DOES THE BOBOLINK NAVIGATE?

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RECENT discussions of celestial cues used by birds to tell direction have centered on the problem of whether these cues provide sufficient information for navigation (Sauer, 1957, 1961; Sauer and Sauer, 1960; Wallraff, 1960*a*, 1960*b*). Matthews demonstrated the navigational abilities of the pigeon (1953*a*) and the Manx Shearwater (Matthews, 1953*b*), and it has been shown that the experimental demonstration of navigational ability is at least partly dependent upon the sun (Matthews, 1953*a*, 1953*b*, 1955) and an internal clock (Hoffman, 1954; Schmidt-Koenig, 1960) compensating the apparent passage of this body. At night stars appear to be the significant celestial cues (Sauer, 1957) and unless Polaris is the essential cue a clock mechanism must also be implicated. But the question posed is not: Do these birds navigate? but: Can they navigate with celestial cues alone? Lest the reader be deceived it should be stated at the outset that this paper contains no definitive answer to either question.

I am especially indebted to Robert and Ann Gammell who captured and shipped the Bobolink reported on here from North Dakota. Dr. Franz Sauer, California Academy of Sciences, and Stephen L. Billeb read the manuscript and offered helpful suggestions. This research was supported by the United States Air Force through the Air Force Office of Scientific Research of the Air Research and Development Command, under Contract No. AF49(638)-825.

METHODS

The orientation testing method has been reported elsewhere (Hamilton, 1962). It consists of a circular apparatus with a vertical screen prohibiting view of all terrestrial landmarks. Since the apparatus is rotated hourly at least 180°, the bird can obtain consistent directional information only from celestial cues and pervasive geophysical forces. Twelve peripheral symmetrically arranged perches register the bird's restricted locomotion.

The experimental data reported here come from a single Bobolink taken 9 August 1959 near Kenmare, North Dakota, and air-shipped the next day to Berkeley, California. It was housed there under artificial lights on a light-dark schedule coinciding with the seasonal schedule for Kenmare, North Dakota.

RESULTS

Orientation following geographic displacement without time shift.—On 29 August at 1800 local standard time this bird was permanently removed from the holding shed and placed in the test apparatus situated atop the

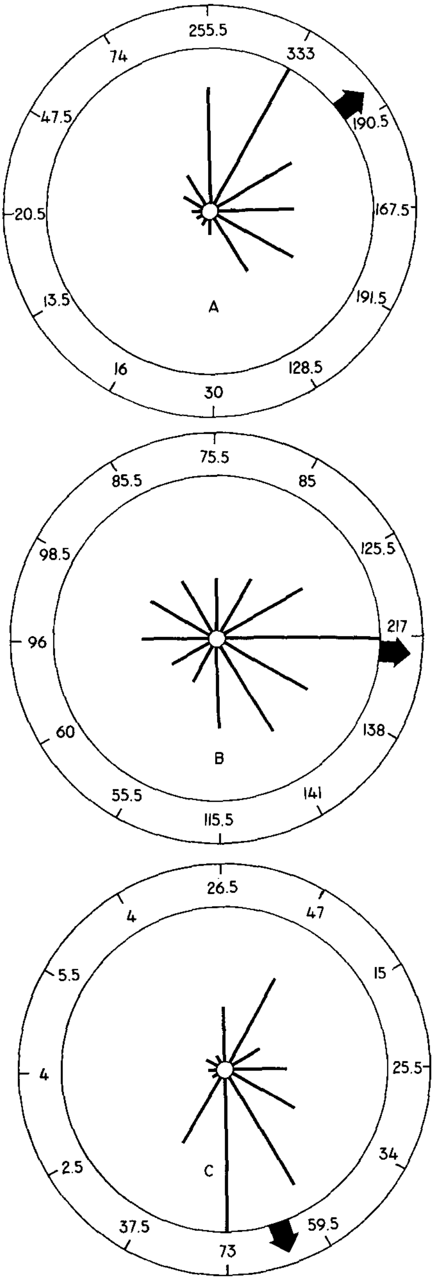

FIG. 1. Preferred directional response of a North Dakota adult female Bobolink recently translocated from North Dakota to San Francisco, held on a time schedule in

Life Sciences Building on the Berkeley campus. This was her first exposure to the natural outdoor Berkeley sky since her capture in North Dakota three weeks earlier. Until this time the overt features of her lighting schedule, i.e., the beginning and end of the day, could have provided no clue permitting the detection of the geographic displacement.

