ORIENTATION BEHAVIOR OF RING-BILLED GULL CHICKS AND FLEDGLINGS

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During 1964, 294 Ring-billed Gull (*Larus delawarensis*) chicks ranging from 2 to 20 days old were subjected to orientation cage experiments designed to test the influence of various landmarks, the presence or absence of the sun, and different intensities of magnetic disturbances on orientation behavior. An additional 15 ring-bill chicks were released in cages after I attempted to modify their sensory faculties by means of blindfolds, sewn eyelids, or ear plugs. These chicks usually spent most of their time attempting to remove the attached devices and no conclusions could be formulated regarding orientation. I also subjected 60 juveniles (young-of-the-year capable of flight) to homing trials at distances ranging from 7 to 18 miles from the colony. Birds used in this study were obtained from a Lake Huron breeding colony near Rogers City, Presque Isle County, Michigan.

The exact age of the experimental subjects was known in many instances because I had color-marked them at hatching in conjunction with another project and these individuals provided a basis for estimating the age of unmarked chicks. I attempted to observe and record variations in activity patterns which seemed to occur during orientation and which might be correlated with chick maturation. Certain behavioral changes (e.g., changes in response to human intrusion) were not associated with orientation and it was necessary to try to evaluate these factors separately in order to avoid misinterpretation of their significance. The responses of chicks to humans entering the territories seemed to develop in the following pattern. For about two days following hatching, chicks remained within or near their nest and made no consistent attempt to hide. Then for several days they atempted to hide behind or under some object such as grass or sticks near the nest. This was followed by a period when they ran a short distance prior to hiding. Next occurred longer runs, which often involved large groups of chicks and usually culminated in particular individuals hiding or the group swimming out into the lake. Finally there was a period of several days prior to departure from the colony when juveniles ran and attempted short flights. Each stage involved changes in locomotor patterns as a result of (1) structural maturation and learning and (2) changes in thresholds associated with the tendencies to run and hide, which enabled young gulls to cover a given distance more rapidly. Because of these changes, it seemed logical to expect older chicks to traverse a course within an orientation cage more rapidly and possibly more directly than younger individuals. I therefore considered it impractical to use speed as a measurement of orientational ability. In fact, the only variable that seemed satisfactory was the compass point at which chicks initially attempted escape from the cage, or their compass bearing after movement had ceased. Duration of trials ranged up to 4 min.

MATERIALS AND METHODS

The orientation cage consisted of a 30-ft diameter circle of 12-inch-high chicken fencing. Markers were used to divide the cage floor into 16 pie-shaped sections and into six concentric circles of increasing diameter, each 5 ft larger than the last. A 5-gal can was inverted in the center of the cage and used as a holding chamber for experimental chicks (fig. 1). An experimental chick was released when an observer, who was concealed by topographical features or by a canvas blind located about 50 ft from the cage, raised the can by a string and pully arrangement.

Orientation cages were placed in six different locations: (1) between the north and south colonies, 40 ft from the south part and 150 ft from the north colony; (2) 200 ft ENE of the ring-bill colony; (3) 300 yards WNW and inland from the colony; (4) 0.25 miles W of the colony; (5) 0.25 miles NW of the colony along Lake Huron; and (6) 200 yards WSW of the colony (fig. 2). Chicks were brought to the cages in closed containers and subjected to tests singly or in groups of two or three. They were returned to the nests immediately thereafter. Each chick was used only once to insure statistical independence of data points. The results from group releases will be discussed in a later paper.

The statistical methods presented by Batschelet (1965) for the analysis of animal orientation data were applied during this study as a result of a computer program prepared by Dr. Jerrold H. Zar of this department. The Rayleigh Test, a statistical test of randomness, was applied to the data presented in this paper. Since the concentration of headings selected by young gulls could be a result of chance, this test is used as an indication of whether the data are significant.

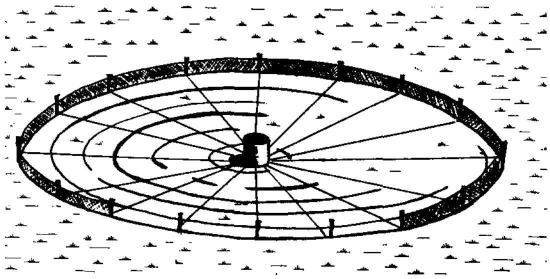

FIGURE 1. Sketch of the orientation cage used in experiments with Ring-billed Gull chicks.

