MIGRATORY ORIENTATION IN THE INDIGO BUNTING, PASSERINA CYANEA

PART II: MECHANISM OF CELESTIAL ORIENTATION

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In Part I of this publication (Emlen, 1967), I discussed the *Zugunruhe* orientation exhibited by caged migratory Indigo Buntings, *Passerina cyanea*. The majority of the experimental birds consistently demonstrated an ability to select the appropriate migration direction when tested under natural or artificial (planetarium) night skies. These results, in conjunction with predictable behavioral changes under manipulated planetarium skies led me to hypothesize that celestial cues provided at least one means of enabling this species to determine its migratory direction.

Since the outdoor experiments were performed on moonless nights, and all planetarium tests were conducted without projecting the planets, the stars themselves are implicated as the informational cues.

In an attempt to study the mechanism by which stellar cues are employed and to determine which particular stars are of importance to this orientation process, several additional series of experiments were performed; the results are presented here, in the second and last part of this report.

METHODS

The Indigo Buntings tested in these experiments were the same individuals used in the previous study. Complete information concerning aviary quarters and general maintenance of captive birds as well as descriptions of the annual physiological cycles of molt, fat deposition, and occurrence of nocturnal restlessness are presented in Part I. Orientational abilities were tested by placing birds in small, funnel-shaped cages which allowed a view of the sky overhead. As a bird jumped up the sloping sides of such a cage, it left inked footprints in the direction of each jump and the accumulation of these prints provided the record of the bird's orientation (for details see Emlen and Emlen, 1966). Experiments were conducted inside the Robert T. Longway Planetarium at Flint, Michigan

(Spitz model B projector; dome diameter, 60 feet). A detailed description of this planetarium, including an evaluation of parallactic and distortion errors can be found in Part I. In addition, a complete, experiment by experiment, listing of the planetarium settings (including the absolute position of the sky measured as the hour angle of the first point of Aries) is presented elsewhere (S. T. Emlen, "Experimental analysis of celestial orientation in a nocturnally migrating bird"; Ph.D. dissertation, Univ. Michigan, 1966).

The footprint records were quantified in the manner described by Emlen and Emlen (1966) and all results obtained from one individual bird under one specific set of experimental conditions were combined and presented in the form of a vector diagram. The null hypothesis of randomness was tested for each set of data and the mean direction, ϕ, and mean angular deviation, s, were calculated by vector analysis (see Part I).

In addition to this purely descriptive analysis, I have here compared the directional behavior of buntings tested under different experimental conditions. This was done by using a modification of the Mann-Whitney U test adapted for circular statistics (Batschelet, 1966: 37–38). Since consecutive jumps by an individual bird in a test cage certainly do not represent independent units of information, only one point from each data distribution, the mean direction, was used in these analyses. The sample size in these tests was therefore equal to the number of birds tested under the experimental conditions in question.

Herein, orientation data are presented in both tabular (see appendices) and diagrammatic form. Throughout, 0° or 360° represents north, 90° is east, 180° is south, and 270° is west.

RESULTS AND DISCUSSION

The Role of the Internal Clock

As a result of the earth's rotation, there is an apparent motion of stars across the sky at 15° per hour relative to the celestial axis. Consequently, the altitude and azimuth positions of stars, as well as the specific stars present in the sky, change greatly during the course of a night.

To determine whether these changes affected the orientation of caged Indigo Buntings, I re-analyzed the results obtained under the natural night sky during the autumns of 1964 and 1965 (discussed in Part I [Emlen, 1967]). These outdoor tests were performed from soon after sunset until just before sunrise. During the first season, three separate tests were regularly conducted each night: 2000–2200; 2300–0100; and 0200–0400 hours. In 1965, the nightly schedule included two tests: 2030–2400 hours and 0030–0400 hours. When the results obtained at these different times were compared (Figures 1 and 2; Appendices 1 and 2), no significant

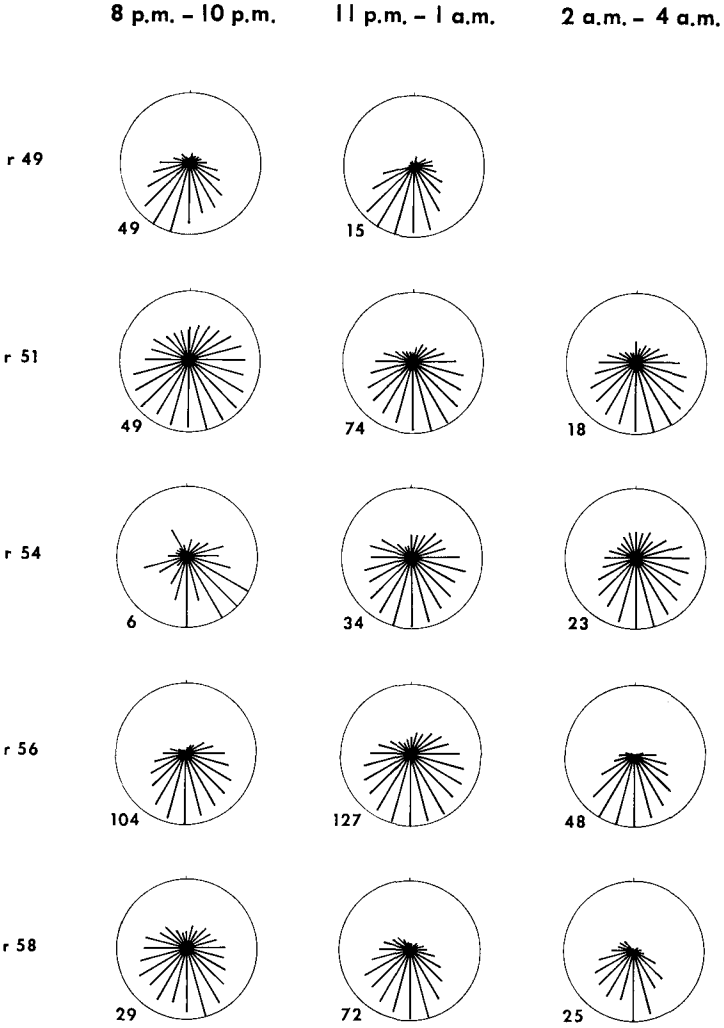**8 p.m. - 10 p.m.   11 p.m. - 1 a.m.   2 a.m. - 4 a.m.**

Figure 1. *Zugunruhe* orientation under the natural night sky analyzed as a function of time of night; autumn, 1964. Here and in other figures, the number at the lower left of each diagram represents the greatest number of units of activity in any one 15° sector.

directional changes appeared. Similar constancy of direction was obtained during planetarium experiments conducted at different times of night.

These findings imply that the buntings are not merely responding photo-tactically to individual bright stars or to general patterns of brightness in the night sky. Rather they are suggestive of a reliance upon a time-

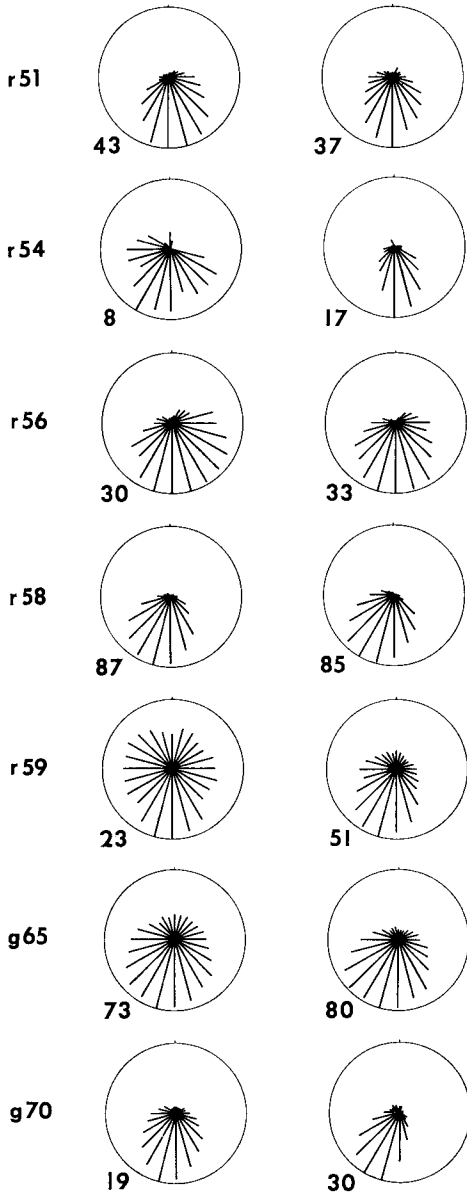## 8:30 p.m. – 12:00   12:30 a.m. – 4 a.m.

