Nocturnal Bird Migration in Opaque Clouds

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It is generally recognized that birds can maintain directional orientation by means of the Sun or stars (ref. 1). But recent radar observations have demonstrated that much migration occurs under overcast skies (ref. 2). Therefore, it is of primary importance for theories of bird navigation to inquire whether birds that migrate on cloudy nights fly above, below, within, or between layers of cloud, and whether the clouds are thick enough to conceal the sky, the ground, or both. If birds do fly within or between cloud layers, how long do they remain cut off from sight of sky or ground, and how does their orientation compare with that displayed on clear nights? Evidence for migratory orientation within cloud layers has been presented by Bellrose and Graber (ref. 3), although flight directions of birds that appeared to be in clouds were distinctly more variable than on clear nights. The radar used in these studies recorded only intermittent positions during short segments of any one flight path, so that straightness and levelness of flight could be estimated only very roughly. Eastwood and Rider (ref. 4) also reported instances in which migrating birds were flying at night within a thick layer of clouds, but they do not report any flight directions under these conditions nor whether the birds were flying level, climbing, or descending.

In hopes of clarifying the degree to which migrants maintain oriented flight in or between clouds, I have employed a tracking radar to measure as accurately as possible the flight paths of migrating birds on nights with opaque stratus clouds at low altitudes. Many colleagues provided indispensable collaboration in essential phases of this work. On three nights during the spring of 1970 when fog and low stratus clouds were present continuously over a broad area, we observed numerous birds flying in appropriate directions for distances up to 3 or 4 km. A special effort was made to analyze all available meteorological data concerning the vertical and horizontal extent of the cloud layers. Local wind velocities were measured when feasible by tracking a balloon with the same radar as it rose through the range of altitudes where birds were observed. The combined evidence strongly supports the conclusion of Bellrose and Graber that birds sometimes migrate in appropriate directions inside opaque clouds.

METHODS

The Radar

The most suitable radar we were able to obtain was a military surplus 3 cm (X band) type AN/GPG-1 unit, otherwise known as a
T-9 tracker from the “Skysweeper” antiaircraft system. It is basically similar to the radar used by Gehring and Bruderer and Joss (refs. 5 and 6). A tracking radar contains the important feature that electronic circuits automatically keep the beam aimed at a given target once the radar is “locked on” to it. Thus the whole track can be measured quite accurately as long as the autotracking circuits are locked on to a given bird or flock.

Radars such as these do not yield pronounced echoes from clouds consisting of small water droplets, although clouds with large droplets or active precipitation are clearly revealed (ref. 7). Hence our radar could track birds through several hundred meters of stratus cloud. We mounted this instrument on a trailer, so that it could be moved to any location accessible to automobiles. Power was supplied from a gasoline-engine driven generator when line power was not available. The nominal peak power output of this radar was 40 kilowatts; its pulse width was 0.25 µsec; and the pulse repetition rate was approximately 3800/sec. The antenna was only 75 cm in diameter which yielded a nominal beam width of 3′, but the autotracking circuits were designed to track with an accuracy of approximately ±0.03′, and in practice this degree of accuracy was apparently achieved. The range dial could be read to within ±3 m, so that in theory a bird at 1000 m slant range (range along the radar beam) could be located within a very few meters. Since ground clutter made it very difficult to calibrate the radar with fixed targets at known positions, the best evidence of the accuracy was obtained from the straightness of the straightest tracks recorded. Instrumental errors or random inaccuracies would be most unlikely to convert an irregular flight path into an apparently straight one. A typical example from the longest and straightest tracks (2134, April 30, 1970) covered a total distance of 3400 m in 144 sec. During this period of tracking the azimuth values shifted gradually from 204° to 055° (North = 000°); the elevation rose from 33° to 68° and then fell to 25° as the bird passed nearly overhead; while the slant range decreased from 1968 to 1144 m and increased again to 2248 m. The altitude of the bird varied between 1025 and 1065 m. Throughout this track all positions recorded by the methods described below fell within 40 m horizontally and vertically of a straight line. The departures from such a line were not random, as can be observed in several of the figures discussed below, so that it seems likely that we were continuously measuring the positions of many birds with an accuracy of ±5 or 10 m.

In the actual operation of this tracking radar, bird echoes could be observed either on a small (7.5 cm diameter) PPI screen or on an A-scope display as the azimuth and elevation controls were operated manually to scan the sky. When appropriate manipulation of the controls caused the radar to lock-on to a bird or other target, the bird's elevation, azimuth, and range could be read from dials. But it was impossible to take full advantage of the information provided by the radar without recording the position of each bird as accurately and continuously as feasible. Slight modifications were therefore made to generate dc voltages proportional to azimuth, elevation, and range. These dc voltages in turn were converted into frequencies from approximately 600 to 6000 Hz that could conveniently be recorded on three channels of a four-channel tape recorder (Precision Instruments model 6100). The fourth channel was used to record voice notes or other signals. Each frequency could be reconverted with the aid of calibration data into azimuth, elevation, and slant range, by use of an electronic counter or frequency meter. The resulting values could then be converted by
simple trigometric calculations into the bird's position. But an accurate and continuous record clearly called for computer data reduction. The tape-recorded analog frequency data were read into a Linc 8 computer which used 1-sec sampling intervals to count the number of cycles per second. An output tape was then prepared with a digital number tabulation for each second of the azimuth, elevation, and range frequencies as played back from the tape recorder. This tape was then utilized in conjunction with a Fortran program prepared by D. K. Riker for processing by the CDC 160G computer at The Rockefeller University Computer Center.

The final output from the computer consisted of a print-out and a graphic plot. The former provided once per second the following quantities in numerical form:

1. The three original frequencies as played back from the tape recorder
2. The corresponding values of azimuth, elevation, and slant range
3. The X, Y, and Z coordinates of the bird (X = East-West, Y = North-South, Z = altitude relative to the radar)
4. The horizontal and vertical distance that the bird had moved between each successive pair of readings

The graphic plot displayed the bird's XY position and separately its altitude as a function of distance traveled over the ground. The XY graphic plots were superimposed on topographic maps photographically enlarged to the same scale, to display any correlations between flight path and topography.

