THE DISTRIBUTION OF NOCTURNAL MIGRANTS IN THE AIR SPACE

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We recently used a new method for obtaining information about nocturnal migrants in the air space. A light aircraft equipped with auxiliary landing lights (Figure 1) was flown on altitudinal and geographical transects to obtain information on the distribution of nocturnal migrants that could not be obtained by other methods.

The possibility of using lights on an aircraft at night to survey birds in the air space developed on a flight with airborne radar. Richard R. Graber of the Illinois Natural History Survey and Glenn E. Stout and Donald W. Staggs, meteorologists with the State Water Survey, watched targets on an aircraft radar the night of 17 September 1962 that they believed to be birds. To identify the targets on the radarscope, they turned on the landing lights and were able to see large numbers of small birds in the air, confirming the nature of the radar targets.

Aircraft surveillance of nocturnal migrants has three advantages: individual birds can be counted, the magnitude of migration at different altitudes can be assessed more accurately than by other methods, and geographic distribution of nocturnal migration can be continuously monitored. Observations from the aircraft can be either continuous in time or continuous in geography, but not both without using more than one aircraft. The relationships of nocturnal migrants to terrain and weather conditions are more apparent when the observer is in the air along with the migrants. For example, air turbulence is infrequently recorded by U. S. Weather Bureau stations, yet the airborne observer is intimately aware of this condition.

We initiated aerial reconnaissance of nocturnal bird migration to supplement our radar surveillance of bird movements, but we make no attempt in this paper to compare findings from radar surveillance with observations from a light aircraft. The objectives are to determine the altitudinal distribution of small birds in the air space, determine the magnitude of migration as influenced by cloud cover and wind, evaluate the influence of topographic features on the distribution of nocturnal migrants, and describe the response of spring migrants to a weak cold front and a warm front.

Methods

The Piper 180 we used is a low-wing, four-passenger aircraft that we cruised at an air speed of 120 mph. In addition to its standard equipped landing light in the nose, we added a landing light to each of the two landing gear struts (Figure 1). We found from a few experimental flights that the best zone of observation was

Figure 1. The Piper 180 aircraft, fitted with auxiliary landing lights on the landing struts, used for surveys of nocturnal bird migration.

between the propeller and the leading edge of the wing, a distance of 70 inches, and laterally 168 inches to the wing-tank gas caps. We could see birds readily for a depth of 60 inches, from near the top of the cabin to the landing wheels. Thus we viewed an area 60 inches vertically by 168 inches horizontally, a lighted zone of 70 square feet. In one statute mile, we scanned 369,600 cubic feet of air space.

Two observers usually accompanied the pilot, and, on occasion, we used a recorder. The observer behind the pilot looked over the pilot's left shoulder. The observer to the pilot's right looked downward at a 45° angle. The birds were recorded by time in order to determine their geographic position, and a log was kept of the time of arrival at towns on the flight course. Thus we could calculate the number of birds per ground mile between known localities.

Radar observations made simultaneously showed no tendency for small birds to be either attracted to or repelled by the lights, possibly because of the aircraft's speed. We have seen flocks of ducks and geese on radarscopes deviate from their flight paths when aircraft passed nearby. We have noted, in over 2,000 hours of diurnal flying, that small birds such as blackbirds, swifts, and swallows, make last-second plunges to avoid aircraft, but ducks and geese take evasive flight at much greater distances ahead of the aircraft. Thus we believe that our aerial transects through the nocturnal sky provide a representative view of the magnitude of small bird passage, but not of waterfowl and similarly wary birds.

We have watched thousands of small birds at night, flashing around the propeller and clearing it and the wings of the aircraft by mere inches. We have struck only three small birds and no large birds at night. Because of the aircraft's speed, the birds are in view for only a split second. Their feathers give a reflected glow in the light beam, creating brilliant streaks against the black sky as they dart by. This reflected glow makes all small birds look somewhat alike.

In clearing the propeller, most small birds pass close to the fuselage of the plane, with about three-fourths passing below the wing. Middle-size and large birds are more likely to pass farther out on the wing, beyond the primary zone of observation. We have often noticed large birds passing near the tips of the wings.

Two types of transects were run—"staircase" transects over the same route night after night to determine altitudinal distribution and to compare nightly differences in the volume of migration, and transects across country at approximately the same altitude above ground level to ascertain geographic distribution.

The altitudinal and nightly transects were flown between the Mackinaw River, south of Pekin, Illinois, and state route 78 south of Canton, Illinois, an east-west distance of 16 miles. As shown by radar (Bellrose and Graber, 1963; Bellrose, 1967), most small birds in this region migrate in a northeasterly direction in the spring and southeasterly in the fall. Intercontinental migrants apparently have an elliptical migration pattern that takes advantage of the westerly and easterly wind belts. Consequently our transects crossed their lines of flight at an angle of 45°-60°. When crossing the paths of migrants at these angles the ground speed of birds does not greatly influence sampling. If the aircraft is moving opposite to the direction of the migrants, the sample size is increased by the ratio of the ground speed of the aircraft to the ground speed of the migrants. Conversely, the aircraft moving with the migrants decreases the sample size by the proportion of the aircraft speed to that of the migrants. Assuming our aircraft had a ground speed of 120 mph and birds were migrating at 40 mph, sample size at the most would increase or decrease by 33.3 per cent. Usually our sampling error was much less because of intersecting most passages at an angle of 45°–60°.

We usually stopped increasing our altitude when two transects passed without seeing a bird. Concurrent radar observations at Havana, Illinois, about 20 miles south of the Pekin-Canton transects, showed that bird targets sometimes occurred at higher altitudes than where we ceased finding them. This suggests that the density of migrants was so low and our field of coverage so limited compared with the field of radar that we failed to observe birds when they were sparsely distributed in the air space.

Geographic transects were conducted east-west across central Illinois into eastern Iowa. A round trip survey was made between Pekin, Illinois, and Lincoln, Nebraska. Another survey extended from Pekin to Daytona Beach, Florida, with a base leg from there to San Antonio, Texas, and the third leg from Houston, Texas, back to Pekin, Illinois. Geographic transects were flown at altitudes 1,000 to 2,000 feet above ground level (abbreviated AGL). We selected altitudes in which the largest number of migrants occurred concomitant to the lowest altitude considered safe for night flying.

On 20 nights during the fall of 1965 we flew 16-mile transects at altitudes 500 feet apart, starting with a base 500 feet above the airport. About one-third of the terrain was 50 feet lower than the airport elevation (500 feet above mean sea level—MSL), and one-third was 100 feet higher. During the spring of 1966, we conducted surveys on 29 nights. Thunderstorms and/or poor visibility prevented flights on other nights. Usually our observations began about one hour after sunset. Surveys at that time gave us an index to local departures enabling us to associate them with local weather conditions. Our radar findings in Illinois (Bellrose, 1967) show that most small birds start migrating shortly after dark and climb quickly to altitude. In addition to the transects at 500-foot intervals, as in the fall of 1965, transects were made at 350 and 750 feet AGL. One other altitudinal survey was made on 2 June 1967 near St. Louis, Missouri, and four surveys during one night, 27-28 May 1970, Pekin to Canton.

So far as we can discover, no nocturnal migration occurs at ground or "on the deck" level, often noted among diurnal migrants such as blackbirds. From ground observations at night, as well as from our aircraft leaving and approaching airport runways, we have no evidence of birds migrating at night below 100 feet AGL.

Radar at Havana showed that most birds migrate north-northeast in the spring and south-southeast in the fall. Winds blowing within 90° ± toward the seasonal direction were considered favorable; other wind directions were considered adverse. Time is always given in local standard hours.

RESULTS

ALTITUDINAL DISTRIBUTION

The magnitude of migration varied greatly from night to night. On a few nights in the spring and fall, the number of migrants was much larger than on all other nights; an analysis of variance test of altitudinal distribution indicated that the mean number of migrants for each altitudinal transect was unreliable. Nevertheless we noticed a consistent pattern to the altitudinal distribution whether the nightly number of migrants was large or small: numbers increased rapidly up to 1,000 feet AGL and decreased gradually with altitude above that level.

Figure 2 compares the abundance of bird migrants between spring and fall on altitudinal transects 500 feet apart. The slight differences in the altitudinal distribution between the seasons are statistically insignificant. During the spring surveys 50 per cent of the migrants occurred at the 500- and 1,000-foot levels; on the fall surveys 48 per cent occurred at those levels.