Figure 2. *Zugunruhe* orientation under the natural night sky analyzed as a function of time of night; autumn, 1965.
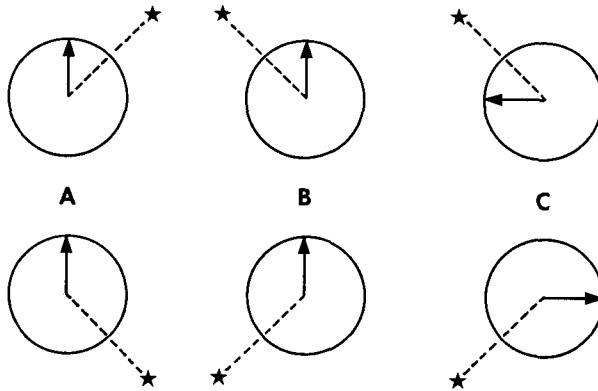
Figure 3. Expected shift in orientation following resetting of the internal clock six hours behind local time, and assuming compensation for motion of a star located in the northern sky (upper diagrams), or in the southern sky (lower diagrams). "A" represents normal orientation early in the evening when 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.

compensating orientational system analogous to the diurnal sun-compass hypothesis proposed by Kramer (1951: 279, 1957: 209–223), Hoffmann (1954, 1960), Schmidt-Koenig (1958, 1961), and others. Such a hypothesis assumes the possession of an internal time-sense, or "clock," which enables the bird to alter its angle of orientation relative to the sun's (or star's) position at a rate which compensates for the movement of the celestial object through the sky.

The requirements for such a system to be operative at night, however, are more demanding than those necessary for diurnal, solar orientation. Instead of one obvious celestial object, many potential cues are available in the night sky and a bird must be able to locate consistently the specific one, or ones, of importance. In addition, the necessary rate of compensation will differ depending upon the specific star or stars employed. A star located near Polaris (the North Star), for example, moves through a much smaller arc than one which culminates in the zenith. Consequently, if a bird were to use several stellar cues of different declinations, the compensation rates would have to be varied accordingly. Alternatively, one might expect nocturnal migrants to exhibit a constant azimuth compensation of approximately 15° per hour, similar to that reported for numerous diurnal species (Kramer and St. Paul, 1950; Kramer and Reise, 1952;
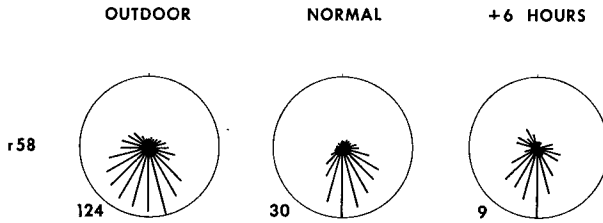
OUTDOOR   NORMAL   +6 HOURS

Figure 4. *Zugunruhe* orientation under a sky advanced six hours from local time compared with results obtained under "normal" planetarium conditions (43° N) and out-of-doors; autumn, 1964.

Kramer, 1953; Hoffmann, 1953, 1954, 1960; St. Paul, 1953, 1956; Matthews, 1955, 1963; Schmidt-Koenig, 1958, 1961; Graue, 1963). Accuracy of the directional response could then be maintained only if the cues used were restricted to the band of stars characterized by an azimuth motion approximating 15° per hour. Finally, the actual *direction* of this compensation varies, being clockwise for stars located in the northern sky and counterclockwise for those to the south (Figure 3).

Experiments.—The importance of temporal compensation to the orientation process can be tested experimentally by creating an artificial situation in which the bird's internal time sense is out of phase with astronomical time. In studies of the sun-compass mechanism, the internal clock is frequently altered by subjecting the experimental birds to appropriately shifted light-dark regimens (e.g., Hoffmann, 1954; Schmidt-Koenig, 1958). With the nocturnally active Indigo Buntings, I was able to achieve the same effect of desynchronization by altering the astronomical time. This was accomplished in the planetarium by rotating the celestial sphere about its axis, thereby presenting artificial skies advanced or retarded from local time. If the time sense is an essential component of this orientation system, a shift in mean direction of orientation should result under these conditions. The extent of this deviation will depend upon which star(s) are used, the amount approaching 15° per hour if the critical cues are located near the celestial equator.

The first experiment of this type was conducted in the fall of 1964. One bird, r58, was exposed to a planetarium sky adjusted for local date (17 November) and latitude (43° N) but advanced six hours from local time. As seen from Figure 4 (and Appendix 3) a westerly shift occurred relative to results previously obtained under planetarium-normal conditions, but not relative to those observed out-of-doors. If these results are to be interpreted as evidence for a clock-correlated mechanism, the compensation rate must be exceedingly slow. Such a mechanism could be

−3 HOURS   **NORMAL**   **+3 HOURS**

g 77

26   86   39

g 63

44   92   31

b 43

11   65   26

g 74

5   23   8

g 71

5   26   6
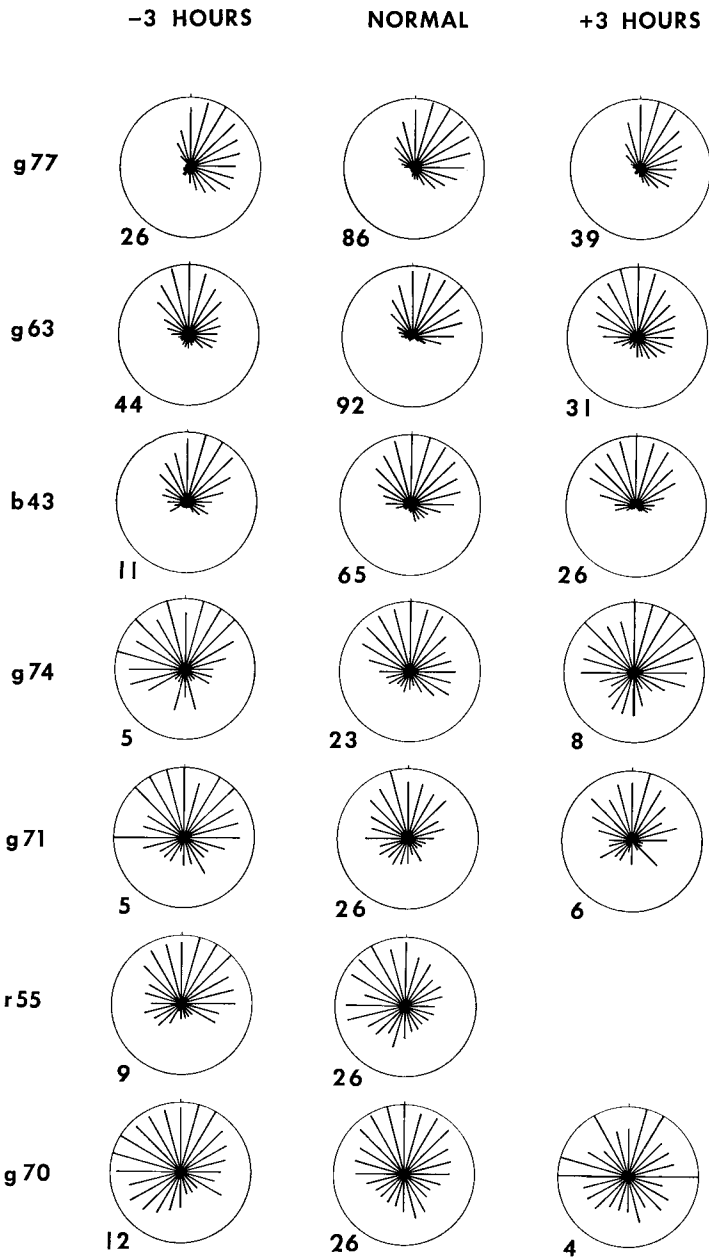
r 55

9   26

g 70

12   26   4

Figure 5. *Zugunruhe* orientation under temporally shifted skies (± 3 hours) compared with results obtained under "normal" planetarium conditions (28° N); spring, 1965.

functional, of course, only if the critical stars were located close to the celestial poles.

