The Ontogenetic Development of Orientation Capabilities

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THE COLLECTION OF PAPERS presented at this symposium attests to the interest that problems of animal orientation have aroused in both physiologists and ethologists. One phase of orientation research, however, has received little mention. This is the question of the ontogenetic development of orientation capabilities.

Early field observers reported that among many species of birds (primarily shorebirds) the young migrate southward independently of adult conspecifics, hence orienting correctly without any prior migratory experience. As a result of such findings, migratory orientation became a classic example of an "innate" behavior (refs. 1 to 4). Unfortunately, this rather arbitrary labeling discouraged further research on the actual maturation of navigation behavior.

Actually, field experiments conducted over a decade ago suggested a dichotomy of navigation capabilities between young and adult birds. When birds of several species were captured and displaced from their normal autumnal migration routes, the adults appeared to correct for this displacement and returned to the normal winter quarters while immatures (birds on their first migration trip) did not, but rather took up courses parallel to the original direction of migration (refs. 5 to 8). This implies an improvement in navigation performance as a result of previous migratory experiences.

I arrived at a somewhat similar conclusion from studies of the migratory orientation of caged indigo buntings. Several years ago I naively was trying to locate the critical star pattern for celestial orientation in this species. My approach was to remove portions of a planetarium sky and look for disorientation among the birds. The results (ref. 9) demonstrated a high degree of redundancy in the celestial orientation system; different individual birds employed different "strategies." Thus one bunting required the entire area within 35° of Polaris for successful orientation while another individual required only a small portion of that circumpolar area. For one additional bird, the northern stars were not essential at all. Such results suggested a level of individual variation hard to reconcile with the idea of a predetermined star map under rigid genetic control.

These considerations have led me to study

TABLE 1.—*Orientation of Young Indigo Buntings, Hand-Raised Under Conditions of Visual Isolation from Celestial Cues, 1965*

Bird	No. of experiments	Units of activity (Total N) [a]	p (Rayleigh test)	p (V test)	Mean direction
w88		211	0.18	0.03	187°
	8		0.24	0.07	(152°)
w89		480	0.55	0.21	....
	9		0.44	0.20	....
w93		119	0.04	0.01	158°
	6		0.23	0.05	168°
w94		754	0.45	0.18	....
	12		0.45	0.11	....

[a] Sample sizes were determined by dividing the total number of units of footprint activity, N, by a correction factor. This divisor was determined empirically and represents the interval at which activity measures become independent of one another.

the orientational capabilities of hand-raised indigo buntings. This paper represents a summary of all such experiments performed to date. Portions have been adopted from studies already published (ref. 10) or currently in press.[1] I am grateful to the National Institutes of Health (through a health science advancement award to Cornell University) and the National Science Foundation (through GB 13046 X) for financial assistance. I also thank Margaret Platt and Carol Conley for help with experimental series II and III, and members of Cornell's Orientation Seminar Group for comments and criticisms.

METHODS

Two groups of buntings have been reared for experimentation, 10 individuals in 1965, and 26 in 1968. All birds were removed from their nests and brought to the laboratory where their visual experience with celestial cues was carefully controlled. I attempted to take birds before their eyes had opened, but this was not always possible. Details concerning the age, sex, fledging date, and "eye condition" of all experimental birds are given in Appendixes 1 and 2. Young birds were kept in nest-cups and fed a diet of cricket abdomens supplemented by several insectivorous mashes. At the time of fledging (when 10 or 11 days old) I transferred the birds to cages 65 × 65 × 65 cm (2 × 2 × 2 feet) in size. The diet gradually shifted to one of dried seeds and the buntings became self sufficient at an age of approximately 25 days.

Birds were housed in windowless rooms where the day length was controlled to duplicate that present outdoors. The young were maintained in both visual and acoustical isolation from adult indigo buntings (with the exception of experimental series IV). These studies, therefore, test only the effects of visual exposure to certain cues. The role, if any, normally played by the parents or other adult birds in influencing the orientational choices of immatures remains a subject for future investigation.

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[1] EMLEN, S. T.: Celestial Rotation: Its Importance in the Development of Migratory Orientation. Science, vol. 170, Dec. 11, 1970, pp. 1198–1201.

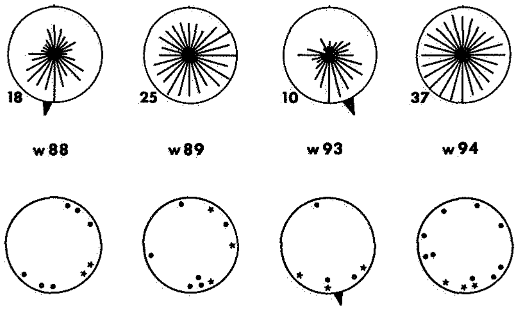

FIGURE 1. ***Zugunruhe*** **orientation of young indigo buntings hand-raised under conditions of visual isolation from celestial cues and tested outdoors under natural night sky. Top: Vector diagram summaries plotted such that radius equals greatest number of units of activity in any one 15° sector. Number represented is at lower left of each diagram. Bottom: Distributions of mean directions for each bird. Stars represent mean headings for first three nights of testing. (Fewer than three stars indicates bird was inactive during early experiments.) Arrows denote statistically significant mean directions.**

Weight, fat level, and molt status were recorded weekly for each bird. Nocturnal activity also was monitored. When the birds completed the postjuvenal molt, acquired visible subcutaneous fat deposits, and exhibited nocturnal activity, I considered them ready for experimentation. I placed each bird in an individual, circular, funnel-shaped cage, and recorded its directional tendencies by means of the "foot print technique" (ref. 11). In experimental series I, birds were tested outdoors under the natural night sky at a location 39 km (24 mi) from any sizeable town. This minimized the possibility of artifact orientation caused by horizon glows from city lights. Experimental series II, III, and IV were performed under the artificial skies of Cornell's research planetarium. This is an air-supported structure, hemispherical in shape, and measuring 9 meters in diameter and 5.5 meters in height. It is equipped with a highly modified Spitz Model A–3–P star projector. All planetarium settings were for a latitude of 42° north.

