

Magnetic polarity fractions in magnetotactic bacterial populations near the geomagnetic equator

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ABSTRACT The relative numbers of North-seeking and South-seeking polarity types in natural populations of magnetotactic bacteria were determined at sites on the coast of Brazil. These sites were South of the geomagnetic equator and had upward geomagnetic inclinations of 1–12°. For upward inclinations >6°, South-seeking cells predominated over North-seeking cells by more than a factor of 10. For upward inclinations <6°, the fraction of North-seeking cells in the population increased with decreasing geomagnetic inclination, approaching 0.5 at the geomagnetic equator. We present a simple statistical model of a stochastic process that qualitatively accounts for the dynamics of the two polarity types in a magnetotactic bacterial population as a function of the geomagnetic field inclination.

INTRODUCTION

Magnetotactic bacteria orient and migrate along geomagnetic field lines (1, 2). Magnetic orientation is due to intracytoplasmic, single-magnetic-domain magnetite (Fe_3O_4) particles (magnetosomes) which are fixed in the cell. The particles are often arranged in chains and impart a permanent magnetic dipole moment to the cell (3). There are two possible cell polarity types: one in which the North-seeking pole of the cellular magnetic dipole is forward with respect to the flagellum (polarity type N) and the other in which the South-seeking pole of the cellular magnetic dipole is forward with respect to the flagellum (polarity type S) (Fig. 1). The former cells migrate along geomagnetic field lines parallel to the field direction, i.e., Northward, whereas the latter cells migrate antiparallel to the geomagnetic field direction, i.e., Southward. Thus polarity type N is North seeking, polarity type S is South seeking. Because of the inclination of the geomagnetic field, cells will migrate upward or downward depending on their polarity and on the sign of the inclination. In the Northern hemisphere where the field is inclined downward, North-seeking cells and South-seeking cells migrate downward and upward, respectively. In the Southern hemisphere where the field is inclined upward, North-seeking cells and South-seeking cells migrate upward and downward, respectively. Downward directed motion is generally favored over upward directed motion because North-seeking cells predominate in the Northern hemisphere whereas South-seeking cells predominate in the Southern hemisphere (4, 5). The differential survival advantage of downward migration over upward migration is presumably related to lower oxygen tension

and higher nutrient availability in the sediments compared with the water surface.

At the geomagnetic equator the geomagnetic field is horizontal, i.e., the inclination is zero. Under these conditions there is no differential survival advantage for either polarity type and North-seeking and South-seeking bacteria coexist in the sediments (6, 7).

Whereas the ability to synthesize Fe_3O_4 and construct magnetosomes is certainly genetically encoded, the polarity of the magnetosome chain cannot be encoded. If a bacterium that lacks magnetosomes starts to synthesize them *de novo*, there is equal probability that, when the particles grow to permanent single-magnetic-domain size, the chain will magnetize with the North-seeking pole forward or with South-seeking pole forward: a population of these bacteria will consist of 1:1 North seekers and South seekers. If however, the daughter cells inherit some of the parental magnetosomes during cell division, they will inherit the parental polarity. As they synthesize new magnetosomes at the ends of their inherited chains, the magnetic field produced by the existing particles will magnetize the new particles in the same direction. Thus North-seeking bacteria predominantly produce North-seeking progeny and South-seeking bacteria produce South-seeking progeny. However, some progeny with the opposite polarity can be produced in each generation. For example, if in the cell division process, some of the daughter cells inherit no parental magnetosomes, these cells will synthesize them *de novo* and about one-half of those will end up with the polarity opposite to that of the parent. So in the Northern Hemisphere where North-seeking bacteria predominate, some South seekers are produced in each population division. Under normal

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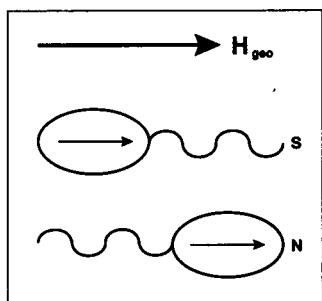


FIGURE 1 Schematic representation of South-seeking (polarity type S) (top) and North-seeking (polarity type N) (bottom) magnetotactic bacteria.

circumstances, these South seekers are unfavored by being directed upwards toward the surface when they are separated from the sediments, and their population remains low compared with the North-seeking population. The reverse situation holds in the Southern hemisphere where South-seeking bacteria are favored.

