

Of the two females replacing collected birds, one was not seen until incubating her own eggs, so I do not know whether she was even exposed to the young of her eventual mate. The other female cared for the three nestlings of the male she courted after an interval of 5 days during which she provided them no services; she successfully nested with that male later in the season.

Assuming that the second female consort was not closely related to the young she aided (which is reasonable if outbreeding is favored), her behavior could be alternatively considered truly altruistic, reciprocally altruistic, or a reproductive error. I dismiss true altruism because her long hesitation in providing care suggests that she was not oriented toward aiding young so much as she was being reproductively primed by them. A truly altruistic bird could be expected to provide care immediately. Indeed, the stepwise hormonal preparation necessary for carrying out the successive stages of nesting in birds (13) is probably a proximate expression of ultimate selection for reproductive selfishness, making altruistic errors infrequent.

Reciprocal altruism (4) is a possible but unlikely explanation. It is considered because the female consort may have increased her chances of nesting by helping her prospective mate. Only three of the ten birds obtaining consorts had additional broods that year, and two of these had only three young in their original brood rather than the usual five or six. Even this small sample suggests the possibility that single birds with normal size broods either cannot or ordinarily will not attempt a second brood. Insofar as helping a prospective mate rear its young leads to successful future nestings more often than not, parental care by consorts might be favored provided it does not also exhaust the consort. But helping rear the young of other birds probably has little influence on their decision to renege because neither two of the three experimentally occurring consorts of 1972, nor the naturally occurring consort of 1970, all of which renege, provided care to the young of their prospective mates. Thus reciprocal altruism does not appear to play an important part in the occasional fostering of apparent nonrelatives in bluebirds.

Williams (2) considered cases similar to the behavior of the consort female as reproductive errors made possible by the unrewarded benefactor having had its own reproduction interrupted at a stage of nesting similar to that of the benefiting bird. Such interruption would place the bird in the proper hormonal state to be stimulated into misdirected parental behavior by the offspring of the aided adult. Paradoxically, selection to avoid altruism could occasion-

ally almost inevitably result in altruistic error because at rare intervals a bird may be confronted with a concatenation of stimuli, more or less inducing it to provide parental care even though those stimuli emanate from other birds' young rather than its own, which otherwise always would be the case and would cause the bird to care only for its own young. That only one of 11 naturally and experimentally occurring consorts in 1970 and 1972 provided care, and that she hesitated 5 days before providing this care, suggests that altruistic behavior is rare and best interpreted as an occasionally inevitable reproductive error.

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17 January 1975; revised 11 March 1975

Orientation of Gull Chicks Exposed to Project Sanguine's Electromagnetic Field

Abstract. *Birds tested on clear days in the normal geomagnetic field showed a significant clustering of headings about a predicted bearing corresponding with the direction of migration. Individuals tested when a large antenna was energized dispersed randomly. Magnetic fields associated with such conductors may be sufficient to confuse orienting birds.*

Publication of Yeagley's (1) findings almost three decades ago generated a continuing controversy regarding the possible existence of an avian ability to use geomagnetic cues for migrational orientation. Recently Keeton (2), Southern (3), Walcott (4), and Wiltschko and Wiltschko (5)

have recorded changes in the direction-finding ability of pigeons (*Columba livia*), ring-billed gulls (*Larus delawarensis*), and European robins (*Erithacus rubecula*) when the birds are subjected to disturbances in the geomagnetic field, superimposed d-c fields (6), or simulated fields

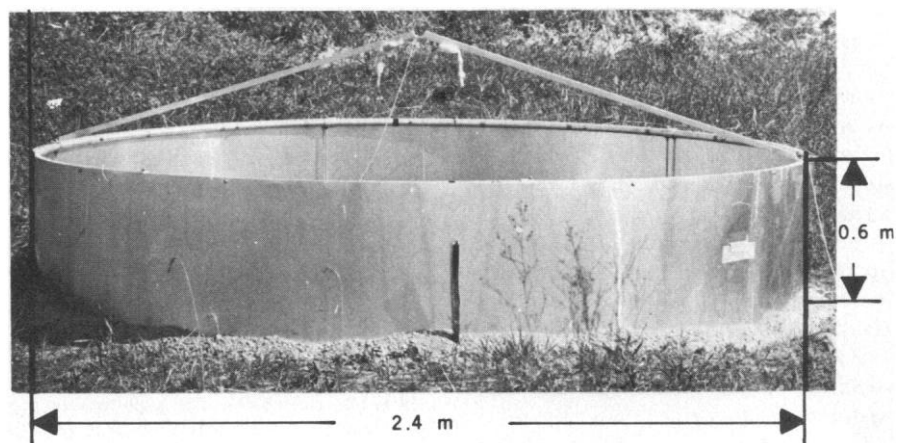


Fig. 1 Orientation cage.

