

BOBOLINK MIGRATORY PATHWAYS AND THEIR EXPERIMENTAL ANALYSIS UNDER NIGHT SKIES

WILLIAM J. HAMILTON III

IN the last decade many new experimental tools have been developed by students of bird migration, while conventional field-observation techniques have been pursued more acutely (Lack and Lack, 1953; Ball, 1952; Hochbaum, 1955) and within new theoretical spheres (Bellrose, 1957). Kramer's (1952) discovery that the diurnal fluttering of a caged Starling was oriented in the species-specific migratory direction provided a new experimental means of migration analysis. With the Starling's visual field restricted to the sky above, Kramer noted that the fluttering remained oriented only when the sun or the sky near it was unobscured by cloud cover. Experiments under an artificial sun confirmed the use of the sun in direction finding and demonstrated the role of an internal clock in compensating for the apparent passage of the sun across the sky (Hoffman, 1954). Sauer (1957) and Sauer and Sauer (1959, 1960), working at night with a device similar to Kramer's, found night-migrating species able to tell direction by the stars, a discovery confirmed by experiments performed under the artificial stars of a planetarium.

During this same period, Lowery and Newman (1955) proceeded with the analysis of the natural night migration by observing the passage of birds across the face of the moon with telescopes. The additional discovery that radar can be used to detect migratory birds led to a flood of new information about the natural migration both during the day and at night (Sutter, 1957; Lack, 1959, 1960). Interest in the calls of passing migrants has also been revived (Graber and Cochran, 1959, 1960; Hamilton, ms), lending new perspective to the analysis of orienting cues used by migrants.

MIGRATORY ROUTE OF THE BOBOLINK

Migratory pathways. In its annual migratory cycle the Bobolink (*Dolichonyx oryzivorus*) travels over 19,000 km (12,000 miles), a movement surpassing that of all other Western Hemisphere passerines. No less interesting than the extraordinary dimension of the migratory pathway is the complex and irregular route followed. These features of Bobolink migration suggest that this species would be an exceptional subject for the analysis of the evolution of migratory pathways and the orienting cues used in the process of passage.

The breeding area of the Bobolink is largely restricted to a band about 800 km (500 miles) wide, stretching across the northern United States and southern Canada, from New Brunswick and central New Jersey in the east to Nebraska and Saskatchewan in the west. Throughout much of this

area the distribution is continuous within ecological limits. Gaps are restricted to peripheral parts of this area.

Western populations. To the west and northwest smaller breeding populations occur at widely separated localities, with vast areas of unoccupied territory intervening (A.O.U. *Check-list*, 1957). It is frequently stated that these westerly populations have invaded the area with the advent of agricultural changes, an interpretation that apparently stems from Ridgway's (1876:500) brief comment that the species "seemed to be spreading over all districts of the 'Far West' where the cultivation of cereals had extended," a reflection apparently prompted by the discovery of birds breeding near wheat fields at Ruby Valley, Nevada, and the report of transients in grain fields near Salt Lake City. From the original statement it seems unclear whether Ridgway was referring to geographic dispersal or population expansion, and the single sentence that he devoted to this interpretation was appropriate to the extent of the then available evidence. But by 1895 the former interpretation tentatively had been ascribed to Ridgway's brief comment (Bendire, 1895), and subsequent recounts became increasingly elaborate and emphatic. This trend reached its culmination when Lincoln (1939) stated: "extension of the breeding range, with the resulting change in the migration of the species, has taken place since the settlement of the country by the white man. Its preferred habitat during the nesting season is damp meadows, and originally it was definitely cut off from existing habitat of this type in the West by the intervening arid regions. But with the bringing of large areas under cultivation, and the advent of irrigation, small colonies of nesting Bobolinks began to appear at various western points."

There seems to be no conclusive evidence, however, to support the claim of recent invasion of these areas. Western populations even today remain small and generally poorly known. In fact, the discovery of the local and restricted western populations closely parallels the ornithological exploration of the west.

Many authors have commented on the sensitivity of local populations of Bobolinks to land-use practices and successional changes. It is possible that existing local populations were favored by the arrival of agriculture in the west. At most, the available evidence indicates that these populations enlarged and expanded locally.

If a trend to westward expansion was established a century ago, it has not kept pace with agricultural developments in the west. The largest western populations continue to be localized in naturally moist areas such as the vicinity of Malheur Refuge in Oregon and the area about Great Salt Lake, Utah. In Idaho, Burleigh (pers. comm.) has found them quite localized but scattered through much of the state. Again, they do not

center their breeding activities about irrigation projects but are concentrated in the vicinity of naturally wet meadows. Why have Bobolinks not expanded into the ever-increasing irrigated areas of the west? I suggest that a part of the answer is that these are in fact relict populations with historically fixed migratory routes and breeding grounds. Certainly the localized nature of these western populations supports the remnant interpretation rather than suggesting an expanding distribution. Since the Great Basin has in the past, probably as little as 11,000 years ago (Broecker, 1947), been much more moist than it is today, this interpretation is in accord with the history of the region. Fresh-water lakes once abounded, and the area must have been generally more moist (Hubbs and Miller, 1948) and more hospitable to a bird such as the Bobolink. Probably at this time the Bobolink occupied very nearly the entire area where today it remains only as a border remnant. Modern invasion of the west by Bobolinks is probably but a myth.

Range shifts. Essentially the same arguments apply to Bendire's (1895) and McAtee's (1919) suggestion that the whole of the Bobolink range has shifted westward. McAtee especially suggests that the western populations were augmented at the expense of the eastern populations. It is true that Bobolink populations in the east were dwindling in the early part of this century, probably due to the extensive market hunting that was directed to the fall flocks along the eastern seaboard. However, the western expansion, if it existed, commenced a good deal earlier, and there is no report to indicate that it might have accelerated at the time that McAtee (*op. cit.*) interpreted the evidence.

Fall migration. With the completion of the breeding cycle in mid-July Bobolinks gather locally about swampy areas, go through a partial molt, and early in August initiate the fall migration. The initial move is apparently to the southeast, at least for the bulk of the eastern populations, and from mid-August to mid-September great concentrations occur along the Atlantic Seaboard from New Jersey (Stone, 1937) south to Florida (Howell, 1932).

Chapman (1909) and Lincoln (1939) use the Bobolink as an example of a species using a traditional migratory pathway over the route of expansion, suggesting that the species departs the country along the path of geographic dispersal. Since the region of regular occurrence along the migratory route leaving the country is much narrower than the breeding area, this assumption seems to be generally correct for most Bobolink populations. Direct banding recoveries are limited (Figure 2, inset), but what evidence there is supports the assumption that the eastern populations gather in the southeastern United States. Lincoln's (*op. cit.*) conclusion that the isolated western populations also retrace this route apparently is based on the very limited number of specimens and sight records in localities to the south of these areas. Absence of regular sightings in Arizona, New Mexico, and Texas suggests that the more direct route through Mexico is ignored. But since the western populations are small, the probability of recovery or sighting transient Bobolinks would not be great, and the migratory pathway of these populations should be regarded as imperfectly known pending banding recoveries or other new evidence.

The path from the southeast in the fall leads across the Caribbean directly to South America, with Cuba (Gundlach, 1874) and Jamaica (Grosse, 1847: 229) lying on

the direct line of passage. What part of these transients stop at these islands we do not know, but great flocks are often encountered and the islands may well be regular stopping places for most individuals. To the east the Bobolink becomes increasingly sparse, and in Puerto Rico it is uncommon in migration (Wetmore, 1927). Observation points are lacking to the west short of the coast of Mexico, so that it is impossible to know what part of the migration departs directly from the Gulf coast between Florida and Texas, but occasional Central American records make this interpretation plausible.

In South America the route and schedule of the Bobolink are poorly known, but the passage follows roughly the western slope of the Andes to the winter quarters in the open grassland of southern Brazil, Uruguay, and northern Argentina. Apparently the species is nomadic in the winter area (Chapman, 1890; Wetmore, 1926), and the southward movement may not be completed before January.

