

## *Chapter 3*

# **MIGRATION: ORIENTATION AND NAVIGATION**

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## **I. Introduction**

For centuries, people have observed birds departing from north temperate areas each fall and returning the following spring. Worldwide programs of banding and recovery have largely answered the question of "where do migrants go?" Birds migrate great distances, often many thousands of kilometers, and with great regularity and accuracy. This information raises other questions of fundamental interest and importance to biologists and laymen alike. How have birds adapted to withstand the high energy cost of long-distance flight? And how have they solved the navigational problems involved in traveling over vast stretches

of unfamiliar terrain between specific breeding and wintering locations? To give an idea of the types of orientational capabilities required for migratory journeys, a small amount of background information on the general behavior of migrants and typical features of migratory flight is outlined below.

The migratory habit is extremely widespread among birds. Fully two-thirds of the species breeding in the northern United States travel south for the winter. Distances covered typically average 1000–3000 km each autumn with a similar return trip in the spring, but one-way trips of 4000–6000 km are not uncommon (e.g., Dorst, 1962). Some shorebirds cover round-trip distances exceeding 20,000 km on their migrations between arctic breeding areas and southern hemisphere overwintering locations.

A migratory journey is usually broken into a series of short, discrete flights. Most songbirds are nocturnal travelers that probably fly singly or in widely spaced, loose groups. They initiate a flight 30 minutes to 1 hour after sunset and fly continuously throughout most of the night. Depending upon the flight speed of the bird and the direction and speed of the winds aloft, a bird may cover 300–600 km on each night of traveling. An individual usually does not fly each night, however, and a 3000 km trip may require 3 or 4 weeks.

Diurnal migrants, in contrast to their nocturnal counterparts, are more prone to fly in flocks and to follow along topographic leading lines. But they, too, travel along their migratory route in a series of discrete one-day flights. Longer flights in which birds travel continuously throughout the 24 hour period commonly occur among some shorebirds and waterfowl. Among passerines, such flights occur when long stretches of inhospitable terrain are crossed. These include the autumnal over-water flights from the east coasts of North America to South America, flights crossing the Gulf of Mexico during both migration seasons, and the trans-Sahara voyage of many European migrants to and from central and southern Africa.

Recaptures of banded birds attest to the navigational accuracy of most migrants. Adults routinely return to breed in the same general location where they bred in previous seasons. Evidence is accumulating that a similar fidelity occurs at the wintering localities; individual birds return year after year to the same specific area where they spent the previous winter.

Young birds show little evidence of possessing predetermined destinations or specific goals for migration (see Section III). Rather, they appear to adopt particular locations, perhaps by becoming imprinted to certain features of the local environment (Perdeck, 1958; Löhrl, 1959; Ralph and Mewaldt, 1975).

One major unknown of migratory behavior concerns the accuracy of birds while en route. This is particularly true in the case of nocturnal migrants. Do birds follow precise pathways that take them to the same intermediate locations year after year? Are experienced birds cognizant of any destinations or goals along the way? Unfortunately, neither banding returns nor experimental results provide sufficient information to answer these questions. What can be said is that many birds undertake long-distance migratory trips, and that they return year after year to rather precise geographic locations at both the breeding and the wintering ends of these journeys. Such travels require considerable navigational skills. In this chapter, I present a personalized overview of our current knowledge of these skills and of the knowns and unknowns of migratory orientation.

## **II. Philosophy of Orientation Research**

Although biologists have been fascinated by migratory behavior for many decades, most of our current knowledge of navigation mechanisms has been obtained in the past 25 years. During most of this period, investigations centered on the development of all-inclusive theories to explain bird navigation. Underlying such studies was the assumption that one orientational cue or one mechanism of usage of a particular cue would provide the key to understanding all aspects of navigation behavior. Such a philosophy, I feel, is wholly inappropriate for this field of research.

The environment contains numerous cues that could give directional information to a migrating bird. Natural selection should favor the development of abilities to make use of all such information. By pooling several inputs, a bird could increase the accuracy of its directional decision. A system involving multiple cues could also provide checks and balances, enabling the bird to maintain its orienting ability in cases where one cue is lacking or provides equivocal information.

Not all sources of directional information are equally useful to the migrant. Some cues undoubtedly yield more accurate information than others. Some might be available throughout the entire route, whereas others would be useful only at specific geographic locations. Some might be available regardless of flight conditions, while others might be functional only under optimal meteorological situations. The probable existence of a hierarchy of redundant cues makes obsolete the search for "the" mechanism of migratory orientation. In all probability, a differential weighting of several directional cues occurs. These weightings should be expected to vary not only between species but, for any individual

bird, with changing meteorological conditions and at different points along the migratory path (Emlen, 1971). Recent studies are confirming this prediction. They suggest that there are changes in the relative importance of different cues used during the spring and fall (S. T. Emlen and N. J. Demong, unpublished observations) and by birds of different ages (Emlen, 1970a, 1972; S. T. Emlen, N. J. Demong, and E. Gwinner, unpublished observations; Keeton and Gobert, 1970; Keeton, 1972).

The belief that most birds utilize multiple cues, some of them repetitive, necessitates changes in our evaluations and interpretations of previous studies. No longer should evidence for the importance of one directional cue be taken to imply, even indirectly, a lack of importance for an alternate cue. Redundancy of information was seldom considered in early experimental designs, and results must be reinterpreted accordingly. For example, let us assume that a bird can use two types of information, A and B, to determine a migration direction. Now suppose I block or modify sensory input to system A, yet find that the bird continues to orient properly. I would not be justified in concluding that system A was unimportant for orientation or that the bird did not have the capability of orienting using system A. The bird might simply have selected its direction using its alternate system, B. The experiment shows only that system A is not essential for proper orientation. This is very different from the conclusion that system A is not or cannot be used for direction determination.

Consider the following case. Several authors have attempted to study the role of magnetic information in orientation by attaching miniature magnets to the wings or bodies of birds and noting their abilities to home. Although the magnetic field surrounding the birds was seriously disrupted, homing ability generally was unimpaired and most authors concluded that the birds could neither detect nor use magnetic cues (Gordon, 1948; Matthews, 1951b; von Riper and Kalmbach, 1952). Unfortunately, almost all of these experiments were conducted either close to the home loft, on clear sunny days, or both. If we grant the birds the ability of using either familiar landmarks or information from the sun for orientational purposes, then the original conclusions of these studies must be reevaluated. No disorientation would have been expected in the presence of either of these alternate sources of directional information. The results did not provide any evidence for the use of geomagnetic cues, but neither did they rule it out.

Similar caution must be exercised in evaluating studies of inertial navigation in which semicircular canals have been severed. Experimentally treated birds performed as well as controls, but again, all releases were made in the close vicinity of home (Sobol, 1930; cited in Matthews, 1968; Huizinger, 1935) or under clear sunny skies (Wallraff, 1965a).

Unfortunately, the list of experiments where redundant cues were not taken into consideration is enormous.

I am the first to acknowledge the difficulties of designing experiments that control for repetitive cues. Often the best that can be done is to affect more than one cue simultaneously. But, at the very least, we must take this redundancy into account when interpreting experimental results.

We must also be careful not to overgeneralize among species. Migratory behavior has evolved independently many times among birds. Birds migrate for different reasons, and the paths taken, the distances traveled, and the hardships encountered en route vary greatly from species to species. The resulting selection pressures must differ accordingly.

Finally, I propose that caution be exercised in extrapolating the results from studies of homing to explanations of orientation during migration. Earlier workers assumed that the two processes were identical and that each could be used as an experimental tool for studying the other. But, as will be seen in the next section, there is little evidence that most migrants navigate to specific goals with the versatility and accuracy shown by homing pigeons. It is possible that the typical migrant switches to a homing-type process only during the terminal phases of its migratory travels. Throughout much of the trip, many migrants might use simple compass orientation. Migrants are faced with the additional problem of maintaining a given direction for periods of many hours, even days. During these long flights, the availability of different cues may change. Celestial cues may be obscured by clouds, features of the terrain may be enveloped by ground fog, the direction of the wind might change unexpectedly, or the bird might pass over a strong magnetic anomaly. The advantage of having redundancy built into the orientational systems is obvious. The orientational repertoire of a migrant, therefore, should be expected to include a number of simpler systems allowing for the *maintenance* of a given flight direction.

The problems faced by a pigeon homing to its loft and a migrant returning to its former breeding site at the end of its long migration may be identical. But the behavior of the migrant on the remainder of its journey may be quite different. At the very least, the weighting of various sources of directional information should be expected to be different in these two circumstances.

The realization that migrants probably use numerous cues and that different species may use them in different ways should not be considered as discouraging or slowing the advance to an understanding of orientational systems. The effect is exactly the opposite. Today there is an increased willingness to consider both a great variety of types of cues and a variety of ways in which they might be integrated. Alternative

hypotheses frequently are viewed as reinforcing rather than competitive. The problem for the ornithologist interested in navigation is no longer searching for *the* mechanism of orientation. It is studying any and all components of the orientation systems and trying to decipher how these are integrated into a navigational complex that determines the directional behavior of the bird at any place in time or space.

### III. Navigational Capabilities of Migrants

Before discussing the types of cues that may provide a migrant with directional information, mention should be made of the actual orientational capabilities exhibited by birds during the course of their migratory travels. In spite of the large number of studies of migration, surprisingly little is known about the accuracy or versatility of birds' navigational abilities. Do they know their geographic location at all times? Are they actually navigating toward a particular geographic goal, or do they rely on a system of simpler compass orientations during much of the migratory flight? Can they determine when they have been blown off course by strong winds, and do they correct or compensate for such displacement?

Many years ago, Griffin (1955) defined three levels of orientation ability. The first, which he called Type I, is a simple piloting based upon familiar landmarks (visual or otherwise). His second level, Type II, describes a bird's ability to fly in a particular compass direction without reference to landmarks. Type III, commonly called true navigation, refers to the ability to orient toward a specific goal from a variety of unfamiliar areas. As Schmidt-Koenig (1965) points out, reference to a goal could be maintained either by means of a complex inertial system ("reverse displacement navigation") or by reference to some grid of coordinates provided by celestial and/or geophysical cues ("bi-coordinate navigation"). Such true navigation has been shown convincingly in homing experiments for only three groups of birds—oceanic seabirds (Lack and Lockley, 1938; Matthews, 1953b, 1964; Kenyon and Rice, 1958; Billings, 1968), swallows (Rüppell, 1934, 1936, 1937; Southern, 1959, 1968), and homing pigeons (Matthews, 1951b; Wallraff, 1967, 1970; Keeton, 1974).

Many authors have assumed that migratory orientation falls under category III because individual birds cover thousands of kilometers and yet return to highly specific breeding and wintering locations. In actuality, there is very little convincing evidence for the widespread occurrence of Type III orientation among migrants.

#### A. DISPLACEMENT EXPERIMENTS WITH FREE-FLYING BIRDS

One way of studying orientational capabilities is to perform displacement experiments. Birds are captured as they migrate through an area and are transported and released at a different geographic location. If the displaced birds reorient back toward the original capture location or on a corrected course toward the normal breeding (in spring) or wintering (in autumn) area, it would imply that they had sensed and correctly compensated for the displacement.

Results from this type of experiment generally are dependent upon reports of recovered banded birds. Unfortunately, recovery rates are extremely low and are strongly biased by the uneven distribution of persons interested in capturing and reporting such birds. An additional error would be introduced if the displaced individuals showed any tendency to be influenced by, or to travel with, local migrants at the release location. Finally, one should consider only those recoveries occurring during the migration season in which the displacement was performed. Even taking this precaution, however, one must realize that an individual bird could travel over a tremendous area during the period before recapture; one cannot assume that the bird moved in a direct line from release to recapture location.

In spite of these potential drawbacks, displacement experiments have provided valuable information on the strategies of direction finding of migrants. The most extensive studies have been those of Perdeck (1958, 1967), who transported almost 15,000 European Starlings (*Sturnus vulgaris*) from Holland to release locations in Switzerland and Spain. From previous banding studies, Perdeck knew that the migrant starlings passing through The Hague each autumn were from a population that bred in eastern Holland, northern Germany, Denmark, and Poland. This population generally migrated west-southwest to wintering areas in western Holland, southern England, Belgium, and northern France (Fig. 1). In his initial experiments, 11,000 birds were displaced from The Hague approximately 750 km south-southeast and released at three locations in Switzerland. Of the 354 recaptures reported, 131 satisfied Perdeck's requirements of being recovered at a distance of more than 50 km from the release site and being recovered in the same autumn or in the following winter season. I have replotted these data in Fig. 2, and it is apparent that a dichotomy exists between the behavior of transported juvenile and adult starlings. The young birds on their first migratory flight continued to travel in the west-southwest compass direction even though this took them far from the population's normal wintering areas. There is no indication that the birds detected the displacement or corrected

for it in any way. Rather, they traveled along a preferred compass direction (Type II orientation). Additional recoveries revealed that many immature birds adopted the new wintering areas in southern France and Spain and even returned in later years (Perdeck, 1958, 1967).

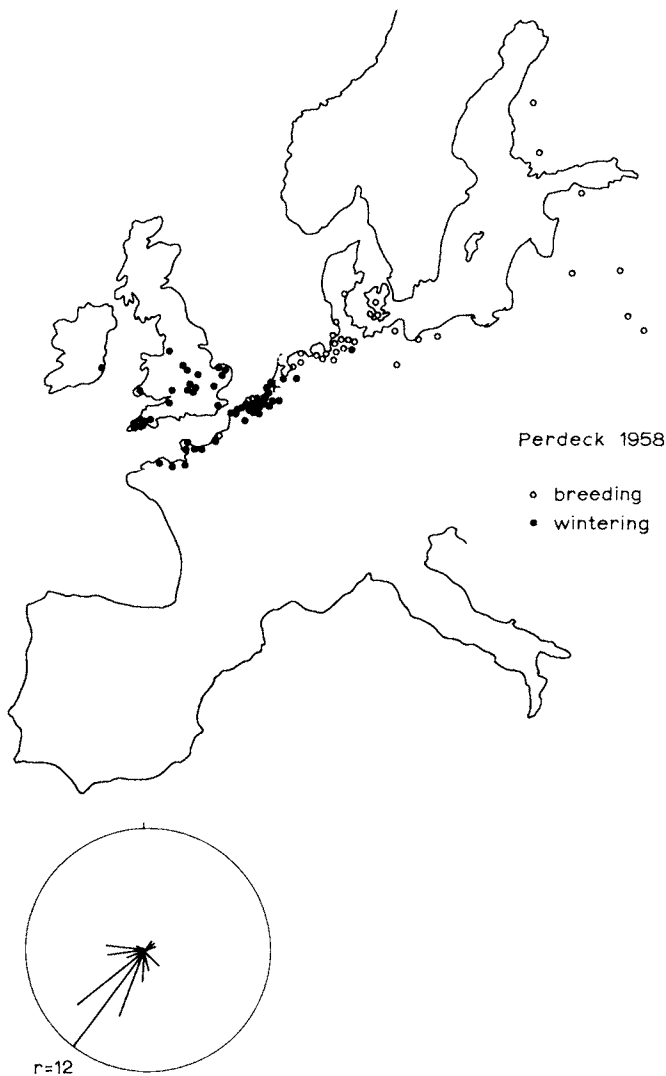


FIG. 1. Top: Recapture locations of breeding (open circles) and wintering (solid circles) of European Starlings banded during autumn passage through The Hague. Banding location is designated by a plus (+) sign. Bottom: Vector diagram of the directions of winter recapture locations relative to The Hague. The data are grouped into 15° sectors and plotted on a proportionality basis with the radius equaling the greatest number of recaptures in any one sector. The number that this represents is presented at the lower left of the diagram. In all such figures, 0° or 360° represents geographic north. (Data from Perdeck, 1958.)



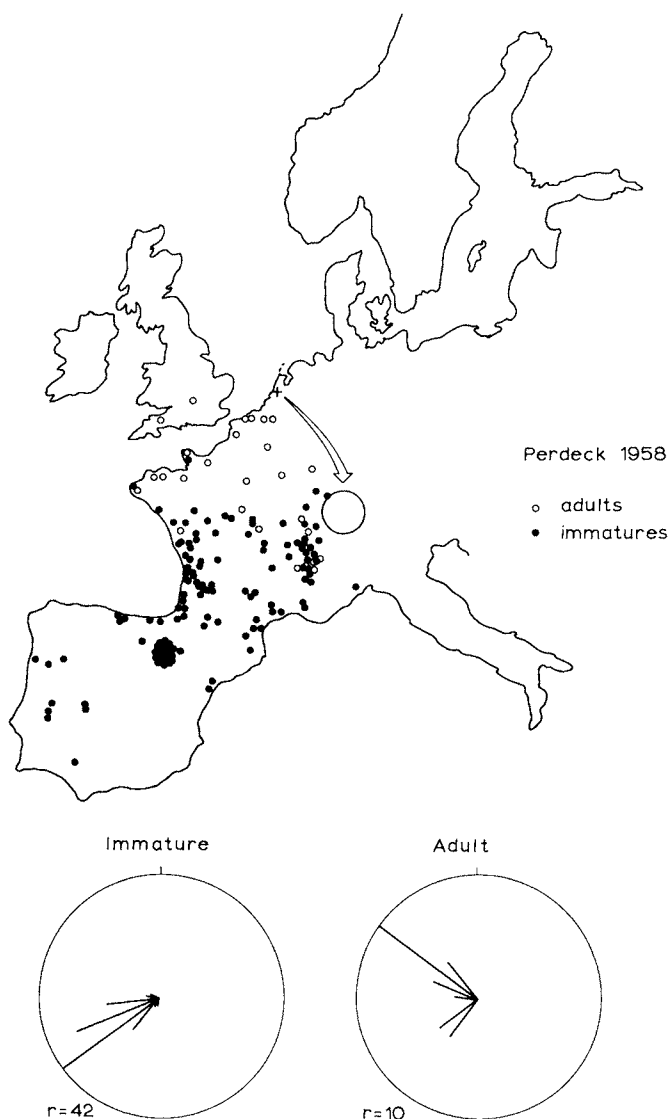


FIG. 2. Top: Recapture locations of adult (open circles) and immature (solid circles) European Starlings displaced from The Hague to three locations in Switzerland during autumn migration. Bottom: Vector diagram of the directions of winter recaptures of immature (left) and adult (right) European Starlings plotted relative to the release sites in Switzerland. (Data from Perdeck, 1958.)

The recaptures of adult displaced starlings showed a weakly bimodal distribution. One group of recaptures ( $N = 8$ ) was to the west-south-west, suggesting a continuation along the previous compass direction.

But a second group ( $N = 19$ ) was distributed to the north-northwest, and 13 of these birds returned successfully to the normal wintering area.

An additional 3600 starlings, also captured migrating through The Hague in the autumn, were transported to Barcelona, Spain (Perdeck, 1967). The recapture locations and directional vector diagrams for their recoveries are replotted in Fig. 3. Again there is a difference in the behavior of juvenile and adult birds. Young starlings continued to fly along the west-southwest compass bearing, seemingly unaware of the 1300 km displacement. The 12 recaptures of adults, however, support the findings of the Swiss experiments. Although there is a considerable spread in recovery locations, most were from the northwest.

One could be hypercritical and point out that the overwintering area for this population of starlings is not northwest, but north of Barcelona (Fig. 1). Only two birds successfully returned to this area. But the combined evidence from Perdeck's experiments clearly shows that most adult starlings did not continue in their "normal" migration directions. Rather, they traveled toward (and often reached) their previous wintering areas. This implies both a recognition of and a correction for the geographic displacement.

In contrast, first-flight migrants showed no change in behavior after transplantation. Either they did not detect the displacements or they were unable to reorient to compensate for them. In either case, Type III navigation capabilities were lacking.

Schüz (1949) conducted analogous experiments with White Storks (*Ciconia ciconia*). These storks breed over much of Europe and migrate considerable distances to winter throughout southern Africa. Individuals from populations breeding from central Germany eastward migrate in a southeasterly direction, passing around the eastern end of the Mediterranean on their way south. Storks from the western population take a southwesterly course, crossing the Mediterranean at the Strait of Gibraltar. Schüz captured young storks from the eastern population and released them in western Germany after the migratory departure of the local storks. Although they were in an area where the normal migration direction would have been to the southwest, recoveries indicated that the displaced young birds continued on a southeasterly compass course. Again we have the suggestion of a simple Type II directional capability.

Rüppell (1944) and Rüppell and Schüz (1948) performed similar displacements with Hooded Crows (*Corvus corone cornix*) during a spring

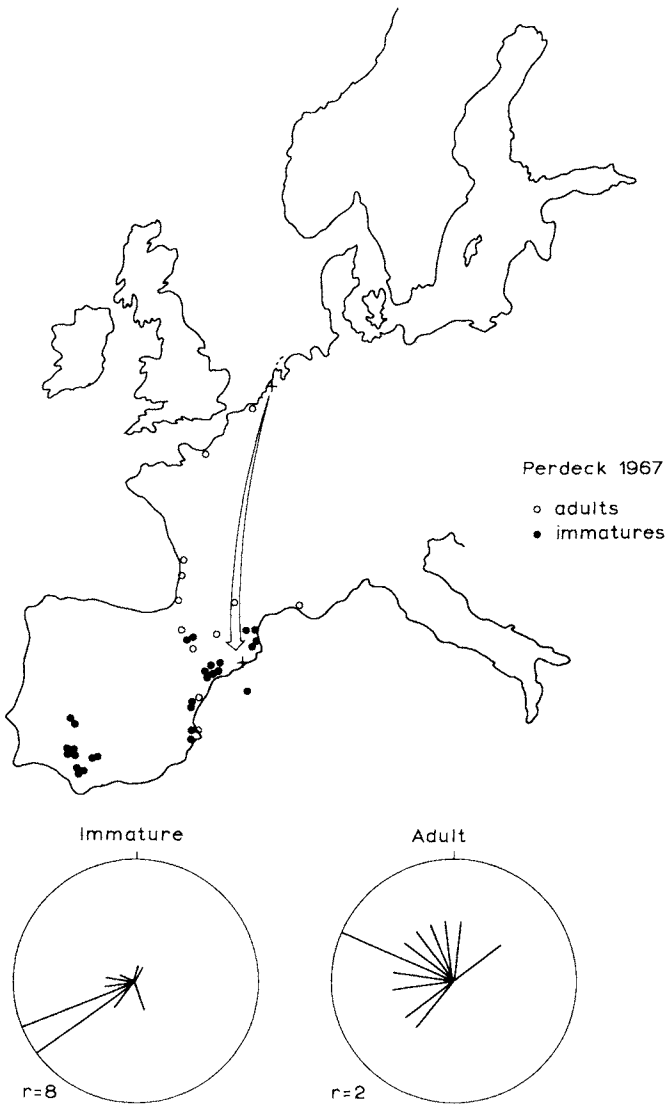


FIG. 3. Top: Recapture locations of adult (open circle) and immature (solid circle) European Starlings displaced from The Hague to Barcelona, Spain. Bottom: Vector diagram of directions of winter recapture locations of immature (left) and adult (right) European Starlings plotted relative to the release site at Barcelona. (Data from Perdeck, 1967.)

migration. Banding studies showed that the birds passing through Rossitten, on the Baltic Coast, migrated northeast to reach breeding areas in northern Poland, southern Finland, and northwestern U.S.S.R. Approximately 900 birds were transported from Rossitten west to central Denmark (770 km) or west-southwest to western Germany (960 km). Recaptures indicated that the dislocated birds continued to migrate to the northeast, failing to compensate and reorient back toward the normal breeding area. Recoveries from succeeding years showed that the birds adopted new, more westerly, breeding locations and even overwintered at points west of their normal wintering quarters. We must tentatively conclude that Hooded Crows, even on their second migration trip, were not goal-orienting but were following a Type II northeast-southwest compass course.