The results from each individual bird are presented both as a summary vector diagram and as a plot of the mean directions obtained from replicate tests. I tested the null hypothesis of randomness by both the Rayleigh test and the "*V*" modification of the Rayleigh test (ref. 12). Mean directions were calculated by vector analysis (ref. 13). Values for these statistics are presented in the accompanying tables. Unless stated otherwise, the figures are drawn with 0 or 360° representing north, 90° east, 180° south, and 270° west.

RESULTS

Experimental Series I

In the autumn of 1965, I tested the orientational abilities of 10 immature indigo buntings that had been hand-raised under conditions of restricted access to celestial information. These experiments have been reported upon elsewhere (ref. 10), and will be reviewed here only briefly.

Four individual birds lived in a windowless room from the time they were taken as nestlings until mid-September when they were tested outdoors under the natural night sky. During the experiments, they were placed outdoors after sunset and returned to their rooms prior to sunrise. Consequently the birds were never allowed a view of the Sun and were denied access to nocturnal celestial information until the migration season. Two experiments of approximately three hours duration were conducted each night, the first between 9 p.m. and midnight and the second from 1 to 4 a.m. As a result, these birds viewed a 105° rotation of the night sky during the experiments.

The results of these birds are shown in figure 1 and table 1. Using the "*V* test" for

TABLE 2.—*Orientation of Immature Indigo Buntings Allowed a One-Month Exposure to Natural Surroundings (Including Celestial Cues) Just prior to the Autumn Migration Season*

Bird	No. of experiments	Units of activity (total *N*)	*p* (Rayleigh test)	*p* (*V* test)	Mean direction
w95		73	0.00	0.00	192°
	4	insufficient sample size..........		....	(189°)
w96		819	0.00	0.00	186°
	13		0.15	0.00	166°
w97		191	0.08	0.01	184°
	3	insufficient sample size..........		....	(180°)

randomness, two birds are seen to show southerly tendencies. (Only w93 is significantly non-random by the Rayleigh test.) Considering the consistency of orientation during consecutive tests, only w93 shows a significant directional preference and then only by the "V" test. The behavior of the remaining birds was random.

A second group of buntings was given greater exposure to celestial information. Until self-sufficient, they were raised by a colleague, John Rice, who housed them in a room with a south-facing window. Although they were covered at night, they frequently were able to observe the daytime sky and, occasionally, the Sun itself. I obtained these birds shortly after their fledging and moved them to the windowless room where they lived until August 15. I then placed them in a large outdoor aviary for a one month period prior to the migration season (August 15 to September 15). This aviary allowed a full view of the sky and natural surroundings. The results from these birds, presented in figure 2 and table 2, show a notable improvement over the previous group. All three birds displayed clear southerly tendencies; the consistency of these directional responses, revealed by the nightly mean headings, also improved considerably.

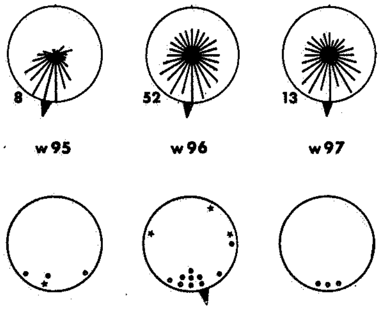

FIGURE 2. *Zugunruhe* orientation of immature birds allowed a 1-month exposure to natural surroundings (including celestial cues) just prior to the autumn migration season.

These early results suggested that some weak orientational ability did develop in some individual buntings without the need of any social contact with experienced birds or any prolonged visual-celestial experience during their early development. They further suggested that exposure to celestial cues resulted in considerably improved performances. Whether this was due to viewing the Sun, the stars, or, perhaps, integrating the two sources of information could not be determined.

A third group of buntings yielded data that are more difficult to interpret. They also were placed outdoors in a large aviary but not until the migration season had begun (from September 15 until late October). These birds showed poor orientational abilities with only one of three individuals consistently directing its activity southward. The possible implications of these results will be discussed in a later section.

Experimental Series II

If a bunting must learn to recognize star patterns, those patterns will be useless as orientation cues unless their positions are learned with regard to some other directional reference system or marker.

In the summer of 1968 I again hand-raised indigo buntings for a series of experiments designed to retest the ability of "naive" birds to use celestial cues, and to determine the possible importance of celestial rotation in providing a reference axis for direction determination.

The first experimental group, group A, consisted of 10 birds that never left their windowless living quarters until I tested their orientational tendencies during the autumn migration season. The actual experiments were conducted under the artificial skies of Cornell's planetarium set to duplicate those present outdoors, with the exception that the experimental sky was held stationary. These birds never were allowed to view either the Sun or the natural night sky.

Each experiment lasted two hours and the hour-angle position of the planetarium sky was set to correspond with the mid-point of that two-hour period.

The results are shown in figure 3 and table 3. Of the 10 individual buntings, none demonstrated a clearcut directional tendency. This was true whether one analyzed the total activity of each bird or the distribution of mean directions from replicate tests. This contrasts strongly with previous results obtained from adult buntings which orient normally under stationary planetarium skies (ref. 9). Since the artificial sky contained the full complement of autumnal stars and star patterns (in their correct positions), the behavior of the young birds argues against a genetic recognition of specific stellar cues.