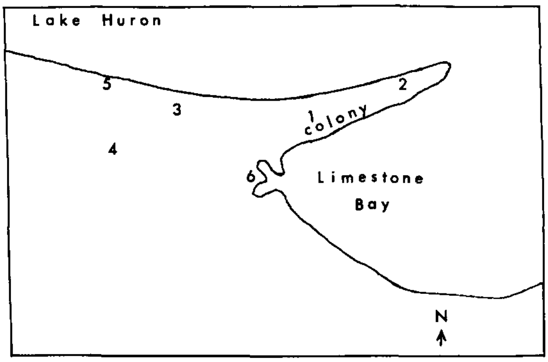

FIGURE 2. Relative positions of the six orientation cage locations. The map is not drawn to scale.

RESULTS FROM TRIALS

Chick movements within the colony were not restricted during development and, as a result, territorial alterations occurred as did changes in brood mates. This observation, which is based on daily checks on the movements of about 200 color-marked chicks in a 50 × 50 ft plot, suggested that ring-bill chicks lacked a strong attachment to one area within the colony; therefore, it was unlikely that they possessed a specialized mode of orientation which would enable them to relocate the territory.

Over half (57.8 per cent) of the chicks tested in the six orientation cages showed preferences for headings of east, south, or southeast and it seemed unlikely that this behavior simply represented escape attempts or orientation toward the nest territory. Instead, the responses for particular course headings were interpreted as representing a basic directional tendency which may be the source for initial migratory headings by juvenile gulls. This possibility is supported by the distribution pattern of band recoveries for ring-bills banded at Rogers City (Southern 1968). On this basis I speculated that the behavior shown by chicks placed in test cages was probably indicative of their future directional responses during dispersal and migration.

Because there was no apparent difference between the preferred directions selected by chicks of various ages or by individuals released at the different cage sites, I grouped the data from the 294 trials for evaluation. Chick movement patterns resembled, to some extent, those of adults used in homing trials (Southern 1967a) and they could be grouped into three similar categories: circling, zigzag patterns, and direct departures. In addition, some chicks exhibited a fourth possibility, that of no response. A typical activity sequence after release might involve the following: a short walk away from the holding container; one or two small diameter circles, either clockwise or counter-clockwise; selection of a directional heading and forward progress for at least a few steps; performance of another circle; pursuit of a new course after much looking around; several more short walks along new routes, possibly involving four or five of the plotted compass directions, each of which might be preceded by more looking around; and finally, selection of a relatively constant course towards the cage boundary. This chain of events typically required 2–4 min.

Variations in this pattern occurred and, in some instances, there were no circles and birds followed a rather erratic course prior to selection of a line of prolonged travel. Sometimes chicks moved slowly (2–3 min to cover the distance) across the cage but occasional individuals, usually older than 15 days, traveled the distance much more rapidly (15 sec or less).

A third type of response was the direct departure during which the chick traveled an almost straight-line course from the holding container to the cage boundary. Travel over the selected route might be slow or fast but usually one minute or less was required.

The final descriptive category, relative to orientation cage results, was that of no response. In these instances, chicks usually squatted down at or near the release site and failed to select and follow a course. Often they looked around and if shade was available near the container they inched into it. About 10.9 per cent of the experimental chicks reacted in this way.