On the assumption that her internal clock was unaffected by the shift, the new outdoor environment might reveal several things which would influence her directional preference. These include the relative duration of the light and dark periods, the temporal schedule of the light and dark periods, and the position of celestial features (i.e., sun, stars, etc.) with declinations temporally out of phase with the setting of the internal clock. The importance of any or all of these features depends on the nature of the orientation mechanism.

Figure 1A indicates the northeasterly response of this bird during the ensuing clear night from 2100 to 0430. The bird was left under the natural outdoor Berkeley sky during the following day, being removed briefly for maintenance of the apparatus. The response during the period 2100 to 0430 on the following night is indicated in Fig. 1B. On this night the response showed a wide scatter with the mode shifted nearly 40 degrees to the south.

The bird was again left in the apparatus except for the brief maintenance period in the middle of the day. That night, from 2100 on 31 August to 0430 on 1 September, she showed a somewhat weaker and bimodal response. The heaviest peak was to the southeast (Fig. 1C). The second mode to the northeast is atypical even of an ambivalent response since the northward trend is not the back azimuth of the southward tendency. No such variations in directional tendency from night to night have been noted for birds time-adjusted to local time (Hamilton, 1962). This result is probably based on the time sense and its relationship to direction. Since the time difference between the light-dark schedule under which the bird was maintained and local time differed by only 100 minutes we are left with a directional shift well in excess of the 15-degree-per-hour shift noted for other species of time-shifted birds responding during the day.

The comparatively wide scatter of the response on these three nights probably stems from her unfamiliarity with the test environment. A comparable scatter has been noted for other birds on the first nights that they were introduced to the apparatus (Hamilton, 1962). However, it may also be due to the conflicting information from the visual field and the internal

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phase with the natural light-dark schedule in North Dakota, and then exposed to the natural night sky in San Francisco. See text for conditions and subsequent data on this bird.

clock. This might provide the bird with less adequate information for making an appropriate directional choice.

In the early morning following the third experimental night the bird escaped as it was being removed from the apparatus.

DISCUSSION

It is important to point out here that navigation has been used with two quite different meanings, both appropriate in the dictionary sense. One is directional response based on geographic position, the Type III homing of Griffin (1952). The other is so-called one-direction navigation (Matthews, 1955), which corresponds to the performance of Mallards (Bellrose, 1958) and Common Terns (Griffin and Goldsmith, 1955).

Possible courses from San Francisco.—In experimenting with spontaneous migratory activity we are dealing either with fixed directional courses in which a directional tendency is taken which has no apparent geographic meaning, or with responses which must be interpreted in relation to an actual migratory pathway. In the case of the Bobolink, we are almost surely dealing with this latter case. For this reason, the experimental result should be interpreted in relation to geographic localities. The bulk of the experiments done to date have been performed in and around San Francisco, California—an area which is not included in the normal pathway of any population of Bobolinks. The experimental results must therefore be interpreted in terms of this geographic displacement. The bird may or may not correct for the displacement under these experimental conditions.

Later in the season all experiments were performed with birds time-adjusted to San Francisco. Subjected to this treatment, the North Dakota birds expressed a preference for the southeast (Hamilton, 1962) as indicated in Fig. 2, Arrow 1. If such a bird were released in San Francisco, what direction would it fly? The southeasterly course extended indefinitely from San Francisco leads through terrestrial areas to the tip of Baja California and then out to sea over vast stretches of ocean (Fig. 2, Arrow 4). Were the bird to actually take such a course it would surely perish. There is only one other possibility which might be in full accord with the experimental result and other available information. Such a bird, time-adjusted to San Francisco, might continue to follow this course as long as it is appropriate with respect to the terrain below (Fig. 2, Arrow 5).