Spring migration. We know still less about the northward migration, but the movement surely is slow in getting under way, for Gundlach and Grosse (*op. cit.*) report nuptial males in the Caribbean Islands only two or three weeks before the main movement through the southeastern United States in May. In their rush northward the birds may pass Cuba without stopping, for Ramsden (1914) reports that at Guantánamo they are rare in spring and usually pass at night without stopping. Probably the route followed through the United States in spring is not greatly different from the fall migration, although it has been suggested that the Mississippi Valley is more favored at this time. This may be due to the location of stopping points more than to a seasonally separate set of routes. In spring the edge of the passage advances slowly; in fall the initial movement may be extensive. An excellent example of this unseen fall migration, leaping over wide geographic areas, is the discovery of four Bobolinks at a television tower kill in Kansas. Only two previous fall records for the state preceded this occurrence (Tordoff and Mengel, 1956), and Bobolinks would not have been recorded this time if they had not perished in an accident.

Daily pattern of migration. The Bobolink is neither a strict nocturnal nor diurnal migrant. It is certainly a prominent night traveller in the fall (Graber and Cochran, 1960) but travels partly by day at this season as well, and the same is true of the spring migration.

Direction changes in migration. Migratory direction changes may be broadly classified into two categories: (1) those accomplished in following the natural course of migration and (2) those that are made by birds off the usual line of movement in initiating their return to the main line of migration. The basic change in direction that most birds must make in Florida in spring and fall is an example of the first kind of change. Are there other shifts of this sort along the way? Chapman (1909) suggests that the Caribbean crossing is along three separate routes, the main one extending directly across Cuba and Jamaica to northern South America with secondary routes extending from Florida "to Yucatan and thence southward along the eastern coast of Central America" and "eastward to Porto Rico and thence southward through the Lesser Antilles." Chapman thus implies direction changes in the Caribbean area in the fall. But I would like to emphasize that these analyses are based on museum specimens and resting flocks of birds, not on directional analysis of flying migrants. It is, therefore, possible to suggest an alternative interpretation, namely that the birds that filter into places such as Yucatan and Puerto Rico are making a direct flight across the Caribbean and have not departed from Florida at all. Just as in the case of the analysis of the path of the western populations, it is a matter of analyzing the volume of migration at potential departure and landing stations. For the Bobolink,

available information does not permit this analysis, and Chapman's (*op. cit.*) interpretation of separate trans-Caribbean routes is not acceptable. The evidence that would be most useful in resolving this question would be reports of flight directions of Bobolinks in flight over the sea, leaving land areas, or making land falls.

With respect to traditional flyways in South America, there simply is no information on which to base a useful discussion.

The second kind of direction change, which is in the nature of corrections, is quite relevant to the following experimental studies and their interpretation. There is only one useful observation in this respect—Bryant's (1859) observation of a flock of spring Bobolinks departing the Bahamas in a westerly direction. Since he does not indicate the exact site of the observation, we cannot be sure that this flock was departing toward the mainland, but the westerly direction of flight is suggestive. It would be most useful if observers in this area or on any of the Caribbean Islands where Bobolinks are birds of passage would observe and record the direction of departing flights.

METHODS

Direct observation of migratory fluttering. Kramer's pioneer experiments were made by observing the facing direction of birds during migratory fluttering in a circular cage. This behavior, with wings extended and bill pointed obliquely upwards, is probably a widespread characteristic of caged migratory passerines. In addition to the Starling it has been reported for a European cuckoo (see Hudson, 1923), five species of *Sylvia* (Saint Paul, 1953; Sauer and Sauer, 1959) and *Lanius* (Kramer, 1949), and occasionally in *Zonotrichia* (Mewaldt, *in litt.*). This behavior was used to measure migratory orientation in the direct observation studies of Bobolinks reported here. The sequence of activities that precede and accompany this behavior in the Bobolink is described elsewhere (Hamilton, ms).

In their studies of night orientation of several species of *Sylvia* the Sauers recorded the duration in seconds of fluttering in each direction. This is perhaps the best measure of the migratory response of these tiny birds, which sometimes flutter continuously. But the Bobolink tends to flutter in spurts, and usually each spurt lasts less than 10 seconds. For this reason the number of fluttering bursts in each direction seems to be a more easily handled response measure. The facing direction was recorded both for fluttering directed to the center of the cage and outward from the ring, but it was rarely necessary to interpret any facing as directed to a point other than perpendicular to the tangent of the bird's position on the ring (Figure 1A). This contrasts with the behavior of the *Sylvia* species observed by the Sauers, which frequently faced obliquely on the ring during fluttering.

For direct observation of migratory fluttering the experimental apparatus (Figure 1A) closely follows the design adopted by Sauer (1957). A circular central perch 40.6 cm in diameter was surrounded by a cylindri-

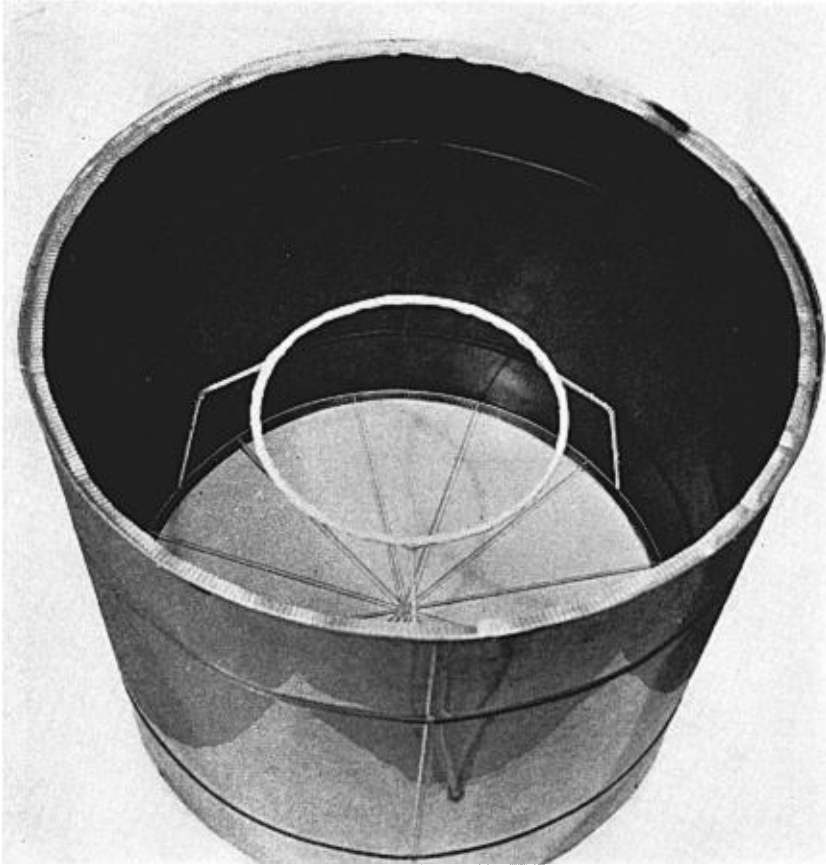


Figure 1A. The experimental apparatus. Direct observation chamber with enclosed central fluttering ring.

cal aluminum screen painted flat black. A Plexiglas top and bottom gives the bird unimpaired visibility of the overhead sky and allows the observer to watch. The bottom plate was marked into 12 sectors, and the observer lay on his back below the apparatus recording time and direction of fluttering with a switch panel connected to an Esterline-Angus operations recorder. Intermediate facings were recorded by simultaneously closing two switches, thus permitting the observer to record the facing direction according to his estimate of the nearest of 24 directions.

The circular peripheral screen was 89 cm in diameter and 76 cm deep. Tripodal legs held the fluttering ring 46 cm from the floor so that from the position of the bird's eye a view of approximately 100 degrees of the sky was available to the bird at any point on the ring.

