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MIGRATORY ORIENTATION IN THE INDIGO BUNTING, *PASSERINA CYANEA*

PART I: EVIDENCE FOR USE OF CELESTIAL CUES

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THE experimental analysis of the orientational cues used by nocturnally migrating birds originated with Kramer's (1949) discovery that caged Blackcaps (*Sylvia atricapilla*) and Red-backed Shrikes (*Lanius collurio*) would, under certain conditions, spontaneously orient their migratory activity or *Zugunruhe* toward the portion of the cage corresponding to the normal migration direction of the species. These preliminary studies were extended by Sauer (1957, 1961) and Sauer and Sauer (1960) who tested the directional responses of three sylviid species placed in cages under the natural night sky. The results indicated that some individuals consistently selected directions coincident with predicted migration routes; thus Sauer hypothesized that the birds were orienting by means of celestial cues. Additional experiments, performed under the artificial skies of a small planetarium, provided strong support for this idea.

Recently, several other species of nocturnal migrants have also been found to orient in "correct" migration directions when tested in circular cages out-of-doors (Merkel and Fromme, 1958; Mewaldt and Rose, 1960; Fromme, 1961; Hamilton, 1962*a, c*; Sauer, 1963; Mewaldt *et al.*, 1964; Emlen, 1967). Most of these studies have additionally shown that such orientation deteriorates or disappears entirely under heavily overcast skies, further suggesting a reliance upon celestial information.

There are, however, several instances in which nocturnal orientation appeared to be unaffected by overcast conditions (Kramer, 1949; Merkel and Fromme, 1958; Fromme, 1961; F. Bellrose, pers. comm.). This discrepancy in findings, coupled with recent evidence suggesting possible geomagnetic determination of *Zugunruhe* orientation (Merkel and Fromme, 1958; Fromme, 1961; Merkel *et al.*, 1964; Merkel and Wiltshko, 1965; Wiltshko and Merkel, 1965), prohibits one from accepting outdoor data as unconditional evidence for celestial orientation.

Attempts to repeat the Sauers' planetarium findings have been unsuccessful (P. H. Klopfer and K. Schmidt-Koenig, pers. comm.; H. G. Wallraff, 1965, pers. comm.; A. Wolfson, pers. comm.). In addition, Wallraff (1960*a, b*) has severely criticized Sauer's statistical analyses, claiming that many of the conclusions drawn are unjustified.

The question of celestial orientation therefore remains controversial, and the need for additional, well controlled experiments is self-evident.

METHODS AND CONDITIONS OF THE STUDY

The Indigo Bunting, *Passerina cyanea*, was selected as a promising species for intensive study because it is a moderately long-distance, nocturnal migrant which is easily maintained in captivity. The species breeds throughout the eastern United States, and winters in the Bahamas, southern Mexico, and Central America south to Panama (Figure 1). Actual distances traveled by different populations vary considerably, but individuals breeding in southern Michigan, where these studies were conducted, would have migratory flights of between 1,800 and 2,500 miles. Migration appears to proceed along a broad front, with some buntings funnelling through peninsular Florida and the Bahamas to the east (Sprunt, 1954: 453-454; Johnston, 1965) and through Mexico along the Gulf coast to the west (Lowery and Dalquest, 1951: 639; Loetscher, 1955: 46). The relative magnitude of these overland flights is incompletely known, but the frequency and dates of observation in the Gulf states, as compared with Mexico and Florida (Cooke, 1905: 5, 1911; Stevenson, 1957: 55, 74), as well as direct sightings of Indigo Buntings from boats crossing the Gulf (Frazar, 1881; J. C. Howell in Lowery, 1946: 187; Bullis, 1954), suggest that the migration route is primarily trans-Gulf, especially during the spring flight.

Capture and maintenance of experimental birds.—A total of 33 birds was obtained for use in these experiments (Table 1), the first 16 (Group I) being mist-netted near Ann Arbor, Michigan, in the late spring of 1964. These birds had completed their migration and consequently were not available for experimentation until the following autumn. An additional 17 buntings (Group II) were netted by Maurice Baker and Thomas Imhof at Dauphine Island on the Gulf coast of Alabama, in late April of 1965. These individuals, in the peak of migratory condition, were shipped air express to Ann Arbor within 24 hours.

During the summer and fall, the birds were maintained in a 6 × 9 × 6 foot outdoor aviary constructed of one-half inch hardware cloth and located in a large, undisturbed field on the University of Michigan Edwin S. George Reserve, 25 miles northwest of Ann Arbor. Shelter was provided at its northern end and food (white millet and canary seed with

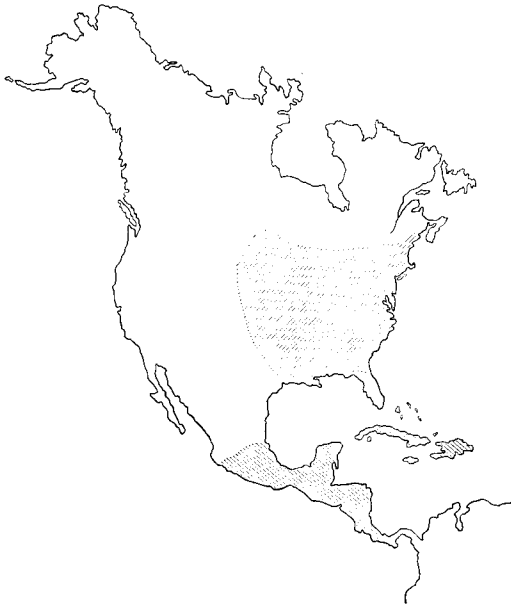


Figure 1. Breeding and wintering ranges of the Indigo Bunting, *Passerina cyanea*.

occasional lettuce greens) and water (with ABDEC liquid vitamins added weekly) were constantly available. Cuttlebone and mineralized grit were also provided. An additional $4 \times 8 \times 6$ foot aviary on the roof of the University of Michigan Museum of Zoology was occasionally employed to relieve crowding. All birds were thus exposed to normal photoperiods and weather fluctuations as well as to a continuous view of the sky.

After the fall experiments, in late October or early November, birds were transported to the winter quarters, a $4 \times 9\frac{1}{4} \times 8\frac{1}{2}$ foot, windowless, indoor room with semi-soundproof, white, masonry walls. Two banks of concealed fluorescent lights plus a 150-watt reflector floodlight furnished a light intensity of 25 to 300 foot-candles at perch levels. Food and water were again constantly available, and the photoperiod was maintained equivalent to that present in the wintering area at 15° N latitude. The birds therefore received the normal photoperiodic stimulation required to initiate prenuptial molt and pre-migratory fat deposition and to enter migratory condition on schedule in the spring.

Annual cycle.—In the autumn of 1964, the 16 birds in captivity (Group I) underwent postnuptial molts which were complete in all cases but 2 (r56 and r59). For 9 of the birds this occurred between early August and early October, while 7 individuals (r47, r50, r55, r56, r57, r59, and b42)

TABLE 1
HISTORIES OF BIRDS USED IN ORIENTATION EXPERIMENTS

<i>Bird</i>	<i>Sex</i>	<i>Age at capture</i> ¹	<i>Date of capture</i>	<i>Place of capture</i>	<i>Comments</i>
GROUP I					
r47	M	1st yr.	10 May 1964	Ann Arbor, Michigan	Sick: spring, 1965
r48	M	1st yr.	"	"	Died: 22 March 1965
r49	M	1st yr.	"	"	
r50	M	1st yr.	"	"	
r51	M	1st yr.	"	"	
r52	M	—	"	"	
r53	M	1st yr.	"	"	Sick: fall, 1965
r54	F	—	14 May 1964	"	Sick: spring, 1965
r55	M	2nd yr.	15 May 1964	"	Died: 1 July 1965
r56	M	1st yr.	"	"	
r57	M	2nd yr.	17 May 1964	"	Sick: fall, 1965
r58	M	1st yr.	23 May 1964	"	
r59	M	1st yr.	"	"	
w43	M	1st yr.	10 May 1964	Detroit, Michigan	Died: 12 June 1965
b42	M	1st yr.	"	"	
b43	M	1st yr.	"	"	
GROUP II					
g61	F	—	24 April 1965	Mobile, Alabama	
g62	M	1st yr.	"	"	
g63	F	—	"	"	
g64	M	2nd yr.	"	"	Died: 21 September 1965
g65	M	2nd yr.	"	"	
g66	M	1st yr.	"	"	
g67	M	2nd yr.	"	"	
g68	M	2nd yr.	"	"	Died: 25 May 1965
g69	M	2nd yr.	"	"	Died: 25 May 1965
g70	M	1st yr.	"	"	Died: 27 October 1965
g71	M	1st yr.	"	"	Escaped, May, 1965
g72	F	—	"	"	Died: 11 November 1965
g73	M	1st yr.	"	"	Injured, spring, 1965
g74	M	1st yr.	"	"	Escaped, May, 1965
g75	F	—	"	"	
g76	F	—	"	"	Died: 7 June 1965
g77	M	2nd yr.	"	"	Escaped, May, 1965

¹ Age category of males determined by color of primary coverts. All birds older than first year are designated second year.

molted two to three weeks later. These dates are in general agreement with the findings reported by Dwight (1900: 211–214).

The situation was similar the following autumn, the birds molting between mid-August and early October. The molt was complete for 19 birds this season, while 3 individuals (g64, g67, and g72) underwent partial molts, and 2 others (r53 and r57) became ill and terminated the molt prematurely.

After the completion of the body molt (but while replacement of retrices was still in progress), the birds began to acquire visible fat re-

serves, a process which required approximately two to three weeks and was rapidly followed by the initiation of nocturnal activity.

Autumnal *Zugunruhe* behavior was generally present from late September until early November, which correlates fairly well with the known times of Indigo Bunting migration. (Wood [1951: 451] states that Indigo Buntings depart from southern Michigan throughout September, rarely staying until the first or second week of October. Reports from Latin America indicate arrival times during the latter part of October [Griscom, 1932: 365; Dickey and van Rossem, 1938: 582; Russell, 1964: 178; Slud, 1964: 373].)