To test this further, a more extensive series of experiments under temporally-shifted skies was conducted in the spring of 1965. Throughout the series, the planetarium date was set at 1 May and the latitude at 28° N (south of the breeding range of the species). The eight buntings which oriented their *Zugunruhe* under planetarium-normal conditions this season (Emlen, 1967) were now exposed to artificial skies 3, 6, and 12 hours out of phase with local time.

To achieve a three-hours-advanced condition, I tested birds between 2000 and 2300 hours under skies normally present between 2300 and 0200 hours. The converse situation, three-hours-retarded, was obtained by testing birds in just the reverse manner. Each experiment was repeated on three different nights.

Neither the seven birds active under retarded skies (r55, b43, g63, g70, g71, g74, and g77) nor the six individuals providing data under advanced skies (all of the above except r55) significantly altered their directional tendencies relative to their behavior under planetarium normal conditions (p > .3) (Figure 5; Appendix 4). Even if the birds relied upon stellar cues located very near the celestial axes with slow rates of azimuth movement, one would expect slight, *consistent*, changes in direction. But, of nine individual instances where minor deviations did occur (averaging roughly 5° per hour), only five were in the directions predicted (r55, g71, and g77 in column 1, and b43 and g63 in column 3, Figure 5). The remaining four deviations (g63, g70, and g74 in column 1, and g71 in column 3) would be explainable only by assuming a counterclockwise compensation rate approximating 5° per hour. Stars fitting this description are located near the southern celestial pole and were never visible during these experiments. Consequently, these results fail to support any hypothesis involving temporal compensation for celestial motion.

Skies advanced and retarded by six hours were also presented to the buntings. Of these two conditions, the former consisted of exposure to a 0500–0730 hours sky when the local time was 2300–0130; testing birds from 2100–2300 hours under skies set for 1500–1700 constituted the latter.

A comparison of the orientation exhibited under these conditions and that obtained under normal planetarium skies again revealed no significant difference (p > .3) (Figure 6; Appendix 4). In general, the birds continued to maintain their normal migratory directions. Where slight deviations did occur, they were neither consistently easterly nor westerly.

However, closer, qualitative examination showed sizeable directional shifts in three instances (g77 in column 1, b43 and g74 in column 3,

−6 HOURS   NORMAL   +6 HOURS   +12 HOURS

g 77

9   86   18   21

g 63

22   92   18   32

b 43

7   65   9

g 74

6   23   4

g 70

6   26   8   8

r 52

6   40
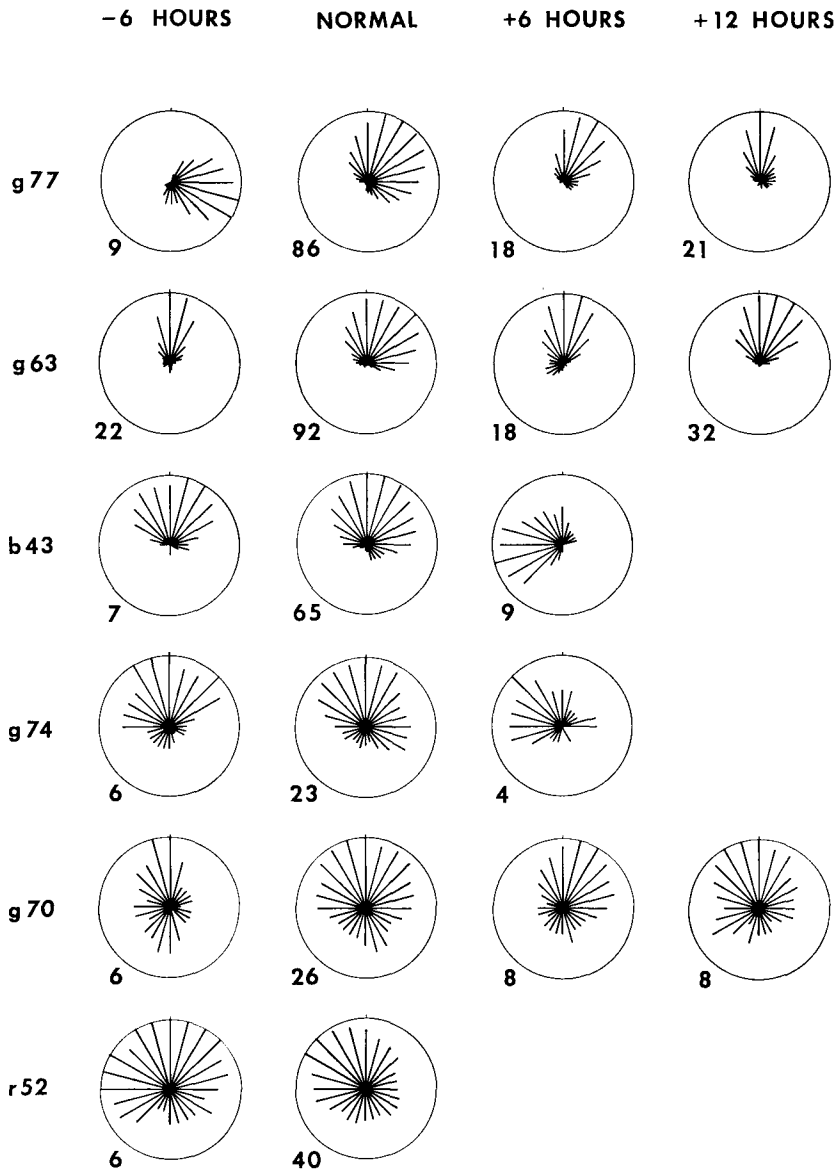
Figure 6. *Zugunruhe* orientation under temporally shifted skies (± 6 and 12 hours) compared with results obtained under "normal" planetarium conditions (28° N); spring, 1965.

Figure 6). Moreover, these shifts were in the direction and of the approximate magnitude (65°, 92°, and 59°, respectively) predictable assuming a clockwise compensation of 10° to 15° per hour and a reliance upon stellar cues in the northern sky. If these behavioral responses are meaningful, it would imply that Indigo Buntings possess the ability to compensate for the motion of certain stars. But over-emphasis should not be placed upon isolated cases. In the great majority of the experiments, the buntings, including b43, g74, and g77, continued their normal, northerly, orientation. Consequently, this compensating ability, if present, generally was not employed.

The final experiments in this series consisted of presenting buntings with a sky advanced 12 hours from local time (the test being conducted from 2100–2300 hours under a sky set for 0900–1100). Under these conditions three birds were active, g77 shifting its orientation from northeast to north, and g63 and g70 continuing their northward tendencies.

To summarize, no statistically significant directional changes occurred when Indigo Buntings were exposed to planetarium skies 3, 6, and 12 hours advanced and retarded from local time. Qualitative examination of each individual case further revealed that the buntings generally maintained their normal migratory orientation in 25 out of the 28 experiments conducted under such time-shifted artificial skies. This strongly suggests that temporal compensation for stellar motion is *not* an essential component in the migratory orientation mechanism of this species.

Discussion.—These findings contrast with results reported by Sauer (1957) and Sauer and Sauer (1960) who studied the nocturnal orientation of European warblers of the genus *Sylvia*. The Sauers performed time-shift experiments with one Lesser White-throat, *S. curruca*, and two Blackcaps, *S. atricapilla*, under the artificial skies of a small Zeiss planetarium. When tested during the autumn under planetarium skies advanced one to four hours relative to local time, the Lesser White-throat (1957: 56–58) and one Blackcap (1960: 466–470) oriented in a westerly, rather than the normal, southerly, direction. The amount of these deviations was commonly far greater than 15° per hour, but the shifts do suggest a counterclockwise allowance for celestial motion. (This would imply that the warblers were using stellar cues located in the *southern* sky.) Results obtained under retarded skies were rather ambiguous and their biological significance is unclear (Sauer, 1957; Sauer and Sauer, 1960; Wallraff, 1960*a*, *b*).

