MIGRATIONAL ORIENTATION IN RING-BILLED GULL CHICKS[1]

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IN a series of papers I (1969, 1971, 1972a, 1972b) have described the responses of Ring-billed Gull (*Larus delawarensis*) chicks (2–20 days old) and juveniles (about 6 weeks old) during orientation experiments. Gull chicks have exhibited consistent preferences for southeasterly, rather than random, headings when provided with adequate environmental cues during 2-min trials in 8-foot diameter orientation cages (Fig. 1). In a choice reaction experiment such as this, gull chicks apparently are subjected to a novel experience that forces them to use all available information for resolving the problem of which direction to select. As they have not previously encountered directional problems, they presumably utilize genetically programmed information that is normally used during migrational orientation. The result, in the experimental arena, is a significant preference (indicated by final headings) for southeast that corresponds with the mean angle for band recovery data obtained for juveniles from the same population.

Recently (1971–73) I have conducted several thousand additional trials with Ring-billed Gull chicks in orientation cages. Groups of gulls used as controls have shown, with one exception, consistent preferences for southeast mean bearings (Southern 1971, 1974a) thereby providing significant baseline orientation against which to compare results for experimental groups. Specific sets of trials and comparisons of data have served as a means of ascertaining the reliability of my technique.

Since the onset of my studies involving gull chicks I have questioned whether I was really obtaining a measurement of their ability to orient during migration. I have been cognizant of the possibility that I was recording a response completely unrelated to migrational orientation but it seemed unlikely because: (1) similar results have been obtained over a period of several years, (2) thousands of individual gull chicks have shown similar responses, (3) several different observers have collected and interpreted data thereby reducing the chance of observer bias, and (4) one of my students (Moore 1973) obtained similar results for Herring Gull chicks (*L. argentatus*). In addition, I have conducted three lines of investigation specifically aimed at determining if chick responses in orientation cages are indicative of their future directional

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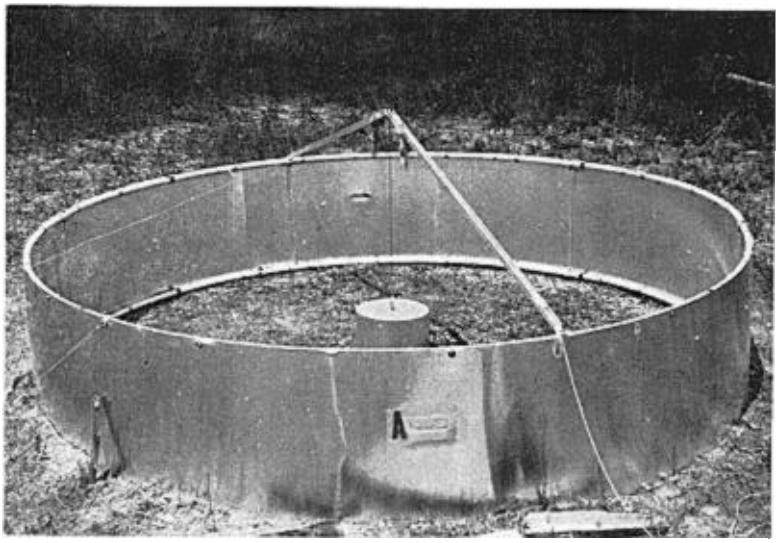

Fig. 1. Southern-type orientation cage showing the centrally positioned holding chamber that is raised by a string to release a gull chick. Observers watch the chick through portals in the side and plot its course on a printed replica of the cage floor. Marks on the cage wall designate 15° sectors. All materials used in construction are nonmagnetic. The structure is 8 feet (2.5 m) in diameter and 2 feet (0.6 m) high.

preferences. These are: (1) an analysis of band recovery data for juveniles from the colony studied (Southern 1974b); (2) a series of replication trials (i.e. three consecutive trials) with the same chick, thereby testing the consistency of its preference; and (3) free-flight trials with juveniles from the same colony (Southern 1972b). I have compared my results from 357 orientation cage trials conducted as clear sky controls with the directional preference indicated in the data for each of these groups. Results from this comparison are discussed in this paper.