It was not possible to maintain continuous tracking of all bird targets that could be observed on the PPI or A-scopes. Consequently only cases where such tracking was maintained for at least 30 seconds without evident discontinuities are considered below (except as noted for a few tracks on May 16-17, 1970). This means that we gathered significant data only from reasonably steady targets. Since the tracking circuits were designed to keep the radar aimed at the strongest target falling within its beam, it would sometimes shift from one bird or flock to another. Such cases were excluded from consideration unless each portion of the track, considered separately, was of adequate length to be of interest.

The longest bird tracks we were able to record continuously were about 5 km. The lowest elevation at which birds could be reliably tracked despite radar echoes from the ground was ordinarily about 10°, although at one location on a ridge, tracking did prove possible down to elevations of 0°, which represented a clear view out into adjacent valleys. The maximum range at which most bird targets could be maintained in the autotracking mode of the radar varied between 2000 and 2500 m. Many birds were lost at shorter ranges for unknown reasons, and an occasional bird target, presumably a very large bird or a dense flock, could be tracked to 3500 m or more. The data presented in this paper are not at all a random sample of birds migrating over the location of our radar. For example, we did not make sustained efforts to search for birds at the highest possible altitudes, since we were primarily interested in obtaining tracks as long as possible, but some birds were tracked as high as 2000 m above the radar. In spring we usually searched for birds with the radar beam pointed roughly south or southwest and at elevations between 20° and 35°, because this facilitated the recording of long tracks as birds approached, passed nearly overhead, and receded to the north or northeast. For tracking we selected primarily birds that were picked up at nearly maximum range and high enough to avoid ground echoes. On the other hand there were often times when no birds could be detected by this procedure, and we then searched in
other directions and at other elevations of the beam. Our procedure tended to exclude birds flying both at the lowest and the highest altitudes. Hence the tracks described here tended to be those of birds or flocks passing fairly close over our radar in the customary direction of spring migration.

Artificial targets, approximate spheres formed from aluminum foil suspended about 0.5 m below meteorological pilot balloons, could also be followed to about the same distances. These metal targets ranged in diameter from about 10 to 30 cm, and one might at first suppose that they would be detectable at much greater distances than birds. But as discussed by Eastwood (ref. 8) and Bruderer and Joss (ref. 6), water reflects 3 cm microwaves more than half as strongly as a metal sphere of the same size. Since the range at which a given radar system can detect a target varies as the fourth root of the target strength, this difference becomes trivial in comparison to the other variables involved in tracking birds by radar. Likewise variations in ground return and fluctuations in echo amplitude from both birds and metallic targets allowed only rough comparison of tracking ranges. But it does seem clear that our artificial targets were tracked to approximately the same distances as birds.

On several occasions we tracked birds in daylight. With $7 \times 50$ binoculars mounted on the antenna supports and aligned with the radar beam, we could see the bird in question if it was the size of a crow or larger. Crows, turkey vultures, and buteos were tracked in this manner to distances of about 1000 m. In daytime the radar would often track what seemed to be small birds, moving somewhat more slowly than the hawks, but these would often not be visible with the binoculars even when within 400 m range. This was partly due to the vibration caused by the autotracking mechanism. While we could not distinguish single birds from flocks with any great confidence, ornithologists experienced in observing migrants visually against the full Moon have the impression that most fly singly or in relatively dispersed flocks (ref. 9). Most of the radar targets we believe to have been birds had fluctuations of the echo amplitude similar to those described by Bruderer (ref. 10) and Bruderer and Joss (ref. 6). These became recognizable with experience and matched the fluctuation patterns when visible birds were tracked in daytime. This criterion is subjective and imprecise by itself (ref. 11), but we found it persuasive in practice. All targets discussed in this paper moved at groundspeeds appropriate for birds, and the times when they were most abundant were appropriate for spring migrants. All tracks were included in the analyses, provided that they were of sufficient length and free from various artifacts discussed below. When feasible, airspeeds were estimated from wind velocities determined by tracking a balloon at the same location. When we did not obtain local balloon tracks, we were obliged to use the radiosonde data discussed below. In most of the former cases airspeeds were clearly appropriate for birds, and unlikely for any other known types of targets such as insects or wind blown material. A complication arises, however, in cases discussed in a separate section of this paper in which birds appear to have spent considerable periods of time in almost stationary flight.

The arrangements for recording range and azimuth sometimes produced artifacts. The potentiometers generating the dc voltages proportional to range and azimuth were attached to shafts that rotated once for each 1000-yd (944-m) interval of range and once per revolution of the radar in azimuth. Consequently the frequencies necessarily shifted from minimum to maximum or vice versa when a bird passed through switch-over val-
ues of range or azimuth. Occasionally a bird was so uncooperative as to remain for several seconds close to a switch-over point or even move back and forth across it. Since the computer counted the total number of waves within each 1 sec interval, each such crossing yielded intermediate values corresponding to erroneous positions of the bird. Such artifacts could readily be eliminated, with only small resulting gaps in the plotted tracks. Such gaps are shown in the figures with broken lines. It was also necessary to note in which 944-m range interval each bird was acquired by the radar. The computer program was then able to apply appropriate corrections when the range frequency passed either upward or downward across a switch-over point.

