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METEOROLOGICAL VARIABLES AND THE NORTHWARD MOVEMENT OF NOCTURNAL LAND BIRD MIGRANTS

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INTRODUCTION

AN investigation into the relationship between nocturnal land bird migration in the spring months and certain meteorological variables was begun early in 1953 at the Meteorology Group of the Brookhaven National Laboratory, Upton, Long Island, New York. Two variables, atmospheric stability and upper air wind direction, were believed on the basis of both logic and observation to be of major importance. The study was planned not only to evaluate the importance of these two factors, but also to reveal any correlation that might exist with other parameters. Owing to the scope of the program, which covered the United States east of the Rockies in area and the months of April and May in time, and owing to the large amount of data used, both meteorological and ornithological, it was necessary to confine the study to basic relationships and to classify the data into rather broad categories. Thus, individual species were not considered separately, but all nocturnal land bird migrants were grouped together. This grouping, however, is not believed to be artificial because years of observation have shown that a large variety of species commonly migrate through the same area on the same night, all of them apparently reacting to the same stimuli. Specific localities were not dealt with as such, but only as part of the whole area. However, each night was studied as a unit and the data later consolidated for the whole period.

MIGRATION PROBLEMS AND METEOROLOGY

For many years, ornithologists have noted what seemed to be relationships between the weather and bird migration, and many attempts to correlate the two have been made with varying success. Most of these attempts have had limited success owing to certain deficiencies in method or data. Few studies have been confined to one species or one group of species that react to similar stimuli. Most studies have been too restricted either in time or in area to give a true picture of any class of migration as a whole, and until recently none have had enough data to use statistical methods. Most studies used only surface meteorological data and some only values obtained at the place of arrival. In spite of these drawbacks, a number of useful studies have been made and some light has been shed upon the problem by earlier investigators.

One of the earliest American ornithologists to call attention to a relationship between bird migration and the weather was Cooke (1888), who found the southerly winds in the warm sector of a low pressure area favorable for spring migration. In a later paper (1913), he concluded that birds prefer to migrate in spring with rising temperatures but that temperature alone is not a controlling factor. He found that surface wind direction was of little importance in spring migration. Eaton (1904) also found warm sector conditions favorable for spring migration whereas Smith (1917) found a relationship between spring arrivals and falling pressures. Main (1938) attributed the beginning of migratory flights particularly early in the season to warming temperatures.

More recently, Robbins (1949) showed a correlation between arrivals in the Washington region and above-normal temperatures, south or southwest winds, and low barometric pressure. Bagg and collaborators (1950) advanced the hypothesis that northward migration begins with falling pressures and southerly winds in the western portion of a high, increases in the warm sector of the following low, and is arrested by the arrival of the cold front from the west or upon arriving at a quasi-stationery front to the north. In an earlier paper, Bagg (1948) pointed out as a favorable condition for spring migration in the northeast a high pressure area moving off the southeastern coast of the United States and a low moving northeastward into the Great Lakes region.

Williams (1950) believed that nocturnal migrants cannot land safely in the darkness and that birds aloft overtaken by an approaching cold front might fly far off their course rather than alight in the darkness or attempt flight into the frontal area. He also suggested that birds might be carried far off course by the movement of the air mass in which they are flying if the skies are overcast and visual navigation is impossible. He observed that overhead migration ceases completely in spring when a strong wind is blowing, regardless of its direction. A study of the arrival of large waves in Minnesota in the spring of 1944 showed a correlation with high maximum temperatures.

Lowery (1951), by organizing telescopic observations of birds crossing the lunar disk and analyzing the data, has made the most significant contributions to our knowledge of nocturnal migration and certain of his conclusions may be briefly summarized. He concluded that nocturnal movements are not continuations of daytime movements, that until 11 P.M. or midnight, there is a progressive increase in the number of birds taking wing and that a gradual decrease takes place after that time. He found that nearly all nocturnal migrants come to earth well before dawn, that migrants are rather evenly spaced throughout the sky and that topography is apparently not important in governing flight densities. He also found that migration usually follows the prevailing air flow, that maximum migration occurs in regions of high barometric pressure, and that the passage of a cold front storm may almost halt migration in spring.

Although this method of study has proven more fruitful than any previously used, certain inherent limitations restrict its more extensive use and the confidence that may be placed in the results obtained. Chief of these is its confinement to the few moonlight nights during the migration season. The question also arises whether moonlight itself has an influence upon nocturnal migration. In addition, a moonlight night implies mostly clear weather, and conclusions drawn from observations made under any one type of weather condition can not be extrapolated to include other weather conditions.

Since previous investigations tend to show that the external stimuli which control or influence the day-to-day movements of migrants are largely meteorological, a large number of observations of actual migration should show a high degree of correlation with those variables that are actually of importance. The fact that different groups of birds respond to different stimuli makes it necessary to confine a study of this type to one homogeneous group. Soaring birds, for instance, depend largely on ascending air currents to keep them aloft, and it is obvious that areas or times lacking such updrafts would be unfavorable for extended migratory flights. Soaring birds normally migrate either on sunny days when thermal updrafts are present or along mountain ranges, coast lines, or other terrain features which cause mechanical lifting of the air.

Likewise those species such as the swallows and swifts which migrate by day and feed as they fly should favor days when considerable vertical motion is present. Glick (1939) has shown a good correlation between instability and the number of insects captured at high levels. It seems probable, therefore, that migratory flights of these birds could be correlated with days and areas of instability.

