Geomagnetic Disturbance and the Orientation of Nocturnally Migrating Birds

Abstract. *Free-flying passerine migrants respond to natural fluctuations in the earth's magnetic field. The variability in flight directions of nocturnal migrants is significantly correlated with increasing geomagnetic disturbance as measured by both the* K *index and various components of the earth's magnetic field. The results indicate that such disturbances influence the orientation of free-flying migrants, but the evidence is not sufficient to show that geomagnetism is a cue in their orientation system.*

Much attention is currently focused on the question of geomagnetism and the orientation of birds. The view that birds are capable of extracting directional information from the earth's magnetic field draws support principally from controlled cage experiments with both passerines and nonpasserines (*1, 2*) and homing experiments with pigeons (*Columba livia*) (*3, 4*). I now report what is, to my knowledge, the first direct visual evidence that the orientation of free-flying nocturnal migrants is affected by natural fluctuations in the geomagnetic field (*5*).

Two means of assessing the effect of magnetism on the orientation of free-flying migrants are (i) tracking birds with radar through an artifically induced magnetic anomaly or during actual geomagnetic storms, and (ii) visually observing migrants aloft and examining statistically the influence of geomagnetic disturbance on the migrants' orientation. Larkin and Sutherland (*6*) recently reported that individual birds tracked by radar may be responding to a low-intensity a-c field created by the antenna system at the Wisconsin Test Facility, Project Seafarer; and Richardson (*7*) found a relationship between geomagnetic disturbance and the flight direction of diurnal migrants by using surveillance radar.

Direct visual observations of migration aloft during the spring and fall of the years 1968 through 1974 were collected by Gauthreaux, in the southeastern United States with ceilometer watches (*8*) and moon watches (*9*); his observations form the basis of this study. Both techniques allow a bird's flight direction (track) and, consequently, the mean track direction and angular deviation or dispersion in tracks to be determined during a watch. The flight directions of nocturnal migrants can be affected by wind (*10, 11*), and the velocity of the following wind in particular can influence the variability in track directions for a watch (*7*). Therefore, only watches made during light [≤ 6 knots (1 knot = 1.85 km/hour)] and calm winds are included in the current analysis (*12*). Other meteorological variables apparently do not influence the dispersion of passerine flight directions (*7, 11*) and, thus, were not included in the analysis. Because the ceilometer technique provides a better sample of migrants below 305 meters than the moonwatch technique, the data gathered according to the two methods were analyzed separately, as were the data gathered during the spring and fall migration seasons (*13*). Emphasis is placed here on the data from ceilometer watches because of better information about wind and the greater number of watches under disturbance conditions. Several measures of the geomagnetic fields were included as independent variables in the study (*14*), the most important being the *K* index, a measure of superimposed geomagnetic disturbance.

In the fall, migrants were well oriented and exhibited significant directionality [Rayleigh test (*15*), $P < .05$] for all but one of 60 ceilometer watches. However, the accuracy of orientation did deteriorate with increasing disturbance to the earth's magnetic field. Angular dispersion (s) in tracks was positively correlated ($P < .05$) with all geomagnetic variables except the magnetic aftereffects of a disturbance (Dst) (*14*), which was negatively correlated ($P < .05$). Multiple linear regression analysis (*16*) of all geomagnetic variables revealed a significant relationship between track dispersion and K-index values (Fig. 1).

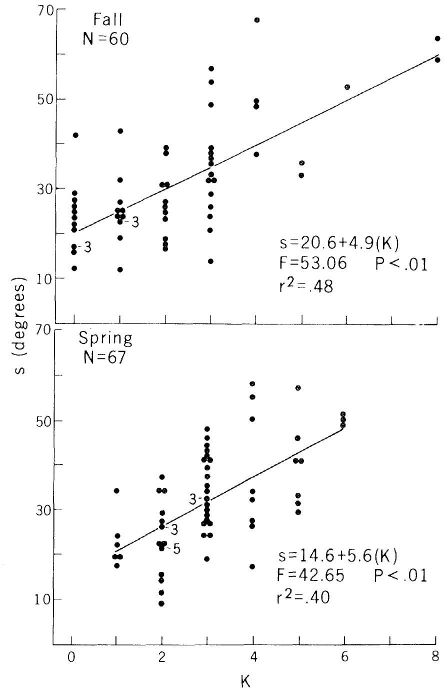

Fig. 1. Angular deviation (s) in flight directions plotted as a function of geomagnetic disturbance (K) for the fall and spring migration season (ceilometer data.)