These results led the Sauers to assign an important orientational role to the internal clock (Sauer, 1957, 1961; Sauer and Sauer, 1960). Sauer further stated (1961: 241–242): "Old World warblers of the genus *Sylvia* do not simply rely on a star-compass. They rather apply their visual

orientation to a grid of two celestial coordinates, azimuth and altitude or hour angle and declination." Such a bicoordinate navigational system could enable birds to determine their geographic location since azimuth or hour angle, coupled with an accurate time sense, could provide longitudinal information, and altitude or declination of a particular star could likewise indicate latitude. The westerly shifts of the sylviids noted under advanced skies might then represent goal-directed compensatory flights toward the wintering ground since the advanced sky at the test longitude could be interpreted as the normal sky at some geographic location to the east. The evidence for this hypothesis, however, has been criticized severely by Wallraff (1960a, b).

Experimental evidence suggesting a bicoordinate navigational ability in the Indigo Bunting is entirely lacking, although the possibility that buntings can determine latitude cannot be ruled out (Emlen, 1967). According to Sauer's hypothesis, skies three- and six-hours advanced or retarded should be interpreted as representing longitudinal displacements of 45° and 90° (3,000 and 6,000 miles at the test latitude of 28° N), respectively. Yet the buntings did not orient in the predicted, goal-oriented direction. It is difficult to imagine how a bird could detect a longitudinal displacement unless it made use of an accurate internal clock rigidly set on home time, and for Indigo Buntings such a time sense does not appear to play an essential role in migratory orientation.

The Importance of Stellar Patterns

Without time-compensation, no *single* star (with the exception of Polaris) can provide sufficient information to allow a bird to maintain a given direction through time. But additional potential information is provided by the presence of numerous stars in the sky and by the constant, two-dimensional, spatial relationships which exist between them. This configurative nature of star positions permits our recognition of specific stellar groupings known as constellations. For example, the Big Dipper, Ursa Major, is easily located by the characteristic spatial pattern of its seven component stars. And, by visually extending the pouring line of the dipper, we can readily locate Polaris, hence geographic north. As long as this *pattern* is visible, we can determine north *regardless of the time of night*, the season, or our geographic location (see Figure 7).

I propose that Indigo Buntings are able to determine their migratory direction in a similar manner, by responding to the *Gestalt* stimuli provided by the patterning of stars. Since each star bears a fixed geometric relationship with all others, it is theoretically possible to obtain directional information from an infinite number of configurations. Such a mechanism operates entirely independently of any time sense and there-
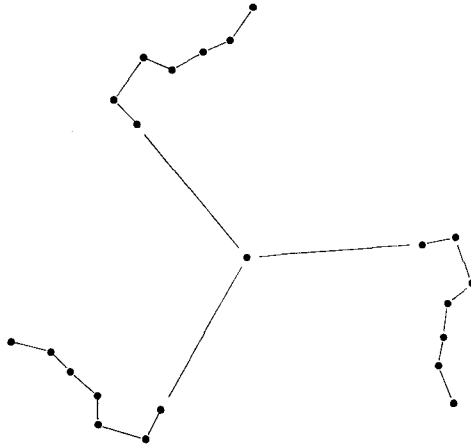
Figure 7. Fixed configurative relationship between Polaris and Ursa Major. Star patterns of this type could provide consistent directional information regardless of the temporal position of the sky.

fore is consistent with the results obtained in the shifted-sky experiments.

This hypothesis is similar to that reached by Matthews (1963), who studied the basis of "nonsense" orientation in Mallards, *Anas platyrhynchos*. When he artificially shifted the ducks' time sense by exposing them to light-dark cycles advanced or retarded 6 and 12 hours, this in no way altered their orientation behavior when released out-of-doors. This led Matthews to state (1963: 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 the star *patterns*, possibly using the same constellations as we do ourselves."

As a second step toward understanding this mechanism of celestial orientation, I attempted to learn *which* stellar patterns were of particular importance to the buntings.

Since the birds maintained their normal, migratory directions regardless of the temporal position of the sky (Figures 4, 5, and 6), we must assume that ample celestial information was always present. This suggests that either several different star patterns were used by the birds (at least one being available in each of the skies presented), or the essential cues were circumpolar in location.

I therefore conducted a series of experiments in which selected stellar configurations or portions of the planetarium sky were artificially blocked

POLARIS AND
NORMAL   SOUTH OFF   POLARIS OFF   URSA MAJOR
OFF

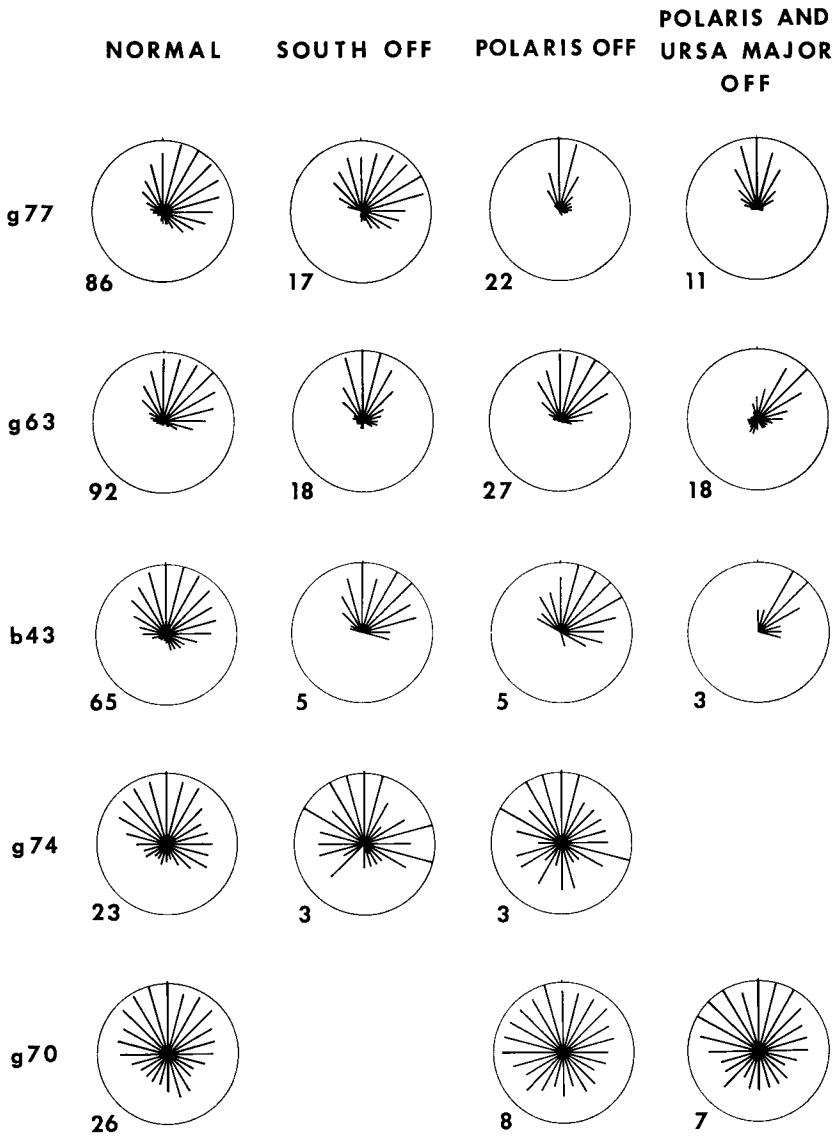Figure 8. *Zugunruhe* orientation under partially blocked skies, compared with results obtained under "normal" planetarium conditions (28° N); spring, 1965.

from view. Throughout these tests, stars with altitudes under 30° to the north and 15° to the south were never visible because of the funnel shape of the test cage itself and the off-center position of the birds in the planetarium (see Emlen, 1967: figure 4).

