The Canadian Journal of Statistics
Vol. 26, No. 3, 1998, Pages 431–443
La Revue Canadienne de Statistique

Elephant-seal movements: Modelling migration*

David R. BRILLINGER and Brent S. STEWART

University of California, Berkeley (D.R.B., B.R.S.) and
Hubbs-Sea World Research Institute (B.R.S.)

Key words and phrases: Animal migration, diffusion process, drift, elephant seal, great-circle route, likelihood, spherical motion, stochastic differential equation.
AMS 1991 subject classifications: 62M05, 62M10, 62M30, 62B99.

ABSTRACT

Elephant seals migrate over vast areas of the eastern North Pacific Ocean between rookeries in southern California and distant northern foraging areas. Several models of particle movement were evaluated and a model for great-circle motion found to give reasonable results for the movement of an adult female. This model takes specific account of the fact that the movement is on the surface of a sphere and that the animal is apparently heading toward a particular destination. The parameters of the motion were estimated. Such a great-circle path of migration may imply that these seals have the ability to assess their position with respect to some global or celestial cues, allowing them to continually adjust their course and achieve the most direct geodesic route between origin and destination of migration. But the navigational mechanism actually used by these seals to accomplish such feats is as yet unknown.

RÉSUMÉ

Deux fois par année, les éléphants de mer entreprennent de longues migrations au nord de l'océan Pacifique. Plusieurs sont porteurs d'instruments qui enregistrent la profondeur et l'intensité lumineuse à intervalles réguliers. Ces instruments sont ensuite récupérés et permettent de faire plusieurs estimations, par exemple les positions à mi-journée. Dans cet exposé on s'interessera à la modélisation des itinéraires de surface des animaux à l'aide d'équations différentielles stochas-tiqeus. Les distances sont suffisament importantes pour être incluses dans le modèle la nature sphérique de la surface terrestre. Une question intéressante est de déterminer si les itinéraires sont des grands cercles de la sphère terrestre.

1. INTRODUCTION

Many marine mammals travel great distances each year between breeding and calving areas and seasonally productive foraging areas. Northern elephant seals (*Mirounga angustirostris*), for example, are exceptional migrators. They spend most of each year at sea and range over vast areas of the eastern North Pacific Ocean during double annual migrations between California rookeries and distant northern foraging areas (Stewart and DeLong 1995, Stewart 1996). Similarly, southern elephant seals (*Mirounga lemina*)

*This research was supported by Office of Naval Research Grant N00014-94-1-0042 and National Science Foundation Grants DMS-9625774, 97-04739 (D.R.B.). Elephant-seal dive data were collected in previous studies with partial support of a contract of B.S.S. from the Space and Missile Command, U.S. Department of the Air Force. Part of the material was presented in the 1997 President's Invited Talk, Annual Meeting of the Statistical Society of Canada, Fredericton, New Brunswick.

range over vast areas of the Southern Ocean (e.g., McConnell and Fedak 1996, Bester and Pansegrouw 1992). Although the navigational mechanisms involved in these remarkable migrational feats are as yet unknown, an initial step of describing the migratory trajectories with various formal models may help to develop testable hypotheses. One possibility is that the seals follow great-circle paths. If so, this would imply that they are able to assess their position relative to some astronomical or global magnetic background and constantly make course corrections, as do oceangoing ships when navigating, to achieve the shortest geodesic distance provided by such a route. Elephant seals dive and forage continuously while migrating. Such behaviour could pull them away from the direct route from origin to destination, and it could be modelled as stochastic fluctuation. Here the fit of the great-circle model of particle movement is evaluated for a particular northern elephant seal, in part to examine the hypothesis that such animals can migrate along great-circle paths.

The top graph of Figure 1 presents the surface track for one seal during the post-breeding-season migration. This figure led to speculation that the seals would sometimes follow a great-circle path. A great-circle path is indicated in the bottom graph for reference.

The paper first mentions some of the work of previous authors on the stochastic modelling of particle tracks. Then some material concerning stochastic differential equations is recorded. Section 3 concerns the motion of a particle on the sphere for the case of the particle heading towards a particular destination. Section 4 focuses on the problem of estimating the parameters of the spherical motion. The next section reviews the data and data-collection procedures. Section 6 describes the analysis and presents results, the principal one being an examination of the hypothesis that the motion is a great circle. The statistical analysis presented involves a rotation of the spherical coordinates so that the destination is the North Pole, followed by a search for systematic departure of longitude changes from noise of mean 0. Section 7 provides some introductory remarks on dealing with measurement error. Finally there is discussion, an appendix on rotating spherical coordinates, and an appendix presenting the data.

2. MODELS FOR PARTICLE MOVEMENT

Various authors have employed random-walk models for animal movement. Some particular cases follow. Okubo (1980) devotes a chapter to the topic. Kareiva and Shigesada (1983) studied butterflies and caterpillars. A general reference is Levin (1986). McCulloch and Cain (1989) studied swallowtails, butterflies and goldenrod. Dunn and Gipson (1977) modelled deer movements, assuming that such data were generated by a multivariate Ornstein-Uhlenbeck diffusion process (see also Dunn and Brisbin 1985). Moore (1985) and Zwiers (1985) modelled iceberg movements as vector ARIMA processes. Some authors (e.g., Hadeler *et al.* 1980, Niwa 1996), sought to describe annual movements by variants of Newton's equations of motion, with Niwa evaluating fish movements. Preisler and Akers (1995) employed an autoregressive scheme to model the heading of a bark beetle attracted towards a source. Malik *et al.* (1994) investigated the motion of microtubules. Oceanographers have studied drifting-buoy movements; see Brink *et al.* (1991). Wagner (1986) and Wehrhahn *et al.* (1982) studied the motion of one fly pursuing another. Bril (1995), in studying hurricane tracks, considered a state-space model with a randomly varying drift.