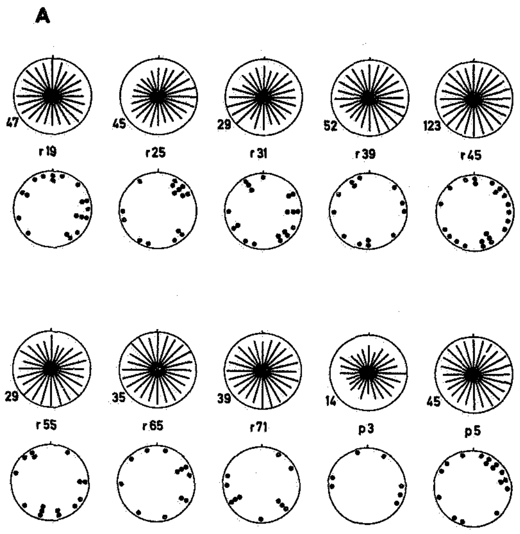

FIGURE 3. **Orientation of young buntings prevented from viewing celestial cues during their early development and tested under a stationary planetarium sky.**

A second group of eight birds, group B, also was housed in a windowless room and prevented from obtaining any view of the natural sky. However, these individuals were taken into the Cornell planetarium and exposed to the artificial sky during the months of August and September. The artificial sky was set to duplicate that present outdoors and the star projector was modified to rotate at a speed of one revolution per 24 hours, thus duplicating the normal pattern of celestial rotation. The young birds continued to live in their indoor quarters, but, three times a week, I transferred them to the planetarium at 9 p.m. and returned them to their indoor cages

TABLE 3.—*Orientation of Young Indigo Buntings Prevented from Viewing Celestial Cues During Their Early Development and Tested Under a Stationary Planetarium Sky*

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh test)	p (V test)	Mean direction
r19		963	0.878	0.649	....
	19		0.261	0.836	....
r25		846	0.144	0.392	....
	15		0.393	0.616	....
r31		573	0.942	0.388	....
	19		0.539	0.261	....
r39		1086	0.522	0.563	....
	13		0.942	0.422	....
r45		2706	0.497	0.147	....
	22		0.449	0.356	....
r55		604	0.528	0.131	....
	15		0.449	0.102	....
r65		762	0.861	0.701	....
	12		0.530	0.751	....
r71		722	0.811	0.270	....
	11		0.316	0.069	(195)
p3		238	0.692	0.500	....
	7		0.067	0.907	....
p5		964	0.644	0.695	....
	16		0.111	0.943	....

between 4:30 and 5 a.m. (Eastern Daylight Time).

During the migration season, these birds were tested under the identical, stationary, planetarium sky described for group A. In fact, birds from both group A and group B usually were tested simultaneously in the planetarium.

The rationale for testing birds under a stationary sky, thereby denying them direct access to rotational information, was to test whether they had integrated information from celestial configurations with the potential reference framework provided by the axis of rotation. The experimental design called for retesting these birds under a moving sky if orientational tendencies failed to appear with stationary sky conditions.

Figure 4 and table 4 show that such an integration apparently did take place. Exposure to stellar cues, including celestial motion, resulted in greatly improved orientation. Of the eight birds, seven exhibited southerly preferences in both total activity and nightly mean headings. In keeping with previous reports, the behavior of immatures was less accurate than that of adults tested under similar conditions (refs. 10, 14, and personal communication from W. J. Hamilton, III), but the directional tendencies were highly significant and all lay between SSE and SSW, well within the normal migratory range for the species.

A third group of buntings, group C, also was exposed to planetarium skies prior to the migration season. After becoming self-sufficient, these birds were taken on three different nights each week and exposed for a similar length of time to an artificial sky. However, this sky was abnormal in several respects.

Once again, I had modified the star projector, this time by constructing a special attachment arm that allowed the celestial sphere to be rotated about any axis of my choosing. For group C, I selected the bright star Betelgeuse as the new "pole star" and the constellation Orion became the dominant pattern in the new "circumpolar" area of the sky. The speed of rotation (15° per hr) and the direction (clockwise) remained as they were before.

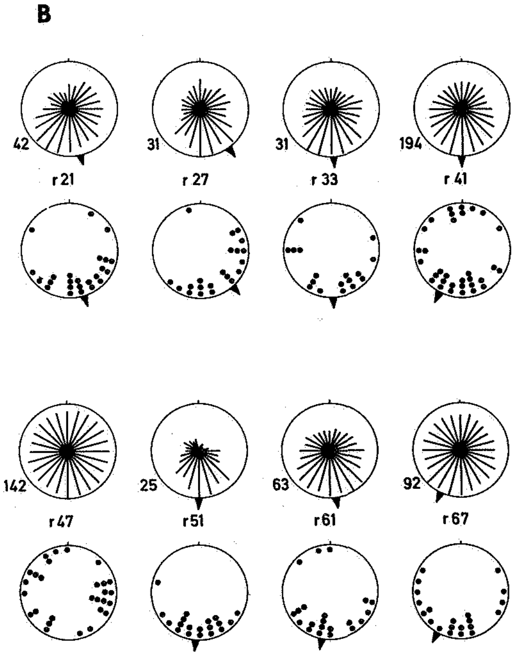

FIGURE 4. Orientation of young buntings permitted regular viewings of a normal, rotating planetarium sky during their early development and tested under a stationary artificial sky.

I selected this new sky setting for several reasons. First, a bright star was located at the pole of the new axis. Second, a very bright constellation was located in the "circumpolar" area, an area shown to be of importance in the celestial orientation process of indigo buntings (ref. 9). Third, the "hour angle" position was selected carefully so that the actual northern circumpolar stars (in particular the constellations Ursa Major and Cassiopeia and the star Polaris) were present in this artificial sky. They were located just to the south of the new "celestial equator" and moved progressively across the sky from east to west as the night progressed.