The results accumulated during chick orientation trials can be compared with those for adults in some other respects. Response patterns fell into four categories, those that were (1) quick and accurate (according to the hypothesis), (2) slower but in directions "toward" the population's wintering grounds,

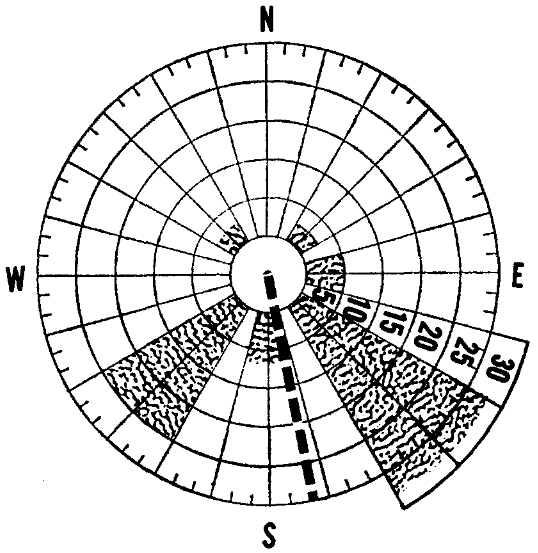

FIGURE 3. Departure directions selected by 63 Ring-billed Gull chicks, 2–20 days old, when released under clear skies. Departure direction was indicated by the chicks' final position within the orientation cage. Numerical scale indicates numbers of birds. The broken line represents the mean angle (168.8°).

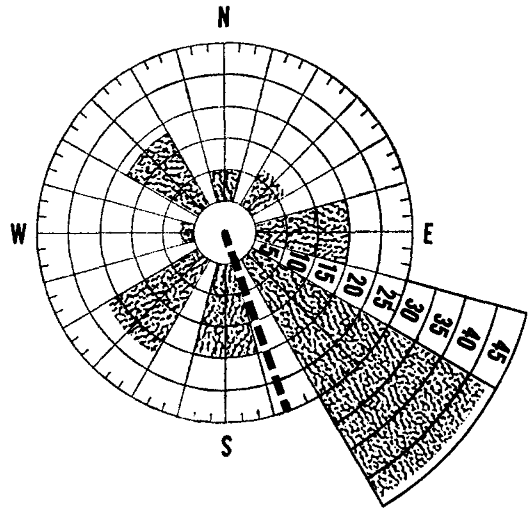

FIGURE 4. Departure directions selected by 118 Ring-billed Gull chicks, 2–20 days old, when released under partly cloudy conditions. Numerical scale as in figure 3. The broken line represents the mean angle (159.7°).

i.e., E, SE, or S (Southern 1968), (3) slow and in directions other than the preceding, and (4) those that failed to respond or "return."

SOLAR CUE CONSIDERATIONS

Three directions, E, S, and SE, were selected by 57.8 per cent (170) of the 294 chicks released in six orientation cages. Southeast headings were indicated by 70.6 per cent (120) of the 170 chicks; E by 14.7 per cent (25); and S by 14.7 per cent. The course taken by each chick was compared with sky conditions existing during the trial in an attempt to evaluate the role of solar cues in orientation. I have plotted the responses of chicks released under clear, partly cloudy, and completely overcast conditions in figures 3, 4, and 5, respectively. The mean directional bearing is also plotted in each figure.

Sixty-three Ring-billed Gull chicks were tested in orientation cages under clear skies. Trials were run at times ranging from shortly after daylight until after dusk. Four individuals were released after dark. The number of nocturnal releases was restricted by lack of infra-red equipment for observing chick movements during darkness. No obvious differences were noted in behavior during the various release times; hence, data for all clear sky trials were grouped for further evaluation.

The three directions postulated as being representative of future migrational headings (E, S, and SE) were selected by 39 (61.9 per cent) of the 63 chicks released under clear skies. Under these conditions, however, orientation approached a bimodal distribution when plotted in figure 3. A large majority (76.2 per cent) of the chicks selected SE or SW courses (mean angle, 169° = SSE). The mean angle is significant at the one per cent level (table 1) where a z value greater than 4.6 is considered as indicative of a unimodal distribution. Figure 4 shows the directions selected during 118 chick trials under partly cloudy skies and points out a continued preference for S, E, and SE (62.7 per cent) headings. Fewer chicks selected SW headings during partly cloudy conditions and more birds picked northward routes, particularly NW. The mean departure angle of 160° (= SSE) was consistent with that selected under clear skies and is also significant (table 1).

During periods of complete overcast 71.6 per cent of the 81 chicks selected E, S, or SE headings (fig. 5). The latter direction was selected by 44 (54.3 per cent) of the chicks.

TABLE 1. Results of the Rayleigh Test applied to chick trials conducted during various sky conditions.

