INFLUENCE OF SOLAR AND GEOMAGNETIC STIMULI ON THE MIGRATORY ORIENTATION OF HERRING GULL CHICKS

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RESEARCH in avian migratory orientation has centered on the environmental stimuli that may serve as cues (see Adler 1970, Bellrose 1972, Emlen 1975). Most such studies have dealt primarily with long-distance migrants or trained homing pigeons (*Columba livia*) (Keeton 1974). Few experiments have explored the orientation mechanism(s) of nonmigrants, partial, or short-distance migrants. As Bellrose (1972) suggested, such studies may help illuminate the evolutionary development of avian migratory orientation.

During June of 1972 and 1973 I studied orientation in the Herring Gull (*Larus argentatus*), generally considered to be rather sedentary (Smith 1959). The previous orientation studies with this species have been homing experiments testing the ability of displaced breeding adults. Griffin (1943) and Matthews (1952) both reported homing ability for Herring Gulls even from distances up to 872 miles (1404 km). Matthews (1952) concluded that visibility of the sun was related to homing success. Williams et al. (1974) likewise concluded that some mechanism other than landmarks may be involved in successful homing. Southern (1969a) found no evidence for the use of solar cues in Herring Gull orientation based on his homing trials (maximum displacement of 242 km). No doubt in close proximity to the breeding colony Herring Gulls use landscape features in homing (Southern 1970), but homing trial experiments have added little to the understanding of orientation cues involved in long-distance movements, particularly by inexperienced juvenile Herring Gulls. Furthermore, evidence for orientation abilities based on this experimental method is open to some question (Southern 1971).

In light of these views and the likelihood that experienced adults have access to multiple cues, I decided to use Herring Gull chicks in indoor and outdoor orientation arena experiments designed to test the influence of various environmental stimuli on orientation behavior. Southern (1969b, 1972a, 1972b) and other investigators (Schüz 1950, 1951; Perdeck 1958, 1967) have shown that juveniles are capable of assuming a direction appropriate for the population's fall migration. Additional evidence for both Ring-billed Gulls (*Larus delawarensis*) (Southern pers. comm.) and Herring Gulls (MS) indicated that individual chicks, when tested in replication trials, consistently selected similar headings, i.e. directions appropriate for postbreeding dispersal. Such results tend to justify the use of chicks in a study of subadult and adult orientation. I conducted 420 trials during the study to analyze the significance of geomagnetic and solar stimuli in this species' orientation.

Fundamental to understanding a species' orientation is the necessity of determining its pattern and schedule of seasonal movements. Few studies (e.g. Southern 1971, 1974a) have correlated the postbreeding dispersal pattern of a species with orientation trial results. This procedure should yield a better understanding of the Herring Gulls' orientation capabilities. The postbreeding dispersal of Great Lakes region Herring Gulls has been the subject, at least in part, of several studies over the past 50 years (e.g. Gross 1940, Smith 1959), but no previous study has analyzed the extensive recovery data available for all Great Lakes region Herring Gulls. Southern (1974b) developed a computer program in his laboratory to analyze such data on eastern U.S. Ring-billed Gull populations. In 1972 I initiated a similar computer analysis of over 12,500 Fish and Wildlife Service band recoveries of Herring Gulls banded in Great Lakes colonies, the results of which will be reported separately. My initial data analysis was limited to gulls banded in Lake Huron colonies because present orientation experiments were done with chicks from a Lake Huron colony near Rogers City, Michigan.

METHODS AND MATERIALS

Herring Gull chicks were obtained from the Calcite Colony near Rogers City, Presque Isle County, Michigan. Orientation experiments were conducted at a site 0.50 km west-northwest of the colony. Chicks were captured and then carried by auto to the experimental area where they were held (5 to 20 min) in opaque-sided containers until subjected to orientation trials. Individual chicks 3 to 10 days old were used for only one trial to ensure statistical independence of data. Later they were temporarily leg-tagged with masking tape or banded for identification and returned to the nest.