An analysis of the spring data set yielded comparable results. Increased variation or spread in track directions (per watch) was associated with more intense geomagnetic disturbances, although only 2 of 67 ceilometer watches showed insignificant ($P > .05$) directionality (*15*). Again s was positively correlated ($P < .05$) with all geomagnetic variables except declination. Regression of track dispersion on K accounted for 40 percent of the variability in s (Fig. 1), while K was the only variable to enter a stepwise regression procedure ($P < .05$). Variables reflecting geomagnetic activity before and after a watch (K_6 and Dst, respectively) were unimportant in both seasons, which suggests that any response to geomagnetic disturbance is immediate (≤ 3 hours). Further comparison of the two migration seasons revealed the relationship between K and s to be nearly identical (Fig. 1), as no statistical difference was found between the two regression slopes, a finding that suggests the effect shown thus far to be independent of season.

I examined separately the relation between s and the individual field components, that is, horizontal (H) and vertical (Z) intensity as well as declination of the field (D), in an attempt to determine whether fluctuations in a given component were important. Recent work with the European robin (*Erithacus rubecula*) and certain sylviid warblers (*2*) suggests that such an analysis might reveal consistent patterns relative to the significance of the components. In spring, a combination of H, Z, and D accounted for only 17 percent of the variability in s, with the vertical component being the only significant variable ($P < .05$). The coefficient of determination was greater for the same combination of variables ($r^2 = .37$) in the fall, but in this season, the horizontal component was the important variable. Track variability was apparently unaffected by fluctuations in declination regardless of season.

Despite the attempt to control wind velocity, considerable residual variability in track dispersion remains after inclusion of geomagnetic variables. This variability may mask the exact relationship between K, for example, and bird orientation. Intuitively, I expected s to be nonlinearly related to K given the quasi-logarithmic nature of the K-index; that is, lower values of K (between 0 and 3) should have little effect on track dispersion, while moderate to severe storm activity ($K \geq 4$) should have a disproportionate influence. To test this expectation, I subdivided both spring and fall ceilometer watches into two groups, $K < 4$ and $K \geq 4$, and found the mean angular deviation in tracks to be significantly greater (t-test, $P < .05$) for the $K \geq 4$ group in both spring (40° versus 29°) and fall (50° versus 28°) (*17*).

The analysis of moon-watch data yielded similar results in terms of the relationship between K and s. With increasing geomagnetic activity, the spread in track direction increased, the relationship being more evident in spring ($r^2 = .46$, $n = 20$) than in fall ($r^2 = .28$, $n = 39$). No field component contributed significantly to the variance in s in either season when K was excluded from the moon-watch analysis. When the data were subdivided into groups of $K < 4$ and $K \geq 4$, the mean angular deviation changed both in the spring (from 25° to 36°) and in the fall (from 32° to 46°). A t-test was not performed on these data, however, because of nonhomogeneity of the variances.

The effect of magnetic disturbance on the actual mean track direction during a watch was also investigated, but I found no obvious relationships. The only hint of such an effect was in the spring ceilometer data set. Under low K values (< 4) the mean flight directions ($\bar{a}_f$) were consistently to the north-northeast ($\bar{a}_f = 20°$), while under K values ≥ 4 a statistically significant shift in mean direction to the northwest ($\bar{a}_f = 326°$) ($F = 8.55$, $P < .01$) (*18*) accompanied a marked increase in the variability of watch flight directions (Fig. 2). Although the distribution of watch means under high K is not significant ($.05 < P < .10$), the leftward or counterclockwise shift in mean direction is especially intriguing in light of similar findings with homing pigeons (*4*) and free-flying migrants over Puerto Rico (*7*). The corresponding wind directions for the watches conducted under high K also showed a northwest bias ($\bar{a}_w = 322°$), although their variability was much greater, resulting in a statistically uniform ($P > .10$) distribution (Fig. 2).

The evidence lends additional credence to the view that birds respond to magnetic stimuli and suggests that the orientation of free-flying migrants is influenced by fluctuations in the geomagnetic field. Magnetic disturbances, however, may act indirectly on the avian orientation system. For example, meteorological phenomena are influenced by solar activity (*19*) as well as by the earth's magnetic field (*20*), but the time course involved is on the order of days, months, or years, which probably precludes their importance in the relationship shown here. Nonetheless, the existence of some (unidentified) intervening variable or variables is not ruled out. Alternatively, a disturbance to the earth's field may impair the normal functioning of some other component of the orientation system. Whether the relationship be direct or indirect, a strong correlation between the orientation of free-flying birds and geomagnetism has been demonstrated.