Many of the tracks recorded by our radar system were remarkably straight, but others showed various sorts of curvature, and a few involved many shifts in direction at close intervals. After considering several methods of expressing the degree of departure from a perfectly straight line, the following two were selected as most helpful for present purposes: (1) a simple straightness index, and (2) the groundspeed ratio, or ratio of net to total distance travelled. The straightness index employed was the length/width ratio of the smallest rectangle that included all bird positions on the XY plot except those that were clearly due to artifacts. This is a conservative criterion, since the straightness index is lowered substantially by either a gradual curve or by one questionable point well off the straight line that best fits the great majority of the points. The groundspeed ratio was the straight line distance between beginning and end of the track divided by the total of the XY distances shown in the print-out for all the 1-sec intervals between bird positions calculated by the computer. Here too we excluded clearly erroneous points where range or azimuth frequencies passed through crossover points. The highest observed straightness indices were greater than 100, and the groundspeed ratio was often 0.98 or 0.99. This shows that radar artifacts did not add appreciably to the recorded length of the flight path.

Location of Radar Observations

Although a number of locations were utilized for preliminary observations, only two will be considered here: (1) The Bronx Zoological Park in the northern part of New York City (73° 52' W. Long., 40° 52' N. Lat.), close to the Bronx River and at an elevation of approximately 15 meters above sea level; and (2) Ice Caves Mountain, approximately 5 km southwest of Ellenville, N.Y. (74° 21' W. Long., 41° 42' N. Lat.). Here the radar was located at 670 m above sea level on a plateau that ranged between 600 and 700 m over an area of several square km. These two observation points are shown in figure 1, together with the airports from which meteorological data were obtained. The terrain was essentially level around the Bronx location, but heavily built up. There were steep hillsides within a few km of the radar location near Ellenville, and these could well have generated obstruction updrafts, as discussed below.

Meteorological Data

Since the basic purpose of these observations was to determine the relationship of the birds to cloud layers, all available meteorological data were obtained from the U.S. Weather Bureau and the Federal Aviation Agency stations in the New York area. Surface observations were available from 11 airports shown in figure 1. Radiosonde data were available at 12-hour intervals from J. F.
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Kennedy Airport, N. Y., and Albany, N. Y. These provided data on wind direction, windspeed, temperature, and humidity at the two airports when the radiosonde balloon ascended. Most of our observations were conducted within 3 or 4 hours after the evening radiosonde ascent (nominally at 0000 Greenwich Mean Time). Ellenville is approximately equidistant from New York and Albany, hence our estimate of Ellenville winds, temperatures, and humidities were made by proportionate interpolation according to the time and location of the observation. The Bronx location was much closer to Kennedy Airport, and Kennedy data were used to estimate wind and cloud conditions there.

We also attempted to obtain local wind data by tracking with the same radar a meteorological pilot balloon beneath which was suspended a radar target. Unfortunately operational difficulties prevented this from being accomplished on April 23 or May 16, 1970, which turned out to be two of the most interesting nights in terms of cloud depths. But on April 30, 1970, two balloons were tracked late in the evening, and these balloon tracks provided more accurate determinations of local windspeed and direction. Airplane pilots reported additional data concerning the upper limit of cloud layers which the Watch Supervisors of the New York Air Traffic Control Center kindly furnished to us by telephone. These were not as numerous nor as close to the location of our radar as would be ideal, but they provided valuable supplements to the other meteorological data.

To facilitate comparison with the directions in which birds were moving, all wind directions discussed below are the direction toward which the air was moving. Thus a north wind in ordinary usage is designated 180°.

RESULTS

Observations during certain nights in the fall of 1969 and the spring of 1970, other than the nights discussed in detail below, showed that many birds were migrating in approximately the appropriate directions under opaque layers of altocumulus or other types of cloud. We could not discern any consistent differences in the straightness of such tracks between overcast and clear nights. No tracks on completely clear nights were straighter than 2121 or 2134 of April 30. This could be interpreted as evidence that when flying under clouds but over well-settled land areas birds may orient by means of artificial lights on the ground. In all such cases lights were available in sufficient
abundance that a bird could probably maintain tracks as straight as we observed by selecting a light approximately straight ahead, flying toward it for a few minutes and then shifting attention to another, more distant, light in the same direction.

On the nights of April 23, April 30, and May 16, 1970, deep and continuous stratus clouds were present. Out of 73 birds tracked many were observed at altitudes that seem to have been well within the cloud layers. These data will therefore be presented in detail.

April 23–24, 1970, Bronx, N. Y.

Occluded fronts were located to the north, west, and south of the New York City area during this night with widespread low clouds and fog. All aviation surface weather observations from 2100 to 0000 at Kennedy, La Guardia, Newark, Teterboro, White Plains, and Bridgeport airports showed low ceilings, with overcast reported at altitudes ranging from 30 to 400 m. At 2000 La Guardia reported broken clouds at 390 m and overcast at 1220 m; Teterboro reported broken clouds at 340 m and overcast at 610 m. But at the other four airports overcast was reported at 370 m or lower at this time. The ceilings lowered throughout the evening, and after 2100 the highest at any of these airports was 300 m. From 2200 until after midnight the nearest airports all reported fog and ceilings below 150 m.

Figure 2 shows the radiosonde data from Kennedy Airport (30 km south of our location). At 1928 very moist air (dew point depressions less than 1.5° C) extended from 200 to 1850 m with a pronounced change to dryer air above this level. In the morning there were variable but relatively low dew point depressions (0.8° to 4.8° C) up to about 3000 m. The Albany radiosonde data also showed dew point depressions of less than 2° up to 1840 m in the evening and up to 880 m in the morning, with other high humidity readings in the morning above 3500 m. At Kennedy the radiosonde recorded a slight inversion from 200 to 1200 m and a nearly isothermal layer up to 2000 m, both evening and morning. At Albany the inversion was more pronounced and extended from 550 to 1500 m both evening and morning.