Sky	$\bar{x}$ Angle	SD	n	z[a]	z_p ($P = 1\%$)
Clear	168.8	41.53	63	34.25	4.61
Partly Cloudy	159.7	58.57	118	26.90	4.61
Overcast	160.1	38.94	81	47.91	4.61

[a] If $z > z_p$ then the distribution is unimodal.

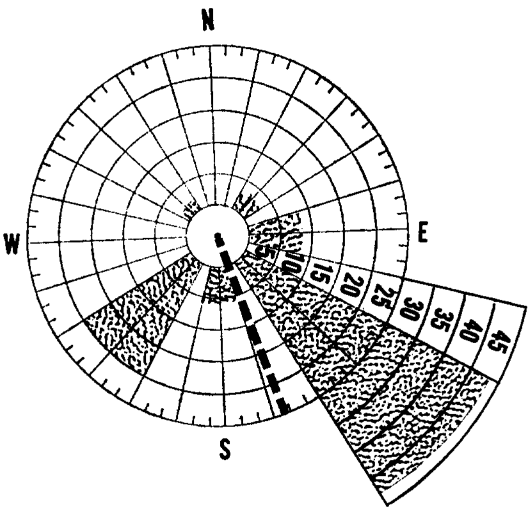

FIGURE 5. Departure directions selected by 81 Ring-billed Gull chicks, 2–20 days old, when released under completely overcast conditions, i.e., the sun not visible to the observer. Numerical scale as in figure 3. The broken line represents the mean angle (160.1°).

Once again SW was selected by 20 (24.7 per cent) of the chicks. However, over twice as many birds selected SE and the mean angle was 160°. The Rayleigh Test shows the mean angle in this instance to be highly significant (table 1).

As mentioned earlier, I consider the SE headings to be correlated with fall dispersal or migration patterns. The statistical significance of the directions selected under each type of sky condition and the similarity between the three mean headings under different sky conditions suggests that other than solar cues are involved in selection of these courses. The likelihood of these headings being the result of chance appears small. The course preferences of chicks were not associated with particular age groups, releases during particular times of day, or with chicks used in any particular orientation cage.

There was no indication that vision of the sun, its path, or a suggestion of its position in the sky was necessary for orientation. Chicks apparently select the preferred courses on the basis of other types of environmental clues. It is possible that chicks from different colonies have specific directional preferences that are influenced by heredity. Performance of such innate responses would probably be associated with some type of environmental cue. The southeasterly preference displayed by newly-hatched and older ring-billed chicks from the Rogers City colony supports this contention. Further studies are being conducted with individuals from several colonies. Whatever the source of this behavior, it provided Ring-billed Gull chicks with a rapid means (4 sec to about 4 min) of direction selection.

INFLUENCE OF MAGNETIC DISTURBANCES

The controversy regarding avian capabilities to sense and interpret magnetic cues has been well covered in the literature (see Dorst 1963). Even though the general consensus is that birds are unable to use clues of this type, I considered this parameter during my search for the environmental factor(s) influencing orientation behavior by gull chicks.

The United States Coast and Geodetic Survey operates the Fredricksburg, Virginia, Observatory which maintains a continuous record of fluctuations in the earth's magnetic field. The variations are expressed as K-indices ranging from 1 through 9, with 5 representing moderate "storm" activity, 6 or 7 referring to moderately severe storms, and 8 or 9 indicating severe storm activity. The record obtained from the observatory is indicative of the approximate amount of magnetic activity at other parts of the world as well since the principal storms occur simultaneously.

Directions selected by chicks used in trials during various intensities of magnetic disturbances are plotted in figure 6. A preponderance of SE headings was apparent during K-values of 1 and 2, but during 3 and 4 there was increased fluctuation and a decline in SE responses. The full significance of this decline was not determined since a small number of releases (8) were made during magnetic disturbances of the K-4 level and none was made during K-5 or stronger storm conditions. Therefore, it was impossible to determine the effect of moderately severe magnetic storms. Nevertheless it is impossible to overlook the correlation between the decline in southeasterly preferences and the increase in magnetic disturbance. Table 2 lists the standard deviations and results of the Rayleigh Test for each magnetic value. The mean angles are highly significant, according to this test, during mild magnetic disturbances of 0 to 2K. But at 3, and particularly 4K, the headings

TABLE 2. Statistics associated with chick trials conducted during various levels of magnetic disturbance.