If celestial rotation provides a reference axis for the use of stellar cues, then the birds of group C might adopt this incorrect axis and orient their migratory activity in an inappropriate direction. On the other hand, if young birds possess a genetically predetermined star map as has been proposed by some authors (ref. 1), then the birds should orient "south" with reference to the normal circumpolar area of the sky. These two "south" directions should be easily distinguishable since they range from 110° to 180° apart in these incorrect planetarium settings.

Figure 5 and table 5 give the results from these birds when plotted relative to true stellar north—with Polaris dictating the northward direction. Of the seven birds, only two showed significant directional tendencies (measured by either the Rayleigh or the "*V*" test): r23 preferred a northwesterly bearing while r57 aimed southward. The accumulation of mean bearings for r57 did not deviate from random. Neither did the orientation behavior of the remaining five individual birds.

Compare these results with figure 6 and

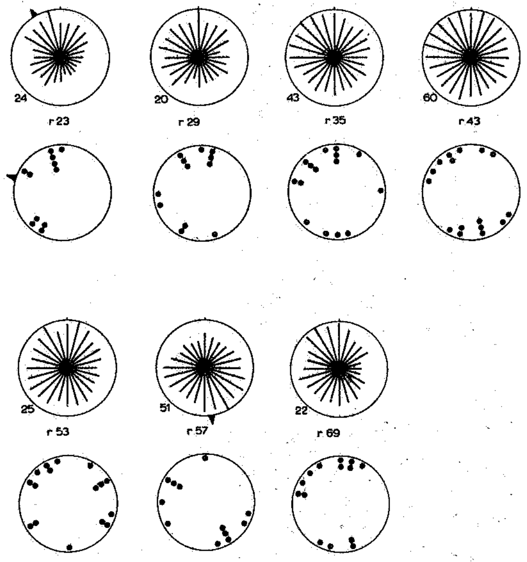

FIGURE 5. Orientation of young buntings exposed to a planetarium sky that rotated at 15° per hour about an incorrect axis during their early development. Data are plotted with reference to true stellar north (position of Polaris dictating north).

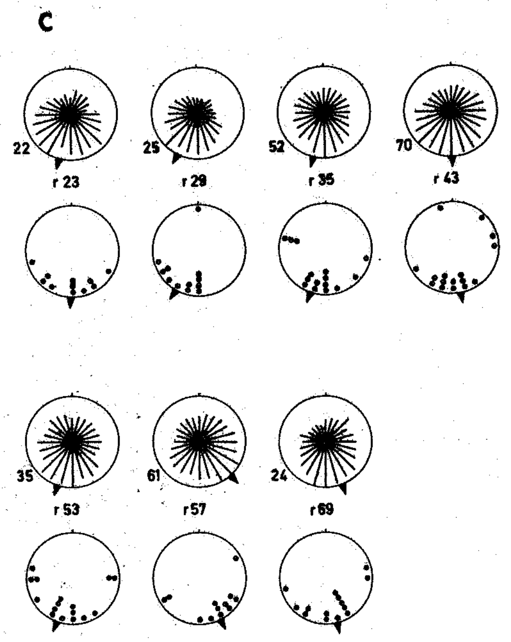

FIGURE 6. Same data as in figure 5 but plotted with new "pole star" (Betelgeuse, of the constellation Orion) designating "north" or 0°.

table 6 in which the data from group C are replotted relative to the new axis of rotation —with the position of Betelgeuse defining north. All seven birds now display a "southerly" orientation indicating a realignment of directional behavior to correspond with the new axis of rotation. The mean bearings range from 138° to 211° and the values obtained from total activity measures and distribution of nightly means are in very close agreement.

Once again these results are inconsistent with the hypothesis of a predetermined template of star positions. Rather they imply an important role of celestial rotation in the maturation of migratory orientation abilities.

Experimental Series III

Previous work has suggested that many individual adult indigo buntings rely for direction determination upon star patterns located near the northern axis of rotation (ref. 9). I was curious to learn whether this was also true for immatures. In particular, might the birds of group C have come to rely upon "wrong" star patterns situated near the artificial axis of rotation?

I tested this by removing selected stellar information from the planetarium sky by attaching a cardboard mold over the appropriate portion of the star projector. As in experimental series II, all observations were made under stationary skies.

I presented birds from group B with a planetarium sky in which the northern circumpolar area, defined as encompassing an area within 35° of Polaris, had been blocked. The results (fig. 7 and table 7) indicate a

TABLE 4.—*Orientation of Young Buntings Permitted Regular Viewings of a Normal, Rotating Planetarium Sky During Their Early Development and Tested Under a Stationary Artificial Sky*

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh test)	p (V test)	Mean direction
r21		684	0.002	0.000	169°
	24		0.000	0.000	165°
r27		455	0.009	0.006	145°
	21		0.001	0.003	138°
r33		487	0.004	0.000	178°
	17		0.005	0.001	182°
r41		3293	0.000	0.000	182°
	32		0.079	0.024	208°
r47		2932	0.440	0.205	....
	28		0.718	0.452	....
r51		251	0.000	0.000	181°
	19		0.000	0.000	186°
r61		1024	0.000	0.000	174°
	21		0.003	0.001	191°
r67		1777	0.088	0.025	207°
	21		0.001	0.001	195°

high degree of individual variability. Of six active birds, only two continued to display southerly tendencies, r33 to the south, and r27 to the southeast. One additional bird, r41, took up a new and inappropriate orientation to the northeast. The behavior of the three remaining birds failed to deviate from random.

These results are consistent with previous findings from adults: Blocking the northern sky adversely affects the orientation of most buntings.

I subjected the birds of group C to two sets of blocking experiments. First, I removed all the stars located in the southern celestial hemisphere. Since the true northern circumpolar stars were located just south of the celestial equator in the C sky, this manipulation eliminated them as potential cues.

