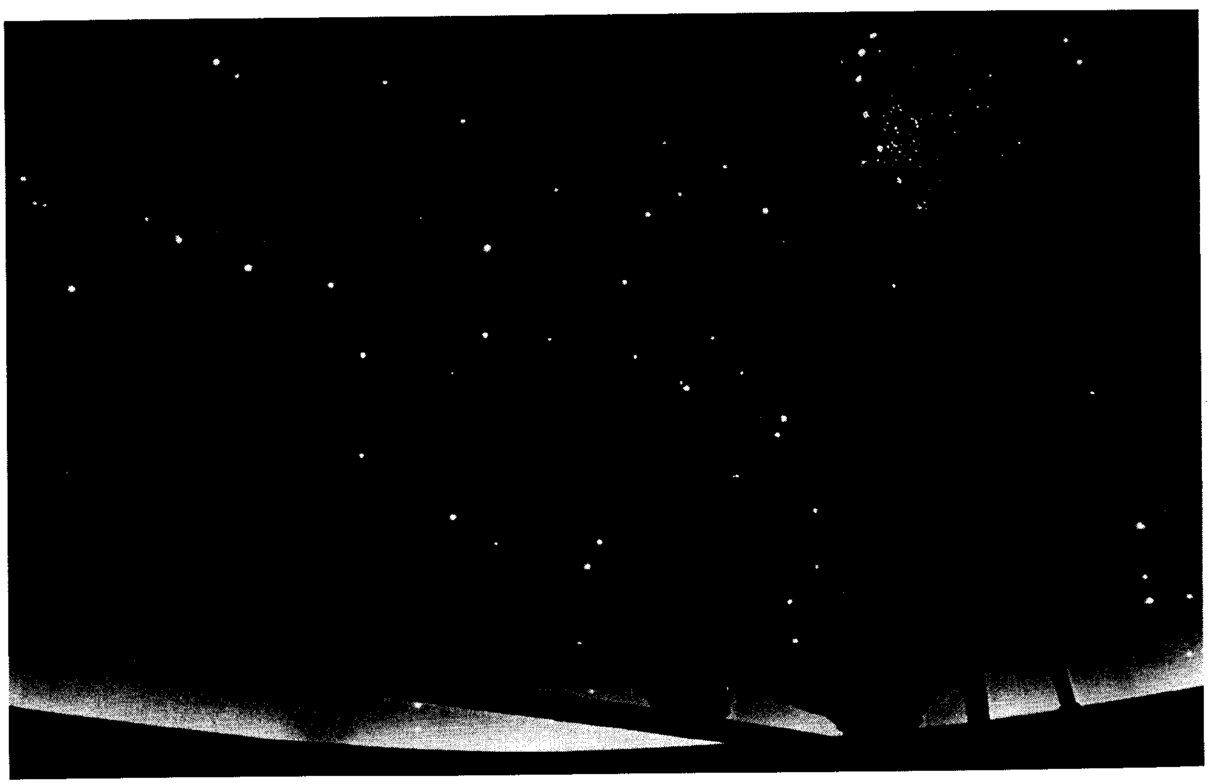
The Stellar-Orientation System of a Migratory Bird

When the indigo bunting is put in a planetarium, it exhibits an ability to orient itself by the stars. This, however, can be only one of the cues it uses for long-distance navigation

by Stephen T. Emlen

The blackpoll warbler is a small, inconspicuous songbird that breeds during the summer in the stunted conifer forests of Alaska and northern Canada. When fall approaches, these birds embark on a remarkable migratory journey. They leave the northern forests and fly east-southeast across the North American continent to the Atlantic coast. During this stage of the journey they stop to feed and build up stores of subcutaneous fat that will serve as a vital energy reserve for the next stage. The blackpolls concentrate near the coast of New England and the Maritime Provinces of Canada, waiting for the right weather conditions. Then, as the next high-pressure cell moves in from the west, bringing with it winds from the north or northwest, the blackpolls depart again, this time over the ocean on a nonstop flight that will take them three to five days. They fly over Bermuda, the Antilles and Puerto Rico, stopping only when they make landfall on the northeastern coast of South America. It is a tremendous feat: a nonstop flight of



EXPERIMENTAL ARRANGEMENT in a planetarium for testing the ability of the indigo bunting to orient by the stars is shown. The photograph was made in the Southern Cayuga Atmospherium-Planetarium in Poplar Ridge, N.Y. Projectors are not visible to birds in the cages. Stars at any latitude and longitude, as well as celestial motion, can be projected onto the planetarium dome.

more than 2,400 miles over water by a bird weighing less than 20 grams! Any error in navigation would obviously lead to disastrous results. Any misinterpretation of the weather would also lead to disaster, since a blackpoll that encounters stiff headwinds or a storm has no chance of landing to rest or to find shelter.

The blackpoll warbler is an extreme but not atypical case of birds that migrate south. Fully two-thirds of the species of songbirds that breed in the northern U.S. travel south in the winter. The distances of migration typically range from 600 to 1,800 miles, but each fall some songbirds make one-way trips of up to 4,000 miles. The following spring the birds fly back to their breeding grounds. Year after year the adult birds return with amazing precision to the same several square miles of territory at both their breeding and their wintering grounds.

How do the migrating birds select the appropriate flight directions? Can they determine when they have been blown off course, and can they correct appropriately? How do they know when they have arrived at the latitude of their destination? What is the fate of young birds flying alone on their first migratory trip?

INDIGO BUNTING is shown hopping onto the side of a test cage. The photograph was made by placing a camera with a "fish-eye" lens at the bottom of the cage. Black marks on the white side of the cage are footprints made by the bird. The screen is the top of the cage.

Biologists have long been intrigued by the phenomenon of bird migration, but it is only during the past two decades that significant progress has been made toward answering the fundamental questions about it. Today scientists around the world are focusing their attention on questions of animal navigation. Hundreds of thousands of migrant birds are being individually marked with a leg band so that field investigators can determine their migratory paths by plotting their recapture locations. In the laboratory other workers are testing the ability of birds to detect different potential directional cues and are examining how such cues are used. Ornithologists are tracking "unseen" migrating birds with radar and following individual migrants by attaching small radio transmitters to them.

The results of these various studies have shown that bird navigation is not a simple affair; it is not entirely dependent on any single cue or sensory system. It seems that migrating birds make use of a variety of cues to determine their direction and maintain it in flight. A recent article by my colleague William T. Keeton describes some of the types of cues available and the interplay among them [see "The Mystery of Pigeon Homing," by William T. Keeton; SCIENTIFIC AMERICAN, December, 1974]. Here I shall concentrate on one cue system that has been studied intensively and that appears to be of major importance to night-migrating birds: orientation by the stars. The reader should bear in mind that I am covering only one aspect of how birds navigate. It is only by dissecting out the various aspects and studying them one at a time that an understanding of the full story will ultimately be achieved.