Five reports from airplane pilots were available during the time of our observations. Three were consistent with the Kennedy Airport radiosonde data in indicating the top of the cloud layer to be around 1800 m (1815 m at Bridgeport at 2030, 1815 m at Carmel, N. Y., 61 km north of the Bronx, at 1900; and 1720 m at 2100 near Northport, 37 km east of the Bronx). But two other pilots reported cloud tops at 1030 m—at White Plains at 2300 and at Bayville, N. Y., 26 km east of the Bronx at 1930. These reports indicate variability in the cloud tops, or possibly emergence of the pilot from one layer with other unreported clouds above his plane. But even the lowest of the five pilot's reports place the cloud tops above 1000 m. April 23 was two days past full moon; the moon rose at 2130 and set at 0628; and hence it was above
FIGURE 3. Radar tracks of birds over Bronx, N. Y., April 23, 1970. Cross near center is radar location. Number at start of each track is local time (EST) when tracking began; other numbers are altitudes in meters. Between numbers, changes in altitude were gradual and of roughly constant slope, within the radar accuracy. Dashed lines replace radar artifacts but with no sign that radar shifted targets. Asterisk indicates period of nearly stationary flight. A few tracks have been displaced slightly, relative to the radar, to avoid crossing other tracks.

Throughout the period of our observations. At the altitudes where we tracked birds, the winds varied from about 000° at 500 m to about 090° at 1700 m. Thus many of the birds tracked were flying in crosswinds. Wind speeds varied in a moderately complex fashion according to the Kennedy radiosonde data, increasing in the evening from 5 m/sec at the surface to 16 m/sec at 560 meters, then falling to 9.5 m/sec between 1100 and 1440 m followed by a gradual rise to 11.5 m/sec at 1780 m. In the morning the winds followed a similar pattern but windspeeds were only 0.5 to 0.6 times the evening values.

Twenty-five birds tracked between 2006 and 0003 EST yielded 17 tracks longer than 1 km, with the longest 4.36 km. But several shorter tracks are also included because of special features. These birds varied in altitude from 540 to 1775 m. Figures 3 through 7 show the tracks and altitudes of all birds except for a few where computer artifacts rendered the track very difficult to plot even though its general direction was evi-

d through the horizon when most of the birds were tracked.

Since we did not succeed in tracking a local balloon on this evening, our best data concerning local winds come from the evening radiosonde ascent from Kennedy Airport (fig. 2). The wind shifted markedly with increasing altitude from surface winds blowing towards 270° through 000° to 096° at 1760 m. The morning radiosonde at Kennedy showed very similar winds up to 1500 m except that the wind shear was considerably less, with surface winds blowing to 340°. Surface winds at the airports within a few miles of our observations were consistently light and blowing towards southwest or west.

FIGURE 4. Radar tracks from Bronx, N. Y., April 23 and 24, 1970 (symbols as in fig. 3).
FIGURE 5. Radar tracks from Bronx, N.Y., April 23, 1970 (symbols as in fig. 3).

FIGURE 6. Radar tracks from Bronx, N.Y., April 23, 1970 (symbols as in fig. 3).

FIGURE 7. Radar tracks from Bronx, N.Y., April 23, 1970 (symbols as in fig. 3).

dent. Here and elsewhere it is convenient to identify each bird by the time when its track began. Three tracks showed such clear turns (2033, 2220, and 0003) that additional track directions were determined for the separate legs. The resulting 29 track directions vary from 315° (second leg of 2220) to 123° (2100), with an average of 035°. All 29 tracks were within 90°, 21 within 60°, and 16 within 45° of the mean. Thus these birds were reasonably well oriented for spring migration.

Many of these tracks were far from straight. The average straightness index defined above was 13.5 (2.35 to 44.6), and the mean groundspeed ratio was 0.72 (0.40 to 0.99). Birds such as 2147 and 2220 circled, looped, zigzagged, or flew in other patterns so that the total distance traveled was more than double the net distance covered. For example 2105 was followed over a total distance from beginning to end of the track of 1.09 km during 107 seconds which is equivalent to a net speed of 10.2 m/sec. But the average speed from the computer print-out was 16.0 m/sec (groundspeed ratio = 0.64), and close inspection of the track showed many small scale zigzags. A few shorter tracks showed even lower groundspeed ratios: 0.47 for 2051, 0.46 for 2346, and 0.40 for the most striking case of all, 2147, in which a total net track of 3.20 km required almost 10 minutes.

It seems unlikely that these non-linear tracks were operational artifacts of the radar, because very straight tracks and very irregular ones were registered within a few minutes. Rapid switching of the autotracking between members of a flock also seems an unlikely explanation, since the second-to-second speeds were reasonably consistent and in
some cases a definite but complex flight pattern was plotted. Clearly many of these birds were making extensive but small scale deviations from a perfectly straight track, while nevertheless maintaining a consistent direction of progress. A possible interpretation of such behavior will be discussed below. Estimates based on the evening radiosonde from Kennedy Airport indicated implausible airspeeds and headings on April 23. These do not seem meaningful in view of the differences on April 30 between Kennedy radiosonde values and local wind data obtained by tracking our own balloons.

On balance the available meteorological data point consistently toward the presence of a low-lying stratus cloud layer extending throughout the period of our observations from ceilings at 200 to 400 m up to cloud tops between 1700 and 2000 m. All birds we tracked were certainly above the cloud base, and appeared to be well within the stratus layer. At least half were below the lowest of five pilot's reports, which as mentioned above were not wholly consistent with the radiosonde data.

Night of April 30-May 1, 1970 Bronx, N. Y.

A very weak and ill-defined occluded front extended from north to south through the New York area with low stratus clouds and fog. Throughout the period of our observations Kennedy, Newark, Teterboro, La Guardia, White Plains, and Bridgeport observations showed either fog, indefinite low ceilings, or overcast at 60 to 250 m. Visibilities were virtually zero to not more than 3 km. Winds were light and blowing to about 315° to 000°. Pilot reports of cloud tops were available from several km north and east of the Bronx and ranged from 900 m to 1830 m. The radiosonde data from Kennedy Airport in the early evening showed an isothermal layer at approximately 10° C from the surface to 550 m and a marked inversion with temperatures of 16° between 800 and 1100 m (see fig. 8). Above this level the temperatures dropped gradually to reach 8° at approximately 2100 m. The humidity sensors in the radiosonde showed a very high humidity (dew point depression less than 2°) up to approximately 500 meters with very much dryer air at higher altitudes. This indicates that the stratus cloud did not extend above 500 meters, although the pilot reports indicated higher cloud tops. Yet it would clearly be unjustified to conclude that any bird flying any higher than 500 meters was cut off from a view of the sky.