In the spring of 1965, the birds of Group I underwent normal, partial, prenuptial molts between early February and early April. All body feathers and wing coverts were replaced, but the retrices and, in most cases, the remiges were retained. Again, this is in general agreement with Dwight (1900: 211-214). Following termination of molt, fat deposition occurred and *Zugunruhe* commenced. This vernal *Zugunruhe* period extended from mid-April until early June, again approximating the dates when buntings are *en route* to their breeding areas. (Buntings leave Central America in late April [Griscom, 1932: 365; Dickey and van Rossem, 1938: 582; Russell, 1964: 178; Slud, 1964: 373] and arrive in Michigan throughout the month of May [Wood, 1951: 451].) The birds of Group II had completed the prenuptial molt when captured.

Two features deserve special mention. First, although all healthy captive birds underwent seemingly normal molts, not all birds displayed *Zugunruhe* behavior. In fact, when the number of available birds in captivity during each migration season is summed, one finds that migratory behavior occurred in only 33, or 45 per cent, of 72 "potential bird seasons" (10 of 16 in the fall of 1964; 10 of 24 in the autumn of 1965; and 13 of 32 in the spring of 1965).

Second, *Zugunruhe* activity was generally present for only five to six weeks during any particular migration season. This contrasts with the situation reported for other caged migrants (Merkel, 1938; Eyster, 1954: 21; Wagner, 1955; Weise, 1956: 285; Helms, 1963: 928) in which vernal nocturnal restlessness continued into the summer and frequently terminated only when the postnuptial molt began. The explanation for these two facts is not presently understood.

General procedure.—As with other nocturnal migrants which have received study (Palmgren, 1949; Eyster, 1954; Weise, 1956; Helms, 1963; Mewaldt *et al.*, 1964), Indigo Buntings are diurnal except during the migration seasons when they become highly active in the evening and remain so until a few hours before sunrise (Figure 2).

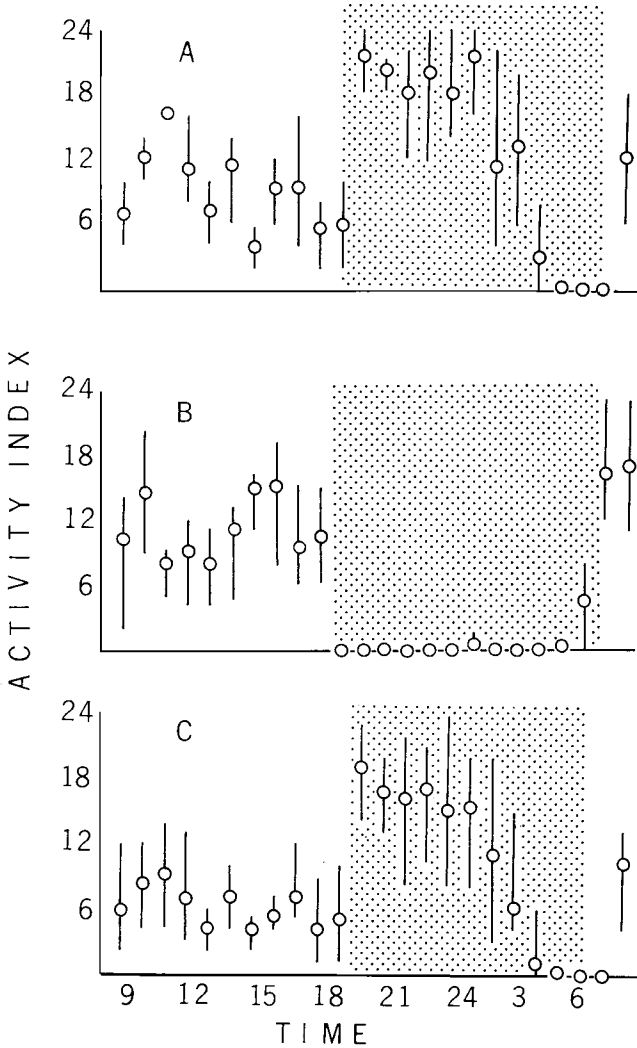


Figure 2. Activity rhythm of an Indigo Bunting, r51, as recorded by automatic perch registration (after C. M. Weise, pers. comm.). Activity index indicates the number of 150-second intervals per hour during which activity occurred. Stippled areas represent periods of darkness. The mean and range of activity values per hour are presented for three seasons: A, 5-8 October 1964; B, 10-17 February 1965; C, 12-16 April 1965.

Note that this measurement is one of total activity and is not related to the index based on footprint records (see Emlen and Emlen, 1966) which is used herein to evaluate the orientation of the birds.

When this nocturnal restlessness appeared, a bird was considered ready for experimentation. It would then be caught prior to each experiment, transported to the selected location in a small, cloth-covered holding cage, and placed in an individual circular test cage.

This test cage, which is described in detail elsewhere (Emlen and Emlen, 1966) consisted of a white blotting paper funnel mounted over an ink pad base and topped with a screen of one-half inch hardware cloth. From inside such a unit, a bird is able to see the sky overhead, but all terrestrial objects comprising the horizon are blocked from view. The orientation of *Zugunruhe* behavior, exhibited as frequent jumps up the sloping blotter paper funnel, is recorded in the form of inked footprints left in the direction of each jump. These can later be evaluated numerically (20 categories indicating increasing activity were used) and subjected to suitable statistical tests (Emlen and Emlen, 1966).

Pilot experiments conducted in the spring of 1964 with White-throated Sparrows (*Zonotrichia albicollis*), Swamp Sparrows (*Melospiza georgiana*), and Slate-colored Juncos (*Junco hyemalis*) indicated that when these birds were tested at an outdoor location four miles northeast of Ann Arbor, they tended to orient directly toward the horizon glow created by the town's lights. Therefore, during the Indigo Bunting experiments, outdoor testing was restricted to moonless nights. Further, each test cage was equipped with a four-inch high shield constructed from thin sheet metal painted flat black. This effectively blocked out the lower portions of the sky (up to 38° from the horizon), thereby limiting visibility to a 104° sector of the sky, a view which increased to approximately 140° as the bird jumped up the sides of the funnel. Finally, all outdoor tests were conducted in a large open field on the University of Michigan Edwin S. George Reserve, a location far from any towns which might produce appreciable horizon glow.

Five levelled saw-horse tables were constructed in this field, each aligned in a north-south direction. During an experiment, five test cages were assembled on each table and their positions (row and column number) recorded. Since individual birds consistently maintained their orientation from night to night regardless of their position in this experimental matrix, I assumed that *Zugunruhe* was not directionally influenced by the activity or calling of birds in nearby units.

Planetarium description.—Numerous experiments were also conducted under the artificial skies of the Robert T. Longway Planetarium at Flint, Michigan. This planetarium has an inner dome measuring 60 feet in diameter and 40 feet in height and is constructed of layered-concrete sprayed over a self-supporting steel frame. The geographic compass bearing of its north polar axis is 229° and is therefore displaced 31° west of true north.

The planetarium's Spitz model B projector allowed great experimental flexibility. I could present skies for any latitude and longitude, turn on the northern and southern celestial hemispheres separately, and easily block out any selected pattern or portion of the artificial sky. The instrument could also project the moon and planets, but I presented only the stars as potential visual cues.

Because the projector could not rotate at a speed slow enough to simulate true celestial motion, experiments were performed under stationary skies which were rotated through four degrees of arc once every 15 minutes to compensate for the passage of time.

The procedure followed in obtaining footprint records was identical to that described previously except that funnel units were not equipped with shields since horizon glows were non-existent. All test units (up to seven could be used simultaneously) were assembled atop an eight-foot-high table, thereby placing the birds on an approximate level with the planetarium horizon (Figures 3 and 4).

The projector occupied the central position in the planetarium, requiring placement of the test cages 10 feet off-center. When the artificial skies were set for north temperate latitudes (all autumn and most spring

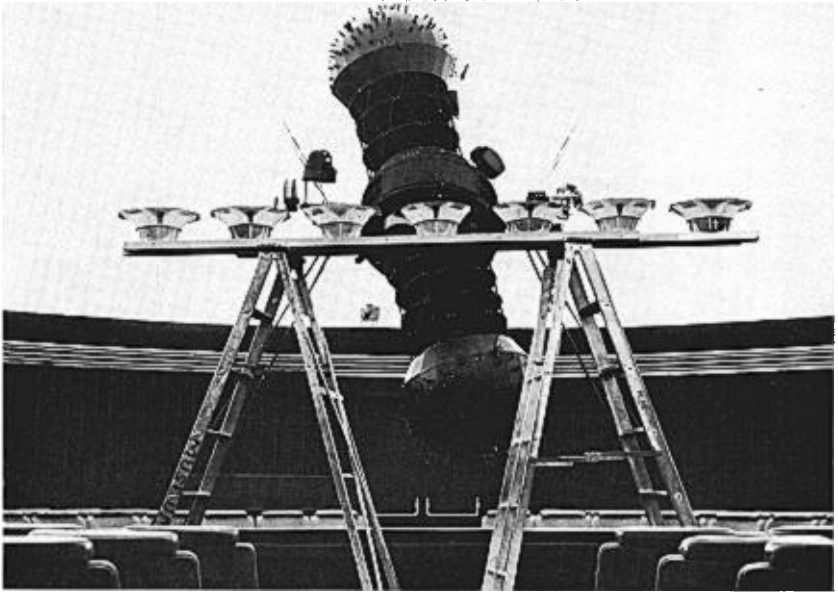


Figure 3. Photograph of the interior of the Robert T. Longway Planetarium at Flint, Michigan, showing the Spitz B projector and the arrangement of the test units.

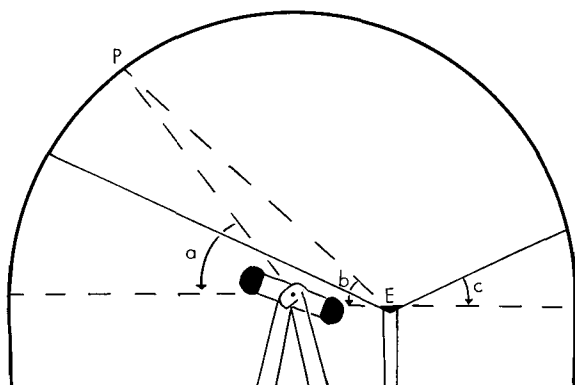


Figure 4. Diagrammatic view of the planetarium with the sky set for 43° N latitude; a, latitude setting of the projector (54°); b, latitude setting from the bird's position (43°); c, horizon area blocked from view (24°); P, position of Polaris; E, experimental bird.

experiments), the tilt of the projector necessitated the placement of the cages to the south of center, since portions of the projector could otherwise have been visible to the birds. Other tests, however, conducted under the more southerly skies of 15° N, permitted placement north of center.