The spring density of small bird migrants is included for the 350- and the 750-foot levels in addition to the altitudes sampled the previous fall (Figure 2). From the 1,000-foot level upwards, the number of migrants decreased at a fairly constant rate: for each 500-foot span of altitude, density declined about one third.

An exception to the general altitudinal distribution found for small birds during the fall of 1965 and the spring of 1966 occurred on 2 June 1967. Tremendous numbers of small birds were aloft that evening averaging 18 per mile (37 per minute) at 1,000 feet AGL between St. Louis, Missouri, and Havana, Illinois. On 2 June 1967 we flew east–west altitudinal transects 20 miles north of St. Louis at 500-foot intervals between 1,000 and 6,000 feet AGL. At the four lower levels we found from 12.7 to 17.8 birds per mile, an unusually large number. A much larger proportion of migrants than previously observed occurred at higher altitudes (Figure 3). For the first time, we found more migrants at 2,000 feet AGL than at 1,000 feet. Even as high as 6,000 feet, migrants averaged 2 per mile.

SKY CONDITION

To increase the size of the sample, both spring and fall data were combined for evaluating the effect of sky cover. The average number

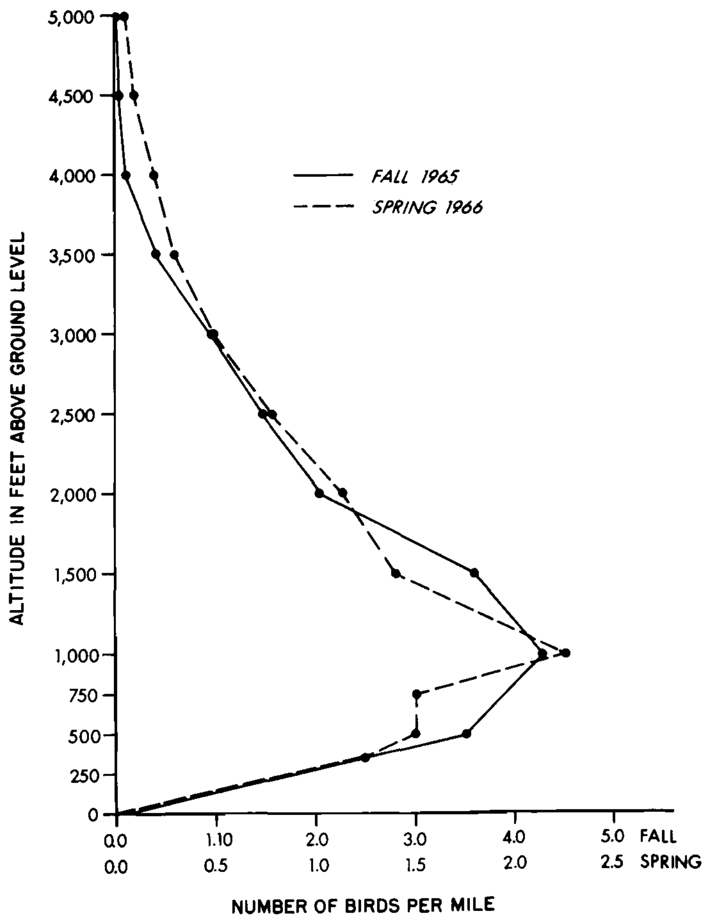

Figure 2. The relative proportion of small bird migrants found at altitude levels 500 feet apart on 20 nights during the fall of 1965 and 29 nights during the spring of 1966. Based upon 5,710 birds counted during the fall and 4,389 birds counted during the spring.

of migrants at 1,000 feet AGL on 30 nights with clear or partly clear skies was 2.9 per mile. On 19 nights when solid overcast occurred, we found an average of 3.1 per mile for the same altitude. A large proportion of the migrants under overcast skies occurred on only one night, 7 October 1965. At the 1,000-foot level we counted 47 birds per mile. The sky had been overcast throughout the day and remained so until 21:45, when the transect at 3,000 feet was completed. At that time breaks in the cloud cover developed and the sky began to clear gradually, but it is

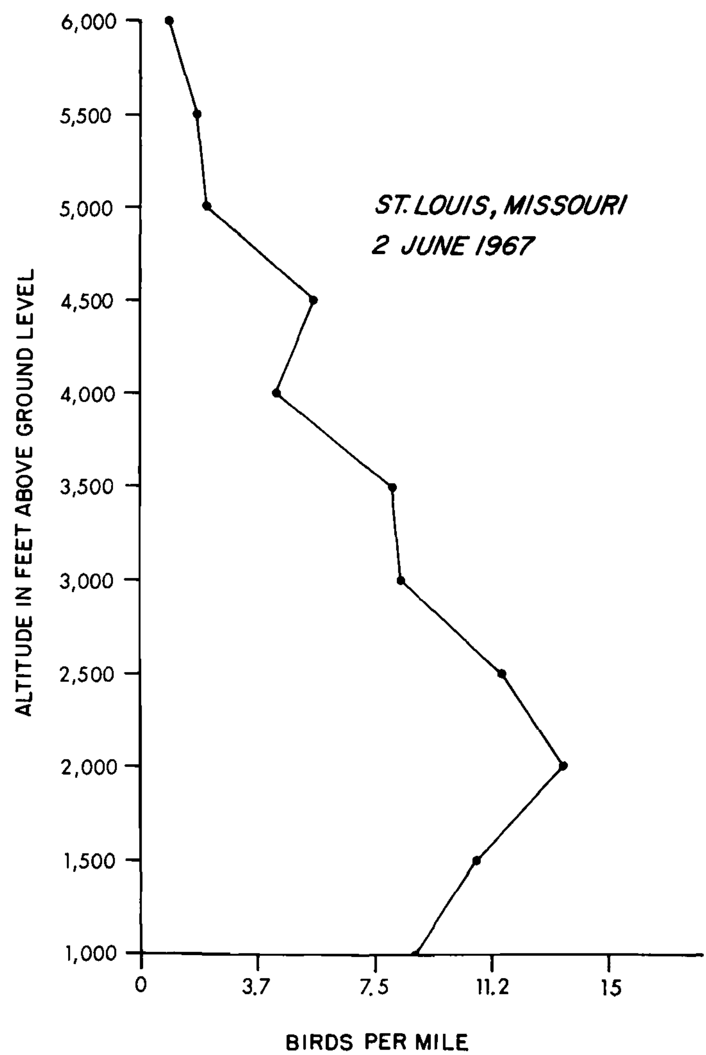

Figure 3. The abundance of small birds by altitudinal transects near St. Louis, Missouri, during an unusually large migration the night of 2 June 1967.

apparent that the number of birds we observed began migrating under overcast skies. Considering spring data only at the 1,000-foot level, there were averages of 3.7 birds per mile on 20 nights with clear skies and 1.8 birds per mile on 8 nights with overcast skies.

On the night of 30 September 1965, we found 2.3 birds per mile at the 1,000-foot level. The entire day and night was overcast, with the

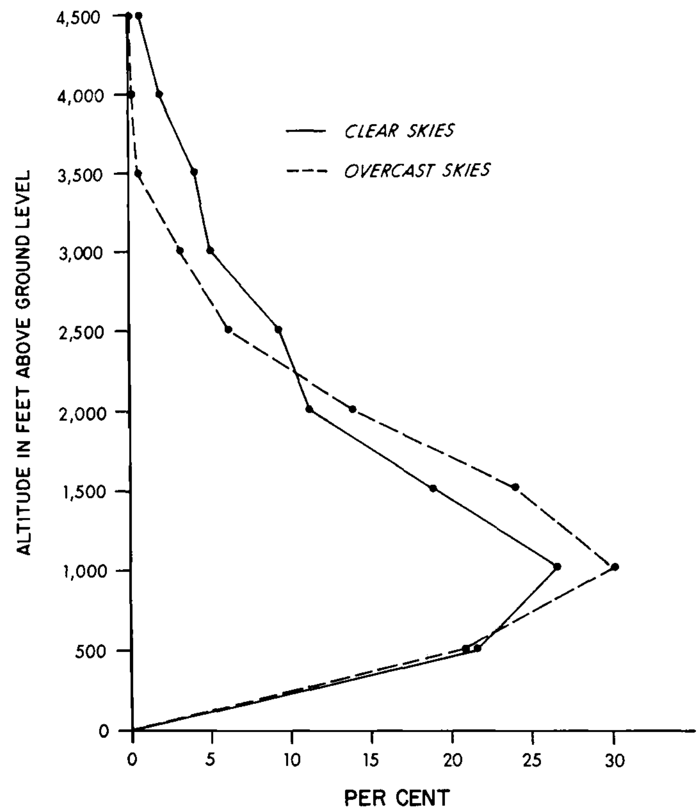

Figure 4. The relative proportion of small bird migrants found at altitude levels under clear and under overcast skies, fall 1965 and spring 1966. Based on surveys made on 30 nights with skies partly clear to clear and 19 nights with skies completely overcast. At the 1,000-foot level we found an average of 2.9 migrants per mile under partly clear to clear skies and 3.1 migrants per mile under overcast skies.