An original term for "stochastic process" is "trajectory", so it is interesting to be returning to the roots of the subject. Stochastic differential equations (SDEs) are a powerful tool for conceptualizing processes and investigating trajectories. These equations have

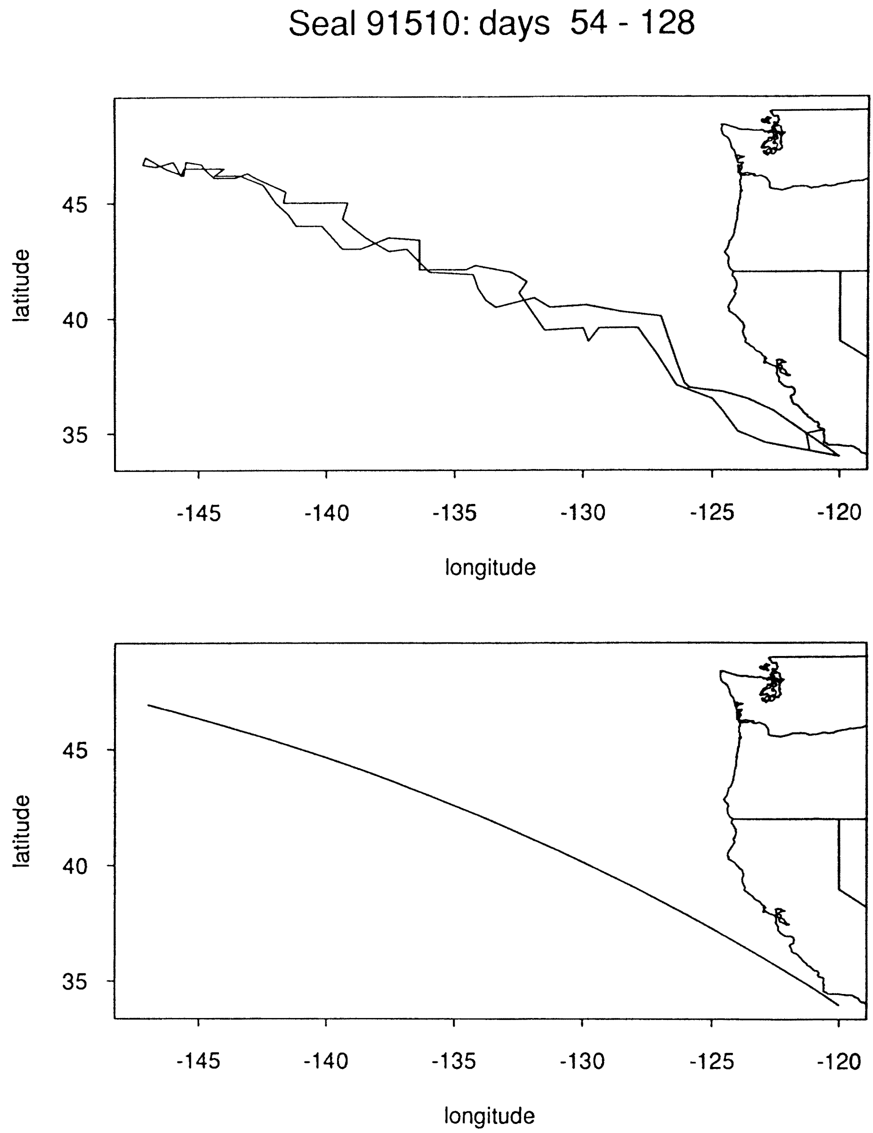


FIGURE 1: The top graph is the track of one seal heading from an island off Santa Barbara to a region in the Northwest Pacific and return. The bottom graph is a great-circle route, for reference.

some surprising properties. Their solutions, when continuous and Markov, are referred to as diffusion processes.

By way of introduction, consider representing a random walk in the plane by a bivariate Brownian. Letting (X_t, Y_t) represent a particle's location at time t, the SDE for the motion may be written

$$dX_t = \sigma \, dU_t, \tag{1}$$

$$dY_t = \sigma \, dV_t \tag{2}$$

with $\{U_t\}$ and $\{V_t\}$ independent standard univariate Brownians, i.e., Gaussian processes with mean 0 and covariance function $\min\{s,t\}$. Suppose one changes to polar coordinates, $r_t = \sqrt{X_t^2 + Y_t^2}$, $\phi_t = \text{atan}\,(Y_t, X_t)$; then the SDEs (1), (2) become

$$dr_t = \frac{\sigma^2}{2r_t}\, dt + \sigma\, dU_t, \tag{3}$$

$$d\phi_t = \frac{\sigma}{r_t}\, dV_t \tag{4}$$

via Itô's lemma (see Karlin and Taylor 1981, Bhattacharya and Waymire 1990, Oksendal 1995). The appearance of the drift term $\sigma^2/2r_t$ in (3) is perhaps surprising. This term dominates the behaviour of r_t near the origin, pushing the particle away. In the case of ϕ_t the change is highly variable when the particle is near the origin. The process $\{r_t\}$ is known as the two-dimensional Bessel process.