Magnetic value (K)	$\bar{x}$ Angle	SD	n	z^a	z_p ($P = 1\%$)
0	162.10	52.35	31	10.52	4.61
1	157.49	46.79	93	41.32	4.61
2	154.02	61.30	105	19.20	4.61
3	140.79	70.90	42	2.31	4.61
4	291.0	77.15	8	0.07	4.20

[a] As in table 1.

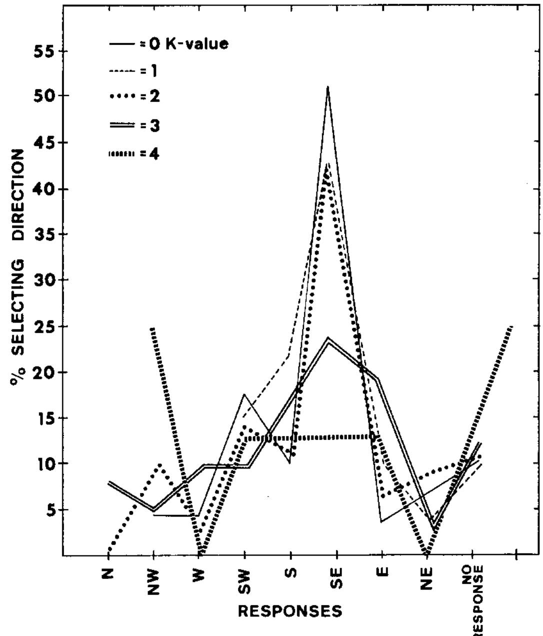

FIGURE 6. Directional responses of 294 Ring-billed Gull chicks released in orientation cages during magnetic disturbances of various intensities as indicated by K-indices. See table 2 for the statistics involved.

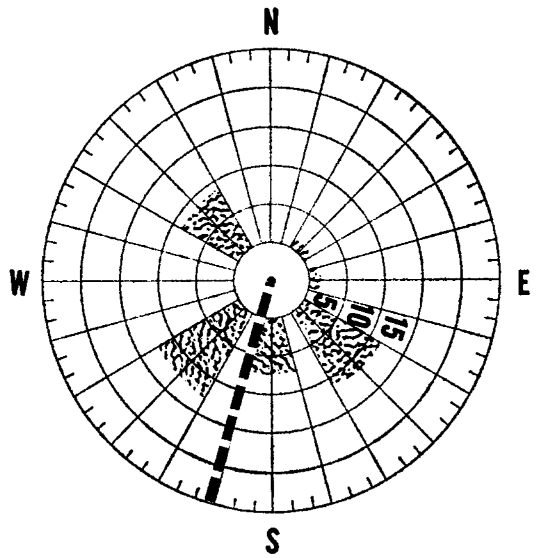

FIGURE 7. Departure directions selected by 43 Ring-billed Gull chicks, 2–20 days old, when released under partly cloudy skies in an orientation cage surrounded by an opaque barrier. Two individuals showed no response. Numerical scale as in figure 3. The broken line represents the mean angle (195.2°).

decrease in significance and the mean angle could be a result of chance. It can be noted, however, that the southeasterly bearing persisted through 3K. In most instances the standard deviations were fairly high.

Releases could not be planned during particular levels of magnetic disturbance since reports were received on a weekly basis. All chick experiments were planned according to sky conditions or the availability of time to devote to this aspect of the project. As a result, the distribution of trials in relation to K-values was determined solely by chance. These data tend to indicate a correlation between the apparently innate preferences for particular directional headings and magnetic cues provided by the earth's magnetic field or with associated factors. But, since correlation is not synonymous with causation, these data are not considered conclusive and further inquiry is planned.