Nocturnal migrants, however, are influenced by other factors. They do not soar; therefore, they are not assisted by rising currents. They do not feed in the air; therefore unstable air is of no advantage to them. In fact, it is my belief that exactly the opposite condition, atmospheric stability, is most favorable for nocturnal migration. It has been generally assumed that most small land birds migrate by night in order to feed by day and although this may well be an important consideration, it will also be shown that flying conditions at night are more favorable for these migrants.

METEOROLOGICAL BACKGROUND

The degree of stability in the atmosphere is a function of the lapse rate, the amount of temperature change with height (Figure 1). If the lapse rate exceeds 1° C per 100 meters as it usually does in the lower layers during the day, the air is unstable. When this condition exists, air which is heated by contact with the earth's surface tends to rise and is replaced by the sinking of cooler air from aloft. Thus, vertical motion is set up in the atmosphere in addition to the horizontal motion represented by the wind direction and velocity. In an unstable atmosphere, the air flow is turbulent. Turbulence may be defined as departure from a mean motion. For example, the mean wind direction over a given period of time may be northwest or from 315° at 10 miles per hour. If the measuring instrument does not deviate from 315° and 10 miles per hour throughout the period, no turbulence on a scale measurable by the instrument exists. If, however, the wind fluctuates between west and north and between 5 and 15 miles per hour, as might commonly be the case, each deviation from northwest and from 10 miles per hour represents turbulent motion.

In a similar fashion an instrument may be set up to measure vertical motion. If this vane remains horizontal throughout a given period, no measurable vertical turbulence is present. If, however, the vane fluctuates up and down over a number of angular degrees in response to the passing up and down drafts, vertical turbulence is present. Studies at Brookhaven National Laboratory (Singer and Smith, 1953), where three bivanes as well as seven Bendix-Friez aerovanes are in continuous use on the 420-foot meteorology tower, show that both vertical and horizontal turbulence are always present whenever an unstable lapse rate exists. When the lapse rate is between 1° C per 100 meters and zero, the air may be either conditionally unstable (unstable only when lifted mechanically) or stable. Under these conditions, turbulence continues to exist but becomes progressively less as the lapse rate decreases.

When temperature increases with height, the condition is termed an inversion since the normal temperature structure is inverted. Inversions near the surface form almost entirely by night, when instead of receiving heat from the sun, the earth radiates heat back to space thereby cooling its surface. As the surface cools, the air near it is also cooled, and when it reaches a temperature lower than that of the air above, an inversion has formed. Inversions form on about two-thirds of all nights over suitable terrain. The two inhibiting

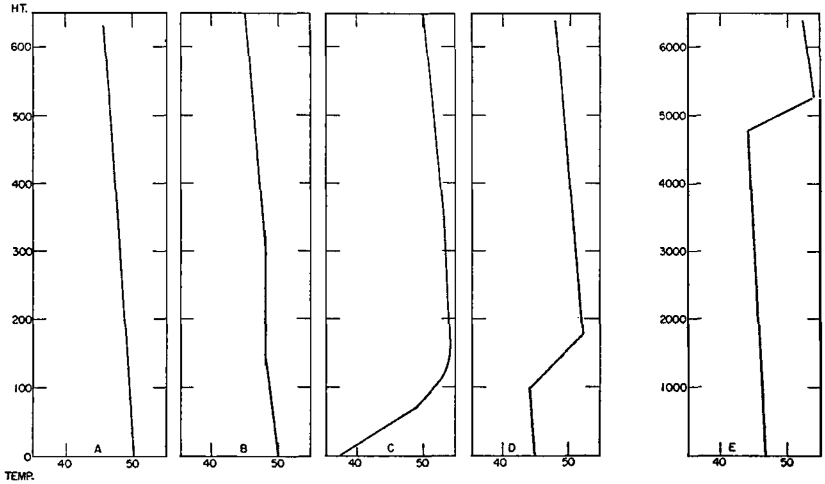

FIGURE 1. Five typical cases of temperature change with height: A, lapse; B, isothermal layer; C, ground inversion; D, low level inversion; E, high level or frontal inversion.

factors that are primarily responsible for preventing inversion formation are cloudiness and wind speed. Clouds reflect and re-radiate most of the outgoing radiation, and if enough are present, prevent the surface from cooling enough to form an inversion. By mixing the cooling lower air with warmer upper air, high wind velocities also prevent inversion formation. Thus, nights with rather low surface wind speed and with the major portion of the sky free of low or middle clouds are most favorable for inversion formation. Either increased wind speed or increased cloud cover may break up an inversion after it has formed, although a cloud layer forming about sunrise may prolong the inversion into the daylight hours. The usual cause of inversion breakup, however, is the appearance of the morning sun which heats the earth's surface. This in turn heats the lower air until its temperature exceeds that of the air aloft. At this point the inversion ceases to exist. Although inversion formation and breakup are usually quite rapid, an intermediate condition, called isothermal, in which temperature remains the same with height, may exist for some time during the change from lapse to inversion or from inversion to lapse.

It has been found that under inversion conditions vertical motion on a significant scale virtually disappears. It is obvious that convective effects can not be operative since the colder, heavier air is now at the bottom and the warmer, lighter air is at the top. Mechanical turbulence also is quickly eliminated in this stable air so that at any appreciable height above the surface, vertical motion on a measurable scale ceases. This may be demonstrated by introducing into the atmosphere a substance such as a smoke which has particles too light to fall out by gravity. Under stable conditions, the smoke trail will remain at the same level, neither rising nor falling to any significant extent.