The wind directions indicated by the evening radiosonde ascent from Kennedy varied from winds blowing to 940° at the surface shifting to 070° at 1400 m. We succeeded in tracking two balloons with our radar after our observations of birds, and these showed the local winds at 0033 and 0100 to be quite consistently toward 005° ± 10° up to an altitude of 900 m where both balloons were lost because of interfering buildings on the horizon. Windspeeds from these two balloon tracks, which were quite consistent, were 7 m/sec from 200 to 400 m, 11 m/sec at 400 to 550 m, 16 m/sec at 550 to 650 m, and 14
m/sec at 650 to 925 m. The wind data from Kennedy Airport radiosonde data (fig. 8) differed by as much as 40° in direction and up to 10 m/sec in speed from these local measurements. This difference demonstrates the importance of local and approximately simultaneous wind measurements for reliable estimates of a bird's airspeed and heading.

A conservative interpretation of these meteorological data indicates a continuous layer of low stratus cloud extending from 200 m or lower up to approximately 500 m. It was 9 days past full Moon and the Moon set at about 2200, so that it was not available during most of our observations.

Twenty-eight out of the 29 tracks obtained between 2121 and 0052 EDST were between 322° and 080°, with a mean of 026°. One track at 147° (2150) clearly lay outside the range occupied by all the rest. The altitudes of these tracks ranged from 230 to 1060 m. Of the 28 tracks between 322° and 080°, 25 were within 60° of the mean, 23 within 45°, and 16 within 30° of the mean. All tracks are shown in figures 9 to 12.

Those tracks that were above 500 m were distinctly straighter than the four tracks that were clearly below this cloud top level, as indicated by the radiosonde data of figure 8 (2150, 2240, 2303 and 2306, all shown in fig. 9). The first was short and highly non-linear, with a straightness index of 4.3 and a groundspeed ratio of 0.36. Furthermore the track direction was 147°, and the heading calculated from local wind data was 178°. This bird's airspeed appears to have been 13.2 m/sec, based on its net track. But of course the actual integrated airspeed over the many changes of direction must have been considerably greater. The two tracks at 2303 and 2306 were also very far from straight, with straightness indices of 9.1 and 10.6 and groundspeed ratios of 0.57 and 0.49, respectively. Both track directions were 35°, and the estimated headings were 230° and 223°. Because these two targets were moving so
nearly downwind, their indicated airspeeds were only 2.2 and 2.4 m/sec. This suggests either that they were insects, or hovering birds, or something moving more slowly than birds, that their turns were even more extensive than indicated by the groundspeed ratios, or that the wind velocity was appreciably different from the winds measured with our balloons 1½ and 2 hr later. In contrast to these non-linear tracks below 500 m, 15 tracks between 500 and 700 m showed an average straightness index and groundspeed ratio of 32.7 and 0.94. For 11 tracks between 750 and 1050 m these values were 49.2 and 0.92.

Track 2240 was the longest within the cloud layer, and it was in an appropriate direction for spring migration (343°). Based on our local wind data, its airspeed was 5.8 m/sec and its heading 316°. This bird's straightness index was 10.1, and its ground-speed ratio was 0.80. The latter value probably means that the actual airspeed was above 10 m/sec when integrated over the several turns evident in figure 9. Estimates of this bird's airspeed, based on the local balloon tracks about 2 hr later, lead to distinctly different headings and air speeds during different portions of the curving flight path shown in figure 9. From 14 to 48 seconds after the radar was locked onto this bird its track was almost exactly 000°, its groundspeed averaged 13.8 m/sec, and estimated heading and airspeed were 355° and 6.8 m/sec. It then turned left with absolutely no sign that the radar shifted to a different target and moved between 49 and 75 sec with a track direction of 320° and an average groundspeed of 14.6 m/sec. This northwesterly leg involved a heading of 293° and an airspeed of 10.8 m/sec according to our local wind data. This is consistent with the reports of Bellrose (ref. 12) and with the recent findings of Bruderer and Steidinger\(^1\) that birds lower their airspeeds in tail winds. But perhaps the most appropriate conclusion to be reached from these data is that calculations of a bird's airspeed and heading should not be taken very seriously unless local wind data are obtained at the same place as the radar tracking data and within a few minutes of the same time. Particularly under conditions of wind shear and complex air movement, local winds may well vary considerably from moment to moment.

On balance there is thus a clear indication on the night of April 30 that those birds flying in the stratus cloud layer were deviating distinctly more from a straight flight path than those that were above the cloud tops. Nevertheless three of the actual tracks of these birds flying in the cloud layer were rea-

\(^1\) See paper by Bruderer and Steidinger in this volume.
FIGURE 12. Radar tracks from Bronx, N. Y., night of April 30, 1970. Symbols are as in figures 3 and 9. 2134: 073°, 14.5; 2234: 082°, 7.8; 2248: 129°, 8.8; 2251: 057°, 18.0; 2307: 105°, 6.0; 2309: 347°, 11.4; 2345: 094°, 13.0; 2353: 044°, 15.6.

reasonably appropriate for seasonal migrating (343°, 350°, and 350°), while the fourth had a quite inappropriate migration direction of 147°.

May 16-17, 1970, Ellenville, N. Y.

A cold front was approaching from the west and passed approximately over our location in the early morning shortly after our last observation. There was widespread low stratus cloud and also very high rows and cells of convective cloud with heavy showers and thunderstorms. The weather bureau radar in New York City showed bands of radar reflective clouds with large water droplets moving from west to east toward and through the Ellenville area throughout the night. The tops of these cumulus clouds were at 9000 to 10 000 m, but this type of radar does not reveal stratus clouds and consequently tells us nothing about the tops of the clouds that lay between the bands of thunderclouds. Shortly after we arrived on the plateau, very thick fog descended and remained throughout the night. In the early morning as we drove down from the plateau, we did not emerge from the bottom of this stratus layer until we were at least 200 m below the radar.