The scientific study of the directional orientation of migratory birds had its breakthrough with the pioneering work of Gustav Kramer, an ornithologist at the Max Planck Institute for Marine Biology at Wilhelmshaven. It had long been known that when migrant songbirds were kept in captivity, they displayed intense activity at night during the periods of their normal spring and fall migration. When Kramer placed songbirds in circular cages during their migratory period, he discovered that they would spontaneously orient their activity in a particular direction. By manipulation of the cues available to the caged birds the determinants of direction finding could be studied. Through this technique migration could be "brought into the laboratory."

In the late 1950's another German ornithologist, E. G. F. Sauer of the University of Freiburg, carried out a long series of experiments with European warblers. It was he who first hypothesized that these warblers determine their migratory direction from the stars in the night sky. Since then much has been learned about star orientation by birds. Numerous species have been examined, and it appears that the ability to orient by the stars is widespread among birds that migrate at night.

For some years I have been studying one night-flying migratory bird, the North American indigo bunting (*Passerina cyanea*). Enough information is now available to piece together a fairly complete picture of how the stellar-orientation system in this species operates. The species breeds throughout the eastern U.S., where the brilliant blue male is a well-known songster. During the fall migration the buntings fly up to 2,000 miles to winter in the Bahamas and in southern Mexico and Central America south to Panama.

When indigo buntings are kept in captivity and exposed to the same pattern of day lengths they would experience in nature, they exhibit intense nocturnal activity in April and May and again in September and October, the times of normal migration. When this restlessness appeared, I tested the birds by placing them individually in circular cages. The cage was constructed of a piece of white blotting paper, rolled and stapled to form a funnel, mounted on a base consisting of an ink pad and topped with either a clear plastic sheet or a hardware cloth screen. A bird inside the cage can see only the sky overhead, since all ground objects are blocked from view.

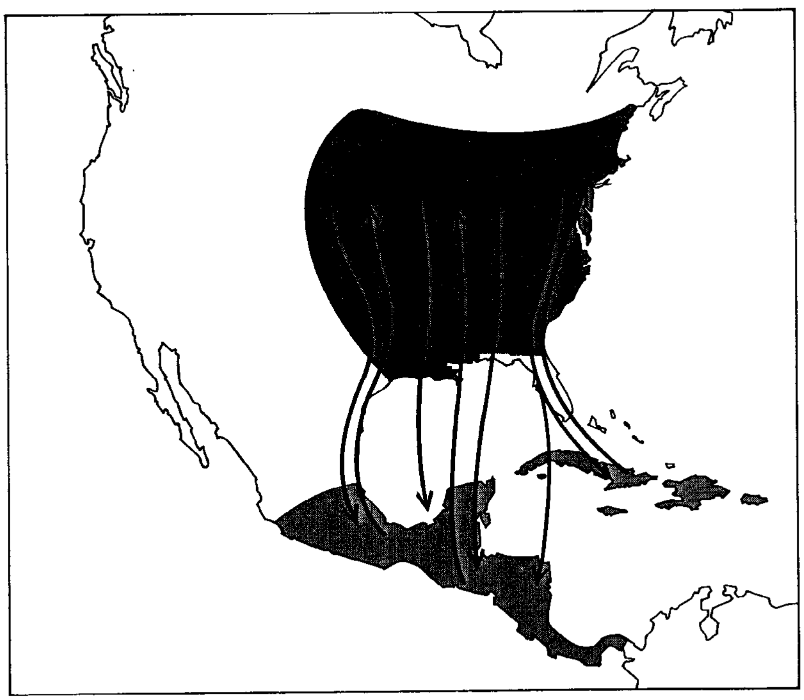
A bunting in migratory condition stands in one place or turns slowly in a circle, its bill tilted upward and its wings partly spread and quivering rapidly. At frequent intervals the bird hops onto the sloping paper funnel, only to slide back and continue its pointing and quivering. Each hop from the ink pad leaves a black print on the paper. The accumulation of inked footprints provides a simple record of the bird's activity; they can later be counted and analyzed statistically.

In the first stage of my studies I placed the buntings in their funnel cages outdoors on clear, moonless nights. In September and October most of the birds exhibited a distinct preference for jumping toward the southern sector of the cage, the same direction in which they would have migrated if they could. When the birds are tested in late April and May, however, the preferred direction is to the northeast, the appropriate direction for spring migration.

Since the wall of the test cage completely screens the horizon from view, it seems likely that the buntings are able to determine their migration direction when the only visual cues are those provided by the night sky. This hypothesis was reinforced by the changes observed when the birds were placed outdoors at night under cloudy conditions. As the stars disappeared behind the clouds, the orientation of the birds deteriorated considerably [*see lower illustration on opposite page*].

In order to test the stellar hypothesis under more rigorous conditions, I took the buntings into a planetarium, an approach also used by Sauer in some of his experiments with European warblers. In September and October, when the birds were exhibiting nocturnal restlessness, I projected the normal fall stars onto the planetarium dome. When the buntings were tested in the funnel cages, they oriented to the south. Birds tested in April and May under a spring sky in the planetarium consistently oriented to the north and northeast. When the North Star in the artificial sky was shifted to the east or west, the buntings changed their orientation to the new "south" or the new "north," depending on the season of the year. The change in orientation behavior was consistent and predictable. In control experiments I turned off the star projector in the planetarium and exposed the birds to a diffusely illuminated dome. Their behavior paralleled their response to overcast conditions outdoors: the accuracy of their orientation deteriorated considerably.

Since indigo buntings are willing to exhibit meaningful orientation in spite of the confinement of captivity, I was able to further modify the visual cues in the night sky and thus dissect out the detailed workings of the birds' stellar-orientation system. The experiments were designed to answer the following questions: Which stellar cues are important? How are such cues employed? What kind of information does the bird obtain? How accurately does it obtain it?