Now consider motion in $\mathbb{R}^3$. One important process, the Langevin or Ornstein-Uhlenbeck, is defined by the SDE

$$d\dot{\mathbf{X}}_t = -\beta\dot{\mathbf{X}}_t\, dt + \Gamma\, d\mathbf{B}_t \tag{5}$$

with $\mathbf{X}$ representing location, $\dot{\mathbf{X}}$ representing velocity, $-\beta\dot{\mathbf{X}}$ representing dynamical friction, Γ a 3-by-3 matrix and $\mathbf{B}_t$ Brownian motion in $\mathbb{R}^3$; see Chandrasekhar (1943) for example. It may be that the particle is moving in a force field, in which case a term $K(\mathbf{X}_t, t)\, dt$ is added to the right-hand side of (5).

What distinguishes the present work is that the particle is supposed to be heading for a specific destination. Kendall (1974) considered the case of a Brownian motion on the plane with an "attractive" polar drift. He worked with polar coordinates (r,ϕ) centered at the target center. The particle, in his case a bird, started at location $(D, 0)$. In a time interval of length dt it moved a distance $\delta\, dt$ towards the target, then was subject to random Gaussian disturbance, of amount $\sigma\, dU_t$ towards the target and amount $\sigma\, dV_t$ at right angles to the path. Here U_t and V_t are independent Brownians with variance σ^2. In Itô form the motion may be described by

$$dr_t = \left(\frac{\sigma^2}{2r_t} - \delta\right) dt + \sigma\, dU_t, \tag{6}$$

$$d\phi_t = \frac{\sigma}{r_t}\, dV_t. \tag{7}$$

These equations reduce to (3), (4) when $\delta = 0$.

For basic material on diffusion processes see Karlin and Taylor (1981), Bhattacharya and Waymire (1990) or Oksendal (1995). Papers and books on inferential aspects of diffusion processes include Basawa and Rao (1980), Burgière (1993), Dohnal (1987), Genon-Catalot *et al.* (1992), Heyde (1994).

3. DIFFUSION ON A SPHERE

The description of a particle moving randomly on the surface of a sphere has been considered by a number of authors, beginning with Perrin (1928). The infinitesimal generator and transition density for spherical Brownian motion were given in Yosida (1949). Following directly from the infinitesimal generator are the Itô SDEs

$$d\theta_t = \frac{\sigma^2}{2\tan\theta_t} dt + \sigma\, dU_t,$$

$$d\phi_t = \frac{\sigma}{\sin\theta_t}\, dV_t.$$

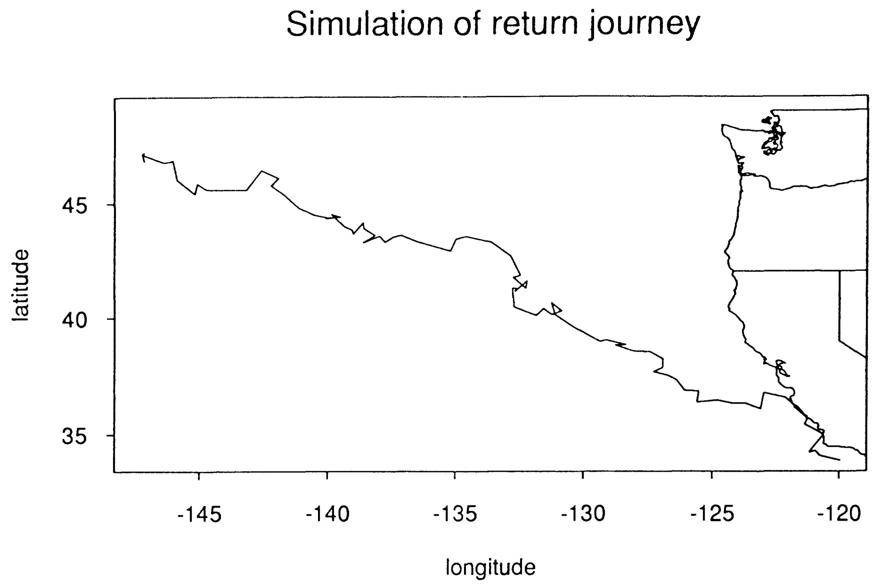


FIGURE 2: A simulation of the process (8, 9) for a seal heading back to the Channel Islands.

Suppose that a particle on the sphere is migrating directly towards the North Pole at speed δ and subject to Brownian disturbances. (The North Pole is taken for convenience.) In analogy with the model of Kendal (1974), the following Itô differential equations are set down in Brillinger (1997):

$$d\theta_t = \left(\frac{\sigma^2}{2 \tan \theta_t} - \delta \right) dt + \sigma \, dU_t, \tag{8}$$

$$d\phi_t = \frac{\sigma}{\sin \theta_t} dV_t, \tag{9}$$

so long as $\theta_t \neq 0$ and with ϕ_t defined mod 2π. It will be supposed that the particle does not start at $\theta = 0$ or π. The latitude, θ_t, is analogous to r_t of (6, 7). If one considers a sphere of infinite radius, the planar and spherical formulations coincide.

Because distances around a constant latitude decrease with increasing latitude, the $1/\sin\theta$ term appears in (9). Figure 2 presents a simulation of the process (8), (9) meant to represent a return trip of a seal to the Channel Islands off southern California. The standard error σ here has been taken to be 0.005 rad.