Orientation arena.—Since Southern (1969b) first described the original "Southern-type" orientation arena, he has modified it somewhat (Fig. 1). The circular arena is 8 feet (2.4 m) in diameter with sides of 2-foot (0.6 m) aluminum sheeting supported by interconnecting upper and lower rings of aluminum conduit. The sides are divided with colored plastic tape into 24 sectors, each representing 15° on a compass card with 0° corresponding to magnetic north. In the center of the arena is a 1-foot (0.3 m) cube holding container that is raised by rope and pulley to release the chick. Indoor control trials were conducted within an 8 × 8 × 6 feet high (2.5 × 2.5 × 1.8 m) plywood chamber with a ventilated roof and lighted by two 200-watt propane lamps. The arena was reduced to 5 feet (1.5 m) in diameter and a floor of sand-roughened plywood was added.

Environmental cues tested.—I used the standard arena in all outdoor trials testing the significance of solar and geomagnetic cues. The opaque siding eliminated the influence of both topographical features and prevailing winds on chick trials. Both overcast and indoor (no sky) trials were conducted as controls in evaluating solar cues on chick orientation.

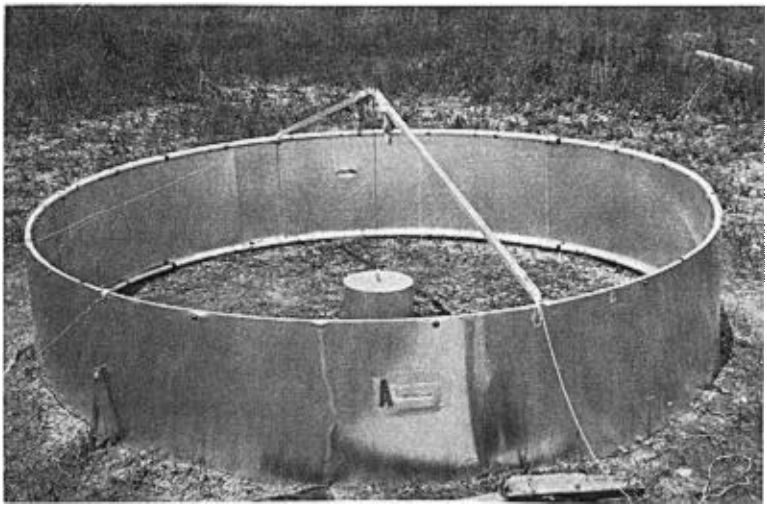

Fig. 1. Southern-type orientation arena at the experimental site.

When testing the effect of geomagnetic cues, a small ceramic disc magnet was attached to a chick's head (see Southern 1972b). Each magnet had a total intensity of about 1 oersted (98,000 gammas). A brass disc of similar weight and size was similarly attached instead of the magnet in control trials.

The trial procedure described by Southern (1971) was followed. No significant differences existed among responses of chicks of various ages or trial time of day, and so results from all trials were grouped accordingly.

Results of each trial were analyzed by the Rayleigh Test (Batschelet 1972, Zar 1974: 316–320), which served as a test for significance of orientation direction for each trial type. The Watson and Williams Test (Zar 1974: 321–324) was used to compare orientation trial mean headings with a pertinent mean heading derived from recovery data analysis.

Results

I conducted 420 orientation trials under five different trial conditions. The relevance of solar cues to chick orientation behavior was tested by contrasting clear sky and overcast (sun not visible) control conditions (200 trials total). The response under both conditions was high: 94% under clear and 92% under overcast. Under clear skies 70% of the chicks selected southeasterly through southwesterly directions (Fig. 2A); of these 60% selected a southerly heading. Rayleigh Test results showed this preference ($\bar{a} = 187°$) to be significant at the 1% level. Recovery data results indicate a southerly heading to be correlated with the species' winter dispersal pattern. Under overcast skies (Fig. 2B), the heading did not deviate from random at either the 1% or 5% level.