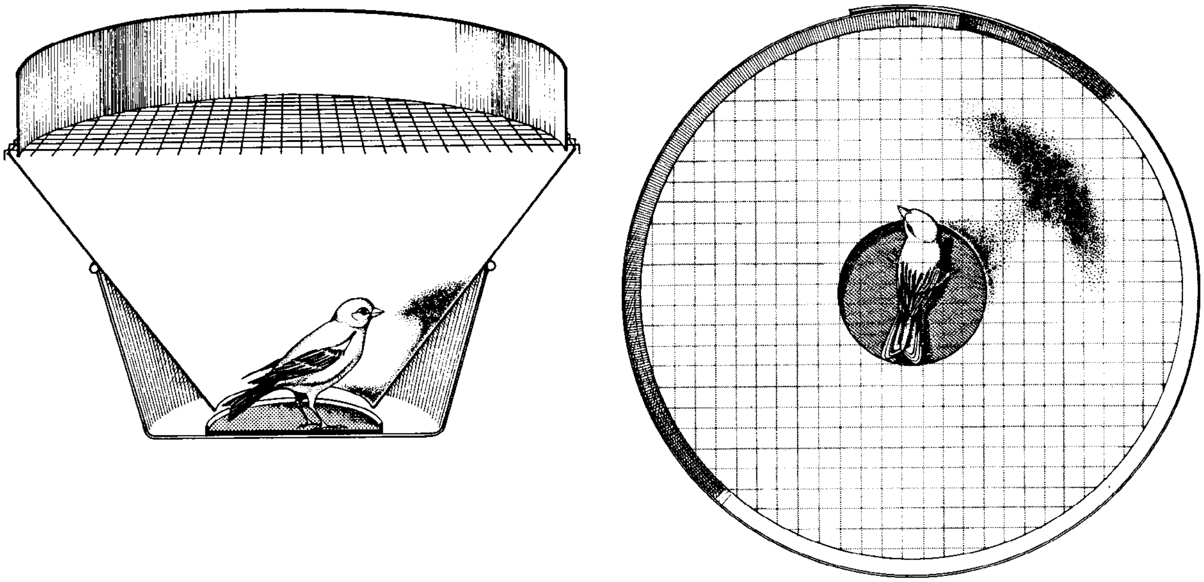


MIGRATION OF INDIGO BUNTINGS proceeds along a broad front. Buntings migrate from their wintering grounds in the Bahamas, southern Mexico and Central America (*gray areas*) in late April and arrive at their breeding grounds in the eastern U.S. (*colored area*) throughout the month of May. They depart for wintering grounds in September and October.

In theory there are two ways birds could determine direction by the stars. One way would be for the bird to locate a critical star or a group of stars and then guide itself by flying at a particular angle with respect to the star or the group of stars. The absolute position of a star, however, is not constant throughout the night: stars shift from east to west as the result of the rotation of the earth. In order to maintain a given compass direction the bird would have to alter its angle of flight with respect to the selected star in such a way as to compensate for the apparent motion of the star [*see top illustration on page* 7]. Such a mechanism would be analogous to the sun-compass orientation in which a daytime bird migrant, making use of an internal time sense, correctly compensates for the daily movement of the sun across the sky.

The requirements for a stellar-navigation system are much more demanding than those for a system that depends on the sun for determining compass direction by day. There is only one sun, and it moves at a regular rate, but there are thousands of stars and different stars are visible above the horizon at different times of the night and at different seasons. A nocturnal migrant presumably would need to be able to consistently locate a specific star or a specific group of stars, and that would require it to possess some form of pattern recognition.

In addition the rate of compensation for apparent motion will differ, depending on the star or stars selected. Celestial motion is an apparent motion produced



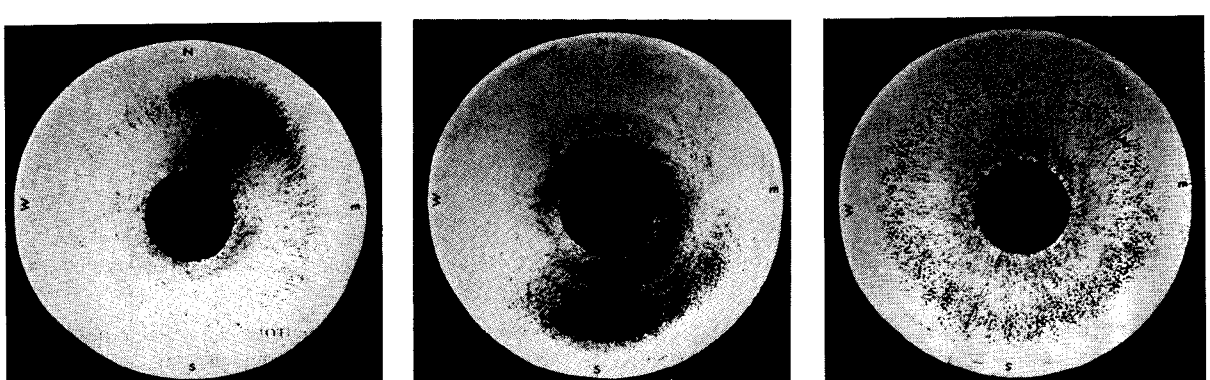
CIRCULAR TEST CAGE for determining the directional preference of an indigo bunting is shown in cross section and in a top view. Funnel portion of the cage is made of white blotting paper. The bunting stands on an ink pad, and each time it hops onto the sloping funnel wall it leaves black footprints. The bird's view is limited to a 140-degree overhead sector of sky when it hops up.

by the earth's rotation once every 24 hours. All stars move with an angular velocity of 15 degrees per hour, as the sun does. The linear velocity of a star will vary, however, depending on how close it is to the North Star. Stars near the North Star move through a small arc, whereas stars near the celestial equator move through a large one. If a bird were to use star groups in different parts of the sky, it would have to compensate at a different rate for each group. Finally, the direction of compensation depends on whether the guiding stars are in the north or in the south: northern stars would require clockwise compensation, southern stars counterclockwise.

According to the second theoretical model, the bird would use patterns of stars to determine directional reference points. Human beings easily recognize the Big Dipper by the characteristic arrangement of its stars. And by visually extending the line joining the two pointer stars of the Big Dipper, they can readily locate the North Star and hence geographic north. Star patterns such as the Big Dipper also move across the sky, but the shape of each pattern remains constant and each preserves a distinct relation to the North Star.

Since each star bears a fixed geometric relation to other stars, it would be theoretically possible for a bird to determine a directional reference point from any number of star patterns [*see middle illustration on page* 7]. The major difference between this model and the first one is that a compass direction can be determined from the geometric patterns of the stars independently of an internal time sense, or "biological clock."

I tested these alternative hypotheses in a planetarium by creating an artificial situation in which the astronomical time would be out of phase with a bird's internal time sense. If a time sense is involved in star navigation, then presenting the stars in positions that are advanced or retarded from local time should cause the bird to orient in the wrong direction. On the other hand, there should be no change if the bird relies only on the geometric patterns of the



FOOTPRINT RECORDS of male indigo buntings tested in a circular cage placed outdoors under the stars on moonless nights are shown. In the spring the bird typically orients its hopping to the north (*left*). In the fall its hopping is oriented to the south (*middle*). When the stars are obscured by clouds, the bunting's activity remains high but orientation of the hopping is random (*right*).

stars. I tested buntings when the planetarium sky was three, six and 12 hours ahead of local time and when it was three, six and 12 hours behind local time. The results were clear: the birds generally maintained their normal migratory orientation under all these conditions. Apparently indigo buntings do not make use of an internal time sense to orient by the stars but obtain directional information from star patterns, much as human beings do.

I then turned to the question of which star groupings are of particular importance to buntings. Once again the planetarium was an invaluable tool, since one can block from view selected stars, constellations or entire areas of the sky. In a series of experiments I systematically removed and later reinserted portions of the artificial sky. I found that most buntings rely for direction finding on the northern area of the sky that lies within about 35 degrees of the North Star. The major constellations in this area are the Big Dipper, the Little Dipper, Draco, Cepheus and Cassiopeia. The birds relied on the northern circumpolar stars not only during the spring migrating season when they normally fly north but also during the fall migrating season when they fly south.

An important corollary finding was that there is considerable redundancy in the buntings' recognition of star patterns. The birds are familiar with several star groups, and the removal of one group of stars, say the Big Dipper, often merely forces them to rely on some alternate constellation. Since birds frequently migrate on nights when there is variable cloud cover, such redundancy is obviously adaptive.