The results of six birds tested under these conditions are shown in figure 8 and table 8. Again, inter-individual variation is high; but four individual buntings continued to orient southward.

This contrasts with the results obtained from the same birds when I removed the *new* "circumpolar stars" (within 35° of Betelgeuse) from the sky. Figure 9 and table 9 reveal that all birds of group C failed to show significant directional preferences under

TABLE 5.—*Orientation of Immature Buntings of Group C Plotted With Reference to True Stellar North (Position of Polaris Dictating North Point)*[a]

Bird	No. of experiments	Units of activity (Total *N*)	*p* (Rayleigh test)	*p* (*V* test)	Mean direction
r23		354	0.04	0.99	328°
	11		0.03	0.86	294°
r29		343	0.25	0.91	....
	12		0.09	0.94	(314°)
r35		813	0.15	0.92	....
	15		0.13	0.91	....
r43		1249	0.20	0.90	....
	16		0.88	0.38	....
r53		592	0.66	0.69	....
	16		0.34	0.93	....
r57		1056	0.20	0.03	173°
	12		0.59	0.17	....
r69		379	0.26	0.75	....
	14		0.14	0.93	....

[a] The eighth bird in this group, r49, developed the habit of "somersaulting" in the orientation cage. Since the resulting ink smudges represented an aberrant behavior pattern, they are not treated in this analysis.

this condition. I only performed two replicate tests under these skies, so the sample sizes of mean directions are insufficient for statistical analyses. However, a qualitative glance shows that a clumping of means occurred for only one bird, r43, and that clumping was in an inappropriate direction. Although Betelgeuse and the constellation Orion were absent in this experimental sky, the true northern circumpolar stars were present. The fact that the buntings were unable to orient implies that these patterns provided insufficient information for direction determination.

The most important area of the night sky thus appears to be defined not by the presence of specific stellar configurations but by a relationship to the axis of celestial rotation.

Experimental Series IV

Many studies of behavioral development have stressed the importance of sensitive or critical periods during which the young animal responds preferentially to certain types of sensory input. In the case of bunting orientation, might such a developmental phase exist prior to the first migration season? Or would a prolonged exposure to celestial cues following the autumn migration period enable birds of group C to re-adopt the normal migration direction in future years?

Following the experiments in the autumn of 1968, I placed the birds from group C in a large, windowless, indoor aviary, 2.4 × 3.7 meters. Photoperiod was maintained by an

TABLE 6.—*The Data of Table 5 Re-analyzed With the New "Pole Star" (Betelgeuse of the Constellation Orion) Designating "North" or 0°*

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh (test)	p (V test)	Mean direction
r23		354	0.017	0.003	195°
	11		0.001	0.000	186°
r29		343	0.001	0.000	207°
	12		0.001	0.001	211°
r35		813	0.015	0.002	194°
	15		0.001	0.000	198°
r43		1249	0.000	0.000	180°
	16		0.006	0.001	172°
r53		592	0.063	0.014	200°
	16		0.001	0.001	201°
r57		1056	0.002	0.005	138°
	12		0.003	0.002	156°
r69		379	0.013	0.003	161°
	14		0.001	0.009	600°

astronomical time-clock set for 18° north latitude. This served to simulate the changes in daylength typical for the wintering grounds of this species. In the spring, I moved these birds outdoors to an aviary, 2.4 × 4.9 meters, providing a full view of natural surroundings and celestial cues (including celestial motion). The birds lived at this outdoor location from early May until the end of autumn migration season in early November 1969.

Six of the original birds molted normally, deposited large quantities of fat, and exhibited nocturnal activity. After six full months of access to normal visual-celestial information, I returned these birds to the planetarium and tested them under the incorrect, stationary skies they had been exposed to a year previously. This sky was selected to present the birds with a choice of southern migration directions. The star Betelgeuse was located at an altitude of 42° in one direction; the pole star, Polaris, was situated at a comparable altitude in a different direction. Neither pole star coincided with the direction of either geographic or magnetic north. (Considering Betelgeuse as 0°, geographic north is 48° and magnetic north, 38°.) I tested the birds only once each night, always at the same sky setting. This prevented them from obtaining indirect information about the axis of rotation by comparing the movement of stars located at different points in the celestial sphere between successive sky settings.

The orientation performances of these birds are shown in figure 10 and table 10. Although the sample sizes are rather small for some birds, five of the six individuals show a clear tendency to orient south relative

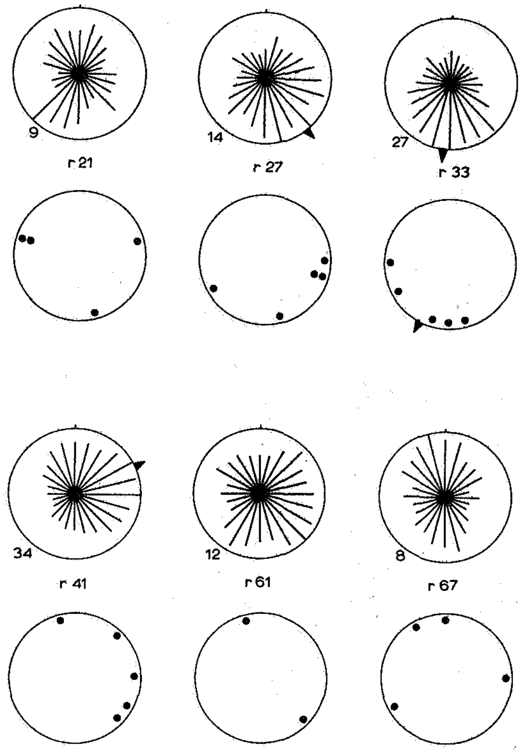

FIGURE 7. **Orientation of immature buntings of group B under a planetarium sky in which the circumpolar stars have been removed.**