(7). While many questions remain unanswered, these studies have added substance to the possibility that factors interfering with the magnetic environment of a bird may also disrupt its orientation. To determine whether man-made structures that generate high-intensity electromagnetic fields have similar effects, I conducted a study during 1973 at the Wisconsin Test Facility (WTF) of the U.S. Navy's Project Sanguine (8). The proposed Sanguine communication system will employ extremely low frequency radio waves between the continental United States and the submarine fleet.

Ring-billed gull chicks were subjected to trials in orientation cages at the site of the WTF to determine if the electric or magnetic fields produced by this large transmitting system would disrupt orientation. Experiments were designed to test the possible effects of various Sanguine characteristics, such as frequency, current, and mode of transmission.

The WTF consists of two 22.6-km-long antennas forming a cross, with a transmitter building at the intersection (9). The transmitter feeds the antennas at their centers, and each of the four antenna ends is terminated in a distributed ground system spread over a distance of about 3.2 km. When these studies were conducted, the north-south antenna was buried at a depth of about 1 m, whereas the east-west antenna was supported on ordinary 10.7-m utility poles.

The test antenna was operated at a frequency of 45 or 76 hertz and a current of 260 or 300 amp. The test field levels were therefore about twice as high as those associated with the proposed Sanguine system. Both antennas could be energized, but only the north-south one was used during these studies. Radiation characteristics of the electric and magnetic fields (10) associated with the energized antenna are presented in Table 1. The electric field level was determined by measuring the voltage induced in a wire of some arbitrary length. The magnetic field at WTF is generated by the current flowing in the earth as well as that flowing in the antenna cable.

Groups of 60 ring-billed gull chicks between 3 and 9 days old were transported by aircraft from a colony near Rogers City, Michigan, to Wisconsin. Chicks were used in trials for 2 or 3 days and then returned to the colony and exchanged for another group. The birds were maintained at a site where only minimal Sanguine effects were recorded, which reduced the likelihood that acclimation to Sanguine conditions would occur before completion of the experiments.

Two orientation cages (11) were centered on the ground (Fig. 1) directly over

Table 1. Magnitude of electric and magnetic fields measured when the north-south antenna was energized with 260 amp at 76 hertz, in the presence and absence of an orientation cage. Noise level corresponded to 60-hertz ambient fields.

Magnetic field (gauss)		Electric field (volt/m)	
At cage center	Over cage floor	Over 1.8-m wire	Over 15-m probe wire
Cage present			
0.429	0.400-0.509	0.244	0.280
Cage absent			
0.607	0.400-0.644	0.290	0.280

the buried north-south antenna, as the field characteristics associated with this antenna most closely resembled those of the proposed operational Sanguine system. The ground served as the cage floor. The schedule for test conditions was arranged with WTF personnel, but when the actual field work was conducted neither the investigators nor the facility staff knew the existing parameters until their diaries were compared. Procedures associated with the chick trials were the same as those I reported earlier (3).

Controls were tested when the antenna system was not energized and were exposed to only the local ambient field of

about 0.6 gauss. All trials were conducted during low-intensity natural disturbances in the geomagnetic field (12). Trials designated as experimental were conducted when the north-south antenna was energized. The birds in these trials were subjected to the maximum-intensity electromagnetic fields produced by the Sanguine test system, as trials were conducted at ground level. Data for control and experimental groups selected for discussion in this report were obtained during periods of clear skies; therefore the sun was available as a potential supplemental cue for orientation. Both types of trials were conducted on the same days but at alternate times. Equivocal results were associated with some of the other experimental conditions (13).

Ring-billed gull chicks tested previously in Michigan showed significant directional preferences for southeast (about 165°). Gulls tested under control conditions (antenna not energized) during four trial days at the WTF indicated a similar preference during 255 trials (Fig. 2A). The sample mean bearing is highly significant according to both the Rayleigh test and the V test (14). These findings show that young ring-billed gulls, although transported about 7° west and 1° north of their home colony, are capable of directional responses consistent with those shown at home.

I conducted 642 trials during eight trial days under the same sky conditions, but with the north-south antenna energized (15). A significant mean bearing was lacking in the resulting data (Fig. 2B), which indicates that the birds dispersed randomly in the test apparatus. From these data it appears likely that the electromagnetic field encountered by gulls at ground level above the Sanguine antenna is sufficient to disrupt their orientation. As these trials were conducted within the maximum fields produced by the test facility, further studies are required to show if chicks tested at various distances from the conductor are similarly affected. Since the magnetic field associated with an antenna conductor decreases rapidly as distance increases, birds migrating over Sanguine might pass unaffected. Important questions must be answered regarding the possible long-term effects at or near ground level.