When setting the artificial sky, the date, time, and latitude were each carefully controlled. (For complete, experiment by experiment tabulation of these data see S. T. Emlen, "Experimental analysis of celestial orientation in a nocturnally migrating bird." Ph.D. dissertation, The University of Michigan, 1966.) The latitude (or altitude of Polaris) was calculated from the bird's position, not from planetarium center. For example, in order to provide a bird located south of center with a sky of 43° N, the projector would be set for 54° N (see Figure 4). Similarly, latitude values of 28° N and 35° N actually represent projector settings of 35° N and 43° N, respectively.

All planetarium studies are subject to parallactic errors created by the closeness of the observer to the dome. Since any individual star remains fixed at a specific location on this dome, its apparent altitude and azimuth position will vary as the observer changes his position. In these experiments this distortion was relatively minor since the area in which the buntings could move, an ink pad 10 cm in diameter, was extremely small in comparison to the 60-foot diameter of the planetarium dome. In fact, the maximum parallactic displacement which an Indigo Bunting could experience while moving about in a funnel unit was equivalent to approximately two degrees of longitude and less than one degree of latitude.

Additional stellar distortion of a different type is created by the off-center positioning of the birds. This produces an inequality in the "close-

ness" of northern and southern celestial objects which, in turn, results in slight configurational aberrations. This effect was unavoidable although the portion of the sky most seriously altered, that near the horizon, was blocked from view by the funnel shape of the test cages.

The most serious problem encountered in the planetarium experiments was an inhibitory effect apparently produced by the sound-absorbing quality of the planetarium chamber. During three pilot experiments under these "echo-less" conditions, buntings which were strongly in migratory condition (as indicated by activity rhythm data and outdoor results) failed to produce footprint records. Yet when this "echo-less" quality was masked by playing a background tape recording, *Zugunruhe* activity reappeared. Thereafter, I continuously played a tape of the call of *Oecanthus fultoni*, the snowy tree cricket, through the 16 equally spaced, circumperipheral speakers of the planetarium's high-fidelity sound system. This sound (168 cricket chirps per minute) provided a broken, yet non-distracting background which was effectively non-directional.

In addition, a recording of the Indigo Bunting's nocturnal call note was used during the autumn experiments of 1964. Hamilton (1962*b*) had reported that a similar procedure increased *Zugunruhe* activity of Bobolinks (*Dolichonyx oryzivorus*), but no such effect was noted in the present study and in later seasons I did not use this recording.

Prior to a planetarium test, the experimental birds were taken from their aviary, placed in cloth-covered holding cages, and transported 50 miles to Flint by car. They then remained in the holding cages for an additional one-half hour while the funnel-cages were assembled and the planetarium sky set for the experiment. At the end of the night's test, the reverse procedure was followed, and birds were returned to the aviary.

Statistical treatment of the data.—After the footprint records were translated into numerical terms, 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. These diagrams are plotted such that, for each, the radius equals the greatest number of units of activity in any one 15° sector (the number which this represents is given at the lower left of each diagram in the figures) and the lengths of the other vectors are proportional to the radius.

These summarized data were evaluated statistically with the use of the University of Michigan IBM 7090 computer. Three different statistics were computed for each summary and these values were spot-checked on a desk calculator.

First, I tested the null hypothesis that the data are distributed randomly. Since the sample sector size of 15° was arbitrary and the footprint data were quantified on a relative rather than absolute scale (Emlen

and Emlen, 1966), it was necessary to employ a statistical measure which was insensitive to the absolute magnitudes of footprint activity. Such a test was derived by D. S. Robson, of the bio-statistics unit at Cornell University (pers. comm.). In this test, the data are considered graphically, activity (Y) being plotted as a function of compass direction (X). To assure independence, every second 15° sector was omitted from the treatment, thereby yielding 12 values of Y . The line representing an oriented response is then described by the cubic regression equation: $Y = a + bX + cX^2 + dX^3$, subject to the constraint that $Y_0 = Y_{12}$. This condition allows the equation to be rewritten:

$$Y = a + b\left(X - \frac{X^3}{144}\right) + c\left(X^2 - \frac{X^3}{12}\right).$$

Under the null hypothesis, the graph would be linear with a regression coefficient of zero. Therefore, the null hypothesis that $b = c = 0$ was tested by multiple regression analysis, randomness being rejected if the F values indicated a probability level of 0.05 or less.

Second, the mean direction, ϕ , was estimated for each set of data by vector analysis (Batschelet, 1965). (In these analyses, activity values for all 24 sectors were included.)

$$\cos \phi = \frac{x}{r} \qquad \sin \phi = \frac{y}{r}$$

in which $r = \sqrt{x^2 + y^2}$

and
$$x = \frac{n_1 \cos 15^\circ + n_2 \cos 30^\circ + n_3 \cos 45^\circ \dots + n_{24} \cos 360^\circ}{n_T}$$

and
$$y = \frac{n_1 \sin 15^\circ + n_2 \sin 30^\circ + n_3 \sin 45^\circ \dots + n_{24} \sin 360^\circ}{n_T}$$

where n_1 is the number of units of activity in the first 15 degree sector, n_2 is the amount of activity in the second such sector, etc.

I also determined a measure of dispersion which is similar to the standard deviation of linear statistical theory. For circular distributions this is the mean angular deviation, or s :

$$s \text{ (in radians)} = \sqrt{2(1-r)}$$

This value was converted into degrees and, together with ϕ and r , allowed the complete description of the distribution of any given footprint record. 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

Outdoor experiments: autumn.—As a first step in studying the orientational mechanism employed by Indigo Buntings, birds of Group I were repeatedly placed in funnel cages outdoors under the natural night sky during the autumn of 1964. The orientation of their *Zugunruhe* behavior was recorded on all rainless nights from 27 September until 15 October, when the moon's appearance in the night sky forced the discontinuance of outdoor experiments. Additional isolated tests were conducted on 7 and 11 September, and 1, 9, and 11 November. (A complete listing of all experiments, with date, time, and weather conditions is presented in Emlen, *op. cit.*)

Nine buntings exhibited *Zugunruhe* and their directional tendencies are presented in Figure 5, in which each vector diagram represents the sum of one bird's migratory activity over the entire season (see also Appendix 1). Although different birds behaved differently, the results for any one individual were consistent from night to night throughout the experimental period.

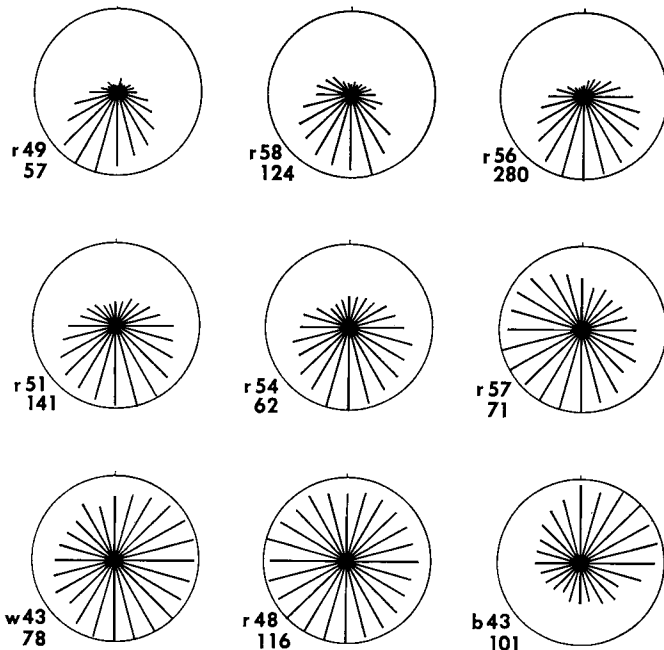


Figure 5. *Zugunruhe* orientation under the natural night sky (43° N), autumn, 1964. Here and in other figures vector diagrams are plotted such that the radius equals the greatest number of units of activity in any one 15° sector. The number which this represents is presented to the lower left of each diagram.

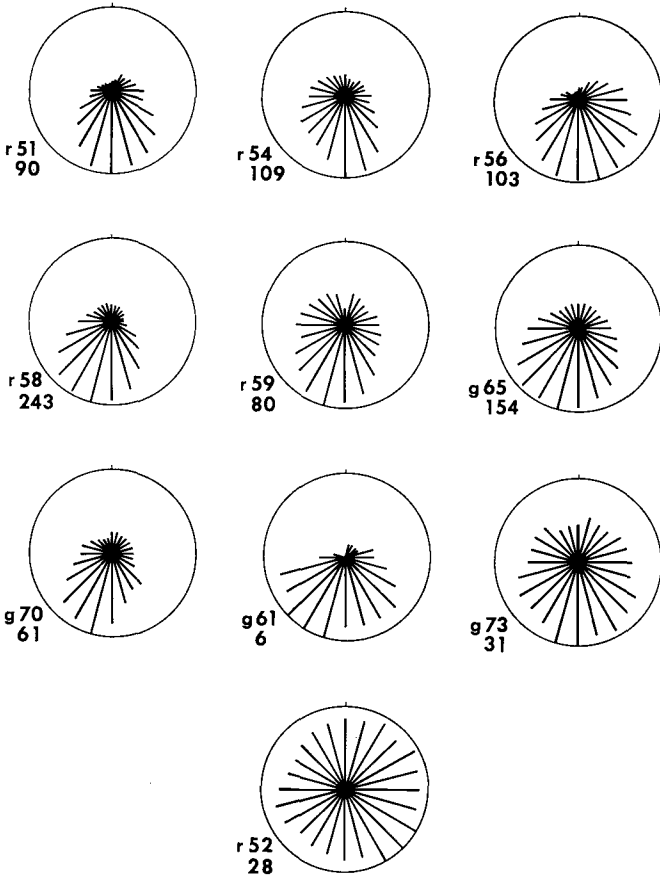


Figure 6. *Zugunruhe* orientation under the natural night sky (43° N), autumn, 1965.

The remaining six birds (r47, r50, r52, r53, r55, and r59) were tested concurrently with the active individuals but failed to exhibit nocturnal restlessness. As mentioned previously, these birds had all progressed through a normal postnuptial molt and no explanation for this absence of *Zugunruhe* is known.