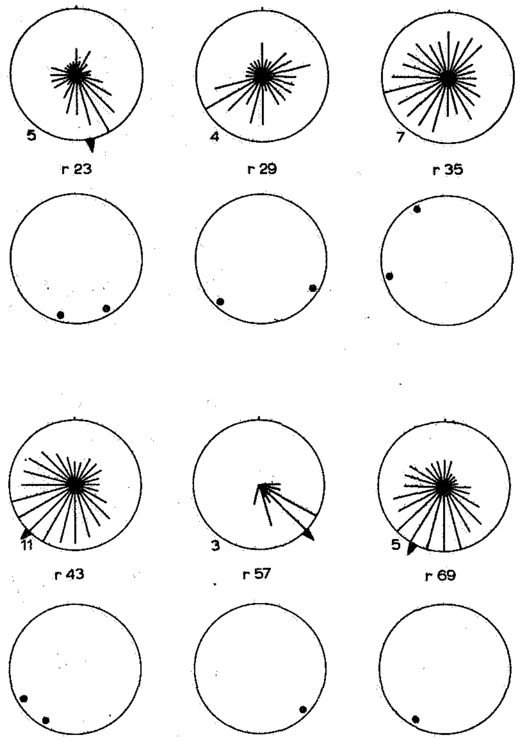

FIGURE 8. **Orientation of buntings of group C under a planetarium sky in which the southern stars have been blocked.**

to the *incorrect* axis of rotation. The birds not only took up directions remarkably similar to those selected the previous year, they also showed a decrease in the amount of scatter in their nocturnal activity.

This implies that the birds had not adjusted to a new axis of rotation; they had not relearned the positions of star patterns relative to a new reference framework. Rather, the results are consistent with the hypothesis of a sensitive period in the development of indigo buntings, a period during which the young are highly receptive to rotational input. During later life buntings show a lesser tendency to modify their behavior as a result of visual-celestial experience.

The poor orientational results of the buntings in group C in experimental series I are of interest in this regard. These birds were placed outdoors and allowed visual exposure to celestial cues after the initiation of the migration season. Yet they failed to show the improvement in orientational ability attained by individuals of a second group given similar exposure prior to the time of migration (figure 2). Therefore the optimal period for learning stellar cues might coincide with the period of pre-migratory development. Stated another way, might this sensitivity decrease with the onset of actual migratory behavior? Answers to these questions must await future experiments employing larger samples of birds.

TABLE 7.—*Orientation of Immature Buntings—Group B—Under a Planetarium Sky in Which the Circumpolar Stars Have Been Removed*

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh test)	p (V test)	Mean direction
r21		134	0.93	0.39	....
	4	insufficient sample size..........		....	
r27		223	0.06	0.03	142°
	5		0.17	0.08	(135°)
r33		394	0.00	0.00	186°
	5		0.03	0.01	205°
r41		552	0.00	0.93	66°
	5		0.14	0.65	....
r61		211	0.46	0.24	....
	2	insufficient sample size..........		....	
r67		124	0.74	0.72	....
	4	insufficient sample size..........		....	

TABLE 8.—*Orientation of Immature Buntings—Group C—Under a Planetarium Sky in Which the Southern Stars Are Missing*

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh test)	p (V test)	Mean direction
r23		47	0.26	0.05	170°
	2	insufficient sample size..........		....	
r29		46	0.65	0.17	....
	2	insufficient sample size..........		....	
r35		112	0.52	0.38	....
	2	insufficient sample size..........		....	
r43		176	0.03	0.04	227°
	2	insufficient sample size..........		....	
r57		12	0.05	0.04	136°
	1	insufficient sample size..........		....	
r69		71	0.09	0.02	206°
	1	insufficient sample size..........		....	

TABLE 9.—*Orientation of Immature Buntings—Group C—Under a Planetarium Sky in Which the "Circumpolar" Stars (Within 35° of Betelgeuse) Have Been Blocked*

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh test)	p (V test)	Mean direction
r23	1	44	0.88	0.69	....
		insufficient sample size.........		....	
r29	2	63	0.88	0.59	....
		....	....	....	
r35	2	167	0.58	0.18	....
		....	....	....	
r43	2	257	0.72	0.79	....
		....	....	....	
r53	2	90	0.95	0.38	....
		....	....	....	....
r57	2	171	0.34	0.93	....
		....	....	....	
r69	2	167	0.44	0.36	....
		....	....	....	

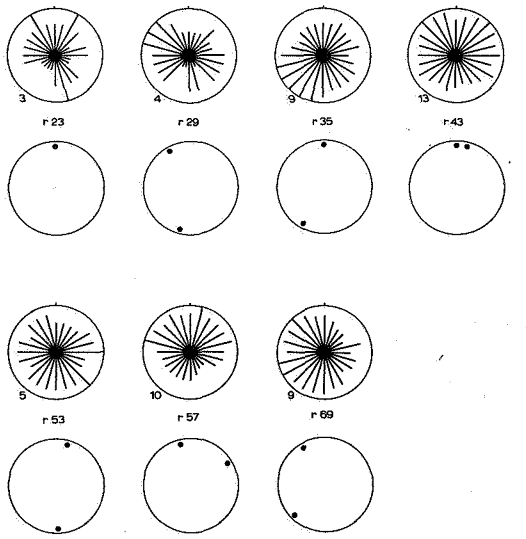

FIGURE 9. Orientation of buntings of group C under a planetarium sky in which the "circumpolar" stars (within 35° of Betelgeuse) have been blocked.

