obscure. Cochran and Graber (1958) observed a fairly constant flight density of migrants throughout the night around a television tower, but these tower observations represent a definitely abnormal situation wherein birds continued to fly in confusion when they might otherwise have landed.

To compromise the lunar-radar observations on temporal pattern with the aural observations, we can hypothesize that migrants reduce altitude after midnight and fly close to the ground where they would go undetected by radar and lunar observations. The aural data indicate that at least some migrants continue to fly, but many may land. Even supposing this to be true, we must account for the timing of the nightly flight and particularly its duration. Odum, Connell, and Stoddard (1961) calculated potential flight ranges of migrants based on energy reserves in the migrant. Their specimen data indicated that long-distance migrants (tanagers, thrushes, and warblers) could fly 600–1,500 miles nonstop, or 12–30 hours even at a speed of 50 mph. Swainson's Thrushes (*Hylocichla ustulata*) killed at 0100 CST near Champaign in September 1959 (Graber and Graber, 1962) still carried a calculated (from fat-free weights, Connell, Odum, and Kale, 1960) fat deposit of about 15 per cent of gross weight, the equivalent of an estimated flight range of 240–400 miles (Odum, et al., op. cit.). This would amount to a minimum of nearly five hours more of potential flying time, or, for the example cited, a flight lasting until 0600, i.e., 10–11 hours total. The flight range potential appears to greatly exceed the actual flight time during one night, judging from the radar temporal curve. Fatigue (accumulation of lactic acid) and/or dehydration of the migrants may be the primary factors in delimiting the flight span, but more basic data are needed on the physiology of individual birds before these factors can be evaluated.

Farner (op. cit.) discussed factors which bring the bird into a state of readiness to migrate, and though we are primarily concerned with the extrinsic factors which appear to stimulate *en masse* flights of nocturnal migrants, the two phenomena, i.e., the condition of the individual bird and the mass flights, are obviously intimately related.

The classic wave pattern of migration has been well documented. It is typically seen by the field observer as an influx of migrants into an area on a given day, several days of static or declining activity, then another conspicuous arrival. Our radar data confirm the reality of these waves in the midwestern United States. Lack (1960*a*) found that the spring emigration from Norfolk proceeded steadily, but with fluctuations in volume, on every night during the season except those few with extremely unfavorable weather, and he did not describe a pattern for this activity. The wave type of migration which occurs in the midwestern United States depends not only on a supply of (physiologically) ready migrants but on secondary extrinsic factors to "release" the flight.

The duration of a migration wave is usually two or three days (example: 4–6 August), and typically the migration volume falls off progressively after the first night. The wave is followed by a period of low migration activity which rarely lasts more than three nights; usually two or less (examples: 3–4, 13–14 August). This periodicity, i.e., duration of wave and lull, is fairly consistent and its significance is still not entirely clear. We have already indicated that the periodicity depends to some extent on the presence of one or more meteorological factors usually associated with a cold front. Yet when the interval between fronts is extended, a migration wave may occur without any apparent meteorological releaser (examples: 4 September and 9 October), and in such instances the wave shows the "usual" periodicity.

Intervals of low migration activity may in some cases represent "stopover periods" for migrants. King (1961) analyzed data from several authors to show that stopover periods for migrant White-throated Sparrows (*Zonotrichia albicollis*) averaged three to five days, which is about the time required for fat deposition in this species prior to flight (Wolfson, 1954). Fat deposition in migrants has been correlated with the onset of *Zugunruhe*, and Weise (op. cit.) showed that *Zugunruhe* in migrant sparrows varied with weather conditions apparently even when the fat condition of the birds remained unchanged. These data and the radar observation showing correlation of mass flights with cold front passage indicate that migrants may wait for an environmental stimulus before taking flight even though they are in (physiological) condition to migrate. The waves of 4 September and 9 October show that migrants will not always wait more than a day or two for the releaser.

Just what extrinsic factors act as stimuli for mass flights is a subject of some controversy. Lack (1960*b*) emphasized the importance of temperature as the meteorological phenomenon most likely to stimulate migration. He concluded, after citing numerous field and laboratory studies, that warmth in spring and cold in autumn are the primary factors in stimulating migration, dismissing wind direction as unimportant. He also stated that (p. 185), "In the United States, nocturnal movements in September normally occur with cold, northerly winds, especially with cold fronts (Bennett, 1952; Lowery and Newman, 1955), but the difficulty, as in spring, is to separate the possible influence of temperature from that of wind direction."

After careful consideration of the work of both Bennett, and Lowery and Newman, we do not believe that either of them intended to imply that they found cold the important factor in initiating autumn migration. Both cited an apparent correlation with cold front passages, but Bennett in particular believed wind direction was the more important factor in stimulating waves of migration; and Lowery and Newman did not discuss the problem in detail.