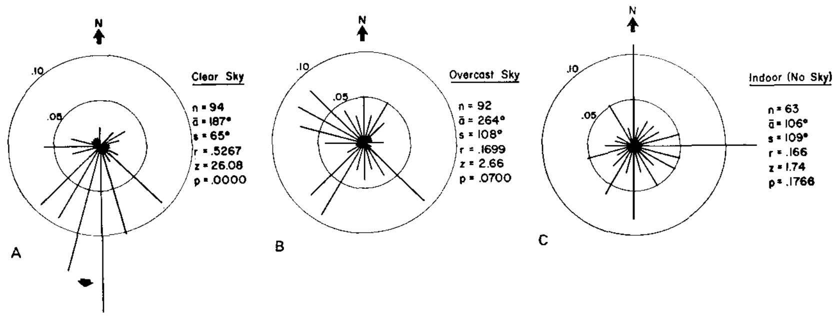

Fig. 2. Arena trial orientation of Herring Gull chicks under clear (A), overcast (B), and no sky (C) conditions. A, mean heading (black arrow) is significant at the 1% level. B, direction is not significant at 5% level, so no mean arrow is shown. C, direction is random at 5% level, and no mean arrow is shown. Here and in other figures vector diagrams are plotted so that the drawn radii are the relative frequencies of response in the 15° compass sectors. The two concentric circles represent a relative frequency of 5% and 10%, respectively. Sample size (n), mean heading (ā), angular deviation (s), Rayleigh's r and z, as well as the probability of z, are given in each figure. Black mean arrow signifies 1% statistical significance, clear arrow 5%. North is 0° or 360°.

Activity was likewise random for 100 indoor control (no sky) trials (Fig. 2C). Only 63% of the chicks selected headings, quite low in comparison to outdoor trials. Such variables as lower light intensity, higher temperature and humidity, and decreased background noise may have caused this low response and possibly biased the results.

Southern's work (1971) with the influence of geomagnetic cues on the migratory orientation of the closely related Ring-billed Gull prompted me to consider the effect of such cues in Herring Gull orientation. Fig. 3 shows the vector diagrams for 60 head magnet (experimental) and 60 head brass (control) trials. Reponse level was high in each case: 97% experimentals and 98% controls. The small ceramic disc magnet tended to disrupt Ring-billed Gull chick orientation (Southern 1972a), whereas Herring Gull chicks with head magnets showed a significant mean heading (ā = 212°) at the 5% level (see Fig. 3A). Both experimentals and controls exhibited directions appropriate for juvenile winter dispersal (Table 1). However comparison of control and experimental trial data (Fig. 3) reveals a clockwise shift of 58° in the preferred directions of experimentals relative to controls. A Watson-Williams two-sample F-test (Zar 1974: 316–320) shows that the two distributions differ significantly ($P < 0.001$: $F = 12.34$; critical $F_{0.01,1,115} = 6.85$). Head magnet chicks also exhibited a much greater angular deviation in individual headings (93° vs. 67° for controls) re-

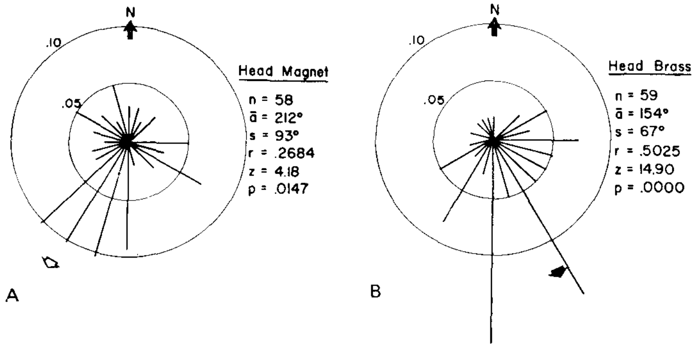

Fig. 3. Arena trial orientation of Herring Gull chicks under clear skies with head magnets (A) and head brass (B) attached. A, direction is significant at the 5% level (clear mean arrow). B, direction is significant at the 1% level (black mean arrow). See Fig. 2 for figure explanation.

sulting in a less pronounced directional preference. Geomagnetic stimuli apparently alter but do not disrupt Herring Gull chick orientation.