In addition to the virtual elimination of vertical turbulence, horizontal turbulence is greatly diminished and in some cases almost eliminated in stable air. Instead of constant rapid fluctuations about a mean direction as occurs in unstable air, only a few very slow and gradual fluctuations occur. As may be seen in Figures 2, 3, and 4, the horizontal as well as the vertical wind trace under these conditions may approximate a single line.

The height of a ground inversion may vary from a few feet to over a thousand with the mean probably about 400–500 feet. Regardless of its height, however, the air in and above an inversion is effectively isolated from turbulence originating from below. Thus, the stratified wind flow is present not only within but also above the inversion structure.

In addition to these low level ground inversions, higher level inversions are fairly common. They are usually caused by warmer air flowing over colder air at a frontal surface, the discontinuity line between two air masses. Frontal inversions are most common and best developed at a warm front surface aloft. At a warm front with a shallow slope the inversion may extend for several hundred miles north and south without being more than a mile above the earth's surface at its northern end, and it may extend for hundreds of miles east and west along a well developed warm front. In contrast to ground inversions, frontal inversions persist independently of wind speed, cloudiness, or time of day.

For the purpose of this study, air is classed as stable only if an isothermal layer or an inversion actually exists. All other cases are classed as unstable although from a strict meteorological standpoint, some of them are stable also. It must be emphasized, however, that areas of stability have no consistent relationship with pressure, temperature, or wind direction. Ground inversions may occur in any situation where sufficient cooling of the earth takes place at night and frontal inversions occur whenever warmer air is lifted by cooler air.

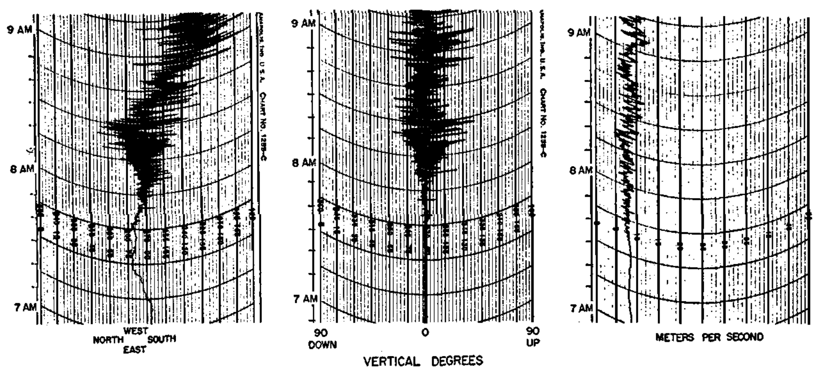

FIGURE 2 (*left*) Horizontal, and Figure 3 (*center*) vertical wind direction traces showing the increase in turbulence from stable to unstable conditions. FIGURE 4 (*right*) Wind speed trace showing the increase in variability under the same change in conditions.

HYPOTHESIS

McMillan (1938) advanced the hypothesis that a bird in flight becomes a part of the air flow and is unaffected by turbulence except when landing or taking off. This would be true if the bird were a weightless body suspended in the air through no effort of its own and content to drift wherever the wind carried it. However, a bird actually remains aloft only by the expenditure of a certain amount of energy, and a bird in flight is normally trying to follow a more or less specific route and reach a definite objective, be it the nearest tree or a breeding area hundreds of miles away. Therefore, the bird in attempting to follow a course and maintain an altitude is necessarily subject to any forces acting upon him. High speed photography has shown us that a bird's flight surfaces are capable of great adjustment in meeting the various forces encountered in flight. It is obvious, however, that such adjustments, each necessitating muscular action, involve the expenditure of a small amount of energy. It is also apparent that a bird flying through unstable air and meeting constant fluctuations in both the horizontal and vertical wind directions as well as frequent variations in wind speed is forced to readjust his flight surfaces continually in order to maintain a constant height and direction. On the other hand, flight through stable air with no significant vertical fluctuations, with only a few gradual horizontal fluctuations, and with little variation in wind speed, would necessitate adjustment to only one relatively constant force. Therefore, such flight should be more economical of energy. Futhermore if, as has been postulated, birds make use of air flow in navigation, it should be much easier to maintain a course in the stratified flow of stable air. It is my belief that nocturnal migrants find flight easier through stable air, that stable conditions are of major importance in triggering such flights, and that a positive relationship exists between atmospheric stability and nocturnal migrations. As far as I can determine, this concept has not previously been advanced.

Comparison of the horizontal and vertical wind direction traces in Figures 2 and 3 and the wind speed trace in Figure 4, gives a good conception of the relative magnitude and frequency of the fluctuations present in stable and unstable air. A numerical indication of the relative difference may be obtained from a gustiness totalizer in use at the Brookhaven National Laboratory Meteorology Group. This device measures all horizontal gusts strong enough to move a Bendix-Friez aerovane in units of angular degrees of rotation of the vane. Thus, each deviation from a mean direction is measured and totalized. Under normal unstable conditions a mean of over 10,000 degrees of rotation per hour or about 1700 per minute has been found. On the other hand, under stable conditions a mean of about 400 degrees of rotation per hour or about 7 per minute has been found. Therefore, we find about two hundred and fifty times as much horizontal variability present in unstable air as is present in stable air. Although such measurements have not yet been made on vertical variability, other studies lead to the belief that a similar proportion and order of magnitude exist there. Although it is impossible to determine how much of this turbulent force is of such a scale as to affect the flight of a small bird, a fair assumption would be that a considerable portion of it is.

As an observational basis for the hypothesis outlined above, observations show that most nocturnal migrations take place under stable conditions. Flights do not usually begin until after the time that inversions normally form in the evening and usually terminate before or at the time of inversion breakup in the morning.