Statistical treatment of the data included use of the Rayleigh test (Batchelet 1965, Zar 1974) to test for a significant sample mean; the modified Rayleigh test or V-test (Batchelet 1972, Zar 1974) to determine if the population sampled was clustered about a predicted mean angle; and the Watson-Williams' two-sample and multiple-sample tests (Zar 1974) to compare the mean angles for each data set, thereby determining if the various mean angles estimate the same population.

Comparison of Band Recovery and Orientation Cage Data

Recently I (1974b) analyzed all of the U.S. Fish and Wildlife Service band recoveries for the Great Lakes Region Ring-billed Gull population.

Recovery information for juveniles from the Rogers City, Presque Isle County, Michigan colony was separated from the rest and compared with orientation cage performances by gull chicks from the same colony. The mean angle between the colony and each recovery site was calculated during a computerized analysis of banding data.

Juvenile Ring-billed Gulls do not depart from the breeding range immediately after leaving the colony. Instead, from July through mid-October, the majority disperse throughout most of Michigan and the Great Lakes Region with the mean distance between the colony and recovery sites gradually increasing with time. The mean direction of movement time, according to the available banding data, is 220° rather than the predicted 165° bearing. There is, however, a significant clustering of headings about the predicted mean angle as indicated by the V-test results (Fig. 2). Several factors may contribute to this apparent failure of the actual and predicted mean bearings to coincide. Young Ring-Billed Gulls may be hesitant to cross the large expanses of Lake Huron. Instead they apparently follow an inland route through Michigan, thereby giving a southwesterly trend to band recovery data. A similar bias, based on the scarcity of observers in Lake Huron, may contribute further to the south-southwest tendency in the data. For these 4 months (July through October) the significant (Rayleigh test, $P = 0.0000$; V-test, $P = 0.0005$) mean dispersal angles range between 209° and 220° (Fig. 2). Very few band recoveries have been received from south of the Great Lakes Region from July through mid-October, which supports my premise that migration does not begin until later.

A distinction has been made between postbreeding dispersal and migration as band recoveries during the former did not include a mean heading corresponding with that found after the onset of migration. During July and most of October many Ring-bills drift southward on the Michigan side of Lake Huron. Upon reaching the end of the lake they cut eastward, thereby assuming the seasonal pattern evidenced in the November–December data and the combined data for the Great Lakes population (Southern 1974b, 1974c). The significant southward trend apparent in the band recovery data for these months has been interpreted as signifying that migration from the breeding range (between 42° and 47° N) is underway. The significant (Rayleigh test, $P = 0.0000$; V-test, $P = 0.0005$) mean angle for the combined November and December recoveries is 172° (Fig. 2).

The mean angles for the July–October and November–December recovery data have been compared with the mean for my 1971–73 orientation cage trials (clear sky controls, $R = 51.57$) by using the Watson-Williams two sample test. The null hypothesis (H_o) states