My studies do disclose the importance of solar cues. Based on the results, I decided to pool all outdoor/clear sky trial responses (Fig. 4), thus increasing the sample size ($n = 211$). The majority (59%) of the responding chicks chose headings of southeast, south, or southwest. The mean direction ($\bar{a} = 182°$) was highly significant by the Rayleigh Test. On the basis of the results, Herring Gull chicks appear to have an unlearned directional preference dependent on the presence of the sun.

Using the Watson and Williams Test, the mean heading (μ_1) of each

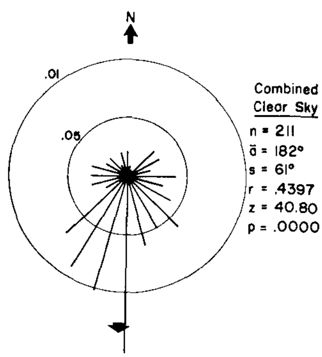

Fig. 4. Arena trial orientation of Herring Gull chicks under combined clear sky conditions (outdoor/clear sky trials, outdoor/head magnet, and outdoor/head brass trials). Mean heading (black arrow) is significant at the 1% level. See Fig. 2 for figure explanation.

TABLE 1

RESULTS OF WATSON AND WILLIAMS TESTS[1] COMPARING ENCOUNTER DATA DISPERSAL HEADING OF 179° AND CHICK ORIENTATION TRIAL MEAN HEADINGS

Trial type	n	ā	Rayleigh R		F	F_c[3]	H_o
			Rec.[2]	Trial			$\mu_1 = \mu_2$
Outdoor/sky clear	94	187°	8.38	49.51	0.16	6.90	Yes
Outdoor/sky overcast	92	264	8.38	15.63	16.59	6.90	No
Indoor/no sky	63	106	8.38	10.46	8.99	7.01	No
Outdoor/with head magnet	58	212	8.38	15.56	2.06	7.01	Yes
Outdoor/with head brass	59	154	8.38	29.56	1.75	7.01	Yes
Combined outdoor clear sky	211	182	8.38	92.78	1.26	6.76	Yes

[1] For Watson and Williams Test: n = sample size; a = mean heading of orientation trial type; F = test statistic.
[2] Rec. = recovery data R.
[3] F_c = critical F at 1% level.

experiment was compared with the pertinent juvenile winter recovery dispersal heading (μ_2 = 179°) determined from recovery analysis (see Table 1). The F values for the different outdoor/clear sky trials did not exceed the critical F; i.e. a high probability existed that the mean headings for both orientation trial and recovery data estimated the same population mean. When solar cues were lacking (overcast and indoor), the null hypothesis of identical mean headings was rejected. Such evidence indicates the chicks selected headings in orientation trials appropriate for winter dispersal, headings that correspond to winter dispersal of juvenile Herring Gulls.

DISCUSSION

My computer analysis of recovery data for Lake Huron Herring Gulls established that only subadults showed extensive postbreeding dispersal; the magnitude of which was inversely related to age. Juveniles (gulls less than 1 year of age) dispersed significantly greater distances than did gulls of all other ages. After remaining near their respective colonies through late summer and early fall, these young gulls began a widespread east-southeast dispersal along the lower Great Lakes and St. Lawrence Seaway during late fall. With the onset of winter conditions over the entire Great Lakes region, the dispersal pattern of young Herring Gulls shifted southward and distances traveled substantially increased to well beyond 300 miles (480 km) from the breeding colonies. This initial southward dispersal could be one-way for many of the juveniles, as spring elicits no mass return northward. On the other hand, young gulls may be less attracted to the breeding grounds (Smith 1959). Adult Herring Gulls remained rather sedentary throughout the year as few ventured farther than 300 miles (480 km) from the breeding colonies.