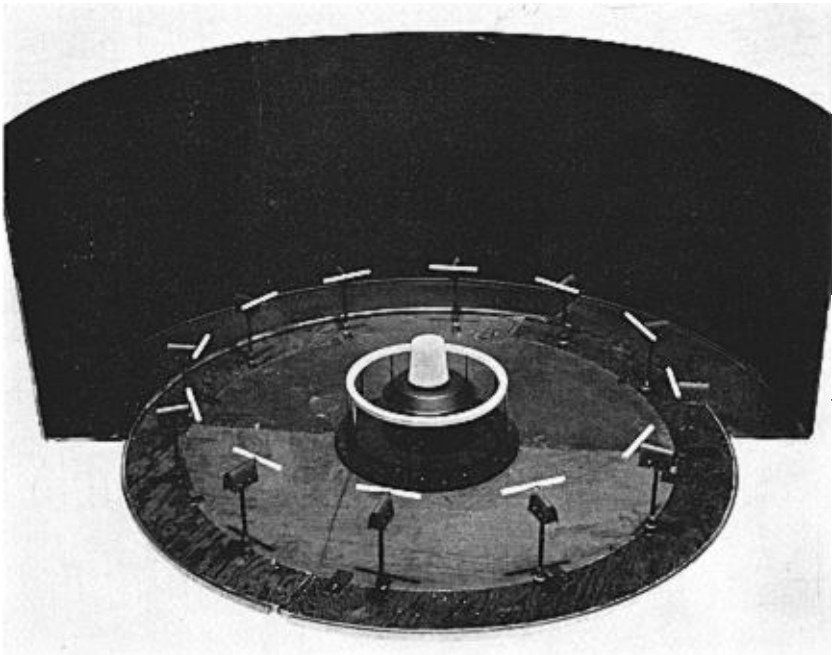


Figure 1B. The experimental apparatus. The automatic registration device with peripheral perches to record the number of times the bird landed on each perch. Only half of the terrain screen is in place, and the holding net has been removed to show the features of the apparatus more clearly.

The apparatus was rotated at 30-minute intervals so that no physical features of the apparatus could provide consistent cues for compass orientation. Occasionally this procedure was omitted because the disturbance of the birds caused associated blockage of migratory activity.

When the migratory call notes were recorded and played back, the birds in the apparatus could often be stimulated to activity. Birds already active could be made to continue activity for longer periods of time than normal by this device (Hamilton, 1962). The playback device was placed at random positions at the side of the apparatus, but these calls apparently did not influence the directional aspect of the response in the enclosed test cylinder. The observer manipulated the playback according to the response of the bird. Increase in both duration and volume was sometimes necessary to induce activity, and often no amount of auditory enticement was effective; but this was only true of birds that had shown no activity earlier in the evening.

Automatic registration of migratory orientation. The automatic registration device was patterned after that used by Mewaldt and Rose (1960).

Their cage was like that employed by Kramer but with peripheral perches replacing the central fluttering ring. These perches activate microswitches to record the activity. A 12-perch arrangement was substituted for the eight perches used by Mewaldt and Rose. A central ring 38 cm in diameter surrounds the peripheral registration perches (Figure 1B). These outer perches are 20 cm high and 40 cm from the edge of the vertical 76-cm landmark screen. From the bird's position on the central perch a section of approximately 102 degrees of sky was visible. At the recording perch the bird could see to within 26 degrees of the horizon, with a total view of 128 degrees of the sky available from all positions of the bird in the apparatus taken together.

A 24-perch arrangement was tried first, but the size of the apparatus combined with a minimum perch size necessitated close positioning of perches with no significant gap between them. Thus the perches formed a nearly complete ring. With this arrangement the behavior of the bird changed. Instead of moving from the central ring to the peripheral perch and back again, or from the recording perch to the enclosing screen and back to the recording perch, the bird sidled along the 24-perch ring. In preliminary tests made with such an apparatus, this sidling behavior seemed to induce a greater scatter into the response record than that indicated by the 12-perch arrangement. Thus, in order to take advantage of additional perches, a much larger apparatus would be required.

In the automatic registration experiments each switch closure was measured by an electric counter. Usually a perching movement recorded only one unit at the counter, but occasionally the bird bounced on the perch and produced a double count. The microswitch was covered with a plastic shield that did not permit the bird to land, but the bird could move back and forth to the vertical enclosing screen and trigger frequent counts. Also, the birds could, and occasionally did, flutter on the perches, lifting the weight from the perch so that the lever arm of the switch was primed to record again at the end of the fluttering action.

Comparison of the two recording methods. The two methods produce essentially the same result. The basic difference is in what is recorded. With the direct observation chamber the bird is required to perform on a small, circular ring, and the facing directions of flight-intention movements are measured. Actual locomotion is prohibited by the dimension and arrangement of the apparatus. On flying up the birds strike the wall of the apparatus or the Plexiglas lid of the chamber and fall to the bottom of the apparatus. The consequences of taking off are soon learned, and after a few attempts takeoffs are rare. It is surprising that the fluttering in place does not condition as well, but there is no evidence that the amplitude of the response is in any way inhibited by the cage environment if other

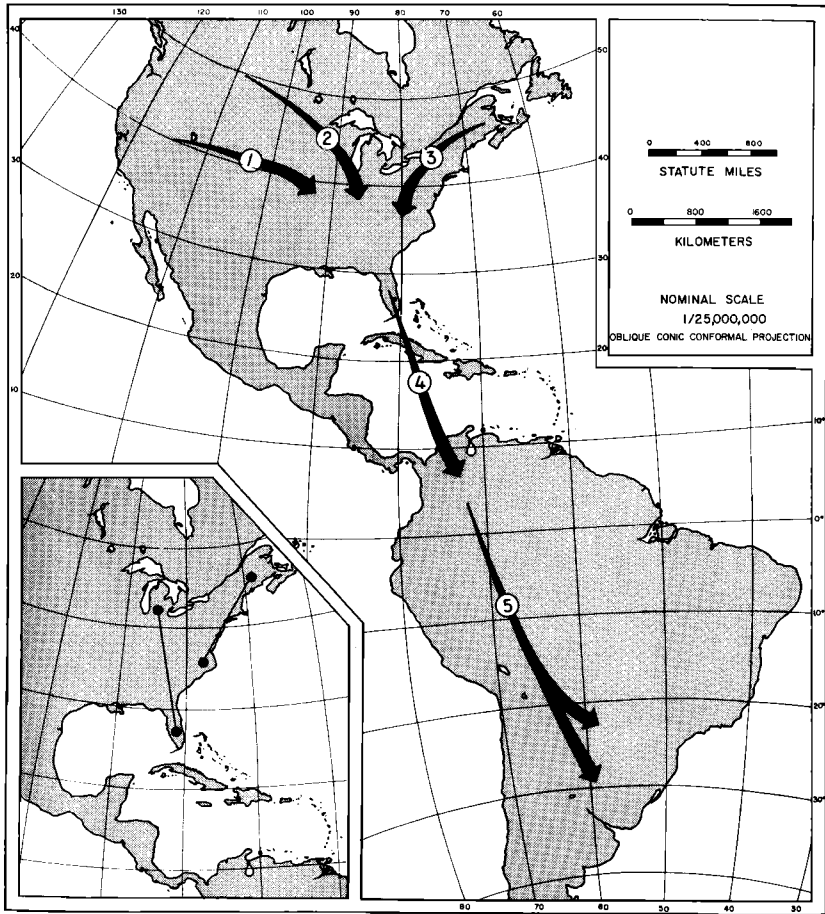


Figure 2. Migratory routes of Bobolinks from the breeding grounds to the winter quarters. See the text for a discussion of the reliability of the interpretations indicated by the map. The inset is a portion of the same map with connected dots showing the only two recoveries of banded Bobolinks.

environmental influences are not disrupting or inadequate. The bird may flutter several hours almost nightly for weeks.

By contrast, the automatic registration device primarily measures overt locomotion. It is, therefore, necessary to place the registering perches well toward the periphery, and the dimension of the cage must be considerably larger to record the directional component accurately. The large automatic registration device measuring locomotion is well suited to work under natural skies. But under the artificial sky of a planetarium (see Sauer, 1957) the dimension of such an arrangement introduces new inaccuracy,



Figure 3. Nocturnal response of an adult male North Dakota Bobolink tested under natural San Francisco skies during two fall months. The response was comparatively strong and directional on clear nights (A-D, F, G) but was weak on two intervening overcast nights (E).

due to magnified parallax problems resulting from the greater range of movement possible to the bird.