base of the clouds varying from 1,600 to 2,800 feet AGL. The wind at ground level was partly adverse (ESE) at 9–13 knots. An indication of the species aloft that night is provided by birds killed striking a TV-transmitting tower near Peoria, 15 miles north of our aerial surveys. Ten birds were picked up on the morning of 1 October: 2 Red-eyed Vireos (*Vireo olivaceus*), 1 Black-and-white Warbler (*Mniotilta varia*), 1 Tennessee Warbler (*Vermivora peregrina*), 1 Chestnut-sided Warbler (*Dendroica pensylvanica*), 2 Bay-breasted Warblers (*Dendroica castanea*), 1 Ovenbird (*Seiurus aurocapillus*), 1 Common Yellowthroat (*Geothlypis trichas*), and 1 Indigo Bunting (*Passerina cyanea*).

Because we began 1 hour after sunset, the birds that we saw

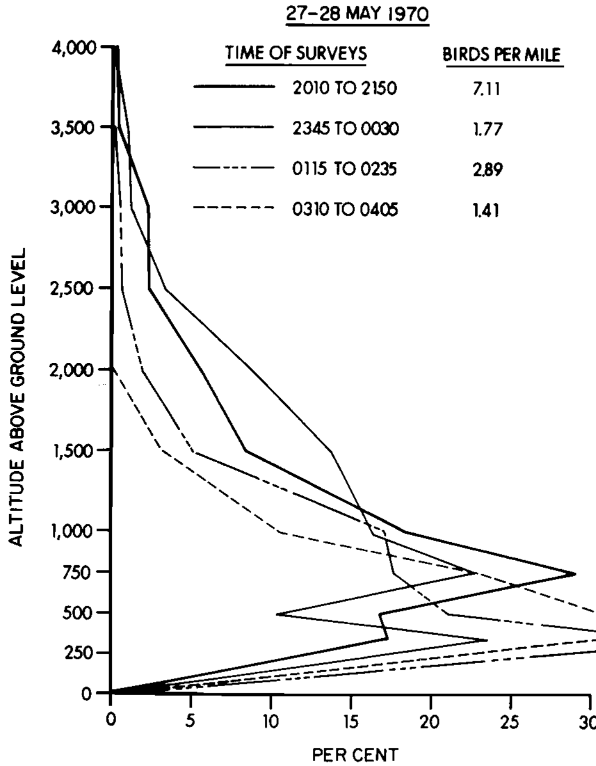

Figure 5. The relative proportion of small birds found at various altitudinal levels on four surveys, Pekin-Canton, Illinois, the same night, 27-28 May 1970.

undoubtedly started migrating within 40 miles of our transect. From our own observations of sky cover and those at the U. S. Weather Bureau station at Peoria, we have confidence in our determination of the sky cover under which birds initiated nocturnal flight. Most of the overcast skies at the time of our observations had been overcast for many of the previous daylight hours, and in 11 instances overcasts occurred prior to 12:00. In the remaining seven cases, overcasts developed several hours before sunset.

Figure 4 compares the relative proportion of migrants found at 500-foot intervals under clear and under overcast skies. Although 48 per cent of the migrants under clear skies and 51 per cent of those under overcast skies occurred at the 500- and 1,000-foot levels, an analysis of variance test showed no statistical significance between the altitudinal distributions under clear and overcast conditions.

Temporal Pattern

We made four survey flights on the night of 27–28 May 1970 to determine the relationship between time of night and altitude of migration. For some unknown reason, small birds were migrating at lower altitudes than customary (Figure 5). We found the largest number of migrants on the first survey flight made shortly after dark (20:10 to 21:50). Density of migrants declined on the second survey (23:45 to 00:30), was appreciably higher on the third survey (01:15 to 02:35), and was lowest on the fourth survey (03:10 to 04:05) made shortly before dawn.

A slightly larger proportion of the migrants were at middle latitudes (1,500–2,500 feet) on the second survey than on the first survey. Mean altitude of the migrants on the first survey was 914 feet AGL and on the second survey 982 feet. Migrants were at lower altitudes (mean, 672 feet) on the third survey, and at still lower altitudes on the fourth survey (mean, 530 feet). Our evidence suggests that shortly after taking off, small birds quickly ascended to their migrating altitude. In the next few hours they climbed slightly, if at all. Shortly after midnight, they began to descend, and, by dawn, were all below the 2,000-foot level.

Wind Conditions

Winds at ground level were in a favorable direction for migration on 27 nights during the fall of 1965 and the spring of 1966 and were in an adverse direction on 22 nights. On evenings when wind direction favored departure, we found 4.0 birds per mile at the 1,000-foot level. On evenings when wind direction was adverse, we counted only 1.6 birds per mile at the same altitude. Since we sampled the magnitude of migration shortly after it started, we assume that the number of migrants aloft was influenced in departure by the direction of winds at ground level. The relative altitudinal distribution of migrants under favorable and under adverse wind directions (Figure 6) indicates that migrants fly slightly higher under favorable winds but that the difference is not statistically significant.

Geographic Distribution

During the altitudinal surveys on 29 nights in spring 1966, we separated our transects into the area east of the Illinois River valley (4 miles), over the Illinois River valley (6 miles), and west of the Illinois River valley (6 miles). The objective was to determine whether small nocturnal migrants were denser over the Illinois valley than elsewhere. A greater density would suggest that birds were using the valley as a guideline in nocturnal flight. Our findings showed an average of 8.6 birds per mile for all altitudes flown each night east of the Illinois River valley, 9.8 birds per mile over the Illinois valley, and 12.4 birds west of the valley.

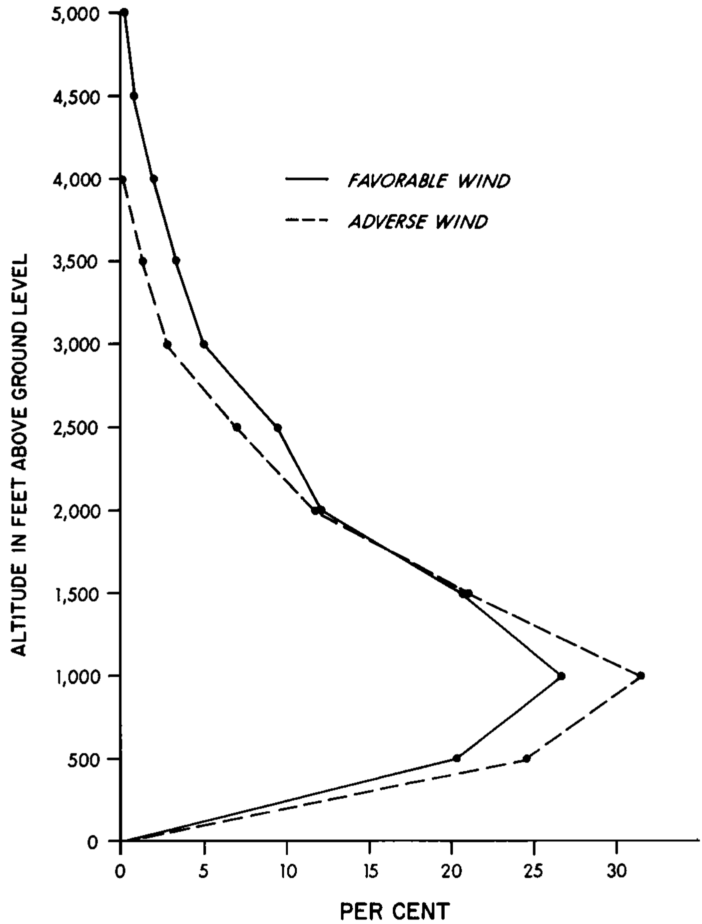

Figure 6. The relative proportion of small bird migrants at altitude levels 500 feet apart when winds were favorable and adverse, fall 1965 and spring 1966. Based upon 27 nights when winds were favorable and 22 nights when winds were adverse. We found an average of 4.0 migrants per mile at the 1,000 foot-level when winds were favorable and 1.6 migrants per mile at the same altitude when winds were adverse.