RESPONSES TO TOPOGRAPHICAL CLUES

It seemed possible, although unlikely, that gull chicks might be responding to some type of topographical clue within their range of vision at the six different test sites. To examine this possibility, I encircled one activity cage with an 18-inch-high opaque barrier. This reduced the likelihood of small chicks viewing the surrounding terrain; however, it permitted vision of the sky. Figure 7 depicts the results from 43 trials conducted in this cage. The most obvious variations in behavior included a reduction in SE headings and an increase in northerly preferences. The mean course angle was 195.2° (z_P at 1 per cent level = 4.61; $z = 13.97$). Since SE courses predominated in previous releases regardless of sky conditions, the reduction in this preference in favor of other headings suggests that chicks may be using one or more terrestrial cues as orientational aids. Currently, however, there is no suggestion as to what these cues might be. Since orientation cages were placed in a variety of situations, including sites never before seen by chicks, it seems unlikely that individuals could obtain orientation clues from local landmarks. Further investigation of this possibility is obviously required. Several trials of free-running chicks showed that birds between 15 and 20 days old were able to return, at least occasionally, to their territories or to "family" groups from distances of 100 ft. Other chicks rapidly pursued a correct course for at least 300 ft toward their part of the colony from localities as much as 0.25 miles away. The sounds of the colony and sight of adults probably influenced these particular responses by chicks.

Indications are that Ring-billed Gull chicks of all ages possess a mechanism for selecting directional headings which may correspond to migration routes. A range of abilities seems to exist, with about 35 per cent of the individuals

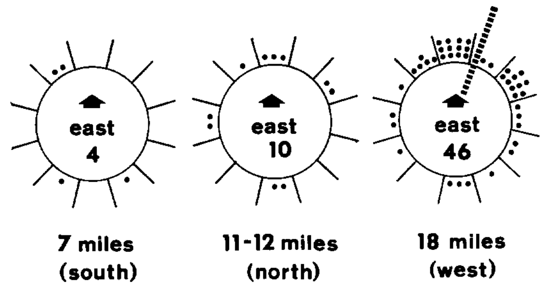

FIGURE 8. Disappearance points for 56 of 60 juvenile ring-bills that responded when released 7–18 miles from the colony. The arrows refer to the direction E, and the numbers within each circle indicate the sample size. The broken line in the 18-mile figure represents the mean angle (112.02°) for the grouped data.

selecting courses other than those corresponding to routes followed during migration. This figure is similar to that representing the number of adults that failed to return during homing trials (Southern 1967a). It is quite possible that the general behavior of chicks during trials, as well as their headings, are comparable to those later performed as adults.

RESULTS FROM HOMING TRIALS WITH JUVENILE RING-BILLS

During 1964 and 1965, 60 juvenile ring-bills were released at sites 7–18 miles S, N, and W of the colony. Four individuals did not respond upon release and were returned to the colony. In most instances I was confident that these birds had not left the colony previously because they had been under observation within the study area. This was, therefore, considered to be their maiden flight and their first experience with orienting over unfamiliar territory. Unless the birds flew at high altitudes which could permit a view of the colony or of Lake Huron, geographical features at the release sites should have been unfamiliar to them. As a result, departure directions were probably selected by one or more of the following methods: random selection, an innate response independent of visual cues, sun-compass or magnetic orientation, or some type of bicoordinate navigation. Figure 8 depicts the departure directions of this group of birds. Statistical analysis of the grouped data for the 56 responses indicates that the ESE mean bearing (112°) is significant and not the result of chance dispersal. This further substantiates the hypothesis that young Ring-billed Gulls possess an orientational ability that is influenced directly by heredity.

The behavior of individuals within this group of gulls was more uniform at release time than was that of adults. In all cases, juveniles spent considerable time making sweeping circles. These were usually performed in one direction, either clockwise or counter-clockwise, but occasionally individuals alternated directions. Most juveniles initiated circling almost immediately and in these instances the loops usually increased in diameter as circling continued. Circles were performed at altitudes estimated to range between 100 and 800 ft, with the higher elevations reached by individuals that circled longest. A departure direction was occasionally selected after several circles and the bird disappeared. After traveling a few hundred yards, several gulls changed their courses by perhaps as much as 90 to 180° and occasionally passed back over the release site. Sometimes this type of indecisive behavior continued for over 20 min within sight of the release area. A new departure direction was usually selected upon completion of circling. This type of behavior may have been repeated after the juveniles left the release area. A similar type of behavior was described for inexperienced Pintails (*Anas acuta*) by Hamilton (1962a).