Navigation can be regarded as involving a two-step process. Consider a man equipped with a map and a compass. In order to determine how to reach a particular geographic destination he must first calculate his position on the map with respect to his goal and then use the compass to select the appropriate direction. The navigation problems of a migrating bird can be viewed in the same way, that is, as a "map and compass" process.

Theoretically an accurate knowledge of the absolute positions of the stars coupled with a stable and highly accurate internal time sense could provide enough map-and-compass information for a bird to determine its absolute geographic position. If the bird retains a precise memory of the temporal position of the stars at its destination point, it could in principle select the appropriate direction to the goal from the displacement of the stars in the sky overhead.

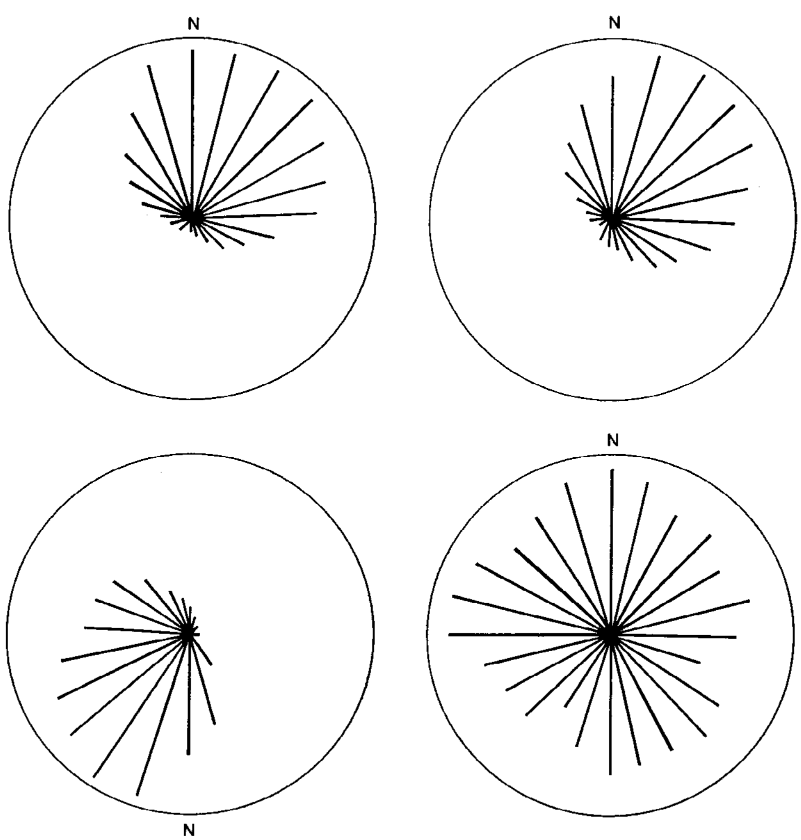
The finding that the indigo bunting does not integrate a temporal component with its use of stellar cues implies, however, that the bird does not detect or correct for longitudinal displacement, at least not by celestial cues. Hence star orientation in the indigo bunting appears to be a compass sense that enables the bird to select and maintain a particular direction but does not provide the information that makes it orient to a particular goal.

What, then, does determine how the star compass will be used? The bunting may be able to locate the Big Dipper or other constellations, but why does it use them to orient north or south rather than east or west? And how does the bunting select north in the spring and south in the fall?

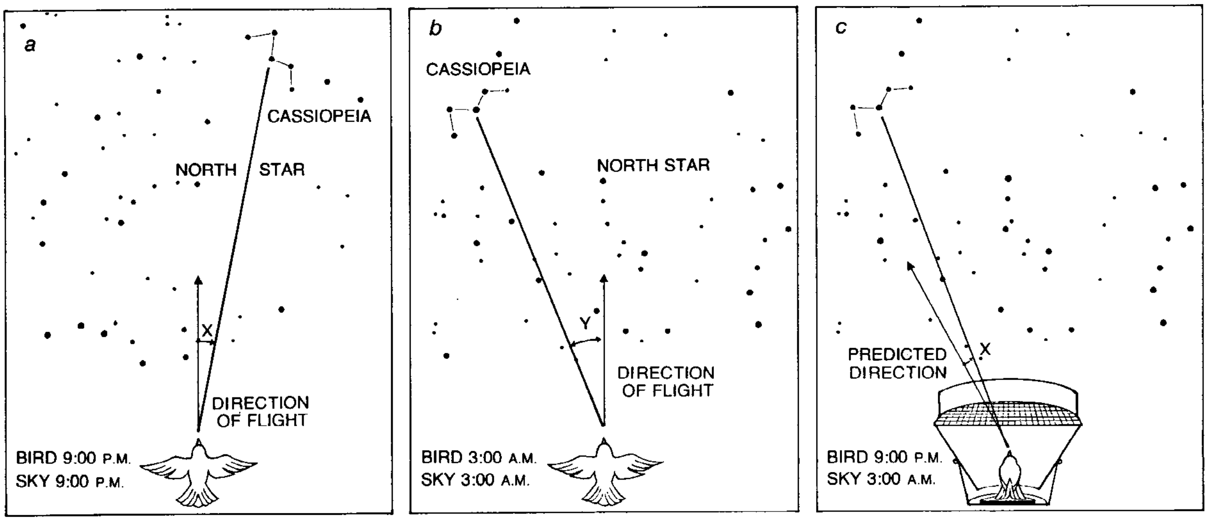
The sidereal, or astronomical, day is four minutes shorter than the solar day. Because of this inequality the temporal positions of the stars change with the seasons, with the result that the stellar information available from the fall night sky is quite different from that available from the spring night sky. Does the indigo bunting have a specific northerly directional response to the stellar stimuli in the spring sky and a southerly response to the stellar stimuli in the fall sky?

To test this possibility I captured 15 adult male buntings in their summer breeding territories near Ithaca, N.Y., and divided them into two groups. The weight, fat level and molt status of each bird was recorded weekly until the testing period the following spring.