Occasionally, a natural experiment occurs in which migrants are blown off their normal course by adverse winds. Many autumn nocturnal migrants of Scandinavian origin leave Norway on a south-southwest flight that takes them over southern England and on to western France and Spain. Evans (1968) believes that such birds normally cross over the eastern coast of Britain at points south of Yorkshire. If, in crossing the North Sea, birds encounter stiff easterly winds, they may be blown off course and be forced to make landfall along the northeastern coast of Britain. Do such birds continue migrating to the south-southwest or do they reorient to the south and south-southeast, thereby returning to their normal migration route?

Birds captured at Northumberland (north of Yorkshire) and believed to have been displaced westward were tested in circular orientation cages. The data are extremely sparse, but many birds did display south or southeast tendencies (Evans, 1968). I hesitate to draw firm conclusions from these data, because no control tests were run with birds not presumed to be off course. But, at the very least, the results are consistent with a hypothesis of compensatory reorientation.

Evans next compared the autumn and winter recovery locations of European Redstarts (*Phoenicurus phoenicurus*) and Pied Flycatchers (*Ficedula hypoleuca*) banded north of Yorkshire with those netted on the coast south of Yorkshire. The recoveries from the northern or "displaced" birds ( $N = 10$ ) showed the same geographic distribution as the recoveries from "normal" birds ( $N = 25$ ), leading Evans to hypothesize that these two species possess the ability to correct for displacement.

Several words of caution are necessary before interpreting these results. Some workers question both the assumptions that all birds of these species on the British coast are of Scandinavian origin, and that those north of Yorkshire necessarily represent individuals that have been blown significantly off course (Evans, 1968, p. 30). Even if these assumptions

are valid, we must ask ourselves what would be the expected distribution of band recoveries if those blown off course did not correct for displacement? Presumably, they would continue south-southwest on a course that would take them out over the Atlantic. Such birds would never be detected. Hence, a difference in recapture locations between the two groups of birds would not be expected regardless of their orientation behavior. Evans' case must rest on a comparison of the numbers or percentages of recaptures. These numbers are quite small and could be explained by alternative hypotheses requiring little in the way of complex navigation capabilities. Scandinavian migrants crossing the North Sea might have the tendency to turn to the east (toward the coast of France and Spain) at dawn after flying long periods over open water. Or they might demonstrate the "dawn ascent" phenomenon of climbing in altitude and turning toward the coast upon finding themselves at sea following a night's migration (Baird and Nisbet, 1960; Myres, 1964; Richardson, 1972). Simple strategies such as these could account for many of the recaptures, and they would seem clearly adaptive for passerines that frequently encounter easterly winds while traveling along the Atlantic coast of Europe.

Finally, radar studies of passerine migration in autumn show that the dominant direction of travel in England is to the south-southeast (Evans, 1966). Consequently, any tendency for displaced Scandinavian transients to associate with British migrants could also explain the apparent "reorientation" of Evans' birds. In view of these considerations, I must regard Evans' data as exciting, but his conclusions as unproven.

#### B. DISPLACEMENT EXPERIMENTS WITH CAGED MIGRANTS

One way to avoid the problems associated with banding-recapture studies is to study the orientation behavior of caged migrants following artificial displacement. Very few such studies have been undertaken and the preliminary results are somewhat confusing. Yet mention will be made of these studies since they constitute a powerful experimental approach that should be extended in the near future.

Russian investigators (Dolnik and Shumakov, 1967) working at Rybachii on the Nehrung Peninsula (longitude 21°E, latitude 55°N; near the Rossitten station used by Rüppell) transported four species of passerines over 3800 km to Dushanbey (69°E, 38°N) and almost 8300 km to Khabarodsk (135°E, 48°N). Two diurnal species, Chaffinches (*Fringilla coelebs*) and European Starlings, were selected as typical short-distance migrants, while two others, Scarlet Rosefinches (*Carpodacus erythrinus*) and Barred Warblers (*Sylvia nisoria*), were taken as examples of long-distance travelers. The birds were displaced in the autumn of

1964 and placed in circular cages exposed to the outdoor sky. The results are difficult to interpret, since all the data obtained from a particular species are presented in pooled form. This pooling includes an unknown number of individual birds, and diurnal as well as nocturnal activity. The latter is especially unfortunate, since it is probable that different mechanisms of orientation are used by day and by night. It is also unfortunate that the birds lived in the circular cages and were constantly exposed to the solar day at the displacement location. This means that the birds were in the process of resynchronizing their biological time senses to local time during the week the experimental data were being collected. Since all results are pooled, it is not possible to factor out the effects of clock-shifting and reentrainment, nocturnal versus diurnal activity, or the relative weighting of the data by different individual birds. Nevertheless, the pooled vector diagrams indicate that the two short-distance diurnal migrants either failed to correct for displacement or showed an overall low level of oriented behavior. The two long-distance nocturnal migrants, however, did shift their mean bearings from southeast at Rybachii to a more bimodal northeast-southwest axis at Khabarovsk. The results from the experiments with Barred Warblers are redrawn in Fig. 4. Since the birds had been transported approxi-

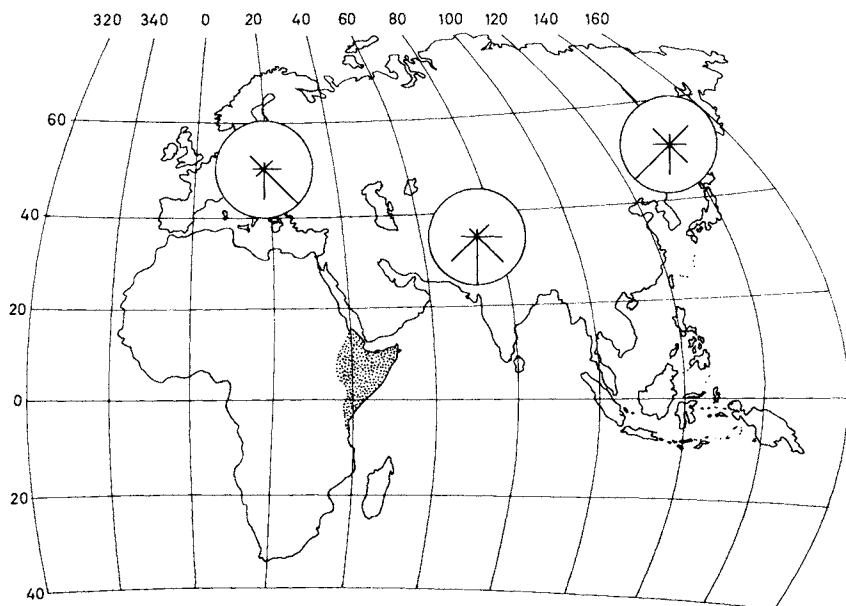


FIG. 4. Orientation of caged Barred Warblers (*Sylvia nisoria*) tested in the autumn at Rybachii (21°E, 55°N) and after artificial displacement to Dushanbey (69°E, 38°N) and Khabarovsk (135°E, 48°N). Stippled area denotes winter quarters. From Dolnik and Shumakov (1967). See text for full explanation.

mately  $115^\circ$  of longitude to the east, these findings are suggestive of a reorientation toward a wintering location and are so interpreted by Dolnik and Shumakov (1967). However, the same shifts in orientation ( $50^\circ$  clockwise at Dushanbey and  $115^\circ$  clockwise at Khabarodsk) would be expected if the birds possessed not a goal-directed orientation (Type III), but rather a simple, celestial compass (Type II) incorporating a biological time sense to compensate for the clockwise motion of the sun or of stars located in the southern sky (see Sections IV,B and C). Unfortunately, the experiments were not designed or presented in a way that allows the reader to distinguish between these two very different interpretations.

One of the participants in the original study, R. L. Potapov, extended the study the following autumn by clock-shifting Garden Warblers (*Sylvia borin*), Scarlet Rosefinches, and Barred Warblers prior to their displacement. He presents his data in the same pooled form and includes results obtained when the birds were clock-shifted to different times as well as their behavior after they had been allowed to reset to local conditions at the points of displacement. Potapov (1966) states, however, that the clock-shifting had no effect upon the directional choices of the birds. The results that are given completely contradict those of Dolnik and Shumakov (1967). No evidence was obtained that the birds either detected or corrected for their eastward displacement. For each species, the overall orientation was similar regardless of test location. Barred Warblers, for example, continued to aim to the southeast at both Dushanbey and Khabarodsk. From this Potapov (1966, p. 892) concludes that his test species do not possess true navigational capabilities. Instead, he hypothesizes they use a simple star compass (Type II) and that this mechanism of orientation is independent of the biological clock.

Taken together, Dolnik, Potapov, and Shumakov must have accumulated exactly the types of data that are required to answer the questions posed in this section. Their sample sizes are large; their displacements are impressive. But as long as these data are presented in such an abbreviated, even cryptic, format, it will be impossible to interpret the results fully or to understand the opposing conclusions of the two studies. I can only plead that the data be reanalyzed and published in full detail. This reanalysis should treat nocturnal and diurnal activity separately and should factor out the effects of displacement, clock-shifting, and reentrainment.

Another experiment with displaced migrants is Hamilton's study of the nocturnal orientation of caged Bobolinks (*Dolichonyx oryzivorus*). Birds were obtained from a breeding population in North Dakota, transported to San Francisco, California, and allowed to resynchronize their

activities with local time. When tested in the autumn under the natural night sky in California, the birds showed a southeasterly orientation, parallel to the normal direction taken by birds in North Dakota. No evidence of a directional shift to compensate for displacement was observed.

One adult female Bobolink was treated somewhat differently (Hamilton, 1962c). It was housed in a separate room where the light-dark cycle was kept in phase with North Dakota time. The bird was first exposed to the San Francisco sky in late August when its *Zugunruhe* orientation was tested. Interestingly, this individual took up a northeasterly direction, approximating the direction to its breeding area in North Dakota. Why a bird in autumnal migratory condition should orient toward its summer home is unclear. During the successive two nights, presumably as the bird's chronometer synchronized with local, California time the directional preference shifted through east to the typical south-southeast. This directional shift of approximately  $100^\circ$  is greater than would be expected if the bird were using a time-compensated compass (Type II). Unfortunately, no additional data are available because the bird escaped prior to its fourth test.

Jørgen Rabøl (1969, 1970, 1972) has recently initiated a series of short-distance displacement experiments with migrants in Denmark. He has transported several species of European warblers distances of  $5^\circ$  to  $8^\circ$  of longitude and latitude. Although his results are quite variable, mention will be made of one test that did provide a suggestion of reorientation (Rabøl, 1969). At Blavand, on the west coast of Denmark, migrant Garden Warblers typically exhibited a southward directional preference when tested in orientation cages. Rabøl transported a group of warblers 500 km east to Ottenby, off the southeast coast of Sweden, and tested them on the night of their arrival. Although the sample was small, the pooled mean direction of those birds that showed oriented behavior did shift westward (mean direction =  $209^\circ$ ;  $N = 5$ , at Ottenby; mean direction =  $165^\circ$ ,  $N = 11$  at Blavand). By the second and fourth nights (it rained on night three), the pooled mean direction had shifted back eastward to south ( $184^\circ$ ;  $N = 6$ ). These results could be interpreted to mean that some birds corrected for displacement, but only as long as their chronometers remained on Blavand time. Within 24 hours their internal clocks had reset to Ottenby conditions and the ability to detect the eastward displacement had disappeared.

If the caged warblers possessed a Type II compass system that incorporated time-of-day information, we also would have expected a clockwise shift in orientation. This shift would be equal to the longitudinal displacement, in this instance,  $8^\circ$ . The magnitude of Rabøl's shift ( $44^\circ$ ) suggests an awareness of geographic displacement, since it exceeds that



predicted for the compass system alone. Additional tests with Garden Warblers, Willow Warblers (*Phylloscopus trochilus*), and European Redstarts have yielded more equivocal results (Rabøl, 1969, 1970).

### C. DISCUSSION

When a bird is "naturally" displaced during a migratory flight, the causal agent is wind and the distance blown usually is small. Migrants don't often find themselves thousands or even hundreds of kilometers off route. When natural displacements do occur, migrants might be able to detect them directly, while in flight, either through reference to visual markers on the ground (Section IV,D,2) or by the exposure to strong winds and storm conditions aloft. Natural selection should operate to insure adequate correction for *these* errors, not necessarily for abilities to detect and compensate for displacements of thousands of kilometers. For small-scale wind displacements, changes of orientation strategy such as (1) reversing the direction of flight the following morning, (2) turning into the direction of the prevailing wind, or (3) reorienting toward a visible coastline, might be sufficient corrective measures. All three behaviors have been reported for songbird migrants on mornings following nights of strong wind or storm activity. All three might get the birds back on course; yet none presupposes geographic location detection or a Type III navigational capability.

Sections III,A and B reveal the meager state of our knowledge concerning the actual navigational capabilities of most migrants and point to the need for additional studies. From the information at hand, it is by no means clear that most migrants are using a bicoordinate navigational grid or are goal orienting. The orientation behavior of many migrants may be fundamentally different from that of goal-directed homing behavior found in shearwaters, petrels, swallows, or pigeons. Some might possess the capability of homing to a learned goal but not invoke this strategy until the final phases of the trip. A bird programmed only to fly in a preferred compass direction could still reach the general vicinity of its wintering quarters if it selectively timed its flights to avoid adverse winds. The accuracy of such a bird would be a direct function of (1) its degree of selectivity in flying with different winds, (2) its accuracy in predicting winds aloft, and (3) its ability to correct for wind drift (see Section IV,E).

Physiological studies have shown that the metabolic cost of flight is extremely high (Tucker, 1971; Berger, and Hart, 1974). Field observations suggest that birds often travel with a low margin of safety. Songbirds making landfall after a long, overwater flight in unfavorable winds frequently are so exhausted that they can be picked up by hand. Individ-

uals are often completely devoid of subcutaneous fat reserves, and some have even metabolized part of their own flight muscles as a last source of fuel (e.g., Rogers and Odum, 1966).

Birds can conserve energy by taking advantage of specific weather situations, i.e., by initiating a journey only when wind conditions are favorable for the preferred direction of flight. By flying with tail winds and by taking advantage of vertical air currents, a migrant can both reduce the energetic cost of flight and increase its potential flight range.

We should expect birds to follow migratory routes that allow a maximum utilization of the various prevailing winds occurring in different geographical areas. This leads to the interesting hypothesis that *the most advantageous route from an energetic viewpoint might be an indirect one*, following a path that is neither shortest in distance nor directly goal oriented.

Bellrose and Graber (1963) used this logic to explain their radar observations of bird migration over central Illinois. They noted that the flight paths of small birds were predominantly to the east of north in the spring and to the east of south in the autumn. The absence of reciprocal flight directions in the two seasons led them to speculate that many species follow elliptical clockwise routes between breeding areas in the north and wintering areas in Central and South America. By following such an indirect path, the birds could take advantage of the high frequency of westerly winds found at northern latitudes and, more importantly, could utilize the westward drift provided by the easterlies that predominate at more southerly latitudes.

A similar explanation may underlie the long-distance flights of passerines and shorebirds that depart the east coast of North America on a nonstop trip to the West Indies or South America. Radar observations indicate that birds leave the coasts of the Canadian Maritimes and New England on southward and south-southeastward bearings (Drury and Keith, 1962; Drury and Nisbet, 1964; Richardson, 1972, 1974, 1975; Williams *et al.*, 1974). The courses of many of these birds would, if extended, pass east of the coast of South America and take the birds to Africa. Recent autumn radar observations in the Antilles (Hilditch *et al.*, 1973) and on Puerto Rico (Richardson, 1974, 1975) detected a moderate volume of birds approaching from the north and north-northeast. Many of these bearings, if extended backward, would suggest a European starting point. The most logical explanation is that these birds are also following a clockwise elliptical course, shifting their bearing more westward as they encounter the prevailing easterly trade winds at low latitudes. We must hypothesize that the energetic savings gained by using the low latitude easterly winds more than offsets the increased mileage of this route to South America.

Peter Evans (1966) further stressed the importance of energetic considerations in the evolution of migratory routes. Banding studies of autumn migrants in Britain show that many species overwinter to the south-southwest in Spain. Yet, birds observed by radar generally depart from Britain on a preferred southeast or south-southeast bearing. Evans hypothesized that this indirect route had evolved to take advantage of the prevailing upper air winds and to minimize the chance of being blown out over the Atlantic.

In cases such as these, it might be selectively advantageous for a bird to orient along a preferred compass bearing (Type II orientation) even though it possessed the capabilities of true goal navigation. In the later stages of migration, such birds might change behavior and locate their specific wintering areas by a variety of means. These could include random search, recognition of familiar topographic landmarks, use of cues emanating directly from the final destination itself, or the use of intermediate cues providing bicoordinate grid information.

At this stage, our knowledge is meager enough to allow a considerable spread of speculation about the orientation strategies of migrants. In fact, a whole spectrum of hypotheses has been advanced in recent years. At one end of this spectrum are Sidney Gauthreaux and Kenneth Able (Gauthreaux and Able, 1970; Gauthreaux, 1972b; Able, 1972, 1973, 1974a; but see Able, 1974b) who believe that passerines in the southeastern United States have no strong directional preferences at all, but merely fly downwind. By this hypothesis, a migratory course would be rather circuitous. It would follow a modified random walk model with a strong bias imposed by the relative frequencies and temporal sequence of winds from different directions, and by the degree of selectivity in the departure behavior of the birds. In an intermediate view, William Cochran (personal communication) believes that thrushes possess a Type II compass capability but do not compensate for wind drift. Consequently, their direction of flight on any given night is merely the vector sum of the wind direction and speed plus their predetermined compass heading and flight speed. Other workers, including William Drury and Ian Nisbet (1964; Nisbet and Drury, 1967) and Frank Bellrose (1963), have proposed that birds not only have a preferred compass bearing but also an accurate ability to control for wind drift aloft (see Section IV,E). Discussing songbird migrants in Massachusetts, Nisbet and Drury state: "they appear to preserve their tracks so precisely that it is unnecessary to suppose that they use any form of bicoordinate navigation" (1967, p. 184).

At the other end of the spectrum, many authors hypothesize that migrants use a bicoordinate navigation system based upon celestial and/or geophysical cues (see Yeagley, 1947; Matthews, 1951a, 1968;

Sauer, 1957; Sections IV,B and C). This view reaches its most sophisticated form in the recent proposals of Jørgen Rabøl (1969, 1970, 1972), who suggests that a migrant is capable of detecting displacement and reorienting toward a goal by means of a bicoordinate system of star navigation. Additionally, he proposes that the coordinates of this goal change through time in an internally programmed sequence that brings the bird to its geographic destination at the end of the migration period.

At this point, it is too soon to look for generalizations about the navigational capabilities of birds. I have tried to point out that migrants undoubtedly make use of a variety of cues, some providing simple, others complex, directional information. In all probability, a whole array of navigational strategies exists. Their study will provide the ornithologist with an exciting challenge in the years ahead.

#### **IV. Cues Used in Direction Finding**

In spite of our ignorance about their actual migratory behavior, birds do reach specific breeding and wintering destinations with great regularity. The remainder of this chapter will be devoted to a survey of the types of directional cues available in the environment and the kinds of information that birds seem capable of extracting from them.

##### **A. THE IMPORTANCE OF TOPOGRAPHIC LANDMARKS**

It is well known that many diurnal migrants are influenced by general topographic features beneath them. Some regularly follow coastlines, avoiding flights over large bodies of water. Others appear to follow river valleys or to make use of updrafts that occur along mountain ridges. All of these landmark effects cause a concentration of diurnal migrants along specific "flight corridors" and are responsible for the mass flights at such famous birding localities as Point Pelee on the Ontario shore of Lake Erie, Cape May at the southern tip of New Jersey, and Hawk Mountain in northeastern Pennsylvania.

Piloting using familiar topographic landmarks is also widely believed to be of importance in the guidance process, particularly in the final stages of migration. This seems logical, since birds have quite good visual acuity and have been shown to be capable of recognizing salient features of the terrain and of retaining this information for long periods of time.

Most migration occurs at considerable heights above the surface of the earth and this has important consequences for the perception of the visual landscape beneath. The higher a bird flies, the greater the

breadth of its field of view. For a bird at 200 feet (60 m), the visual horizon is approximately 30 km away, giving a breadth of vision of 60 km (Hochbaum, 1955). For a bird migrating at 2000 feet (610 m), the landscape stretches 100 km in all directions (visibility conditions permitting). Together with this increase in field of view, there is a decrease in the angular velocity of the apparent ground movement. Hochbaum (1955) correctly noted that this would give the migrant more time for visual inspection of the landscape below.

In spite of these facts, there are obvious drawbacks to basing an orientation system exclusively on topographic cues. Specific landmarks must be learned and thus are not available for first-flight migrants that travel separately or become separated from experienced adults. This system is useful only for traversing areas that have already become familiar as a result of previous flights. If a bird were blown off course or made an incorrect turn along the way, it would leave its zone of familiarity and, with it, the possibility of landmark orientation. Recognition and retention of landmark information becomes increasingly difficult as the distance covered in migration increases, and as the terrain covered becomes more homogeneous.

Natural selection should favor a reliance upon cues that can provide directional and/or geographical information and are available over large areas of the earth's surface. Landmark recognition probably is of considerable importance at specific areas along the migratory route—in finding familiar stopover points and in locating the final destination. But I would expect landmarks to take a secondary, supplemental role in the direction finding process en route.

Waterfowl show one of the strongest tendencies to return to traditional stopover locations during migration. Since ducks and geese typically travel in family groups, information about the migratory route and the guideposts along it could easily be transmitted from generation to generation. Not surprisingly, waterfowl provide some of the best examples of landmark orientation. Hochbaum (1955) and Bellrose (1967b) mention the importance of landscape features both at the breeding grounds and in the vicinities of migratory staging areas. "In addition to the use of landmarks for local orientation, large rivers, lakes and similar features of the landscape are used by diurnally migrating waterfowl as guidelines and guideposts" (Bellrose, 1967b, p. 95). Yet, even among waterfowl, other orientational cues play the major role in determining the direction and course of the migratory flights (Bellrose, 1958, 1963, 1964, 1967a, 1971).

In contrast, there is a growing body of evidence from radar studies that birds migrating at night generally ignore even the most obvious landscape features beneath them. This has been reported almost uni-

formly for waterfowl and waders (shorebirds), as well as for nocturnally migrating songbirds. It holds true in a variety of geographic locations ranging from southeastern Canada and the New England coast of North America (Drury and Keith, 1962; Drury and Nisbet, 1964; Nisbet and Drury, 1967; Richardson, 1971, 1972, 1974), the Great Lakes area (W. W. Gunn, unpublished observations) through the northern Mississippi Valley (Bellrose, 1964, 1967b) to the southeastern Gulf area of the United States (Gauthreaux, 1971), and the west coast of the Gulf of Mexico (Bellrose, 1967a, 1971). Similar reports come from a variety of locations in Europe (Lack, 1962; Gehring, 1963; Bergman and Donner, 1964; Evans, 1966; Eastwood, 1967).