Experiments during the spring migration season.—During northward migration, Indigo Buntings depart from Central America under a sky in which Polaris is located at an altitude of 10°–20° and stars 75° south of the celestial equator are just visible on the southern horizon. As the birds continue northward, the altitude of Polaris increases until, at the breeding areas, it has reached an elevation of 30°–45°, while stars with declinations exceeding 45°–60° S have disappeared from view (Emlen, 1967: figure 1).

To test the importance of southern stars, birds which previously had demonstrated northerly tendencies were presented with a planetarium sky adjusted for local conditions of 28° N latitude but with only the northern celestial hemisphere projected. This was accomplished by shutting off the lamp which projects the entire southern half of the sky. In this situation all four active birds (b43, g63, g74, and g77) continued to exhibit northward preferences (Figure 8, column 2; Appendix 5), indicating that stars in the southern hemisphere were not essential for orientation. The converse experiment, testing buntings with the northern sky turned off, failed to produce conclusive results since all birds ceased activity under these conditions.

As discussed previously, there is only one star which, by itself, could provide consistent directional information irrespective of the passage of time; that star is Polaris, located at the north celestial axis. Yet when the North Star was selectively blocked by covering its projection lens with several layers of masking tape, all birds tested (b43, g63, g70, g74, and g77) continued to display northerly tendencies (not statistically significant for g74) (see column 3 of Figure 8, and Appendix 5).

This finding, that Polaris is not essential for correct orientation, is strengthened by results reported in Part I of this publication. Three buntings, r52, r55, and b43, were tested in mid-April under planetarium normal conditions set for 15° N, the latitude of Guatemala in the wintering range of the species. Each of these birds was able to orient in the spring migration direction (Emlen, 1967: figure 11) although at this planetarium setting the North Star and its near neighbors would not have been visible.

The seasonal rotation of the celestial sphere is such that during the late evenings of spring, Ursa Major is near its culmination. Since this constellation contains some of the brightest stars in the northern sky, an experiment was conducted in which the eight stars of both Polaris and Ursa Major were blocked from view. The results show that this manipulation of the planetarium sky was again without effect upon the behavior of the buntings; all four active birds continued to orient their *Zugunruhe* to the north (Figure 8, column 4; Appendix 5).

To summarize, it appears that during the spring migration flight, the

NORMAL   SOUTH OFF   CASSIOPEIA OFF   MILKY WAY OFF

r54

79   14   20   0

r56

13   13   6   2

r58

34   20   15   12

g65

14   13   0

g70

*16   14   20
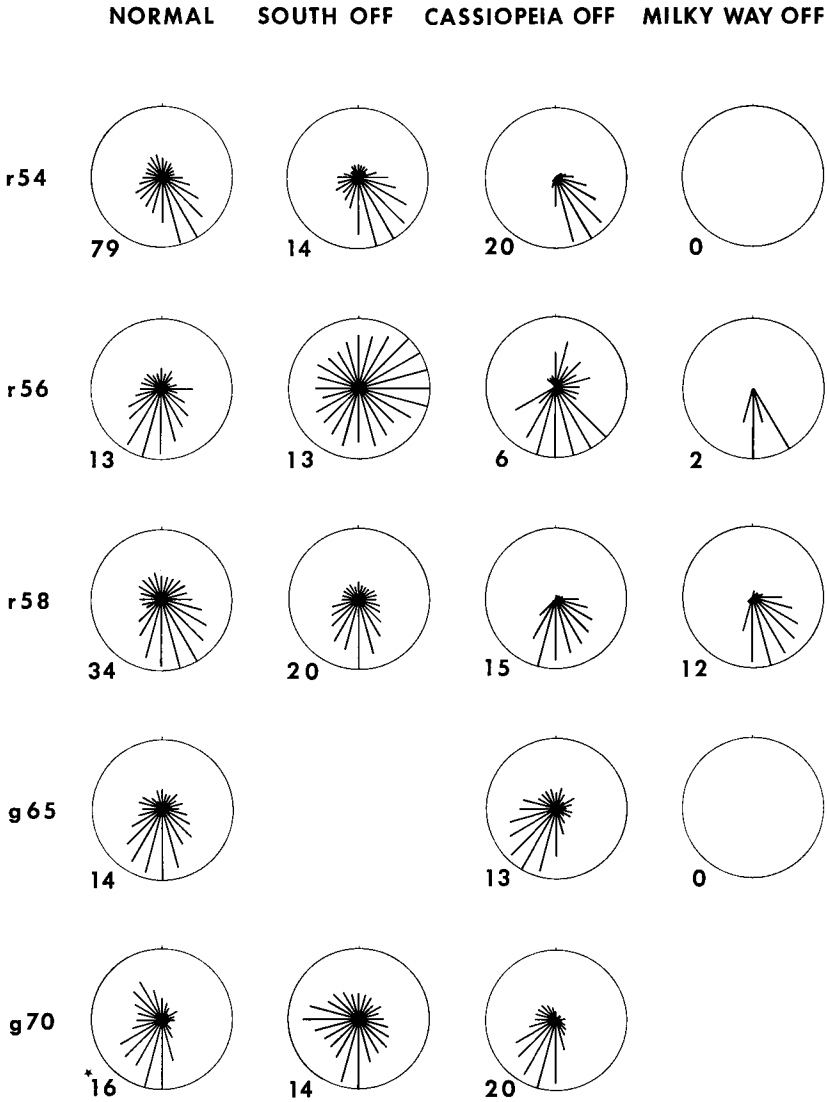
Figure 9. *Zugunruhe* orientation under partially blocked skies, compared with results obtained under "normal" planetarium conditions (35° N); fall, 1965.

northern sky is sufficient to allow direction determination. Attempts to localize further the specific patterns employed failed. Neither the Big Dipper nor the North Star was essential for orientation. This does not necessarily mean, however, that these stars may not be important cues.

It merely indicates that sufficient directional information is present in their absence.

Experiments during the autumn migration season.—A more extensive series of blocking experiments was conducted in the fall of 1965 using birds which exhibited a clear migratory orientation both in the planetarium and out-of-doors. During these tests the planetarium sky was set for 1 October and 35° N latitude; the time element varied between 2130 and 0330 hours but was always synchronous with local time.

Since the normal migration direction in autumn is southward, I was interested in learning whether the important stellar cues were likewise located in the southern sky. Consequently I exposed these buntings to a sky containing only northern celestial hemisphere stars. Under these conditions one bird, r56, failed to orient, its *Zugunruhe* being random. The remaining three individuals (r54, r58, and g70), however, continued to demonstrate southerly preferences (Figure 9, column 2; Appendix 6). These results suggest that (1) individual variation exists with regard to the specific stellar cues used by different buntings, and (2) the northern sky again provided sufficient information for the orientation of the latter three birds.

One prominent northern constellation which nears its culmination in the late evenings of autumn is Cassiopeia. However, elimination of this pattern of stars did not seriously alter the behavior of the buntings. Neither did the removal of the Milky Way from the artificial sky (Figure 9; Appendix 6).

I must reiterate the need for exercising caution in interpreting results of this kind. Continued orientation in the absence of a particular star pattern is not necessarily evidence for the unimportance of that pattern. If a bird were familiar with a large portion of the night sky, removal of one group of stars might merely force it to rely upon some alternate constellation. I therefore performed a series of experiments in which entire portions of the northern sky were blocked from view.

One such test involved blocking all of the area within a 35° radius of Polaris, thereby eliminating all northern circumpolar stars. Besides Polaris, this included the constellations of Ursa Major, Ursa Minor, Cassiopeia, Cepheus, and Draco, as well as a significant portion of the Milky Way (see Figure 10). In this situation, the *Zugunruhe* orientation of two birds, r54 and g65, became random, while that of another, r56, deteriorated considerably. Only one individual, r58, continued southward and its direction shifted from south-southeast to southwest (Figure 11, column 2; Appendix 6).