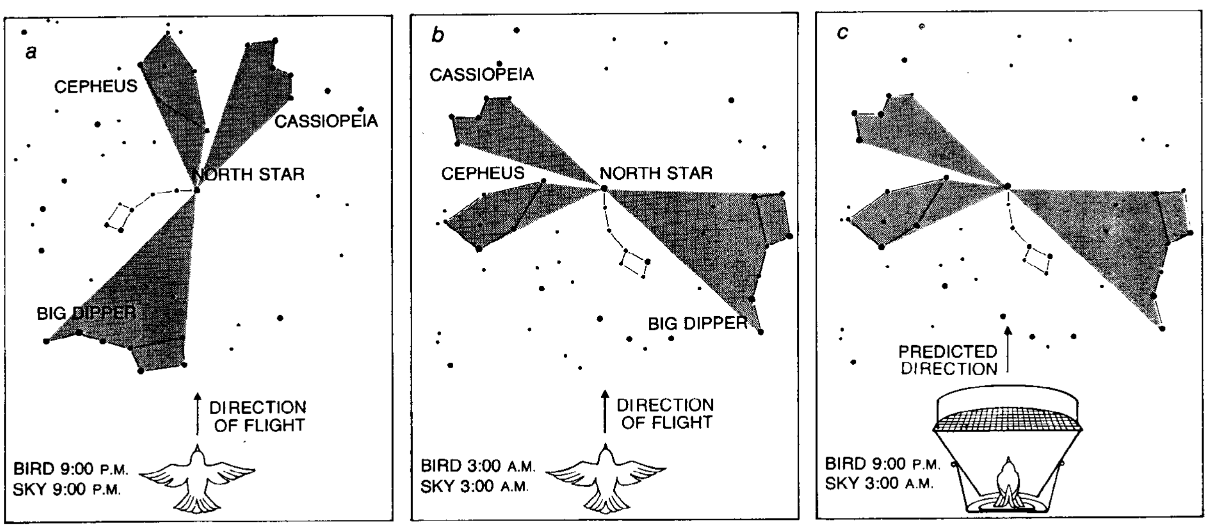
The control group of eight birds lived in a flight room where the length of the day simulated what they would have normally encountered in nature. An astronomical time clock maintained a day length equivalent to the day length at



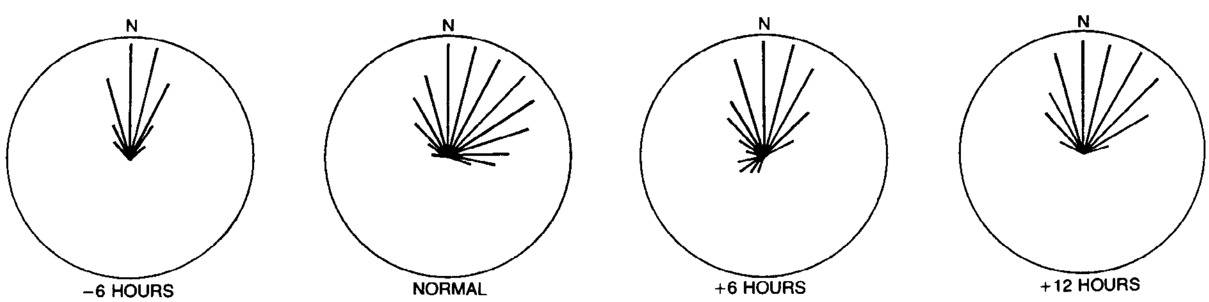
VECTOR DIAGRAMS show the similarity of the orientation of a bunting outdoors under the stars in the spring (*top left*) and under a simulated spring night sky in a planetarium (*top right*). When the planetarium stars were shifted so that the North Star was at the true south, the bird reversed its orientation (*bottom left*). When the stars were turned off and the planetarium was diffusely illuminated, the bunting's orientation became random (*bottom right*). The radius of each circle is equal to the largest amount of activity in any one 15-degree sector, and the vectors for the other 15-degree sectors are proportional to the radius.



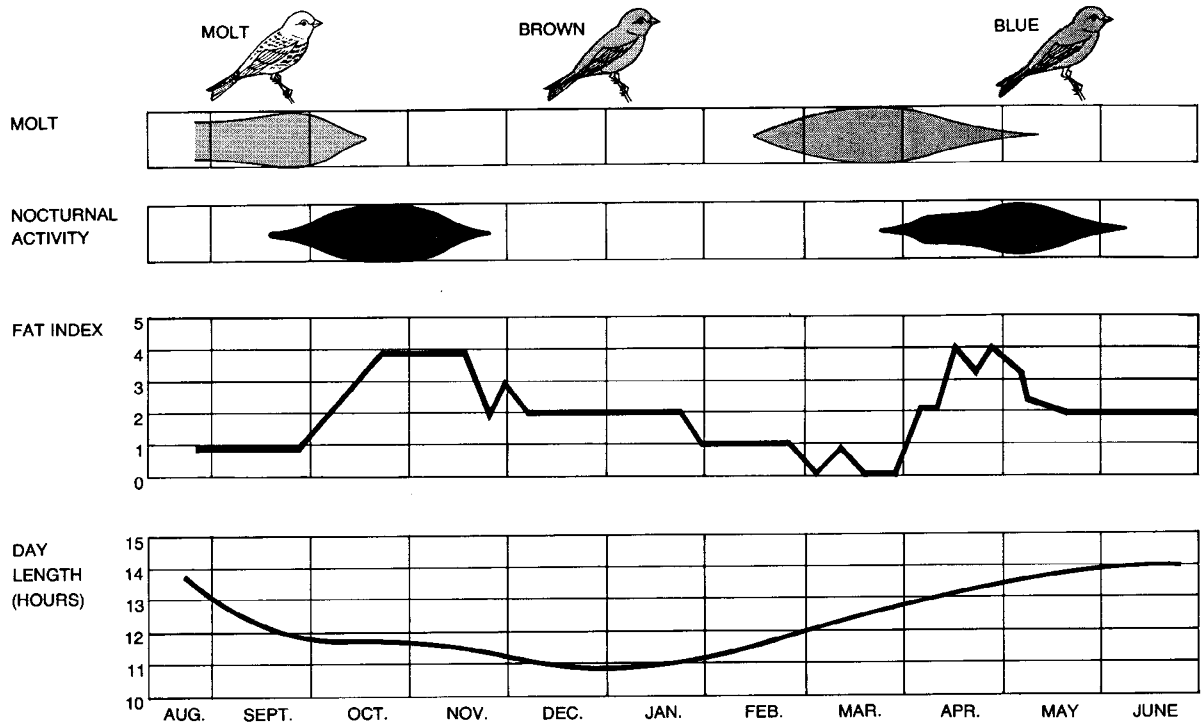
STELLAR-ORIENTATION HYPOTHESIS I proposes that the indigo bunting guides itself by flying at an angle to a particular star or group of stars. Since the positions of the stars change throughout the night, the bird would have to use an internal time sense to compensate for the motion of the stars. For example, a bunting going north at 9:00 P.M. would fly at angle X with respect to a critical star (*a*). At 3:00 A.M. the bird compensates for the rotation of the stars by flying at angle Y to the critical star (*b*). According to the hypothesis, when a bunting whose physiological time is at 9:00 P.M. is presented with a 3:00 A.M. star pattern in a planetarium, it should compensate in the wrong direction, that is, it should orient at angle X with respect to the critical star instead of at angle Y (*c*).