In this paper we consider the effect of the inclination of the geomagnetic field on the fractions of the two polarity types of magnetotactic bacteria in natural populations. In particular, we are interested in how much inclination of the geomagnetic field is required to select one polarity type over the other. In April, 1982 we surveyed the number of each polarity type in magnetotactic bacterial populations at aquatic sites on the coast of Brazil, South of the city of Camocim, Ceará, where the magnetic inclination varies between 1 and 12° (geomagnetic field inclined upwards). The survey shows that an upward inclination of ~6° is sufficient to effectively select the South-seeking polarity type. For upward geomagnetic inclinations <6°, the fraction of North-seeking bacteria at each site increases with decreasing inclination, although the fraction can vary from point to point within the sediments at that site. We present a simple statistical model of a stochastic process that qualitatively accounts for the relative populations of the two polarity types as a function of geomagnetic field inclination. The model, similar to that proposed by Lumsden (8), is mapped onto a linear system which can be described by a set of differential equations or by an iterative procedure. Although the model does not account for the total population, both descriptions lead to the same fixed point which represents the ratio of polarity types in the population.

SURVEY OF NATURAL ENVIRONMENTS

Samples were collected at nine sites on the Brazilian coast between the cities of Camocim, Ceará, and Natal, Rio

Grande do Norte. The sites were brackish mangrove swamps at the mouths of rivers on the coast. Eight or more samples were examined at each site during low tide with a Zeiss aus Jena microscope set up nearby. The procedure for each sample was to draw up an aliquot of sediment and water with a Pasteur pipette. A drop of the sediment-water mixture was deposited on a glass cover slip. The drop was hung by turning the cover slip upside down and placing it over a small rubber O-ring situated in the center of a microscope slide and held in place with vacuum grease. The slide was placed on the microscope stage, together with a small bar magnet that produced a magnetic field of several gauss across the drop. The magnet was oriented so that the south pole, that is, the pole that attracts the North-seeking pole of a magnetic compass needle, was closest to the drop. The edges of the drop closest to and opposite to the bar magnet were surveyed microscopically for up to 30 min. Coccoid-shaped bacteria ~2 μm in diameter were the most common magnetotactic cells at all the sites. Bacteria that accumulated at the edges of the drop were checked for magnetotaxis by observation of their response when the bar magnet was moved or rotated, then counted. Magnetotactic bacteria that accumulated at the edge of the drop closest to the bar magnet were North-seeking bacteria; those that accumulated on the edge of the drop opposite to the bar magnet were South-seeking bacteria. The magnet was periodically rotated and moved to the other side of the drop to avoid counting bias. The procedure was repeated with several drops of sediment and water at each site.

The geomagnetic field intensity and inclination at each site was measured with a fluxgate magnetometer (model DM2220; Schoenstedt Instruments Co.). A block of lucite with three orthogonal holes (X, Y, and Z) just large enough to hold the magnetometer probe was mounted on the platform of an aluminum camera tripod with a brass screw and leveled. Then with the probe in the X hole, the block was rotated in the horizontal plane and the meter adjusted until both $R(X)$ and $R(-X)$ were zero, meaning that the axis of the probe was orthogonal to the geomagnetic field and the meter was properly zeroed. Then readings along the vertical direction $R(Z)$, and parallel and antiparallel to the horizontal component of the geomagnetic field, $R(Y)$ and $R(-Y)$, were made. The measurements were considered acceptable if $R(Y)$ was equal to $-R(-Y)$ to <0.001 Gs. Because $R(X) = 0$, the field strength H_{geo} is given by

$$H_{geo} = ([R(Y) - R(-Y)]/2)^2 + R(Z)^2)^{1/2}. \quad (i)$$

The inclination β of the geomagnetic field is given by

$$\beta = \arctangent \{R(Z)/[R(Y) - R(-Y)]/2\}. \quad (ii)$$

TABLE 1 Geomagnetic field intensity and inclination, and the fraction of North-seeking (polarity type N) magnetotactic bacteria in natural populations at sites on the coast of Brazil, South of the geomagnetic equator. Data were collected in April, 1982

Locality	H_{geo}	β	Polarity type N fraction
	<i>gs</i>	<i>degrees</i>	
Camocim (CE) [‡]	0.268	-1.3	0.38 ± 0.03
Acaraú (CE)	0.272	-2.2	0.32 ± 0.04
Fortaleza (CE)	0.277	-4.2	0.16 ± 0.02
Iguape (CE)	0.268	-5.6	<0.1
Fortim (CE)	0.269	-6.4	<0.1
Mossoró RN [‡]	0.269	-8.6	<0.1

*Upward inclined geomagnetic fields are conventionally considered to have negative inclinations.