When the headings of the 56 juveniles are compared on the basis of the amount of magnetic disturbance that existed at release time, it is apparent that the preference for ESE declined with increased K-values (table 3). At an average disturbance of 1.5K the mean angle is highly significant but the courses selected during 2.5 through 3.8K are probably random.

After about half (51.8 per cent) of the extended periods of circling, the direction selected was easterly or southeasterly. The remaining departure directions were more randomly dispersed ($\bar{x}$ angle = 112°). It is possible that some of the birds I observed for shorter periods also selected these two bearings after additional circling. Some of the gulls (6) returned to the colony but no careful check was maintained for their return. Perhaps this is the type of behavior Matthews (1961) called "nonsense" orientation. Adult

TABLE 3. Statistics associated with juvenile homing trials during various intensities of magnetic disturbances.

$\bar{x}$ Magnetic value (K)	$\bar{x}$ Angle	SD	n	z[a]	z_p ($P = 1\%$)
1.5	113.57	30.56	17	12.51	4.42
2.5	151.81	55.59	8	2.24	4.20
3.8	7.40	67.74	18	1.63	4.43

[a] As in table 1.

gulls released in homing trials during this study (Southern 1967a) did not indicate similar preferences. Bellrose (1958, 1963) and Matthews (1963a) have reported nonsense orientation for adult waterfowl and the departure directions appear to vary according to the species or particular population involved. Thus far no satisfactory explanation of the survival value of this action has been developed. The term "nonsense" orientation does not accurately describe the type of behavior performed by the birds; instead it indicates the inability of the investigators to adequately explain the functional significance of the directional responses. As mentioned earlier, I believe that the ESE headings selected by young Ring-billed Gulls are indicative of the future migration patterns of the particular population under study.

The departure courses selected by experimental juvenile ring-bills might represent a "blueprint" depicting the pattern of the apparent pre-migratory dispersal from the colony. Banding recoveries indicate that young ring-bills from the Rogers City colony scatter over most of northern Michigan during August and that southward migration is intensified during September (Southern 1968). Matthews (1963a) indicated some skepticism about nonsense orientation being associated with pre-migratory dispersal, at least in the case of several species he investigated. However, Schüz (1949), Sauer and Sauer (1955), Perdeck (1957), and Hamilton (1962b) all agree that the direction indicated by experimental birds corresponds to the ancestral migratory direction specific for the actual season.

DISCUSSION

The results of this study suggest that a sizeable proportion, if not all, of the young ring-bills from the Rogers City colony possess an innate ability for selecting a flight-path suitable for reaching the major wintering grounds of the population. The relationship of environmental cues to this ability has not been positively determined. There were observable modifications in chick responses as a result of terrestrial cues being occluded and fluctuations in the level of magnetic disturbances. There was no apparent breakdown in SSE orientation by gull chicks or free-flying juveniles during overcast conditions. In contrast, Matthews (1963b) concluded, on the basis of rather sparse data, that Mallårds use the sun as a diurnal cue for nonsense orientation and the stars as nocturnal cues. Griffin and Goldsmith (1955) also noted flights oriented in a southerly direction during experiments with Common Terns (*Sterna hirundo*) and Goldsmith and Griffin (1956) found that terns released in the eastern United States (Maine and Connecticut) immediately headed SE if the sun was visible, but they did not if it was hidden behind heavy clouds. They attributed this orientation to the fact that terns on the east coast of the United States tend to fly SE or E when lost or released over land, thereby eventually reaching the coast. However, at this time I strongly believe that it is a mistake to apply the findings discussed in this paper directly to other species or to expect that most species of birds will use a common mode of orientation.