DISCUSSION OF EXPERIMENTS

These series of experiments furnish strong evidence that early visual experience plays an important role in the maturation of celestial orientation abilities in indigo buntings. In the hopes of stimulating both discussion and future experimentation, I offer the following working hypothesis. I propose that young buntings have a predisposition to respond to the apparent rotational motion of the night sky. This responsiveness is not dependent upon prior migratory experience; neither is it rewarded in the conventional sense of the term. The experiments in series IV suggest that the peak in responsiveness to rotational information is present during the first summer of life, prior to the first migration season.

The fact that stars located near the celestial axis move through much smaller arcs (have slower linear velocities) than those near the celestial equator could allow the

TABLE 10.—*Orientation of Indigo Buntings of Group C in the Autumn of 1969, Following One Full Summer of Exposure to Natural Surroundings and Celestial Cues*

Bird	No. of experiments	Units of activity (Total N)	p (Rayleigh test)	p (V test)	Mean direction
r23		54	0.00	0.00	181°
	4	insufficient sample size..........	....		
r29		134	0.00	0.00	223°
	5		0.28	0.09	(218°)
r43		391	0.88	0.32	....
			0.92	0.34	....
r53		214	0.01	0.00	190°
	6		0.03	0.01	191°
r57		234	0.01	0.00	150°
	6		0.21	0.04	160°
r69		28	0.03	0.01	183°
	2	insufficient sample size..........	....		

birds to locate a north-south directional axis. Stars and patterns of stars are of no value for direction finding until their positions are learned relative to some reference location. If the birds come to associate certain patterns of stars with areas of either fast or slow rotation, the axis of motion can become one such reference system. The results from experimental series III suggest that young buntings tend to concentrate their attention on areas of slow rotation, thereby coming to rely upon the circumpolar sky areas. Within this broad constraint, individual birds could learn a variety of star groupings. Such a hypothesis is consistent with the high degree of individual variability obtained in blocking experiments with adult buntings. This redundancy in pattern recognition could be highly adaptive since clouds frequently obscure portions of the sky from view. A preferential reliance upon circumpolar sky areas further assures the presence of familiar star groupings at all seasons and times of night since such cues are rarely below the horizon at the northern latitudes through which indigo buntings migrate.

Once an integration of stellar and rotational information has occurred, a bird should be able to locate the rotational axis (and, hence, a reference direction) from the geometry of star configurations alone. This implies that celestial motion *per se* need not be an important cue for adult birds. In point of fact, the accurate orientation of several species of caged migrants under stationary planetarium skies (refs. 1, 15, unpublished observations by S. T. Emlen, and personal communication from S. A. Gauthreaux, Jr.) demonstrates that such motion is not essential for direction determination. But lack of essentiality need not imply that rotational cues cannot be used as a source of directional information. Two of four birds in group A of experimental series I showed southerly biases when tested under the natural night sky although I had prevented them from viewing the sky during their early development. These results differed from those obtained

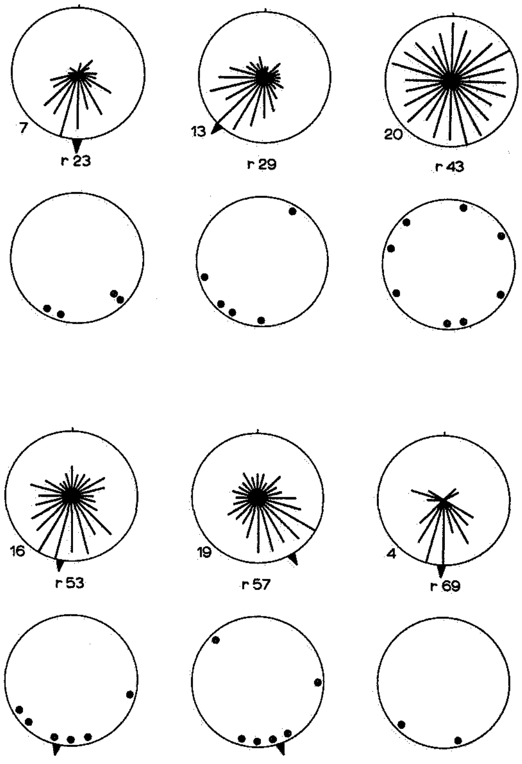

FIGURE 10. Orientation of buntings of group C in the autumn of 1969 following a summer of exposure to natural surroundings and celestial cues.

from birds kept in similar visual isolation but tested under a stationary starry sky (group C, experimental series II). It is conceivable that the former birds integrated pattern information with the visible rotation during the first few hours of exposure to the natural night sky; or, the two buntings might have used rotational information directly as an orientation cue. (This hypothesis need not imply that buntings directly perceive the slow rate of celestial motion. One could locate the axis of rotation by making observations over longer periods of time and comparing the degree of movement of stars located at different points in the celestial sphere.)

All of this speculation avoids the question of why the young migrant orients southward on its first flight. Rotation, in this hypothesis, merely provides a stable reference axis. The use of this reference to select a southerly heading as opposed to any other remains a topic for future investigation.

This paper has concentrated on only one aspect of the migratory orientation problem, the use of stellar cues. Future experiments should consider the possible integration of other types of directional information into adult guidance systems. For example, we know that most nocturnal migrants are daytime animals except during the migration season, and experiments by St. Paul (ref. 16) and Shumakov (ref. 17 and 18) show that several such species possess an ability to orient by the Sun. The integration of stellar information with information about the path of the Sun and, in particular, the position of sunset might lead to a more accurate orientation ability. A possible selective advantage for such a system is easy to imagine for birds that migrate over large bodies of water and might be unable to land with the coming of sunrise.

Similar arguments could be made for the coupling of celestial information with other types of guidance cues, be they topographic, magnetic, or meteorological.