[‡]CE, State of Ceará; RN, State of Rio Grande do Norte.

Measurements of H_{geo} and β were made in three different locations at each site and the results were averaged. The measured values are in good agreement with geomagnetic survey results from 1985, if the latter are corrected for annual variation back to 1982.

The measured fractions of North-seeking cells in the populations at various sites are presented in Table 1 together with the magnetic field intensities and inclinations. It can be seen that for sites with upward inclinations $>6^\circ$, the number of North-seeking cells is less than one-tenth the number of South-seeking cells. For upward inclinations $<6^\circ$, the relative numbers of North-seeking cells become appreciably greater, approaching the number of South-seeking cells as the inclination goes to zero. However, whereas the averaged values for samples at a given site vary smoothly with inclination for inclinations $<6^\circ$, there were large variations from sample to sample at the same site. This is illustrated by the data for seventeen samples from Camocim in Table 2. This suggests that microenvironmental factors as well as gross environmental factors such as the geomagnetic field play a role in determining the polarity ratio. One microenvironmental factor could be texture or roughness of the sediment/water interface on a scale that is large compared with the size of a bacterium. As shown in Fig. 2, this could favor one or the other polarity at any point on the interface. If one randomly samples many points of the interface, the average polarity type fractions will presumably be obtained.

We can summarize the experimental results as showing that an upward inclination of the geomagnetic field of the order of 6° is sufficient to select polarity type S over polarity type N. For upward inclinations between 0 and 6° , an appreciable fraction of polarity type N exists in the populations, and can even predominate in certain microenvironments.

TABLE 2 Numbers of South-seeking (polarity type S) and North-seeking (polarity type N) magnetotactic bacteria in individual samples collected at Camocim (CE)

Sample	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
(S)	40	10	23	26	10	129	03	06	49	06	05	09	107	28	04	17
(N)	13	03	14	13	07	03	01	130	27	21	01	01	13	14	01	27

Totals: (S) 472; (N) 289.

THEORETICAL MODEL

We now consider a model for the effect of the geomagnetic inclination on the ratio of the two magnetic polarity types in the population. The model is based on the following assumptions: (a) North-seeking (polarity type N) and South-seeking (polarity type S) cells are identical except for their polarity. In particular the division rate of the bacteria is independent of polarity type; (b) when bacteria divide, there is a probability k that they produce daughter cells with the same polarity, and probability $1-k$ that they produce daughter cells of the opposite polarity. k is independent of the magnetic field strength and inclination. (c) the survival probability of each polarity type is equal to the probability that it will migrate downward from the horizontal plane. If p is the probability that South-seeking cells migrate downward in the Southern hemisphere, $1-p$ is the probability that North-seeking cells migrate downward. So the survival probabilities of South-seeking and North-seeking cells are p and $1-p$, respectively. p is a function of the magnetic field strength H and inclination β , and of the magnetic dipole moment M of the cells.

The dependence of p on H , β , and M can be calculated as follows. First consider the case of H vertical (i.e., $\beta = 90^\circ$) and further consider the bacteria as point magnetic dipoles. Then the probability that a particular

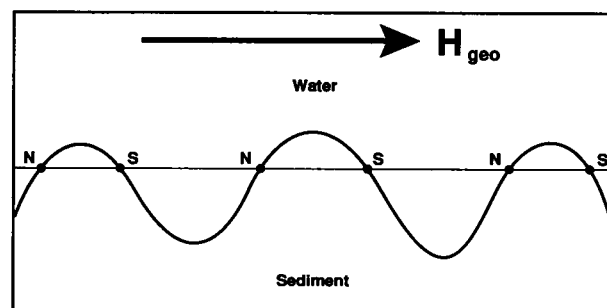


FIGURE 2 Schematic representation of the sediment/water interface at the geomagnetic equator, showing how motion along the horizontal geomagnetic field lines could favor one or the other polarity types at different points of the interface.