Social stimulation appears to be a very significant factor in Bobolink migration. The night call notes, for example, have a strong stimulatory effect on the migratory behavior of experimental birds (Hamilton, MS). And like many other birds Bobolinks are reluctant to leave a land area to pass over open water alone (Stone, 1937).

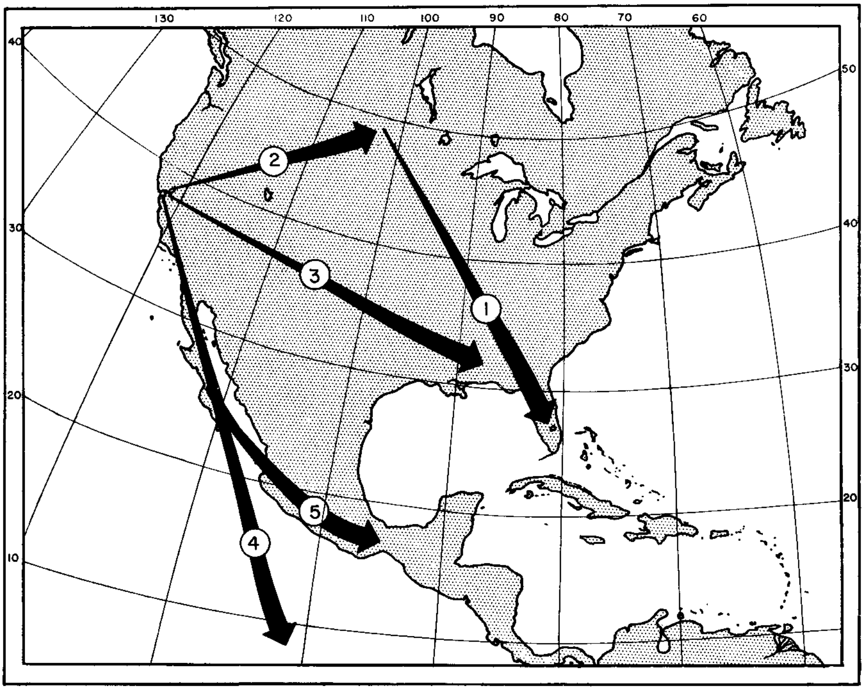

Fig 2. Possible courses of a Bobolink from the North Dakota breeding population upon release in San Francisco. The most probable route of migration is shown by Arrow 1. The bird might return to the home area (2), intersect the migratory route (3), fly a parallel course (4), or fly a parallel course as long as it covers overland areas (5). The map is an oblique conic conformal projection.

A Bobolink responding to the southeast in San Francisco in the experimental apparatus might, therefore, if given its freedom, follow such a course as long as it covered overland areas but shift when it intersected open water and fly as close as possible to such a course without leaving terrestrial areas. There is no reason to believe that the bird would stubbornly stick to a fixed direction unless it were satisfactory in relation to other aspects of the environment such as the relative positions of land and water masses, mountains, weather fronts, etc.

The experiment reported here for a bird held on the time schedule of its home area indicates that under these conditions a homing tendency may be witnessed. This bird took an almost absolutely correct homing course the first night it responded in the apparatus.

The directional shift to the southeastern sector in subsequent nights brought the vector of the response on the final night of testing into agreement with the performance of other North Dakota Bobolinks with internal clocks in phase with local San Francisco time. When thus time-shifted to San Francisco these displaced birds take a course in the apparatus paralleling the natural migratory route from North Dakota to Florida (Hamilton, 1962). It seems then that the performance of the bird reported on here, shifting direction drastically over a period of three nights, indicates that the internal clock shifts rapidly to local time. Such a relatively labile timing mechanism would be advantageous to birds which traverse great east-west distances such as the North Dakota Bobolinks and other more westerly populations in their move to Florida. If the internal clock did not shift, birds relying only on the innate directional information provided by the internal clock and the stars would encounter considerable difficulty in continuously maintaining a direct and accurate course. This would be true since in shifting to the east these birds no longer encounter the same stellar pattern 24 hours later but a stellar pattern out of phase by the degree of the geographic shift to the east and south. The labile timing mechanism would be disadvantageous in relation to homing, especially if homing were delayed for a considerable period of time. But probably the homing response of birds shifted from their home area is initiated almost at once, and the birds would not depend on a rigid internal clock mechanism and could at once be under way in a homeward direction or at least immediately determine the direction of home.