Surface observations at Binghamton, N. Y. (140 km west of Ellenville), Newark, Teterboro, White Plains, and Poughkeepsie showed overcast throughout the night at altitudes lower than our radar. The New York City airports, Wilkes Barre—Scranton, and Albany also showed continuous overcast, although at times it was above our altitude. Because the weather was so bad, no pilot reports were available from anywhere close to our area during the night.

The radiosonde data from both Kennedy Airport (fig. 13) and Albany (fig. 14) showed virtually saturated air (dew point depressions 2° C or less) from well below the altitude of our radar up to 2000 m. There was also some indication of higher clouds, but it seems conservative to assume that birds flying within range of our radar must have encountered stratus clouds from below our altitude up to about 2000 m above sea level. There was heavy but intermittent rain during the night, and the 3 cm radar itself showed much cloud echo when used at low

FIGURE 13. Radiosonde data from J. F. Kennedy Airport, May 16 and 17, 1970. Time, EST.
elevations. We searched for birds from 2030 to 0320 EDST, whenever it was not actively raining. There were many fewer birds than on April 23 or April 30, but during this period of about 7 hr we tracked 21 for distances ranging from 200 to 3680 m. On many other occasions what appeared to be a bird would be observed on the A-scope, but it would prove impossible to maintain it for more than a few seconds in the autotrack mode. Hence several relatively short tracks are included in figures 15 to 17. It seemed likely that the many failures to track birds were due to interfering echoes from the clouds, although this cannot be established with certainty.

Since we were in thick fog we could not manage to locate a balloon in order to lock the radar on to it. Wind direction at the altitudes where we tracked birds can be estimated only from the New York and Albany radiosonde data. The evening radiosonde ascents showed almost identical wind directions at these two stations, 350° at 1000 m shifting to approximately 025° at 2400 m. At both stations the winds at lower elevations showed a clockwise shift during the night. A reasonable average interpolated value of wind direction would appear to be 020°, and the maximum discrepancy from this interpolated average wind at either airport, morning or evening, at the altitudes where birds were observed was only about 40°. The windspeeds were reasonably consistent for the four radiosonde ascents at New York and Albany, and an interpolated value of 12 m/sec at 1000 m rising to 17 m/sec at 2400 m seems a reasonable approximation. It was 5 days before full Moon,
but the Moon set about 2230 and hence was unavailable for most of the night.

The 21 birds tracked were much more consistent in track direction than on any other night when extensive data were gathered. The average track was 016° (340° to 050°). All tracks were within 45° of the mean and 19 out of 21 were within 30°. All the birds tracked were flying very nearly downwind, and their groundspeeds ranged from 20 to 37 m/sec with the higher groundspeeds being those of birds at higher altitudes, as would be expected. All tracks were quite straight with practically no deviations of the types so prominent on April 23rd and below 500 m on April 30th. The straightness index varied from 8.75 to 91.3 (av 30.15), and the groundspeed ratio averaged 0.93 (0.88 to 0.99). Unless the New York and Albany radiosonde data were grossly misleading with respect to our location, the majority of these birds must have been migrating within the stratus layer with no opportunity to see sky or ground. The possible role of obstruction updrafts will be discussed below.

"Stationary" Flight

A few of the tracks recorded by our radar showed periods of several seconds during which the X, Y, and Z coordinates remained almost unchanged. If a target did not move when first acquired, we would ordinarily assume it was some peculiar form of ground echo. Such stationary targets were observed in many locations, but they were especially common in the Bronx. They could be identified as fixed targets because some had the azimuth of prominent buildings and because the radar would remain locked on to them indefinitely, giving constant values of azimuth, elevation, and range. They were much more common at low elevations, but some would be found consistently from night to night in the same location, and these appeared to be reflections of side lobes of the radar beam from buildings, even though the elevation was much too high for the building in question to lie in the main beam. But what will be called here for convenience "stationary birds" were clearly distinguishable from such fixed ground targets because they moved at speeds appropriate for birds before and/or after a period when the radar coordinates remained approximately constant. The following specific cases on April 23 in the Bronx demonstrate this phenomenon most clearly.

The bird tracked at 2033 (fig. 5) was unusual in making a gradual turn of about 90° at 200 to 205 sec after tracking began. Unlike many other tracks with pronounced turns, there was no sign that the radar had shifted to another bird—such as a discontinuity in altitude or an unusually high XY speed registered near the time of the turn. The average groundspeed was 8.2 m/sec during the first leg and 6.7 m/sec during the second leg when the bird moved roughly east. The altitude rose very slowly and gradually with minor variations during this long track from
700 to 835 m, and between 170 and 235 sec it varied only between 831 and 846 m. Shortly after the 90° turn, at the point marked with an asterisk in figure 5, the bird's position remained stationary for 7 sec, all points in that interval falling within a horizontal area of $5 \times 11$ m and a vertical range of only 6 m. This is approximately the accuracy of the radar. Yet immediately before and after this stationary period the track showed regular horizontal motion at speeds typical of the rest of the track with no sign that the radar switched to a new target. The winds at the bird's altitude, according to the Kennedy Airport radiosonde less than an hour earlier, was blowing to about 005° at about 12 m/sec. This wind velocity would mean that during the first leg the bird was heading about 191° and flying at an airspeed of about 5.5 m/sec, in other words being blown backwards at double its airspeed!

After the turn the estimated airspeed and heading become 15.6 m/sec and 164°. During the first leg the groundspeed ratio was 0.71 and the straightness index 9.4, indicating, as is clear from figure 5, that the track was deviating considerably from a straight line.