Figure 5 indicates that five birds (r49, r51, r54, r56, and r58) demonstrated definite southerly directional preferences (between SSE and SSW), the normal migration direction for Indigo Buntings at this season. A sixth and much less oriented bird, r57, exhibited a weak southwesterly tendency while b43 oriented northeast, a direction more closely resembling that typical of spring migration. The behavior of the two remaining birds, w43 and r48, however, was consistently random. Whether these indi-

viduals actually lacked the ability to determine their migratory direction under these conditions or behaved abnormally due to some facet of the experimental situation is not known.

Similar experiments were conducted in the fall of 1965 when 10 birds were active (6 from Group I and 4 from Group II). Data were collected from 23 through 29 September and 24 through 29 October. The data for these 10 birds (Figure 6 and Appendix 2), show that 9 (r51, r54, r56, r58, r59, g61, g65, g70, and g73) oriented their *Zugunruhe* southward (SSE to SSW) while the tenth, r52, failed to display any directional preference.

These results indicate that the majority of the buntings were able to obtain the information necessary to determine their migratory direction even though the funnel cages restricted the cues visible overhead to a 104° – 140° sector of the sky.

It is of interest that four birds (r51, r54, r56, and r58) exhibited *Zugunruhe* during both autumns and comparisons indicate that their directional behavior was remarkably similar during the two seasons, the principal difference being a general reduction in the mean angular deviation in 1965.

When the response of individual birds in September, 1965, was compared with their behavior one month later (with the exception of r59, g61, and g65 which did not commence *Zugunruhe* until early October) a pronounced difference in the orientation of three of seven birds was noted. In each of these cases (r58, g70, and g73), activity early in the season was random or near-random, yet by late October a definite SSE to SSW orientation was evident (Figure 7; Appendix 3). It is, therefore, possible that, in certain individuals, the ability (or perhaps the motivation) to orient develops after the initiation of nocturnal activity, a hypothesis also proposed by Mewaldt *et al.* (1960, 1964) for White-crowned Sparrows, *Zonotrichia leucophrys*. Such disorientation early in the season was not apparent, however, in other individuals during either 1964 or 1965.

The general finding that buntings are able to determine their migratory direction when the only visual cues are those provided by the sky itself may tempt us to conclude that the birds must be relying upon stellar information. However, other, non-visual, geophysical factors (such as the earth's magnetic field) are also present and, theoretically, could serve as directional cues (see Merkel and Wiltschko, 1965; Wiltschko and Merkel, 1965).

Responses under overcast skies.—If the essential cues are of a celestial nature, then orientation should break down as stars become occluded—under conditions of complete overcast. To examine this, I re-analyzed the data from the autumn of 1964 on the basis of the cloud conditions

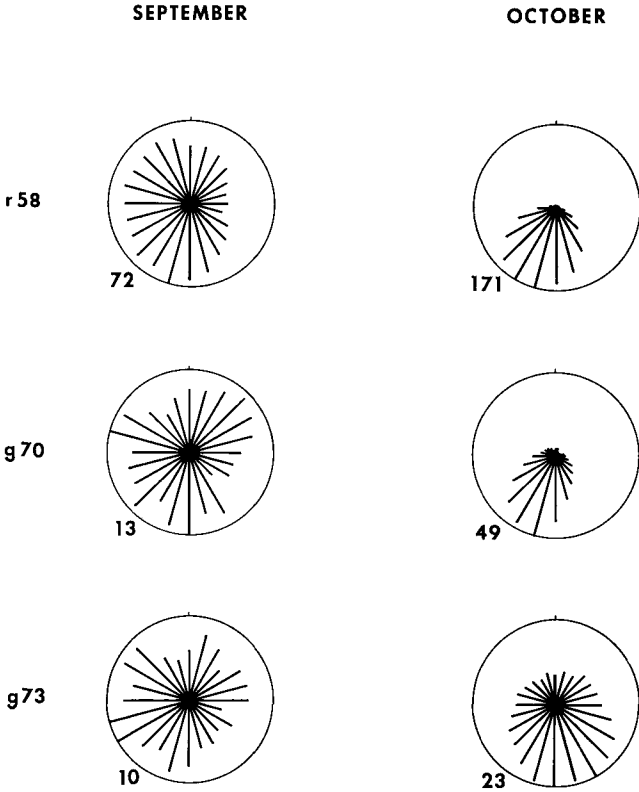


Figure 7. Comparison of *Zugunruhe* orientation obtained under the natural night sky in September and October of 1965.

present at the time of experimentation. (Overcast conditions were extremely rare during the outdoor test periods of 1965.) Four arbitrary categories of increasing cloud cover were adopted.

- $\frac{1}{10}$ cloud cover = clear
- $\frac{1}{10}$ to $\frac{4}{10}$ cloud cover = slight overcast
- $\frac{5}{10}$ to $\frac{8}{10}$ cloud cover = moderate overcast
- $\frac{9}{10}$ to $\frac{10}{10}$ cloud cover = heavy overcast

Unfortunately, no conditions of complete ($\frac{10}{10}$) overcast were encountered and, with $\frac{9}{10}$ cloud cover, small patches of clear sky are still visible, and different stars and star patterns are exposed as the clouds move overhead. Since it could be possible that viewing a few stars is sufficient for orientation, it becomes exceedingly difficult, if not impossible, to correlate increasing *partial* cloudiness with decreasing cue availability.

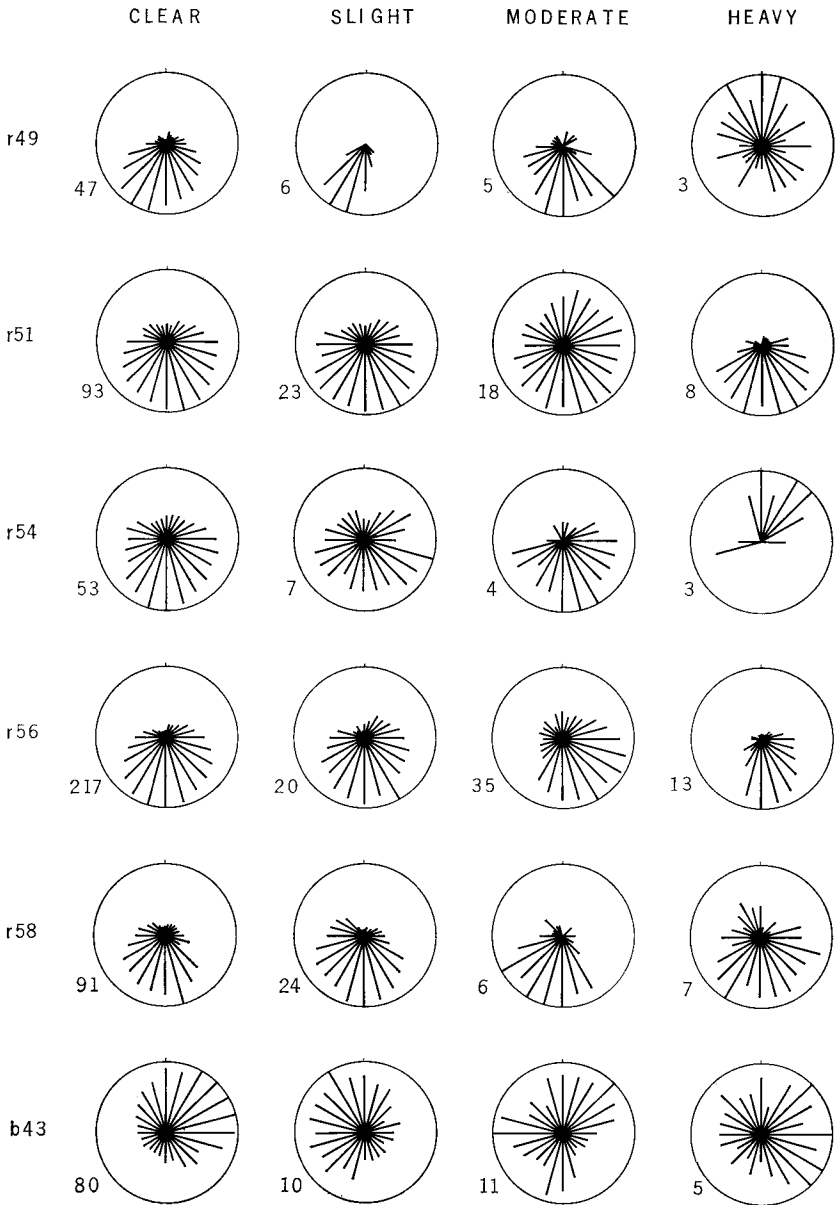


Figure 8. *Zugunruhe* orientation under various conditions of overcast, autumn, 1964.

The results obtained under different conditions of overcast are illustrated in Figure 8 (Appendix 4). While some birds experienced a decrease in orientational accuracy with slight or moderate overcast (r51, r54, and b43), others (r49, r56, and r58) did not. Under 10% cloud cover, the variability of responses was even greater; the angular deviation of r58 increased while the behavior of r49 and b43 became random, and r54 reversed its direction, aiming northward. Yet r58's orientation remained southward and r51 and r56 continued to exhibit southerly preferences.

Even more puzzling is the behavior of r51 which became decreasingly oriented under slightly and moderately cloudy skies, yet aimed accurately southward under 10% overcast.

Considering the absence of conditions of complete overcast, I can only state that while some increase in angular deviation (and occasionally complete disorientation) did occur under overcast, several birds were able to obtain sufficient directional information when only a very few stars were visible. This, of course, fails to provide convincing evidence concerning the hypothesis that Indigo Buntings rely upon celestial cues for directional determination.

The intensity of *Zugunruhe*, however (measured in units of footprint activity per hour), did correlate with overcast, decreasing as cloud cover increased (regression coefficient = -10.4; $p < 0.025$).

Planetarium experiments: autumn.—In order further to investigate the problem, buntings were tested under the artificial skies of the planetarium in late autumn, 1964 (Figure 9, column 2; Appendix 5). In these experiments, all birds which had not ceased *Zugunruhe* activity were exposed to skies which mimicked those present outdoors. Three birds which had oriented southward outdoors (r51, r56, and r58) continued to display a preference for "planetarium south" under the artificial sky, while a fourth bird, b42, which first exhibited nocturnal activity during these experiments, likewise oriented southward. The behavior of the remaining active individual, r48, was random, again resembling that displayed under the natural sky.

Although differences did occur (r51 aimed slightly west and r58 east of its mean outdoor direction), the planetarium results were generally similar to those obtained from the same birds out-of-doors.