An additional difference between the two methods of registration pertaining to the detection of ambivalent behavior and its interpretation will be discussed with results demonstrating this phenomenon.

In the wheel diagrams, which accompany the presentation of data, the actual number of responses is indicated in the marginal ring. The heavy black arrow is a mean computed from the mode plus the three choices on either side of it. In the case of the direct observation record, observations were made in 24 sectors, and the intermediate sectors were divided between the bordering divisions before the vector was tabulated.

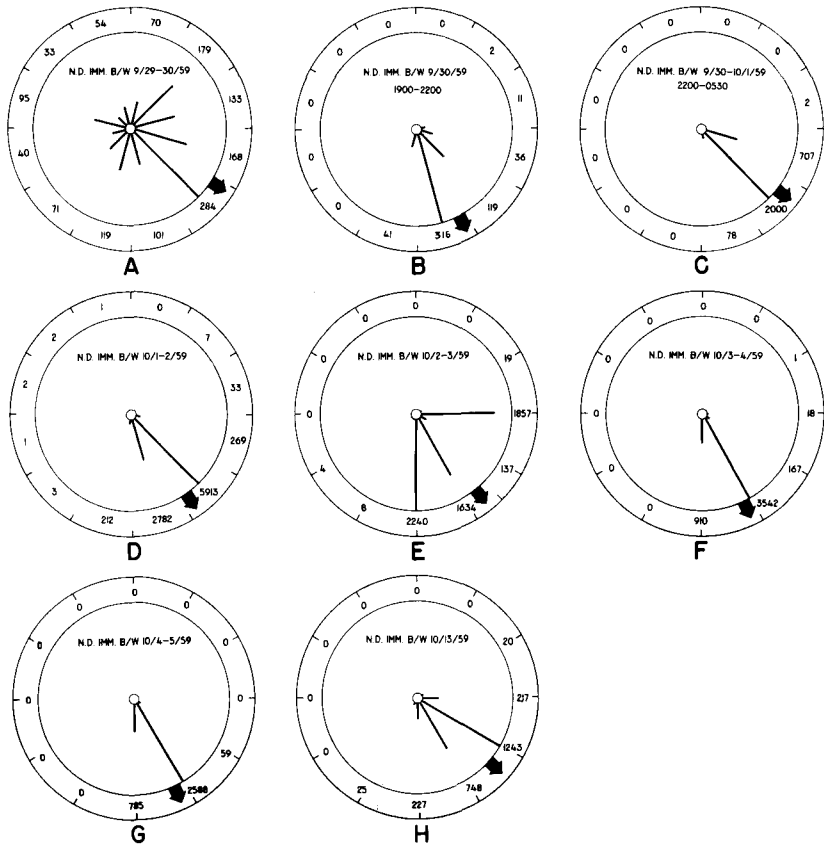


Figure 4. Nocturnal response of a young North Dakota Bobolink tested under natural San Francisco skies in the automatic registration apparatus. The result shown for Diagram A was the first night this bird had been in the apparatus. Diagram E shows the possible influence of searchlights.

POPULATION ANALYSES

North Dakota birds under the clear, moonless fall sky. Birds from Kenmare, North Dakota ($48^{\circ} 40' N$, $102^{\circ} 05' W$), were the subjects of the majority of experiments. These birds were taken in the postbreeding period of the first week of August 1959 and 1960. Mrs. Ann Gammell, who captured the birds with mist nets, reported that at the time the birds were taken no migratory concentrations had appeared, making it seem likely that they were breeding birds from the immediate vicinity of Kenmare. These birds were flown to San Francisco and immediately exposed to the natural San Francisco sky ($37^{\circ} 46' N$, $122^{\circ} 27' W$).

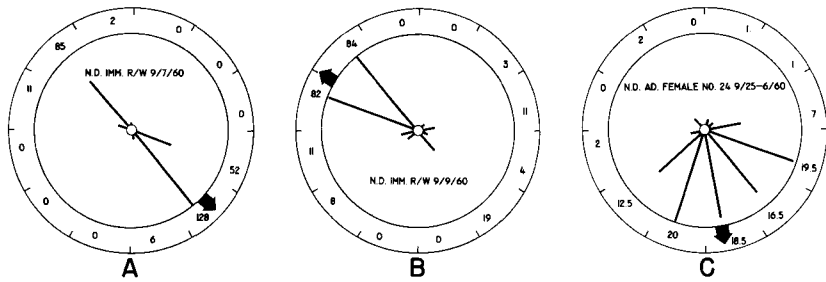


Figure 5. Some tests of North Dakota Bobolinks using the direct observation technique. The numbers represent number of fluttering movements in each direction.

The directional heading recorded under the natural San Francisco sky showed a remarkable uniformity in preferred direction, both in experiments done in the automatic registration cage (Figures 3 and 4) and the direct observation record (Figure 5). The trend is to the southeast, with the vector of the preferred direction ranging from 131° to 154° . In these and all subsequent figures the longest bar denotes the mode of the choices while the shorter bars indicate per cent of the mode in other directions. The average fall vector of experimental North Dakota birds held under natural skies two weeks or more was 140° . Extended from the experimental site (Figure 10), this course would lead the birds along the west coast for some distance and out to sea. Such a course leads neither to the winter quarters nor returns the bird to the migratory pathway but closely parallels a direct course from North Dakota to northern Florida (135°), a probable point on the fall migratory route of most Bobolink populations. This result suggests that the orientation mechanism of birds held under these conditions does not permit navigation, *i.e.*, determination of position and direction. But it does not mean that these same birds are unable to

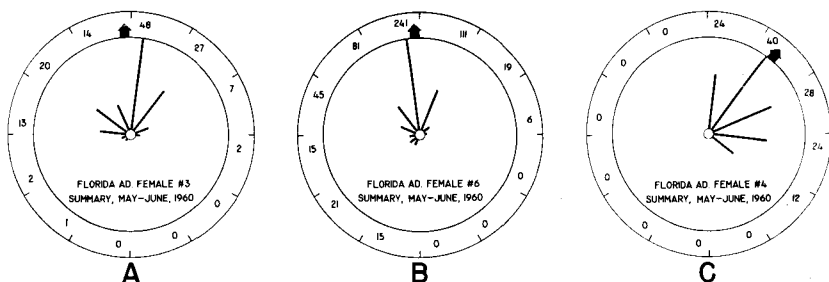


Figure 6. Spring orientation of three different adult Bobolinks taken from transient flocks at Gainesville, Florida, and tested after two weeks or more of residence in San Francisco.

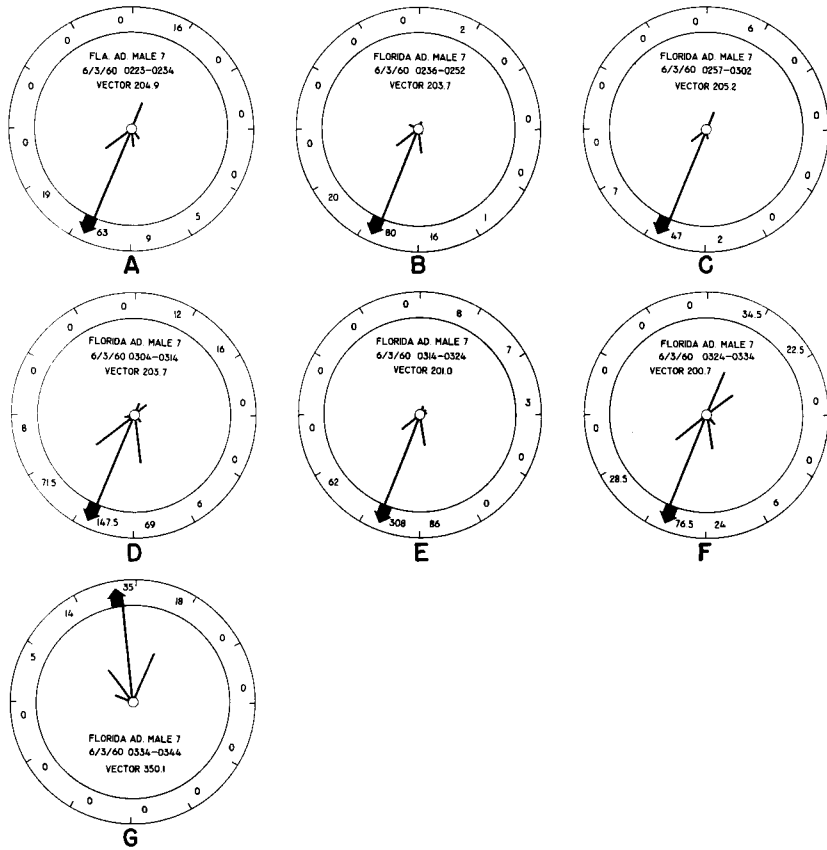


Figure 7. A continuous record of a night's performance by a Florida-caught male. The numbers represent number of seconds of fluttering in each direction.

make such a determination under other more favorable or more appropriate circumstances. Interpretation of the parallel course accompanies the discussion of the internal clock.