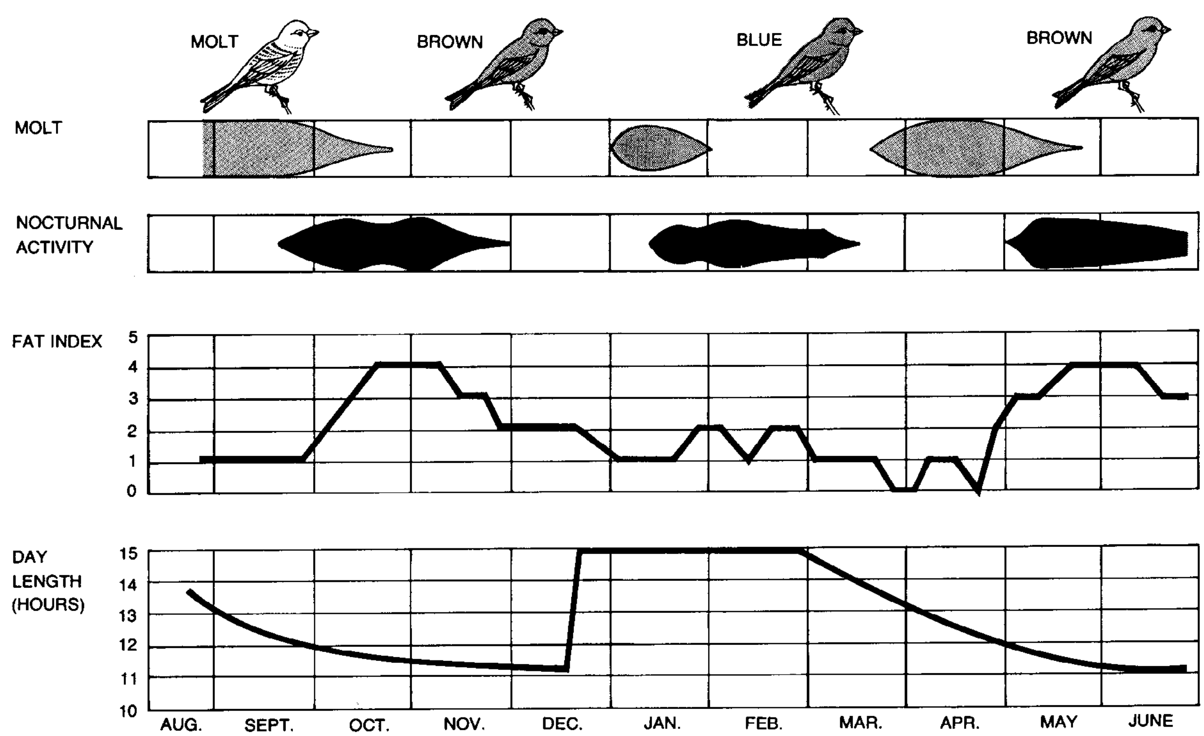
STELLAR-ORIENTATION HYPOTHESIS II states that the bunting obtains directional information from the configuration of the stars. The bird can determine a reference direction such as north from fixed geometric relation of the stars regardless of the time of night (*a, b*). When the bunting is exposed to a time-shifted sky in a planetarium, there should be no change in its orientation (*c*).



RESULTS OF PLANETARIUM TEST of the two star-navigation hypotheses show that buntings continue to orient correctly regardless of whether planetarium stars are shifted ahead of or behind the bird's normal physiological time. This indicates that the bunting does not incorporate its biological clock in the star-orientation process and obtains only directional information from star patterns.



CONTROL GROUP OF ADULT MALE BUNTINGS lived in a flight room where an astronomical time clock maintained the day length equivalent to length at their wintering grounds. The birds molted normally in the fall and again in the spring. After each molt they built up fat reserves and became active at night. In May directional preference of the birds was tested in a planetarium.

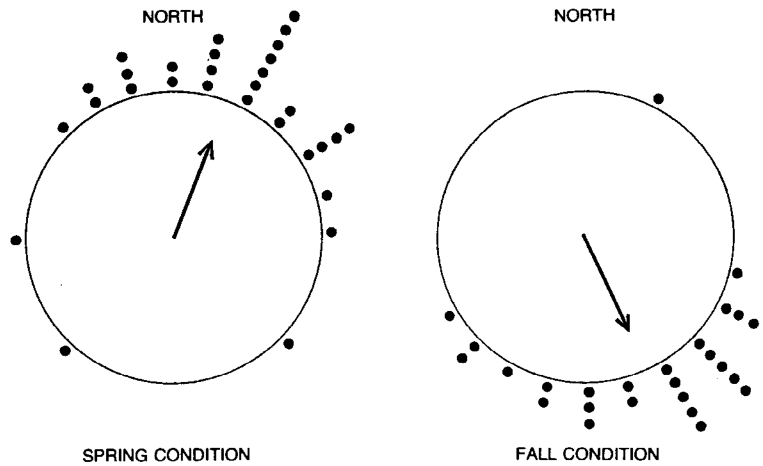


EXPERIMENTAL GROUP OF ADULT BUNTINGS was given an accelerated photoperiod regimen. Beginning in mid-December birds were exposed to the longer day lengths typical of spring. They molted into their blue spring plumage in January. The day lengths were shortened in March, and the birds molted into their brown winter plumage. Their directional orientation was tested in May.

their wintering ground in Guatemala. The male buntings in this group molted normally and acquired their bright blue prenuptial plumage between February and early April. After molting they built up substantial reserves of subcutaneous fat. They became nocturnally restless in April and May.

The experimental group of seven buntings was subjected to the same day-length regime as the control group until mid-December. The birds were then exposed to a spring day length of 15 hours, which caused them to molt into their blue spring plumage in January. Beginning on March 1 the day length was progressively shortened to simulate the day lengths of fall in the buntings' summer breeding territory, and the birds molted out of their blue plumage and into their brown winter coloration. After the molt the buntings built up fat reserves, and nocturnal activity began in May.

The directional preferences of the control group and the experimental group were tested in the planetarium under identical spring night skies. There was a marked dichotomy in the orientation behavior of the two groups. The control group of blue buntings, which were ready for their normal spring migration, oriented to the north and northeast, whereas the experimental group of brown buntings, which were ready for their normal fall migration, oriented to the south.



DIFFERENCE IN ORIENTATION of indigo buntings in the control group (*top illustration on opposite page*) and the experimental group (*bottom illustration*) shows that the physiological state of the bunting affects its migratory direction. The control group, which was physiologically in the normal spring migratory condition, oriented to the north-northeast. The experimental group, which was in an induced fall migratory condition, oriented to the south-southeast. The mean vector of the birds in each group is shown by the arrow. The length of the vector represents degree of agreement among the birds in selecting a direction.

The results indicate that the physiological state of the indigo bunting affects its migratory orientation. We have already seen that the same northern circumpolar stars are used as the chief stellar reference in both spring and fall. It now appears that the polarity of the migratory orientation—whether it is toward or away from the northern circumpolar stars—is under hormonal control. Recent studies by Albert H. Meier and D. D. Martin of Louisiana State University support this hypothesis. They report being able to reverse the orientation behavior of another nocturnal migrant, the white-throated sparrow, by altering its physiological state with the administration of two hormones, prolactin and corticosterone, which appear to have a synergistic effect in stimulating the birds' migratory activity.

The finding that the physiological state of the indigo bunting affects the direction in which it orients does not, however, fully answer the question of how it chooses a specific direction for its migration. The young of many species of birds migrate independently of the adults, setting out on a course they have never traveled before and without the benefit of experienced companions. What causes young, inexperienced birds to select a southerly direction for their first migration? To many investigators the fact that they do so implied that early experience was not important in the development of normal orientation abilities. Some workers even proposed that birds possess a genetically inherited "star map."