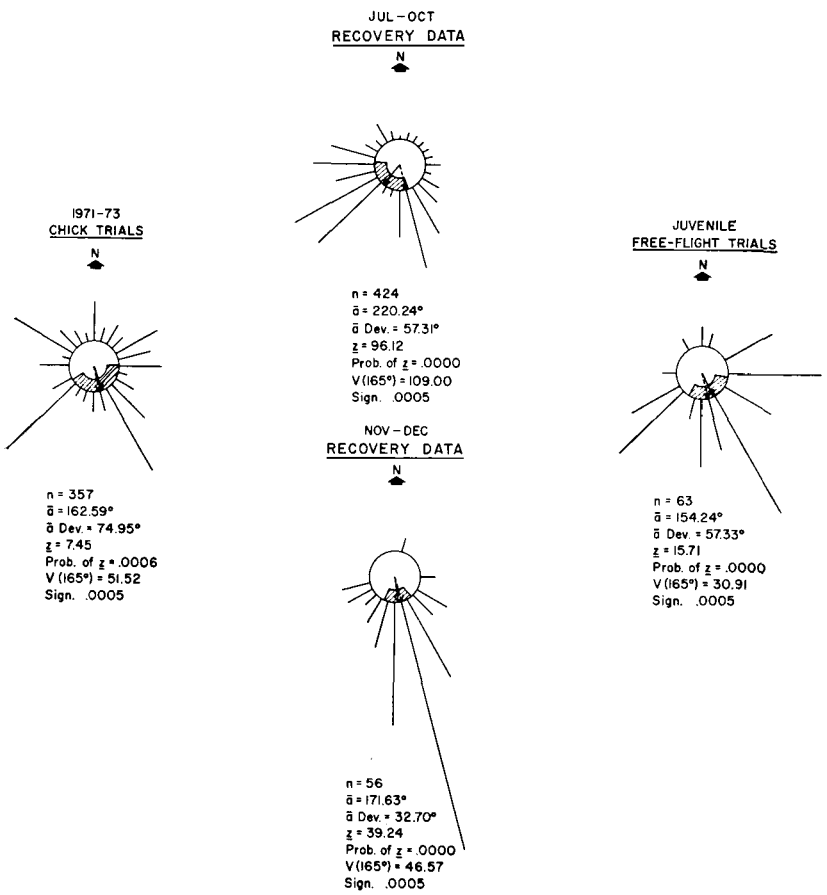

Fig. 2. A comparison of results from chick orientation cage trials (left), band recovery data (top center: June thru October; bottom center: November–December), and juvenile free-flight trials (right). Radiating lines represent relative frequencies of final headings; solid arrow = mean angle for sample (ā); broken arrow = predicted population mean (165°) used in the V-test; and the shaded area represents one angular deviation (ā dev.).

that the two sample mean angles estimate the same population. In this case, the hypothesis is rejected for the July–October dispersal data ($R = 192.37$, $F = 35.47$, $F_c = 6.69$) but accepted for the November–December migration data ($R = 46.88$, $F = 1.34$, $F_c = 6.72$, $P = 0.01$). For the reasons expressed above, I believe that these results substantiate my earlier conclusion that young Ring-billed Gulls display an unlearned preference for a bearing indicative of the route they will follow during

fall migration. The November–December data are considered the most accurate measure of the species' directional tendencies whereas the June–October data are rendered less representative because of data recovery bias.

RESULTS FROM REPLICATION TRIALS WITH CHICKS

During all of my previous gull chick experiments I used an individual bird in a single 2-min trial. Mean bearings are calculated from the final headings of the number of chicks making up the sample size for the particular experiment. This was done to reduce the chance of habituation to test procedures that could bias results and mitigate the value of this choice reaction experiment. This procedure differs from that of averaging means derived from the multiple responses of individual birds as has been the practice in some studies (e.g. Merkel 1971, Wiltschko 1971). My method may provide a more accurate measure of the directional preference of a given population as more individuals are sampled.

In 1971 I conducted a series of replication trials with 60 Ring-billed Gull chicks to determine if they consistently selected a particular heading and if the grouped headings would give results similar to those obtained from single trials. Each bird was used in three consecutive trials spaced about 5 min apart. The significant mean angles for the three trials are similar (range, 150 to 167°) and compare favorably with the mean for the combined trials ($\bar{a}$ = 153°, Fig. 3). The mean angles for each trial set (first, R = 17.50; second, R = 20.79; third, R = 12.92) were compared by the Watson-Williams three-sample test and also with results for November–December band recoveries and standard orientation cage trials. Occasionally a chick failed to respond during one of the replication trials, therefore, the sample sizes in Fig. 3 are not always 60. The results from this statistical test (R_c = 50.76, F = 0.51, F_c = 4.73, P = 0.01) verify that gull chicks are reasonably consistent in their selection of a preferred heading and that the population sampled by each method (examination of November–December band encounters, single trials in orientation cages, and replication trials) is the same.

The three headings taken by individual birds during each set of trials vary with respect to consistency and the sample size is too small for treatment with the usual circular statistics. However, 10 individuals followed essentially the same course each time; 10 others had final headings separated by 10° to 30°; and, in all, 43 of the 60 had all three headings within the same 90° sector.