Experiments with Florida-caught birds. In the spring of 1960 a group of birds was taken from migratory flocks near Gainesville, Florida. These transient Bobolinks showed exceptionally strong migratory responses in the experimental apparatus during the following month. In Figure 6 the number of fluttering responses of three of these birds is indicated for the period 15 May-6 June. All had been exposed to the San Francisco sky for at least a week prior to the initiation of experimentation. In Figure 7 a series of responses of another Florida-caught bird are indicated in number of seconds of fluttering rather than number of fluttering bouts. A different

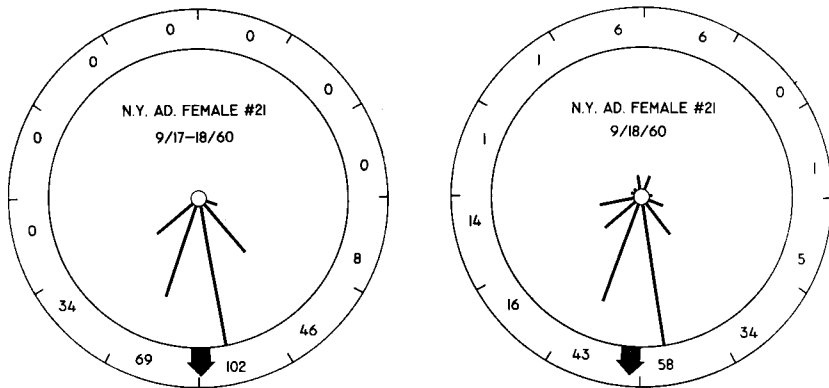


Figure 8. Migratory response of a New York adult female Bobolink on two consecutive nights.

measure of responsiveness was used here in order to indicate more accurately the strength of the response of this bird, and to compare the response directions over shorter periods of time.

The vector of the response among these Florida-caught birds differs widely. Females 3 and 6 and male 7 all showed general agreement in preferred direction just to the east of north, but female 4 preferred a direction well to the east. Perhaps this may be explained by the heterogeneous breeding origin of this transient population. Because the bulk of all North American Bobolinks apparently enter the country through Florida, it is possible that a sizable transient flock at a locality such as Gainesville would be composed of individuals of diverse breeding origin. If this is true, then northern Florida is probably a critical dispersal point for such flocks. The preferred directions of Florida-caught birds are in general agreement with anticipated courses leading from Florida to the breeding grounds. No individual demonstrated a westward tendency, which is perhaps not surprising since the western populations are small and the probability of taking such a bird from a transient flock even if these populations move through the southeast would not be high.

These considerations suggest that orientation determinations may permit the analysis of migratory and breeding origins of transient populations.

Experiments with New York breeding population. A small number of birds were taken near Ithaca, New York, in June 1960. Usable data (for moonless nights, see p. 225) were obtained from only one New York bird. This bird responded on two consecutive nights in an almost due south direction (Figure 8). While these limited data are not conclusive, the response on these two nights was nearly the same, and does not overlap the range of variation exhibited by the North Dakota population, suggesting

that local populations have different preferred migration directions based on their geographic origins.

Two hand-reared New York birds were used in a number of experiments. The response of these hand-reared birds alternated between north and south, with the southward trend almost due south. Because the response was mixed, it is difficult to be certain that the southward part of the response does in fact measure the directional choice in this sector rather than the back azimuth of the northward tendency. There is no assurance at this time that these two measures are the same, and it thus seems inappropriate to utilize such data to determine preferred migration direction in relation to geographic locality.

Reversed migration. The response of Florida male 7 on the night indicated in Figure 7 was largely reversed, *i.e.*, directionally appropriate for fall rather than spring migration. Through the earlier hours of the evening this male made only sporadic fluttering attempts, all directed to the southeast. After 02:00 the response level increased, and activity was nearly continuous the rest of the night. The response was partly ambivalent (see below), with brief flutterings to the north (Figure 7, A,C,F). In the last minutes before dawn, however, the basic heading changed (G), and this male fluttered strongly facing north until he ended his nocturnal activity. At the time of the final fluttering, migrating thrushes were still passing overhead, but the early-morning Robin chorus had already begun and the dawn sky had lightened noticeably.

Sauer (1957) and Sauer and Sauer (1959) interpret seasonally inappropriate responses such as this as the experimental equivalent of reversed migration. They point out that such ambivalent responses occur in numerous stressful situations such as partial overcast, physical disturbance, and conflicting orienting cues.

Ambivalent behavior. On several occasions ambivalent directional choices were noted, *i.e.*, frequent alternation in directional choice between spring and fall directions. No behavior such as this was noted in the experiments with North Dakota birds in the fall of 1959 for birds held under natural skies. The Florida male whose record appears in Figure 7 was the only bird that demonstrated such an ambivalent response in the spring of 1960. Perhaps of particular interest is the strong tendency toward the north in the final minutes before fluttering stopped.

In experiments conducted in the fall of 1960 under natural skies, a more pronounced tendency toward ambivalent response and reversed migration was noted. Two hand-reared New York birds that were used in most of the experiments in the fall of 1960 showed a strong northward fluttering tendency. These are the only experiments done under clear, moonless skies that are not presented in full here. At the time these experiments

were performed, the northward tendency was assumed to be an artifact of either the experimental situation or of the location of the apparatus. For that reason the apparatus was moved to different localities in and around San Francisco to alter local situations. However, the trend, almost true north, persisted and was the choice of both of these birds. There was also a small amount of fluttering toward the south.

While my hand-reared birds were kept on a natural lighting schedule, they were not exposed to a fully natural horizon situation. During the month prior to the initiation of migration activity (15 July–15 August 1960) they were housed on the balcony of an apartment. Here the horizon was raised in all directions and was especially high toward the face of the building.

Based on Kramer's (1957) discovery concerning the role of artificial experimental horizons in creating "orientation cripples," it seems possible that these birds may have encountered similar difficulties. The Sauers noted no tendency for their hand-reared garden warblers to be less effective in their directional choice than adults, even though their birds were held in soundproof rooms without view of the natural horizon.

In addition to these two hand-reared birds, a North Dakota juvenile (Figure 5) showed a similar tendency to orient either in an ambivalent fashion or in the reverse of the anticipated migratory direction on two of three nights that it was tested.

These ambivalent responses were noted only by the direct observation technique. It cannot be stated at this time whether this difference is due to the actual lack of such responses in the experiments done in the automatic registration cage or whether it may be due to an actual difference in the behavior of the birds in these two series of experiments.