Several potential environmental guides exist by which this species may gain directional information during its movements. The use of landmarks is not only feasible, but also probable (Southern 1969a, 1970). Recovery data indicate that this species is usually found in association with rivers or lakes and ocean shores. Such features probably play a major role in Herring Gull postbreeding movements, especially for the rather sedentary adults. The use of landscape features for establishing direction is questionable for inexperienced gulls, especially during long distant movements. The use of wind cues, particularly when astral or solar cues are obscured, has also been suggested as a possibility (Bellrose 1967). That winds may influence direction or simplify flight is one thing, but that they may function as an orientation cue for Herring Gulls is quite another and merits investigation.

Evidence presented here suggests that Herring Gulls respond to geomagnetic stimuli. Walcott and Green (1974) reported *altered orientation* rather than *disorientation* in homing pigeons when the polarity of an induced magnetic field was reversed under overcast sky. Also, Keeton et al. (1975) discovered a systematic shift in the mean vanishing bearings of pigeons in a series of releases under varying K values (measure of geomagnetic disturbance). The effect was not randomness under high K values as with Ring-billed Gulls (Southern 1972a) but rather a tendency for mean bearings to shift counterclockwise when values of K were high. My results are also rather subtle in suggesting a geomagnetic influence on Herring Gull orientation. Such a response is not surprising in light of the growing body of evidence that various birds are affected by or may be using geomagnetic cues in orientation. In homing pigeons magnetic cues are probably most important when solar cues are lacking (see Keeton 1972, Walcott and Green 1974), but in some species a magnetic compass may function regardless of sky conditions (see Wiltschko and Wiltschko 1972, Wiltschko 1974, Southern 1974a). Herring Gull chicks, on the other hand, become disoriented under overcast skies, suggesting that geomagnetic stimuli are not used in the absence of solar cues. Whether such stimuli function as cues for this species is thus still open to question. Demonstrating an animal's sensitivity to a particular environmental stimulus (e.g. geomagnetism) is not necessarily evidence that such a stimulus functions as a cue in the animal's orientation needs. More study is certainly warranted relative to this problem.

Results do indicate that gull chicks are capable of gaining directional information from solar cues and probably have a sun compass. According to Kramer (1957), a sun compass only allows the bird to find and maintain its direction. This orientation is probably type II (Griffin 1952, Adler 1970), with the sun functioning as an external referent that enables the bird to determine a fixed direction. Although considerable evidence (Matthews 1968) suggests many long distance migrants have a sun compass, few investigators offer evidence for such a mechanism among nonmigrants or partial migrants. Bellrose (1972) postulated the existence of such a mechanism in at least some nonmigrants. The evidence at hand suggests that the Herring Gull may be such an example.

Significantly, chicks preferred a southerly direction under clear sky trial conditions, which correlates well with the winter dispersal pattern of juvenile Herring Gulls. This pattern is characterized by both southerly direction and greater distances traveled than older age groups. Given their inexperience with landscape features, particularly at great distances from the breeding grounds, the functional existence of a sun compass in subadult postbreeding dispersal is not unlikely. This is probably their primary guide until familiarization with landmarks develop.

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SUMMARY

I conducted 420 orientation trials with Herring Gull chicks to test the effect of solar and geomagnetic stimuli on orientation behavior. Results indicate the existence of a sun compass mechanism in this species. Under clear sky conditions chicks exhibited a statistically significant southerly heading (182°), a direction that corresponds to the heading juveniles selected during winter dispersal (179°). When solar cues were lacking, the headings were random. Geomagnetic stimuli possibly influence orientation as the preferred heading of experimentals (head magnets—212°) deviated significantly from that of controls (head brass—154°). Such stimuli may alter but do not disrupt chick orientation.

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