These results support the hypothesis that different individual buntings rely upon different stellar information. Equally important, they demon-
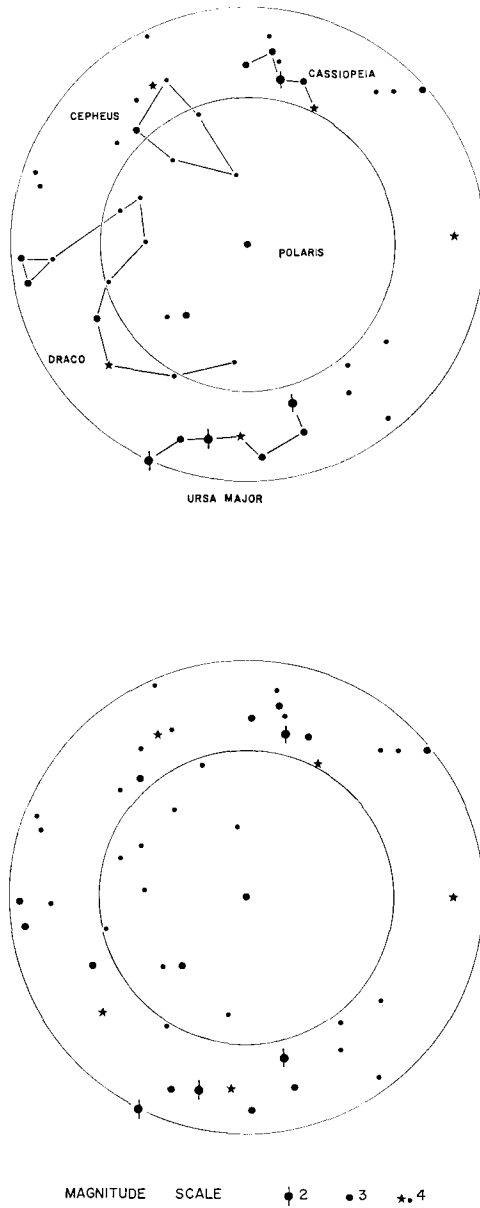
Figure 10. Polar azimuthal equidistant projections of the northern circumpolar sky within 35° of Polaris. The inner circle represents an area within 25° of Polaris.
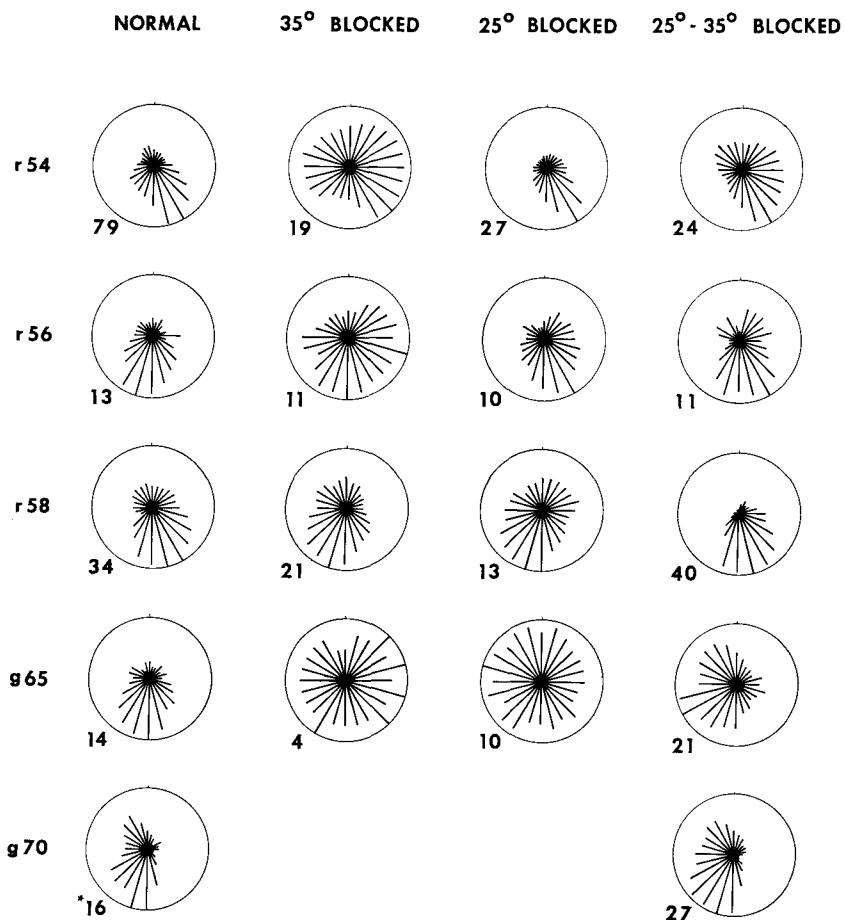
Figure 11. Additional results under partially blocked skies, compared with data obtained under "normal" planetarium conditions (35° N); fall, 1965.

strate that the entire sky other than that within 35° of Polaris did not contain sufficient celestial cues to enable r54 or g65 to aim southward; the specific stars or star patterns *essential* for their orientation were located within this area. In the case of r56, accurate orientation was apparently dependent upon some information within this 35° circle. But other cues, presumably in the southern sky (see Figure 9), enabled it to assume a weak orientation in the absence of circumpolar stars. Finally, r58 appeared able to rely entirely upon non-circumpolar information. As a result of this individual variation, the behavior of each bird must be considered separately.

An examination of Figure 10 reveals that most low magnitude (bright) stars within the circumpolar area are located in a band between 25° and 35° from Polaris. This doughnut-shaped zone contains all of Ursa Major, Cassiopeia, and the major stars of Draco and Cepheus. Consequently, in another experiment, these bright stars were projected while the circular area within 25° of the North Star was blocked. As shown in column 3 of Figure 11, this resulted in a general improvement in orientational responses, with r54, r56, and r58 aiming their *Zugunruhe* southward. (The directions taken by r56 and r58 continued to be shifted relative to their behavior under normal planetarium skies.) Only g65 continued to be random.

One might conclude that it is indeed the bright stars within this 10° band which were essential for accurate direction determination by r54 and r56. But when the "converse" experiment was conducted in which these major stars were selectively eliminated and the 25° circle projected, the birds continued to orient southward (again with the exception of g65). In this experiment, all second- and third-order magnitude stars within the 25°–35° zone were blocked as well as those of fourth magnitude indicated by "stars" in Figure 10. Dimmer stars were not obstructed. Yet r56, r58, and g70 all displayed southerly tendencies, while r54 oriented to the east-southeast (Figure 11, column 4; Appendix 6).

These experiments suggest that adequate directional information for r54 was present in both the inner and outer portion of the circumpolar area. This, in turn, suggests that two or more groupings of stars could be relied upon. For g65, the removal of either portion prohibited correct orientation. Possibly this indicates a critical celestial pattern which overlaps both zones, in which case the necessary *Gestalt* stimulus would not be provided by either area alone.

I wish to emphasize, however, that in light of the great amount of variation in these data and the small sample size of birds, these interpretations must be considered as highly speculative.

(The results of the blocking experiments furnish additional, indirect, evidence relating to the role of the internal clock. If buntings employed a time-compensating mechanism of celestial orientation, "optimal" cues presumably would be those possessing an azimuth motion approximating 15° per hour, an approximation not applicable to circumpolar stars. Such "optimal" cues are located near the celestial equator and were visible throughout the blocking experiments. The general deterioration of orientation occurring when certain northern areas were blocked can only be interpreted as indicating that such equatorial cues generally were not used by the buntings.)