Consider, for example, the expected travel time for the process (8), (9). Suppose the particle starts at $\cos\theta = x$ and heads to $\cos\theta = d$, $1 > d > x > -1$. In Brillinger (1997) it is shown that the expected travel time is given by

$$\int_x^d \frac{2}{\sigma^2} \int_{-1}^{y} \exp\left(-\frac{2\delta}{\sigma^2} \cos^{-1} z \right) dz \exp\left(\frac{2\delta}{\sigma^2} \cos^{-1} y \right) \frac{1}{1 - y^2} \, dy, \tag{10}$$

which may be evaluated in specific cases.

4. ESTIMATION

Following Brillinger (1997), the log likelihood ratio of the process, relative to that of the case $\delta = 0$, is

$$\frac{1}{\sigma^2} \left\{ (-\delta) \int_0^T d\theta_s - \frac{1}{2} \int_0^T \left(-\frac{2\delta\sigma^2}{\tan \theta_s} + \delta^2 \right) ds \right\} \tag{11}$$

In the case that σ is known this leads to the maximum-likelihood estimate

$$\hat{\delta} = \frac{1}{T}\left((\theta_0 - \theta_T) + \sigma^2 \int_0^T \frac{1}{\tan\theta_s}\,ds\right). \tag{12}$$

Because the particle reaches the region of its destination eventually, this estimate becomes unreasonable in practice if $T \longrightarrow \infty$.

One can actually obtain an exact estimate of σ^2; specifically, it is the case that

$$\sum_i (\tilde{\phi}_{t_{i+1}} - \tilde{\phi}_{t_i})^2 \xrightarrow{p} \sigma^2 \int_0^T \frac{1}{\sin^2\theta_s}\,ds. \tag{13}$$

Here $\{t_i\}$ is a partition of the interval that gets finer under the limiting process. The stated result is conditional on the given (continuous) realization of $\theta_s, 0 \leq s \leq T$, and it is assumed that there exists $\epsilon > 0$ such that $|\sin\theta_s| \geq \epsilon$. The curve $\tilde{\phi}_t$ refers to a continuous curve obtained from the curve ϕ_t either by patching together continuous segments or by reflecting ϕ_t whenever it reaches the barriers $\phi = 0, \pi$. (It is assumed that $0 < \phi_0 < 2\pi$.)

In practice the data will be available at discrete time points and the above likelihood ratio (11) is not available. However, with a model such as (14)–(15) below, describing the position of the particle's successive time steps, one can set down the likelihood function and obtain estimates of the parameters. An approximate approach is to do what a ship's navigator has done traditionally. Specifically, at the start of a day, based on a ship's position, the navigator determines the heading of the great-circle course. That heading is followed for the whole day. The next day the navigator determines the ship's new position, then the great-circle course based on that position. The new heading is followed for that day. Unless the ship is heading due north or south, during its travels it will be pulled off the great circle route, but with the course revisions the destination is approached. This method leads to approximating the desired conditional density by a succession of planar motions with different headings.

A discrete approximation to the model (8), (9) is provided by

$$\theta_{t+1} - \theta_t = \frac{\sigma^2}{2\tan\theta_t} - \delta + \sigma\epsilon_{t+1}, \tag{14}$$

$$\phi_{t+1} - \phi_t = \frac{\sigma}{\sin\theta_t}\eta_{t+1}, \tag{15}$$

$t = 0, 1, 2, \ldots$, with the errors independent standard white noise processes and the ϵ_t, η_t independent normal with mean 0 and variance 1. One notes that the conditional expected value of θ_{t+1} given the past is $-\delta + \sigma^2/(2\tan\theta_t)$ and that the conditional variances of the increments are σ^2 and $\sigma^2/(\sin^2\theta_t)$ respectively. Estimates of the parameters may be derived by the method of moments or by maximizing the likelihood. In this discrete case an "exact" estimate of σ^2 is not available. Then minus twice the log likelihood is

$$2T\log\sigma^2 + \frac{1}{\sigma^2}\sum(\sin^2\theta_t)(\phi_{t+1} - \phi_t)^2 + \frac{1}{\sigma^2}\sum\left(\theta_{t+1} - \theta_t + \delta - \frac{\sigma^2}{2\tan\theta_t}\right)^2,$$

which may be minimized to obtain estimates of δ and σ. Such estimates will be presented for the data of Figure 1.

5. THE DATA

The data studied in the present work are from the postbreeding migration of an adult elephant-seal female (*Mirounga angustirostris*). This species breeds on offshore islands and at a few mainland sites along the coasts of California and Baja California (Stewart and Huber 1993, Stewart *et al.* 1994, Stewart 1996). Adults are ashore briefly in winter to breed, and again in spring (females) or summer (males) to molt, but they spend the remainder of the year, 8–10 months, at sea foraging. They make two precise, long-distance migrations each year between islands in southern California and offshore foraging locations in the mid North Pacific, in the Gulf of Alaska and along the Aleutian Islands, covering 18,000 to 20,000 km (surface movements alone) during the double migrations (Stewart and DeLong 1995). The navigational mechanisms employed by these superlative migrators are, as yet, unknown.

The data on diving and movements studied were obtained by a microprocessor-controlled event recorder which was harmlessly glued to a seal's hair (e.g., Stewart and DeLong 1995, Bengtson and Stewart 1992, Stewart *et al.* 1989). The instrument was attached at the end of the breeding season and then recovered when the animal returned to land several months later.