Results of similar planetarium experiments conducted between 4 and 22 October 1965 support these findings (Figure 10, column 2; Appendix 6). Four birds which had oriented southward under the natural sky (r54, r56, r58, and g65) continued to aim southward in the planetarium. (The fifth oriented individual in Figure 10, g70, was not tested under planetarium skies set for local conditions.) One additional bird, r52, failed to display any directional preference either outdoors or under the artificial

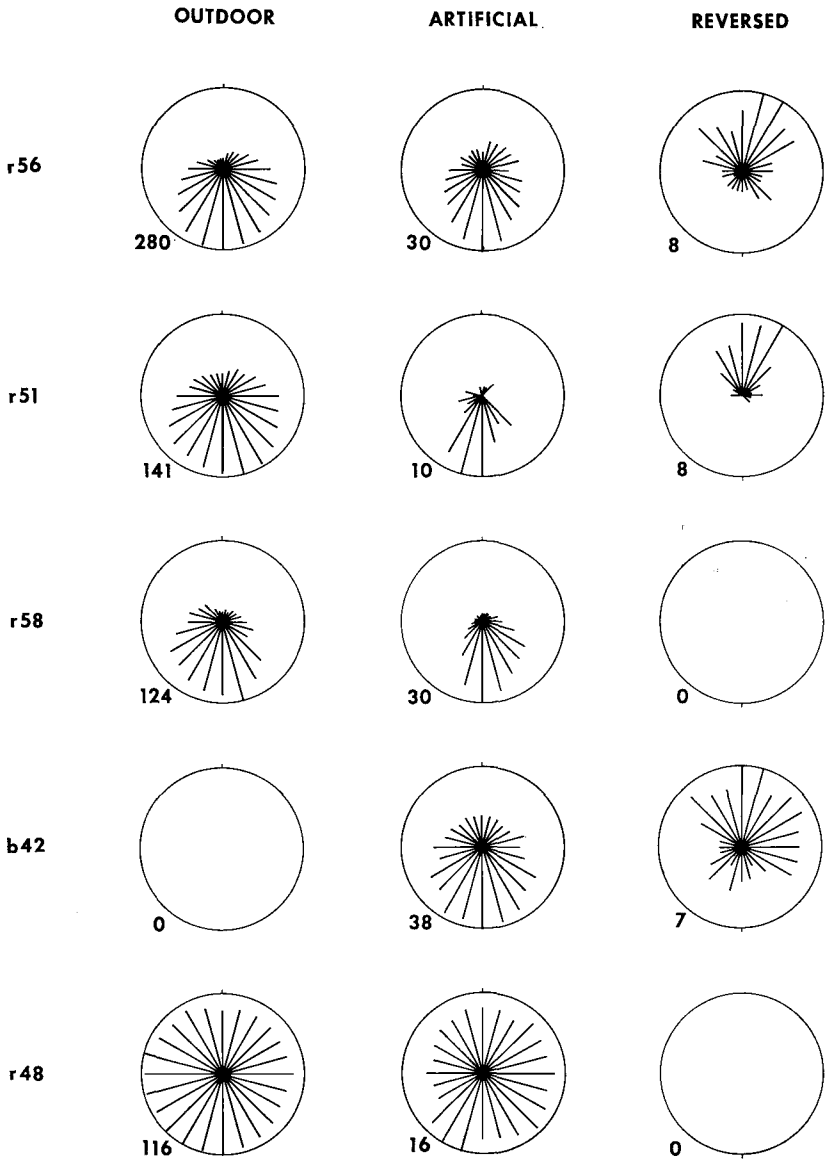
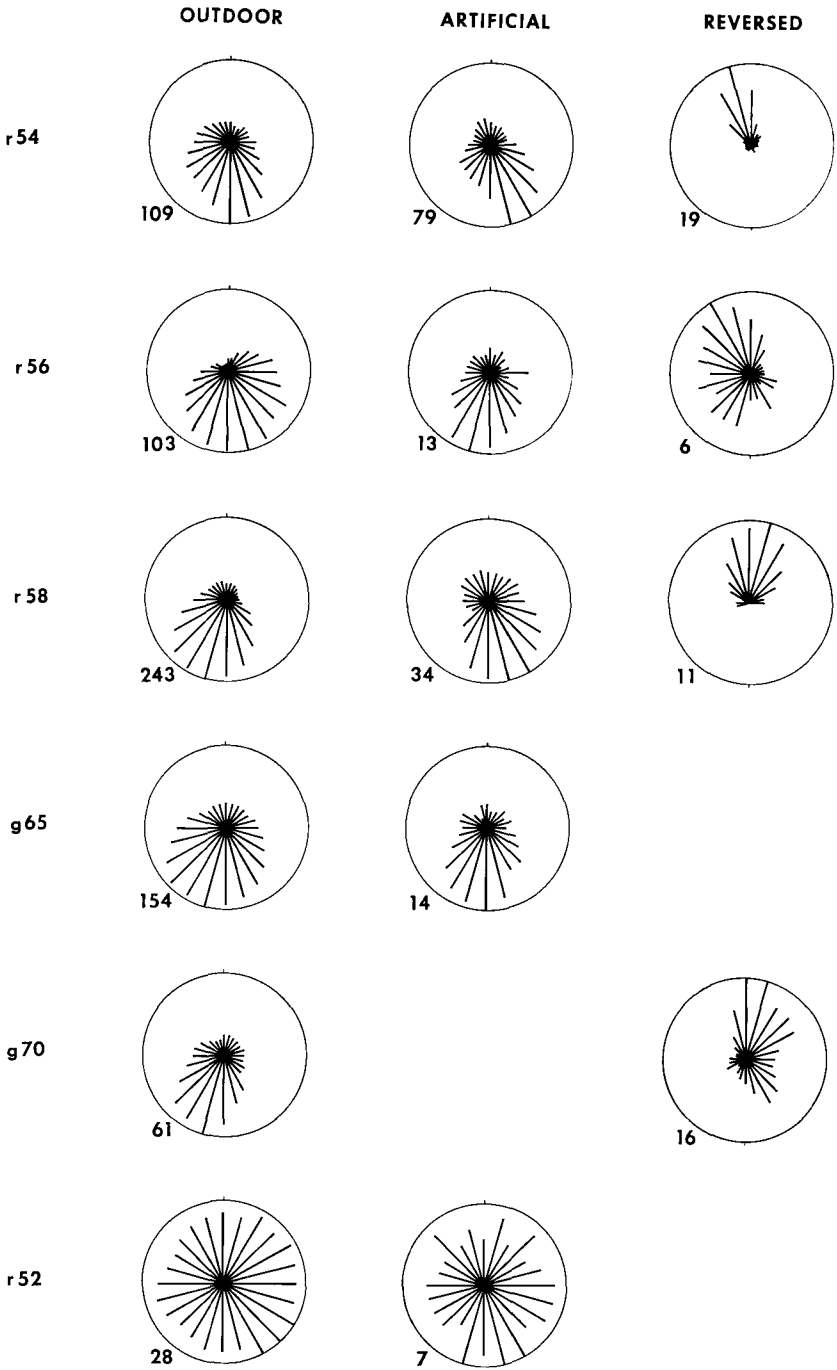


Figure 9. *Zugunruhe* orientation under "normal" and "reversed" planetarium skies of 43° N, compared with results obtained out-of-doors, autumn, 1964.

→

Figure 10. *Zugunruhe* orientation under "normal" and "reversed" planetarium skies of 35° N, compared with results obtained out-of-doors, autumn, 1965.



sky. Once again, therefore, an agreement between indoor and outdoor behavior is apparent.

Considering that planetarium north is actually 31° west of true north, one would predict that if the birds relied upon geophysical factors, and if these factors were present within the planetarium dome, the buntings would orient their behavior with respect to true south rather than planetarium south. The vector diagrams should then indicate consistent shifts of approximately 30° to the west. But, although slight differences in the *Zugunruhe* orientation of some birds were noticeable, these deflections were by no means consistently westerly.

The apparent absence of a dependence on geophysical factors was demonstrated more clearly when the birds were presented with an artificial sky in which the north-south axis had been reversed 180° (Polaris therefore being projected onto the southern portion of the north-south meridian).

In this situation, all seven active birds (r51, r56, and b42 in 1964; r54, r56, r58, and g70 in 1965) tended to reverse their direction, continuing to aim toward stellar south although this now corresponded to true NNW (see column 3 in Figures 9 and 10). The accuracy of this reversal varied from bird to bird, but in each case, a definite directional shift to the previously north side of the planetarium occurred.

Planetarium experiments: spring.—Experiments of a similar nature were conducted in the spring of 1965 during the season of normal northward migration. Precautions were taken to prevent the birds from viewing the sky at the latitude of Ann Arbor (43° N is near the northern limits of the breeding range of the Indigo Bunting) by housing them indoors and conducting planetarium experiments under artificial, low latitude skies until late in the season. Only in late May and early June, after the termination of normal migration, were birds exposed to the natural sky.

Nocturnal restlessness, commencing in mid-April, was displayed by only three of the birds which had over-wintered in the indoor aviary (Group I). These birds were immediately tested in the planetarium under skies coincident with local time and season, but with the latitude set for 15° N, the latitude of southern Guatemala, the center of the wintering range of the species.

In this situation, all three birds oriented northward with r52 tending toward NW, r55 toward NNW, and b43 toward NE (Figure 11; Appendix 7). And, as in the autumn experiments, when the north-south axis of the planetarium sky was reversed 180° , this orientation was reversed.

