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Celestial Rotation and Stellar Orientation in Migratory Warblers

In his study of the ontogenetic development of stellar orientation in indigo buntings, Emlen (1) develops the hypothesis that fledgling buntings react to the apparent rotational motion of the night sky. By learning the birds establish a reference system for using certain stars or star patterns to guide their nocturnal migrations. Subsequently, through the correlation of stellar and rotational information, experienced birds can locate the polar axis from the specific star patterns alone, so "that celestial motion per se should become a secondary or redundant orientational cue for adult birds."

The results of Emlen's studies seem to support his view that early visual experience is an important factor in the development of stellar orientation in indigo buntings. In support of his hypothesis Emlen cites the accurate orientation of our caged Old World warblers of the family Sylviidae when they were tested under stationary planetarium skies (2). Although the migratory orientation of our captured adult warblers, exposed to the stationary sky of a 6-m Zeiss planetarium, may support Emlen's hypothesis, there are notable exceptions. The spontaneously precise and species-specific reactions of inexperienced juvenile and adult migrants, as well as those of birds with very limited exposure to the natural sky, suggest that the warblers utilize a different system of stellar orientation under the same experimental conditions and even under the natural starry sky.

Garden warblers (*Sylvia borin*), blackcaps (*S. atricapilla*), and lesser whitethroats (*S. curruca*) were optically isolated in diffusely lit chambers from the date of hatching, and from the 9th, 14th, and later days of their life. The birds were prevented from viewing the sky until their first orientation tests during their first or later migratory periods. These birds then chose their specific migratory directions within minutes of their first exposure to the natural starry sky [figure 3 in (2)] or to the stationary planetarium sky

[for example, figure 13a in (2)]. These birds were just as reliably and lastingly oriented as their counterparts in the wild who were familiar with the natural sky during day and night and were experienced with previous migrations. Particularly impressive are the spontaneous responses, for example, of the garden warbler kept isolated since hatching and of the lesser whitethroat kept optically isolated for more than 1 year from the 14th day of its life (before it had begun any premigratory wanderings and night activity) until its second autumnal migratory period.

It seems hardly conceivable that the sylviid warblers were able to deduce and establish a knowledge of the location and angular position of the polar axis within a few minutes after their first confrontation with the natural or artificial starry skies. The inexperienced birds were accurately oriented under the stationary planetarium sky even when forced to accept an unnatural zenith (2-4); since the azimuth and altitude positions varied from experiment to experiment, this suggests that, in the absence of any visible rotational axis, the birds must have related the key stars or star patterns to a fixed axis, plain, or point in space whose identity is not yet known (3).

When the birds were shown a stationary planetarium sky for a length of time, they began to shift their preferred direction of orientation slowly but steadily around the compass opposite to the apparent direction of rotation of the natural night sky. The fact that the visually oriented birds "invented" compensatory angular movements of approximately 15 degrees per hour, thereby "inducing" an otherwise nonexistent motion of the fixed starry sky, strongly suggested the existence of a primary reference system established by other than visual cues. This should not exclude the possibility that the birds may visually recognize the polar axis if they can view a rotating starry sky for a certain time.

Polaris and the circumpolar region of

the night sky, seemingly of such importance to indigo buntings (5), proved of little significance for the warblers. They made and maintained their precise directional choices when this section of the starry sky was experimentally eliminated in the planetarium or was covered by clouds in nature.

If one accepts the buntings' system of stellar orientation, and for that matter that of the Sylviidae too, the birds' knowledge or experience of the canopy of stars is not sufficient of itself to account for their specifically and seasonally distinct and varying choices of migratory directions. The spontaneously accurate responses of the sylviid warblers without training and experience, their selection of compass bearings in line with the migratory pathways of their species, their upset and compensatory behavior under temporally maladjusted planetarium skies (2-4), and their quick adjustments to simulated north-south displacements under latitudinal shifts of the planetarium skies (2) provide strong evidence for a genetic substrate. This determines, in the first place, the birds' ability to navigate by the stars and to project their orientation along the lines of specific routes. On the basis of this substrate, learning by association or by imprinting (6) can yield new efficiencies and safety mechanisms for their migratory flights. We do not know by what genetically predetermined means the inexperienced Old World warblers are able spontaneously to choose and to follow the long-established migratory routes of their respective species, guided by the starry sky. Contrary to the opinion expressed by Emlen (1), we never meant to propose that the young warblers possessed a "genetically predetermined star map." We rather stressed the importance of vision and visual configurational qualities in the warblers' star orientation, their reliance on a grid of two celestial coordinates and on an internal chronometer. We pointed out the enormous variability, qualitatively and quantitatively, in stellar information that enabled the birds to take their bearings (2). We also stressed the limitations of our planetarium experiments and of our study, which dealt with only one of the factors that govern the nocturnal flights of these birds. That the inexperienced warblers responded spontaneously to the canopy of stars requires no genetic blueprint of a star map. With the exception of the warblers' probable configurational perceptive