ORIENTING CUES

Response under overcast. The area where these experiments were carried out, a coastal area bathed regularly by high fog during the migratory period, offers an exceptional opportunity to study the effect of complete overcast on nights when other meteorological conditions are essentially the same. The most frequent response to overcast was waning response intensity and subsequent termination of activity. This aspect of the response under overcast skies is demonstrated by the response of an adult male North Dakota Bobolink during two moonless periods in the fall of 1959. During the first of these periods (Figure 3) the response amplitude was consistent throughout. In the second moonless period, however, two completely overcast nights were correlated with a completely changed response pattern. On these nights the response was faint and the direc-

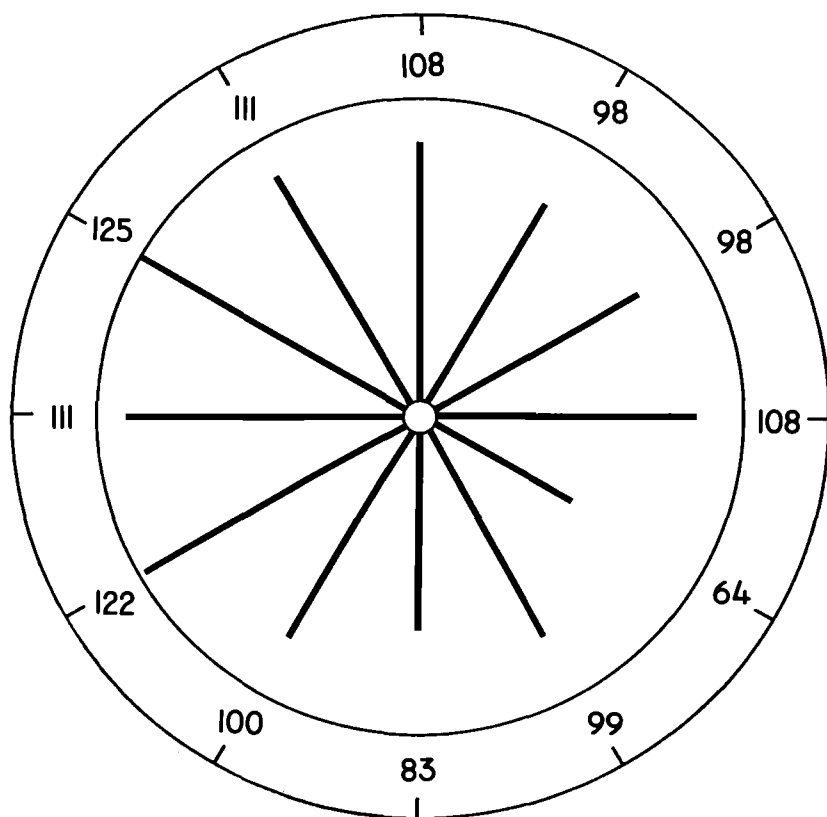


Figure 9. Combined "directional" response of three Florida-caught birds under conditions of complete overcast.

tional aspect of the response that had been so consistent on clear nights was lacking.

When condensation formed on the Plexiglas lid of the direct observation apparatus, the response amplitude faded, and when the brighter stars were no longer visible to the observer looking through this apparatus from below, the experimental bird usually stopped fluttering. Thus, it was extremely difficult to obtain data on the directional aspect of migratory fluttering under conditions of complete overcast. In the spring of 1960, however, a group of birds originally taken from migratory flocks in Florida showed exceptionally heavy migratory responses that persisted under fully overcast skies (Figure 9). The random scatter contrasts with the highly oriented behavior of these same birds under clear skies.

These data suggest that the orienting cues in the night sky are motivating as well as orienting, but we should reserve judgment on this conclusion

pending more rigidly controlled experiments. It is possible that the darkening (or brightening in urban areas) of the sky on overcast nights influences the responsiveness of the bird. Experiments conducted by Wagner (1957) with caged birds lend support to this interpretation. He found a maximum responsiveness at illumination levels of approximately 10 lux (0.1 foot candles). Under brighter or darker conditions the amplitude waned.

The response under overcast conditions is one of the most important aspects of bird orientation research at this time. In experiments with trained ducks I found (Hamilton, 1962) that they could not determine direction in the dawn and dusk periods when neither the sun nor the stars are visible to man. Probably the comparatively homogeneous sky at these times is for orientation purposes equivalent to an obscured overcast sky. Bobolinks seldom respond in the test apparatus or in a registration cage during the evening twilight period. But the vertical screen of the test apparatus, restricting the field of view of the bird to 26 degrees above the horizon, obviously delays the time of apparent sunrise for the bird in the apparatus. Yet the activity of the bird starts on schedule, soon after actual sunrise. At this time the response has been nearly random. We cannot say with any assurance that this response represents migratory locomotion as opposed to the usual (and perhaps usually random) daily activity, but the result is suggestive. No adequately controlled experiments at later times in the day when the sun has risen above the artificial skyline have been made as yet, but the little response that has been measured seems to be directional.

THE ORIENTATION MECHANISM

The use of stars as orienting cues. Directional response under clear skies and scattered response under overcast suggest that the experimentally detected directional trend may be based on some feature of the clear night sky. The moon is certainly not essential, since in the experimental situation it only disrupts the directional tendency (see below) and fully appropriate responses are possible in its absence. A host of other potential orienting features in the night sky prevent the conclusion that the stars are in fact the orienting feature, but the persistence of appropriately directed fluttering under partial overcast seems to rule out such features as the zodiacal light and perhaps the Milky Way.

Behavior under moonlit skies. The orientation data presented here represent results on nights when the moon was not in the sky or after moonrise or moonset.

With the moon visible, the birds in the apparatus faced either the moonlit wall or the moon itself. This effect could be detected easily by noting the gradual shift in preferred direction on moonlit nights, a result con-

trasting with the fixed course that the same birds maintained throughout clear, moonless nights. The results of such experiments under moonlit night skies seem to contribute little to an understanding of the orienting cues used by migrating Bobolinks, and they are excluded from further consideration of migratory pathways here. Heavy migrations do pass on moonlit nights (Kramer, 1957; Lowery and Newman, 1955), so it seems probable that these phototactic responses are experimental artifacts. This is not to say that these responses are inadapative, for they may have adaptive bases in other contexts such as giving direction to the initial surge from the ground, or simply in the basic physiological organization of the bird in relation to other stimulus situations.

In view of the preceding statements and discussion of the influence of moonlight, most of the data obtained in the automatic registration device must be eliminated from further consideration. This is because there was a moon visible most nights during the experimental seasons. No other data have been omitted from experiments done to date except for a few experiments with hand-reared birds previously discussed.

Influence of searchlights. Figure 4E indicates the response of a bird during a period of heavy searchlight activity, a seasonal phenomenon of the fall California sky closely correlated with the appearance of new automobiles on local markets. The directional aspect of the response remains essentially the same, and the exceptional scatter can probably be attributed to the bright, sweeping overhead lights.

Orientation following geographic displacement with time shift to local time. Displacement of the experimental birds to San Francisco naturally introduces new lighting schedules and the internal clock is probably reset in a few days. Schmidt-Koenig (1960) found three or four days sufficient to alter the clock setting of pigeons, and, based on preliminary results with Bobolinks, nearly the same time requirement seems implicated. Once reset the clock provides no information about the bird's location, for the bird could be anywhere along the parallel passing through San Francisco (the experimental site) and extending around the world. If the experimentally determined vector for the North Dakota population is plotted from the point where this parallel crosses the migratory route of this population, then this direction coincides with the continuation of the pathway from this point (Figure 10). The close fit of the experimental result to this interpretation seems to be a further demonstration of the correctness of the celestial orientation interpretation of the result.

These experiments with birds in phase with local time but from different geographic areas, which provide the bulk of the data presented here, throw additional light on the role of the internal clock in relation to the orientation mechanism. This result rules out the possibility that the birds are

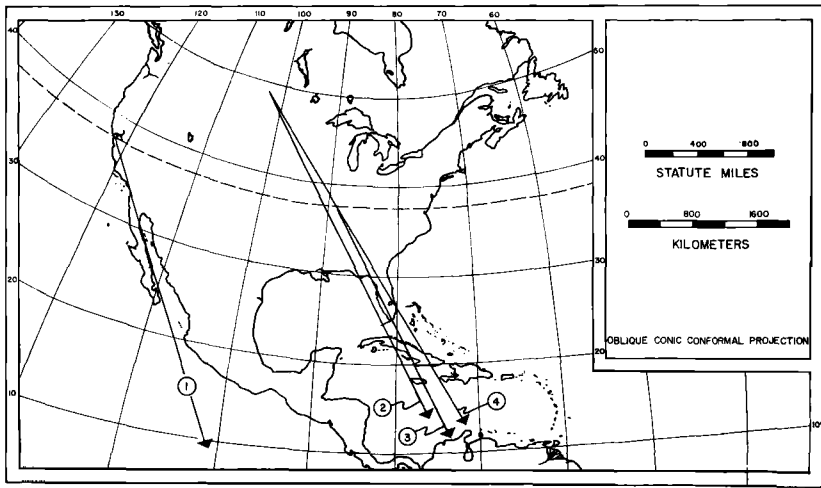


Figure 10. A geographic interpretation of the result of the performance of North Dakota Bobolinks in California. See the text for a full discussion.