Features of the landscape are less distinct on very dark nights. If migrants relied heavily upon these cues, they might be expected to compensate for the decreased visibility by flying at lower altitudes. Yet there is no indication that nocturnal migrants fly lower under overcast or on nights with no moon (Bellrose, 1971).

All of this implies that although a great deal of potential information is available in the form of major topographic cues, it is not of critical importance to most birds migrating overhead at night. Since the major features of the terrain are visible on all but the darkest of nights, it is difficult to avoid concluding that under most circumstances landmarks are openly ignored by the majority of nocturnal migrants.

Even in homing studies, there is a growing consensus that pilotage based on learned landmarks becomes crucial only in the immediate vicinity of the final destination. While tracking homing pigeons by airplane, Michener and Walcott (1966, 1967) and Walcott and Michener (1967) found that birds approaching home lofts in eastern Massachusetts did not turn and fly directly toward the loft location until they came within sight of a tall building in the Boston area. By plotting the track location at which pigeons made their final correction toward home, they estimated that landmark guidance occurred only within 15 to 20 km of the loft. Pigeons that approached the home area but whose paths were in error by more than this distance continued on past the loft, giving no indication of landmark recognition. Michener and Walcott further report that pigeons routinely flew over areas where they previously had flown many times without showing any apparent sign of recognition.

Wagner (1972) followed pigeons by helicopter as they homed to lofts in Switzerland. The mountains and valleys provided striking topographic features, and his birds often departed in directions dictated by the terrain. They were particularly prone to follow along valleys, provided that the discrepancy between the orientation of the valley and the direction of home was not great. But the pigeons changed strategies shortly after release and turned toward the home location.

Several investigators have shown that when pigeons whose internal clocks have been shifted are released at a familiar site, they ignore the landscape. Their initial bearings are significantly and predictably deflected from homeward. Similar results are obtained even when releases are made within a kilometer or two of the home loft [Graue, 1963; Matthews, 1968; Alexander (in Keeton, 1974)]. As long as the actual home loft is hidden from view, the clock-shifted birds choose deflected bearings even though they are within the area in which they have taken their daily exercise flights all their lives. Schmidt-Koenig (1972, p. 281) and Alexander (in Keeton, 1974) even report instances where the pigeons took shifted bearings when the loft building was in direct view.

Most recently, Schlichte and Schmidt-Koenig (1971), Schmidt-Koenig and Schlichte (1972), and Schlichte (1973) have equipped pigeons with miniature translucent contact lenses that prevent resolution of images at distances greater than about three meters. The position of the sun can still be localized but recognition of topographic landmarks becomes impossible. Yet such birds, when released 15 and 130 km from the loft, showed a homeward initial orientation that was quite comparable to control birds wearing transparent lenses. Even more astonishing, some individuals with translucent lenses still in place fluttered down and landed in the immediate vicinity of the home loft itself. When birds wearing frosted lenses were equipped with miniature radios and tracked by airplane (Schmidt-Koenig and Walcott, 1973), they showed typical homeward paths, except that they often failed to locate the loft and fluttered to the ground prematurely, terminating flights at distances several kilometers from home. In a few instances, a bird "missed" the loft, flying past at a distance of a few kilometers; but, shortly after the overflights, the birds reversed direction and returned toward the loft. These findings imply that pigeons can pinpoint the location of their home loft to within a kilometer or two in the absence of visual landscape cues.

While these studies do not imply that familiar landmarks cannot play an important role in orientation, they do provide strong evidence that they are rarely essential and that alternative cues generally take precedence in the guidance systems of both homing and migrating birds.

## B. THE USE OF THE SUN

### 1. *Evidence of Sun Orientation*

Early workers (Schneider, 1906; Rüppell, 1944) mentioned the possibility that migrants might use the sun, but it was the late Gustav Kramer who provided the first experimental evidence of its importance as a

directional cue. He found that caged European Starlings exhibited a spontaneous migratory restlessness when placed outdoors in a circular cage (Kramer, 1950, 1951). This activity was oriented in an appropriate migratory direction in both the spring and fall as long as the sun was visible (Fig. 5a). Kramer then placed his cage inside a small, six-windowed pavilion that obscured all landmarks from view. The birds' orientation continued under clear skies but deteriorated under overcast conditions when the sun was not visible (Fig. 5b). This test was repeated and the results were confirmed by Perdeck (1957) a few years later. Further, the directional choices of the starlings were altered in a predictable way when Kramer (1951) changed the apparent position of the sun by using mirrors to deflect sunlight entering the pavilion (Fig. 5c and d).

These experiments implied that starlings could select a direction by orienting at a particular angle relative to the sun. But to use the sun

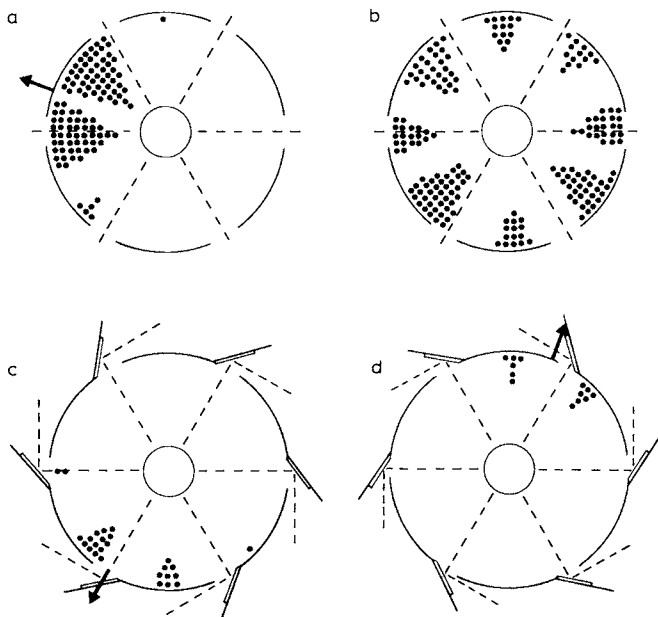


FIG. 5. Orientation of spontaneous diurnal migratory activity in a caged European Starling under various conditions of sun exposure. Bird was tested outdoors in a pavilion with six windows during the spring migration season. (a) Behavior under clear skies. (b) Behavior under total overcast, when the sun was not visible. (c) Behavior when the image of the sun was deflected  $90^\circ$  counterclockwise by means of mirrors. (d) Behavior when the image of the sun was deflected  $90^\circ$  clockwise by mirrors. Each dot represents 10 seconds of fluttering activity. Dotted lines show incidence of light from the sky. Solid arrow denotes mean direction of activity. (Redrawn from Kramer, 1951.)



as a cue during a long migratory flight, a bird must allow for the apparent motion of the sun across the sky; it must change its angle of orientation relative to the sun's position in a manner that correctly compensates for the earth's rotation.

To study this, Kramer and his co-workers developed the technique of training a bird to find food in a particular compass direction in a circular cage (Kramer and von St. Paul, 1950). Starlings, pigeons, and Western Meadowlarks (*Sturnella neglecta*) were trained during one part of the day and then tested at other times when the sun was in very different positions. Most birds continued to orient in their training directions (Kramer and von St. Paul, 1950; Kramer, 1952; von St. Paul, 1956). This implies that the birds had adjusted correctly for the sun's passage through the sky. The birds would even orient to an artificial sun consisting of a 250 W light bulb. If this source was held stationary, they shifted the angle of their movements through the day in such a way as to compensate for the nonexistent motion of this artificial sun (Kramer, 1953).

The most powerful technique for studying the role of a chronometer or time sense in sun orientation is the so-called clock-shift experiment. If a bird is exposed to a light-dark cycle whose onset and termination are shifted earlier or later than local time, it quickly resynchronizes its behavioral and physiological rhythms to be in phase with the new day-night regimen. This makes it possible to study the use of the sun by a bird whose biological clock is out of phase with local time. The rate of apparent motion of the sun is approximately  $15^\circ$  per hour. This leads to the prediction that a bird whose time sense has been retarded by 6 hours should take up an inappropriate orientation angle from the sun and make a clockwise error of approximately  $90^\circ$ . Hoffmann (1954), in a classic study, confirmed these predictions and provided convincing evidence of the integration of the time sense with sun orientation. Using European Starlings trained to find food in a particular compass direction, he was able to shift the directional choice of the birds at will by means of appropriate shifting of their biological clocks. As seen in Fig. 6, the starlings showed the predicted shift of  $15^\circ$  per hour when their clocks were slowed by 6 hours; when allowed to resynchronize with local time, their directional choices shifted back  $90^\circ$  counterclockwise.

After confirming Hoffmann's results using caged homing pigeons, Klaus Schmidt-Koenig (1958, 1960, 1961) studied the importance of sun orientation in free-flying birds. When clock-shifted pigeons were released at a variety of locations, they made large predictable errors in their selection of departure directions. Later studies have yielded similar results (Graue, 1963; Keeton, 1969).

The use of a sun compass has also been found among migratory waterfowl. Several species of ducks captured in Illinois showed a tendency

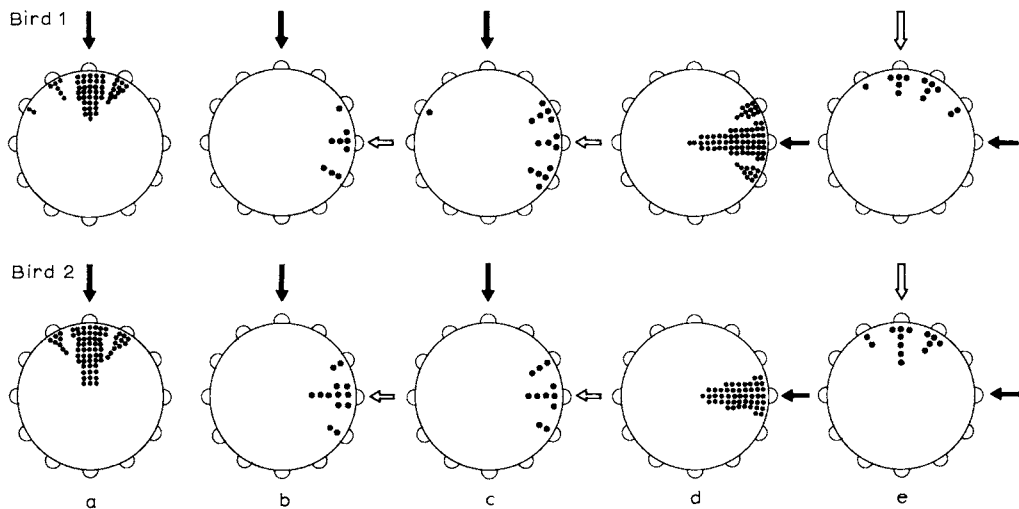


FIG. 6. Directional choices of two European Starlings trained to find food in a particular compass direction. From left to right a, tests during the training time in the natural day; b, tests following the artificial shifting of the birds' clocks 6 hours behind local time; c, tests after 3–28 days in constant conditions following the shift; d, results during training sessions in the artificial (shifted) day; e, results 8–17 days after reentrainment to the natural day. Each dot represents one critical choice (without reward); the black arrows indicate the training directions; the open arrows show the expected direction if the clock is used in sun-compass orientation. (Redrawn from Hoffmann, 1954.)

to depart in a specific northwesterly direction when released (Bellrose, 1958, 1963). This direction did not appear to be migratory and its meaning is unclear. Yet, whatever its biological significance, the direction is taken with reference to celestial cues. Orientation continued under clear skies by both day and night but disappeared under conditions of total overcast (Bellrose, 1958, 1963). Matthews (1961, 1963) made analogous observations on a sedentary population of Mallards (*Anas platyrhynchos*) in Britain. He extended the study to include clock-shifted ducks and found that their departure bearings were deflected in the predicted way when they were released under sunny skies (see Fig. 16).

Even species that are primarily nocturnal migrants seem capable of sun orientation. Von St. Paul (1953) placed two such species, the Red-backed Shrike (*Lanius collurio*) and the Barred Warbler, in orientation cages under the daytime sky and noted that each species took up its appropriate training direction.

## 2. Models of Sun Orientation

In the 20 years since Kramer first demonstrated the importance of the sun for orientation of the European Starling, sun-compass capabilities have been found to be widespread throughout the animal kingdom. The use of solar cues has now been documented in such diverse groups as decapod crustaceans, amphipods, arachnids, and insects, as well as in most classes of vertebrates. The Cold Spring Harbor Symposium volume of 1960 provides a good starting point for the reader interested in pursuing this topic in more detail.

Experiments such as those discussed above define a sun-compass mechanism in which the azimuth position of the sun is integrated with a biological time sense. But such a mechanism does not necessarily provide either the migrating or homing bird with sufficient information to orient toward its destination. Rather, the sun compass merely enables a bird to maintain a bearing once that bearing has been selected. Kramer was acutely aware of this distinction when, in 1953, he suggested that navigation be considered a two-step process. In the first, or map, step the bird determines its location relative to some goal, while in the second, or compass, step it takes up and maintains the appropriate bearing to that goal.

In principle, the sun could provide the necessary map information as well as serving as a compass. Matthews (1951a, 1951b, 1953a, 1955) was the first to propose a theory of complete bicoordinate navigation by means of the sun. He suggested that a displaced bird might determine its latitudinal displacement by observing the sun's movement in arc and extrapolating that arc to its zenith (noon) position. Comparison of the noon altitude at the new location with the remembered noon

altitude of the sun at home would indicate whether the bird was north or south of its destination. Similarly, a bird could determine its longitudinal displacement by noting the sun's position along its arc and interpreting it with reference to a chronometer set on home (not local) time. If the bird is east of home, the sun will appear to have moved too far along its path; if west, the sun will not be far enough along its arc. With this information, the bird could take up the appropriate direction of flight to reach its destination.

An alternative model of bicoordinate sun navigation was proposed by Pennycuick (1960), who suggested that birds compare the sun's altitude and rate of change of altitude at their location with remembered values for the same time of day at their destination. The lines of equal values of these two parameters of the sun's position form a spatial grid that would also allow determination of distance and direction of displacement.

### 3. *Theoretical Considerations*

Although bicoordinate solar theories are attractive, both theoretical consideration and experimental evidence have failed to support them, and they have not gained wide acceptance. The theories demand extraordinarily accurate measurement of the sun's altitude, azimuth, and angular motion by a flying bird whose movement would result in changing parallactic errors in using landmarks as fixed reference points. Furthermore, the theory requires great precision in the bird's internal clock. A time change of one hour translates into a  $15^\circ$  change in the sun's position or, alternatively, to an east-west displacement of  $15^\circ$  of longitude. This means that a clock accurate to only  $\pm 10$  minutes would be geographically accurate to only  $\pm 200$  km (at a latitude of  $40^\circ\text{N}$ ). A timing error of as little as 2–3 minutes might preclude the use of true sun navigation at distances of less than 40–50 km from home. Chronometers with this degree of accuracy have yet to be demonstrated in birds (Adler, 1963; Meyer, 1964; Miselis and Walcott, 1970).

Models of bicoordinate sun navigation assume that when a bird is displaced, its time sense remains in phase with the local time of the area from which it was displaced. But studies of behavioral and physiological circadian rhythms uniformly show that such rhythms readily and rapidly re-entrain (resynchronize) to new local conditions. Birds can be clock-shifted by as much as 6 hours in a matter of 2–6 days (Hoffman 1954; Schmidt-Koenig, 1958). This makes it difficult to believe that a migrant retains a memory of the local time of its overwintering location after migrating a thousand or more kilometers and spending several months on its breeding territory (and vice versa).

There are also difficulties associated with a migrant's use of a circadian clock to determine longitudinal displacement en route. The principal agents of displacement for migrating birds are crosswinds. Displacement distances of more than 200–300 km are probably extremely rare. These distances correspond to time differences of only 10–15 minutes, and it is logical to assume that the migrant would have resynchronized its time sense by this amount within a day or two. In other words, if a migrant is blown off course but remains in its new location for more than 24 hours, it may well have lost the ability to detect its displacement.

I would further suggest that migrants might be faced with a "latitude clock-shift" problem. The time of spring migration coincides with a time of increasing day lengths in the northern hemisphere. Birds traveling north compound this day-length change, since the days are longer at higher latitudes. If a bird took off from the Gulf Coast of the United States in early May and flew north all night, covering a distance of 550 km, dawn would find it at a locality where the day length had "suddenly" increased by 20 minutes. Sunrise would occur 10 minutes earlier than expected. Although the bird had flown due north, the sunrise information would be equivalent to an eastward displacement of some 200 km. How a migrant copes with this problem, if indeed it is a problem, is totally unknown.

For any model of bicoordinate sun navigation to be operative, the migrant must either correct for its displacement immediately and return to its original longitude before its chronometer has had the opportunity to reset, or else the bird must possess a second, stable time sense that is resistant to changes in environmental cues. To date, evidence for the existence of such a stable clock is lacking. One final possibility remains. If we view navigation as a two-step process, the migrant could perform the map step immediately following its displacement and determine a new, corrected preferred direction at that time. To take up this new bearing at some later time, the bird need only refer to the sun for compass (Type II) information. Ironically, this can be done accurately only *after* the chronometer has resynchronized with local time. This should be investigated by transporting birds longitudinally and comparing their preferred orientation before and after being allowed to resynchronize to the new local time.

#### *4. Experimental Evidence*

Aside from these theoretical considerations, a growing body of empirical results argues against Type III models of sun navigation and in favor of a much simpler use of solar information.

First, and most important, the results of many clock-shift experiments are contrary to the predictions of a bicoordinate model. Let us consider

the example of a homing pigeon whose chronometer has been advanced by 6 hours. The pigeon now is released at 9:00 AM local time at a location 60 km north of the home loft. According to a bicoordinate model, the bird should interpret the sun's position with reference to its internal time sense, which indicates it is 3:00 PM. The sun is not as far along in arc as it would be at the home location, and it is rising rather than falling. The bird would interpret this time shift as a geographic displacement of  $90^\circ$  of longitude to the west. The 60 km north displacement would be inconsequential compared with the westward displacement of over 7000 km, and the bird would depart toward "home" to the east. If the bird had been displaced 60 km south, it would make little difference, since this distance also is minuscule compared with the apparent  $90^\circ$  westward displacement. This bird also would depart in an eastward direction (Fig. 7.)

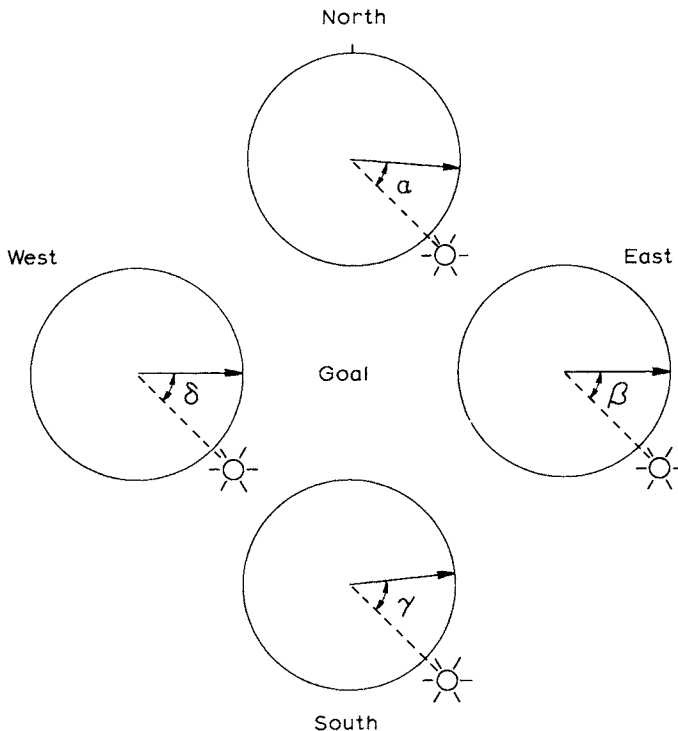


FIG. 7. Predicted orientation of clock-shifted birds according to Matthew's sun navigation hypothesis. The birds are released from the north, east, south, and west of home in the mid-morning. Their internal clocks have been reset by 6 hours and indicate mid-afternoon. Regardless of local release location, the birds should interpret the clock-shift as a massive displacement ( $90^\circ$  of longitude; 7000 kilometers) to the west, and reorient toward "home" in the east. (See text for full explanation.)

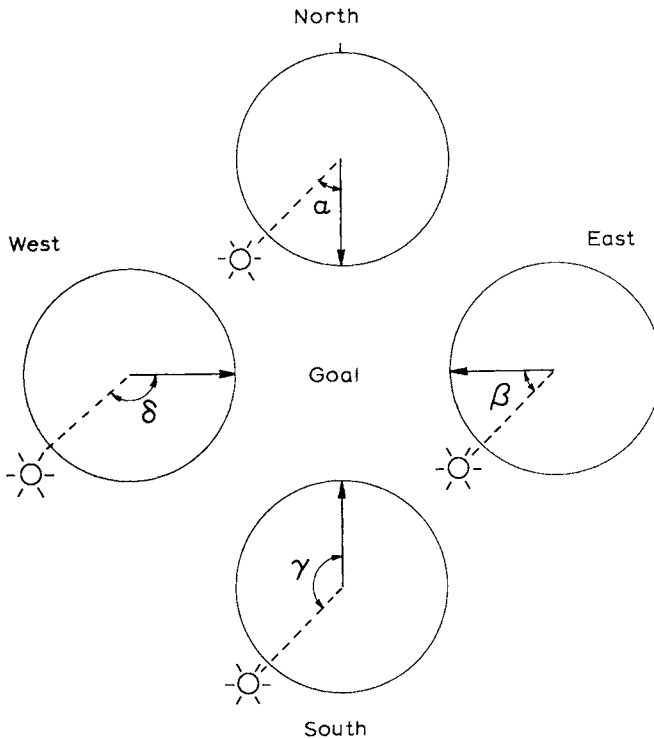


FIG. 8. Correct homeward orientation of birds released in the mid-afternoon when their internal clocks are in synchrony with local time.

If, on the other hand, the bird obtained its map information from some alternative source and merely used the sun as a compass, a very different set of predicted departure directions would be generated. When released 60 km north of home, the bird would determine (by unknown means) that home was to the south and it would take up a southward bearing relative to the sun's position. Under normal conditions, the sun is in the southwestern sky in the midafternoon, and south is approximately  $45^\circ$  counterclockwise from the sun (angle  $\alpha$  in Fig. 8). In our experimental situation, the bird's chronometer indicates it is midafternoon, whereas in actuality, it is 9:00 AM. The pigeon will make a predictable error and fly off at angle  $\alpha$  relative to the sun. Since the sun is rising in the southeastern sky, this results in an eastward departure, a shift of  $90^\circ$  counterclockwise from home (Fig. 9). Similar calculations for releases conducted east, south, or west of home all give the same predicted shift of  $90^\circ$  counterclockwise from homeward (Figs. 8 and 9).