SEASONAL REVERSAL OF MIGRATION DIRECTION

Since the sidereal (stellar) day is approximately four minutes shorter than the solar day, a fact caused by the earth's rotation around the sun, the stars visible overhead at any one time of night will vary with the season. Consequently, when presenting birds with skies six hours retarded or advanced relative to local time, one is actually presenting the skies typical of seasons three months earlier or later: winter and summer, respectively. The Sauers performed such an experiment with one Lesser White-throat (Sauer, 1957: 54–56) and one Blackcap (Sauer and Sauer, 1960: 466–470) and reported that both birds were completely disoriented under these skies characteristic of non-migratory seasons. A 12-hour shift yields a sky typical of the opposite migration season. The Sauers (1957, 1960), testing three Blackcaps, one Lesser White-throat, and one Garden Warbler, *Sylvia borin*, under these conditions found that each bird displayed a bimodal orientation between north and south, perhaps indicative of a conflict between antagonistic migratory drives. This suggests that sylviids may possess a specific northward directional response to the stellar stimuli of the spring night sky, and a different, southerly, response to the different stellar stimuli present in the autumn sky. Similarly, summer and winter skies might not contain essential celestial cues and, hence, would not elicit directional behavior.

The responses of Indigo Buntings under skies shifted 6 and 12 hours were entirely different. Neither disorientation nor conflict behavior generally was observed. In fact, the tendency to maintain the normal spring migration direction under all these conditions (Figure 6) indicates that the stellar information necessary for northward direction determination was present *regardless* of the temporal position of the sky (through the full 360° rotation). I therefore hypothesize that the celestial stimuli present in different seasonal skies do not specify which migration direction an Indigo Bunting will select. Rather, the north-south reversal between spring and fall migration may depend on physiological changes in the birds. This hypothesis should be easily testable by artificially inducing vernal migratory restlessness and then examining directional tendencies under autumn skies, and vice versa. (Studies of this nature are currently being initiated.)

(The differences apparent in the orientational mechanisms of sylviids and Indigo Buntings should serve as a warning against over-generalization between species. Migratory behavior has undoubtedly evolved independently many times in the class Aves, and it is not unreasonable to assume that different groups may have developed different means of solving the problems of long-distance orientation.)

SUMMARY

The *Zugunruhe* orientation of caged Indigo Buntings was tested under artificially manipulated planetarium skies during the fall of 1964 and the spring and fall of 1965.

When exposed to skies advanced and retarded 3, 6, and 12 hours from local time, the buntings generally continued to maintain their normal migration direction. This implies that the birds were not relying upon a bicoordinate celestial navigation system; neither were they employing a form of time-compensation analogous to that proposed in sun-compass orientation. Rather, it is hypothesized that the birds make use of additional information provided by the existence of numerous stars and by the constant, two-dimensional, spatial relationships which exist between them; they determine the migration direction by responding to *Gestalt* stimuli provided by star *patterns*.

Attempts to determine which configurations are of especial importance met with only partial success. Although considerable variation seems to exist in the specific cues used by different individual buntings, results of blocking experiments generally indicated that the northern celestial sky was especially important during both migration seasons. Both theoretical considerations and empirical evidence further suggested that the circumpolar area within 35° of the North Star may be important if not essential to this orientation process. More detailed conclusions must await further experimentation on a larger sample of birds.

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APPENDIX 1

ZUGUNRUHE ORIENTATION UNDER THE NATURAL NIGHT SKY ANALYZED AS A FUNCTION
OF TIME OF NIGHT: AUTUMN, 1964 (SEE FIGURE 1)

Bird	Experiment	Hours tested	Hours active	Mean direction	Angular deviation
r49	outdoors:				
	2000–2200	17h 30m	15h 30m	192°	58°
	2300–0100	7h 0m	5h 0m	185°	52°
	0200–0400	0h 0m	0h 0m	—	—
r51	outdoors:				
	2000–2200	23h 30m	16h 30m	168°	74°
	2300–0100	27h 20m	22h 20m	171°	65°
	0200–0400	12h 0m	10h 0m	173°	66°
r54	outdoors:				
	2000–2200	27h 30m	8h 0m	150°	65°
	2300–0100	26h 20m	22h 20m	174°	70°
	0200–0400	14h 0m	12h 0m	157°	70°
r56	outdoors:				
	2000–2200	27h 30m	23h 30m	169°	68°
	2300–0100	28h 20m	24h 0m	168°	58°
	0200–0400	14h 0m	12h 0m	176°	47°
r58	outdoors:				
	2000–2200	16h 0m	12h 0m	189°	70°
	2300–0100	26h 20m	22h 20m	194°	60°
	0200–0400	12h 0m	6h 0m	197°	51°

APPENDIX 2

ZUGUNRUHE ORIENTATION UNDER THE NATURAL NIGHT SKY ANALYZED AS A FUNCTION
OF TIME OF NIGHT: AUTUMN, 1965 (SEE FIGURE 2)

Bird	Experiment	Hours tested	Hours active	Mean direction	Angular deviation
r51	outdoors:				
	2030–0000	21h 30m	14h 30m	165°	51°
	0030–0400	10h 0m	10h 0m	186°	56°
r54	outdoors:				
	2030–0000	26h 40m	26h 40m	198°	56°
	0030–0400	6h 30m	3h 0m	173°	40°
r56	outdoors:				
	2030–0000	30h 10m	30h 10m	161°	59°
	0030–0400	10h 0m	10h 0m	174°	55°
r58	outdoors:				
	2030–0000	32h 40m	25h 20m	196°	41°
	0030–0400	10h 0m	10h 0m	204°	42°
r59	outdoors:				
	2030–0000	15h 0m	13h 30m	204°	76°
	0030–0400	7h 0m	7h 0m	207°	65°
g65	outdoors:				
	2030–0000	28h 50m	28h 50m	195°	70°
	0030–0400	10h 0m	10h 0m	196°	62°
g70	outdoors:				
	2030–0000	25h 10m	21h 10m	191°	57°
	0030–0400	6h 30m	3h 0m	213°	48°

APPENDIX 3

ZUGUNRUHE ORIENTATION UNDER A SKY ADVANCED SIX HOURS FROM LOCAL TIME COMPARED
WITH RESULTS OBTAINED UNDER "NORMAL" PLANETARIUM CONDITIONS (43° N)
AND OUT-OF-DOORS: AUTUMN, 1964 (SEE FIGURE 4)

Bird	Experiment	Hours tested	Hours active	Mean direction	Angular deviation
r58	outdoors	54h 20m	40h 20m	195°	62°
	planetarium: normal	11h 10m	5h 40m	161°	53°
	planetarium: six hours advanced	1h 30m	1h 30m	200°	62°

APPENDIX 4

ZUGUNRUHE ORIENTATION UNDER TEMPORALLY SHIFTED SKIES COMPARED WITH RESULTS
OBTAINED UNDER "NORMAL" PLANETARIUM CONDITIONS (28° N), SPRING, 1965
(SEE FIGURES 5 AND 6)

Bird	Experiment	Hours tested	Hours active	Mean direction	Angular deviation
g77	planetarium (28° N): 6 hours retarded	2h 30m	2h 30m	109°	46°
	planetarium (28° N): 3 hours retarded	5h 0m	5h 0m	57°	59°
	planetarium (28° N): normal	11h 0m	11h 0m	44°	57°
	planetarium (28° N): 3 hours advanced	6h 15m	6h 15m	41°	57°
	planetarium (28° N): 6 hours advanced	2h 0m	2h 0m	33°	44°
	planetarium (28° N): 12 hours advanced	2h 0m	2h 0m	14°	49°
g63	planetarium (28° N): 6 hours retarded	2h 0m	2h 0m	7°	47°
	planetarium (28° N): 3 hours retarded	5h 0m	5h 0m	13°	62°
	planetarium (28° N): normal	8h 30m	8h 30m	27°	51°
	planetarium (28° N): 3 hours advanced	6h 15m	6h 15m	7°	67°
	planetarium (28° N): 6 hours advanced	2h 30m	2h 30m	349°	52°
	planetarium (28° N): 12 hours advanced	2h 0m	2h 0m	13°	40°
b43	planetarium (28° N): 6 hours retarded	2h 0m	2h 0m	11°	47°
	planetarium (28° N): 3 hours retarded	2h 30m	2h 30m	19°	60°
	planetarium (28° N): normal	14h 30m	14h 30m	18°	60°
	planetarium (28° N): 3 hours advanced	6h 15m	6h 15m	355°	53°
	planetarium (28° N): 6 hours advanced	2h 30m	2h 30m	286°	54°
	planetarium (28° N): 12 hours advanced	2h 0m	0h 0m	—	—
g74	planetarium (28° N): 6 hours retarded	2h 0m	2h 0m	353°	66°
	planetarium (28° N): 3 hours retarded	2h 30m	2h 30m	342°	69°
	planetarium (28° N): normal	24h 0m	11h 15m	10°	69°
	planetarium (28° N): 3 hours advanced	4h 15m	2h 30m	11°	73°
	planetarium (28° N): 6 hours advanced	2h 30m	2h 30m	311°	61°
	planetarium (28° N): 12 hours advanced	2h 0m	0h 0m	—	—
g70	planetarium (28° N): 6 hours retarded	2h 0m	2h 0m	random	—
	planetarium (28° N): 3 hours retarded	5h 0m	5h 0m	329°	73°
	planetarium (28° N): normal	16h 0m	11h 15m	356°	74°
	planetarium (28° N): 3 hours advanced	2h 0m	2h 0m	random	—
	planetarium (28° N): 6 hours advanced	2h 30m	2h 30m	33°	70°
	planetarium (28° N): 12 hours advanced	2h 0m	2h 0m	341°	71°