dipole moment \mathbf{M} makes an angle between θ and $\theta + d\theta$ with \mathbf{H} is given by

$$h(y, \theta) d\theta = y \exp(y \cos \theta) \sin \theta d\theta / 2 \sinh(y), \quad (1)$$

where $y = MH/k_B T$ ($k_B T$ = Boltzmann's constant times temperature). Then the probability p that a dipole is oriented above the horizontal plane is

$$p = \int_0^{\pi/2} h(y, \theta) d\theta. \quad (2)$$

Because South-seeking cells migrate opposite to the orientation direction of their magnetic dipole (Fig. 1), p is the probability that South-seeking cells migrate downward. Because North-seeking cells migrate parallel to their orientation, $1-p$ is the probability that North-seeking cells migrate downward. The probabilities are just reversed in the case of the magnetic field pointing straight down.

Now let us consider the more general case of the magnetic field inclined upward at the angle β ($0 \leq \beta \leq \pi/2$) with respect to the horizontal plane (Fig 3). If the Z direction is taken parallel to \mathbf{H} , and X and Y are chosen properly, the normal \mathbf{n} to the horizontal plane is given by

$$\mathbf{n} = (-\cos \beta, 0, \sin \beta) \quad (3)$$

and the equation of the horizontal plane is defined by

$$\mathbf{n} \cdot \mathbf{r} = 0, \quad (4)$$

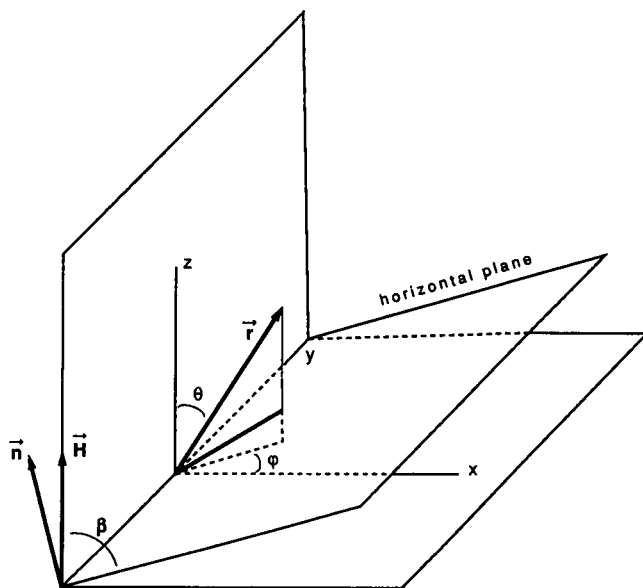


FIGURE 3 Diagram for the calculation of the probability that a magnetic dipole is oriented above the horizontal plane for an arbitrary upward inclination of the geomagnetic field above the horizontal plane.

where

$$\mathbf{r} = r(\sin \theta \cos \phi, \sin \theta \sin \phi, \cos \theta) \quad (5)$$

with θ and ϕ defined with respect to \mathbf{H} . Now the probability that the magnetic dipoles will be oriented above the horizontal plane is given by

$$p = \frac{\int_0^{2\pi} d\phi \int_0^{\alpha(\phi)} \exp[y \cos \theta] \sin \theta d\theta}{\int_0^{2\pi} d\phi \int_0^{\pi} \exp[y \cos \theta] \sin \theta d\theta} \quad (6)$$

where

$$\tan \alpha(\phi) = \tan \beta / \cos \phi. \quad (7)$$

From these equations we obtain

$$p = \frac{\exp[y]}{2 \sinh(y)} - \frac{\int_0^{\pi} \exp[y \cos \alpha(\phi)] d\phi}{2\pi \sinh(y)}. \quad (8)$$

In Fig. 4, p is plotted as a function of the inclination β for several values of y . For values of $y = 10-40$, it can be seen that inclinations $\beta \sim 20-40^\circ$ are required for p to approach 1. This means that the probability of downward direction motion alone does not explain the observed fact that South-seeking cells are selected at upward inclinations $\beta > 6^\circ$. Thus we must take cell division as well as survival probability into account to understand the effect of the magnetic inclination on the equilibrium or steady-state ratio of the two polarity types in a population. This leads us to the dynamic model outlined below.