A comparison of the abundance of migrants east of the valley with those over the valley revealed that $t = 5.1$, which was significant at the 0.05 level with 22 df (2.07). The number of birds per mile west of the valley was significantly greater ($t = 10.5$) than the density over the Illinois valley. Therefore, nocturnal migrants were significantly more abundant on a gradient from east to west. It was also apparent that the

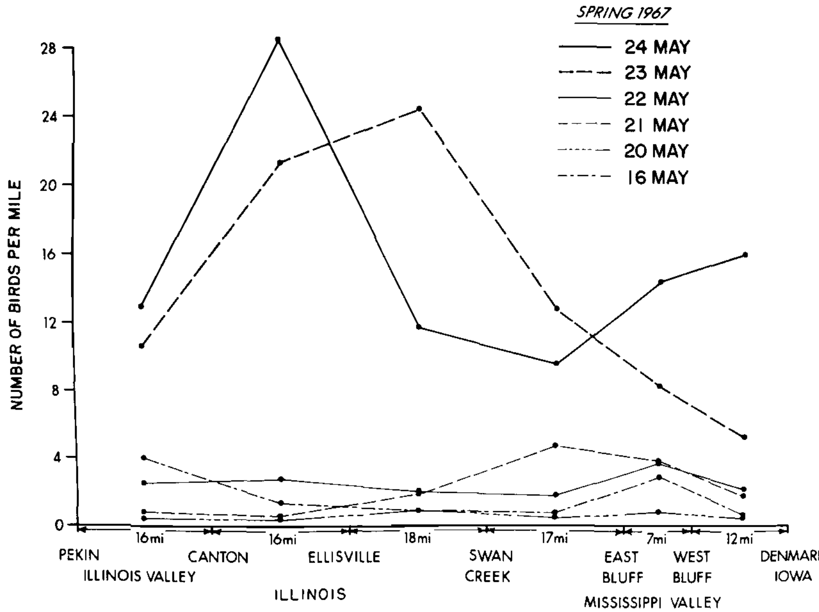

Figure 7. The geographic distribution of small birds across west-central Illinois at the 1,000-foot level on six nights, 16-24 May 1967.

flight of small nocturnal migrants was not concentrated along the channel of the Illinois River nor its 6-mile-wide valley.

Six surveys to determine the density distribution of nocturnal migrants across the west-central region of Illinois were flown 16–24 May 1967. At that period small bird migration is usually at its peak in this region. The flight course was at 1,000 feet AGL from near Pekin, Illinois, to Denmark, Iowa, and return, a round trip distance of 172 miles.

Figure 7 presents the results of these surveys. Four surveys, 16–22 May, found low densities of migrants aloft. Across the agricultural lands and small watersheds of western Illinois, the migrants were quite uniformly distributed. On 16 May and 22 May there was a two- to threefold increase over the Mississippi valley. On 21 May, the greatest density of migrants occurred in the region east of that valley. The night of 20 May, migrants were at a low density all across western Illinois. On 23–24 May, we found a tremendous influx of migrants with a five- to tenfold increase in numbers aloft over previous nights. Peak densities occurred over agricultural lands between the Illinois and Mississippi river valleys. Part of the decline in extreme western Illinois and eastern Iowa on 23 May was the result of a weather front, described later.

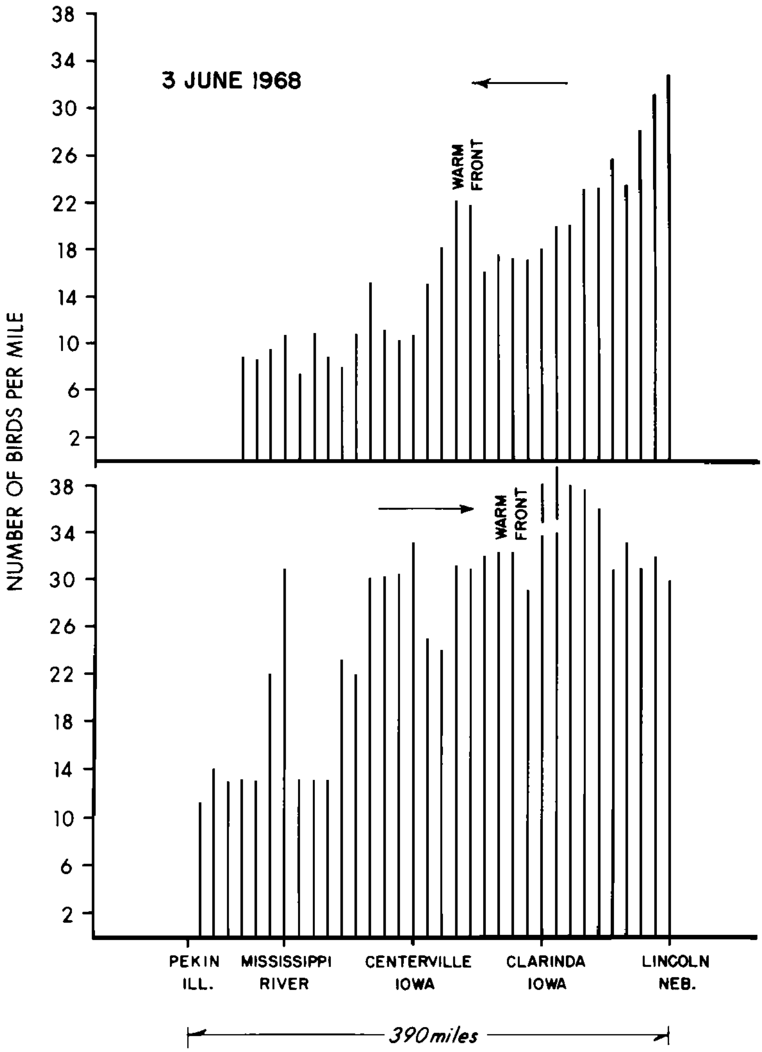

Figure 8. The geographic distribution of small birds east to west and west to east between Pekin, Illinois, and Lincoln, Nebraska, at the 1,000-foot level, the night of 3-4 June 1968. Time of departure from Pekin: 20:40; arrival at Lincoln: 23:50; departure from Lincoln: 00:05; and arrival at Pekin: 03:35.

A survey of nocturnal migrants across the Midwest from near Pekin, Illinois, to Lincoln, Nebraska, and return was undertaken on 3–4 June 1968. The flight course was about 390 miles one way and was conducted at 1,200 feet AGL. Sunset was 19:25 and departure was at 20:40. We