In late April, I received the second group of buntings, birds which had been captured on the Gulf coast *en route* north and air-lifted to Ann Arbor. After an adjustment period of several days during which the birds became accustomed to the indoor aviary and replenished their fat deposits,

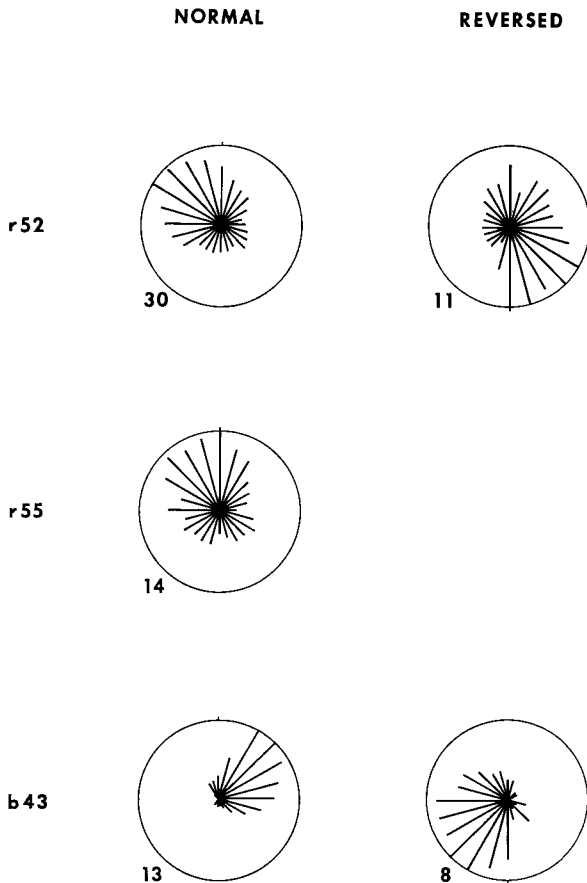


Figure 11. *Zugunruhe* orientation under low latitude "normal" and "reversed" planetarium skies (15° N), spring, 1965.

they were tested in a long series of planetarium experiments under skies of 28° N, a latitude south of the species' breeding range, but close to the location at which they had been captured.

Of these 17 birds, 10 continued to exhibit nocturnal restlessness in Ann Arbor, thereby increasing to 13 the number of available experimental subjects. Of these, 8 individuals (r52, r55, b43, g63, g70, g71, g74, and g77) oriented their *Zugunruhe*; and in all cases this orientation was northward, the normal migration direction (Figures 12 and 13, column 1; Appendix 8). Again, there was considerable variation from bird to bird, but all aimed between NE and NW, and the behavior of each was consistent from test to test.

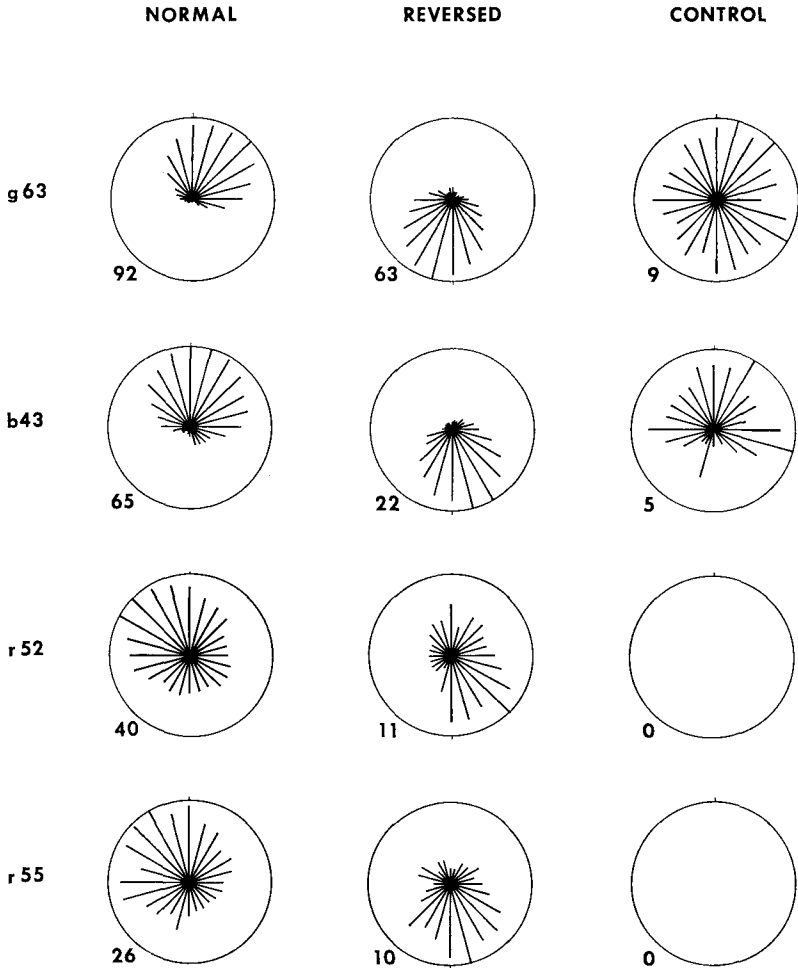


Figure 12. *Zugunruhe* orientation under "normal" and "reversed" planetarium skies of 28° N, compared with results obtained with the stars shut off ("control"), spring, 1965 (see also Figures 13 and 14).

The remaining five active birds (g61, g65, g72, g75, and g76) failed to display any marked orientation (Figure 14, column 1; Appendix 9). The activity of both g72 and g76 resembled escape behavior as was evidenced by direct observation from below (frequent jumps into the wire top and long, scratching, fluttering "runs" up the funnel sides) and by the footprint records obtained (primarily streaky scratch marks and feather smudges as opposed to clean prints). Whether these birds would have

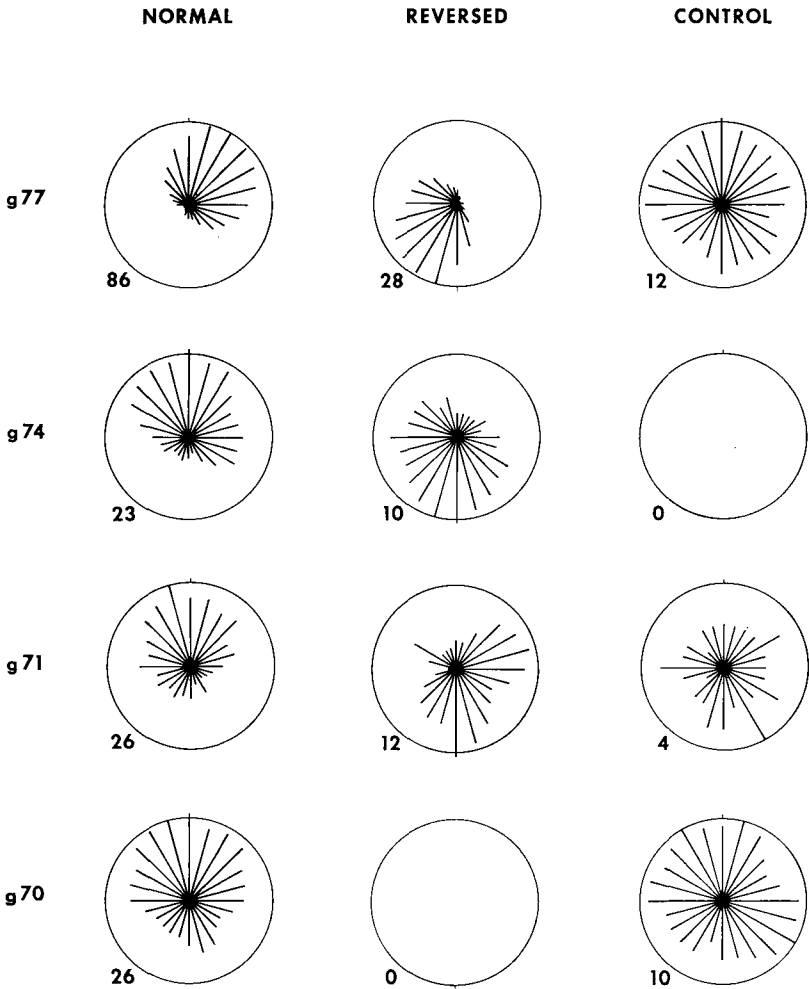


Figure 13. *Zugunruhe* orientation under "normal" and "reversed" planetarium skies of 28° N, compared with results obtained with the stars shut off ("control"), spring, 1965 (see also Figures 12 and 14).

oriented their behavior under more normal conditions is not known.

When the north-south axis of the planetarium sky was reversed 180°, all seven "orienters" which were tested (r52, r55, b43, g63, g71, g74, and g77) reversed their direction, continuing to aim toward *stellar* NE to NW, while the *Zugunruhe* of the three "non-oriented" birds (g65, g72, and g76) continued to approximate randomness (column 2 in Figures 12, 13, and 14).

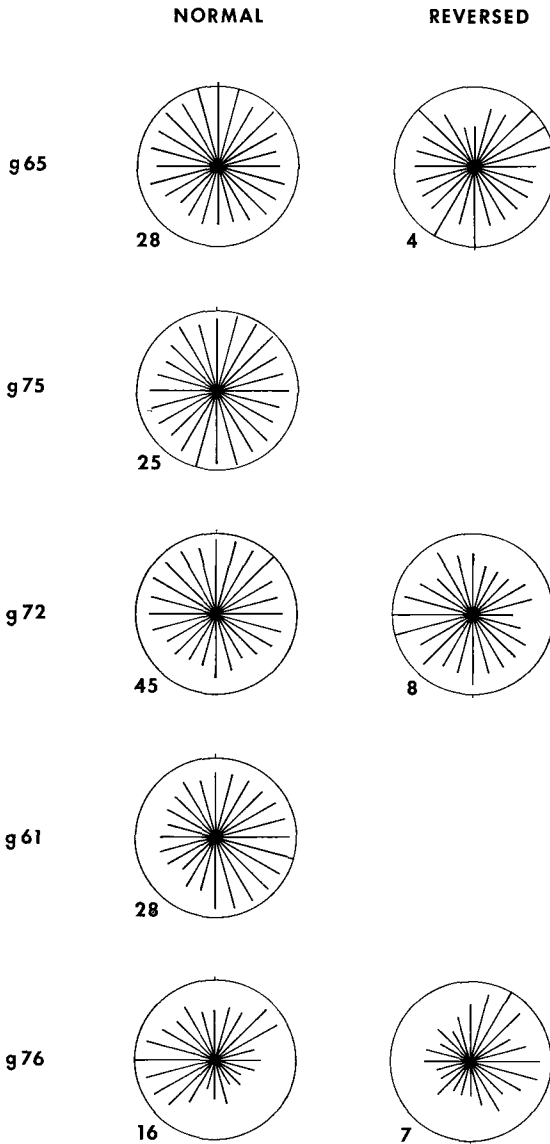


Figure 14. *Zugunruhe* orientation under "normal" and "reversed" planetarium skies of 28° N, spring, 1965 (see also Figures 12 and 13).

As an added precaution, to make certain that artifacts within the planetarium itself were not influencing the directional behavior of the birds, a control experiment was designed in which the stars were turned

off. The dome was then diffusely illuminated by a circumperipheral set of concealed blue lights located at the horizon level, their intensity approximating that of full moonlight. (Complete darkness proved impractical since birds ceased activity under this condition.) All other factors (playing of background tape recording, position of projector, placement of funnel units, etc.) were unaltered.