A second and even more striking case was the bird tracked at 2210. For the first 2 minutes of tracking it remained within an area about 100 meters square, marked with an asterisk in figure 3. While the indicated position moved back and forth irregularly during the first 2 minutes, there was a 20 sec period during which all recorded positions fell within a 20 m square horizontally while the altitude varied irregularly over a total range of only 23 m. During this period the bird gained considerably in altitude, rising from 620 to 710 m. Then without any indication that the radar had switched to a new target it moved off on a somewhat irregular southeasterly course with a gradual curve, covering 1440 m horizontally in 153 sec while climbing about 135 m. Judging by the radiosonde data, this bird also faced into a 12 m/sec wind blowing toward the north during its first 2 min of climbing with virtually no horizontal progress. Its subsequent movement along a curved path was also studded with short zigzags, and the groundspeed ratio was only 0.61. Its indicated airspeed and heading during this time were 16.8 m/sec and 174°. Both these birds might have been flying in tight circles or other small scale patterns not accurately plotted by our radar, and we cannot be certain that the radiosonde data are accurate for the air in which these birds were flying.

**DISCUSSION OF FINDINGS**

Although many of the weak, low velocity radar targets that used to be considered mysterious "angels" have been accounted for by evidence that they are birds or insects, there remain others that have been explained, with some difficulty, as meteorological phenomena (ref. 13). It is often taken for granted that if a target is stationary or moves at the estimated velocity of the local wind it cannot be a bird. The two cases discussed in the previous section, and others for which the evidence is not so complete, were apparently birds that spent a considerable period of time almost stationary. But of course we have no way of knowing whether they were soaring in circles of small radius, hovering, executing small scale and rapid zigzags, or employing other types of flight behavior. It is even possible that flight patterns not ordinarily seen in daytime may be used when flying among clouds at night.

A final possibility that seems worthy of consideration is that some form of dynamic soaring was being practiced by the birds which indulged in so many rapid, small scale
changes in direction of flight. Our computer program calculated the position of each radar target only once per second, so that very rapid changes in heading would not have been detectable. The fact that some birds changed course so frequently, sometimes in fairly regular patterns, suggests that further detailed observations might disclose some pattern of dynamic soaring such as those suggested long ago by Breguet (ref. 14).

Unfortunately on April 23 we did not obtain data on winds from local balloon tracks, and the differences between these local data and radiosonde data from Kennedy Airport on the night of April 30 warn us not to rely too heavily on the latter for estimating airspeeds and headings of birds tracked 30 km away. Hence we can only speculate about the patterns of air movement in which these birds were maintaining almost stationary flight. But figure 2 shows that on April 23 there was considerable wind shear and probably convective currents inside the stratus layer where these birds were apparently flying. Other birds such as 2125, 2147, and 2220 of April 23 were also flying in very complex patterns. It is, therefore, tempting to speculate that some of these birds were riding updrafts in ways roughly similar to the soaring flight of hawks, gulls, or vultures in daytime under cumulus clouds or along ridges.

Bellrose (ref. 12) reports a puzzling variation in airspeeds of nocturnal migrants flying in various windspeeds and directions. While only average values are presented, they indicate that birds tended to maintain a constant groundspeed, flying at lower airspeeds in tail winds and vice versa. While it is difficult to make direct comparisons between Bellrose's data and ours, the complex tracks described above would appear as very slowly flying birds if one could not plot the fine details of each flight path. Particularly when flying inside stratus clouds, birds may alter their flying tactics to take advantage of rising currents at some sacrifice in groundspeed, as speculatively discussed elsewhere (ref. 2).

Finally we must ask whether the meteorological data discussed above are adequate to establish whether or not the birds tracked on the nights of April 23, April 30, and May 16 were in fact inside of opaque clouds. Cloud layers are well known to have gaps, to be variable in thickness, and to have both tops and bottoms that deviate considerably from a horizontal plane. The possibility that extensive gaps occurred in the cloud layers on these three nights can be discounted to a considerable degree by our own local observations. One of us looked carefully at close intervals for any signs of stars, or the Moon when present. No such indications of breaks in the cloud layer were seen during the periods of observation described above. Since our radar was limited in its range, it seems unlikely that there were holes in the cloud where any of the birds we tracked were flying. Furthermore the bottoms of the clouds were in all cases visibly low, and on the night of May 16 unquestionably well below the altitude of the radar.

The only serious doubts about the adequacy of our meteorological data concern the tops of the cloud layers, which were of course invisible to us. The principal evidence about cloud tops was the radiosonde data indicating layers of nearly saturated air up to certain altitudes. But these samplings of the atmosphere occurred at different times and places from our radar observations. Thus it is always possible that the birds we tracked were flying through local depressions in the cloud tops. It seems highly unlikely, however, that under the conditions prevalent on these three nights the cloud top level would have been below the altitudes indicated by radiosonde data for extended periods. Had the stratus clouds
been this variable, the ceilings would probably have varied more than they did at the six neighboring airports from which reports were obtained, and stratus clouds of highly variable thickness would probably also have presented occasional breaks through which we could have seen the Moon or stars.

Nevertheless it is quite appropriate to be skeptical of evidence that birds can maintain reasonably accurate orientation without visual cues, in view of the evidence that Sun- and star-compass orientation is well within the capabilities of birds. Conservatively we might assume that the stars or Moon were visible to all birds above 500 m on April 30 and even to those above 1000 m on April 23 (on the basis of pilots' reports of cloud tops well below the level where the radiosonde data showed a marked change from moist to dry air). We might further assume that over the plateau, where our radar was located on May 16 and 17, there were strong ridge updrafts in which the birds were riding and maintaining straight tracks by sensing the wind direction from turbulence patterns despite the stratus cloud. The only steep hillside within range of our radar was about 1 km to the west where the ridge was approximately parallel to the wind direction and hence not likely to produce a consistent updraft. Many birds were flying roughly over this steep hillside, but others were not, as shown in figures 15 to 17. One can speculate from the topographic map (Napanoch quadrangle, U.S. Geological Survey 7½-min series) that these birds were riding updrafts from the steep cliffs running approximately southwest-northeast that are located about 2 to 3 km south and southeast of our location. But the topography appears equally suitable to generate updrafts in other areas within range of our radar where no birds were tracked. In short, strong ridge updrafts were undoubtedly present in the area, but no convincing correlation is evident between topography and the bird flight paths actually observed.