It appears to me that young Ring-billed Gulls have a directional "sense" which sets their general course for migration. This innate tendency or ability is their primary guide until learning or imprinting has established a goal, and related landmarks for breeding and wintering areas (Southern 1967b). Thereafter the birds seek these particular sites and employ both learned and innate abilities. The former provides the variation needed for dispersal of the species, setting up new breeding areas and dispersal of family groups; whereas the second is significant because it insures the likelihood of the seasonal reproductive cycle. The birds usually return to areas previously satisfactory for breeding. Continued experience acquired within the familiar area (home range) results in a repertoire of responses available to the bird for application in orientational situations. The extent of this variability is affected by individual differences in learning. The sum total of these variables is expressed during homing experiments with adults and, therefore, it is extremely difficult to recognize and separate the basic stimuli and responses associated with orientation.

SUMMARY

Two hundred and ninety-four Ring-billed Gull chicks were used in orientation cage experiments. Over half (57.8 per cent) of the chicks indicated preferences for headings of E, S, or SE, which correspond to the primary fall migration routes for members of the Rogers City, Michigan, population. Response patterns of experimental chicks resembled those of adults used in homing trials.

During clear skies 61.9 per cent of the chicks selected S, E, or SE. Under a complete overcast 71.6 per cent of the birds showed preferences for these headings. The Rayleigh Test was applied to the circular distributions discussed in this paper.

Selection of E, S, and SE headings decreased as the intensity of magnetic disturbances increased. However, only mild intensity magnetic storms were experienced during these experiments and the results are, therefore, inconclusive. The extent of correlation between fluctuations in the earth's magnetic field and orientation behavior by gull chicks has reopened the possibility of this type of cue being associated with the apparently innate directional preferences. Limited evidence also exists which suggests that topographical clues of some type may influence chick orientation behavior. Fifty-six juvenile ring-bills were released in homing trials and about half (51.8 per cent) selected E or SE courses during their maiden flight.

It appears that young ring-bills innately select their initial migratory headings and thereafter their responses are modified as a result of experiences (learning) associated with migration, the home range, and other activities.

ACKNOWLEDGMENTS

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LITERATURE CITED

BATSCHELET, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. AIBS Monograph, Washington, D.C.

BELLROSE, F. C. 1958. The orientation of displaced waterfowl in migration. Wilson Bull. 70:20–40.

BELLROSE, F. C. 1963. Orientation behavior of four species of waterfowl. Auk 80:257–289.

DORST, J. 1963. The migration of birds. Houghton Mifflin, Boston.

GOLDSMITH, T. H., AND D. R. GRIFFIN. 1956. Further observations of homing birds. Biol. Bull. 111:235–239.

GRIFFIN, D. R., AND T. H. GOLDSMITH. 1955. Initial flight directions of homing birds. Biol. Bull. 108:264–276.

HAMILTON, W. J. 1962a. Initial orientation and homing of inexperienced Pintails. Bird-Banding 33:61–69.

HAMILTON, W. J. 1962b. Celestial orientation by juvenal waterfowl. Condor 64:19–33.

MATTHEWS, G. V. T. 1961. "Nonsense" orientation in Mallards (*Anas platyrhynchos*) and its relation to experiments on bird navigation. Ibis 103a: 211–230.

MATTHEWS, G. V. T. 1963a. "Nonsense" orientation as a population variant. Ibis 105:185–197.

MATTHEWS, G. V. T. 1963b. The astronomical basis of "nonsense" orientation. Proc. XIII Intern. Ornithol. Congr., Ithaca, p. 415–429.

PERDECK, A. C. 1957. Stichting Vogeltrekstation Texel. Jaarverslag over 1957. Limosa 30:66–74.

SAUER, F., AND E. SAUER. 1955. Zur Frage der nächtlichen Zugorientierung von Grasmücken. Rev. Suisse Zool. 62:250–259.

SCHÜZ, E. 1949. Die Spätauflassung ostpreussischer Jungstörche in Westdeuschland 1933. Vogelwarte 15:63–78.

SOUTHERN, W. E. 1967a. The role of environmental factors in Ring-billed and Herring Gull orientation. Ph.D. dissertation, Cornell Univ., Ithaca, N.Y.

SOUTHERN, W. E. 1967b. Colony selection, longevity, and Ring-billed Gull populations: Preliminary discussion. Bird-Banding 38:52–60.

SOUTHERN, W. E. 1968. Dispersal and migration of Ring-billed Gulls from a Michigan population. Jack-Pine Warbler 45:102–111.

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