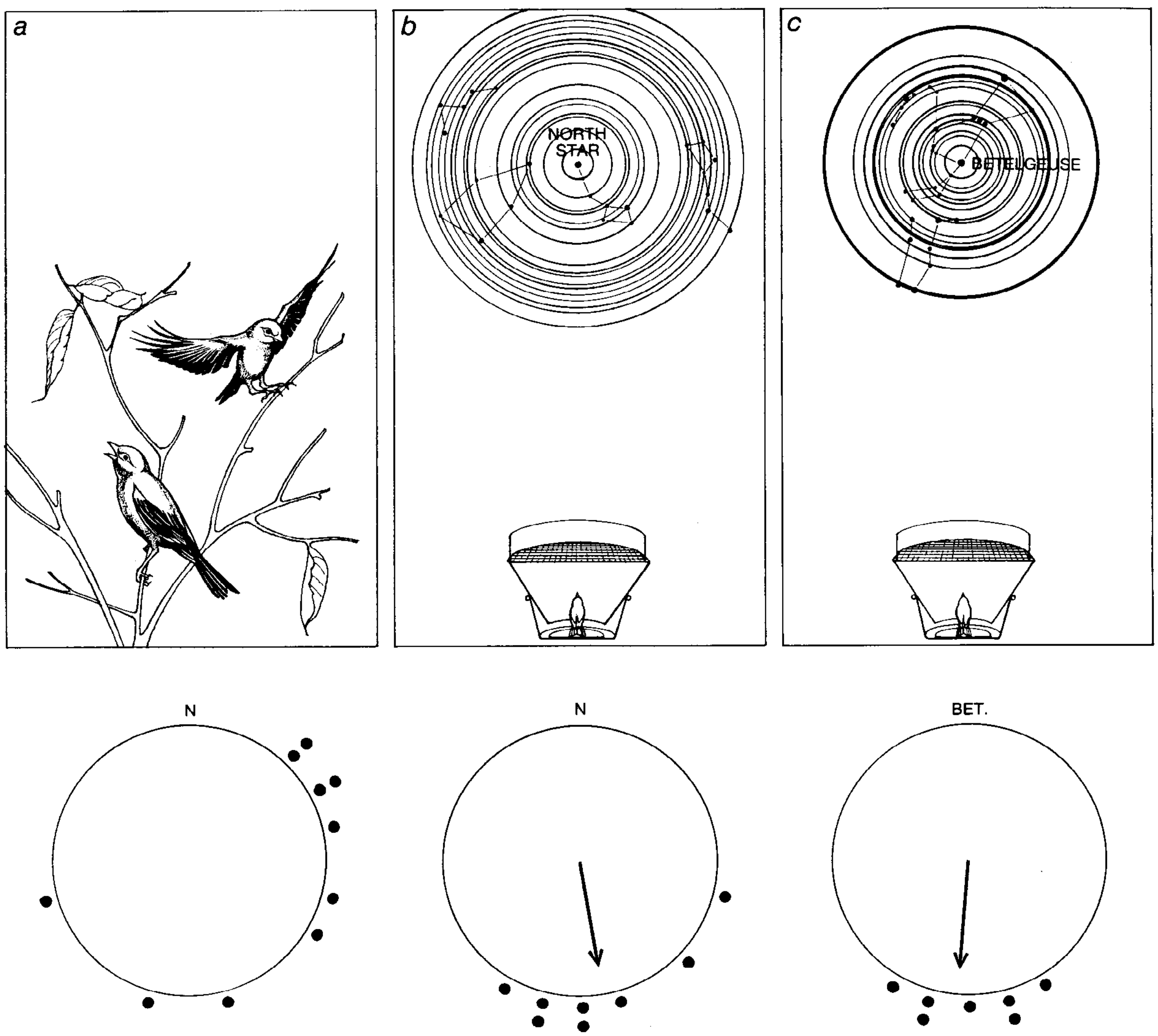
Field studies have produced evidence that makes the inherited-star-map hypothesis unlikely. These investigations reveal that there are differences between the navigational abilities of young birds and those of adult birds. When birds of some species, for example the European chaffinch, are captured and displaced from their normal fall migration routes, the adults may correct for the displacement and fly to their regular winter grounds, but young birds on their first migration do not. Prior experience obviously improves the navigational ability of birds.

In my studies adult indigo buntings have always been more accurate and consistent in their orientation than young birds. If very young buntings are prevented from the time of their capture from viewing the normal night sky, aberrant orientation behavior develops. One summer I located numerous nests of indigo buntings near Ithaca, and I carefully removed the young birds when they were between four and 10 days old. The nestlings were hand-reared in the laboratory, where their visual experience with celestial cues could be controlled. One group of young buntings never saw a point source of light. They lived in a windowless room with diffuse fluorescent lighting until they began depositing migratory fat and exhibiting intense nocturnal activity in September and October. When I tested these birds in the planetarium under a night sky that matched the normal one for the season, they were unable to select a migratory direction. The young birds were highly motivated, jumping with great frequency in the test cages, but the orientation of the jumps was random. They were unable to obtain directional information from the stars.

A second group of young birds was prevented from seeing the sun, but the birds were allowed to view the night sky in a planetarium every other night during August and September. The star projector rotated at a speed of one revolution every 24 hours, thus duplicating the normal pattern of celestial rotation. When these birds began displaying nocturnal activity, they were tested in the planetarium under the same sky as the group of birds that had had no visual experience with the stars. Unlike the inexperienced birds, the buntings that had already been exposed to the night sky were able to orient to the south. In some way the exposure to the stars was of extreme importance for the normal maturation of star-orientation abilities. Finally, a third group of young buntings was exposed to the night sky in the planetarium but with one important difference. I modified the star projector by constructing a special arm that allowed the projector to be rotated around any axis of my choosing. I selected Betelgeuse, a bright star in Orion, as the new polestar around which all other stars rotated. The star patterns and constellations remained unchanged; only their positions and movements with respect to the new axis of rotation were altered.

The young buntings of the third group were exposed to the sky with the Betelgeuse polestar every other night for two months. When they became nocturnally active, they were tested under a normal sky with the North Star at the pole position. The buntings consistently oriented their activity 180 degrees away from Betelgeuse—the appropriate "southerly" direction as defined with respect to the polestar of their early experience [*see illustration below*].