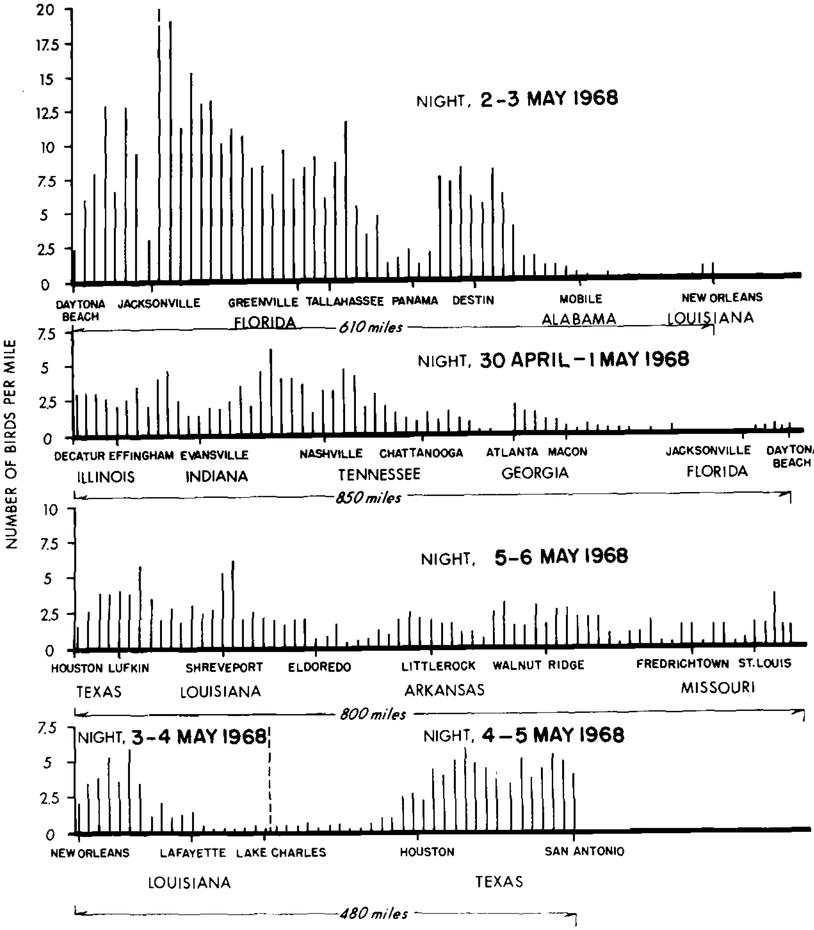

Figure 9. The geographic distribution of small birds at night from Pekin, Illinois, to Daytona Beach, Florida, 30 April-1 May 1968; from Daytona Beach to New Orleans, 2–3 May; from New Orleans to Lake Charles, Louisiana, 3–4 May; from Lake Charles to San Antonio, 4–5 May; and from Houston, Texas, to Pekin, Illinois, 5–6 May. Times of departure, local standard time, were: Pekin, 19:05; Daytona Beach, 21:20; New Orleans, 17:45; Lake Charles, 20:15; Houston, 19:20. Arrival times were: Daytona Beach, 04:50; New Orleans, 03:15; Lake Charles, 21:10; San Antonio, 23:45; Pekin, 02:50. The first night the altitude flown was about 1,500 feet AGL; all other nights the altitude was 2,000 feet AGL.

landed at Lincoln at 23:50, left there at 00:55, and arrived back at Pekin at 03:35.

The number of migrants encountered per mile every 11 miles is plotted in Figure 8. A tremendously large number of small birds were aloft, and

Figure 8 shows that migration was on a broad front; migrants abounded along the entire 390-mile transect. Birds were twice as abundant across Iowa as across western Illinois. Except for an upsurge of migrants at the Mississippi River valley on the westward flight, the abundance of migrants bore no relation to the courses of major rivers, the Illinois, the Iowa, or the Missouri. The fairly continuous decline in numbers of migrants on the return flight east from Lincoln, Nebraska, appears to be from birds dropping out of migration as the night waned. The flight ended about 55 minutes before sunrise, but even during the last 30 minutes of the survey the landscape was distinctly visible from the air, long before the sun appeared at the horizon.

Radar surveillance of small, nocturnal migrating birds has revealed that they usually reach peak numbers about midnight and gradually drop out of the air space between 01:00 and dawn (Hassler et al., 1963; Bellrose, 1967), indicating that the numbers of birds found aloft on nocturnal surveys of long duration are influenced by time as well as by geography.

Three extensive aerial surveys were conducted to explore the breadth and depth of small bird migration in eastern United States. One survey, extending 900 miles southeastward from Pekin, Illinois, to Daytona Beach, Florida, was made on the night of 30 April–1 May 1968. A second survey westward from Daytona Beach to San Antonio, Texas, 480 miles, was made on two nights, 3–4 May and 4–5 May. A third survey, 850 miles, north-northeastward from Houston, Texas, to Pekin, Illinois, was flown the night of 5–6 May.

The findings of these surveys are given in Figure 9. Each bar represents a horizontal distance of 10 to 12 miles, varying among graphs because air speed and ground speed were not always identical. Although we departed Pekin at 19:05, it was not dark enough to see migrants reflected in the light beams until 19:30 at Decatur. Our altitude was held to approximately 1,500 feet AGL. On all other nights our altitude was maintained at 2,000 feet AGL.

Only moderate numbers of migrants were aloft, varying from 1.2 to 4.7 per mile between Decatur, Illinois, and Evansville, Indiana. The lower density of birds found in the Evansville area suggested that the Wabash and Ohio rivers had no influence on the distribution of birds aloft. The density of migrants reached a peak, for reasons that are not apparent geographically, almost midway between Evansville and Nashville, Tennessee. As we approached the first ridge of the Appalachian Mountains, 30 miles northwest of Chattanooga, Tennessee, the density of birds aloft declined markedly; none were observed over the ridge proper. An increase in birds occurred in the valleys southeast of

Chattanooga, but they were absent from the air space above the ridges between there and Calhoun, Georgia.

Southeast of Atlanta, Georgia, the number of migrants aloft steadily declined. Very few were found between Macon, Georgia, and Jacksonville, Florida. We left Atlanta at 01:25 and arrived over Jacksonville, at 03:05.

On the night of 2–3 May, we left Daytona Beach, Florida, at 21:20 and flew north along the Atlantic Coast to Jacksonville. There we turned westward to Tallahassee, then west-southwestward to Panama City, where we followed the Gulf Coast to New Orleans, landing at 03:15.

A tremendous number of birds were aloft (Figure 9), especially just west of Jacksonville. The number of migrants remained large across the Florida peninsula to the panhandle, where a marked decrease occurred. Along a 75-mile stretch of the Gulf Coast centered by Destin, Florida, the density of migrants again increased. Farther west between Mobile, Alabama, and New Orleans we found very few birds. As we were flying either along the shore of the Gulf of Mexico or only a few miles inland, the sparsity of birds could not be attributed to an early morning descent.

We left New Orleans at 17:45, 3 May, and flew east to Gulfport, Mississippi, to see if any birds were coming in over the Gulf. We saw none during daylight hours, but upon returning to New Orleans we saw birds as soon as the landing lights projected a beam in the gathering dusk. Birds might have been flying from over the gulf during late afternoon; if so, we were unable to discern them against the blue sky. For about 60 miles west of New Orleans a moderate number of migrants were aloft, but west of the Mississippi River Delta numbers declined to about 1.2 birds per mile as far as Lafayette, Louisiana. From Lafayette to Lake Charles, Louisiana, we counted fewer than 0.5 birds per mile.

Because of low clouds and the approach of a severe thunderstorm, we stopped counting small birds at Lake Charles and aborted the trip at Beaumont, Texas, 21:35. The next night, 4–5 May, we surveyed the area between Lake Charles and San Antonio, Texas. Few birds were aloft between Lake Charles and Houston, but their numbers increased tenfold between Houston and San Antonio, Texas.

The flight from Houston to Pekin, Illinois, the night of 5–6 May, revealed about the same density of birds aloft as the initial flight leg to Florida. Small birds were migrating northward in a mass that extended 700 miles in depth from south to north. Only in a few areas were there any notable changes in density of migrants. An increase in density occurred over the Red River Valley at Shreveport, Louisiana, and a decrease occurred over the Ouachita River Valley, north of El Dorado, Arkansas. A slight increase in bird density occurred over the Angelina River northeast of Lufkin, Texas.

Our findings on the geographic distribution of nocturnal migrants represented two variables: geography and time. We planned to use U. S. Weather Bureau WSR-57 radar stations along the Gulf of Mexico to determine the temporal pattern at the time of our aerial surveys. Unfortunately, for various reasons the radar record for this period was inadequate for the purpose. We therefore had recourse to earlier records of the temporal pattern for WS7-57 radar stations at Daytona Beach, Tampa, and Apalachicola, Florida; Lake Charles, Louisiana; and Galveston and Brownsville, Texas. Radar surveillance of bird migration at these stations in April 1963–1965 showed an almost continuous flow of migrants around the clock, night and day, with birds crossing the Gulf of Mexico and adjacent land areas.

Peaks and valleys occurred in the hour-to-hour magnitude of passage. The hourly fluctuation was greater at the Florida stations than at the Lake Charles, Galveston, and Brownsville stations. Considering nocturnal hours only, the largest passage of migrants occurred at the following hours: Daytona Beach, 21:00 to 02:00; Tampa, 22:00 to 02:00; Apalachicola, 21:00 to 03:00; Lake Charles, 19:00 to 03:00; Galveston, 19:00 to 03:00; and Brownsville, 21:00 to 04:00.

Most of our surveys, in point of time (Figure 9), appeared to coincide with the time of the largest nocturnal passage of birds. An important exception was the low density of migrants found between Atlanta and Daytona Beach (02:25 to 04:50, 1 May 1968). The low density in this region appears attributable to the temporal pattern of migration rather than to geography. Variations on the transect along the Gulf of Mexico appear to be more the result of geography than of time.