using some feature of the "goal" to orient the migration behavior shown in the apparatus. If the birds were using this category of cues, then the orientation direction at the displaced experimental site would be to either the winter quarters, the home (breeding site), or some stop along the migratory route. But this was not the result. Instead, there was a preference for a course paralleling the natural migratory route. Such a pathway could be based only on some cue (such as the earth's magnetic field, Coriolis Force, or celestial bodies) providing basic directional information at any point on the earth's surface. Since other data demonstrate the stars to be the probable orienting cues, it seems likely that the parallel course is based on an internal clock shifted to local time and an interpretation of the celestial patterns on the basis of this local time rather than a compensation for geographic displacement. It is possible, of course, that the time shift, which must be a physiological phenomenon, impinges on the memory of the bird so that the bird is not left without information about its geographic location on the parallel. All that can be said is that under the conditions in the orientation cage the response provides no evidence that such a recollection has been made.

The annual clock. While an internal clock has been found in every thoroughly investigated organism, these clocks seem adapted to only short-term cycles. In migratory birds, however, an endogenous clock with an annual periodicity seems implicated. The sidereal (stellar) day is approximately four minutes shorter than the solar day, a difference indicating the rate of annual advance of the earth in its orbit about the sun. This

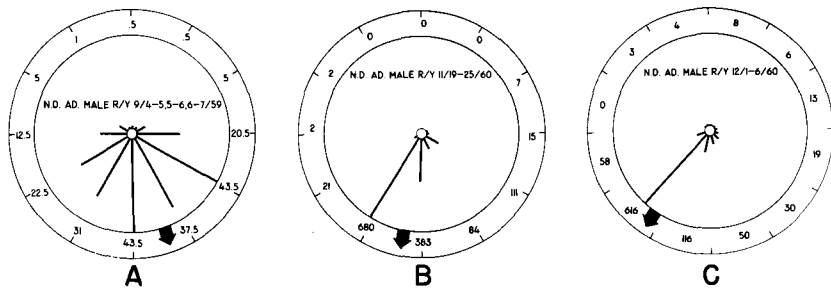


Figure 11. Fall migratory orientation of an adult North Dakota Bobolink. **Diagram A** shows the response during these moonless nights at the beginning of the migratory season. **Diagram B** and **C** summarize the response of this same bird under similar conditions nearly three months later.

simply means that a particular star rises four minutes earlier every night. If a bird's time schedule is based on only the solar schedule, then star-compensated directional tendencies would become increasingly inaccurate by the directional component of this four minutes each day. On the basis of the experiments reported here, it seems likely that the stars involved are culminating south of the 38° latitude of the experimental site. If this assumption is correct and the bird does not compensate for the stellar day, then the orienting cues and thus the directional tendency would shift clockwise (to the west) through the season.

One bird, an adult North Dakota male, responded very early in the season in a direction close to that obtained for other members of this population (Figure 11A). This bird was not tested again under moonless conditions for 74 days. At that time in late November and from then into early December the response was no longer southeasterly but had shifted to the southwest (Figure 11B, C). The direction of this shift is that predicted if the bird did not compensate for seasonal stellar-time advance. The direction of the late-fall result does not agree with the result obtained from any other North Dakota bird earlier in the fall. The apparent acceleration of the rate of shift during the relatively short period between the result presented in Figures 11B and 11C suggests that the shift is not based on a single, linear time shift of a fixed number of degrees per day. And the total shift is well under the $75^\circ+$ shift anticipated if a celestial body with the sun's apparent motion were not being compensated for.

These results were, of course, obtained at a time when Bobolinks have normally vacated the latitudes where the experiments were conducted. The experimental birds were thus presented with the "unnatural" problem of taking a direction based on skies that they would not normally see.

The preceding discussions do not imply that star patterns are the only

cues used by Bobolinks in migration. It seems more likely that directional choices in migration are oriented, at least occasionally, by additional information. Much of the migration is during the day, perhaps especially so in spring, at least in the United States. It seems likely that the sun and other cues will be used during this part of migration. Elsewhere (Hamilton, ms) I emphasized the role of social phenomenon in direction maintenance during migration.

Terrain features may play an important role in correcting courses and perhaps even in maintaining a basic direction (Hochbaum, 1955) in relation to familiar landmarks, especially when celestial cues are obscured by overcast. The celestial heading of the Bobolink may be an intercept course, adapted to intersecting coastlines with subsequent landmarked-based coasting (Lack and Lack, 1953) or celestial correction rather than direct overseas departure. The directional trend of the New York population, for example, does not lead directly to Florida but to the Atlantic Seaboard. We know that great flocks of Bobolinks gather along the coastal marshes in these areas, subsequently reaching departure points in Florida.

A number of other species also apparently fly intercept courses. For example, the flight direction of the massed movements of waterfowl in the Midwest, when traversing great stretches of open and relatively featureless prairie country, is roughly to the southeast. When these movements reach the Mississippi River the flight direction turns to the south, following this major waterway (Bellrose, 1957). The flight of displaced Common Terns to the southeast (Griffin and Goldsmith, 1955) may be explained in a similar fashion, the southeasterly course being an adaptation to intersecting the coastline that runs northeast-southwest. And it is possible that the fixed direction flights that Bellrose (1958) has observed for several species of displaced waterfowl have a similar adaptive basis. Even so, the basic direction of flight is probably based on celestial cues. This statement seems to have increasing comparative applicability.

ACKNOWLEDGMENTS

I am indebted to Dr. and Mrs. Robert Gammell, Kenmare, North Dakota, for trapping and shipping North Dakota Bobolinks. Their cooperation and enthusiasm was a strong impetus in the initiation of these studies and continued throughout the program.

The continual support of Dr. Robert C. Miller, Director of the California Academy of Sciences, together with the free use of the Academy's facilities and the cooperation of the technical staff, made these studies both possible and pleasurable.

Dr. E. G. Franz Sauer, California Academy of Sciences, reviewed the manuscript and provided stimulating discussion of ideas presented here.

Preliminary experiments were supported by a faculty research grant from the University of California at Berkeley. The Zoology Department at Berkeley provided space and supplies. Subsequent support for work at the California Academy of Sciences came from the United States Air Force through the Air Force Office of Scientific Research of the Air Research and Development Command, under contract No. AF 49(638)-825.

SUMMARY

The orienting cues used by Bobolinks, a transequatorial migrant, were experimentally analyzed. By observing or recording automatically the facing direction or the restricted locomotion of a bird confined to an experimental apparatus, the orientation of migratory behavior was analyzed.

Since vertical shields prevented the bird from seeing local landmarks, and since the experimental apparatus was rotated from experiment to experiment, the only constantly available orienting cues were features of the sky. The results can be best interpreted on the basis of the use of stars or star patterns and the internal clock as the bird's direction-finding mechanism. Under complete overcast, orientation becomes random or, more often, the bird fails to respond at all.

Birds used in these experiments were largely from a North Dakota breeding population. The experiments were all done in and around San Francisco, California, with the birds held on local San Francisco time either in indoor cages or under the natural sky. These birds responded by taking a migratory course in the apparatus paralleling the natural migratory route of this population from North Dakota to Florida. A limited number of experiments with a New York population indicate that this breeding population possibly takes a preferred migration course different from the North Dakota population. The course is directed generally to the south close to the direction of the natural migration from this area.

A consideration of the course taken by geographically displaced birds suggests that the preferred migration direction depends upon a shifted timing mechanism. The parallel flight observed for the populations tested is a result of the shifting of the bird's internal clock to local San Francisco time and the lack of compensation for geographic displacement once the internal clock has come into phase with local time.