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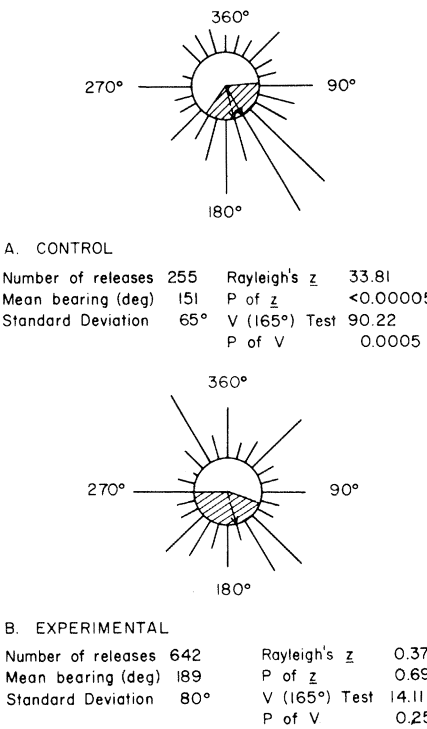


Fig. 2. Relative frequency of headings (shown as percentage of total) for control (A) and experimental (B) gull chicks. The hypothesized preferred heading is indicated by a broken arrow; a solid arrow designates the significant mean angle, if any.

6. This refers to magnets or battery-powered coils attached directly to a bird.
7. This refers to the production of an artificial ambient field over a relatively large area, in which the bird is subjected to orientation problems.
8. The facility is located in the Chequamegon National Forest near Clam Lake, Ashland County, Wis. The proposed system will employ two 88-km-long antennas with an interconnecting grid. There has been concern about the environmental impact of the electric and magnetic fields emitted by the operational system. Because of public concern in states proposed as possible sites for Sanguine, construction has been delayed, Congress has been critical of budget matters, and the scientific feasibility of the system has been questioned [see N. Gruchow, *Science* **166**, 850 (1969)]. This study and others have been conducted to determine if any detrimental effects are evident. Most studies have shown Sanguine test fields to have no undesirable effects. But, in most cases, the organisms tested or the methods used were not known indicators of electromagnetic field effects.
9. For further details see *Sanguine System Final Environmental Impact Statement, Technical Annexes* (Department of the Navy, Electronic Systems Command, Washington, D.C., April 1972).
10. Field measurements at WTF were arranged for by the Navy and performed by Illinois Institute of Technology Research Institute (IITRI) personnel. The magnetic field intensities listed in Table 1 are for the a-c field produced by the energized antenna. I measured the d-c geomagnetic field separately with a Radio Frequency Laboratories model 101 magnetometer. I requested information from the Navy and IITRI to show the interaction of the two fields, but the necessary data were not provided.
11. For details of orientation cage design and trial procedure see W. E. Southern, *Wilson Bull.* **86**, 256 (1974). The structure was made of nonmagnetic materials but formed a closed conductor when exposed to a-c fields. This is why the test fields (Table 1) were reduced when the cage was present. The resultant field was still within the range proposed for the operational Sanguine system.
12. Data on *K*-indices of magnetic activity were received from the World Data Center, Denver, Colo.
13. Results obtained on overcast days are inconsistent with those obtained on clear days. On overcast days the experimental and control groups showed statistically significant mean angles of 138° and 146°, respectively. Because there were fewer overcast days, these data are not comparable with the data for clear days. Only portions of 2 days were completely overcast, and during this time 491 trials were conducted. This necessitated scheduling the same group of 60 gull chicks for more individual trials per unit time than were scheduled for any other test situation. The chance of habituation or some other phenomenon biasing the results seemed likely. However, when the data for overcast days are combined with those for clear days ($N = 1133$) there is a statistically significant mean angle of 146° ($P = .0005$). Further fieldwork is necessary to resolve the causes of this inconsistency.
14. The Rayleigh test indicates whether a significant mean bearing exists in the distribution; the *V* test determines whether there is a significant grouping of headings about a hypothesized bearing, in this case 165°. See E. Batschelet, in *Animal Orientation and Navigation*, S. R. Galler, L. Schmidt-Koenig, G. J. Jacobs, R. E. Belleville, Eds. (NASA SP-262, National Aeronautics and Space Administration, Washington, D.C., 1970), pp. 61–91.
15. The data were divided into several subsets that could be considered as replicate experiments. Each subset was used to evaluate the possible effects of various aspects of the operational Sanguine system, such as mode of transmission, frequency of signal, and antenna type. The results for each subset are consistent with those for the main data set for clear days.
16. Supported by the Naval Electronic Systems Command through ONR contract N00014-72-A-0050-0002. Field assistance was provided by F. J. Cuthbert, F. Loomis, C. Lovekin, F. Moore, and J. O'Brien.