EFFECT OF CERTAIN WEATHER CONDITIONS

Cold front.—We had the opportunity to determine the influence of a weak cold front on birds aloft on 23 May 1967. The effect of the front was measured by the number of birds aloft ahead of the front and behind it. The location of the front was apparent to us in the aircraft: the trip westward over west-central Illinois at 1,000 feet AGL was smooth until suddenly the plane began to pitch and roll in the turbulent air of the leading edge of the front. After about 10 miles the turbulence lessened, and it was apparent that we were behind the front. Radio contact with the FAA flight control station at Burlington, Iowa, revealed that the front reached there at 18:40. At 12:00 the weather map showed that the front trailed from a low pressure area in northeast Iowa, about 150 miles north of Burlington, that was moving south-southeastward at about 20 mph.

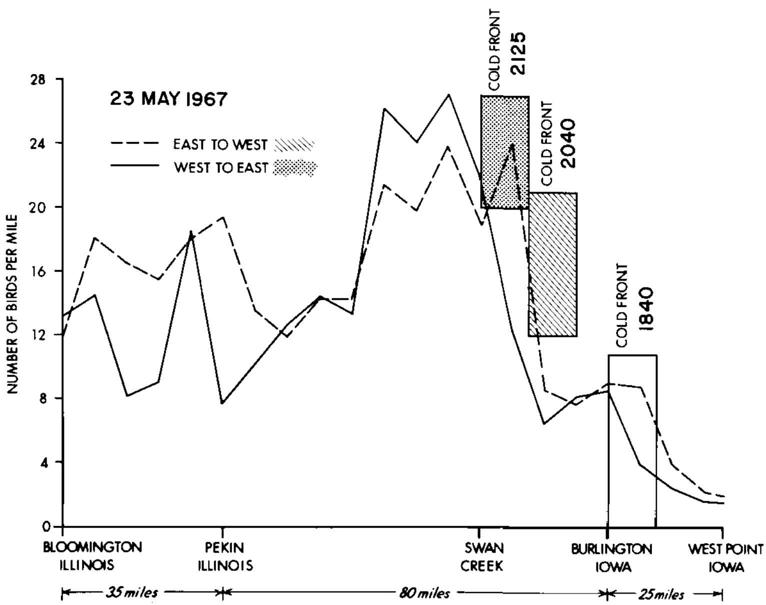

Figure 10. The geographic distribution of nocturnal bird migrants between Bloomington, Illinois, and West Point, Iowa, in relation to passage of a cold front 23 May 1967.

A wind shift usually determines the arrival of a weather front. At Burlington (18:40) the wind shifted from 210° at 8–10 knots to 360° at 8–10 knots. An hour later it was at 20° at 8 knots. At 18:00 the temperature was 81° F; at 19:00, 75° F; at 20:00, 73° F; at 21:00, 73° F; at 22:00, 72° F. This "cool" air mass was only a few degrees cooler than the air mass it was replacing. Because the cool air was wedging under the warm air, pushing it upwards, the outside thermometer in our aircraft actually rose 2° shortly after we entered the front.

Immediately upon arriving at the weather front we noticed a sharp decrease in the abundance of birds (Figure 10). A reduced number of migrants continued as far west as West Point, Iowa, where we turned around and headed eastward. In the 45 minutes during our absence the cold front had moved 11 miles eastward. A reduction in the abundance of migrants also extended a comparable distance eastward. On four of the other five surveys over this area of the Mississippi Valley, we had found an increase in the abundance of nocturnal migrants (Figure 7); on the one exceptional night (21 May), we found only a slight decline in migrants.

The change in abundance of nocturnal migrants aloft was evidently directly related to the weather front because a great decrease in migrants occurred in a region where decrease was unlikely to be due to the terrain. The change started simultaneously with the leading edge of the cold front, and the decline in migrants shifted eastward concomitant with the leading edge of the front. The turbulent air at the leading edge was not likely to be responsible for the change in abundance of migrants, because the turbulence lessened 10 miles behind the leading edge, with a continued decline in the number of birds aloft.

Of the weather factors associated with the front, only the shift in wind direction appeared important. The 6-degree drop in temperature at ground level appears inconsequential, especially as the temperature above the ground actually increased. Barometric pressure changed very slightly: 29.83 to 29.80 to 29.83. Skies were clear throughout the survey.

Warm front.—We passed through a weak warm front on our survey flight from Pekin, Illinois, to Lincoln, Nebraska, the night of 3 June 1967. The front was between Centerville and Clarinda, Iowa, moving eastward. Its weakness was apparent in the slight turbulence we encountered at its leading edge. On our outbound survey, the abundance of birds increased immediately behind the front (Figure 8). On the inbound survey, density of migrants increased concomitant with the leading edge of the front. These changes in bird abundance were so slight as to suggest that this weak front had only a slight effect on the numbers aloft and, possibly, the distribution observed was a matter of chance.

Air turbulence.—We noted some evidence that small nocturnal migrants were prone to fly in the turbulent strata of the air mass rather than in the smooth strata. On 6 May 1965, when we were first exploring the use of aircraft to make observations at night, small birds were found in turbulent air below 2,800 feet AGL but none above 2,800 feet in smooth air. A temperature inversion that night resulted in a ceiling of ground haze and turbulent air at 2,800 feet.

Severely turbulent air extended up to 1,000 feet AGL on the night of 4 May 1966. Moderately turbulent air prevailed from 1,000 to 4,000 feet, and smooth air occurred above that level. Nocturnal migrants were distributed as follows: 44 per cent from ground level to 1,000 feet; 55 per cent from 1,000 to 3,900 feet; 1 per cent at 4,000 feet and above. The following night, 5 May, moderately turbulent air occurred from ground level to 1,500 feet. Of the 57 migrants found aloft, with smooth air above that level, 56 of them were in the stratum of turbulent air.

On 10 May 1966, moderately turbulent air occurred up to 1,500 feet AGL, light turbulence up to 2,000 feet, and no appreciable turbulence above that level. We found 40 migrants in the moderately turbulent air, 6 in the lightly turbulent, and none in three levels, 2,250–2,750 feet, sampled in the smooth air stratum.

Richard R. Graber found nocturnal migrants in turbulent air below a temperature inversion while viewing bird targets on airborne radar the night of 17 September 1962. The temperature inversion was at about 2,600 feet AGL; multitudes of bird targets occurred between 1,100 and 1,600 feet. None were found in the smooth air above the temperature inversion. On these nights, when turbulent air was restricted to definite strata, migrants occurred at lower altitudes than customary (Figures 2–5). Even though smooth air strata occurred at altitudes well within their normal zone of flight, few migrants were encountered in smooth air.

The distribution of small birds in the turbulent air strata at night is contrary to two of the author's experiences with migrating ducks during the daytime. On both occasions flocks of migrating ducks were in calm air just a few feet above a haze layer that marked the boundary between turbulent and calm air strata. Each day all duck flocks were close to the same altitude, 1,550 feet (25 October 1961) and 2,500 feet AGL (3 March 1967).

Precipitation.—We flew several nights when light rain fell at least part of the time during the survey flights. On 22 April 1966 we encountered about 0.2 migrant per mile until light rain began at 21:40, after which we saw none. We recorded only two migrants in 100 miles of flying through intermittent rain on the night of 26 April.

The only survey on which no birds were recorded was on the night of 12 May 1966. A solid overcast covered the sky, with a cloud base only 500–800 feet AGL. Haze restricted visibility to 5 miles. Surface winds were light and variable; light rain was intermittent. Transects at 350 and 500 feet AGL, Pekin to Canton, revealed no migrants.

Grouping of Birds

We concluded from our observations of nocturnal migrants in the air space that small birds migrate both singly and in groups. Birds judged to be singles were encountered from 2 seconds to several minutes apart. Birds considered to be grouped consisted of those that passed the aircraft almost simultaneously. At our cruising speed we covered 176 feet per second, so those appearing at intervals longer than 2 seconds were unlikely to be associated with each other.

Single birds appeared to predominate in the air space when the volume of migration was light. When the volume of migration ranged from moderate to heavy, groups of birds predominated. We would see a number of birds almost simultaneously, followed by an interval of from several seconds to several minutes before another flurry of birds passed. We had the impression that most small birds migrating at night were not in compact flocks, but were in loose aggregations that might be termed "cells."