Finally, one might inquire about the possible selective advantage of a maturation process that integrates experience-dependent and experience-independent factors and rotational and configurational information. One possible explanation lies in the long-term unreliability of stellar cues themselves. Agron (pp. 525–526 of ref. 19) has noted that the positions of stars are not constant through evolutionary time. This is due, primarily, to the precession of the Earth's axis. Agron likened this to the wobbling of a spinning top and states:

> The angle of tilt of the Earth's axis remains constant, but the direction of the axis changes. In a period of 25,800 years, the gyrations, in a cone, of the earth's axis cause the celestial pole to make one circuit about a circle of 23.5° radius.

This motion produces marked seasonal and latitudinal changes in the apparent positions of stars, the "spring" stars of the present becoming "autumn" stars in 13 000 years, and vice versa. The values of declination also change; as the axis moves through its circle of 47°, Vega becomes the new pole star and the declination of Polaris shifts from 90° north to 43° north. Similar changes occur for all stars with the result that the stellar information typical for any given latitude or season is altered markedly.

The implications of these changes for the evolution of celestial navigation are obvious. If migrants are to rely on a genetically fixed star map that they have inherited, the rate of genetic change must be rapid enough to allow for these changes in celestial position.

A maturation process involving the coupling of stellar information with a secondary set of reference cues would minimize this problem. The axis of apparent celestial rotation is well suited to function as one such cue because this axis is aligned with geographic north-south regardless of what particular stars are located at its "poles."

Over a decade has passed since Lehrman (ref. 20) issued his warning to ethologists that simple categorization of behaviors as "innate" could serve to discourage research on behavioral development. The lack of data on the maturation of guidance mechanisms bears witness to the truth of his statement. Hopefully this paper will provide a small stimulus to others to initiate studies in this area, for I feel that such investigations may lead to new discoveries concerning the functioning of animal orientation systems.

APPENDIX 1

Age and Sex Data for Hand-Raised Birds Used in Experimental Series I

Bird	Sex	Age at capture	Fledging date	Group	Eyes at capture
w88	M	8 days	21 June	A	open
w89	F	10 days	30 June	A	open
w90	F	9 days	26 July	C	open
w91	F	8 days	27 July	C	open
w92	M	8 days	27 July	C	open
w93	M	3 days	8 August	A	closed
w94	F	3 days	8 August	A	closed
w95	F	4 days	8 July	B	closed
w96	F	4 days	8 July	B	closed
w97	F	3 days	30 June	B	closed

APPENDIX 2

Age and Sex Data for Hand-Raised Birds Used in Experiment Series II, III and IV

Bird	Sex	Age at capture	Fledging date	Group	Eyes at capture
r19	F	5 days	June 30	A	slits
r21	F	9 days	June 21	B	open
r23	M	9 days	June 21	C	open
r25	M	4 days	July 11	A	closed
r27	M	4 days	July 11	B	closed
r29	M	4 days	July 11	C	closed
r31	M	4 days	July 11	A	closed
r33	M	5 days	July 10	B	slits
r35	F	5 days	July 10	C	slits
r39	F	8 days	June 30	A	open
r41	F	8 days	June 30	B	open
r43	F	8 days	June 30	C	open
r45	M	8 days	June 30	A	open
r47	M	9 days	July 18	B	open
r49	F	9 days	July 18	C	open
r51	F	4 days	July 22	B	closed
r53	M	4 days	July 22	C	closed
r55	F	4 days	July 22	A	closed
r57	M	9 days	July 23	A	open
r61	F	9 days	July 23	B	open
r65	F	8 days	July 23	A	open
r67	F	8 days	July 23	B	open
r69	F	9 days	July 29	C	open
r71	M	6 days	July 27	A	open
p3	F	5 days	August 3	A	slits
p5	F	5 days	August 3	A	slits

DISCUSSION

Question: Do you know of any data that suggest that motion, *per se*, in celestial bodies is a cue? Can birds see the movement of Sun, Moon, or stars directly?

Emlen: That is a good question. However, I have no new information that pertains directly to it. In order to use celestial motion as I am suggesting, one need not perceive it directly. One easily can locate the axis of rotation by making observations over long periods of time and comparing the degree of movement of stars located at different points in the sky. Whether celestial motion itself is actually visible is a debated subject. Horridge has concluded that some crabs can detect movements well below the rate of celestial rotation. For birds, however, this remains an unresolved question.

Question: The data for group C are plotted in two ways. How can one be oriented and the other not?

Emlen: Experiments were performed twice a night. A typical experiment lasted two hours and the hour-angle position was set for the mid-point of that two-hour period. Consequently, the birds of group C oriented under two different skies each night. Since the times of the experiments also varied somewhat, this resulted in the accumulation of oriented responses under a variety of hour-angle settings. The position of the "pole" star, Betelgeuse, did not change during these sky shifts, but the position of the real north star, Polaris, did. If the birds were orienting relative to a "Betelgeuse axis," then plotting the data relative to Polaris would be equivalent to rotating each data distribution by an amount equal to the difference in azimuth positions of Polaris and Betelgeuse. This difference is not constant but changes with changes in hour-angle settings, so an increase in scatter results.

QUESTION: Where is magnetic north in the Cornell planetarium?

EMLEN: This is variable since the experimenter can orient the star projector to make stellar north correspond to any direction of his choosing. To guard against a misinterpretation of planetarium results, various types of controls are imperative. One of these involves testing birds under a starless dome, or placing a sheet of frosted glass over the top of an individual orientation cage to simulate "instant overcast." Another control is to change the north point and then note whether the birds change their behavior in keeping with the artificial sky. In experimental series II, the birds of groups A and B were subjected to both control procedures. Depending upon the sky setting, magnetic north was located at either 130° or 310°. True geographic north would be at 140° and 320°. With the star projector modified to rotate abnormally for group C, the control of reversing the north point became impractical. For these birds magnetic north was 40°, true geographic north 50° (considering Betelgeuse as 0°).

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