In this situation two marked changes occurred in the birds' behavior. First, there was a general reduction in activity; three different nights of tests produced very few data from most individuals and none from others. This may indicate that sight of the stars is in itself stimulatory to buntings in migratory condition, a suggestion also supported by the inverse relationship between activity and cloud cover obtained under the outdoor sky.

The second change, more pertinent to this discussion, was the severe deterioration which occurred in the birds' orientational abilities (Figures 12 and 13, column 3). The *Zugunruhe* of all five active birds which had previously been orienting northward (b43, g63, g70, g71, and g77) became random. This demonstrates that the artificial starry sky was necessary for direction finding and that potential artifacts within the planetarium itself were not being used as cues, a conclusion previously supported by the behavior of birds under reversed skies.

It is now of interest to reconsider the hypothesis proposed by Merkel and Wiltshcko (1965) that the earth's magnetic field is of great importance in enabling caged European Robins, *Erithacus rubecula*, to orient their *Zugunruhe*. Through the generosity of the Bendix Systems Division, I was able to obtain a Bell model 110 Gauss-meter and directly measure the magnetic field present both outside and within the planetarium. Inside the dome, at the height of the funnel units (eight feet), the field was remarkably constant, with a total intensity of 0.51 ± 0.02 Gauss and a horizontal component direction of approximately 30° east of planetarium north, in other words, magnetic north. Outside the building, the intensity of the magnetic field was 0.54 ± 0.02 Gauss. It thus appears that the layered concrete construction of the planetarium does not appreciably alter the normal magnetic field, and the geomagnetic information available inside is no different from that outdoors.

Interpreted in the light of this finding, the buntings' behavior under reversed planetarium skies suggests either that they were unable to use information from the magnetic field or that they employed celestial information in preference to it. The results from the control experiments, in which no stars were visible, provide evidence for the former interpretation since the caged birds failed to orient although in the presence of a normal geomagnetic field.

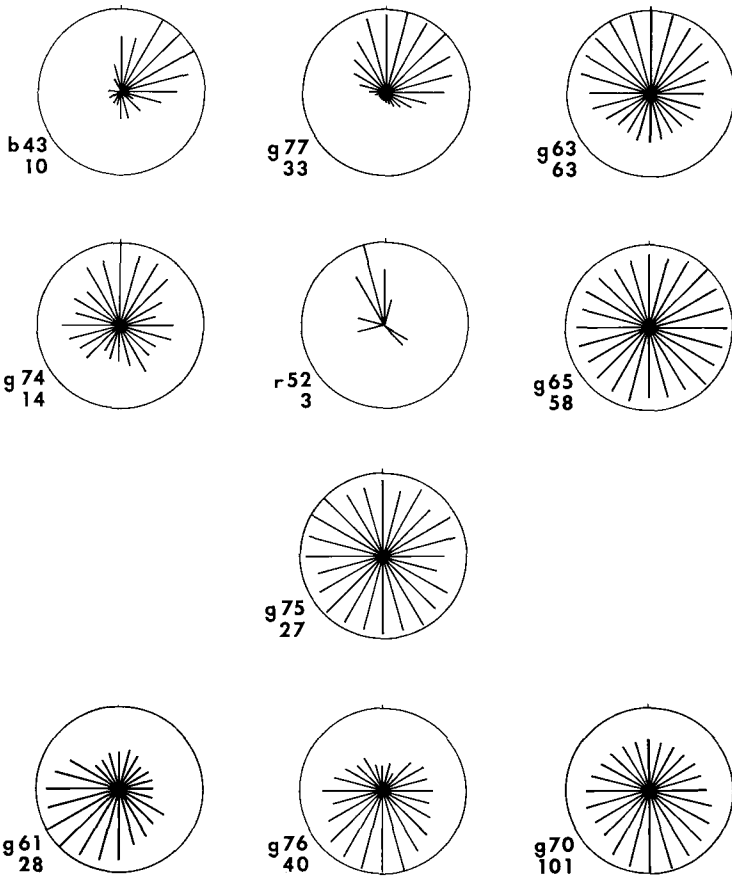


Figure 15. *Zugunruhe* orientation under the natural night sky (43° N), late spring, 1965.

Outdoor experiments: spring.—After the completion of the spring planetarium experiments, buntings still exhibiting *Zugunruhe* were taken outdoors and their behavior examined under the natural sky of 43° N latitude. The results, obtained between 20 May and 4 June 1965, are depicted in Figure 15 (Appendix 10). Of the six “orienters” still active, five (r52, b43, g63, g74, and g77) directed their *Zugunruhe* roughly northward as they had in the planetarium set for a more southerly latitude. (This tendency, however, was not statistically significant for r52, and the mean direction of g63 was altered appreciably.) In addition, g65 and g75 were consistently random as they had been indoors.

Changes did occur, however, in the behavior of three birds: g61, which had previously failed to display any strong directional preference, now

oriented its *Zugunruhe* toward the southwest, while g76, previously inconsistent to random in its behavior, and g70, a northward orienter in the planetarium, both exhibited a tendency to aim southward.

Whether these behavioral changes were a result of the different environmental conditions or the lateness of the season, or both, or whether the birds were actually responding in a different manner because of the presence of a more northerly sky is not known. Since these birds had been captured in Alabama, it is probable that some were far north of their actual breeding areas. This raises the possibility that they somehow perceived this displacement and altered their behavior accordingly. But g63, g74, and g77, also Alabama-caught birds, continued to head northward. At present, no additional data pertinent to this question are available and the possibility of latitude determination must remain highly speculative.

CONCLUSION

The general agreement in *Zugunruhe* orientation obtained under natural and artificial skies, coupled with consistent behavioral changes produced by experimental manipulation of the planetarium sky, furnishes strong evidence that celestial cues can provide at least one means of enabling Indigo Buntings to determine their direction for migration.

These findings, in addition to representing an independent confirmation of some portions of Sauer's (1957) study, supply one more example to add to the increasing list of species thought capable of using celestial information.

The mere amassing of such lists, however, in no way indicates either *which* stellar cues are of importance to the orientation process, or *how* such cues are employed. These topics will be the subject of the second part of this paper.

ACKNOWLEDGMENTS

This investigation is based upon a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree at the University of Michigan. I am grateful to Harrison B. Tordoff, my chairman, and to Richard D. Alexander, William S. Benninghoff, Francis C. Evans, and Robert W. Storer, for their advice and criticism. For assistance in obtaining experimental birds, I thank Maurice F. Baker, Thomas A. Imhof, and Walter P. Nickell. Maurice G. Moore made available, without cost, the exceptional facilities of the Robert T. Longway Planetarium. Advice on statistical matters was offered by James S. Farris, Douglas S. Robson, Frederick E. Smith, and Hans G. Wallraff; Mr. Farris also programmed the data for computer evaluation. The assistance of my wife, Kate, in all aspects of this study is also gratefully acknowledged.

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SUMMARY

The *Zugunruhe* orientation of caged Indigo Buntings was tested both outdoors under the natural night sky and inside the Robert T. Longway Planetarium in the fall of 1964 and the spring and fall of 1965. During these three seasons, data were obtained from 23 different birds for a total of 33 "bird seasons." In 24 of these cases (73 per cent), the birds displayed a consistent tendency to orient in the direction appropriate for the migration season in question; random results were obtained in an additional 8 cases (24 per cent).

The individuals demonstrating directional preferences under the night sky continued to orient correctly under artificial planetarium skies set for local conditions, reversed this direction when the north-south axis of the planetarium sky was reversed 180°, and lost all ability to orient when the stars were turned off and the dome diffusely illuminated.

These results support the hypothesis that Indigo Buntings are able to obtain directional information from the starry sky.

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APPENDIX 1

ZUGUNRUHE ORIENTATION UNDER THE NATURAL NIGHT SKY (43° N), AUTUMN, 1964 (SEE FIGURE 5)

<i>Bird</i>	<i>Hours tested</i>	<i>Hours active</i>	<i>Mean direction</i>	<i>Angular deviation</i>
r49	26h 30m	20h 30m	190°	57°
r58	54h 20m	40h 20m	195°	62°
r56	69h 50m	59h 50m	170°	63°
r51	62h 50m	48h 50m	171°	69°
r54	67h 50m	42h 20m	172°	71°
r57	30h 0m	26h 0m	229°	75°
w43	66h 20m	48h 20m	random	—
r48	71h 50m	61h 50m	random	—
b43	72h 50m	63h 50m	39°	72°

APPENDIX 2

ZUGUNRUHE ORIENTATION UNDER THE NATURAL NIGHT SKY (43° N), AUTUMN, 1965 (SEE FIGURE 6)

<i>Bird</i>	<i>Hours tested</i>	<i>Hours active</i>	<i>Mean direction</i>	<i>Angular deviation</i>
r51	31h 0m	24h 30m	170°	59°
r54	33h 10m	29h 40m	197°	66°
r56	40h 10m	40h 10m	163°	62°
r58	42h 40m	35h 20m	206°	62°
r59	22h 0m	20h 30m	205°	71°
g65	38h 50m	38h 50m	198°	68°
g70	31h 40m	24h 10m	207°	65°
g61	5h 0m	1h 30m	185°	55°
g73	27h 40m	17h 50m	176°	74°
r52	35h 10m	28h 40m	random	—

APPENDIX 3

ZUGUNRUHE ORIENTATION OBTAINED UNDER THE NATURAL NIGHT SKY DURING SEPTEMBER AND OCTOBER OF 1965 (SEE FIGURE 7)

<i>Bird</i>	<i>Dates</i>	<i>Hours tested</i>	<i>Hours active</i>	<i>Mean direction</i>	<i>Angular deviation</i>
r58	23–29 September	18h 10m	14h 50m	253°	75°
	24–29 October	24h 30m	20h 30m	199°	41°
g70	23–29 September	18h 10m	15h 10m	random	—
	24–29 October	13h 30m	6h 0m	204°	53°
g73	23–29 September	18h 10m	11h 50m	random	—
	24–29 October	17h 0m	7h 0m	167°	70°

APPENDIX 4

ZUGUNRUHE ORIENTATION UNDER VARIOUS CONDITIONS OF OVERCAST, AUTUMN, 1964 (SEE FIGURE 8)