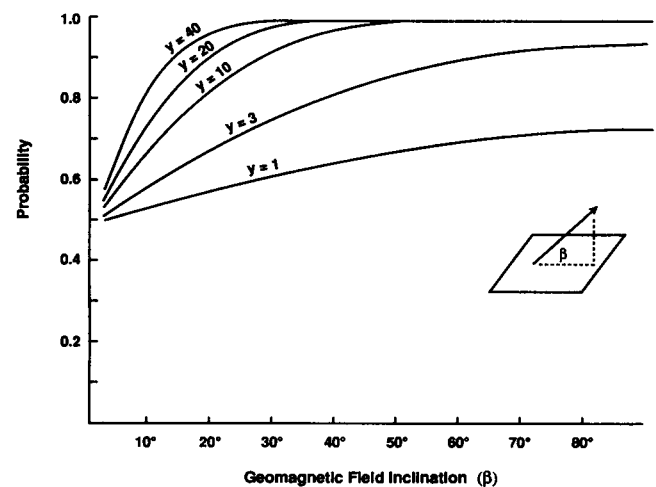


FIGURE 4 Probability p of orientation of cellular magnetic dipoles above the horizontal plane plotted as a function of geomagnetic field inclination for several values of $y = MH/k_B T$.

Discrete model

If n_S and n_N represent the South-seeking (S) and North-seeking (N) magnetotactic bacterial polarity type subpopulations, respectively, of a species in a given habitat, then as a result of the differential survival probability due to the magnetic field directed motion, new subpopulation of each polarity type will result which are given by

$$n'_S = (p)n_S; \quad n'_N = (1-p)n_N. \quad (9)$$

If we write

$$\mathbf{n} = \begin{pmatrix} n_S \\ n_N \end{pmatrix}; \quad \mathbf{n}' = \begin{pmatrix} n'_S \\ n'_N \end{pmatrix}. \quad (10)$$

Eq. 7 can be written in matrix form

$$\mathbf{n}' = \mathcal{P}\mathbf{n}, \quad (11)$$

where

$$\mathcal{P} = \begin{pmatrix} p & 0 \\ 0 & 1-p \end{pmatrix}. \quad (12)$$

If we now consider the division process, then the resulting subpopulations are

$$n''_S = k n'_S + (1-k)n'_N, \quad (13)$$

and

$$n''_N = k n'_N + (1-k)n'_S, \quad (14)$$

where k is the probability that type S and type N cells give rise to type S and type N cells, respectively. $1-k$ is the probability that type S and type N cells give rise to type N and type S cells, respectively. The new subpopulations can be written

$$\mathbf{n}'' = \mathcal{H}\mathbf{n}', \quad (15)$$

where

$$\mathcal{H} = \begin{pmatrix} k & 1-k \\ 1-k & k \end{pmatrix}. \quad (16)$$

We have neglected a scaling factor of 2 which affects the total population but not the ratio of the polarity type subpopulations.

Only symmetrical sequences of operators give results which are independent of the boundary conditions, i.e., whether the subpopulations are observed before or after the last cell division. Therefore we consider symmetrical combinations of \mathcal{P} and \mathcal{K} , the simplest of which is \mathcal{PKP} . This corresponds to cell division occurring in the middle of a time interval in which the bacteria are subject to the selection pressure associated with the geomagnetic field.

Then

$$\mathbf{n}''' = \begin{pmatrix} n'''_S \\ n'''_N \end{pmatrix} = \mathcal{PKP} \begin{pmatrix} n_S \\ n_N \end{pmatrix}, \quad (17)$$

where

$$\mathcal{PKP} = \begin{pmatrix} p^2k & p(1-p)(1-k) \\ p(1-p)(1-k) & (1-p)^2k \end{pmatrix}. \quad (18)$$