Some observers who recognize the stimulus of frontal passage upon autumn migration may tend to envision the cold front as being invariably followed by sharply reduced temperatures. In the midwestern United States during August and much of September, we have observed that such fronts as occur are often weak and slow-moving or stationary. Frontolyses are not uncommon. These nearly static fronts represent rather broad, indistinct boundaries between air masses which are very similar in temperature and humidity. Bennett (1952: 213), in discussing the early fall migration of warblers through Chicago, also observed that "most summer cyclones and anticyclones are not strongly developed circulations, and the summer cold fronts are ordinarily mild." This weather is typical over the midwestern United States from the Canadian border south at least to Kentucky. Half or less of the fronts which occur in this area at this season produce a significant (5 F or more) temperature decrease (Figs. 2, 3), and the decrease often requires 24 hours to become evident. Nevertheless, the radar record shows that these fronts are, indeed, promptly followed by increases in migration.

It is difficult to imagine that birds which are regularly experiencing diurnal temperature variations of 15 to 20 F would be stimulated to take flight by such a slow temperature decrease from one day to the next as is produced by the weak, early season fronts.

The greatest difficulty, when discussing the effects of temperature on migration, is not to separate the effects of temperature from those of wind, but to establish the degree of temperature change which might prove to have significant influence on the birds. Most laboratory studies on nocturnal migration have had as their primary objective something other than the correlation of *Zugunruhe* with temperature, and are not conclusive on this point.

The statistical evaluation made by Lack (1960*a*) of the relationships between spring departures of migrants from Norfolk and various weather elements illustrates one approach to the problem of what might constitute a significant temperature effect. He concluded that spring emigration from Norfolk was favored by a temperature (at 1800 hours) of 45–49° between 1 and 23 February and by a temperature of 40–44° from 24 February to 31 March. He also noted that temperature apparently had no influence on emigration in April.

Baird, et al. (1959) indicated that declining temperature was important in stimulating fall migration on the east coast of the United States, stating that a migration wave of 19–21 September 1958, was initiated under overcast skies "apparently influenced by a temperature drop a few days earlier." These authors correlated temperature drops and good catches of migrants at recovery netting stations. It is important to realize that diurnal observations do not always reflect the previous night's migration at a given locality (Drury, et al., op. cit.). Graber and Cochran (1960) found correlation poor between field observations and their audio record, and suggested several explanations for the discrepancies. Quantitative correlation between field observations of migration and the radar record is equally unsatisfactory. The pattern of continuing but decreasing activity on nights following the initial movement, and the existence of numerous small waves go virtually unnoticed in the field.

In 1958, the cold front which crossed Illinois on 15–16 September crossed New England on 16–17 September. In Illinois, heavy migration was recorded at night within two hours of the passing of this front (Graber and Cochran, 1960). In New England heavy mortality of night migrants occurred widely at ceiliometers and TV towers in the wake of the front on 16–17 September (Baird, et al., 1959), yet diurnal observations in New England showed no great influx of migrants until 19 and 20 September. The same frontal system released mass flights in Illinois and New England, but in Illinois temperature could not have affected the release because there was no temperature decrease associated with the front. In this example we can see an apparent and unaccountable lag between the night migration and what daytime observers found in the way of grounded migrants. At Champaign, heaviest flights occur typically on the same night or the first night after frontal passage. Baird, et al. (1959) stated that the **second** day after cold front passage often produced the greatest density of migrants, based on diurnal observations. Because temperature decline often lags behind both the trough and wind shift of the front, we can see why this factor correlated well with the flights detected by daytime observers. Furthermore, temperature decreases with frontal passage are probably more pronounced at coastal stations in New England than in Illinois, because the widespread precipitation which is more likely near the marine environment tends to hold down temperatures. In such cases the front is not the direct cause of the lower temperature.

Both Weise (op. cit.) and King (op. cit.) indicated that night restlessness in certain fringillids appeared to be correlated with temperature change. These fringillids were short-distance (Odum, et al., op. cit.), late fall migrants, and it is possible that the flights of these species are released by temperature change, since marked temperature declines are more often associated with late fall and winter fronts. By contrast, the flights of long-distance migrants which pass Champaign for the most part in early and mid-autumn (to 10 October) do not appear to be "triggered" by falling temperatures. It is not uncommon for mass flights in this season to depart from Champaign even with slightly rising temperatures. We do not deny that temperature change may release migration flights, but at least some mass flights are triggered by some other frontal characteristic than temperature change.

SUMMARY

The migration-weather relationship is complex. Among the factors contributing to this complexity may be differences in environmental situation, physiology, and specific behavior of the many species of migrants under investigation.

Radar and lunar data yield nocturnal temporal patterns which correspond closely with one another and with some observations of the activity of captive migrants but contradict the pattern obtained by aural methods. Potential flight range of migrants apparently exceeds actual flight time. Additional physiological data are needed to resolve these differences.

Our radar data indicate that mass departures of nocturnal migrants, particularly long-distance migrants in early and mid-fall, are "released" in the Champaign area by a change in wind direction from south to north. Such wind shifts almost always accompany cold fronts, but the migrants may react to the wind shift whether or not a cold front is involved. How rapidly migrants respond to the wind shift is indicated. A following wind would seem to be especially important to these long-distance passerine migrants. Recognition and response to such a wind condition would appear to have real survival value both from the standpoint of energy conservation in the migrant and the reduction of total migration time. On the other hand, it is difficult to see survival value in a response to the subtle temperature changes which accompany cold fronts in mid-fall.