An estimate of daily location was computed from measurements of ambient daylight made and stored in the recording instruments. Briefly, estimates of sunrise, sunset, and local apparent noon were made from those data, and then latitude and longitude were computed [see DeLong *et al.* (1992) and Stewart and DeLong (1995) for description of methods]. The error varies with season and latitude.

The movement data for the journey of the seal studied in our work are given in Appendix B. It is to be noted that days 85 and 111 are missing. This was handled in this preliminary study by simply using the average of the adjacent values. Brillinger and Stewart (1996) carry out some frequency-domain studies of the series of depth values recorded during this particular migration, and Brillinger and Stewart (1997) develop typical shapes for individual dives and study their temporal occurrence.

6. RESULTS OF SOME ANALYSES

To begin, consider the path of the top graph of Figure 1. Figure 3 provides a corresponding smoothed path. This smooth path was determined via the procedure loess of Cleveland *et al.* (1990). One notes the bowing of the route typical of great-circle travel. The variability represented in Figure 1 represents both foraging movements and measurement error for location.

For the next analysis it is necessary to take note of the fact that the seal's positions are given in latitude and longitude with the destination not the North Pole as was assumed the model in (8), (9). Appendix A indicates the formulae for the necessary change of coordinates to make the data correspond to the North Pole model. The rotated coordinates are denoted by $\tilde{\phi}_t$ and $\tilde{\theta}_t$.

The model (14), (15) was fitted to the outbound and inbound daily positions, merged appropriately, by minimizing the minus twice the log likelihood (16). The estimates obtained are

$$\hat{\delta} = -0.0113 \text{ rad/day} = -72.0 \text{ km/day},$$
$$\hat{\sigma} = 0.00805 \text{ rad/day} = 51.3 \text{ km/day}. \qquad (16)$$

The estimated standard error of $\hat{\delta}$ is 0.0011.

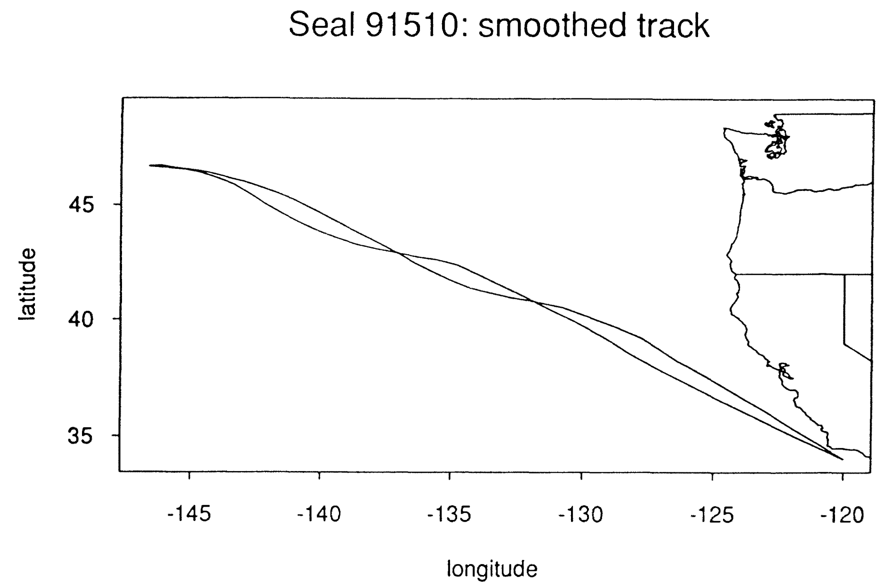


FIGURE 3: Smoothed track of seal 91510.

Figure 4 plots the values

$$\frac{(\sin\tilde{\theta}_t)(\tilde{\phi}_{t+1}-\tilde{\phi}_t)}{\hat{\sigma}} \tag{17}$$

for $t = 0, 1, \ldots$, separately for the outbound and inbound trips. This plot provides a means to examine the hypothesis of a great-circle route. For the great-circle case the points plotted should simply fluctuate about 0. A smoothed loess line has been added to each figure to provide an estimate of some systematic route. Also graphed are ± 2-standard-error levels placed about 0. One does not see evidence against the great-circle hypothesis.

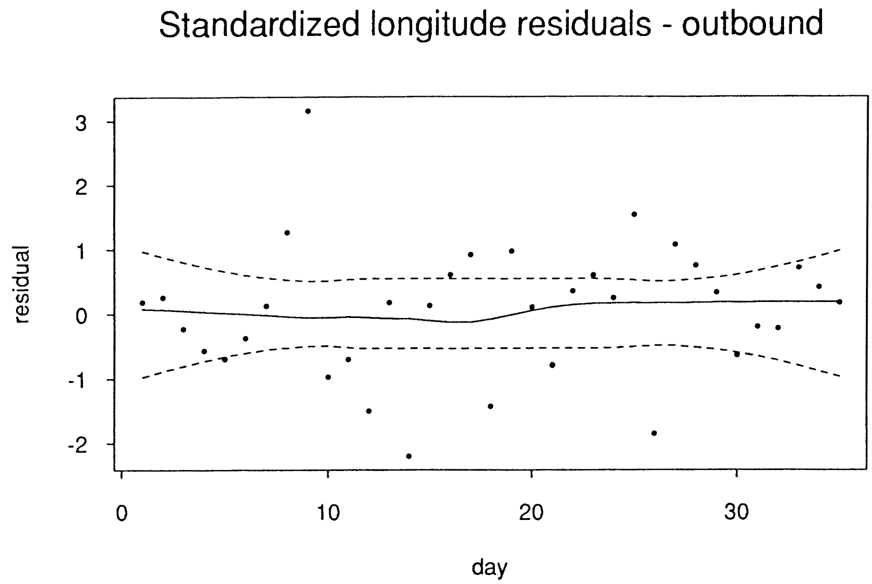
In these computations the procedure adopted is to act as if the uncertainty in the destinations is negligible. The seal appears to have the location of its rookery specifically in mind when it begins the return movement, so the assumption is certainly reasonable then. In the case of the outbound trip the destination was taken as the average of the extreme points in the Northwest.