Experiments now can be designed with clock-shifted birds in which opposite results are expected according to the two types of sun orientation hypotheses. In such experiments, it has been shown repeatedly that

pigeons choose bearings consistent with a simple sun-compass (Type II) model (Schmidt-Koenig, 1958, 1960, 1961; Graue, 1963; Keeton, 1969). To dramatize this point, I enlisted the cooperation of my colleague William Keeton. Clock-shifted pigeons were released in the four cardinal compass directions from the Cornell lofts. Their initial departure bearings are presented in Fig. 10. The results confirm the use of the sun as a simple compass, as can be seen by comparing the predicted directions of Fig. 9 with the actual bearings of Fig. 10.

A second way of testing sun navigation hypotheses is by means of slight clock shifts involving time changes of an hour or less. According to a bicoordinate theory, a time error of 1 hour should be interpreted as a displacement of  $15^\circ$  of longitude along an east-west line. As mentioned previously, at a latitude of approximately  $40^\circ\text{N}$ , this is equivalent to a displacement of approximately 1200 km. Similarly, a 20 minute shift is equivalent to a 400 km displacement, and a 5 minute shift to

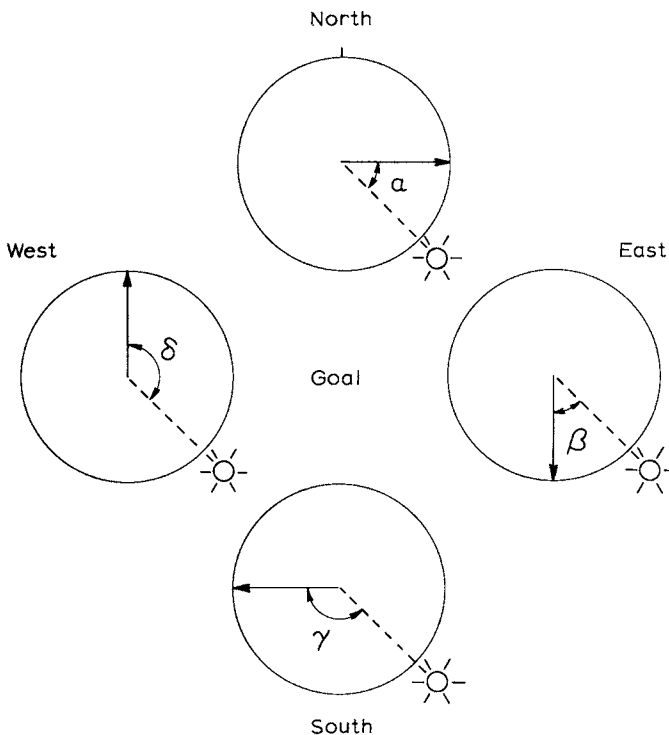


FIG. 9. Predicted orientation of clock-shifted birds according to a sun-compass model. The birds determine the direction home by some other means, then take up the appropriate compass bearing with reference to the position of the sun. The angles are as in Fig. 8, but the resulting directions are shifted  $90^\circ$  counter-clockwise since the sun is in the mid-morning position. (See text for full explanation.)



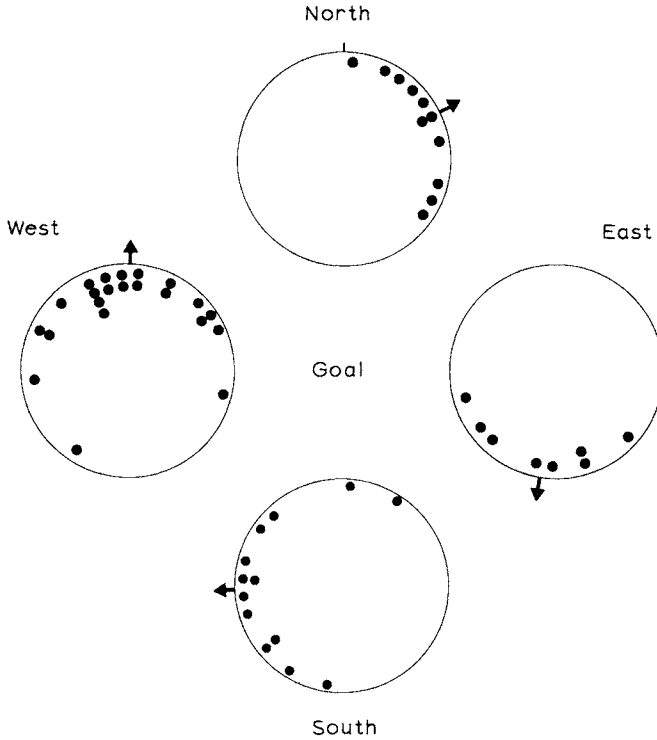


FIG. 10. Observed departure bearings of pigeons whose clocks have been advanced by 6 hours and then released 30 to 80 kilometers to the north, east, south, and west of the Cornell lofts. Solid arrows denote mean directions.

approximately 100 km. Thus, minor shifts in the time sense should give rise to major changes in predicted "homeward" bearings. If the sun is being used merely as a compass, however, the predicted deflection from the true homeward bearing should only approximate  $15^\circ$  per hour. Consequently, clock-shifts of 20 or 5 minutes should produce changes in departure bearings so slight as to be almost undetectable.

Two such series of experiments have been performed to date (Walcott and Michener, 1971; Schmidt-Koenig, 1972). Although the results are somewhat meager, no large-scale deflections in departure bearings were observed, and both authors concluded that the sun was being used solely as a compass.

Other experiments have attempted to dissect out the latitudinal component of bicoordinate models by confining pigeons out of sight of the sun at the time of the autumnal equinox. At this time of year, the sun's day-to-day changes in zenith altitude are considerable, and a bird that has been prevented from viewing the sun for a week or more should detect a significant decrease in the height of the sun at noon. According

to Matthews' theory, this should indicate to the bird that it is north of home. It now becomes possible through a careful manipulation of time and distances to transport a pigeon to the south of its home loft and still have the sun's altitude lower at the release location than it was when *last viewed* at home. Matthews (1953a) performed such an experiment and found that the "deprived" pigeons departed to the south, away from home, in accordance with the hypothesis. Attempts to repeat these observations, however, have yielded negative results; deprivation of a view of the sun has not caused any significant change in homeward bearings (Rawson and Rawson, 1955; Kramer, 1955, 1957; Hoffmann, 1958; Keeton, 1970).

To summarize, a large body of evidence demonstrates that the sun is an extremely important directional cue for diurnally migrating and homing birds. Support for the idea that the sun provides accurate information about geographic location or the precise direction toward a pre-determined goal remains unconvincing. Rather, the general use of the sun appears to be as a dominant cue for maintaining a bearing that is determined by some other means.

### C. THE USE OF STELLAR CUES

#### 1. Evidence of Star Orientation

Since the 1930's, physiologists have known that when birds are held in captivity for long periods of time they often exhibit intense activity at night (Palmgren, 1937, 1938, 1949a,b; Merkel, 1938, 1956). This activity seems almost entirely restricted to species that migrate at night; further, the seasonal timing of this behavior coincides with the periods of spring and fall migration.

Hypothesizing that this nocturnal restlessness, or *Zugunruhe*, is a direct expression of migratory behavior, Gustav Kramer decided to study its orientation. He placed Blackcap Warblers (*Sylvia atricapilla*) and Red-backed Shrikes outdoors under the night sky and recorded their spontaneous locomotor activity in a circular cage. He discovered that these species oriented in a particular direction (Kramer, 1949, 1951). As long as the sky was clear, orientation was consistent from night to night (although it was not in the predicted direction of migration). Activity decreased in magnitude and lost its directionality when the sky clouded over.

Franz Sauer (1957) extended these findings and reported that Blackcaps, Garden Warblers, and Lesser Whitethroats (*Sylvia curruca*) took up appropriate southerly directions when tested in cages outdoors under the autumn night sky. As long as the brightest stars were visible, the migratory direction was maintained; but if the stars were hidden by

dense overcast, the birds circled randomly or ceased nocturnal activity altogether. Two Blackcaps were tested in the spring, and they both selected north-northeast bearings, in keeping with the predicted direction of spring migration.

Since this early study, star orientation has been reported for a wide variety of bird species ranging from waterfowl (Bellrose, 1958, 1963; Hamilton, 1962b; Matthews, 1961, 1963) and shorebirds (Sauer, 1963; S. T. Emlen, unpublished observations) to a large number of songbirds (Sauer and Sauer, 1960; Mewaldt and Rose, 1960; Mewaldt *et al.*, 1964; Hamilton, 1962a, 1966; Shumakov, 1965, 1967a; Emlen, 1967a,c; Dolnik and Shumakov, 1967; Sokolov, 1970; Rabøl, 1969, 1970, 1972; C. J. Ralph, personal communication; P. De Sante, personal communication). Few studies, however, do more than demonstrate that a caged bird can select its direction under starry skies or, perhaps, that orientational accuracy decreases under overcast.

Sauer (1957) was the first to investigate detailed mechanisms of star orientation. To do this, he exposed warblers to the artificial skies of a small planetarium. When he adjusted the star projector so that it accurately duplicated the sky outdoors, the birds again took up their migratory directions. Under autumn skies, Lesser Whitethroats selected a southeasterly direction, while a Garden Warbler and a Blackcap oriented to the southwest. Only a single Blackcap was studied under a spring sky in the planetarium; it adopted a northeasterly bearing in agreement with this species' migratory route in this season. By means of appropriate control experiments, Sauer was able to demonstrate that his birds definitely were responding to information provided in the artificial starry sky and not just to visual or acoustical artifacts that are so commonplace in planetarium settings. When he shifted the star projector so that the position of stellar north was reversed 180°, the birds shifted their orientation accordingly.

I have also conducted planetarium studies (Emlen, 1967a,b) on a North American migrant, the Indigo Bunting (*Passerina cyanea*). These birds selected southerly bearings in the autumn when they were tested under the natural night sky in small, circular cages. Individuals maintained approximately the same direction when they were brought indoors and tested under the artificial autumn skies of a large planetarium (Fig. 11). These birds also took up appropriate north to northeasterly directions in the spring when they were exposed to low-latitude spring skies. Results of control experiments were similar to those of Sauer; the buntings reversed their orientation when the direction of stellar north was reversed, and nocturnal activity either became random or ceased when the artificial stars were turned off and the planetarium dome was diffusely and dimly illuminated (Emlen, 1967a).

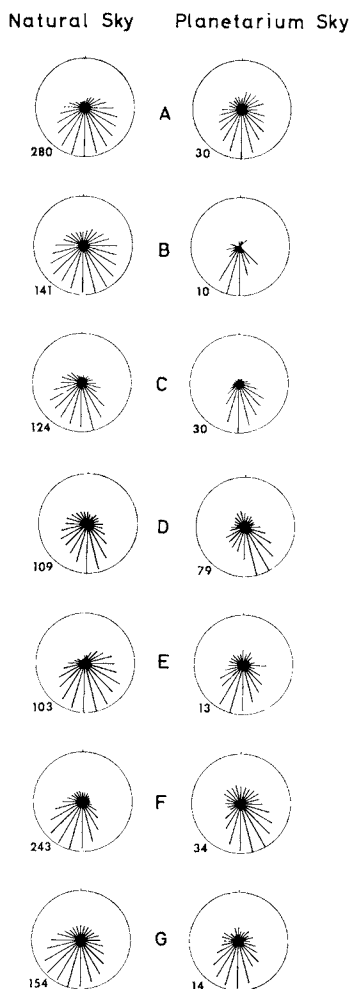


FIG. 11. *Zugunruhe* orientation of caged Indigo Buntings (*Passerina cyanea*). Left: Behavior when tested outdoors under clear night skies. Right: Behavior when tested in a large planetarium under artificial skies set to simulate outdoor conditions. Vector diagrams are plotted on a proportionality basis with the radius equaling the greatest amount of activity in any one 15° sector. The number that this represents is presented at the lower left of each diagram. (From Emlen, 1967a.)

The finding that a caged migrant will take up its migratory direction when in the confines of a planetarium has provided the ornithologist with a powerful experimental tool. By appropriate manipulations of the artificial sky, the investigator can tease out the different components of star orientation mechanisms.

## 2. *Models of Star Orientation*

Theoretically, sufficient information is available in the night sky to allow bicoordinate navigation. In a manner analogous to the sun navigation model described above (Section IV,B,2), a migrant could compare the altitude and azimuth position of a selected star or group of stars with their remembered positions at some goal. When coupled with an extremely accurate and stable time sense, such information could tell the bird its distance and direction of displacement.

Alternatively, stellar cues might provide the migrant with only compass (Type II) information. There are two basic ways of obtaining such directional information. In the first, a migrant could select a specific star or group of stars and orient by flying at a particular angle from them. This would require the integration of an internal time sense, since the bird could not maintain a straight course unless it changed its angle of orientation relative to the selected stars to compensate for their apparent motion. I wish to emphasize that the requirements for such a system to be operative at night are much more demanding than would be necessary for diurnal, solar orientation. Different stars are visible above the horizon at different times of night and at different seasons. Instead of one obvious celestial object, many potential cues are available in the night sky and the migrant must be able to locate consistently the specific one or ones of importance. This presumably requires some form of pattern recognition. Additionally, the necessary rate of compensation differs depending upon the position of the star or stars being used. Celestial motion is an apparent motion produced by the earth's rotation of one revolution each 24 hours. All stars appear to move with an *angular* velocity of  $15^\circ$  per hour. But the *linear* velocity of a star located near Polaris (the North Star), which moves through a very small arc, is quite small compared to that of a star located near the celestial equator. Consequently, if a bird were to use several star groupings located in different parts of the sky, it would have to have several compensation rates at its disposal and be able to pair specific stars and rates of movement appropriately. Finally, the actual direction of this compensation would have to vary, being clockwise for stars located in the northern sky and counterclockwise for those to the south (see Fig. 12).

Without time compensation, no single star (with the exception of Polaris) could provide sufficient information to allow a bird to maintain a given direction through time. In the second model, the bird would make use of additional, configurational, information available in the night sky and use patterns of stars to locate directional reference points. For example, the Big Dipper, Ursa Major, is localizable because of the characteristic spatial pattern of its component stars. By visually extending

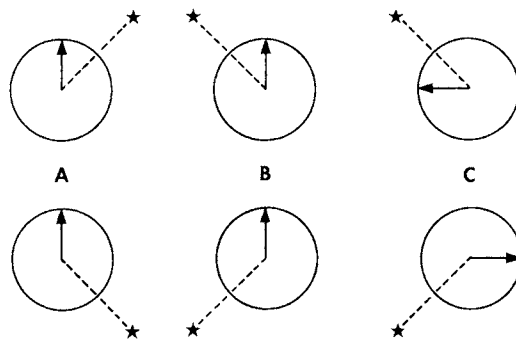


FIG. 12. Expected shift in orientation following resetting of the internal clock six hours behind local time, and assuming compensation for motion of a star located in the northern sky (upper diagrams), or in the southern sky (lower diagrams). (A) represents normal orientation early in the evening when the critical star is located to the NE or SE respectively. Later in the night, in (B), orientation continues although the stars have rotated to a more westerly position. In (C), the bird's time sense has been shifted to coincide with time (A) while the actual time and, hence, the position of the stars, coincides with situation (B). Thus, the direction of the predicted error is dependent upon the north-south location of the critical star. (After Emlen, 1967b.)

the pouring line of the dipper, one can find Polaris and hence geographic north. The Ursa Major pattern moves across the sky, but its shape remains constant and it preserves its relationship to Polaris. Since each star bears a fixed geometric relationship with all others, it is theoretically possible for a bird to locate a directional reference point from an infinite number of configurations. The principal difference between this model and the one presented above is that a compass direction can be located as long as the important star patterns are visible, regardless of any knowledge of the time of night, the season, or the geographic location.

### 3. Clock-Shift Experiments

These two alternative hypotheses can be separated by means of clock-shift experiments. The usual procedure is to confine birds for several days to a week under an altered light-dark regime. With a planetarium, however, one can create a situation in which the bird's internal time sense is out of phase with astronomical time without subjecting the bird to the trauma of confinement. The star projector can be altered to present a sky that is advanced or retarded from local time. If the chronometer is an integral component of the star orientation system, predictable shifts in migratory orientation should result.

A demonstration that the chronometer is important for nocturnal orientation would not, by itself, allow us to distinguish a bicoordinate navigation system from a time-compensated star compass similar to the sun compass discussed previously (Section IV,B). To separate these possibili-

ties, we must examine the direction and magnitude of the resulting shifts in the bird's orientation. This can also provide valuable information about the portion of the sky and, thus, the critical stars used in orientation. If nocturnal migrants are responding solely to configurational information in the night sky, no directional change would be expected under the clock-shift situation. Note, however, that without integration of temporal information, a migrant could not obtain bicoordinate information from the stars alone.

Two different questions thus are posed by planetarium clock-shift experiments. First, is the chronometer an integral part of star orientation? And, second, does the system provide sufficient information for direct goal orientation or for reorientation following displacement? To date, only a few experiments have been performed, and different species performed differently. Because of their theoretical importance, these studies will be discussed in some detail.

The Sauer's studied the behavior of three individual warblers—one Lesser Whitethroat (Sauer, 1957) and two Blackcaps (Sauer and Sauer, 1960)—under clock-shifted planetarium skies. Their technique was to observe the birds directly from underneath the circular orientation cage and to record the length of time the birds spent fluttering their wings while aiming in a particular direction. Periods without wing quivering were not considered *Zugunruhe* and were omitted from the analyses.

The Lesser Whitethroat was studied in the autumn of 1956 and oriented to the south-southwest when tested under a "normal" planetarium sky. When the projector was manipulated to give a sky that was advanced relative to local time (equivalent to the bird's chronometer being slow) the bird altered its directional behavior. When the discrepancy between local and planetarium time was 1 hour, the whitethroat headed southwest; when the discrepancy was  $1\frac{1}{2}$  hours, it aimed to the west; and when the difference was 3–5 hours, it either oriented west-northwest or was random. When the sky's position was retarded from local time (equivalent to the bird's chronometer running fast) the results were less clear cut. The whitethroat continued to orient south-southeast in directions not significantly different from normal under skies phase shifted 1 and 3 hours (Sauer, 1957; Wallraff, 1960a,b).

An incorrect planetarium sky could be interpreted in one of three ways: either the bird's chronometer is wrong, the season has changed, or the bird has been displaced geographically to the location where the experimental sky would be in phase with local time. Sauer (1957) interpreted his experiments in terms of projected geographic displacements and considered his results as support for a hypothesis of bicoordinate stellar navigation. His advanced skies would be "equivalent" to instantaneous relocations  $13^\circ$  to  $73^\circ$  of longitude to the east. The white-

throat's westerly shifts in orientation under these skies are in accord with such a hypothesis, as is the fact that the amount of the shift exceeds the  $15^\circ$  per hour predictable on the basis of a time-compensated star compass alone. But the results under the retarded skies fail to provide evidence for the incorporation of a chronometer at all, much less for a bicoordinate system. These skies were equivalent to geographic displacements of  $17^\circ$  and  $51^\circ$  of longitude to the west. Yet the whitethroat showed no significant tendency to compensate with a more easterly orientation.

In the autumn of 1958, Sauer and Sauer (1960) repeated planetarium clock-shift experiments with two Blackcap Warblers. Under a normal planetarium sky, both individuals displayed a southwesterly directional preference. When exposed to skies advanced from local time, one individual (no. 632) changed its behavior in a manner similar to that of the whitethroat. Its orientation shifted more westward (clockwise) as the sky was altered from 1 to 5 hours out of phase with local time. (I have recalculated, pooled, and replotted the original data for this bird in Fig. 13.) The Sauers interpreted these results as confirmation of their Type III star navigation hypothesis. I feel, however, that the magnitude of the Blackcap's directional shifts is not significantly different from  $15^\circ$  per hour. Consequently, this bird's behavior is also consistent with a time-compensated star compass model. The direction and amount of change further implies the use of stars located in the southern sky, close to the celestial equator.

When the planetarium sky was set behind local time, the Blackcap's behavior was highly variable. With skies 1, 3, and 6 hours behind local time (equivalent to the chronometer being advanced equivalent amounts), orientation did shift to the south and southeast, although the degree of scatter increased considerably. In the first two cases, the amount of shift was more than would be expected from a star compass alone, while in the last case, it was somewhat less than such a model would predict. Interspersed with these results, the Blackcap showed a weak southwesterly orientation (no change from normal) under a sky 2 hours retarded, and its activity was random under skies deviating 4 and 5 hours from local time.

In one final experiment, another Blackcap (No. 652) was observed for  $2\frac{1}{2}$  minutes while exposed to a sky 3 hours behind local time. The bird did shift its behavior to the southeast, but the importance of such a short observation period is questionable.

All in all, the results of these experiments are difficult to interpret and have been the cause of considerable controversy (see Wallraff, 1960a,b). Personally, I feel that they provide a strong suggestion of the use of a time sense in star orientation. As support for a model



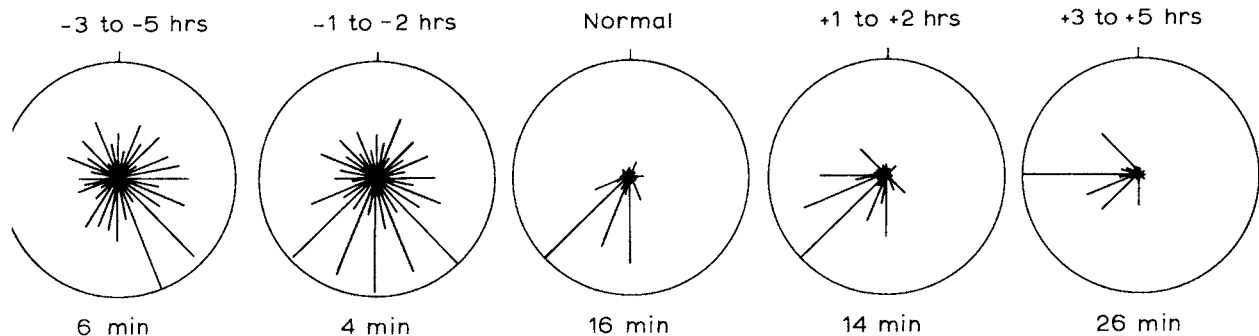


FIG. 13. *Zugunruhe* behavior of a Blackcap (*Sylvia atricapilla*) (No. 632) under planetarium skies adjusted to be out-of-phase with local time. Data were taken from Sauer and Sauer (1960, Figure 5) and translated into amounts of time that the bird fluttered its wings while aiming toward different sectors of the cage. Several experiments have been pooled and replotted in this figure. The number shown below each diagram represents the total amount of time (rounded to the nearest minute) spent in "active *Zugunruhe*" under that planetarium condition. The actual groupings used were the following: for tests under skies retarded 3 to 5 hours, (Sauer and Sauer, 1960) Figure 5t, a, and v; for -1 to -3 hours, Figure 5w and x; for "normal" skies, Figure 5y and z; for +1 to +2 hours, Figure 5a, b; and for skies advanced 3 to 5 hours, Figure 5d and e.

of bicoordinate star navigation (Sauer, 1957, 1958, 1961; Sauer and Sauer, 1960), I find them less convincing.

My studies (Emlen, 1967b) suggest a very different orientational strategy for Indigo Buntings. Pilot experiments conducted during the autumn migration season under temporally altered planetarium skies failed to produce any deflection in orientation (S. T. Emlen, 1967b; unpublished observations). I performed a more extensive series of experiments under clock-shifted skies in the spring of 1965. Eight different buntings were active for a total of 39 experiments, each approximately 2 hours in duration. The north to northeast orientation of these birds under planetarium-normal conditions was compared with their behavior when exposed to artificial skies 3, 6, and 12 hours out of phase with local time.