<i>Bird</i>	<i>Overcast condition</i>	<i>Hours tested</i>	<i>Hours active</i>	<i>Mean direction</i>	<i>Angular deviation</i>
r49	clear	15h 0m	15h 0m	189°	58°
	slight	4h 0m	2h 0m	200°	25°
	moderate	5h 30m	3h 30m	192°	55°
	heavy	2h 0m	2h 0m	random	—
r51	clear	43h 50m	31h 50m	172°	68°
	slight	5h 30m	5h 30m	176°	69°
	moderate	9h 30m	7h 30m	144°	76°
	heavy	4h 0m	4h 0m	170°	53°
r54	clear	48h 50m	32h 50m	174°	62°
	slight	5h 30m	3h 30m	random	—
	moderate	9h 30m	4h 0m	159°	60°
	heavy	4h 0m	2h 0m	16°	47°
r56	clear	50h 50m	42h 20m	174°	62°
	slight	5h 30m	4h 0m	170°	64°
	moderate	9h 30m	9h 30m	141°	66°
	heavy	4h 0m	4h 0m	157°	51°

APPENDIX 4 (CONTINUED)

<i>Bird</i>	<i>Overcast condition</i>	<i>Hours tested</i>	<i>Hours active</i>	<i>Mean direction</i>	<i>Angular deviation</i>
r58	clear	37h 20m	28h 50m	195°	62°
	slight	5h 30m	5h 30m	197°	61°
	moderate	7h 30m	4h 0m	207°	50°
	heavy	4h 0m	2h 0m	185°	69°
b43	clear	47h 20m	33h 20m	47°	70°
	slight	5h 30m	5h 30m	301°	72°
	moderate	9h 30m	7h 30m	random	—
	heavy	4h 0m	2h 0m	random	—

APPENDIX 5

ZUGUNRUHE ORIENTATION UNDER "NORMAL" AND "REVERSED" PLANETARIUM SKIES OF 43° N,
COMPARED WITH RESULTS OBTAINED OUT-OF-DOORS, AUTUMN, 1964 (SEE FIGURE 9)

<i>Bird</i>	<i>Experiment</i>	<i>Hours tested</i>	<i>Hours active</i>	<i>Mean direction</i>	<i>Angular deviation</i>
r56	outdoors	60h 50m	59h 50m	170°	63°
	planetarium: normal	13h 10m	10h 10m	171°	69°
	planetarium: reversed	1h 30m	1h 30m	7°	67°
r51	outdoors	62h 50m	48h 50m	171°	69°
	planetarium: normal	12h 40m	5h 40m	191°	47°
	planetarium: reversed	1h 30m	1h 30m	12°	40°
r58	outdoors	54h 20m	40h 20m	195°	62°
	planetarium: normal	11h 10m	5h 40m	161°	53°
	planetarium: reversed	1h 30m	0h 0m	—	—
b42	outdoors	65h 50m	0h 0m	—	—
	planetarium: normal	9h 40m	8h 40m	186°	71°
	planetarium: reversed	1h 30m	1h 30m	33°	72°
r48	outdoors	71h 50m	61h 50m	random	—
	planetarium: normal	5h 30m	5h 30m	random	—
	planetarium: reversed	1h 30m	0h 0m	—	—

APPENDIX 6

ZUGUNRUHE ORIENTATION UNDER "NORMAL" AND "REVERSED" PLANETARIUM SKIES OF 35° N,
COMPARED WITH RESULTS OBTAINED OUT-OF-DOORS, AUTUMN, 1965 (SEE FIGURE 10)

<i>Bird</i>	<i>Experiment</i>	<i>Hours tested</i>	<i>Hours active</i>	<i>Mean direction</i>	<i>Angular deviation</i>
r54	outdoors	33h 10m	29h 40m	197°	66°
	planetarium: normal	20h 30m	20h 30m	166°	67°
	planetarium: reversed	5h 30m	5h 30m	347°	53°
r56	outdoors	40h 10m	40h 10m	163°	62°
	planetarium: normal	13h 0m	7h 30m	191°	66°
	planetarium: reversed	5h 30m	2h 15m	285°	69°
r58	outdoors	42h 40m	35h 20m	206°	62°
	planetarium: normal	9h 30m	9h 30m	206°	70°
	planetarium: reversed	2h 15m	2h 15m	8°	37°

APPENDIX 6 (CONTINUED)

<i>Bird</i>	<i>Experiment</i>	<i>Hours tested</i>	<i>Hours active</i>	<i>Mean direction</i>	<i>Angular deviation</i>
g65	outdoors	38h 50m	38h 50m	198°	68°
	planetarium: normal	4h 0m	4h 0m	189°	65°
	planetarium: reversed	2h 15m	0h 0m	—	—
g70	outdoors	31h 40m	24h 10m	207°	65°
	planetarium: normal	0h 0m	0h 0m	—	—
	planetarium: reversed	2h 15m	2h 15m	52°	67°
r52	outdoors	35h 10m	28h 40m	random	—
	planetarium: normal	8h 30m	6h 30m	random	—
	planetarium: reversed	3h 15m	0h 0m	—	—

APPENDIX 7

ZUGUNRUHE ORIENTATION UNDER LOW LATITUDE "NORMAL" AND "REVERSED"
PLANETARIUM SKIES (15° N), SPRING, 1965 (SEE FIGURE 11)

<i>Bird</i>	<i>Experiment</i>	<i>Hours tested</i>	<i>Hours active</i>	<i>Mean direction</i>	<i>Angular deviation</i>
r52	Planetarium: normal	8h 45m	8h 45m	314°	69°
	Planetarium: reversed	3h 30m	3h 30m	113°	71°
r55	Planetarium: normal	6h 30m	6h 30m	339°	71°
	Planetarium: reversed	3h 30m	0h 0m	—	—
b43	Planetarium: normal	6h 30m	5h 30m	59°	44°
	Planetarium: reversed	7h 0m	4h 0m	240°	57°

APPENDIX 8

ZUGUNRUHE ORIENTATION UNDER "NORMAL" AND "REVERSED" PLANETARIUM SKIES OF 28° N,
COMPARED WITH RESULTS OBTAINED WITH THE STARS SHUT OFF ("CONTROL"),
SPRING, 1965 (SEE FIGURES 12 AND 13)

<i>Bird</i>	<i>Experiment</i>	<i>Hours tested</i>	<i>Hours active</i>	<i>Mean direction</i>	<i>Angular deviation</i>
g63	Planetarium (28°N): normal	8h 30m	8h 30m	27°	51°
	Planetarium (28°N): reversed	8h 30m	8h 30m	196°	57°
	Planetarium: control	10h 15m	10h 15m	random	—
b43	Planetarium (28°N): normal	14h 30m	14h 30m	18°	60°
	Planetarium (28°N): reversed	5h 0m	5h 0m	164°	55°
	Planetarium: control	10h 15m	5h 30m	random	—
r52	Planetarium (15°N and 28°N): normal	21h 45m	14h 15m	330°	75°
	Planetarium (15°N only): reversed	3h 30m	3h 30m	113°	71°
	Planetarium: control	0h 0m	0h 0m	—	—
r55	Planetarium (15°N and 28°N): normal	27h 30m	23h 0m	319°	72°
	Planetarium (15°N and 28°N): reversed	3h 30m	3h 30m	165°	67°
	Planetarium: control	1h 45m	0h 0m	—	—

APPENDIX 8 (CONTINUED)

<i>Bird</i>	<i>Experiment</i>	<i>Hours tested</i>	<i>Hours active</i>	<i>Mean direction</i>	<i>Angular deviation</i>
g77	Planetarium (28°N): normal	11h 0m	11h 0m	44°	57°
	Planetarium (28°N): reversed	8h 30m	5h 0m	235°	52°
	Planetarium: control	10h 15m	10h 15m	random	—
g74	Planetarium (28°N): normal	24h 0m	11h 15m	10°	69°
	Planetarium (28°N): reversed	5h 0m	5h 0m	203°	70°
	Planetarium: control	10h 15m	0h 0m	—	—
g71	Planetarium (28°N): normal	25h 30m	21h 30m	343°	69°
	Planetarium (28°N): reversed	10h 30m	10h 30m	126°	71°
	Planetarium: control	8h 30m	8h 30m	random	—
g70	Planetarium (28°N): normal	16h 0m	11h 15m	356°	74°
	Planetarium (28°N): reversed	0h 0m	0h 0m	—	—
	Planetarium: control	7h 15m	7h 15m	random	—

APPENDIX 9

ZUGUNRUHE ORIENTATION UNDER "NORMAL" AND "REVERSED" PLANETARIUM SKIES OF 28° N, SPRING, 1965 (SEE FIGURE 14)

<i>Bird</i>	<i>Experiment</i>	<i>Hours tested</i>	<i>Hours active</i>	<i>Mean direction</i>	<i>Angular deviation</i>
g65	Planetarium (28°N): normal	10h 0m	10h 0m	random	—
	Planetarium (28°N): reversed	2h 0m	2h 0m	random	—
g75	Planetarium (28°N): normal	14h 0m	14h 0m	random	—
	Planetarium (28°N): reversed	0h 0m	0h 0m	—	—
g72	Planetarium (28°N): normal	16h 30m	16h 30m	random	—
	Planetarium (28°N): reversed	8h 30m	8h 30m	random	—
g61	Planetarium (28°N): normal	16h 30m	14h 45m	98°	77°
	Planetarium (28°N): reversed	2h 0m	0h 0m	—	—
g76	Planetarium (28°N): normal	9h 45m	9h 45m	random	—
	Planetarium (28°N): reversed	3h 30m	3h 30m	61°	75°

APPENDIX 10

ZUGUNRUHE ORIENTATION UNDER THE NATURAL NIGHT SKY (43° N), LATE SPRING, 1965 (SEE FIGURE 15)

<i>Bird</i>	<i>Hours tested</i>	<i>Hours active</i>	<i>Mean direction</i>	<i>Angular deviation</i>
b43	26h 0m	6h 30m	53°	57°
g77	31h 0m	16h 0m	27°	58°
g63	31h 0m	22h 30m	347°	75°
g74	31h 0m	12h 30m	5°	75°
r52	31h 30m	3h 0m	random	—
g65	31h 0m	29h 0m	random	—
g75	31h 0m	23h 30m	random	—
g61	31h 0m	19h 30m	224°	72°
g76	31h 0m	27h 0m	188°	71°
g70	31h 0m	25h 30m	184°	76°