7. MEASUREMENT NOISE

A difficulty is the presence of measurement noise. It and the foraging variability are confounded in the above analysis. One way to take note of measurement error is to set down the additional equations

$$\begin{aligned} \theta_t' &= \theta_t + \epsilon_t', \\ \phi_t' &= \phi_t + \eta_t'/\sin\theta_t' \end{aligned} \tag{18}$$

with (θ_t', ϕ_t') now representing the available data and supposing ϵ_t', η_t' noise. If these last are assumed independent normals with mean 0 and variances τ^2, then, amongst other procedures, a Kalman-filter-type analysis may be employed to develop a full likelihood and corresponding estimates. The results of this analysis are presented in Brillinger (1998). The Kalman filter is employed with wildlife data in Anderson-Sprecher (1994) and Anderson-Sprecher and Ledolter (1991).



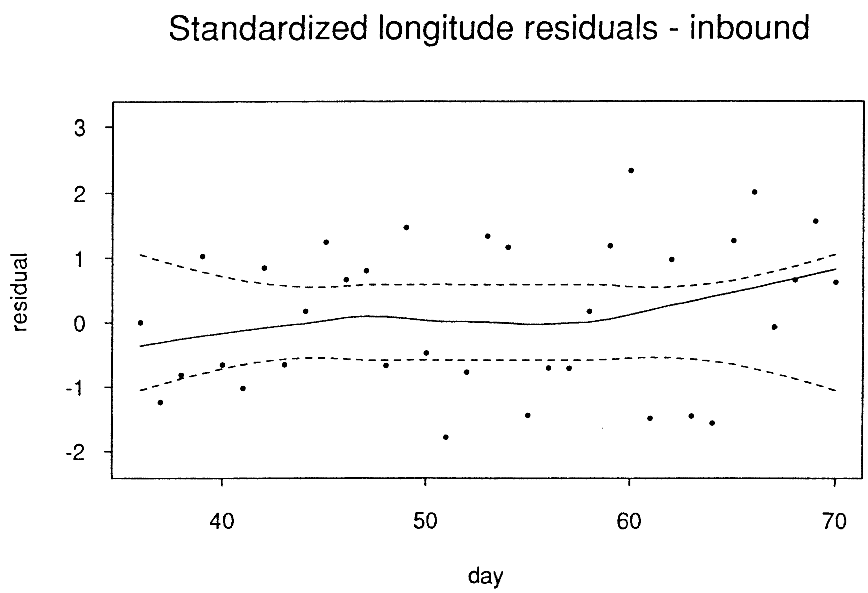


FIGURE 4: The scaled longitude differences of (17) with a smoothed line as produced by loess. The dashed lines are ± 2 standard error limits about 0.

8. DISCUSSION

Future work will incorporate explanatory variables in the model, will employ a recursive filter, will better handle the missing values and will analyze other data sets.

The great-circle path hypothesis was not contradicted by the immigration of one northern elephant seal female. The results suggest that a great-circle path model is a possible navigational strategy in this species. They also suggest that the seals have a destination in mind when departing from an origin (i.e., terrestrial rookery or haulout and pelagic foraging area) and that they are able to continually adjust course en route to achieve the most direct route. Further, they imply that natural selection has favoured the development of neural and sensory mechanisms that permit great-circle navigation. However, the sensory clues actually used are as yet unknown, although several have been suggested and studied to various extents in a variety of other animal taxa (e.g., Able 1996, Dingle 1996, Dittman and Quin 1996, Lohmann and Lohmann 1996, Wehner *et al.* 1996, Weindler *et al.* 1996, Wiltschko and Wiltschko 1996).

Navigation by learned reference to geophysical characteristics would seem to play only a minor role, as elephant seals are generally far from coastlines and in areas of great water depth and little submarine features during most of their migrations. But the fit of a great-circle model suggests that some kind of compass may be central to the seals' rather precise migration and navigational performances, allowing them to continually determine the appropriate direction of each subsequent movement to keep en route to the shortest distance between origin and destination. Celestial navigation may be involved to some extent, but the brief and sporadic appearance of migrating seals at the sea surface, where such clues could be assessed, and their propensity to travel mostly at great depths, where such cues are obscured, would argue that it is not a primary mechanism. Large-scale magnetic field orientation may be the most plausible of potential compasses. But the rather precise navigation of the seals may also imply either the existence of a cognitive map to apply the compass to or perhaps simply remarkable fidelity to vectors and assessment of distance travelled, independent of any map. At present, no such mechanism of magnetic sensory ability or cognitive mapping is known for elephant seals. However, knowledge of the ecological and physiological conditions under which northern elephant seals find their way while migrating and foraging, which have come to be known recently (e.g., Stewart and DeLong 1995, Stewart 1996), coupled with the descriptive theoretical model of navigational strategy developed here, can help focus questions properly on navigational and orientational mechanisms in this and other long-distance, deep-dwelling ocean migrators.