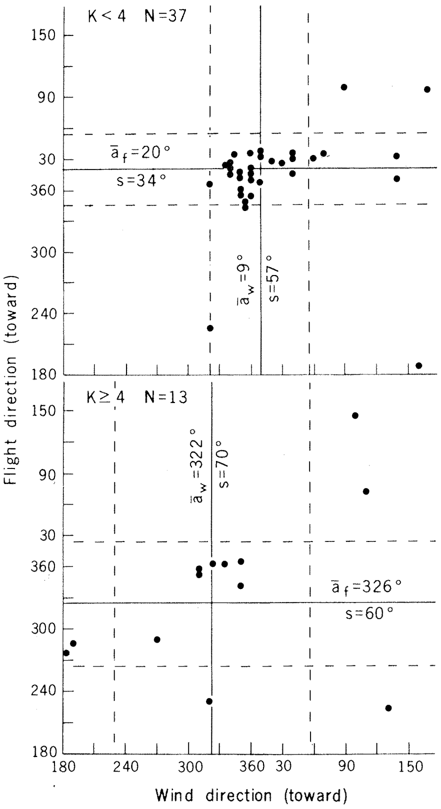

Fig. 2. Scatter plot of migration flight directions and corresponding wind directions under conditions of geomagnetic disturbance $K < 4$ (top) and $K \geq 4$ (bottom). Horizontal solid line represents the mean flight direction ($\bar{a}_f$) and the vertical solid line the mean wind direction ($\bar{a}_w$). Dashed lines delimit ± the angular deviation (s). North is 360°.

FRANK R. MOORE
Department of Zoology,
Clemson University,
Clemson, South Carolina 29631

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12. Information concerning winds aloft was obtained either at the watch site or from the National Climate Center, Asheville, North Carolina.
13. Cloud cover was recorded for each watch. Nocturnal migrants are well oriented in spite of overcast skies (stars not visible); geomagnetic cues would presumably be especially important during such conditions. Only a few overcast observations are included in this analysis (2 moon and 10 ceilometer watches), which makes comparisons between clear and overcast conditions difficult.
14. The K-index value for the 3-hour interval in which the watch was taken was included as a measure of superimposed transient fluctuations in Earth's magnetic field resulting from solar activity (magnetic storms). The index is determined for each 3-hour interval (universal time) after subtracting the effects of quiet-day solar variation, lunar variation, solar flare effects, and the aftereffects of the disturbance field. The variable K is defined in terms of the field component (horizontal or declination) showing the largest fluctuation (the vertical component has been excluded since 1964). The relationship between the actual fluctuation of the intensity of the magnetic field (measured in gamma) and K is defined by a quasi-logarithmic scale ranging from 0 to 9. For the Fredricksburg, Virginia, station from which the original data were collected, the gamma related to each K is (for each K, gamma is shown in parentheses): 1 (0 to 5), 2 (10 to 20), 3 (20 to 40), 4 (40 to 70), 5 (70 to 120), 6 (120 to 200), 7 (200 to 330), 8 (330 to 500), 9 (> 500). In addition, K values for the two 3-hour intervals before a watch were added, creating a new variable, K_6. Possibly events preceding the actual sampling might be influencing the migrants' orientation. The values of *Dst* were also included as measures of the aftereffects of a magnetic storm. In practice, these values represent changes in the horizontal component only. The remaining variables were a function of the individual field components or elements (H = horizontal, Z = vertical, and D = declination)at the time of the watch. The value of the components used in the study represent the difference in gammas between the 5-day magnetic quiet day value for the month in which the watch was made and the actual intensity of the component at the time of the watch. From April 1968 through October 1974, the horizontal component increased by 516 gamma, the vertical decreased by 595 gamma, and the declination moved westward 33 minutes. Thus, actual hourly values at the time of the watch could not be used as variables. All geomagnetic data used in connection with this study were obtained from WDC-A for *Solar-Terrestrial Physics* (Geomagnetism).
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21. I thank S. A. Gauthreaux, Jr. for making available his ceilometer and moon-watch data and, especially, for his advice and encouragement throughout this study. I also thank S. Emlen, W. Keeton, and R. Larkin for their helpful and critical comments on an earlier draft. J. Waide also reviewed the manuscript and offered statistical advice, as did J. Holman. C. W. Helms made available financial support for the study through the Department of Zoology, Clemson University. This work was completed while I held a research assistantship under U.S. Air Force grant AFOSR-75-2787.

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Drug Tolerance in Biomembranes: A Spin Label Study of the Effects of Ethanol

Abstract. *Ethanol in vitro increased the fluidity of spin-labeled membranes from normal mice. Membranes from mice that had been subjected to long-term ethanol treatment were relatively resistant to this fluidizing effect. The data suggest that the membranes themselves had adapted to the drug, a novel form of drug tolerance.*

Ethanol is one of a large group of drugs that can produce general anesthesia and (at much higher concentrations) can block nerve conduction. Most of these drugs lack the structural complexity expected of a drug that acts by combining with a specific receptor. Because the anesthetic potencies of such drugs correlate with their lipid solubilities, they are thought to exert their biological effects by entering the lipid portion of biomembranes and disrupting membrane function. Cell membranes and model membranes expand (*1*) and become more fluid (*2, 3*) when immersed in nerve-blocking concentrations of such drugs. We have recently shown (*4*) that the fluidizing effects of ethanol in biomembranes can be measured at very low concentrations with a sensitive electron paramagnetic resonance (EPR) technique. We report here that tolerance to this effect develops in mice, which suggests that mammalian cells can control the physical properties of their membranes in response to drugs.