Even granting these conservative assumptions, there remain at least 15 to 20 birds tracked over the Bronx on April 23 and 30 that appear to have been well within the stratus cloud layer. In the Bronx there are no topographic features adequate to provide orienting updrafts at altitudes of several hundred meters. Chimneys could well have provided artificial thermal updrafts, but we could discern no correlations between specific buildings and the flight paths of those birds tracked on April 23 and 30 that appear to have been inside the clouds. Many were flying over the Zoological Park or Botanic Garden which have no large heat sources. This part of the city does not have large power plants or factories that operate at night, so that this type of patterned updrafts does not seem likely.

It thus seems probable that these birds tracked within stratus cloud layers were using one or more of the non-visual mechanisms of orientation which I have recently discussed elsewhere (ref. 2). But descriptive observations of flight paths can scarcely tell us which sensory mechanisms of orientation were employed, except that some of the non-linear tracks suggest soaring on updrafts.

**SUMMARY**

1. Detailed flight paths of migrating birds on nights with widespread low stratus cloud were measured with a tracking radar during the spring of 1970. Each bird's position was continuously recorded within 5 ± 10 m. Meteorological data showed that on three nights stratus cloud was continuous throughout the area during the hours when birds were being tracked.

2. On these three nights many birds were tracked for distances up to 3 or 4 km at
altitudes that seemed to be occupied by opaque cloud layers, judging by surface observations, radiosonde data, and airplane pilots' reports. It is difficult to escape the conclusion that these birds were unable to see the sky or the ground. Nevertheless almost all were migrating in appropriate directions.

3. Some tracks of birds apparently within the stratus layers were reasonably straight and level, others were climbing or descending. Several were highly non-linear with zigzags, curves, reverse turns, and in one case a series of loops similar to the path of a hawk soaring on updrafts from a ridge. These birds may have been using convective patterns of air flow within the stratus cloud.

4. A few radar targets that gave every evidence of being birds remained almost stationary for many seconds while apparently located within the stratus cloud. The wind was strong enough that this must have required heading into the wind. Before or after such a period of near stationary flight these birds moved progressively in a reasonably appropriate direction for spring migration. Such non-linear flight paths may account in part for some previous observations of "angels" that do not move as fast as typical birds. Previous reports of migrants flying at surprisingly low airspeeds may be birds flying in non-linear patterns adapted to take advantage of updrafts. But local winds should be measured directly and at the same time birds are tracked before confidence can be placed in calculated airspeeds of birds flying in air that is moving in complex patterns.

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DISCUSSION

CARR: On some of your tracks the zig-zags and loops seem to be a bit more regular than you would expect from pure chance. They have a certain periodicity about them. Have you considered the possibility that perhaps this reflects correction on the part of the bird?

GRIFFIN: I have thoughts about this, but they are purely speculative with no data. It is conceivable that these birds in the cloud are, in fact, getting some lift or at least some directional information from turbulence. I don't have any data as to just how turbulent the air was except on the night of the 30th with the balloon tracks, and then there was not any support for any very great turbulence. It is, however, an interesting thought.

CARR: Do you think that there was any periodicity at all or were they all completely random?

GRIFFIN: Some of them looked quite periodic. I am quite sure they were not random. It looked as though the bird was first making mild turns one way and then another, but we need more data.

GAUTHREAUX: On the particularly erratic tracks, what is the probability that you were not tracking a bird but tracking a bat?

GRIFFIN: It was too early and too cold for bats in New York. The most erratic ones were April 23. It was earlier than one sees bats. I have worried quite a bit about whether these things are all birds. I think probably they are. Furthermore, in the spring they are mostly going north and in the fall they are mostly going south. This rather circum-
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substantial evidence makes it rather likely that most of them, at least, are birds.

WILLIAMS: Can we rule out red bats?

GRIFFIN: We can't entirely, but bats are not nearly as numerous.

SCHMIDT-KOENIG: Has anyone seen radar evidence or other evidence on dragonfly migration?

GAUTHREAUX: There are dragonfly movements that are detectable on radar. They appear on the radar screen as bands extending for several miles and perhaps half a mile wide. If one looks up with a 30-power telescope, one sees literally hundreds of dragonflies in a band flying at great altitudes. The bands are oriented with the wind, and the radar display is very different from those produced by migrating birds.

GRIFFIN: What was the spacing and were the conditions favorable for roll vortices?

GAUTHREAUX: Roll vortices could very well be involved. The bands of dragonflies might coincide with rows of updrafts, but I do not have the necessary data to show this. The spacing of the bands is on the order of perhaps 2 or 3 miles based on measurements taken from the radar screen.

WILLIAMS: In our work in Texas we found that the bulk of the insects were well below 500 meters. There were very few insects at the same heights as migratory birds.

David Wingate in Bermuda has been compiling the dates of major arrivals of birds as well as insects on Bermuda. He finds that there are quite often huge numbers of one or two species of butterflies or moths that arrive suddenly on the islands.

EMLEN: I would like to comment that radar tracking of birds already aloft will not allow us to determine whether birds merely maintain a bearing under overcast conditions (that they may have selected previously when other navigation cues were available) or whether the birds have the ability to determine a goal or compass direction under overcast. This is an important distinction. I feel that the question can best be resolved by radio- or radar-tracking individual birds that the experimenter releases from the ground. In this way, the actual decision making process at the initiation of a migratory departure can be studied. This should constitute a powerful technique for future studies, since the experimenter can control the cues available to the departing bird by selecting to release birds under specific meteorological conditions and by experimentally modifying the sensory capabilities of the migrants prior to their release.

REFERENCES