All birds tended to maintain their normal spring migratory directions. The results from one of the individuals whose orientation was most concentrated are given in Fig. 14. Even if the birds were relying upon stellar cues located very near Polaris with slow rates of movement, one would expect slight, consistent, changes in direction. But, although variations in orientation did occur, they were neither consistently clockwise nor counterclockwise in direction. In Fig. 15, I have replotted the deviations between the mean bearings from individual clock-shift tests and the mean directions obtained under planetarium-normal conditions. In the case of the 3-hour shifts (which, according to a bicoordinate model, would be indicative of a longitudinal displacement of  $45^\circ$  or approximately 3600 km), the mean bearings are remarkably close to the normal spring migration directions. The same is true for the results obtained under the 6-hour retarded and 12-hour advanced skies. Only in the case of the 6-hour advance (chronometer 6 hours behind local time) is there a slight suggestion of a counterclockwise shift in orientation. This difference is not statistically significant, and the magnitude ( $21^\circ$ ) is too minor to be considered as compensatory for an eastward displacement of over 7000 km. Rather, if these results were to be interpreted as evidence for the integration of a clock mechanism at all, they would imply a star compass based upon stars with slow rates of movement and located in the northern sky.

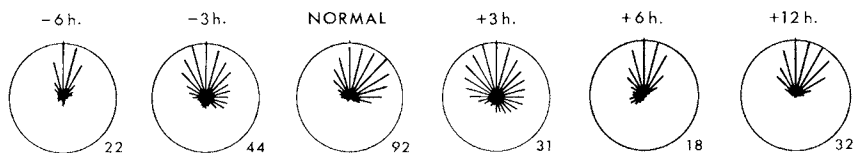


FIG. 14. *Zugunruhe* orientation of a caged Indigo Bunting exposed to planetarium skies advanced and retarded from local time. Vector diagrams are plotted as in Fig. 11. (Redrawn from Emlen, 1967b.)

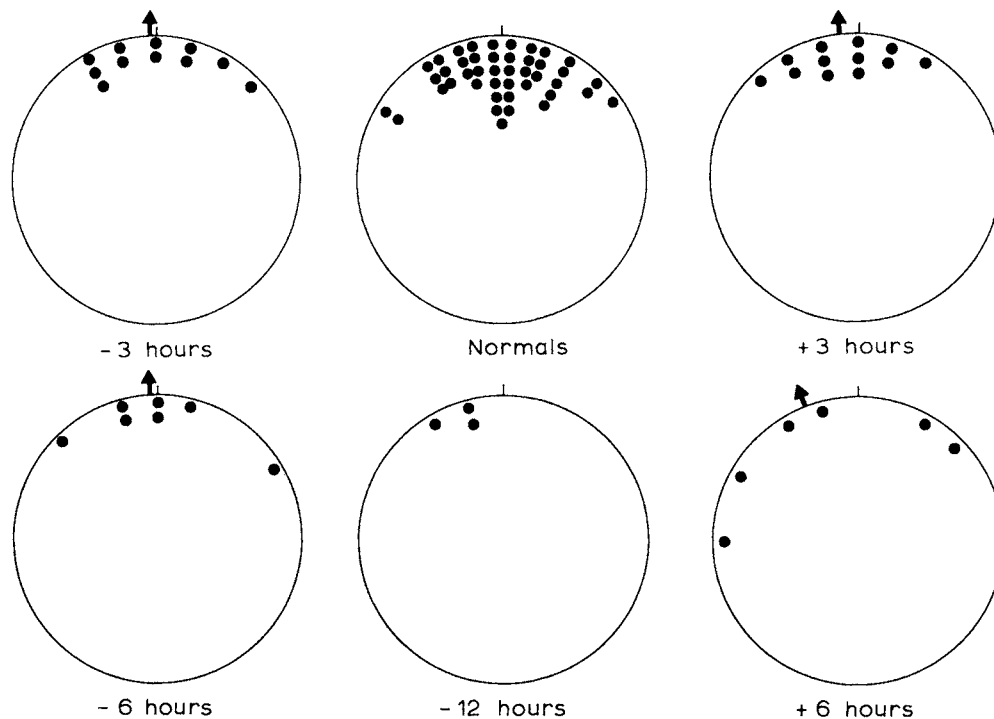


FIG. 15. Mean directions taken by caged Indigo Buntings under temporally altered planetary skies. Results from 39 clockshift and 43 control (planetary "normal") experiments, each of two hours duration and representing eight individual buntings are pooled in these diagrams. Each dot represents the mean direction from one such experiment. The data are plotted in  $15^\circ$  sectors with  $360^\circ$  representing the mean direction under unmanipulated planetary conditions. The "normal" diagram gives an indication of the consistency of orientation from night to night. The remaining vector diagrams (with overall mean directions given by the black arrows) show any shift in orientation caused by resetting the planetary sky 3, 6, and 12 hours out-of-phase with local time. No significant directional changes occurred. (Recalculated from Emlen, 1967b, and unpublished data.)

Since the buntings maintained their north to northeastward orientation under phase-shifted skies, I hypothesized (Emlen, 1967b) that temporal compensation for stellar motion was *not* an essential component in the migratory orientation mechanism of this species. Indigo Buntings presumably can determine their migratory direction from configurational information provided by the patterning of stars. This would give them a directional reference and hence a compass capability.

White-throated Sparrows (*Zonotrichia albicollis*) may also use the patterning of stars to determine direction. Preliminary studies involving radar tracking of free-flying clock-shifted birds failed to yield consistent deflections in migratory bearings (S. T. Emlen and N. J. Demong, unpublished observations). Gauthreaux (1969) also studied the directional preferences of nine individual White-throated Sparrows that he caged for extended periods of time under stationary skies in a small planetarium. With one exception, the birds maintained a stable migratory direction throughout the night, failing to compensate for the expected rotation of the sky.

Finally, Matthews (1963), in his studies of the orientation of Mallards, found that clock-shifted birds released in the daytime exhibited typical deflections in their departure bearings (Fig. 16, top). However, when similarly treated individuals taken from the same population were released at night under starry skies, they continued to orient northwest in the same direction as the controls (Fig. 16, bottom). This led Matthews to state (1963, p. 426), "we are forced to the conclusion that the time element does not enter into star-compass orientation, that measurement of the movement of certain stars in azimuth is not the concern of these birds. From this it does not seem possible to escape the implication that the birds are finding their compass direction by reference to the orientation of star *patterns*, possibly using the same constellations as we do ourselves."

Only one attempt has been made to study which star patterns are of particular importance to migrating birds. Using Indigo Buntings, I conducted a series of experiments in which selected stellar configurations or portions of the planetarium sky were blocked from view (Emlen, 1967b). My initial finding was that most major star groups could be removed one at a time with no discernable effect on the buntings' behavior. When I removed entire sections of the sky, however, orientation deteriorated considerably. A general tendency emerged for most buntings to rely upon the northern, circumpolar area of the sky within about 35° of Polaris.

Of equal importance, perhaps, were two corollary findings. First, there appears to be considerable redundancy in the pattern recognition process of buntings. Several individuals were disoriented when the circumpolar

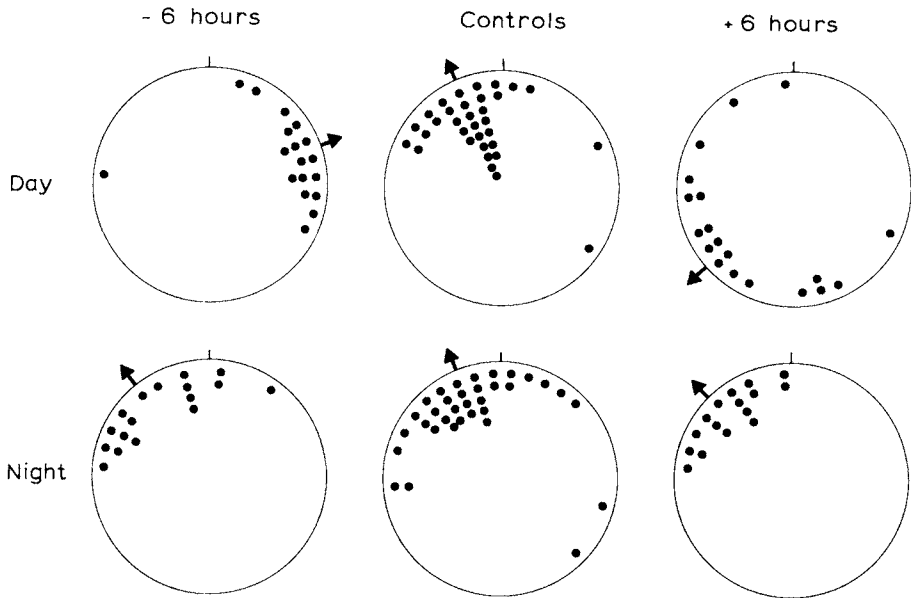


FIG. 16. Effect of clock-shifting upon the departure directions selected by Mallards (*Anas platyrhynchos*) when released in the daytime (top) and at night (bottom) near Slimbridge, England. Arrows denote mean bearings. (Redrawn from Matthews, 1963.)

portion of the sky was blocked but oriented properly when major groups of stars within this zone were removed individually. If a bird is familiar with a particular portion of the night sky, removal of a group of stars might merely force it to rely upon some alternative constellation. Because of this redundancy, continued orientation in the absence of a particular star pattern cannot be interpreted as evidence for the unimportance of that pattern. All one could state would be that sufficient directional information remained in its absence.

Second, different individual buntings were relying upon different cues in the night sky. This variability is inconsistent with any hypothesis of a predetermined, genetically fixed "star map" of constellations and suggests that the maturation of star orientation abilities is a complex, individualistic process. [For a fuller discussion of the ontogenetic development of star orientation capabilities, the reader is referred to Emlen (1969b, 1970a, 1972) and Wallraff (1972).]

#### 4. Seasonal Changes in Orientation

If some birds do not possess a celestial map and compass capability, what factors determine the directions they select as their preferred com-

pass bearings? And what is responsible for the major reversal of migratory directions between spring and fall? Does stellar information play a role in either process? The first of these questions is largely unanswered; the second is only beginning to receive attention.

The stars that are present in an autumn night sky are very different from those available in the spring. The slight inequality of the length of the solar and sidereal days produces a seasonal change in the temporal positions of stars. Because of these seasonal differences, a migrant might possess a specific northward directional response to the stellar stimuli present in a spring night sky and a different, southerly, response to the stellar stimuli of the autumn sky. This hypothesis has been tested with European warblers (Sauer, 1957, 1961; Sauer and Sauer, 1960) and Indigo Buntings (Emlen, 1967b), again with differing results.

When a planetarium sky is adjusted to be 6 hours behind local time, the new sky simulates the conditions that will be present at the same location and same time of night but at a season 3 months later. While performing clock-shift experiments, the Sauers noted that the Lesser Whitethroat and a Blackcap frequently showed random activity under skies phase shifted from 5 to 10 hours. [The actual conditions under which disorientation resulted were the following: for the Lesser White-throat, under skies 7 hours retarded and 4 hours advanced from local time; for the Blackcap, under skies 2, 4, 5, and 7 hours retarded and 6, 7, 8, 9, 10, and 11 hours advanced from local time.] Since these skies are those of summer and winter, they hypothesized that the warblers were unable to orient because the stellar cues essential for navigation are only present at the actual times of migration. Further, when the warblers (one Garden Warbler and three Blackcaps) were confronted with a planetarium sky typical of the opposite migration season, they exhibited "conflict" behavior, concentrating their locomotor activity to the north and south, along an axis parallel to the line of migratory flight.

The behavior of Indigo Buntings under skies adjusted by 6 and 12 hours was very different. Even with the sky advanced 12 hours, the celestial equivalent of the opposite migration season, the buntings continued to orient in their typical migratory direction, to the northeast (Figs. 14 and 15). The visual stimuli typical of the opposite migration season failed to evoke any change in directional response. This, coupled with the finding that the northern circumpolar area of the sky was most important during *both* spring and fall migration seasons (S. T. Emlen, 1967b; unpublished observations), raised the possibility that Indigo Buntings may use the same stellar cues during both their northbound and southbound travels. Perhaps it is not the visual features of the spring or fall sky per se, but rather some feature of the bird's physiologi-

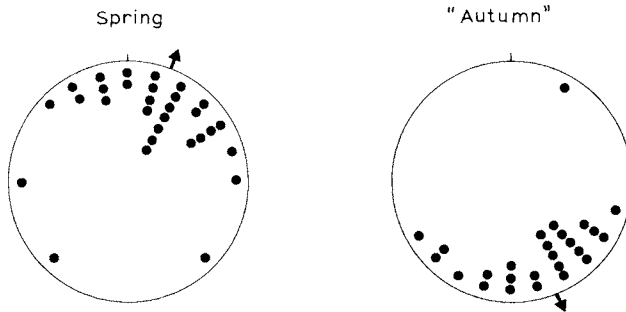


FIG. 17. *Zugunruhe* orientation of Indigo Buntings artificially brought into the physiological states appropriate for spring (left) and autumn (right) migration. Birds from both groups were tested simultaneously, in May, under a spring planetarium sky. Each dot represents the mean direction from one experiment. The results from 6 and 5 birds, respectively, are pooled in these diagrams. Mean direction in spring =  $22^\circ$ ; probability by Rayleigh test = 0.000. Mean direction of "autumn" birds =  $157^\circ$ ; Rayleigh probability = 0.000. (Replotted from Emlen, 1969a.)

cal state that dictates the preferred migratory direction. By appropriate photoperiod manipulations, I brought two groups of male Indigo Buntings into spring and autumn migratory conditions synchronously (Emlen, 1969a). When their directional preferences were tested under identical spring planetarium skies, the two groups showed different behavior. Birds that physiologically were anticipating a spring migration oriented to the north-northeast; those in autumnal condition headed south-south-east (Fig. 17). Important differences must exist between the physiological states of migration in the spring and autumn, and I hypothesized that seasonal changes in the hormonal state of the birds would be found to play a key role underlying the seasonal reversals of preferred migration directions (Emlen, 1969a). Recent studies by Martin and Meier (1973) with White-throated Sparrows support this prediction. They report being able to reverse the polarity of orientation in caged sparrows by administering exogenous prolactin and corticosterone at different times of day.

### 5. Discussion

Planetarium experiments suggest that at least two different strategies of star orientation may have evolved among nocturnal migrants. As additional studies are conducted, still other mechanisms may emerge.

The Indigo Bunting is a moderate-distance migrant that breeds throughout much of the eastern United States and winters in the Bahamas, southern Mexico, and Central America. For most individuals, the journey is probably 1500–2200 km in length. Even the southernmost extension of the species' wintering range lies well north of the equator

(10°N latitude). For such a migrant, use of the northern circumpolar area of the sky makes good sense. These stars are constantly above the horizon and hence are visible at all seasons and along the entirety of the migration route.

But consider the problems of a transequatorial migrant that travels far into the southern hemisphere each winter. Stars close to the northern celestial pole sink below the horizon and are no longer visible to guide the bird on the southern portion of its journey. Star orientation by pattern recognition alone might be more difficult for such long-distance migrants. Presumably they would have to be able to use several patterns of stars having different declination values. If a north reference point is to be extrapolated from star patterns alone, this extrapolation becomes less accurate as the angular distance between the critical stars and Polaris increases. The stars that might be optimal from the standpoint of visibility at all latitudes along the flight path would be those located in the southern sky, close to the celestial equator. This is precisely the area of the sky where the rate of apparent motion of stars approximates that of the sun. Consequently, it might be advantageous for these birds to employ some form of clock-compensated star orientation system, using the same rate and direction of compensation that they presumably use for sun-compass orientation during the day.

All this will remain speculative until many more comparative studies are performed. But it is interesting in this respect that several species mentioned as providing hints of time-compensated nocturnal orientation [Blackcaps, Whitethroats, Barred Warblers, Scarlet Rosefinches, and Lesser Golden Plovers (*Pluvialis dominica*)] migrate farther and to lower latitudes than do Indigo Buntings or White-throated Sparrows.

#### D. BEHAVIOR UNDER OVERCAST SKIES

As evidence of the importance of celestial cues accumulated in the 1950s and 1960s, it produced a bandwagon effect, and claims soon began appearing in the popular literature that scientists had solved the mysteries of bird navigation. But the bandwagon was short-lived. However attractive the hypotheses of true celestial navigation might be, experimental support was still lacking. Directional orientation by means of a celestial compass alone cannot fully explain migratory behavior; such orientational systems can just as well enable a bird to select and maintain an inappropriate bearing as a proper one. Current knowledge of celestial orientation simply does not provide answers to the rather fundamental questions: What factors operate in the initial selection of one direction rather than another? What causes young, inexperienced birds to select an appropriate direction for their first migration?



### 1. Orientation under Cloud

While the attention of experimentalists was focussing on laboratory studies of celestial orientation, other ornithologists were studying broad patterns of migration by means of surveillance radar. Early radar investigations concentrated on describing the directional patterns of migration at different geographic localities and on assessing the volume of migration and the behavior of migrants under different meteorological conditions (see Eastwood, 1967).

It soon became apparent that the presence of overcast skies had only a slight, if any, inhibitory effect upon the volume of migration aloft. There are reports of birds changing direction and thereby avoiding or skirting around areas of cloud (e.g., Williams *et al.*, 1972; Richardson, 1974), and Bellrose and Graber (1963) believed that passerine migrants changed altitude on many overcast nights, apparently attempting to climb above the cloud layer if it was sufficiently low. But, in general, radar studies have shown that migrants continue to fly along straight well-oriented paths under totally overcast skies. Both the mean direction of flight and, in many instances, the angular spread of individual tracks are comparable under clear and cloudy conditions. To date, documentation of orientation under complete cloud cover has been reported for birds migrating over the flat agricultural lands of Illinois (Hassler *et al.*, 1963; Bellrose and Graber, 1963), inland in the Canadian Maritimes and upstate New York (Richardson, 1971, 1974; Griffin, 1972, 1973), and along the Atlantic Coast from Nova Scotia (Richardson, 1971, 1974) to Massachusetts (Drury and Nisbet, 1964; Nisbet and Drury, 1967) and Virginia (Williams *et al.*, 1972; S. T. Emlen and N. J. Demong, unpublished observations), and the southeastern United States, including Georgia on the Atlantic Coast (S. A. Gauthreaux, Jr., personal communication) and Louisiana on the northern coast of the Gulf of Mexico (Gauthreaux, 1971; Able, 1974a). Similar observations have been made in Europe, both in Britain (Evans, 1966, 1968, 1972) and in Switzerland (Steidinger, 1968). Taken together, these observations have been made both in the daytime and at night and include shorebirds and waterfowl as well as passerines.

Vector diagrams of the orientation of nocturnal migrants passing over a radar site in New Brunswick are presented in Fig. 18. These data, generously provided by W. John Richardson, clearly show the birds maintaining an accurate northeastward orientation on both clear and totally overcast nights. Figure 19 is a photograph of the display of a height-finding radar taken on the night of May 12, 1971. It shows that the birds whose orientation is depicted in Fig. 18 were flying at altitudes well below the layer of overcast.

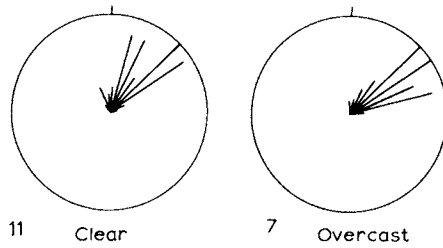


FIG. 18. Flight directions of nocturnal migrants near St. Margarets, New Brunswick, as determined by radar analysis. Left: Orientation under clear skies on the night of 11 May 1971. Right: Orientation under total overcast during the following night of 12 May 1971. Surface winds on 12 May were from the south-southwest at 13 knots. Diagrams plotted on a proportionality basis with the greatest number of birds in any one  $10^\circ$  sector shown to the left of the figure. (From Richardson, 1974.)

Instances of disorientation are rarely observed on radar, but where they have been reported, they have invariably been associated with conditions of fog, total overcast, or both (Lack and Eastwood, 1962; Drury and Nisbet, 1964; Bellrose, 1967a). But the growing list of studies cited above demonstrates that overcast per se does not result in disorientation. This suggests that although overcast skies obscure the sun and stars and therefore eliminate one system of direction finding, most migrants possess alternate guidance systems that are at least sufficient to enable the birds to *maintain* their flight directions. Only when these alternative cues are simultaneously eliminated does disorientation result.

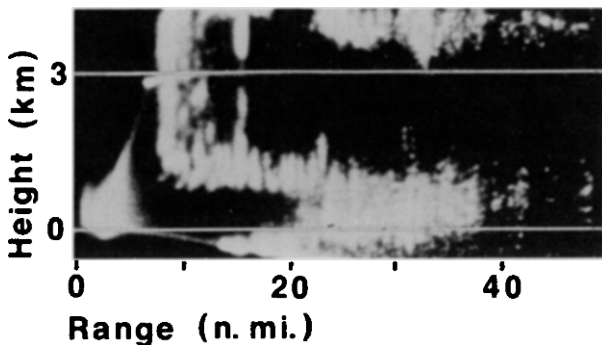


FIG. 19. Height distribution of birds and clouds on the night of 12 May 1971. Photograph shows the display of a high-power nodding-height finder radar located at St. Margarets, New Brunswick. Cloud echo occurs at 4000 meters while the bird echoes are concentrated well below this, near 1000 meters. Echoes within 15 nautical miles of the radar site are obscured by ground clutter. (From Richardson, 1974.)

## 2. *Use of Visual Reference Markers*

What sources of information might a migrant use to maintain its directional track in the absence of celestial input? The most obvious would be to use visual features of the landscape as points of reference. The bird would merely note the location of some visual marker on the ground below that is ahead of it along the desired line of flight. As long as two or more such markers remained visible, a migrant could easily maintain its course by successively piloting toward first one reference point and then another. In this way the bird could detect any slight displacement, turning, or wind drift and correct its heading to keep the same resultant track. This would require neither a familiarity with the landscape beneath nor an unrealistic degree of visual acuity.

On the basis of several hundred hours of night flying in a small aircraft at the altitudes where birds migrate, Bellrose (1971) reports that several features of the landscape are visible on even the darkest of nights. Landscape features, such as hills, mountains, and land-water interfaces, were the most prominent. On clear nights when the moon was in the sky, all but the smaller details of the landscape were detectable. On dark, overcast nights, topographic features were much less distinct, but major features, such as rivers, could be distinguished from 300 m and the shoreline of the Atlantic Ocean was clearly visible from at least 600 m. Artificial lights produced by human civilization could also provide optimal reference points for nocturnal migrants. Considering the apparent ease of maintaining a direction through the use of visual reference markers, it is not surprising that oriented flight continues under occluded skies.

## 3. *Flight in Cloud*

But what happens if visual contact with the ground is obscured by low overcast or fog? Can birds continue to orient properly in the absence of all visual cues? This question is of considerable importance and has led to a concerted search for cases in which nocturnal migrants are flying between cloud layers or in clouds. Understandably, birds do not often fly under these conditions; and when they do, ornithologists are rarely on hand or prepared to record all of the information necessary to document the event. This documentation requires an accurate assessment of the altitude of the flying birds, the horizontal extent of the total overcast conditions, and the height of the bottoms and tops of the cloud layers. Because of the difficulty of obtaining such information, no single instance yet compiled provides entirely convincing evidence that birds can maintain normal tracks while traveling through cloud.