DISCUSSION

The activity of nocturnal bird migrants in the air space has been previously studied with four techniques: watching their passage across the face of the full moon, recording bird targets on the radarscope, tracking individual birds by radiotelemetry, and watching passage through a light beamed vertically from the ground. Each method has certain advantages, but unfortunately no one method provides all the information desired on the behavior of nocturnal migrants in the air space. Leaving aside species identification, which all techniques but radiotelemetry fail to provide, we appraise some of the shortcomings of each method as follows:

1. Moon watching is limited to largely cloudless skies when the moon is nearly full. The zone of observation is small, and constantly changes in area as the earth rotates. It provides no information on the altitude of bird migrants, and the direction of migration can be only approximated.

2. Because of beam shape, inclination, and/or ground return echoes, few radars record bird targets near the ground. The space between the earth and the acquisition of bird targets is usually about 1,000 feet, but may vary from a few hundred to 2,000 feet.

It is difficult to assess the number of individual birds in each target on a radarscope. Only the most sophisticated radar, such as that operated by NASA on Wallop's Island, is capable of differentiating individual birds in the air space. A bird target on most radarscopes may consist of one large bird or a number of small birds at the same signal strength, and large flocks of ducks or geese create only a single blip, although the signal is stronger. Hence it is impossible to determine accurately the number of individual birds in a blip on a radarscope. Most often a blip represents an aggregation of birds (Eastwood, 1967: 243).

At times temperature inversions cause the radar beam to bend downward (ducting) and either greatly complicate the identification of bird targets or obscure them completely. At some radar stations, temperature inversion makes it impossible to compare the magnitude of migration over a long sequence of nights.

3. Tracking the flight of a migrant by a tiny radio transmitter is both expensive and time consuming. A single bird must be followed by aircraft or ground vehicle with a radio receiver. If the bird passes beyond the 25-mile range of the radio receiver, its signal is usually lost. Also the effect of the radio transmitter upon the normal behavior of the migrant is unknown. Because of variability in individual behavior and in

environmental conditions, many individuals must be tracked before sufficient knowledge is acquired to permit meaningful deductions.

4. A vertical light beam for studying nocturnal birds was first used by Graber and Hassler (1962). This technique was improved and amplified by Gauthreaux (1969), who built a portable ceilometer in which birds were visible up to 1,000 feet and, occasionally, up to 2,100 feet AGL. Because the narrow beam of the light provides only a small observation area, altitude of the migrant is difficult or impossible to determine, and migration at altitudes above the effective beam height is overlooked. However it is an inexpensive technique and provides a means of surveillance of low level migration usually missed by radar.

Our method of studying bird migration also has its deficiencies. The two greatest weaknesses are: (1) lack of knowledge of direction of flight; (2) and lack of identification of species in passage, which can be classed only according to approximate size.

Astral Cues

The abundance and vertical and horizontal distribution of nocturnal bird migrants provide important information for evaluating the complexity of cues birds use in orientation-navigation. Numerous experiments (Bellrose, 1958; Sauer and Sauer, 1960; Matthews, 1961; Hamilton, 1962; Mewaldt et al., 1964; Emlen, 1967) demonsrate that birds are able to use star patterns at night to determine direction.

Our observations from an aircraft at night showed numbers of small birds aloft under overcast skies when the stars and/or moon could not be seen. We viewed the sky constantly for breaks in the cloud cover, and hourly observations by meteorologists 20 miles away at the U. S. Weather Bureau station, Peoria, Illinois, confirmed our classification of sky conditions.

Radar surveillance made concurrent with the aerial surveys on several overcast nights showed that direction of migration was oriented. Our radar findings in previous years revealed that migrants were directionally oriented almost as well under overcast skies as under clear skies (Bellrose and Graber, 1963; Bellrose, 1967). Yet we find increasing evidence that skies displaying star patterns are advantageous to small migrating birds. During the present study we counted more birds aloft on our aerial surveys when skies were partly or entirely clear than when they were overcast. Our previous radar findings (Bellrose, 1967) showed comparable numbers of bird targets under clear and under overcast skies in the springs of 1962 and 1963, but markedly fewer migrants were aloft under overcast skies in the falls of those years.

More detailed analysis may show that seasonal and yearly differences in the magnitude of migration under overcast skies depend upon the urgency to migrate. When migration is long delayed (as frequently happens in the spring with precipitation, unseasonably low temperatures, and adverse winds), birds appear more likely to depart when adverse conditions diminish. When no prolonged holdup occurs, small birds apparently prefer to migrate at night under clear skies rather than under overcast skies, suggesting that the birds find it advantageous to view a sky entirely or partly clear of clouds. On the other hand, the inability of birds to see the sky does not preclude their migrating in an oriented fashion. I deduce from this behavior of nocturnal migrants that astral cues are advantageous but not essential for oriented migration. The resulting corollary is that when migrants cannot use astral cues they are forced to rely on some other cue or cues, which are either more difficult to utilize or less reliable.

Landscape Cues

Landscape is one seemingly ubiquitous cue available to nocturnal migrants. From my several hundred hours in the air viewing the landscape under various sky conditions I conclude: (1) Overcast skies at night make for a very indistinct landscape. (2) A moon between half and full under clear skies illuminates the landscape so that all but the smaller details are readily visible. (3) On clear moonless nights the landscape is indistinct except early in the night (when afterglow persists) and for an hour or more prior to sunrise. (4) Landscape features visible from 100 to several hundred feet on even the darkest nights are the boundaries between land and water and ranges of hills or ridges of mountains. (5) The lower the altitude, the more distinct the landscape, especially on dark nights.

On the darkest nights that we flew, from directly overhead I could distinguish the Illinois, Mississippi, and Ohio rivers readily from 500 feet, with difficulty at 1,000 feet, and not at all from 1,500 feet. On the other hand, the shoreline of the Atlantic Ocean and of the Gulf of Mexico was clearly visible from 2,000 feet on dark nights by the waves breaking against the land.

Available evidence suggests that birds not specialized for nocturnal feeding (such as are goatsuckers and owls) cannot see objects at night any better than humans can. Adler (1963) concluded on the basis of his experiments and those of other workers: "robins, starlings, and pigeons must find the world at night much darker than it seems to us." If most nocturnal migrants cannot see the landscape at night any better than humans can, then their recognition of landscape features at night is similarly indistinct.

On our cross-country flying at night, I could find little, if any, evidence to suggest that migrating birds were using large rivers as guide lines. As discussed previously, in the vicinity of the Illinois River valley the highest density of migrants in the spring consistently occurred west of the valley. This distribution of migrants early in the night appears related to the distribution of woodlands in this region. If birds departed north to northeast from wooded areas (as shown by radar; Bellrose and Graber, 1963), then we would expect to find the largest numbers of migrants where indeed we did find them. In this area, the Illinois River valley runs south-southwestward.

Increased density of migrants over and east of the Mississippi River valley appears to be associated with the distribution of woodlands from which the migrants had recently departed. The number of migrants actually declined over and adjacent to the river channel. The exceedingly large numbers of nocturnal migrants found between Canton and Swan Creek, Illinois, on the nights of 23 and 24 May (Figure 6) appear attributable to birds departing from woods along the Spoon River and its tributaries, which lie between the Illinois and Mississippi valleys.

Possibly migrants we observed the night of 30 April (Figure 8) were using the ridges of the Appalachian Mountains as landscape cues. On this rather dark night, the ridge tops were visible against the sky from altitudes slightly lower than the ridge tops. The fact that we found migrants only over the mountain valleys, where the ridges were visible, rather than over the actual ridges, which were invisible looking earthward, might account for this singular distribution.

Early radar surveillance indicated (Bellrose, 1967) that at night small birds did not show an affinity for, nor alter their flight course because of, the Illinois, Mississippi, and Ohio rivers. However, along the Gulf of Mexico the course of flight was noted to change occasionally when nocturnal migrants over the water came near land.

On the night of 22 March 1969, when I was watching the northward passage of ducks and geese on FAA long-range radar at North Aurora, Illinois, I saw flocks of Canada Geese change flight direction from due north to east and northeast upon approaching the shore of Lake Michigan north of Chicago. The targets of Canada Geese could be identified by their large size on the scope (as large as airliners) and ground speed (60 mph). The geese were known to have left southeastern Illinois that day. They apparently flew straight north until Lake Michigan was visible, then abruptly changed direction to fly out over the lake toward Michigan (Flock and Bellrose, 1970).

Lowery and Newman (1966) considered that the Mississippi River and its tributaries had only a slight influence, if any, on the direction and distribution of nocturnal migrants. They found no clear relationship of mountain ranges to direction of passage, but they did find that the Gulf Coast influenced the course taken by part of the migrants.