APPENDIX A. THE CHANGE OF COORDINATES

A transformation $(\phi, \theta) \longrightarrow (\tilde{\phi}, \tilde{\theta})$ is constructed. Suppose that the sphere is rotated so that the particular point (Φ, Θ) becomes the North Pole $(0,0)$, and the great circle (ϕ, θ) to (Φ, θ) becomes the great circle $(0,0)$ to $(0, \tilde{\theta})$. The required change of variables may be derived to be

$$\cos \tilde{\theta} = \cos \Theta \cos \theta + \sin \Theta \sin \theta \cos (\phi - \Phi),$$

$$\tan \tilde{\phi} = \frac{\sin \theta \sin (\phi - \Phi)}{\cos \Phi \sin \theta \cos (\phi - \Phi) - \sin \Theta \cos \theta}.$$

Retaining the signs of the numerator and denominator in the last expression will lead to an appropriate choice of quadrant for the transformed longitude.

APPENDIX B. NUMERICAL DATA

The data are shown in Table 1.

ACKNOWLEDGEMENT

We thank Haiganoush Preisler and the two referees for some very helpful comments.

TABLE 1

Day	Latitude (N)	Longitude (W)	Day	Latitude (N)	Longitude (W)
54	34.0	120.0	92	46.5	146.3
55	35.0	121.3	93	47.0	147.1
56	36.0	122.6	94	46.7	147.2
57	36.5	123.6	95	46.6	146.7
58	36.8	124.6	96	46.8	146.0
59	36.9	125.4	97	46.2	145.7
60	37.0	125.9	98	46.5	145.6
61	37.2	126.1	99	46.5	144.0
62	38.1	126.4	100	46.2	144.4
63	40.1	127.0	101	46.2	143.4
64	40.3	128.5	102	45.8	142.5
65	40.6	129.9	103	45.0	142.0
66	40.5	131.3	104	44.5	141.5
67	40.9	131.9	105	44.0	141.2
68	40.5	133.4	106	44.0	140.2
69	40.8	133.8	107	43.0	139.4
70	41.3	134.1	108	43.0	138.7
71	41.9	134.3	109	43.5	137.6
72	42.0	136.0	110	43.4	136.4
73	42.9	136.8	112	42.1	136.4
74	43.0	136.9	113	42.1	134.6
75	42.9	137.6	114	42.3	134.2
76	43.5	138.5	115	42.0	132.8
77	44.1	139.2	116	41.6	132.2
78	44.3	139.4	117	41.1	132.5
79	45.0	139.2	118	39.5	131.5
80	45.0	141.7	119	39.6	130.0
81	45.5	141.6	120	39.0	129.8
82	46.1	142.8	121	39.6	129.4
83	46.3	143.1	122	38.5	127.2
84	46.1	143.6	123	37.1	126.4
86	46.1	144.4	124	36.5	125.0
87	46.5	144.8	125	36.0	124.6
88	46.7	144.9	126	35.0	124.0
89	46.8	145.5	127	34.6	122.9
90	46.8	145.5	128	34.0	120.0
91	46.2	145.6			

REFERENCES

Able, K.P. (1996). The debate over olfactory navigation by homing pigeons. *J. Exp. Biol.*, 199, 121–124.

Anderson-Sprecher, R. (1954). Robust estimates of wildlife location using telemetry data. *Biometrics*, 50, 406–416.

Anderson-Sprecher, R., and Ledolter, J. (1991). State-space analysis of wildlife telemetry data. *J. Amer. Statis. Assoc.*, 86, 596–602.

Basawa, I.V., and Rao, B.L.S.P. (1980). *Statistical Inference for Stochastic Processes*. Academic Press, New York.

Bengtson, J.L., and Stewart, B.S. (1992). Diving and haulout patterns of crabeater seals in the Weddell Sea, Antarctica during March 1986. *Polar Biol.*, 12, 635–644.

Bester, M.N., and Pansegrouw, H.M. (1992). Ranging behaviour of southern elephant seal cows from Marion Island. *South African J. Sci.*, 88, 574–575.

Bhattacharya, R.N., and Waymire, E. (1990). *Stochastic Processes with Applications*. Wiley, New York.

Bril, G. (1995). Forecasting hurricane tracks using the Kalman filter. *Environmetrics*, 6, 7–16.

Brillinger, D.R. (1997). A particle migrating randomly on a sphere. *J. Theoret. Probab.*, 10, 429–443.

Brillinger, D.R. (1998). Some examples of random process environmental data analysis. *Handbook of Statistics, Vol. 17*. North-Holland, Amsterdam. To appear.

Brillinger, D.R., and Stewart, B.S. (1996). Elephant seal movements: some frequency based studies. *Brazilian J. Probab. Statist.*, 10, 15–33.

Brillinger, D.R., and Stewart, B.S. (1997). Elephant seal movements: Dive types and their sequences. *Modelling Longitudinal and Spatially Correlated Data* (T.G. Gregoire, D.R. Brillinger, P.J. Diggle, E. Russek-Cohe, W.G. Warren, R.D. Wolfinger, *eds.*), Lecture Notes in Statistics 122, Springer-Verlag, New York, 275–288.

Brink, K.H., Beardsley, R.C., Niiler, P.P., Abbott, M., Huyer, A., Ramp, S., Stanton, T., and Stuart, D. (1991). Statistical properties of near-surface flow in the California coastal transition zone. *J. Geophys. Res.* 96, 14693–14706.