16 December 1974; revised 5 February 1975

Behavior of *Hymenaea courbaril* When Its Predispersal Seed Predator Is Absent

Abstract. *Members of lowland Costa Rican forest populations of Hymenaea courbaril (Leguminosae) have longer intervals between seed crops, a later age at first reproduction, larger seed crops, and more resin in the pod walls than do the H. courbaril native to Puerto Rico. The primary predispersal seed predators of H. courbaril in Costa Rica, Rhinocenus spp., are absent from Puerto Rico, and it is postulated that this is a major cause of the interpopulation differences.*

The hypothesis that supra-annual fruiting periodicity in individual trees is adaptive primarily in satiating seed predators with a large seed crop has anecdotal and theoretical support (1–3) but has not been subject to direct tests. One kind of test would be to record predispersal seed predation on individual conspecific and sympatric seed crops that are (i) out of phase with other conspecifics' crops, (ii) exceptionally many years apart (and therefore exceptionally large), or (iii) of different sizes in an asynchronously fruiting population (4). A second kind of test would be to compare the behavior of the tree in an area where the seed predators have been absent over evolutionary time with its behavior in habitats rich in seed predators and fruit parasites. Such a comparison is generally difficult, with one exception: tree species with both mainland and island populations. Here, I contrast a Costa Rican deciduous forest population of *Hymenaea*

courbaril (a caesalpinaceous legume known as "guapinol" in Central America) with that on Puerto Rico, with respect to four traits that I expect have been influenced by selective pressures exerted by Costa Rican *Rhinocenus* weevils (Curculionidae), the only severe predispersal seed predators of *H. courbaril* in Costa Rica (5).

Hymenaea courbaril is the only member of its genus in Central America. In Costa Rica, it occurs as scattered large trees in the forests of the Pacific coastal plain and foothills of the provinces of Guanacaste and Puntarenas [as well as from lowland tropical Mexico to much of lowland tropical South America (6)]. Here, in this highly seasonal habitat, most adults flower in March or April (the last half of the dry season), but in a given year about 10 percent or less of individuals in relatively undisturbed sites (7) produce fruit crops of 100 to 500 pods and do so at 3- to 5-year

intervals. This fruit production is annually asynchronous among members of the population (8) but synchronous within the year (9). When growing in a forest (7), only trees whose diameter at breast height (DBH) is more than about 20 inches (0.5 m) produce these large pod crops (10). Smaller and sick trees reproduce only by pollen production (11). By counting annual rings, I have determined that a 20-inch-DBH tree is usually 80 to 150 years old (12).

Hymenaea courbaril pods are immature, green, and full-sized for about 8 to 11 months, and then drop after maturing in the middle of the dry season (9). They are 10 to 20 cm long and may weigh 25 to 125 g. Indehiscent and extremely hard, they must be opened by a dispersal agent. During the last third of the fruit maturation period (October to December), 10 to 50 female *Rhinocenus* weevils begin to oviposit in the pod crop of a single tree (13). It appears that the female can oviposit in the pod wall for only about a month. During this short period, the copious resin in the pod wall is beginning to dry, and it does not well out when she cuts an oviposition hole with her mouthparts nor when the first instar larva bores further through the pod wall. This susceptible period is terminated when the pod wall becomes so hard with solidified resin that it is impenetrable (14). The total seed predation by *Rhinocenus* weevils in the seed crops of specific trees ranges from less than 5 to more than 90 percent, and the absolute number of pods whose contents are destroyed is usually between 30 and 100 in forest situations (15). On emerging from the pods, the adult weevils disperse from the tree. This dispersal is expected, since in a forest situation there will be no pods on that tree the next year (16). After they disperse, I have not been able to locate adult *Rhinocenus* until they appear at a new pod crop on a different tree in the next fruiting season. Thorough collection of seeds of other potential hosts has shown that a second generation does not occur on other plant species (5).

According to seed predator satiation theory (1–3), the production of large seed crops at intervals of n years rather than a crop $1/n$ times as large every year is selected for because (i) it causes the seed crop to be attacked only by weevils that can "colonize" the crown anew each time it fruits rather than weevils that might wait at the tree from crop to crop if it fruited annually, and (ii) it gives a tree time to accumulate enough reserves to make a crop large enough to satiate the oviposition abilities of beetles that do arrive at its crop. For example, if the beetles arriving at a crop can kill the seeds in 100 pods, then the