METEOROLOGICAL DATA

In order to test the hypothesis described above, an extensive analysis of the 1953 spring migration and its relationship to a number of meteorological variables was undertaken. Three separate maps of selected meteorological conditions were prepared for each night from April 1–2 to May 30–31, 1953. The first set of maps, Figure 5, prepared from data taken from the 10 P.M. EST radiosondes, delineates stable and unstable areas. About 53 stations in the area regularly take radiosondes, but on any given night a number of reports is usually missing. The mean number of reports from which each night's map was prepared was 44. From an inspection of the coded data as obtained from the teletype reports, it was possible to determine whether or not an inversion existed at each station.

If an inversion or an isothermal layer existed below 3,000 feet, the area was classified as stable. If no inversion existed in the lower layers the area was classified unstable. The three types of areas were distinguished on the maps by different colors. Normally, the stable and unstable stations grouped themselves into homogeneous areas and little problem existed in determining the approximate boundary lines. In a few doubtful cases, reference to surface conditions was often helpful. In a few cases of missing data, certain areas could not be classified. Migration reports from these areas were not used.

It was found that an average of 67 per cent of the area was stable each night and 33 per cent unstable, but considerable change took place from night to night both in the percentage and areas in each category. It is realized that a measurement taken once a night at each station is not necessarily indicative of conditions existing throughout the night. It is probable that in some areas an inversion formed after the sounding was taken and that in other cases the inversion was destroyed later in the night. However, no other measure of stability is available and the data are undoubtedly representative of conditions throughout the night at the stations and in surrounding areas on most occasions. Studies at Brookhaven National Laboratory where continuous temperature measurements are made at various levels up to 410 feet show that most inversions have formed by 10 P.M. EST and generally persist for most of the night.

A second set of maps was prepared showing wind direction and velocity at 2000 feet over the same region. In the light of measurements on the height of nocturnal migrants given by Chapman (1888), Winkenwerder (1902), Carpenter (1906), Stebbins (1906), and Wetmore (1926), it was felt that this level is as close to the mean flight level as can be obtained. These wind data were obtained from pilot balloon observations taken at the same hour as the radiosondes. Approximately 107 stations in the area regularly take pilot balloon measurements, but because of unfavorable conditions, runs are not always successful. An average of 79 stations per night was obtained and plotted, giving an adequate sample in all cases. Pibal reports are available every six hours, but since important changes in upper air flow are seldom rapid, the one report may be considered representative of the night.

The third set of maps was prepared from surface data taken from the 1:30 A.M. EST Weather Bureau maps as a test of the possibility of judging favorable migration nights from surface conditions. Areas were classified as favorable, intermediate, or unfavorable for migration. The first category included areas with mostly clear skies and light surface winds. Unfavorable areas were those with precipitation, heavy fog, or strong winds and frontal zones. Intermediate areas were all other.

In addition, the 1:30 A.M. EST Weather Bureau maps were used directly in correlating movements with surface conditions. All maps were prepared as the data became available and before any migration data were received. Thus, no bias was introduced into the maps by a prior knowledge of bird movements.

MIGRATION DATA

Migration data were obtained from many sources. When the project was initiated, a form letter was sent to several hundred observers in the area covered, requesting definite dates of arrival or departure or actual observations of nocturnal migrants overhead. Although the response was not as good as anticipated, a considerable amount of reliable data was obtained in this manner. Other reports were obtained from Audubon Field Notes, from various local publications, and from the files of the U. S. Fish and Wildlife Service. In addition, the data from the co-operative migration study initiated by Mr. James H. Zimmerman, were made available and furnished the largest class of data obtained. About 2500 usable reports were received, some from all portions of the area but relatively few from areas with few observers. Because of the varying reliability of the data, it was judged best to divide it into two classes. Class 1 data included all reports in which no doubt existed as to the actual night of movement while in Class 2 reports, the possibility exists that some arrivals or departures were not actually on the night specified. Although this classification is arbitrary and many of the Class 2 reports probably deserve to be in Class 1, the value of the separation is shown by the fact that Class 1 reports show a better correlation with the expected meteorological variables than the Class 2 reports.

As the data were received, they were placed on each of the maps using appropriate symbols for each type of movement and for each class of data. Major waves were separated from other arrivals by the number of species and individuals involved. Figure 5, a map of the area on the night of April 27–28, illustrates the method of plotting migration reports. It will be noted that all the major waves and the bulk of the arrivals occurred in stable areas. Although some arrivals