Subsequent travels of the experimental bird.—The North Dakota bird discussed here provided some exciting information relative to the previous discussion. As previously noted, this bird escaped while being removed from the experimental apparatus for routine cleaning and rotation of the apparatus following the third experimental night (Fig. 1C). The bird was marked with plastic bands. This was on 1 September 1959. On 1 June 1960, Mrs. Gammell phoned to say that she had taken a color-banded female Bobolink in the meadows south of Kenmare, North Dakota, where she had trapped the birds she shipped the previous fall. She took color photographs of the bird and its bands and forwarded them. Without question it was the bird which had escaped from my hand on the first day of September the previous fall! Where had this bird spent the intervening period and how had she found her way back to North Dakota after so great a displacement in a closed cage? She might have returned directly to North Dakota before initiating the fall migration (Fig. 2, Arrow 2). Based on her directional response the night before the escape it seems much more likely that she headed south through California and made her journey to the wintering grounds without returning to North Dakota. It is most improbable that she remained in the United States through the winter. Bobolinks are not known even as rare winter stragglers in the United States, and have never been reported at the time of the annual

Christmas Bird Count. She may have rejoined migratory flocks of Bobolinks anywhere along the migratory route between North Dakota and Florida (Fig. 2, Arrow 3) but her behavior in the experimental apparatus does not indicate this as a probable course.

The directional tendency of Bobolinks which are time-shifted and thus in phase with San Francisco time (Hamilton, 1962) indicates only a capacity to take a fixed direction. There is no indication in these experiments that the birds attempt to return home or to any part of the migratory course. While the birds obviously use the internal clock to maintain this heading, the course observed is a parallel one and suggests that the bird has no information indicating to it that it is displaced from the migratory route. A bird with an internal clock in phase with a displaced locality would not necessarily be unable to home, however. When exposed to the total stimulus of an unfamiliar environment, either upon release or under other experimental conditions, the bird might respond quite differently. All we can presently say is that under experimental conditions the bird gave no indication that it would do so.

The route following the extension of the directional tendency of the North Dakota population from San Francisco out to sea cannot have been pursued indefinitely since the bird obviously did not perish at sea. The most likely explanation seems to be that the bird followed the final course which it indicated in the experimental apparatus, just to the east of south and where this course left the coastline, the lone bird, reluctant to leave such a coastline alone, perhaps followed other birds or the coastline on south along the Central American isthmus to South America. At this point the track would come close to rejoining the natural migratory pathway. Since this bird had made the journey from North Dakota to the winter quarters in South America and back at least once before, the subsequent route of travel could have been based on landmarks. Also, if the directional response is based on a labile timing device, then clock resetting at the point where the coasting course (Fig. 2, Arrow 5) intersects the natural migratory route in South America would permit continued use of celestial cues throughout the rest of the migration.

It is interesting to consider the possible role of social phenomena in the homing and natural migration of these birds. Elsewhere (Hamilton, 1962) I pointed out that the call notes of the Bobolink probably play an important role in natural migration, serving both to stimulate grounded birds which are in migratory condition to fly up and join migrants aloft and perhaps also to maintain flock structure by closing the ranks of the travelers. Such flocking mechanisms are probably particularly important under overcast conditions when celestial patterns are not easily visible or are completely masked. It seems quite possible that the bird just discussed may have joined flocks of other passerines such as the Russet-backed Thrush which has a very similar call note and which follows the Central American peninsula to South America.