If we let \mathcal{PKP} operate on each successive population, the polarity-type subpopulation ratio after the r th iteration is

$$x(r+1) = \frac{p^2k x(r) + p(1-p)(1-k)}{(1-p)^2k + p(1-p)(1-k) x(r)}, \quad (19)$$

where

$$x(r) = \frac{n_S}{n_N}. \quad (20)$$

The equilibrium ratio can be obtained from the condition $x(r+1) = x(r) = x$. Then

$$x = \frac{\alpha + (\alpha^2 + 4)^{1/2}}{2}, \quad (21)$$

where

$$\alpha = \frac{2p-1}{p(1-p)} \cdot \frac{k}{(1-k)}. \quad (22)$$

This procedure is equivalent to the matrix iteration

$$\mathbf{n}(j+1) = \mathcal{PKP}\mathbf{n}(j) \quad (23)$$

and the equilibrium values are given by the eigenvalue equation

$$\mathcal{PKP}\mathbf{n} = \lambda\mathbf{n}. \quad (24)$$

If we define the fraction of polarity type S in the population $f = n_S/(n_S + n_N)$ then from Eq. 21

$$f = \frac{2}{(\alpha^2 + 4)^{1/2} - (\alpha - 2)}. \quad (25)$$

The fraction of polarity type N is $1-f$. Then

$$f(p) + f(1-p) = 1 \quad (26)$$

and

$$f = 1/2 \quad \text{for} \quad p = 1/2. \quad (27)$$

This last result means that if both polarity types have equal survival probabilities (inclination zero), their subpopulations are equal, as expected.

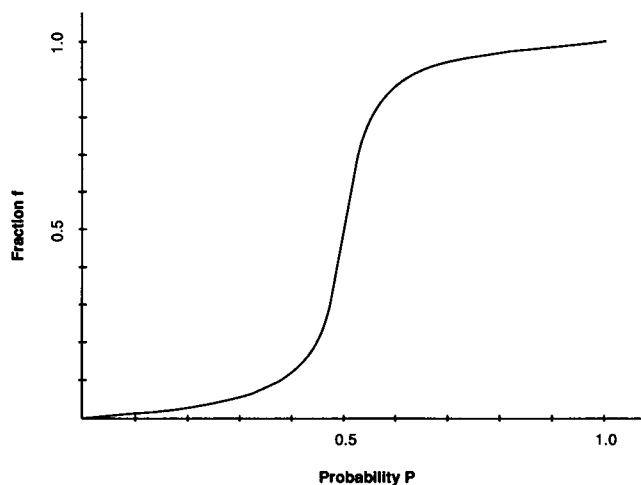


FIGURE 5 Theoretical fraction f of South-seeking cells (polarity type S) in the population from Eq. 25 plotted as a function of survival probability p at constant $k = 0.9$.

Continuous model

The results obtained with the discrete model can also be obtained using linear differential equations. Let λ be the rate of decrease or increase in the total bacterial population. Then considering the symmetrical sequence of events outlined above,

$$dn_s = \lambda p^2 k n_s dt + \lambda p(1-p)(1-k)n_N dt \quad (28)$$

and

$$dn_N = \lambda(1-p)^2 k n_N dt + \lambda p(1-p)(1-k)n_s dt,$$

yielding

$$\frac{1}{\lambda} \frac{dx}{dt} = (2p-1)kx + p(1-p)(1-k)(1-x^2), \quad (29)$$

where $x = n_s/n_N$. The equilibrium solution at $dx/dt = 0$ is

$$x = [\alpha + (\alpha^2 + 4)^{1/2}]/2, \quad (30)$$

where α is given in Eq. 22. This is the same solution obtained with the discrete model (Eq. 21).

DISCUSSION

The fraction f of polarity type S in the population from Eq. 25 is plotted as a function of p at constant k in Fig. 5. It can be seen that f changes rapidly for values of p close to 0.5. In terms of the geomagnetic field, $p = 0.5$ corresponds to zero inclination, i.e., the situation exactly at the magnetic equator. As one moves South of the geomagnetic equator the upward geomagnetic field inclination increases with a consequent increase in p and rapidly increasing and decreasing fractions of polarity type S cells and polarity type N cells, respectively, in the population. The theoretical fraction of polarity type N cells is plotted as a function of geomagnetic field inclina-