However, several cases are extremely suggestive, and if one pools the available evidence it is difficult to avoid the conclusion that at least some birds are capable of maintaining fairly straight tracks while flying without visual contact with either celestial cues above or landscape cues below.

Bellrose and Graber (1963) provided the first suggestion of orientation in cloud. On the night of 27 May 1960, northern Illinois was covered by heavy cloud that extended from 300 m above ground to an estimated top of 1200 or 1500 m. The height distribution of the birds migrating aloft indicated that most were enveloped by the clouds. The mean direction of the radar targets was to the north-northeast, appropriate for spring migration through Illinois. However, the spread of tracks was quite large, with standard deviations ranging from  $44^\circ$  to  $82^\circ$  for samples of birds migrating at different altitudes. On 15 October 1960, clouds again extended from 200 m to an estimated 1050 m above ground, while birds were distributed up to 1500 m with a slight increase in density in the 300 m above the presumed cloud tops. Approximately half of the birds were flying within the cloud while the remainder were traveling above it. The flight directions of birds at all altitudes were well oriented to the south. No differences were apparent between the behavior of birds traveling in and above the overcast (standard deviation ranged from  $20^\circ$  to  $33^\circ$ ).

The second report of possible orientation in overcast comes from Williams *et al.* (1971, 1972) who used NASA tracking radars at Wallops Island, Virginia, to obtain long, detailed tracks of individual bird targets. All targets are presumed to be shorebirds or waterfowl on the basis of their air speeds. On the night of 2 April 1969, heavy fog or low clouds covered the sky at an altitude of about 185 m. Using the radar in an RHI mode, the Williamses located an upper cloud layer at approximately 5000 m. They state that "surface observations and satellite photographs before and after our tracking indicated that this was a totally opaque cloud layer." Unfortunately, the surface observations taken at Wallops cannot be relied upon, since all five of the birds tracked that night were followed at distances of from 20 to 80 km out to sea. Furthermore, the resolution of satellite photographs is insufficient to rule out the possibilities of even sizable gaps in the upper layer of cloud. The assumption that a coastal fog would have extended without gaps for a distance of 80 km out to sea is also questionable. Nevertheless, the birds certainly were flying in conditions of heavy cloud. Of the five targets, one was traveling downwind to the east-southeast, while three tracks were oriented northeast to east-northeast, the typical direction for spring migration at this location. The last bird was descending in altitude and maintaining a constant heading while its track curved

counterclockwise toward land. It is difficult to interpret these tracks considering the uncertainty of the meteorological information. But, with one exception, the birds were maintaining straight tracks and three were traveling in the appropriate migration direction.

Griffin (1972, 1973) used a low power, 3 cm, tracking radar to plot the courses of individual migrants. By specifically seeking out conditions of thick overcast, he was able to obtain accurate information on short segments (up to 5 km) of tracks of targets moving in or near cloud. His data also provide us with the most reliable information available concerning the specific nature and extent of the clouds.

His most impressive evidence of orientation in overcast comes from the night of 16 May 1970 at a location in upstate New York. The radar site was enveloped by fog, and available evidence (dew point depression information from evening radiosondes 150 km to the north-northeast and south-southeast, respectively, as well as surface observations from a variety of nearby locations) indicated the continuous presence of cloud to an altitude of approximately 2000 m. Twenty-one birds were tracked, all within this cloud zone. The behavior of the targets appeared perfectly normal; they were traveling downwind and all tracks were within  $45^\circ$  of a mean direction to the north-northeast. Furthermore, the tracks were straight.

On 23 April 1970, birds were tracked as they passed over New York City. Meteorological information indicated the presence of continuous cloud from a few hundred meters up to at least 1000 m and possibly much higher. The birds tracked were flying in directions ranging from  $315^\circ$  through  $0^\circ$  to  $123^\circ$ , although the mean direction was still to the north-northeast. More interestingly, many of these tracks were extremely circuitous, the birds apparently looping or zigzagging as they traveled. "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" (Griffin, 1972, p. 178). Only about one-third of the targets showed the straight, north to northeastward track typical of migration under clear skies.

I interpret the tracks obtained on the night of 30 April 1970, as suggesting a dichotomy in the behavior of migrants traveling inside and out of cloud. Neighboring airports reported fog and low-lying clouds, and radiosonde data suggested a well-defined cloud top at 500 m. Birds were tracked at a variety of altitudes although only four individuals definitely can be placed below the cloud tops. Each of these four tracks was quite nonlinear and showed twists, turns, or zigzags. The overall direction of three tracks was to the north-northwest to north, while the fourth curved to the southeast. The twenty-five tracks that were above 500 m in height (hence, presumably out of the cloud layer)

were distinctly straighter than the four low tracks. They were also tightly clumped around a mean direction to the northeast.

I would summarize the available evidence as follows: (1) most birds avoid flying through thick layers of cloud; (2) when confronted with this situation, many birds seem able to maintain a general direction of travel; (3) the accuracy of orientation is considerably decreased; (4) some birds exhibit a totally different flying strategy, twisting and looping their way along their course.

#### *4. Selection versus Maintenance of Direction*

An important distinction must be made between *maintaining* a direction taken up previously, either on the ground prior to departure or at times during the flight when visual cues might be visible through breaks in cloud, and *selecting* a correct course under or in total overcast. The former requires much less navigational versatility. For example, if a bird could localize discrete and repetitious sound sources on the ground, it might use them as acoustical reference points in a manner analogous to the use of visual markers (D'Arms and Griffin, 1972). The call notes given by many species of nocturnal migrants could, under some conditions, provide an additional indirect source of directional information. If the altitudinal distribution of birds aloft extended above or below the layers of overcast (as in the cases described by Bellrose and Graber, 1963), the birds within the cloud might hear the call notes of birds flying at different altitudes where additional directional cues were available. By comparing the locations of successive call notes, a bird might be able to extrapolate and follow the flight direction of an unseen companion (Griffin, 1969; Steidinger, 1972).

Other possible nonvisual guidance systems might include flying at a constant angle relative to the direction of the wind (see Section IV,E), using some crude form of inertial dead-reckoning system (see Section IV,F), or determining direction from cues provided by the earth's magnetic field (Section IV,G). Of these five possible means of maintaining direction (and undoubtedly there are others), only geomagnetism, a complex form of inertial guidance, or an accurate prediction of winds aloft could be used for selecting a migratory direction.

One way of learning whether most migrants are able to *select* an appropriate direction of flight in the absence of visual cues is to observe departure behavior under conditions of total overcast. While on the ground, a bird presumably integrates the various types of directional information at its disposal. If the sky is clear, these might include the position of the sun, and perhaps most importantly, the position of sunset as well as the early evening location of the stars. The topographic features of the immediate surroundings could serve as reference points.

Wind could be an important additional cue that might be integrated into this system. If discrete, cumulus clouds were present in the sky, the migrant presumably could determine the direction of the wind (at least at the altitude of the clouds) relative to its celestial and topographic framework without ever leaving the ground. If no clouds were present, the bird theoretically could still determine the wind direction by circling and noting changes in its ground speed using topographic features as reference points. Geomagnetic information might also be incorporated into this selection process.

If celestial information is removed, do the additional cues provide sufficient information for selection of the migratory direction? While studying autumn migration on the southeast coast of Louisiana, Hebrard (1972) conducted a "natural" experiment when a cold front brought low, continuous overcast to his study area. The clouds arrived in mid-afternoon on 13 October 1969 and persisted without a break until the morning of 15 October. Birds departing under the total overcast on the night of 13 October did so after a 2 hour deprivation of solar information and without access to stellar cues (clouds arrived at 3:15 PM; sunset was at 5:32 PM). Yet these birds (passerines) took off downwind in meaningful migration directions (see Fig. 20A). Birds departing under the overcast on the night of 14 October had been unable to view either the sun or the stars for over 24 hours. The orientation of these birds was quite poor, although the statistical mean direction remained significantly oriented to the south (Fig. 20B).

One interpretation of these results is that some birds are able to "remember" the position of the sun or the extrapolated position of sunset by using landscape cues as reference markers. In this way, the sun could provide critical compass information even if it were absent at the time of departure; the bird would select its bearing with reference to topographic features that had taken on directional significance. Such transferring of information onto a topographic reference system should

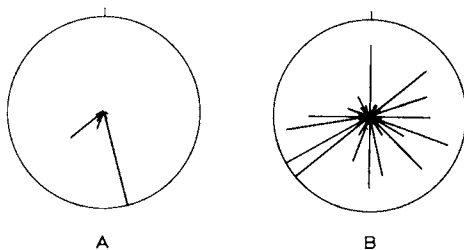


FIG. 20. Orientation of passerine migrants observed crossing through a ceilometer beam on the overcast nights of 13 October (A) and 14 October 1969 (B). See text for discussion. (Redrawn from Hebrard, 1972.)

become more difficult the longer the primary cue is unavailable. The accuracy should also decrease whenever the bird changes its position significantly, since this introduces a parallax error onto the landmark cue.

Many authors have reported normal migratory departure under 10/10 overcast (Bellrose and Graber, 1963; Drury and Nisbet, 1964; Evans, 1966, 1968; Nisbet and Drury, 1967; Bellrose, 1971; Gauthreaux, 1971; W. J. Richardson, 1974). Such cases deserve additional study and re-analysis, giving consideration to the time intervals between disappearance of the sun and oriented migratory departure.

A second way of distinguishing between the capabilities of maintaining and selecting directions under overcast involves bringing the departure behavior of free-flying migrants under experimental control. We have recently devised techniques for artificially releasing birds into the air space and following them with NASA tracking radars as they make their directional decisions and depart on migration (Emlen, 1974; S. T. Emlen and N. J. Demong, unpublished observations). In this way the experimenters can choose the meteorological conditions for departure. The birds can be deprived of the opportunity to integrate sunset information with other directional cues. For the first time, it becomes possible to experimentally manipulate the orientational systems of a free-flying migrant. We are just beginning the analysis of our results from three seasons of radar tracking; hence, it would be unwise to weight our preliminary findings too heavily. However, we have been able to release White-throated Sparrows deep within cloud during the spring migration season. The spread in departure directions suggests that this species, at least, does *not* seem able to select its normal northeastward course under these conditions. Further, the detailed tracks showed multiple loops and zigzags very similar to those reported by Griffin (1972) when he was tracking unidentified bird echoes flying through clouds and suggestive, we feel, of a shift to an alternative flight strategy.

Finally, I feel that valuable information about possible nonvisual orientation systems can be obtained from detailed analyses of the spread of track directions obtained from surveillance radar studies. A bird that is maintaining a predetermined course will make flight errors that should accumulate through time (unless it possesses a complex inertial system). This should result in an increasing scatter between the directions of individual migrants. Comparisons of angular deviations from nights when birds are believed to be flying in clear skies, under cloud, and within cloud would be extremely valuable as would analyses of the changes in angular deviation occurring between the beginning and the end of such migratory flights. Information of this sort should be forthcoming from Richardson (1974), who is conducting analyses of this type on several seasons of radar data of migration over the Canadian Maritimes.



In summary, there are very few data available from free-flying migrants pertinent to the important question of direction *determination* in the absence of both celestial and topographic cues. What data there are seem more reconcilable with the hypothesis that most migrants can only *maintain* their flight course under these conditions.

In contrast to the scanty evidence from migrants, Keeton (1969) has reported well-oriented homing behavior in pigeons under total cloud. Birds from the Cornell lofts were given routine exercise flights and short training flights on overcast days so they became accustomed to flying under these conditions. Both control and clock-shifted birds then were taken to release sites 48 km north and 33 km east of the home loft. Under sunny skies, the vanishing bearings of control pigeons were oriented roughly homeward, while those of clock-shifted birds were deflected approximately  $90^\circ$  (Section IV,B). Under total overcast, however, both groups of birds oriented homeward.

To exclude the possibility of pilotage by familiar landmark cues, two additional tests were performed at a site 160 km east. Both clock-shifted and control birds departed toward home when released under opaque cloud. The data from all control birds used in these experiments have been pooled and replotted in Fig. 21. The similarity in orientation under clear and cloudy skies caused Keeton to conclude that "the sun is used as a compass when it is available, but . . . the pigeon navigation system contains sufficient redundancy to make accurate orientation possible in the absence of both the sun and familiar landmarks" (Keeton, 1969, p. 922). Although these findings conflict with many earlier reports, they have recently been corroborated by Baldaccini *et al.* (1971), Wagner (1972, discussion following his paper), and Walcott and Green (1974). W. T. Keeton believes that the discrepancies between his and previous

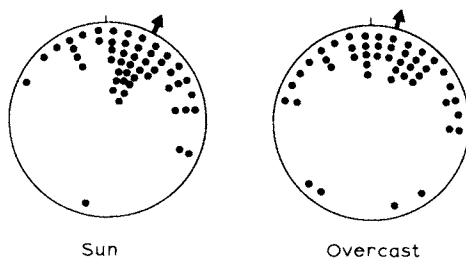


FIG. 21. Departure bearings of homing pigeons released under clear and cloudy skies at distances of 33 to 160 kilometers from the home loft. The results from several experiments are pooled with  $360^\circ$  representing the home direction. With the sun visible, the mean direction,  $\phi$  is  $27^\circ$ ; probability by Rayleigh test = 0.000; probability by "v" test with home the expected direction = 0.000. Under overcast,  $\phi = 13.5^\circ$ , Rayleigh probability = 0.000 and "v" probability = 0.000. (Recalculated from Keeton, 1969.)

studies may relate not to the navigational capabilities of the pigeons involved but rather to their motivation to fly under suboptimal conditions (personal communication).

Keeton's results again raise the possibility of differences in orientation strategies, if not in capabilities, between pigeons and migrants. The pigeons are homing to a loft from which they have just been transported. The migrants are traveling to a destination where they have not resided for many months, if at all.

These findings of migrants traveling through, and pigeons homing under, cloud are of extreme theoretical importance. They raise intriguing questions about nonvisual guidance systems in animals. The search for these alternative sources of directional information stands as one of the most exciting challenges in the field of avian orientation today.

#### E. THE IMPORTANCE OF METEOROLOGICAL CUES

Birds have evolved into excellent meteorologists. Much of their lives is spent in the air space, and during migratory flights they are often aloft at considerable heights for long periods of time. This is especially true for long-distance travelers, particularly those making nonstop flights over inhospitable terrain such as the Sahara Desert or portions of the Atlantic and Pacific Oceans. A strong selective premium must be placed on the ability to predict the weather correctly, particularly the winds aloft.

For decades, it has been known that birds are selective in timing their migration departures. Both ground observations and radar studies have shown that the bulk of migration at north temperate latitudes occurs on a small percentage of the days and nights of the migration season. The times of these dense migrations are quite predictable and coincide with "favorable" meteorological conditions. Stated overly simply, large autumn movements generally occur on the east side of a high-pressure cell following the passage of a cold front, while large spring flights concentrate on the west side of a high pressure area and ahead of an advancing low with its associated cold front (for reviews, see Drury and Keith, 1962; Richardson, 1971, 1972).

Until recently, weather factors were viewed primarily in a negative light, as possible sources of navigation error or disaster. Migrants might be caught up in storms and be blown far off course; they might encounter stiff cross or head winds and fail to reach their destinations; they might find themselves in fog or heavy rain and lose their way. The ornithological literature is filled with notes of severe exhaustion or mass mortality of migrants that misread meteorological information and encountered snowstorms, overtook cold fronts, or battled headwinds aloft. The birds'

selectivity in choosing a time of departure was considered a safeguard against going aloft under hazardous conditions.

In reality, the migrant is probably seeking optimal flight conditions as well as avoiding dangerous ones. The metabolic cost of flight is extremely high, and most migrants lay down sizable fat deposits that serve as energy stores for long-distance flights. If a migrant could correctly predict the winds aloft and initiate a flight only when those winds approximated a tailwind situation, the energetic savings would be immense. A small passerine with an air speed of 20 knots flying with a 20-knot tail wind would effectively double its flight range without significantly increasing the energy cost of the trip. This leads to a selective advantage not just to avoid unfavorable weather conditions, but to postpone departures until optimal or near optimal winds are present. Significantly, most recent radar studies show a marked tendency both for songbirds to migrate downwind, and for migration to be heaviest when the winds are in the predicted migratory direction.

Some migrants show considerable accuracy in interpreting wind information. On nights when wind directions differ at different altitudes, birds often concentrate in those height strata most favorable for migratory travel (Bellrose, 1967a; Blokpoel, 1970; Richardson, 1971; Bruderer and Steidinger, 1972; Gauthreaux, 1972a; Steidinger, 1972). Other studies have raised the interesting possibility that some migrants adjust their air speed as a function of the wind velocity, resulting in the maintenance of a more constant ground speed (Bellrose, 1967a; Bruderer, 1971; Emlen, 1974). If migrants are this closely attuned to interpreting the winds, might they not use them more directly, as a source of directional information?

Gauthreaux and Able (1970; Gauthreaux, 1972b; Able, 1972, 1973, 1974a) feel that wind is the dominant directional cue for many songbirds moving through Georgia and coastal Louisiana. Their observations show birds moving almost directly downwind regardless of the wind direction. This indicates, they feel, that many passerine migrants have only weakly developed directional preferences and will ride the prevailing winds rather than attempt to fly on a predetermined course.

Alternatively, songbirds might be so precise in choosing their flight conditions, that the only species going aloft on a particular night are those whose preferred directions are approximately downwind. According to this model, the changes in mean flight direction observed by Gauthreaux and Able (1970) could be due partly to different species of migrants being aloft on different nights. Evans (1966), Nisbet and Drury (1967), Lack (1969), and Richardson (1972, 1974) each advance this hypothesis to explain similar, but less pronounced, correlations between mean flight and wind directions.

The upper winds present in most areas are primarily dependent upon the location of high- and low-pressure centers. Within any given sector of such a pressure cell, wind direction is quite predictable. Evidence suggests that many birds have evolved the ability to identify and respond to synoptic weather situations favorable for migration. Many spring migrants, for example, will depart on the east side of a low pressure cell, presumably using their full complement of guidance systems to select their flight directions. Suppose, however, that all principal cues were unavailable, and the birds had no direct means of determining their migration directions. The recent increase in temperature and humidity, the drop in barometric pressure, and the buildup of stratus clouds all would indicate the passage of a warm front (and hence a low pressure system to the west). If, under these stimulatory conditions, the migrants that departed adopted a strategy of flying downwind, they would usually travel on a course at least approximating the general migration direction. The predictability of the upper winds from meteorological information available on the surface could make this a crude means of selecting as well as maintaining a direction in the absence of celestial, magnetic, or inertial information.

What happens when a migrant departs on a preferred direction that is not directly downwind? If the bird has a northward heading but the winds are from the east, it will travel along the resultant vector of the two, to the northwest. Its exact direction will depend upon its air speed relative to the speed and direction of the wind. To reach a destination to the north, therefore, the bird must change its heading and aim somewhat east of north. Only by flying at some angle relative to the wind and changing this angle as the wind direction shifts could the bird compensate for wind drift.

Do migrants detect and correct for such drift? This has been a major question since the advent of radar ornithology two decades ago. Different workers have voiced conflicting opinions and there is no general consensus (e.g., Gauthreaux and Able, 1970; Evans, 1970). Much of the disagreement might be due to different species responding differently to drift or to individual species changing their flight strategies depending upon the strength and inappropriateness of the wind.

Many excellent studies provide strong evidence that at least some migrants do correct for drift, although such corrections may not be complete (Drury and Keith, 1962; Drury and Nisbet, 1964; Evans, 1966, 1972; Bellrose, 1967a; Nisbet and Drury, 1967; Lack, 1969; Bruderer and Steidinger, 1972; Gauthreaux, 1972b; Steidinger, 1972; Williams *et al.*, 1972). This evidence is based primarily on comparisons of the mean and spread of tracks and headings on nights with different wind conditions. Tracks generally show less scatter than headings. This implies

that the birds alter their headings in different winds, thereby maintaining more constant tracks. When the wind direction shifts during the course of a single night, Drury and Nisbet (1964), Evans (1966), and Nisbet and Drury (1967), but not Gauthreaux and Able (1970) report that passerine migrants compensate for the wind change and keep the same mean track.

Small-scale wind drift cannot be detected using a celestial or magnetic compass sense alone. Detection requires a crude integration between compass information and some measure of forward progress along the ground (presumably by means of visual reference markers). Once this integration has taken place and the bird has adjusted its heading appropriately, the track could be maintained simply by flying at a constant angle to the wind.

Vleugel (1954, 1959, 1962) has repeatedly stressed that birds could maintain their bearings by using the wind. He proposed that nocturnal migrants use the position of sunset to select their flight direction and then maintain it through the night by keeping their angle to the wind constant. This seems plausible for cases where wind direction can be noted with reference to features of the landscape. But what happens when visual contact with the ground is eliminated by low clouds or fog?

Under these conditions, a bird traveling in a totally homogeneous air flow would have no means of detecting the direction or speed of the wind. But air flow near the surface of the earth is seldom homogeneous. Friction resulting from the passage of air over the ground produces patterns of turbulence that are related to the direction of the wind. Similar patterns may be produced whenever there is wind shear (Stewart, 1956, cited in Griffin, 1969). Nisbet (1955) pointed out that this turbulence takes the form of a series of gusts that should be detectable to a bird as sudden changes in velocity. These gusts have a characteristic structure consisting, at the onset, of a sharp increase of wind velocity in the direction of the mean wind stream, followed by a much more gradual decrease (Nisbet, 1955, p. 558). Consequently, if a bird were flying at right angles to the wind direction, it would be buffeted most strongly on its upwind side. By sampling the turbulent structure of the air a bird might be able to determine the downwind direction or to fly at a particular angle relative to the wind without visual reference to the ground. Bellrose (1967a,b) believes that such patterns of wind turbulence provide the necessary information enabling migrants to maintain their courses when traveling under or in thick cloud.

If many migrants possess this capability, then cases of disorientation should be even rarer. Presumably migrants do not take off unless sufficient directional information is available for the selection of a preferred

direction. Disorientation should occur only when a variety of cues become unavailable after the initiation of a normal flight. Such conditions might include overcast skies (loss of celestial information), ground fog or low clouds (loss of visual contact with the ground), *and* relatively uniform air flow prohibiting the use of wind turbulence.

Massive disorientation has rarely been observed on radar. When recorded it has been associated with total overcast, low visibility, and the presence of rain and/or fog (Lack and Eastwood, 1962; Drury and Nisbet, 1964; Bellrose, 1967a). Bellrose (1967a, p. 307) argues that rain tends to reduce whatever gust structure is present, while fog often indicates a general lack of air turbulence. Drury and Nisbet (1964) make the additional interesting point that the same weather situation is frequently associated with mass bird mortality at television towers and with conspicuous calling of nocturnal migrants.