ability, their spontaneous response should find an explanation along the lines of the same mechanism that, for example, makes a wax moth larva that has been raised in the dark leave the light the very moment it is placed in the open. Similarly, my son had no training in astronomy and had never been taught Gestalt psychology when, at the age of three, he suddenly pointed to the night sky and exclaimed excitedly, "Papa, the stars have made a train." His eyes were fixed, in fascination, on the twinkling stars of Orion's belt.

Emlen's excellent studies indicate that indigo buntings seem to have evolved a system of stellar orientation different from that of the Sylviidae and from that which we studied in the Pacific golden plover, *Pluvialis dominica fulva* (6). But one cannot help recognizing that the buntings' system of orientation through maturation and learning must also have an organic (that is, a genetically determined) basis. Emlen might have had this in mind when he noted that his hypothesis could not explain why the young migrant orients southward on its first flight (and, I may add, at the right time of the year). His latest results on the star orientation of indigo buntings remind me of the development of the song we studied in another sylviid warbler (7). The whitethroat (*Sylvia communis*) under natural conditions develops a species-typical song, and it will sing the same song when growing up isolated in a soundproof room with no external acoustical stimulation. In fact, this typical song will mature even latently, when the bird is prevented from singing it at the proper age of development. Yet, as Heinroth and Heinroth (8) once showed, the same whitethroat male will sing forever with the voice of a stranger when raised in company with a dominantly singing linnet. Certainly, we do not ask if the whitethroat's song or stellar orientation is entirely inborn or entirely learned, but rather what strikes the balance between these two components of life.

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Sauer comments that European warblers of the family Sylviidae appear to utilize a system of star orientation different from that described for a North American fringillid, the indigo bunting (1). Sauer's results differ from mine in that extensive visual exposure to celestial cues, and in particular to celestial rotation, is not a necessary prerequisite for the development of normal orientational abilities in three species of Old World warblers. This conclusion is based upon the results of pioneering experiments conducted during the 1950's on hand-reared birds. Sauer and his wife raised a total of 16 warblers, but relevant data are available for only six (2). Of these, four were obtained as nestlings after the eyes had opened (9 days of age) or after they had left the nest (14 days of age). During captivity they were housed in rooms in which there was a window facing either west or north, thereby allowing a partial view of the day and night sky. Only two individuals, a garden warbler ("Grungelb") and a blackcap ("Rot"), satisfied the requirements of complete visual-celestial isolation, having been kept in complete isolation from view of the sky from the time of hatching. Unfortunately, only one short experiment was performed on each of these individuals. No replicate experiments or control tests were conducted. Consequently, there still remains a need for additional studies of the maturation of orientational capabilities in a wide variety of species, including sylviiids.

Nevertheless, the autumnal migratory behavior of each of Sauer's six birds (two garden warblers, three blackcaps, and one lesser whitethroat), none of which had more than minimal exposure to celestial cues and rotation, was clearly oriented in the appropriate, species-typical direction. This certainly suggests that the degree of visual-celestial experience necessary for the normal development of orientational abilities in young warblers is far less than that required for the maturation of star orientation in indigo buntings.

The discovery of different types of orientation systems in different groups of migratory birds should not be unex-

pected. Migratory behavior has evolved independently many times among birds. 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.

Most animals have several sources of directional information at their disposal. Natural selection should favor the development of abilities to make use of all such cues. Some cues might yield more accurate information than others do; some might be available throughout the entirety of the route, whereas others would be useful only at specific geographic locations; some might be available regardless of flight conditions, whereas others might be functional only under optimum 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 would 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.