Male DBA/2J mice were maintained for 8 days on a liquid diet (Slender, Carnation Company) to which ethanol was added to provide 33 percent of the calories. Controls were pair-fed the same diet with sucrose replacing ethanol calories. We used membranes from the animals whose ethanol intake patterns met our previously defined criteria for development of physical dependence (*5*). They had consumed an average of 18 g of ethanol per kilogram of body weight per day during the last 4 days. Their mean blood ethanol concentration at the time they were killed was 3.4 ± 0.87 mg/ml (mean ± standard deviation).

Since these animals were known to be physically dependent, we considered them to be in a "tolerant-dependent" state. Although we did not make numerical estimates of the extent of functional tolerance, we did note that none of the mice had lost their righting reflex at blood ethanol concentrations that would be hypnotic for most normal animals.

Cardiac blood from five to seven mice was pooled in each of three replicate experiments. Erythrocyte membranes were prepared under conditions that minimize membrane disruption (*4, 6*). From the combined whole-brain homogenates of the same mice, we isolated myelin, mitochondrial membranes, and synaptosomal plasma membranes by a flotation-sedimentation technique (*4, 7*). Each of these four membrane preparations was then spin-labeled by incubation for 30 minutes at 37°C with 5-doxylstearic acid (*N*-oxyl-4′,4′-dimethyl-oxazolidine derivative of 5-ketostearic acid, SYVA Company, Palo Alto). This fatty acid spin label tends to align itself with the fatty acid chains of phospholipids in the membrane bilayer. Its EPR spectrum is affected by its motion; that is, by the fluidity of its environment. The EPR spectrum of a rapidly tumbling spin label consists of three evenly spaced peaks. When the spin label is immobilized, the peaks become broader and farther apart. The spectrum can be characterized by an order parameter, S (*8*), determined from the separation of the peaks, along with reference data from crystals oriented in the magnetic field. In model membranes, the order parameter can vary between the limits of 1.0 (completely ordered) and 0 (completely fluid). In natural biomembranes, order parameters indicate intermediate fluidity: $S \simeq .6$. Our EPR spectra were obtained at 37°C with a modified Varian EM-500 spectrometer and a PDP 8/e computer (*9*).

Spectra were obtained for portions of each of the four kinds of spin-labeled preparations in the presence of various concentrations of ethanol (tested in random order). Measurements of the baseline order parameter with no ethanol added to the membranes were interspersed among the measurements where ethanol was added. The last column in Table 1 shows that the baseline order parameter differed among the various membrane types; mitochondrial membranes were the most fluid, the erythrocyte and synaptosomal membranes were of intermediate fluidity, and myelin was the most ordered. These results confirm those of our previous study (*4*). There were small differences between the three replicate experiments, reflecting the variability in spectral characteristics seen in similar preparations to which the spin label is separately added. We could not detect consistent differences in the baseline order parameter between membranes from groups receiving long-term ethanol treatment and the corresponding membranes from their sucrose-control mates.

When the same membrane preparations were tested in the presence of eth-

Table 1. Baseline order parameters. Membrane fractions were prepared from cardiac blood and from whole-brain homogenates pooled for five to seven ethanol-treated animals in each of three experiments, and from their sucrose-treated partners in the pair-feeding experiments. The fractions were spin-labeled with 5-doxylstearic acid and a portion of each preparation was analyzed by EPR to determine the order parameter in the absence of added ethanol. Since the ethanol and sucrose groups were not significantly different, the data for the six preparations were combined to allow comparison of membrane types (last column); SEM, standard error of the mean.

Source of membrane	Long-term treatment	Order parameter				
		Experiment			Mean of treatment	Mean of membrane type ± SEM
		1	2	3		
Erythrocyte	Sucrose	.589	.588	.597	.591	.589 ± .0038
	Ethanol	.573	.600	.589	.587	
Synaptosome	Sucrose	.590	.592	.604	.595	.595 ± .0023
	Ethanol	.590	.593	.599	.594	
Mitochondria	Sucrose	.570	.579	.571	.573	.574 ± .0017
	Ethanol	.570	.573	.579	.574	
Myelin	Sucrose	.607	.624	.631	.621	.617 ± .0044
	Ethanol	.602	.620	.618	.613	