Does the Bobolink navigate?—Most bird species studied to date which show an oriented response under experimental conditions with familiar landmarks excluded can maintain this directional tendency only when the overhead sky is unobscured by overcast. In a number of animals the response is in a particular compass direction regardless of the direction of home. The Mallard is a good example of a bird taking a fixed direction in this manner. When Bellrose (1958) released Mallards in open fields away from the familiar migratory pathway the birds responded by taking a northerly course. This response persisted through the seasons, night and day, but scatter resulted under overcast conditions. Similarly the Common Tern (Griffin and Goldsmith, 1955), when released at inland points which in all likelihood the birds had never seen before, fly to the southeast. This course is taken regardless of the location of the release in relation to the home. In similar fashion an aquatic bug, *Velia* (Birukow, 1957) heads south when agitated in an experimental situation. While there has been some speculation, there is no adequate adaptive explanation of the directional feature of such responses.

On the other hand a number of species initiate homeward flight immediately when released in unfamiliar country. Matthews (1953*b*), for example, showed that Manx Shearwaters, released at various inland localities which these birds had surely never before visited, initiated homeward flight almost at once. This was true regardless of the direction of displacement. In a similar manner pigeons apparently initiate homeward flight immediately from unfamiliar areas regardless of the direction of displacement (Matthews, 1953*a*; Kramer, 1952). However, Matthews (1961) has recently pointed out that the homeward tendency may be partially masked by a north-flying tendency.

The very limited data for the bird not time-adjusted to local time but maintained on a photoperiod in phase with the home area suggests that under these circumstances the response can be quite different and, furthermore, that the response indicates the possibility of navigation under these circumstances. Many species of birds, and certain populations of Bobolinks in particular, have migrations traversing, in addition to the north-south spans, extensive east-west movements. Such movements to the east or west would present additional problems in orientation to a bird with a rigid internal clock not rapidly adjusting to local time. Especially for an inexperienced bird, using no other orienting information, a particularly difficult problem would be involved in maintaining a compass direction of any sort in relation to the internal clock if this clock were not in phase with local time. These considerations lend support to the hypothesis presented here that the circadian clock rapidly shifts into phase with local time.

The migratory route of the Bobolink in itself demonstrates conclusively that something more than a fixed compass direction is involved in the oriented movement between summer and winter quarters. For the North Dakota population the summer and winter quarters and points along the known migratory route lie approximately on a straight line. But this is not true of other populations such as those in the far west and in the northeast where a directional change must be made in Florida. Of course, we do not yet know whether these changes and subsequent orientation are made on the basis of celestial cues. However, experiments with birds time-adjusted to San Francisco show that the New York population probably heads in a direction approximately paralleling a course from New York to Florida (Hamilton, 1962). From Florida a difficult part of the migration lies ahead with vast stretches of water remaining to be crossed. A shift to topographic features at this point will not suffice and the celestial course taken by the New York population will be inappropriate for further celestial orientation. We might, therefore, anticipate direction shifts based on latitude in the Bobolink such as those noted by the Sauers for the *Sylvia* species. These shifts will not be based on the circadian clock mechanism. The information may be derived either from the latitude through interpretation of the declination of celestial bodies or be part of a programmed circannuan migratory schedule (Hamilton, 1962).

SUMMARY

On 1 September 1959, a captive adult female Bobolink escaped from captivity at Berkeley, California. This bird had been taken from its breeding locality in North Dakota on 9 August 1959 and shipped to Berkeley where it was held on a light-dark schedule coinciding with the natural photoperiod for its home locality in North Dakota. On the three nights prior to escape this bird was held in an experimental cage automatically registering the directional component of migratory activity at night. On the first of these nights the preferred direction almost coincided with the home direction while on the third the direction was parallel to the natural route of migration of the population from which this bird was derived. The direction on the second night was intermediate.

On the first day of June of the following year this same bird was recaptured at the location where it was originally trapped in Kenmare, North Dakota. Since the experimental site in California is not on a migratory pathway of Bobolinks, some navigation capacity permitting the eventual return seems to be implied. The orientation mechanism and the possible travels of this bird prior to recapture are discussed.

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CALIFORNIA ACADEMY OF SCIENCES, GOLDEN GATE PARK, SAN FRANCISCO 18, CALIFORNIA, 16 OCTOBER 1961