Consequently, I would join with Sauer in stressing the importance of avoiding overgeneralization with regard to both the importance of celestial cues and to the detailed mechanisms of celestial orientation. Many more species must be studied before we will have an understanding of the full spectrum of adaptive strategies involved in long-distance direction finding.

Finally, a comment on Sauer's assertion that I have played down the importance of genetic predetermination in orientation behavior. Certainly I recognize that "the buntings' system of orientation through maturation and learning must also have an organic (that is, a genetically determined) basis." Both the types of information learned and the phases of development when an organism is maximally responsive to such information may have a partially genetic basis. But the artificial division of behavior patterns into "innate" and "learned" categories has dominated behavioral thinking and stifled research for too long. If nothing else, my study (1) should point out the complexity of the interactions of experience-dependent and experience-independent components in the maturation of orientation behavior in buntings. I hypothesized that young birds spon-

taneously respond to the rotational motion of the night sky. No obvious reward or change in external motivation can account for this importance of rotational information. Yet this visual exposure not only is necessary but must occur at a certain stage of development (3) if normal stellar orientational capabilities are to develop. I further hypothesized that there is no genetic template for recognition of certain star groupings. Rather, patterns of stars are learned. Yet there is a predisposition for inexperienced buntings to learn patterns located in the northern circumpolar area of the sky (1, 3), the region of least rotation.

Through this complex ontogenetic process, a young bunting acquires a celestial reference system, a necessary prerequisite for stellar orientation. The use of this reference to select a southerly heading in preference to any other

remains a topic for future investigation.

Many questions remain unanswered. We need additional ontogenetic studies of orientation systems. We need more comparative studies of the types of cues used in long-distance direction finding. What we do *not* need is a premature categorization of orientation behavior according to outdated nature-nurture controversies.

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Man-Made Climatic Changes: Seeding by Contrails

Landsberg's review of the impacts of man's activities upon climate (1) is certainly to be appreciated for its comprehensiveness and conciseness. His paragraph on the effects of "pollution caused by jet aircraft," however, and, in particular, his statement that evidence for the nucleation of precipitation by ice crystals falling from aircraft vapor trails is lacking, move me to offer the following comment.

It is true that appreciable effects of

such cloud seeding in modifying rainfall patterns cannot be expected except in a heavily clouded area, because only there will sufficient cloud water be present to generate appreciable precipitation. At the same time, the observation of a contrail seeding a massive cloud system is unusual because the cloud system obscures the sky for the ground-based observer. Only an airborne observer can see such an event.

However, the seeding effect of "air-

plane cirrus" upon lower cloud decks is easily seen under less stormy conditions. On 19 November 1969 a high, thin altocumulus deck under contrails at Ann Arbor showed this seeding effect, and high-level snow showers were produced (Fig. 1). Had these clouds overridden a thicker cloud system, there is little doubt that the seeding effect would have affected the rain pattern. The difficulty of getting adequate photographs of this phenomenon is an important problem in acquiring the needed documentation, but the effect itself is frequently and easily observed.

A more detailed documentation of the seeding effect of cirrus upon lower clouds has been reported by Braham and Spyers-Duran (2). Although this report does not specifically refer to "airplane cirrus" or "contrails," it should be clear that the ice crystals from contrails are just as effective for cloud seeding as those from natural cirrus clouds or from PbI_2 and AgI nucleation.

Within the context of my own observations, associated with the teaching of cloud-watching to students of meteorology over the last 23 years, I have had the strong impression that the cirrus cloud cover over the continental United States has been appreciably enhanced by aircraft exhaust products placed in the layer at 30,000 to 40,000 feet (9145 to 12,190 m). This impression has been vindicated by work recently reported by Machta and Carpenter (3) on the frequency of cirrus clouds at Denver. This increment of cirrus cloud cover must certainly have its effect upon the precipitation distribution. The total effect, however, even though it may be substantial, is at most a small fraction of the observed variability of rainfall amount patterns (4). Thus, again, the direct observation of precipitation changes attributable to airplane cirrus is not likely in the context of currently accepted procedures for measuring and recording precipitation.

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Fig. 1. Snow showers from an altocumulus deck under contrails.