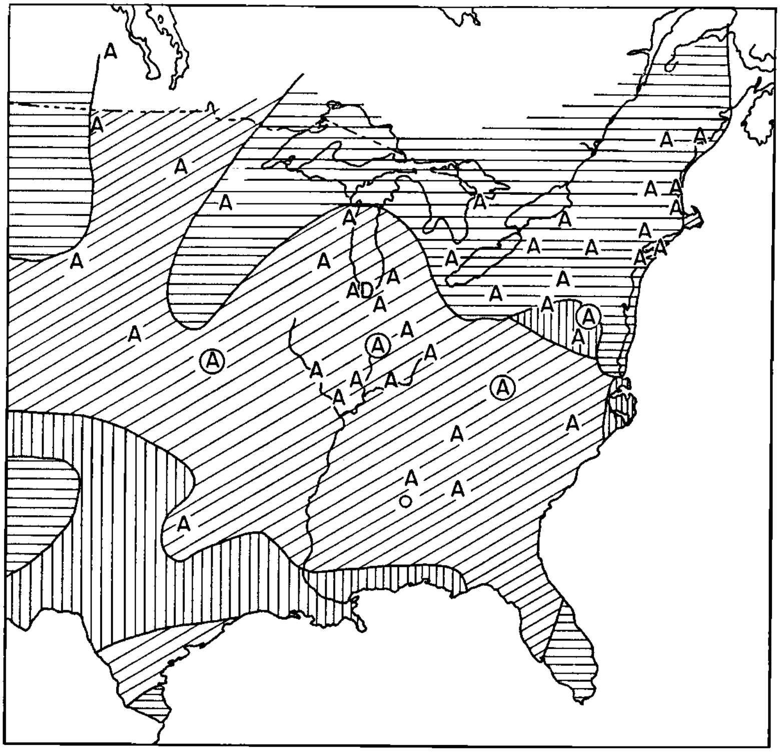

FIGURE 5. Map illustrating method of mapping stable and unstable areas and of plotting migration reports. Slanted hatching, stable area; horizontal hatching, unstable area; vertical hatching, isothermal area; A, arrival; A circled, wave arrival; D, departure; O, overhead observation.

were recorded in the unstable area in the northeast, the number is small considering the large number of observers there and the numerous reports received from that area under stable conditions. All reports received were plotted separately except where different observers reported the same movement from the same or closely adjacent localities. In this case, the reports were plotted as one. No distinction was made between species since it was assumed that all nocturnal land bird migrants react to similar conditions. Separating the data into classes for each species would have hopelessly complicated the study.

METHOD AND RESULTS

When all data received had been plotted, correlations were made with each of the meteorological variables. In all analyses, each night, each class of data, and each type of movement were analyzed separately for each meteorological condition. Grouping into broader categories was accomplished later.

Correlations with areas of stability and instability were undertaken first. All movements were divided into four categories as follows:

1. The entire flight through stable air.
2. The flight mainly through stable air but terminating at the edge of or a short distance into an unstable area.
3. The flight originating in an unstable area but ending in a stable area.
4. The flight entirely through an unstable area.

This classification, of course, is dependent for accuracy on my judgment of how great a distance was travelled by each flight. In arriving at such an estimate, an average flight of about 8 hours at an air speed of 20 to 25 m.p.h. was assumed, and the direction and speed of the wind were considered. The migration and weather pattern was such, however, that a possibility of error existed in only a few cases.

On each date, occurrences in each of the above categories were counted separately for each type of movement and for each class of data. In the final analysis, categories 1 and 2 were combined since both represent flight through stable air. Categories 3 and 4 were also grouped together as representing flight through unstable air.

2,414 reported movements were available for correlation with atmospheric stability. These cases were divided into 155 major waves, 2,075 arrivals, 175 departures, and 9 overhead observations. They were also divided into 363 Class 1 movements and 2,051 Class 2 movements. These cases are summarized in Tables 1 to 3 where the number and percentage of occurrence in stable air of each type of movement are given. It will be noted that the Class 1 data show that about 88 per cent of all movements occur in stable air compared to 74 per cent of Class 2 movements. The arrival of major waves reported in the two classes of data compares more favorably, 88 and 85 per cent. It is apparent that a report of the arrival of a large flight is much less subject to error than a report of the arrival of one or a few individuals.

TABLE 1

PERCENTAGE OF CLASS 1 MIGRATORY MOVEMENTS OCCURRING IN STABLE AIR

Type of movement	*Number of cases*	*Percentage in stable air*
All movements	363	88.4
Major waves	69	88.4
All other movements	294	88.4
Arrivals	234	89.3
Departures	51	84.3
Overhead	9	88.9

TABLE 2

PERCENTAGE OF CLASS 2 MIGRATORY MOVEMENTS OCCURRING IN STABLE AIR

Type of movement	*Number of cases*	*Percentage in stable air*
All movements	2051	74.0
Major waves	86	84.7
All other movements	1966	73.4
Arrivals	1842	73.5
Departures	124	73.4

TABLE 3

PERCENTAGE OF ALL MIGRATORY MOVEMENTS OCCURRING IN STABLE AIR

Type of movement	*Number of cases*	*Percentage in stable air*
All movements	2414	76.1
Major waves	155	86.4
All other movements	2259	75.4
Arrivals	2075	75.3
Departures	175	76.6
Overhead	9	88.9

In order to obtain a mathematical evaluation of these results, the following procedure was followed. An analysis of the radiosonde data showed that 67 per cent of the area was stable during the period studied and 33 per cent unstable. Therefore, if birds flew at random without regard to stability or the factors associated with it, 67 per cent of the flights would be expected through stable areas and 33 per cent through unstable areas. However, 76 per cent of all movements, 86 per cent of all major waves, and 88 per cent of all Class 1 movements occurred under stable conditions. To test the significance of this, the assumption was made that the flights were randomly distributed with respect to stability and the method given by Kenney (1944) was followed.

The evaluation was obtained by use of the formulas:

$\overline{X} = SP$ and $\sigma^2 = SPG$ where $\overline{X}$ = the mean number of flights expected through stable air, S = the total number of cases, P = the probability of flight through stable air, G = the probability of flight through unstable air, and σ = the standard deviation.

Substituting data from the total of all movements, $\bar{X} = 2414 \times 0.67$ or 1617 and $\sigma^2 = 1617 \times 0.33$ or 533.6. Therefore $\sigma = 23$. Subtracting $\bar{X}$ from the number of cases observed of flight through stable air, we obtain 1838−1617 or 221 which is 9.6 σ. The odds against obtaining this result by chance are greater than 99.99 to 1, so we may conclude that the results are highly significant.