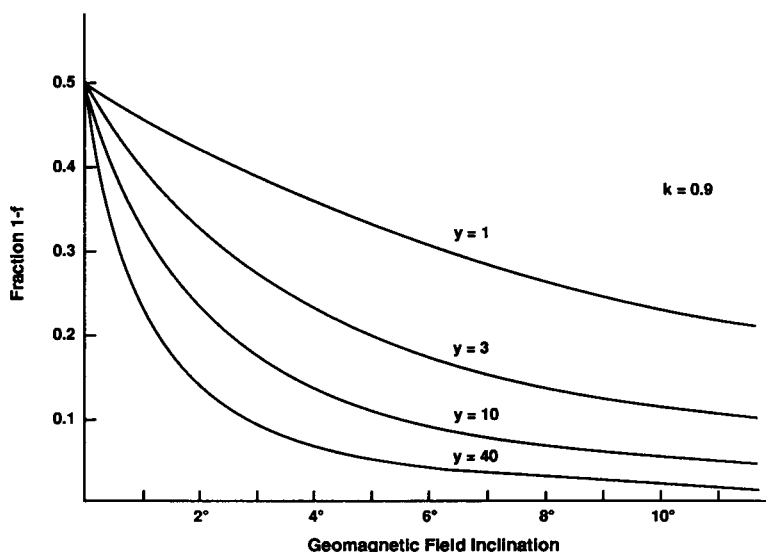


FIGURE 6 Theoretical fraction $1-f$ of North-seeking cells (polarity type N) in the population plotted as a function of geomagnetic field inclination for various values of y at $k = 0.9$.

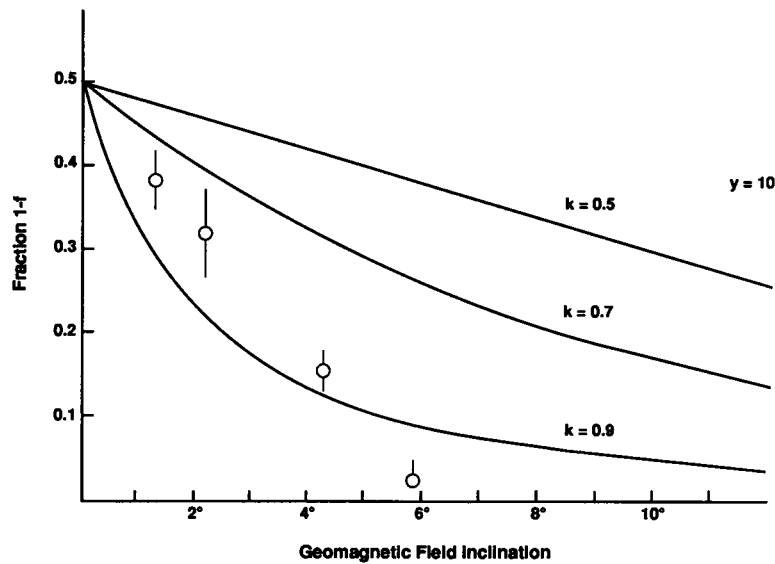


FIGURE 7 Theoretical fraction $1-f$ of North-seeking cells (polarity type N) in the population plotted as a function of geomagnetic field inclination for various values of k at $y = 10$. Results from the survey (Table 1) are superposed.

tion for various values of k at $y = 10$ in Fig. 6, and for various values of y at $k = 0.9$ in Fig. 7. The survey results from Table 1 are superposed on Fig. 7. Although the values for y and k are not known, it is clear that the model can qualitatively account for the fraction of North-seeking bacteria in the population as a function of the inclination of the geomagnetic field, assuming reasonable values of y and k . From the symmetry of the situation, the model should also account for the fraction of polarity type S cells in the population as one moves North of the geomagnetic equator.

We have shown that a simple statistical model of a stochastic process qualitatively accounts for the dynamics of the polarity types in the bacterial population. The model is able to describe the relative populations of the two polarity types even though the total population size is not limited. That is, even if the population goes to infinity, the relative populations go to a fixed point. This is equivalent to letting a statistical system go to the thermodynamic limit (9). Although the dynamics have been constructed from spatially localized, linear processes, and dissipative terms have not been explicitly included, the result is distinctly nonlinear with respect to the geomagnetic field inclination. Thus even a small change in the inclination close to zero inclination leads to a large change in the relative populations of the two polarity types.

We dedicate this paper in memory of Prof. Jacques Danon, who was instrumental in developing research on magnetotactic bacteria in Brazil. We thank Dr. J. H. Sobral for providing geomagnetic inclination data.

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