On the basis of experiments of this kind I have hypothesized that young buntings respond to the apparent rotational motion of stars in the night sky. The stars near the North Star move through much smaller arcs than the stars near the celestial equator, and this enables the young birds to determine a



EARLY VISUAL EXPERIENCE of young indigo buntings was found to play an important role in the development of their celestial-orientation abilities. Three groups of nestlings were captured and hand-reared in the laboratory. The first group (*a*) lived in a windowless room with diffused lighting and never saw a point source of light. In the fall the birds began to display intense nocturnal activity. When they were tested under a stationary night sky in a planetarium, they were unable to select a migratory direction. The second group (*b*) never saw the sun and was exposed to a night sky in a planetarium every other night for two months. Normal celestial rotation was simulated. When the birds were tested in a planetarium under a normal sky during their fall migratory period, they oriented to the south. The third group (*c*) also never saw the sun and was exposed to a modified night sky in a planetarium every other night for two months. Betelgeuse, a star in Orion, became the new polestar around which all other stars rotated. When the birds were tested in the fall under a normal night sky, they continued to regard Betelgeuse as the polestar and oriented their activity away from it. The experiment shows that young buntings initially learn the north-south axis from the rotation of stars and that star patterns by themselves are not useful cues to a naïve bunting. Star patterns take on directional meaning only after they have become part of the bird's general orientational framework, the formation of which is influenced, at least in part, by observing the rotation of stars.

north-south directional axis. Individual stars and patterns of stars are of no value for direction finding until their positions with respect to some reference framework have been learned. The axis of the rotation of the stars appears to function as one reference system. Once the stellar information and the rotational have been coupled, however, the bunting can locate the rotational axis from star patterns alone. This is suggested by the finding that adult indigo buntings orient accurately even under stationary planetarium skies. Celestial motion thus becomes a secondary or redundant cue for adult birds.

One cannot help but speculate about the possible selective advantage of a maturation process that makes use of celestial rotation for a directional reference system. One possible explanation lies in the long-term unreliability of the stellar cues themselves. The rotation of the earth can be viewed as being analogous to the spinning of a top. And like most spinning tops, the spinning earth wobbles. This slight wobble, usually described as the precession of the equinoxes, causes the direction of the earth's spin axis to shift. Over a period of 26,000 years the precession of the equinoxes causes the earth's spin axis to trace on the celestial sphere a full circle with a radius of 23.5 degrees. This motion gives rise to marked seasonal and latitudinal changes in the apparent position of stars. The spring stars of the present become the fall stars in 13,000 years, and vice versa. The values of declination also change: as the polar axis moves through its circle Vega becomes the new polestar, and the present North Star shifts to 43 degrees north [*see illustration on this page*]. Similar changes occur for all stars.

The possible implications of these changes for the star-navigation system of birds are obvious. If birds were to rely on a genetically fixed star map, the rate of genetic change would have to be extremely rapid to allow for the change in position of the stars. A maturation process in birds that involves finding the north-south axis by the rotation of stars, however, minimizes the problem. Of course, several reference cues may play a role, but the axis of celestial rotation is well suited to function as one such reference because that axis is aligned with geographic north-south regardless of which particular stars and patterns of stars are located near the celestial pole.

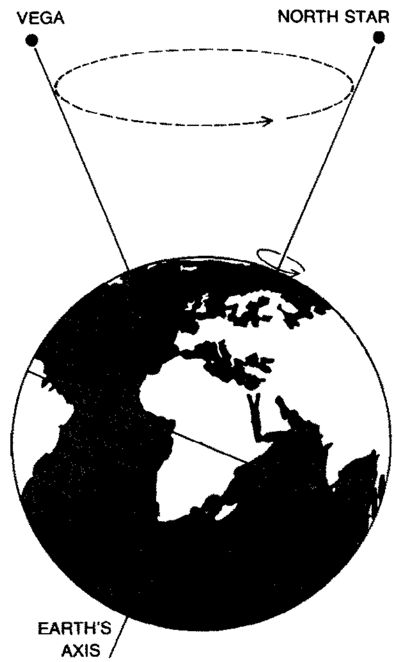
Experiments in the planetarium have enabled us to learn a great deal about the orientation of night-migrating birds. Young birds develop a north-south reference axis as a result of early exposure to celestial rotation. Then they learn the patterns of stars around the northern celestial pole, which they use in a configurational manner to determine a direction of migration. The precise direction that is selected depends on the hormonal and physiological state of the bird and not on seasonal differences in the position of the stars. The star-orientation process of the indigo bunting is basically one of pattern recognition that does not involve an internal time sense.

The experiments described here are equally important for what they do not explain about migratory orientation. Although the star-orientation process enables a bird to maintain a given course during its migratory trip, as an explanation for the orientation abilities of birds the process by itself is not entirely adequate and not absolutely essential. I say not entirely adequate because the direction-finding system described for the indigo bunting is basically only a star-compass system that enables the bird to select and maintain a given direction. The system does not provide any information about actual geographic location.

The star compass does not tell the bird it has been blown off course to the east or to the west, nor does it tell the bird when it has reached the latitude of its destination. That is because the star-orientation capability I have described still lacks the map component of the map-and-compass hypothesis. It is quite possible that most migrating birds are not at all goal-oriented during the major portion of their migratory flight. Their process of orientation may be fundamentally different from that of homing pigeons and they may only revert to a homing type of process during the very final stages of the migratory flight.

I say not absolutely essential because we now know that migratory birds have numerous directional cues available to them. In addition to the use of the sun and the stars, experiments have shown that songbird migrants can make use of the position of the sunset, the directionality of the winds aloft, the direction of the earth's magnetic field, the presence of topographic landmarks and the activity and the call notes of other birds of the same species as sources of information, enabling them either to select or at least to maintain a given migratory direction.

Birds thus have access to many sources of directional information, and natural selection has favored the development of abilities to make use of them all. Some cues may give more accurate information than others; some may be available throughout the flight, whereas others may be useful only at specific geographic locations; some may be available regardless of flight conditions, whereas others may be functional only under optimal meteorological situations.



PRECESSION OF EARTH'S AXIS produces change in the apparent position of the stars. In 13,000 years, as the polar axis moves through half of its circle, the star Vega will become the new polestar and the present North Star will shift to 43 degrees north.

The realization that birds have multiple cues at their disposal is in itself a finding of major importance. Although I have concentrated here on the star compass, I do not mean to imply that the other cue systems are not important. The discovery of a hierarchy of redundant directional cues makes the search for a single mechanism of migratory orientation obsolete.

The nocturnally migrating bird should be viewed as an animal whose behavior has been shaped by aeons of intensive selection pressure. It is the combination of the bird's skill as a meteorologist and as a navigator that accounts for its successful traversing of thousands of miles of environmentally inappropriate terrain each fall and spring. Although our understanding of the migratory navigation of birds has come a long way since Kramer began the experimental approach some 20 years ago, the total of our knowledge is still not enough to fully explain how an individual bird finds its way between its breeding territory and its wintering grounds.

The Author

STEPHEN T. EMLEN is associate professor of animal behavior at Cornell University. After graduating from Swarthmore College in 1962, he went to the University of Michigan, where he obtained his Ph.D. in zoology in 1966. He writes: "I now split my time between two quite different research areas within animal behavior: migration, orientation and navigation on the one hand and social behavior on the other.... This summer my wife (who is also a researcher on animal behavior) and I will be traveling to the Arctic to collect eggs and baby chicks of sandpipers to bring back to Cornell for in-depth studies of the ontogenetic development of orientational abilities."

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