Repeating the procedure with the major waves from both classes of data, we find a probability of 104 cases and an occurrence of 134 cases. The deviation of 30 is 5.2 σ and again highly significant.

A similar procedure was followed with the 2,000-foot wind data. Winds were classed as favorable if they were more with than against the assumed direction of flight and unfavorable if they were more against. The flight direction was assumed to be normal in the area involved, northerly in the mid-west, north to northeast in the northeastern states and north to northwest in the plains states. The few borderline cases were classed as side winds. 4737 wind observations were available, 2306 favorable, 1739 unfavorable, 671 side, and 19 calm. Using only the 4045 distinct cases we find 57 per cent favorable and 43 per cent unfavorable. Therefore, if the birds flew at random in respect to wind direction we would expect 57 per cent of the flights with favorable winds and 43 per cent with unfavorable winds, omitting the side wind flights. Tables 4 to 6 give the actual number of cases observed. It will be noted that 67 per cent of all Class 1 cases, 79 per cent of all major waves, and 63 per cent of all movements occurred with favorable winds.

Considering all cases we find a probability of 1284, an occurrence of 1416 and a deviation of 132 or 5.6σ. Using only the major waves, we obtain a deviation of 29 or 4.8 σ. These results are again highly significant.

Since it is evident that both atmospheric stability and wind

TABLE 4

PERCENTAGE OF CLASS 1 MIGRATORY MOVEMENTS OCCURRING WITH FAVORABLE WINDS ALOFT

Type of movement	*Number of cases*	*Percentage with favorable winds*
All movements	340	67.1
Major waves	66	77.3
Other movements	274	64.6
Arrivals	218	66.1
Departures	47	57.4
Overhead	9	66.7

TABLE 5

PERCENTAGE OF CLASS 2 MIGRATORY MOVEMENTS OCCURRING WITH FAVORABLE WINDS ALOFT

Type of movement	*Number of cases*	*Percentage with favorable winds*
All movements	1931	62.1
Major waves	79	79.7
Other movements	1834	61.3
Arrivals	1717	61.2
Departures	117	62.4

TABLE 6

PERCENTAGE OF ALL MIGRATORY MOVEMENTS OCCURRING WITH FAVORABLE WINDS ALOFT

Type of movement	*Number of cases*	*Percentage with favorable winds*
All movements	2253	62.8
Major waves	145	78.6
Other movements	2108	61.7
Arrivals	1935	61.2
Departures	164	61.0
Overhead	9	66.7

direction are of importance in nocturnal bird migration, it was desired to evaluate their combined importance and to test the influence of each separately. For these purposes only the major waves were used since they were judged more reliable than the bulk of the data. The 153 usable waves were divided into four categories as follows:

1. Flight through stable air with favorable winds.
2. Flight through stable air with unfavorable winds.
3. Flight through unstable air with favorable winds.
4. Flight through unstable air with unfavorable winds.

The number of cases, the percentage in each category and the percentage of probability are given in Table 7. In the first category, we find 98 cases with a probability of 58. The deviation, 40, is 6.7 σ and is highly significant. In the second category, we find 24 per cent of the flights or 83 per cent of the probable number. In the third category, however, we find only 10 per cent of the flights or 53 per cent of those probable. The last category contains only 14 per cent of the number expected.

From the above figures it is evident that the overwhelming majority of all flights took place in areas of stable air and favorable winds, but the fact that the cases in Category 2 are much closer to the probability than the cases in Category 3 indicates that stability is probably of greater importance than wind direction. In the light of these

TABLE 7

PERCENTAGE OF MAJOR WAVES OCCURRING AND PROBABILITY OF OCCURRENCE UNDER VARIOUS COMBINATIONS OF STABILITY AND WIND DIRECTION

Category of movement	*Number of cases*	*Percentage*	*Percentage of probability*
With stable air and favorable wind	98	64	38
With stable air and unfavorable wind	36	24	29
With unstable air and favorable wind	15	10	19
With unstable air and unfavorable wind	4	2	14

findings, it was decided to examine in greater detail the 55 cases in the last 3 categories in the hope of finding why these flights did not conform to the normal pattern.

The 36 cases of flight through stable air but against the wind were examined first. No case was found with flight against wind speeds greater than 18 m.p.h. 18 cases were of flight over a warm front and therefore the flights almost certainly took place with favorable winds at a higher level even though they terminated in areas of unfavorable winds at 2,000 feet. Two cases were doubtful and might have taken place with favorable winds. Four cases had favorable winds a short distance to the south. These flights were evidentally terminated shortly after the unfavorable winds were encountered. The remaining 12 flights took place against light winds, mostly 5 to 10 m.p.h. and none greater than 18 m.p.h. It might be mentioned here that a number of cases taken from Class 2 data reported arrival in an area of strong unfavorable winds. In some cases flight may have been made at a different level with lighter winds, but it is believed that most of these observations are in error.

The 15 cases of flight with favorable winds but unstable air were examined next. Four cases were of flight over a warm front surface, most probably in a higher level inversion not plotted on the map. Five cases occurred in the warm sector of a low with strong southerly winds and a stable area to the south. It is probable that these flights originated in the stable area and were carried beyond by the high wind speed. Four other cases might have originated in a stable area some distance to the south while no explanation was found for only the two remaining cases.

The four cases occurring with unfavorable winds and unstable air were next examined. One case occurred over a warm front surface where favorable winds and stable air existed at a higher level. The other three cases were in regions where a stable area with favorable wind existed to the south. The flight was evidently maintained for some time into the unfavorable conditions.