It appears, therefore, that Ring-billed Gull chicks have a fairly per-

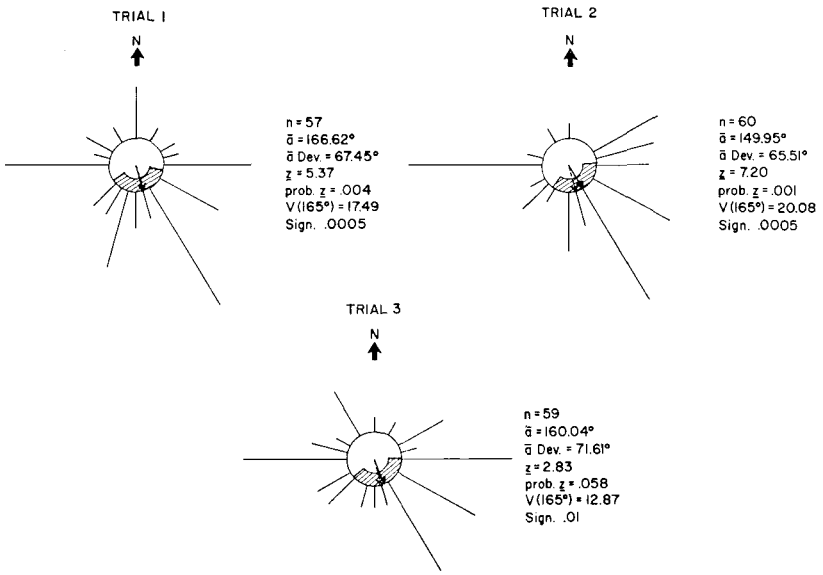

Fig. 3. Relative frequency of final headings during each of three replication trials.

sistent preference for a particular range of headings. In addition, the final heading a chick selects during its first trial seems to be indicative of the bearing it will select in subsequent trials. A higher level of accuracy may not be possible if only a magnetic compass is being used (Southern 1974a, 1974b).

Results from Juvenile Free-flight Trials Compared with Other Data Sources

In 1971 I (1972b) released 113 juvenile Ring-billed Gulls on what was considered to be their maiden flight away from the colony. Each bird was about 6 weeks old when captured in the colony, transported to a site approximately 18 miles away, and released. The bearing of a gull, when it disappeared from the line of sight of three observers equipped with binoculars, was recorded as the final heading used in statistical analysis. These releases were made to determine if: (1) juveniles had a preferred heading, (2) their responses were comparable to that of chicks in orientation cages, and (3) similar cues were used by both groups for selecting a course to follow. The 63 individuals released as controls had a significant ($P = 0.00000$) mean angle of 154° (Fig. 2).

The Watson-Williams' test was used to compare results for free-flight

trials with the mean angles from November–December band encounter data ($R = 46.88$, $F = 3.63$, $F_c = 6.85$) and chick orientation cage trials ($R = 31.46$, $F = 1.69$, $F_c = 6.72$). In each instance the null hypothesis was accepted ($P = 0.01$), indicating that each method was sampling the same population. It appears, therefore, that the directional preferences of migrating juvenile Ring-billed Gulls from the Rogers City, Michigan colony (based on band recoveries), 2- to 20-day-old chicks in orientation cages, and juveniles released in unfamiliar localities are comparable. This conclusion supports my hypothesis that the directional preferences of Ring-billed Gull chicks are indicative of their future directional preferences during migrational orientation. Every caution possible should be taken to document that we are dealing with biologically significant phenomena during studies of this type and not a distribution of data points that is simply of mathematical significance. By using actual migration data for comparison and the results from a variety of trials, I have attempted to abide by this recommendation. I have not, however, devised a dependable method of distinguishing between the two types of information.

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SUMMARY

Evidence is provided in this paper to substantiate that young Ring-billed Gulls: (1) express a significant directional preference in orientation cages corresponding to the mean bearing resulting from analysis of juvenile band recovery data for the same colony, (2) are consistent in their directional responses during successive trials, and (3) respond similarly during orientation cage and free-flight trials. These findings further support my hypothesis that the responses of gull chicks during choice-reaction experiments are indicative of the direction they will head during fall migration. This is one of the few studies having a variety of data for the same species showing statistically significant similarities between experimental orientation data and actual migration data for the same population of birds. It appears that this procedure is producing reliable information to assist in explaining the mechanisms associated

with avian orientation. By comparing migration and orientation data, I have attempted to affirm that my statistically significant results are also of biological significance.

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