It was possible to measure directional tendencies relating to the geographic migration trend of this species only under clear, moonless skies. When the moon or incident light from the moon shines into the apparatus the birds respond in a phototactic manner, heading toward the moon, to the center of the lighted area, or to a corner of the illuminated area of the apparatus. The diagrams presented in this paper are based only on responses on clear, moonless nights. The phototactic response under

moonlit conditions is probably an artifact of the experimental situation not materially influencing the directional choice under natural skies.

Spring-migration trends to the north have so far been obtained only for a population of birds taken in migration in Florida. Since these birds were probably of heterogeneous breeding origin, it is impossible to relate adequately the northward tendencies exhibited by these birds to geographic areas. The responses of these Florida birds showed wide scatter contrasting with the comparatively homogeneous result obtained from the North Dakota population.

Taken as a whole the experiments done to date with Bobolinks suggest that this species is capable of telling direction by some feature of the clear night sky. Both immature birds, which have never made a migration before, and adults are capable of making such directional determinations. The directional choice is probably based on the stars and the internal clock. The clock apparently does not compensate for the advance of the sidereal day in relation to the solar day. Each population of Bobolinks throughout the breeding area may have a unique preferred migration direction, at least until the migration becomes a common pathway in the southeastern United States. While the stars are obviously important to directional choices at night, other orienting cues such as terrain features and other birds of the same species, and perhaps other species in flight at the same time, may provide additional information upon which the directional course is based.

LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds. 5th ed. 691 pp.
- BALL, S. C. 1952. Fall bird migration on the Gaspé Peninsula. Peabody Mus. of Nat. Hist., Yale Univ., Bull. 7. 211 pp.
- BELLOSE, F. C. 1957. A spectacular waterfowl migration through central North America. Illinois Natural History Survey, Biological Notes No. 36.
- BELLOSE, F. C. 1958. Celestial orientation by wild Mallards. *Bird-Banding*, **29**: 75-90.
- BENDIRE, C. 1895. Life histories of North American birds. Smithsonian Inst., U.S. Natl. Mus. Special Bull. No. 3. 518 pp.
- BROECKER, W. S. 1947. Evidence for a major climatic change close to 11,000 years B.P. *Bull. Geol. Soc. Am.*, Vol. 68, pp. 1703-1704 (abstract).
- BRYANT, H. 1859. A list of birds seen at the Bahamas, from Jan. 20th to May 14th, 1859, with descriptions of new or little known species. *Proc. Boston Soc. Nat. Hist.*, **7**: 102-134.
- CHAPMAN, F. M. 1890. On the winter distribution of the Bobolink (*Dolichonyx oryzivorus*) with remarks on its routes of migration. *Auk*, **7**: 39-45.
- CHAPMAN, F. M. 1909. The Bobolink. *Bird Lore*, **11**: 137-140.
- GRABER, R. R., AND W. W. COCHRAN. 1959. An audio technique for the study of nocturnal migration of birds. *Wils. Bull.*, **71**: 220-236.

- GRABER, R. R., AND W. W. COCHRAN. 1960. Evaluation of an aural record of nocturnal migration. *Wils. Bull.*, **72**: 253-273.
- GRIFFIN, D. R., AND T. H. GOLDSMITH. 1955. Initial flight directions of homing birds. *Biol. Bull.*, **103**: 264-276.
- GROSSE, P. H. 1847. *The birds of Jamaica*. London, John Van Voorst. 447 pp.
- GUNDLACH, J. 1874. Neue Beiträge zur Ornithologie Cubas. *J. f. Ornithologie*, **22**: 113-166.
- HAMILTON, W. J. III. 1962. Celestial orientation in juvenal waterfowl. *Condor*, **64**: 19-33.
- HOCHBAUM, H. A. 1955. *Travels and traditions of waterfowl*. Univ. of Minn. Press. 301 pp.
- HOFFMAN, K. 1954. Versuche zu der im Richtungsfinden der Vögel enthaltenen Zeitschätzung. *Zeit. f. Tierpsych.*, **11**: 453-475.
- HOWELL, A. H. 1932. *Florida bird life*. Fla. Dept. of Game and Fresh Water Fish. 579 pp.
- HUBBS, C. L., AND R. R. MILLER. 1948. The Great Basin with emphasis on glacial and postglacial times. II. The zoological evidence. *Bull. Univ. Utah*, Vol. 38, Biol. ser., Vol. 10, pp. 16-166.
- HUDSON, W. H. 1923. *A hind in Richmond Park*. Dutton & Company, New York. 296 pp.
- KRAMER, G. A. 1949. Über Richtungstendenzen bei der nächtlichen Zugruhe gekäfigter Vögel. *Ornithol. als biol. Wissenschaft, Festschrift für E. Stresemann, Carl Winter, Heidelberg*. Pp. 269-283.
- KRAMER, G. A. 1952. Experiments on bird orientation. *Ibis*, **94**: 265-285.
- KRAMER, G. A. 1957. Experiments on bird orientation and their interpretation. *Ibis*, **99**: 196-227.
- LACK, D. 1959. Migration across the North Sea studied by radar. Part I. Survey through the year. *Ibis*, **101**: 209-234.
- LACK, D. 1960. Migration across the North Sea studied by radar. Part II. The spring departure 1956-59. *Ibis*, **102**: 26-57.
- LACK, D., AND E. LACK. 1953. Visible migration through the Pyrenees: An autumn reconnaissance. *Ibis*, **95**: 271-309.
- LINCOLN, F. C. 1939. *The migration of American birds*. Doubleday, Doran and Co., New York. 189 pp.
- LOWERY, G. H., JR., AND R. J. NEWMAN. 1955. Direct studies of nocturnal bird migration. *In Recent studies in avian biology*, University of Illinois Press. Pp. 238-263.
- MCATEE, W. L. 1919. Observations on the shifting range, migration and economic value of the Bobolink. *Auk*, **36**: 430-431.
- MEWALDT, L. R., AND R. G. ROSE. 1960. Orientation of migratory restlessness in the White-crowned Sparrow. *Science*, **131**: 105-106.
- RAMSDEN, C. T. 1914. The Bobolink (*Dolichonyx oryzivorus*) as a conveyor of Mollusca. *Auk*, **31**: 250.
- RIDGWAY, R. 1876. United States geological exploration of the fortieth parallel. Part III. Ornithology. Pp. 303-669.
- SAINT PAUL, U. v. 1953. Nachweis der Sonnenorientierung bei nächtlich ziehender Vögeln. *Behav.*, **6**: 1-7.
- SAUER, E. G. F. 1957. Die Sternorientierung nächtlich ziehender Grasmücken (*Sylvia atricapilla*, *borin*, und *curruca*). *Zeit. f. Tierpsych.*, **14**: 29-90.

- SAUER, E. G. F., AND E. M. SAUER. 1959. Nächtliche Zugorientierung europäischer Vögel in Südwestafrika. *Vogelwarte*, **20**: 4-31.
- SAUER, E. G. F., AND E. M. SAUER. 1960. Star navigation of nocturnal migrating birds. *Cold Spring Harbor Symposia on Quantitative Biology*, **25**: 463-473.
- SCHMIDT-KOENIG, K. 1960. Internal clocks and homing. *Cold Spring Harbor Symposia on Quantitative Biology*, **25**: 389-393.
- STONE, W. 1937. Bird studies at old Cape May. Vol. II. Publ. by the Delaware Valley Orn. Club at the Acad. of Nat. Sci. of Philadelphia. Pp. 521-941.
- SUTTER, E. 1957. Radar als Hilfsmittel der Vogelzugforschung. *Ornithol. Beob.*, **54**: 70-96.
- TORDOFF, H. B., AND R. M. MENGEL. 1956. Studies of birds killed in nocturnal migration. *Univ. of Kansas Publ., Mus. of Nat. Hist.*, **10**: 1-44.
- WAGNER, H. O. 1957. The technical basis of experimental research on bird migration. *Ibis*, **99**: 191-195.
- WETMORE, A. 1926. The migrations of birds. Harvard Univ. Press. 217 pp.
- WETMORE, A. 1927. The birds of Porto Rico and the Virgin Islands. Scientific Survey of Porto Rico and the Virgin Islands, Volume IX, part 4. New York Academy of Sciences. Pp. 409-571.

California Academy of Sciences, Golden Gate Park, San Francisco 18, California.