In the light of these findings, it is evident that only a very few valid cases can be found of large flights through an unstable area or against an opposing wind and that the overwhelming majority of mass flights took place under favorable wind and stability conditions.

Surface conditions were considered next and again only major waves were used. At the beginning of the study, I felt that it might be possible to determine which areas were favorable for nocturnal migration from an inspection of the surface map. Accordingly, the third set of maps showing areas that were, in my judgment, favorable, intermediate, and unfavorable, was examined. Although a precise determination of probabilities is not possible, I estimated that about 50 per cent of the area fell into the intermediate category and about 25 per cent into each of the other two. However, only 28 per cent of the reported flights took place in the intermediate areas, 27 per cent in the favorable areas, and 45 per cent in the unfavorable areas. The latter class, of course, includes the warm front areas now found to be favorable for nocturnal migration. It is obvious, however, that the classification used is of little value and my estimate of favorable conditions as judged from surface data only is not shared by the birds.

The next step was to test for relationships between the major waves and the various surface variables. Pressure systems were considered first. It was found that 47 or 31 per cent of the flights took place through high pressure areas. Of these, 10 were through the eastern portion of a high where opposing winds normally prevailed, 25 through the central portion where winds were usually light and variable, and 12 through the western section where winds were favorable. Ground inversions are most common near the center of highs where skies are relatively clear and winds light.

28 flights or 18 per cent of the total took place in the immediate vicinity of a cold front. It was not always possible to determine if they arrived ahead of or behind the front since their time of arrival during the night was not known, but nearly all the flights could have and probably did arrive before or at the time of the frontal passage while favorable winds still prevailed. It is evident that spring migrants do not favor cold frontal areas. Indications are that flights encountering such areas are usually terminated.

78 or 51 per cent of the total took place in the vicinity of a warm front. 14 terminated in the vicinity of the front, 29 apparently flew over the surface front and came down in the cooler air not far to the north, while 35 terminated more than 100 miles to the north.

All of these flights, however, probably flew through the warm air and southerly winds aloft rather than through the less favorable conditions below. Thus, it is obvious that warm front inversions are of considerable importance in the northward movement.

58 or 37 per cent of the flights took place wholly or partly in a precipitation area. 29 flights ended near the edge of the area, 17 ended some distance into the area, 7 passed through or over the area, and 5 may have originated in a precipitation area. These flights are mostly the same ones discussed above as taking place in warm front areas. It may be assumed that in all cases the flight was over rather than through the precipitation until the time of descent.

A comparison with surface temperature trends was made next. Computations showed that 57 per cent of the area was in a region of rising temperatures and 43 per cent in a region of falling temperatures. 88 or 56 per cent of the flights took place in the former areas and 65 or 44 per cent in the latter showing that flights were apparently random in respect to temperature trends. Although previous studies have shown a relationship between rising temperatures and spring migration, rising temperatures are predominant in spring and they co-exist with favorable winds. Therefore, although the major portion of spring migration may take place with rising temperatures, this study fails to show a correlation greater than the probability.

A similar comparison was made with pressure trends. It was estimated that about 50 per cent of the area had rising pressures and 50 per cent falling pressures. 68 or 47 per cent of the flights took place in regions of rising pressure while 76 or 53 per cent occurred in areas of falling pressure. The deviation of 4 is 0.67 σ. Although a slight relationship appears to exist, pressure as such is judged to be of no importance. Areas of falling pressure are associated with other conditions that are important as discussed above.

The only surface variable that showed a correlation comparable to the upper air variables was wind direction. The percentages of favorable and unfavorable direction at the surface were identical with those at 2,000 feet, namely 57 and 43 per cent. 75 per cent of the flights were made with favorable surface wind and 25 per cent with an unfavorable direction. The deviation of 25 is 4.3 σ, only slightly less than that found at 2,000 feet.

Although the frequency percentages of northerly and southerly winds are identical over the area and the period as a whole at both levels, it does not necessarily mean that they always occur simultaneously. In the majority of cases they do, but at a warm front surface in particular, surface winds may differ radically from those aloft over a wide area. If this situation is taken into account, it is possible that surface winds may be nearly as useful as winds aloft for correlation with migration data.

As mentioned above, the relationship of moonlight to nocturnal movements needs investigating. Two periods of full moon occurred during the time covered by this study and neither was accompanied by a significant increase in reported movements. Many additional data must be accumulated, however, before any conclusions can be drawn.

DISCUSSION

Although the conclusion can be drawn that stable air and favorable winds aloft are of the utmost importance in springtime nocturnal bird migration, it must be regarded as tentative until more than one season can be studied. However, the length of time used, the large area covered, the large number of observations considered, and the excellent relationships found, all tend to increase the probable reliability of the results.

If, for the sake of discussion, we regard the results as valid, certain questions arise. Although the relationship with wind direction is simple, the correlation apparently found with stability could be with stability itself or with conditions associated with stability. An examination of the conditions causing and associated with stability leads to the conclusion that the relationship must be with stability itself. The two types of inversions causing stable air are caused by and are associated with widely differing weather conditions. Yet, each has been found favorable for nocturnal migration. Since stable air is the only variable common to both regimes its importance can not be minimized.

It is also necessary to consider how birds recognize stability and what stimuli are actually operative in triggering a migratory movement. Although this problem is susceptible to experimental solution and should be so tested, we can consider at present only indirect evidence. It seems well established that birds' sensory systems are no less sensitive than are those of humans. If that is so, changes in temperature and wind structure that accompany an inversion can easily be detected by the bird. I have many times had the experience of standing on a tower or other elevated structure during an inversion and feeling the smooth, stratified wind flow which is readily distinguishable from the normal, turbulent flow present during lapse conditions. During a well developed inversion, the temperature increase with height is also readily detectable upon an ascent of 50 feet or less. Therefore, if humans can sense the changes that accompany an inversion, it seems reasonable to believe that birds can also and may be stimulated to begin a flight by these changes.