In this study we found migrants flying only slightly lower under overcast skies than under clear skies, but we did not search in or above the clouds. Our radar studies in 1960 (Bellrose and Graber, 1963) showed that migrants flew higher under overcast than under clear skies, but in 1962 (Bellrose, 1967) we found no significant difference between overcast and clear skies, and in 1963 migrants were at lower altitudes under overcast than under clear skies. Eastwood and Rider (1965) determined, with height-finding radar in England, that the median altitude of migrants on cloudy nights was 2,000 feet and on clear nights 1,700 feet.

If landscape were essential or even desirable for navigation at night, birds would need to fly at low altitudes on dark nights when the landscape is indistinct. Details of landscape that can not be seen at high altitudes are revealed at low altitudes. Usually the landscape is less distinct under solid overcast skies than under clear skies. Yet we find that under overcast skies nocturnal migrants fly at altitudes similar to or higher than those utilized under clear skies. Both geographic and altitudinal distributions of small bird migrants at night imply that landscape is not essential to their "in course" navigation, but even on dark nights landmarks would be visible to departing migrants in the evening and again upon their descent near dawn.

Birds in circular cages are known to use minute irregularities as references to determine direction (Matthews, 1968: 23). Since birds in cages can base direction of movement on their physical surroundings, it is likely that birds in the wild can employ landmarks for directional selection at the start of a night's flight under overcast skies. How nocturnal migrants are able to maintain a course when they lack both astral and landscape cues is more difficult to fathom.

WIND CUES

Radar observations of migrating birds in relation to wind direction and speed reveal that birds affect an advantageous behavior response to this element (Bellrose, 1967), suggesting that birds are capable of using the wind to maintain direction. The turbulent structure of the wind has characteristics that birds could employ to determine their position in the air relative to the earth.

The advantage of the gust-structure of the wind for orientation purposes may be the reason that we found nocturnal migrants concentrated fall, was 2.9 per mile at the 1,000-foot level. We found 3.1 birds per in the layers of turbulent rather than calm air. In a recent paper Griffin (1969) thoroughly reviews the nature of air currents and their possible application to bird navigation. As to the relative value of turbulent versus stable air for migrants, Griffin states: "Perhaps the advantageous feature from the bird's viewpoint [of orientation] is the inversion and resulting shear waves, rather than the stability."

The ability of birds while airborne to diagnose wind change is implied by their descent with the arrival of a cold front (Figure 9) on 23 May 1967.

Several recent investigators (Brooks, 1965; Richardson, 1966; Curtis, 1969) have found a correlation between favorable wind and magnitude of migration. On the other hand, Nisbet and Drury (1968) found a spurious correlation between migrant density and tail winds.

We consistently find more birds aloft in the Midwest with following winds. In this study we found slightly over twice as many birds aloft with following as with adverse winds. Our radar findings (Bellrose, 1967) also showed that the numbers of migrants aloft were much greater with following winds than with adverse winds.

The Influence of Physiography

One survey along the coast of the Gulf of Mexico is obviously too limited to enable us to draw any firm conclusions, but it does show that small birds migrate across the gulf over its entire length. The tremendous numbers migrating up the east side of the Florida peninsula indicate that the Lesser and Greater Antilles and Bahama Islands form an important "land bridge" for migrants between Venezuela and the United States. The upsurge in migrants in the Destin, Florida, area may have occurred as a result of migrants leaving the western end of Cuba.

The increase in density of migrants in the New Orleans area appears to represent birds migrating across the gulf from the Yucatan peninsula. The increase in density of migrants from Houston to San Antonio probably represented migrants that moved northward along the east coast of Mexico. Chance alone does not seem sufficient to account for the decreased abundance of migrants along the Gulf Coast opposite the Yucatan Channel and Gulf of Campeche. Birds leaving Central America south of these bodies of water would have had much longer overwater flights. Hence cursory evidence suggests that most intercontinental migrants use land areas either to bridge or to circumvent the Gulf of Mexico.

Altitude of Migration

The altitudes at which we observed nocturnal migrants from an airplane are generally lower than those reported from radar surveillance (Lack, 1960; Nisbet, 1963; Eastwood and Rider, 1965). All agree that few passerine birds migrate above 5,000 feet AGL. Nisbet (1963) believed that few birds migrate at night below 600 feet, but we found large numbers of migrants at 500 feet, and, in the spring of 1966, almost as many at 350 feet AGL as at 500 feet (Figure 2).

A partial explanation for these differences lies in the fact that Nisbet (1963) found migrants 10 per cent lower 1–2 hours after sunset than 2 hours later. As most of our surveys were made 1–2 hours after sunset, many of the birds we saw may not have reached their peak altitude for the night, but our survey on 27–28 May 1970 showed only a slight increase in altitude later at night. Even with a 10 per cent increase in altitude, the bulk of migrants over Illinois were at lower altitudes than shown by radar in Massachusetts (Nisbet, 1963) and in England (Eastwood and Rider, 1965).

ACKNOWLEGMENTS

I am grateful to James Waddell for donating his services as pilot and to William Mailey for donating his services as observer in our flights. My wife, Esther, often served as recorder. Eugene A. Mueller and Arthur L. Sims of the State Water Survey aided in interpreting weather data. Glen C. Sanderson, Richard R. Graber, William W. Cochran, Jr., and Owen F. Glissendorf of the Illinois Natural History Survey made helpful suggestions on improving the manuscript. Richard Sheets prepared the graphs and William Zehr took the photograph. The National Science Foundation provided financial support for the radar studies.

SUMMARY

1. A small aircraft with added landing lights was used as a platform in the sky from which to enumerate small birds migrating at night.

2. To determine the distribution of small birds in the air space, two types of transects were made—altitudinal and geographic. In the fall of 1965, the altitudinal intervals were 500 feet AGL; in the spring of 1966, a transect at 350 feet and one at 750 feet AGL were added to the 500-foot intervals. The surveys began about one hour after sunset.

3. We found little difference between the altitudinal distribution of migrants on spring and fall transects. In the spring, 50 per cent of the birds between ground level and 5,000 feet occurred at the 500- and 1,000-foot levels; in the fall, 48 per cent of the birds were found at those levels. Except on the night of 2 June 1967, we saw few small migrants at 5,000 feet or above.

4. The altitudinal distribution of small nocturnal migrants under clear and under overcast skies was similar: 48 per cent of the migrants under clear skies occurred at the 500- and 1,000-foot levels; 51 per cent occurred at those levels under overcast skies.

5. The average number of migrants under clear skies, both spring and

mile under overcast skies, but we saw an unusually large number on only one night, 7 October 1965.

6. We made four surveys on the night of 27–28 May 1970 between Pekin and Canton, Illinois. Migrants increased slightly in altitude from shortly after dark to midnight with a decline in altitude shortly after midnight and a further decline prior to dawn.

7. Slightly over twice as many birds were aloft when winds were favorable at departure than when they were adverse, but there was no significant change in altitudinal distribution with wind conditions.

8. The density of migrants aloft increased from east to west from 4 miles east of the Illinois River valley to 6 miles west of the valley. Even though the axis of the valley coincides with the direction of migration, there was no indication that the volume of migration increased along the Illinois River or its valley as if it were used for guidance.

9. Several extensive surveys in the Midwest showed small birds moving on a broad front, which early in the evening appeared more related to the distribution of woodlands than to watercourses. One front of migrants extended at least 390 miles between Pekin, Illinois, and Lincoln, Nebraska.

10. An in-depth survey of spring migrants aloft was made between Pekin, Illinois, and Daytona Beach, Florida, and between Houston, Texas, and Pekin. A moderate number of migrants were found aloft for 585 miles, Pekin to Macon, Georgia, and for 800 miles, Houston to Springfield, Illinois.

11. A survey along the coast of the Gulf of Mexico revealed the largest number of migrants across the Florida peninsula, followed by a decline, with an upsurge in density near Destin, Florida, followed by a decline, with another upsurge at New Orleans, followed by a decline, and another upsurge in density of migrants between Houston and San Antonio, Texas. Further surveys are needed to determine if it was coincidental that the largest density of migrants occurred where "land bridges" circumvented or crossed the Gulf of Mexico.

12. A weak cold front, characterized more by a wind switch than a temperature change, resulted in a sharp decline in small birds aloft. While airborne at night, migrants appeared able to detect the change in wind direction.

13. On several nights when turbulent and smooth air were in well-defined strata, we were surprised to find most birds in the turbulent air strata even though smooth air prevailed at altitudes well within their range of flight.

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