Regardless of which factor triggers a mass departure, it is apparent that cloud cover can modify the response by deterring at least some of the migrants. Thus, while the heaviest concentration of migrants typically passes Champaign on the first night of a mass flight, overcast can postpone the heavy flight one or more nights.

ACKNOWLEDGMENTS

Throughout this project we have depended greatly on others for technical assistance and information. We are especially grateful to William W. Cochran who engineered the project, and to members of the staff of the Illinois State Water Survey Meteorology Laboratory, particularly Glenn E. Stout, Donald Staggs, Eugene Mueller, Don H. Summers, Douglas Jones, Kenneth E. Wilk, and Stanley A. Chagnon, Jr. Robert O. Ellis and David B. Cooley of the State Natural History Survey helped with numerous equipment problems. Earl E. Rumbaugh and Robert E. Potter of the coordinated Science Laboratory, University of Illinois, loaned us radar equipment; and Leslie A. Bryan and Nelwin C. Grimm provided work space at the University of Illinois Airport. Student assistants John White and Donald Hyson helped with radar film analysis and data tabulation.

LITERATURE CITED

Bagg, A. M., W. W. H. Gunn, D. S. Miller, J. T. Nichols, W. Smith, and F. P. Wolfarth
1950 Barometric pressure-patterns and spring bird migration. *Wilson Bull.*, 62:5–19.

Baird, J., A. M. Bagg, I. C. T. Nisbet, and C. S. Robbins
1959 Operation Recovery—report on mist-netting along the Atlantic coast in 1958. *Bird-Banding*, 30:143–171.

Baird, J., C. S. Robbins, A. M. Bagg, and J. V. Dennis
1958 "Operation Recovery"—the Atlantic coastal netting project. *Bird-Banding*, 29:137–168.

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

Bennett, H. R.
1952 Fall migration of birds at Chicago. *Wilson Bull.*, 64:197–220.

Cochran, W. W., and R. R. Graber
1958 Attraction of nocturnal migrants by lights on a television tower. *Wilson Bull.*, 70:378–380.

CONNELL, C. E., E. P. ODUM, AND H. KALE
1960 Fat-free weights of birds. *Auk*, 77:1–9.

DRURY, W. H., JR., I. C. T. NISBET, AND R. E. RICHARDSON
1961 The migration of angels. *Nat. Hist.* (J. Amer. Mus. Nat. Hist.), 70(8): 11–17.

EYSTER, M. B.
1954 Quantitative measurement of the influence of photoperiod, temperature, and season on the activity of captive songbirds. *Ecol. Monog.*, 24:1–28.

FARNER, D. S.
1955 The annual stimulus for migration: experimental and physiologic aspects. *In* Recent Studies in Avian Biology. Ed. A. Wolfson. Univ. Ill. Press, Urbana, pp. 198–237.

GRABER, R. R., AND W. W. COCHRAN
1959 An audio technique for the study of nocturnal migration of birds. *Wilson Bull.*, 71:220–236.
1960 Evaluation of an aural record of nocturnal migration. *Wilson Bull.*, 72:253–273.

GRABER, R. R., AND J. W. GRABER
1962 Weight characteristics of birds killed in nocturnal migration. *Wilson Bull.*, 74:74–88.

GRABER, R. R., AND S. S. HASSLER
1962 The effectiveness of aircraft-type (APS) radar in detecting birds. *Wilson Bull.*, 74:367–380.

KING, J. R.
1961 The bioenergetics of vernal premigratory fat desposition in the White-crowned Sparrow. *Condor*, 63:128–142.

LACK, D.
1960*a* Migration across the North Sea studied by radar. Pt. 2. The spring departure, 1956–59. *Ibis*, 102:26–57.
1960*b* The influence of weather on passerine migration. A review. *Auk*, 77:171–209.

LOWERY, G. H., JR.
1951 A quantitative study of the nocturnal migration of birds. *Univ. Kansas Publ. Mus. Nat. Hist.*, 3:361–472.

LOWERY, G. H., JR., AND R. J. NEWMAN
1955 Direct studies of nocturnal bird migration. *In* Recent Studies in Avian Biology. Ed. A. Wolfson. Univ. Ill. Press, Urbana, pp. 238–263.

ODUM, E. P., C. E. CONNELL, AND H. L. STODDARD
1961 Flight energy and estimated flight ranges of some migratory birds. *Auk*, 78: 515–527.

SUTTER, E.
1957 Radar-Beobachtungen uber den Verlauf des nachtlichen Vogelzuges. *Rev. Suisse Zool.*, 64:294–303.

WEISE, C. M.
1956 Nightly unrest in caged migratory sparrows under outdoor conditions. *Ecol.*, 37:274–287.

WOLFSON, A.
1954 Weight and fat deposition in relation to spring migration in transient White-throated Sparrows. *Auk*, 71:413–434.

STATE NATURAL HISTORY SURVEY DIVISION, URBANA, ILLINOIS, 26 JUNE 1962