APPENDIX 4 (CONTINUED)

Bird	Experiment	Hours tested	Hours active	Mean direction	Angular deviation
g71	planetarium (28° N): 3 hours retarded	2h 30m	2h 30m	354°	71°
	planetarium (28° N): normal	25h 30m	21h 30m	343°	69°
	planetarium (28° N): 3 hours advanced	3h 45m	3h 45m	354°	66°
r55	planetarium (28° N): 3 hours retarded	5h 0m	2h 30m	12°	67°
	planetarium (28° N): normal	27h 30m	23h 0m	319°	72°
	planetarium (28° N): 3 hours advanced	2h 0m	0h 0m	—	—
r52	planetarium (28° N): 6 hours retarded	2h 0m	2h 0m	332°	73°
	planetarium (28° N): normal	21h 45m	14h 15m	330°	75°

APPENDIX 5

ZUGUNRUHE ORIENTATION UNDER PARTIALLY BLOCKED SKIES, COMPARED WITH RESULTS
OBTAINED UNDER "NORMAL" PLANETARIUM CONDITIONS (28° N), SPRING, 1965
(SEE FIGURE 8)

Bird	Experiment	Hours tested	Hours active	Mean direction	Angular deviation
g77	planetarium (28° N): normal	11h 0m	11h 0m	44°	57°
	planetarium (28° N): southern stars off	3h 0m	3h 0m	39°	48°
	planetarium (28° N): Polaris blocked	2h 0m	2h 0m	20°	40°
	planetarium (28° N): Ursa Major and Polaris blocked	2h 0m	2h 0m	356°	37°
g63	planetarium (28° N): normal	8h 30m	8h 30m	27°	51°
	planetarium (28° N): southern stars off	3h 0m	3h 0m	10°	51°
	planetarium (28° N): Polaris blocked	2h 0m	2h 0m	22°	42°
	planetarium (28° N): Ursa Major and Polaris blocked	2h 0m	2h 0m	51°	62°
b43	planetarium (28° N): normal	14h 30m	14h 30m	18°	60°
	planetarium (28° N): southern stars off	4h 0m	3h 0m	25°	42°
	planetarium (28° N): Polaris blocked	2h 0m	2h 0m	35°	47°
	planetarium (28° N): Ursa Major and Polaris blocked	2h 0m	2h 0m	48°	27°
g74	planetarium (28° N): normal	24h 0m	11h 15m	10°	69°
	planetarium (28° N): southern stars off	3h 0m	3h 0m	6°	70°
	planetarium (28° N): Polaris blocked	2h 0m	2h 0m	random	—
	planetarium (28° N): Ursa Major and Polaris blocked	2h 0m	0h 0m	—	—

APPENDIX 5 (CONTINUED)

Bird	Experiment	Hours tested	Hours active	Mean direction	Angular deviation
g70	planetarium (28° N): normal	16h 0m	11h 15m	356°	74°
	planetarium (28° N): southern stars off	0h 0m	0h 0m	- -	---
	planetarium (28° N): Polaris blocked	2h 0m	2h 0m	338°	76°
	planetarium (28° N): Ursa Major and Polaris blocked	2h 0m	2h 0m	347°	74°

APPENDIX 6

ZUGUNRUHE ORIENTATION UNDER PARTIALLY BLOCKED SKIES, COMPARED WITH RESULTS
OBTAINED UNDER "NORMAL" PLANETARIUM CONDITIONS (35° N), FALL, 1965
(SEE FIGURES 9 AND 11)

Bird	Experiment	Hours tested	Hours active	Mean direction	Angular deviation
r54	planetarium (35° N): normal	20h 30m	20h 30m	166°	67°
	planetarium (35° N): southern stars off	9h 30m	2h 30m	152°	74°
	planetarium (35° N): 35° circle blocked	3h 30m	3h 30m	random	—
	planetarium (35° N): 25° circle blocked	3h 30m	3h 30m	146°	66°
	planetarium (35° N): 25°–35° band blocked	7h 15m	3h 45m	118°	73°
	planetarium (35° N): Milky Way blocked	1h 15m	0h 0m	——	—
	planetarium (35° N): Cassiopeia blocked	2h 0m	2h 0m	140°	29°
r56	planetarium (35° N) normal	13h 0m	7h 30m	191°	66°
	planetarium (35° N): southern stars off	9h 30m	5h 0m	random	—
	planetarium (35° N): 35° circle blocked	3h 30m	3h 30m	152°	76°
	planetarium (35° N): 25° circle blocked	3h 30m	3h 30m	149°	70°
	planetarium (35° N): 25°–35° band blocked	7h 15m	3h 45m	147°	70°
	planetarium (35° N): Milky Way blocked	1h 15m	1h 15m	169°	16°
	planetarium (35° N): Cassiopeia blocked	2h 0m	2h 0m	149°	64°
r58	planetarium (35° N): normal	9h 30m	5h 30m	154°	70°
	planetarium (35° N): southern stars off	7h 0m	2h 30m	188°	66°
	planetarium (35° N): 35° circle blocked	3h 30m	3h 30m	219°	72°
	planetarium (35° N): 25° circle blocked	3h 30m	3h 30m	200°	75°
	planetarium (35° N): 25°–35° band blocked	7h 15m	7h 15m	150°	51°
	planetarium (35° N): Milky Way blocked	1h 15m	1h 15m	144°	37°
	planetarium (35° N): Cassiopeia blocked	2h 0m	2h 0m	160°	41°

APPENDIX 6 (CONTINUED)

Bird	Experiment	Hours tested	Hours active	Mean direction	Angular deviation
g65	planetarium (35° N): normal	4h 0m	4h 0m	189°	65°
	planetarium (35° N): southern stars off	7h 0m	0h 0m	—	—
	planetarium (35° N): 35° circle blocked	2h 0m	2h 0m	random	—
	planetarium (35° N): 25° circle blocked	3h 30m	3h 30m	random	--
	planetarium (35° N): 25°–35° band blocked	5h 45m	3h 30m	257°	72°
	planetarium (35° N): Milky Way blocked	1h 15m	0h 0m	—	—
	planetarium (35° N): Cassiopeia blocked	2h 0m	2h 0m	229°	65°
g70	planetarium (35° N): normal[1]	2h 15m	2h 15m	232°	67°
	planetarium (35° N): southern stars off	9h 30m	2h 30m	244°	75°
	planetarium (35° N): 35° circle blocked	0h 0m	0h 0m	—	—
	planetarium (35° N): 25° circle blocked	0h 0m	0h 0m	—	—
	planetarium (35° N): 25°–35° band blocked	7h 15m	5h 15m	246°	65°
	planetarium (35° N): Milky Way blocked	1h 15m	0h 0m	—	—
	planetarium (35° N): Cassiopeia blocked	2h 0m	2h 0m	217°	56°

[1] g70 was inactive under planetarium-normal conditions. These data represent results of the planetarium-reverse experiment (plotted with planetarium and stellar south coincident).