This, of course, does not imply that a bird is capable of recognizing a frontal inversion from the ground even though it was found that many flights took place over such an inversion. It seems more probable that in such cases the migration started in the ground inversion to the south of the warm front and continued over the warm front inversion. The strong southerly flow usually existing in such situations would make possible flights of considerable length.

As far as I can ascertain, no ornithologist has ever witnessed the actual departure of migrants upon a nocturnal flight; their pre-departure behavior is therefore unknown. One account, however, given by Lowery (1945) may be interpretable as pre-departure activity and seems highly significant in view of the hypothesis advanced above. He quoted a letter from Weston who towards sunset on a clear, mild, spring day noted a group of migrants congregated in the tops of the tallest trees. The birds occasionally made short upward flights beyond the tree tops, returning each time to the trees. This activity continued until after dark, and in the morning the birds were gone. Similar activity was observed on another occasion. It will be noted that the weather conditions described were favorable for ground inversion formation. It seems probable that the birds were testing the wind or temperature structure by their short upward flights and that migration began when conditions became favorable.

Since we now have a reasonable theory to explain how and why nocturnal migratory flights are initiated, we must consider how and why they are terminated. It is apparent that termination may be either voluntary or involuntary. The former would include cases in which the bird arrived at his destination or remained aloft until a normal hour for descent, probably shortly before sunrise or somewhat later in certain species. Involuntary terminations would include those cases in which the bird found himself faced with unfavorable or impossible flying conditions. These probably include strong, adverse winds, precipitation at the flight level, and turbulent air. The relatively large number of cases in which arrivals occurred at the edge of a precipitation area, at a frontal zone or at the southern edge of an area of opposing wind or unstable air suggests that many flights may not be terminated voluntarily. Numerous instances in the literature of birds arriving in an area of widespread rain and of being "precipitated out" in an area of thunderstorms support this belief.

It seems probable that many flights above warm fronts may be so ended. As the bird flies northward in the warm air, he has the advantages of stable air and favorable winds. Below him, however, lies unstable air, and usually unfavorable winds or precipitation. In order to stay in the warm air, he must constantly increase his altitude since the front slopes upwards from south to north. Eventually an altitude may be reached at which the bird will no longer be willing or able to continue flight. In this case, he will be forced to descend even though most unfavorable conditions may exist below. It is probable that the various cases of mass destruction overtaking spring migrants were caused in this way.

Although the cases have not been investigated individually, it seems probable that many of the instances wherein spring migrants apparently overshoot their mark and arrive either exceptionally early or well north of their normal range can be explained in a similar fashion. A bird flying above a frontal surface with adverse conditions below might well prefer to prolong his flight rather than descend until descent became necessary. Winds of 40 to 50 miles per hour are not uncommon at a few thousand feet in such situations. Thus, a bird with a flight speed of only 20 miles per hour could easily cover 600 or 700 miles in a single night. Such a flight could take a migrant from the Carolinas to the New England area and from the Gulf Coast to central Illinois, Indiana, or Ohio in a single night.

Although the controversial subject of trans-Gulf migration is beyond the scope of this paper, it might be pointed out that colder air over warmer water is subject to considerable instability but that warmer air over cooler water is relatively stable. Therefore, if stability along the route is a factor in over-water flight, northward movements should be correlated with the presence of air warmer than the water. This condition exists with a southerly circulation so that over the Gulf, favorable temperature structure and favorable wind direction should co-exist.

On the other hand, it is possible that only conditions at the starting point govern the time of trans-Gulf flights. Data obtained by Lowery (1945) tend to show a correlation between good weather (favorable for inversions) and southerly winds in Yucatan and arrivals on the Gulf coast when such arrivals are arrested there by a cold front.

Although the data show that migratory movements are correlated with certain favorable meteorological factors, it must not be expected that flights will occur whenever such conditions exist. If birds in the area are not yet ready to migrate or if all birds that were ready have departed on a previous, favorable night, no migration will take place. On the other hand, a limited amount of migration may take place even under unfavorable conditions if the bird's urge to migrate outweighs his reluctance to fly under such conditions. It seems probable that if favorable conditions are long delayed, considerable movement will take place anyway.

It should be pointed out that the relationships found cannot be extrapolated to another area, to another season, or to another type of migrant. Data available indicate that the fall movement is influenced by quite different synoptic situations although it is believed that stability and wind direction are again of importance. It is expected that weather-migration relationships may be quite different in mountainous regions such as the Rockies, and there is considerable doubt whether the same factors are operative in other continents where migration patterns differ quite widely from those in America. For this reason, references have been confined to work on this continent.

CONCLUSIONS

Of the various meteorological variables studied, only two, atmospheric stability and wind direction, give a good correlation with springtime nocturnal land bird migration. The two together give a better correlation than either separately, but stability seems somewhat more important than wind direction. Therefore, it is evident that such migration normally taken place with favorable winds in stable air which may be caused either by ground or frontal inversions. Such movements usually begin in areas of ground inversions but may continue above frontal inversions. Migration is probably initiated by changes in temperature or wind structure or both, and these act as stimuli to the migrant. Migratory flights are often terminated at the edge of an unstable area or a region of unfavorable winds. A number of previously puzzling migration problems may be explainable on the basis of these findings.

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