#### F. INERTIAL ORIENTATION HYPOTHESES

The possibility that birds orient their flights by means of inertial navigation has been reviewed by Barlow (1964, 1966). Basically, such models require that the animal accurately sense both angular and rectilinear motion. By integrating information from all changes in flight speed and direction, a bird could, in theory, always know its position relative to an arbitrary starting point. For cases of homing orientation, this starting point presumably would be the breeding territory or, for pigeons, the home loft. Thus, a pigeon that accurately detected and integrated the accelerations produced by each twist and turn of its outgoing path (as it was transported to a release site) should be able to select the homeward bearing without resort to visual or geophysical cues.

Numerous attempts have been made to eliminate inertial cues from homing experiments. Birds have been rotated or spun during transit to their release sites with no significant decrease in performance (Rüppel, 1936; Griffin, 1940; Matthews, 1951b). Other investigators, the most recent being Walcott and Schmidt-Koenig (1973), transported birds under deep anesthesia, again with no noticeable effect upon homing success. Wallraff has bisected the horizontal semicircular canal (1965a) and extirpated the cochlea and lagena (1971) in pigeons and reported normal orientation and homing success when they were released approximately 150 km distant at several different release locations. Most of these experiments, however, were performed on clear days when the sun was visible as a possible alternative cue. Keeton and Money (in Keeton, 1974) conducted tests on pigeons with the sacculi removed. When released at unfamiliar sites under conditions of total overcast, performance was unimpaired and both test and control birds oriented homeward.

Errors in inertial systems occur if the animal unknowingly enters a gradual turn that is below the threshold of detection by the vestibular system. Measured thresholds for angular and linear acceleration are approximately  $0.2^\circ \text{ sec}^{-2}$  and  $6 \text{ cm sec}^{-2}$ , respectively (Barlow, 1964). These levels of sensitivity are insufficient for accurate position localization. The acceleration-sensing elements of the inertial systems of aircraft are commonly  $10^3$ – $10^4$  times this precise (Barlow, 1964).

The case of long-distance migration poses an additional constraint upon inertial navigation hypotheses. To navigate to a migration destination, a bird would have to rely upon information obtained and integrated many months earlier, on the previous migratory flight. For the immature bird embarking on its first migration, such information does not even exist.

Drury and Nisbet (1964) have postulated that a much simpler form of inertial dead reckoning might help explain a bird's ability to maintain its bearing during periods when alternate cues are unavailable. If absolute position is not required, the demands on the vestibular apparatus are greatly reduced. If birds have to rely upon this crude inertial system for only short periods of time and can double-check their position and/or direction by frequent reference to other cues, the requirements become even less stringent. Whether migrants actually use such a simplified form of inertial guidance is unknown. Unfortunately, there have been very few experimental tests of inertial hypotheses and even fewer are under way at the present time. Consequently, this remains as a theoretically appealing and yet inadequately studied area of animal orientation.

### G. POSSIBLE USE OF GEOMAGNETISM

#### *1. Introduction*

The hypothesis that the earth's magnetic field plays an important role in bird orientation has had a cyclical history of acceptance since first being proposed over a century ago. The first experimental support was provided by Yeagley (1947) who initially reported that attaching miniature magnets to the carpal joints of the wings of pigeons had a detrimental effect on the birds' homing ability. These findings received wide attention and stimulated considerable thought. Much of this thought was critical, however, and Yeagley's ideas were seriously challenged on theoretical grounds (Davis, 1948; deVries, 1948; Slepian, 1948; Varian, 1948; Wilkinson, 1949). Later attempts to repeat the experiments, including one by Yeagley himself, failed to produce positive results (Gordon, 1948; Matthews, 1951b; Yeagley, 1951; von Riper and Kalmbach, 1952). Following this surge of negative reports, the field lay dormant for nearly

a decade. It was not until the mid-1960's that positive evidence obtained from new techniques began to restimulate serious discussion of magnetic orientation.

Theoretically, a tremendous amount of navigational information could be obtained from geomagnetic cues. A bird might learn the magnetic "topography" of an area and orient by magnetic piloting or by following familiar magnetic contours of the terrain. Alternatively, a bird might localize the direction of the magnetic pole and use it as a reference for compass orientation. Geomagnetic cues could also form part of the basis of a bicoordinate navigation system. Yeagley originally proposed that birds determine latitude from the Coriolis force while obtaining longitude information from the strength of the vertical component of the magnetic field. An earlier model (Viguier, 1882, cited in Matthews, 1968) proposed that the bird measures both the intensity and the dip angle of the earth's field. Over some portions of the earth's surface, the lines of equal intensity and equal dip angle intersect and form a potential navigational grid; in other localities, these lines are parallel and such a model would be inoperative. Hybrid models can also be envisaged. A bird might obtain crude latitude information from the inclination angle while receiving longitude information from the integration of its chronometer with the position of the sun, to mention just one possibility.

Can birds detect magnetic fields, and are they sensitive to intensities of the magnitude of the earth's field (approximately 0.5 G)? To be useful for orientational purposes, sensitivities should be considerably in excess of this value, since birds presumably would need to respond to minor differences in the strength or direction of different components of the magnetic field. Physicists are quick to point out that the intensity of the earth's field at any location is not constant through time but shows both daily and seasonal fluctuations. Superimposed on these changes are irregular perturbations caused primarily by changes in solar storm activity. It is against this backdrop of unpredictably fluctuating magnetic fields that a bird would have to make its measurements and comparisons if it were to use geomagnetic information for navigational purposes.

## *2. Conditioning Experiments*

What is the evidence that birds can detect magnetic fields at all? Several workers have tried to condition birds to respond to magnetic stimuli. Griffin (1952) and G. Bartholomew (personal communication) each attempted unsuccessfully to train homing pigeons to strong magnetic fields. Meyer and Lambe (1966) reported negative results in attempts to condition pigeons to detect slight changes in the intensity



of an artificial field whose strength approximated that of the earth. I also obtained negative results trying to train Indigo Buntings to respond to changes in the direction of a magnetic field of 0.55 G (Emlen, 1970b). Griffin (1952), Yeagley (cited in Griffin, 1952), and Orgel and Smith (1954) all exposed pigeons to oscillating magnetic fields. The bird remained stationary while magnetic lines of force moved through it, thereby inducing an electromagnetic force considerably greater than might be experienced by a free-flying bird. Once again, all experiments failed to produce positive results.

One must be extremely cautious, however, in the interpretation of negative results from conditioning experiments. Psychologists correctly stress the importance of coupling a particular conditioned stimulus with an appropriate behavioral response. While this makes sense ethologically, it is difficult to predict what type of behavior would be optimally associated with presentation of a magnetic stimulus. To date, most studies have used some form of locomotor activity as the conditioned response. Pigeons have moved through T-mazes, walked across electric grids, or pecked at standard response keys, while the Indigo Buntings jumped from the floor of their cage.

Autonomic conditioning provides an alternative and, in all probability, a much more sensitive means of studying magnetic detection. A physiological response such as heart rate is monitored while the animal is presented with test stimuli. Each stimulus presentation is immediately followed by an electrical shock. If the animal can detect the stimulus its cardiac rhythm should show an involuntary increase at each stimulus presentation in anticipation of the forthcoming shock. Using this approach, Reille (1968) reported initial success in conditioning pigeons to magnetic stimuli. Positive responses were greater to oscillating fields of 0.80 G (frequencies 300–500 Hz) than to a continuous, static field of the same strength. These exciting data spurred several laboratories to try to corroborate the findings. None has been successful. Kreithen (Kreithen and Keeton, 1974) has, perhaps, performed the most extensive series of replicate tests to date. Using ninety-seven pigeons from the Cornell loft, he found no indication that responses to magnetic fields were significantly different from control levels.

### 3. *Zugunruhe Experiments*

Several recent behavioral studies have linked magnetic effects more directly with migratory activity and orientation. El'Darov and Kholodov (1964) exposed caged migrants [European Bullfinches (*Pyrrhula pyrrhula*), Greenfinches (*Carduelis chloris*), Coal Tits (*Parus ater*), Red Crossbills (*Loxia curvirostra*), and Chaffinches (*Fringilla coelebs*)] to an artificial magnetic field produced by a large pair of Helmholtz coils.

When the field was increased from 0.6 to 1.7 G, the locomotor activity of the birds increased significantly. A similar finding was reported by Shumakov (1967a,b), who studied the behavior of five species of passerine migrants at the site of a strong magnetic anomaly. First, the activity and orientation of the birds was tested in circular cages at a location on the Baltic. Then the birds were transported to the center of the Kursk magnetic anomaly (located in the town of Gubkin), where the field intensity is significantly increased and the direction of magnetic north is altered by 60°. When tested at this location under overcast skies, the birds failed to show any orientation. However, their level of general activity was double or triple that observed on the Baltic. The biological significance of these findings is unclear, but they could suggest a sensitivity and responsiveness to magnetic information.

William Southern (1971, 1972) has obtained indirect evidence that geomagnetism affects gull orientation. He placed juvenile Ring-billed Gulls (*Larus delawarensis*) in outdoor, circular arenas measuring 2.4 or 9 m in diameter and noted a significant tendency for birds to walk to the southeast. This direction persisted under both clear and overcast skies and was present in gull chicks ranging in age from 2 to 20 days (Southern, 1969). Southern interprets this orientation as evidence for a spontaneous preference for what will later become the autumn migration direction.

Next, Southern grouped all of his tests according to the intensity of magnetic disturbance present during the 3-hour period closest to the time of each experiment. These fluctuations in the earth's magnetic field are primarily a result of differential solar activity and are classified by the United States Coast and Geodetic Survey on a 0-9 scale of *K* values. A disturbance is quantified by the amount of change that it produces in the intensity of the earth's magnetic field. The *K* value represents the greatest amount of change (measured in gammas, with  $1 \gamma = 10^{-5}$  G) occurring during a 3-hour period. Indices of 1-4 signify low amounts of magnetic storm activity; 5 refers to moderate storm activity; and values of 6-9 indicate increasingly severe disturbances.

When the accuracy of the gull chicks' orientation was analyzed as a function of *K* values, the southeast orientation was strong with *K* indices of 0, 1, or 2, became weak at 3, and disappeared at *K* = 4, 5, and 7 (Fig. 22). The behavior under moderately severe storm activity (*K* = 5 and 7) showed an intriguing tendency for reorientation in the opposite direction, to the north.

Southern concludes that magnetic disturbances (or some factor correlated with magnetic disturbances) are responsible for the observed deterioration of gull orientation. If replicable, his findings would suggest an amazing sensitivity to minor fluctuations in the magnetic field. Orien-

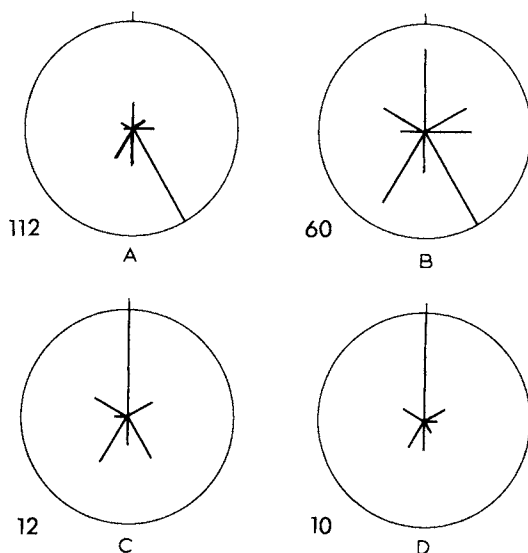


FIG. 22. Walking orientation of Ring-billed Gull (*Larus delawarensis*) chicks tested in a circular arena. Data are grouped according to the amount of magnetic disturbance present at the time of the experiments. (A) Orientation during periods of very low magnetic storm activity. K indices = 0, 1 and 2. Mean direction =  $155^\circ$ ; Rayleigh probability  $< 0.01$ . (B) Orientation when K indices were 3 or 4. Mean direction =  $152^\circ$ ;  $p < 0.01$ . (C) Orientation during moderate storm activity, K index = 5. Mean direction =  $321^\circ$ ;  $p > 0.05$ . (D) Orientation under moderately severe magnetic disturbance, K = 7. Mean direction =  $360^\circ$ ;  $p > 0.05$ . Vector diagrams are drawn on the proportionality basis with the radius equaling the greatest number of gull chicks choosing a particular  $30^\circ$  sector. The number this represents is given adjacent to each diagram. (Regrouped, calculated and plotted from data of Southern, 1971.)

tation broke down at K values between 3 and 4, values signifying a disruption of 20–70  $\gamma$ . This is equivalent to approximately 1/1000 of the intensity of the normal earth's field.

In a series of important papers, F. Merkel and W. and R. Wiltschko have hypothesized that European Robins (*Erithacus rubecula*) actively use the geomagnetic field to determine their migratory direction. In initial tests, caged robins spontaneously oriented their nocturnal activity in the appropriate seasonal direction, even when placed in a room isolated from "normal visual environmental cues" (Merkel and Fromme, 1958; Fromme, 1961; Merkel *et al.*, 1964). If the birds were placed in a large steel chamber that greatly reduced the total intensity of the magnetic field (from 0.41 G to 0.14 G) this orientation ability disappeared (Fromme, 1961; Merkel and Wiltschko, 1965; Wiltschko, 1968). Later tests showed that migratory activity became random if the magnetic field surrounding the cage was artificially decreased to values below

0.34 G or increased to values greater than 0.68 G in intensity (Wiltschko, 1968). Interestingly, if the robins were allowed to adjust to the abnormal magnetic intensities by living under these test conditions for a period of 3 days or more, they redeveloped the ability to orient in the appropriate directions (Merkel and Wiltschko, 1965; Wiltschko, 1968). This led Wiltschko (1968) to conclude that the magnetic detection system of the European Robin is finely attuned to fields approximating the earth's in strength.

Next, these investigators built a large pair (diameter 2 meters) of Helmholtz coils around their octagonal test cage. By rotating these coils and adjusting the strength of the electric current passing through them, they could generate a fairly homogeneous static dc field and control both its direction and intensity. In a series of experiments encompassing both spring and fall migration seasons, they found that the orientation of caged robins could be altered quite predictably by changing the direction of the horizontal component of the artificial magnetic field (Merkel and Wiltschko, 1965; Wiltschko and Merkel, 1965; Wiltschko, 1968; Merkel, 1971). In Fig. 23 I have pooled, replotted, and recalculated all of the results from experiments performed during the autumn migration seasons on robins that were housed and tested under magnetic fields approximating the earth's in strength. Although tested in a closed room, the distribution of the nightly means shows a clear southward trend (mean bearing  $187^\circ$ ; Rayleigh probability  $<0.001$ ) (Fig. 23a). When magnetic north was rotated to coincide with geographic east-southeast (Fig. 23b), the robins kept orienting toward magnetic south although this corresponded to geographic northwest (expected direction  $299^\circ$ ; actual mean bearing  $328^\circ$ ; Rayleigh probability = 0.007). The robins also maintained a magnetic south-southwest preference when magnetic north was rotated to coincide with geographic west (expected direction  $97^\circ$ ; actual mean bearing  $128^\circ$ ; Rayleigh probability = 0.045) (Fig. 23d). In only one condition did the birds shift in an unpredictable manner. When magnetic north was rotated  $45^\circ$  counterclockwise (to geographic northwest) in both 1964 and 1965, the mean directions of the robins rotated clockwise, producing a deviation of  $80^\circ$  between predicted and observed headings (expected direction  $142^\circ$ ; actual mean bearing  $222^\circ$ ; Rayleigh probability  $<0.001$ ) (Fig. 23c). The Wiltschkos have recently extended their investigations to include European warblers (*Sylvia communis*, *cantillans*, and *borin*) and report these species also show magnetically directed *Zugunruhe* (Wiltschko and Merkel, 1971; Wiltschko and Wiltschko, 1973; and unpublished observations).

In their most recent experiments, the Wiltschkos have manipulated the inclination as well as the direction of the artificial magnetic field. When the polarity of the vertical component was reversed (from  $-66^\circ$

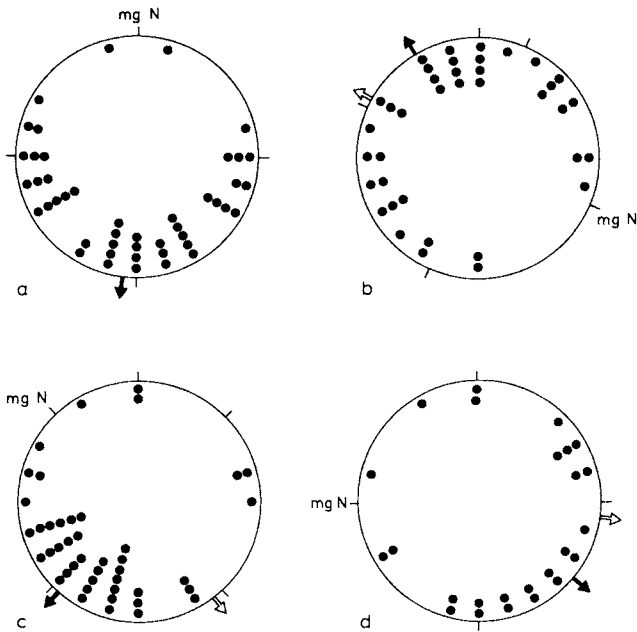


FIG. 23. Migratory orientation of caged European Robins (*Erithacus rubecula*) tested during the autumn migration seasons while in the "absence" of meaningful visual cues. (a) In the presence of a magnetic field of normal direction and strength (pooled from Wiltschko, 1968, Figure 4b and 6b). (b) When the horizontal component of the magnetic field was altered by Helmholtz coils such that magnetic north coincided with geographic east-southeast. (From Wiltschko, 1972, Figure 2a). (c) When the horizontal component of the artificial magnetic field was situated in the northwest. (From Wiltschko, 1968, Figure 9b and Merkel, 1971, Figure 1b.) (d) When magnetic north was aligned with geographic west (From Wiltschko, 1968, Figure 14d.) These diagrams include all of the results obtained to date from experiments performed during the autumn migration season on robins that were housed and tested under magnetic fields approximating the earth's in strength. Each dot represents the mean direction of one bird on one night of testing (here grouped into 15° sectors). Black arrows show overall mean direction. Open arrows give the "expected" direction (186°, see a) measured relative to magnetic north. See text for full discussion.

to  $+66^\circ$ ), robins tended to reverse their orientation even though the horizontal direction of magnetic north remained unchanged (Fig. 24A and B). Orientation also changed if the horizontal component of the field was reversed, while the inclination was held constant at  $-66^\circ$ . But if the horizontal direction of the magnetic field was reversed  $180^\circ$  and the inclination was changed (from  $-66^\circ$  to  $+66^\circ$ ), the birds did not alter their directional behavior (Wiltschko, 1972; Wiltschko and Wiltschko, 1972). In an artificial field with a strong horizontal but a zero vertical component, activity became random (Fig. 24c).

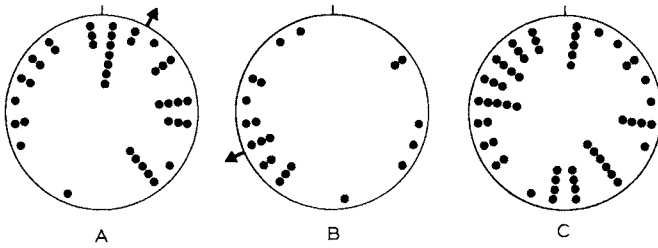


FIG. 24. Migratory orientation of captive European Robins tested in the spring of 1971 under the following artificial magnetic fields: (A) Normal magnetic information available; magnetic north =  $360^\circ$ , inclination =  $+66^\circ$ , total intensity = 0.46 G. (B) Horizontal component normal ( $360^\circ$ ) but polarity of the vertical component reversed ( $-65^\circ$ ). Total intensity = 0.46 G. (C) Horizontal component much stronger but still oriented to  $360^\circ$ . Vertical component eliminated (inclination =  $0^\circ$ ). Total intensity = 0.46 G. Symbols as in Fig. 23. (From Wiltschko and Wiltschko, 1972).

On the basis of these surprising results, Wiltschko and Wiltschko (1972, p. 62) hypothesize that European Robins "do not use the polarity of the magnetic field for detecting the north direction. The birds derive their north direction from interpreting the inclination of the axial direction of the magnetic field lines in space, and they take the direction on the magnetic north-south axis for 'north' where field lines and gravity vector form the smaller angle."

Although most workers in the orientation field have been stimulated by the findings of the Frankfurt group, many have questioned the biological significance of the data. In part, this is because the degree of orientation found by Merkel and the Wiltschkos is relatively weak, frequently demonstrable only on second-order statistical analysis. The activity of an individual robin is recorded by microswitches on eight directional perches in an octagonal cage and a mean direction is calculated. All such means representing one experimental situation then are pooled together. Differing numbers of birds and different numbers of replicates per bird are included in these diagrams. These means are the raw data from which a grand mean bearing is calculated. Frequently this resultant vector attains only borderline significance, even though considerable sample sizes are employed. Merkel (1971) and Wiltschko (1972; W. Wiltschko, personal communication) state that few of their birds display a clearcut orientation and that 40% of the individual bird-nights do not deviate significantly from uniform distributions. The fact that statistical significance is reached by pooling the means from such bird-nights suggests that the robins are displaying extremely weak but consistent directional preferences under the test conditions. Although one may wish

to debate the biological meaning of such weak tendencies, there is a definite shift in these preferences when the direction of the magnetic field is altered.

In 1970, I published "negative" data from an attempt to observe orientation under visually cueless conditions (Emlen, 1970b). Ironically, these data actually provide confirmation of some of Merkel and Wiltschko's findings. They also point up the difficulties involved in attaching biological significance to statistically significant data. Twelve Indigo Buntings were placed in "cueless" cages for from 5 to 13 nights each during the autumn migration season. The pooled total activity for each individual bird is shown in Fig. 25. Statistical treatment of these data (Rayleigh test) showed no case where the activity distribution deviated significantly from a random or uniform distribution.

I also calculated the mean direction for each bird on each night by vector analysis. These means are shown in Fig. 26. A second-order analysis, calculating the mean of the means for each individual bird, revealed only two cases in which the distribution of means differed from random (birds P35 and R45). It was on the basis of these analyses that I concluded "birds tested repeatedly in the presence of a normal geomagnetic field but in a 'visually cueless' chamber failed to develop any significant directional preferences" (Emlen, 1970b, p. 223).

Since publishing that statement, I have performed two additional analyses of these results. First, all of the activity from all of the birds on all of the nights was pooled (Fig. 27A). Although the sample size became enormous ( $N$  of independent activity units = 7531), these data still failed to deviate from a uniform distribution (probability = 0.63 by Rayleigh test; probability = 0.17 by "v" test with  $180^\circ$  as the predicted direction). Finally, I pooled all of the nightly means from all of the birds and calculated the grand mean (Fig. 27B). Recall that this is the test statistic employed by Merkel and the Wiltschkos. Analyzed in this way, the Indigo Bunting data showed a highly significant trend in the appropriate migration direction, to the south-southeast (mean direction  $173^\circ$ ; probability  $<0.001$  by Rayleigh test; probability  $<0.001$  by "v" test). Thus, although the concentration of orientation for individual birds or bird-nights was extremely low, the pooled results show a definite nonrandom clustering in the migration direction.

Another source of confusion arises from attempts to replicate "cueless" experiments. This concerns the relative advantages and disadvantages of different cage designs. Merkel and the Wiltschkos employed an eight-sided cage equipped with radially aligned perches. In such a cage, a bird is prone to circle, and a great deal of extraneous "noise" is introduced into the system (Merkel, 1971; H. C. Howland, 1973). Further,

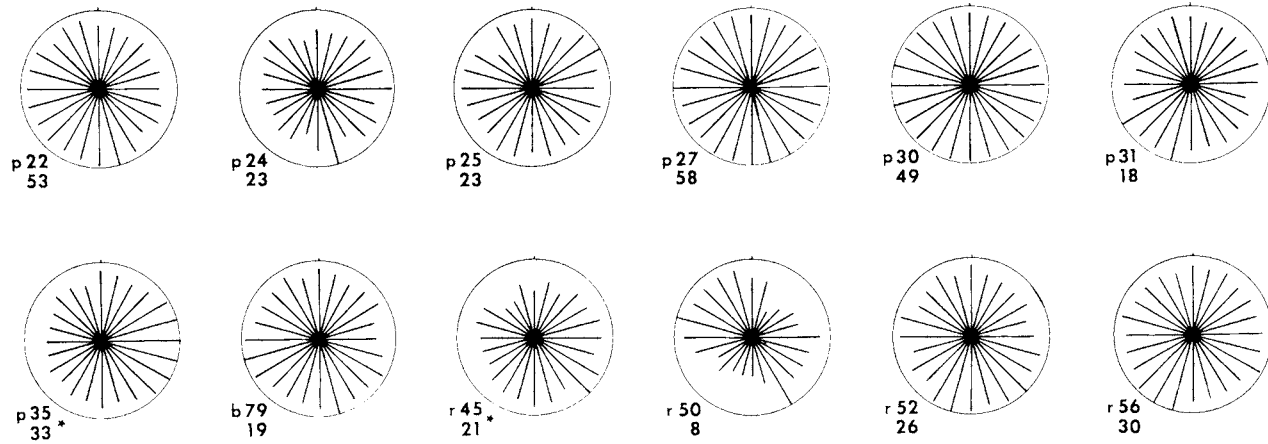


FIG. 25. Vector summaries of migratory orientation of 12 adult Indigo Buntings tested in the presence of a normal geomagnetic field but in the "absence" of visual cues. Diagrams plotted as in Fig. 11. (From Emlen, 1970b.)



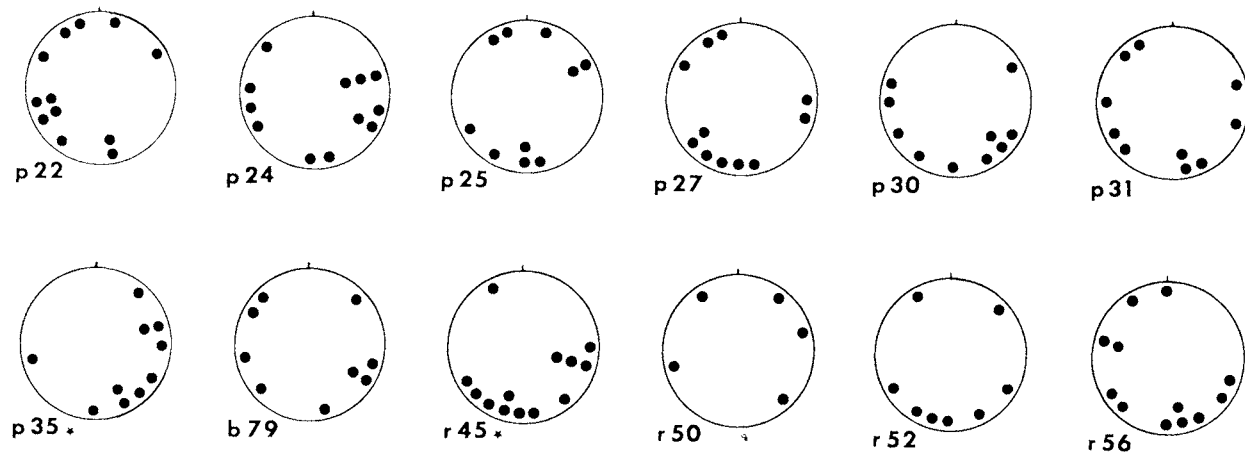


FIG. 26. Nightly mean headings of individual buntings tested in the presence of a normal geomagnetic field in the "absence" of visual cues. (From Emlen, 1970b.)

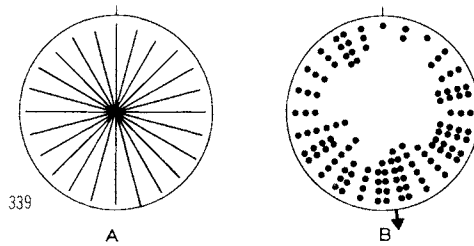


FIG. 27. Pooled results of migratory orientation of Indigo Buntings tested in the "absence" of meaningful visual cues. (A) Vector summary of *all* of the activity from *all* of the birds (total sample size = 7531 activity units). (B) Summary of all nightly means from all of the birds ( $N = 122$ ). Arrow denotes mean direction ( $173^\circ$ ). See text for full discussion. (Recalculated and replotted from data of Emlen, 1970b.)

when a bird depresses a particular radial perch (e.g., northeast) its body axis typically is aligned perpendicular to this direction (the bird is facing northwest or southeast).

Most attempts to obtain oriented *Zugunruhe* in the absence of visual cues have been performed in cages with tangentially arranged perches. A perch registration to the northeast in such a cage should indicate that the bird is facing either northeast or southwest. Interestingly, all attempts to repeat Merkel and Wiltschko's "cueless" results performed in such cages have yielded negative results (Perdeck, 1963; Shumakov, 1965, 1967b; Wallraff, 1965b; Liepa, 1970; Shumakov and Vinogradova, 1970). Recently, Merkel (1971) reported that he, too, was unable to obtain orientation in a closed room when he switched his birds to a cage with tangential perches. To add to the confusion, Wallraff (1972) borrowed one of Merkel's original radial-perch cages and *was* able to repeat their observations. His robins oriented in the migratory direction, although they had failed to do so in previous tests with the other cage design.

In an attempt to better comprehend the controversial data from magnetic orientation experiments, we invited the Wiltschkos to come to Cornell and join us for a year of collaborative studies. Using Indigo Buntings, we set about to repeat "visually cueless" and magnetic deflection experiments, using both funnel (Emlen and Emlen, 1966) and radial-perch cage designs. Extreme care was taken to minimize potential artifact cues and to rigidly control for possible sources of unconscious bias (Howland, 1973). Preliminary results (S. T. Emlen, N. J. Demong, W. Wiltschko, R. Wiltschko, and S. Bergman, unpublished observations) indicate that buntings in early spring selectively oriented to the north under control conditions, but shifted to the east-southeast when the horizontal component of the magnetic field was deflected clockwise  $120^\circ$ . The concentration of orientation for most birds was low, but their

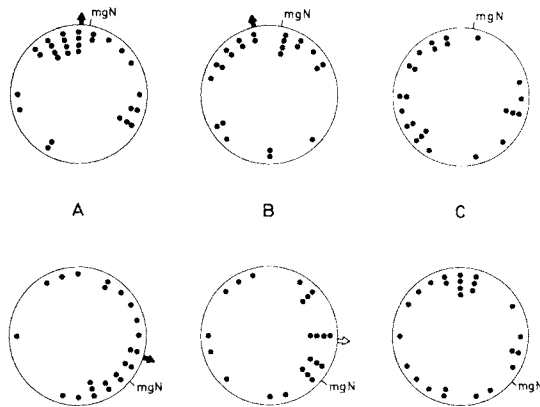


FIG. 28. Pooled mean directions of Indigo Buntings tested in a “visually cueless” environment. Top: With a normal magnetic field ( $mN = 10^\circ$ ). (A) Results from early in the spring migration season, April 24 to May 15. Mean direction =  $3^\circ$ ; Rayleigh probability = 0.002. (B) Results from mid-season, May 16–31. Mean direction =  $347^\circ$ ; Rayleigh probability = 0.019. (C) Results late in the migration season, June 1–15. Mean direction =  $261^\circ$ ; Rayleigh probability = 0.265. Bottom: With the magnetic field shifted  $120^\circ$  clockwise ( $mN = 130^\circ$ ). (A) Early season. Mean direction =  $110^\circ$ ; Rayleigh probability = 0.011. (B) Mid-season. Mean direction =  $95^\circ$ ; Rayleigh probability = 0.089. (C) Late in the season. Mean direction =  $1^\circ$ ; Rayleigh probability = 0.49. The data distributions under the two magnetic conditions are significantly different throughout the migratory period (using the Watson and Williams F test,  $p < 0.01$  in A and B,  $p < 0.05$  in C).

consistency was great enough to give a clear statistical separation between the pooled bearings under the two experimental conditions (magnetic north equals  $10^\circ$ ; magnetic north equals  $130^\circ$ ) (Fig. 28A and B). Later in the season, possibly when migratory motivation was waning, the orientation of birds under these “visually cueless” conditions deteriorated considerably (Fig. 28C).

In summary, second-order poolings of Indigo Bunting data reveal a significant tendency for orientation to the south in autumn and north in spring under visually cueless conditions, and this orientation shifts predictably in accordance with an artificial deflection of the magnetic field. Interestingly, the orientation is more clear-cut and the deflection more pronounced in the radial-perch cage design.

The biological explanation for these discrepancies remains unclear. But, at the very least, they should serve to emphasize the importance of a little-studied aspect of navigation experiments: the effect of different cage designs.

#### 4. Homing Experiments

The older literature is full of accounts of homing experiments performed on birds to which small magnets had been attached to the head,

dorsum, or wings (Wodzick: *et al.*, 1939; Yeagley, 1947, 1951; Gordon, 1948; Matthews, 1951b, 1952; Bochenski *et al.*, 1960). The species used included gulls, ducks, and storks, as well as homing pigeons. With the exception of Yeagley's original experiment, all studies yielded negative results; homing performance was unaffected by the magnetic disturbances. However, most of these experiments were performed under sunny conditions, close to the home location, or both. Consequently, alternative celestial and topographic cues might have been available.

Keeton's (1969) finding that pigeons can take up an initial bearing toward home when released under total overcast made it possible, for the first time, to study the importance of magnetic information in the absence of celestial input. He glued miniature magnets (weighing approximately 3 gm) to the backs of experienced homing pigeons. These magnets were somewhat variable in strength but were designed to produce a field of roughly 0.5 G in the vicinity of the birds' heads. Control birds wore a nonmagnetic brass bar of similar size and weight. All birds were housed together and had identical exercise and training schedules. For the critical tests, Keeton transported the birds to release locations 27–50 km distant and released them under total overcast. The bars were attached to the birds just prior to release; "brasses" and "magnets" were released alternately.

During preliminary experiments, performed when the sun was visible, both groups of birds oriented toward the home loft (Keeton, 1971, 1972). This confirmed the findings of previous investigators; magnets did not disrupt homing. But when releases were conducted under total overcast, the two groups of birds showed significant differences in their initial departure behavior. In five of seven tests, the birds wearing brass bars oriented toward home, while those with magnetic bars scattered at random (Keeton, 1971, 1972). In one additional release, both groups of birds departed toward home, while in the other, neither group showed any preferred orientation. Figure 29 shows the pooled bearings from these series of experiments. These results provide some of the clearest evidence to date of a magnetic effect upon bird orientation. They also serve to emphasize the importance of designing tests that take into account the redundancy of orientation systems.

The behavior of young, inexperienced pigeons was quite different from that of the experienced adults. Keeton and Gobert (1970) previously had reported that first-flight birds were unable to orient homeward when the sun was not visible. It appeared that homing experience was necessary for the maturation of the "overcast system" or, perhaps, for its coupling with some directional reference provided by other cues. Attaching a magnet to a young bird produces yet another decrement

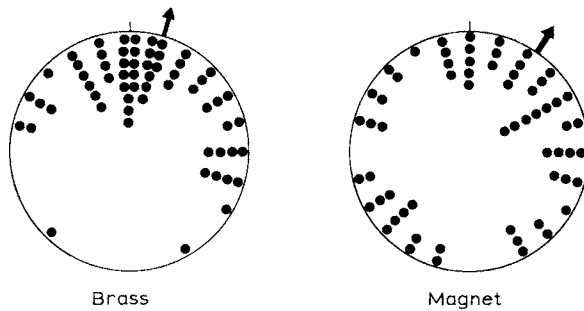


FIG. 29. Pooled departure bearings of experienced homing pigeons released under conditions of total overcast at distances 27 to 50 km from the home loft. Home direction =  $360^\circ$ . Left: Results from birds with brass bars glued to their backs. Mean direction =  $15^\circ$ ; Rayleigh probability  $<0.001$ . Right: Results from birds with a magnetic bar attached. Mean direction =  $31^\circ$ ; Rayleigh probability = 0.04. (Data recalculated from Experimental Series III in Keeton, 1971, 1972.)

in its orientation capabilities. Such birds departed randomly even when released on clear, sunny days (Keeton, 1971, 1972). This suggests that during their first flights, young birds cannot tolerate the elimination or disruption of either solar or magnetic information. As the birds become older and more experienced, less information is required and disorientation results only when both inputs are disrupted simultaneously.

Interestingly, the magnets used in Keeton's tests did not seriously disrupt the pigeons' ability to reach the home loft. Homing speeds frequently were somewhat slower than for control birds, but only occasionally was this difference statistically significant. Further, homing success, as measured by the number of birds returning to the loft, was comparable in the two groups. This suggests that whatever disruptive effect the magnets produce, it is short-lived and the pigeons are able to compensate for the disturbance and reorient toward the home loft soon after being released.

Walcott and Green (1974) have designed a pair of miniature Helmholtz coils that fit around the head of a pigeon. The larger of the two coils slips over the head and fits like a collar around the neck while the smaller is glued directly to the top of the head. In experimental birds the coils are connected to a battery, thereby producing a magnetic field of approximately 0.6 G. Control birds are similarly equipped, but the batteries are not connected to the coils. When pigeons were released at localities 60–90 km west of the home loft under sunny conditions, no effects of the coils were detected. When released under overcast, however, the behavior of the pigeons differed depending on the polarity

of the magnetic field produced by the coils. If the current produced a field where magnetic north pointed toward the larger coil around the neck of the pigeon (SUP) the birds tended to depart in a normal homeward direction. But if the current in the coils was reversed (NUP), the birds tended to reverse their direction and departed nonrandomly in the direction away from home (Fig. 30).

These results must be considered preliminary, awaiting the outcome of additional, replicate releases. But they raise the exciting possibility of a common thread running between migratory and homing studies of magnetic orientation. The difference between NUPs and SUPs may be interpretable in terms of the Wiltschkos' model. They suggested that birds use the inclination of the magnetic field, taking north to be the direction in which the magnetic field vector and gravity vector make the smallest angle. Reversing the current flow through the coils around a pigeon's head would reverse the magnetic field vector which, in turn, would reverse the direction interpreted as north (Walcott and Green, 1974).

The lure of finding a new sensory modality is attracting an increasing number of laboratories into studies of the biological effects of magnetism. No longer can magnetism be brushed aside on theoretical grounds. The recent surge of positive results demands an explanation. Southern's work with gulls and that of Keeton with pigeons shows a deterioration of direction-finding capability when magnetic information is disturbed. It is tempting to conclude from this that magnetic cues are directly involved in the orientation process. But an equally plausible alternative is that a magnetic storm or the presence of a strong bar magnet disrupts the normal sensory input to some other component of the orientation system. At present, the work of Merkel and Wiltschko and Walcott and Green stands as the most tantalizing evidence that magnetic information is actively used by birds in the selection of flight directions.

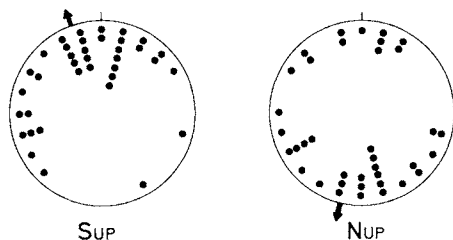


FIG. 30. Vanishing bearings of pigeons equipped with miniature Helmholtz coils. Birds were released 59 to 92 km west of the home loft under total overcast. Diagrams plotted with  $360^\circ$  = home direction. SUP and NUP are defined in the text. Data are pooled from Walcott and Green (1974).

## V. Conclusions

One of my purposes in writing this review was to point out the major areas in migratory orientation research where active work either is being or should be performed. In so doing I have stressed that a migrant has many potential sources of directional information at its disposal. These range from topographic, through meteorological and inertial, to magnetic and celestial cues.

But the subdivision of this chapter into discussions of different sensory cues contradicts my second principal aim. That was to stress the inter-relationship of different sources of directional information—to emphasize the redundant nature of orientation systems. The realization that different cues function as components in a complex navigational repertoire opens an entirely new forefront in orientation research. What are the relative advantages of one type of cue over another? Does the simultaneous use of multiple components result in increased accuracy of orientation? Is there a hierarchy in the relative importances of different types of information?

We have just reached the stage in which these interactions between components are being studied. The principal technique is to manipulate two or more cues simultaneously in such a way as to provide the animal with conflicting information. Preliminary findings suggest that a differential weighting of different cues does exist. In the case of experienced homing pigeons, clock-shifted birds make predictable errors when released under sunny conditions but orient homeward under overcast. This implies that the sun compass takes precedence over the overcast system when the two are in conflict. Clock-shifted birds also vanish in the predicted incorrect direction when released at familiar sites, including locations within a few miles of the home loft. Consequently, the sun compass must also predominate over familiar landmarks in relative importance to the pigeon. W. T. Kecton (personal communication) plans to conduct experiments in which experienced birds wearing magnets are released under total overcast from familiar sites. The results should enable him to rank the relative importance of landmarks with the overcast system.

Similar speculations can be made for migrants. Not all species would be expected to have similar weighting systems, however, and one must be careful not to overgeneralize. In the case of nocturnal songbird migrants, stellar cues seem to predominate over any possible geophysical (including magnetic) effects in at least four species. When the starry skies of a planetarium are adjusted so that “stellar north” does not coincide with either geographic or magnetic north, Indigo Buntings (Emlen,

1967a), European warblers (Sauer, 1957), and White-throated Sparrows (S. A. Gauthreaux, Jr., personal communication) shift their orientation in keeping with the new position of the artificial sky. Wiltschko *et al.* (1971, in preparation) believe that an alternative weighting system, in which magnetic information dominates over celestial cues, functions in the European Robin and in some *Sylvia* warblers. They report being able to deflect the *Zugunruhe* orientation by means of Helmholtz coils, even when the caged bird is provided with a view of a 95° sector of the natural night sky. The findings are difficult to interpret, however, since the zone of the sky that may be of most importance for northern hemisphere migrants (the northern circumpolar region) was blocked from the bird's view during the conflict experiments.

Although experimental evidence is not yet available, I expect that the position of sunset will be found to play a vital role in the initial selection of direction by the great majority of nocturnal fliers. Sunset seems a logical cue to use in the transfer between cues and reference systems employed during daylight and those operative after dark. Several fragments of information support this idea. Kramer (1949, 1951), in his pioneering studies of caged *Zugunruhe*, found that songbirds frequently oriented directly toward the horizon glows produced by city lights. But if birds were placed in their outdoor cages during the daytime and exposed to the normal sunset transition into night, they appeared less confused and normally took up directions appropriate for the migration season, ignoring the phototactic attraction of the same city lights. Hebrard's (1972) observation that nocturnal songbird migrants oriented appropriately under total overcast if the previous sunset had been visible, yet became disoriented when a view of the sun, including sunset, was obscured for long periods of time, is also of interest here. Finally, the fact that the position of sunset can be used directly as an orientational cue is born out by some of my own work (S. T. Emlen and N. J. Demong, unpublished radar observations) in which White-throated Sparrows consistently selected the appropriate spring migration direction when released and tracked during the transition period after the sun's disk had dropped below the horizon yet before the stars were visible to the human eye.

Winds aloft probably play a secondary role in migratory orientation. Although a direction may be maintained by flying at an angle relative to the wind, the selection of that initial direction presumably is based on other cues. When S. T. Emlen and N. J. Demong (unpublished observations) radar tracked White-throated Sparrows that were released artificially in the air space, the birds' behavior differed depending on the meteorological situation. Under clear skies in the spring, the birds consistently departed to the northeast; but they reverted to a downwind ten-



dency under total overcast. This suggests that celestial predominated over downwind orientation in this species.

Finally, the indirect evidence from numerous radar studies tends to place topographic cues near the bottom of the hierarchy for passerine night migrants. However, it is possible that the weighting scheme changes at some point along the migratory route and that topographic features may play a more central role in the final phases of locating a specific breeding or wintering location.

The relative importance of different sources of information also changes with age and experience. Young birds frequently require several types of input in order to select an appropriate direction. These different sources of information appear to be integrated with each other and into a general orientational framework during early development. For example, Indigo Buntings learn star patterns and come to relate them to a directional reference axis provided by the rotational motion of the night sky (Emlen, 1969b, 1970a, 1972). Birds deprived of viewing the night sky in early ontogeny are unable to select the migratory direction. Of equal interest, birds given exposure as young are later able to select their direction under stationary planetarium skies. The implication is that celestial rotation is essential in providing a reference framework in which star patterns take on meaning. Once this framework is learned, however, rotation per se is not necessary and star patterns alone are sufficient for direction determination. A parallel story concerning the possible integration of magnetic and celestial reference systems is being proposed by the Wiltschkos (in preparation).

Young, inexperienced birds are generally much more plastic than adults in their orientation behavior (Emlen, 1972; S. T. Emlen, N. J. Demong and E. Gwinner, unpublished observations; Keeton and Gobert, 1970; Keeton, 1972). Not only are they receptive to a wide variety of cues, but the hierarchy of relative importance of different inputs is less fixed. To understand the adaptiveness of this, consider a young migrant, familiar only with cues available at its site of hatching. When it departs on its first migratory journey, it may travel 2000–3000 km, bringing it to southerly latitudes where the sky overhead is totally unfamiliar and where magnetic cues and prevailing wind patterns are vastly different from those to which it previously has been exposed. Selection and imprinting to a specific overwintering location has yet to occur. Obviously, behavioral plasticity and a receptivity to a wide range of orientational cues would be of crucial importance for such young birds.

As the bird matures and gains experience, this plasticity decreases. The navigational capabilities may change (e.g., Perdeck, 1958, 1967), accuracy improves (Emlen, 1969b, 1972), the amount of information needed for direction determination decreases (Emlen, 1969b, 1970a,

1972; Keeton and Gobert, 1970; Keeton, 1972, 1974), and the relative weighting of cue systems becomes more rigid. These trends seem to hold for both migratory birds and for homing pigeons.

As stated earlier, "the problem for the ornithologist interested in navigation is no longer searching for *the* mechanism of orientation. It is studying any and all components of the orientation systems and trying to decipher how these are integrated into a navigational complex that determines the directional behavior of the bird at any place in time or space."

The field of bird orientation has come a long way since Kramer's (1961) review in the predecessor to this volume. We have developed new techniques for studying the behavior of free-flying migrants. We have proposed various models to explain the functioning of different components in the orientation system. We have enumerated the redundant ways a bird could maintain its migratory direction. But we have a long way to go. We are no closer to an understanding of the "map" than Kramer was two decades ago. We have little knowledge of the types or accuracy of the navigational capabilities of most migrants. In short, the sum total of our knowledge today is still insufficient to explain how an individual migrant finds its way over the thousands of kilometers between its breeding territory and its overwintering destination.

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