Burgière, P. (1993). Théorème de limite centrale pour un estimateur non paramétrique de la variance d'un processus de diffusion multidimensionelle. *Ann. Inst. H. Poincaré Probab. Statist.*, 29, 357–389.

Chandrasekhar, S. (1943). Stochastic problems in physics and astronomy. *Rev. Modern Phys.*, 15, 1–89.

Cleveland, W.S., Grosse, E., and Shyu, W.M. (1990). Local regression models. *Statistical Models in S* (J.M. Chambers and T.J. Hastie, *eds.*), Wadsworth, Pacific Grove, Calif., 300–376.

DeLong, R.L., Stewart, B.S., and Hill, R.D. (1992). Documenting migrations of northern elephant seals using day length. *Marine Mammal Sci.* 8, 155–159.

Dingle, H. (1996). *Migration: The Biology of Life on the Move*. Oxford Univ. Press, Oxford.

Dittman, A.H., and Quin, T.P. (1996). Homing in Pacific salmon: Mechanisms and ecological basis. *J. Exp. Biol.* 199, 83–91.

Dohnal, G. (1987). On estimating the diffusion coefficient. *J. Appl. Probab.*, 24, 105–114.

Dunn, J.E., and Brisbin, I.L. (1985). Characterization of the multivariate Ornstein-Uhlenbeck diffusion process in the context of home range analysis. *Statistical Theory and Data Analysis* (K. Matusita, *ed.*). Elsevier, Amsterdam, 181–205.

Dunn, J.E., and Gipson, P.S. (1977). Analysis of radio telemetry data in studies of home range. *Biometrics*, 33, 85–101.

Genon-Catalot, V., Laredo, C., and Picard, D. (1992). Non-parametric estimation of the diffusion coefficient by wavelets methods. *Scand. J. Statist.* 19, 317–335.

Hadeler, K.P., de Mottoni, P., and Schumaker, K. (1980). Dynamic models for animal orientation. *J. Math. Biol.* 10, 307–332.

Heyde, C.C. (1994). A quasi-likelihood approach to estimating parameters in diffusion-type processes. *J. Appl. Probab.*, 31A, 283–290.

Kareiva, P.M., and Shigesada, N. (1983). Analyzing insect movement as a correlated random walk. *Oecologia (Berlin)*, 56, 234–238.

Karlin, S., and Taylor, H.M. (1981). *A Second Course in Stochastic Processes*. Academic Press, New York.

Kendall, D.G. (1974). Pole-seeking Brownian motion and bird navigation. *J. Roy. Statist. Soc. Ser. B*, 36, 365–417.

Levin, S.A. (1986). Random walk models of movement and their implications. *Mathematical Ecology* (T.G. Hallam and S. Levin, *eds.*). Springer-Verlag, Berlin, 149–154.

Lohmann, K.J., and Lohmann, C.M.F. (1996). Orientation and open-sea navigation in sea turtles. *J. Exp. Biol.* 199, 73–81.

Malik, F., Brillinger, D., and Vale, R.D. (1994). High-resolution tracking of microtubule motility driven by a single kinesin motor. *Proc. Natl. Acad. Sci. U.S.A.* 91, 4584–4588.

McConnell, B.J., and Fedak, M.A. (1996). Movements in southern elephant seals. *Canad. J. Zool.* 74, 1485–1496.

McCulloch, C.E., and Cain, M.L. (1989). Analyzing discrete movement data as a correlated random walk. *Ecology*, 7, 383–388.

Moore, M. (1985). Modelling iceberg motion: A multiple time series approach. *Canad. J. Statist.* 13, 88–93.

Niwa, H. (1996). Newtonian dynamical approach to fish schooling. *J. Theoret. Biol.*, 181, 47–63.

Oksendal, B. (1995). *Stochastic Differential Equations*. Fourth Edition. Springer-Verlag, New York.

Okubo, A. (1980). *Diffusion and Ecological Problems: Mathematical Models*. Springer-Verlag, New York.

Perrin, M.F. (1928). Mouvement brownien de rotation. *Ann. École Norm. Sup.*, 45, 1–51.

Preisler, H.K., and Akers, R.P. (1995). Autoregressive-type models for the analysis of bark beetle tracks. *Biometrics*, 51, 259–267.

Stewart, B.S. (1996). Uncommon commuters. *Natur. Hist.*, 105, 58–63.

Stewart, B.S., and DeLong, R.L. (1995). Double migrations of the northern elephant seal. *J. Mammalogy* 76, 196–205.

Stewart, B.S., and Huber, H.R. (1993). *Mirounga angustirostris. Mammalian Species*, 449, 1–10.

Stewart, B.S., Leatherwood, S., Yochem, P. K., and Heide-Jorgensen, M.P. (1989). Satellite telemetry of locations and dive durations of a free-ranging harbor seal (*Phoca vitulina richardsi*) in the Southern California Bight. *Marine Mammal Sci*, 5, 361–375.

Stewart, B.S., Yochem, P.K., Huber, H.R., DeLong, R.L., Jameson, R.J., Sydeman, W., Allen, S.G., and LeBoeuf, B.J. (1994). History and present status of the northern elephant seal population. *Elephant Seals: Population Ecology, Behaviour and Physiology* (B.J. LeBoeuf and R.M. Laws, *eds*.), University of California Press, Los Angeles, 29–48.

Wagner, H. (1986). Flight performance and visual control of flight of the free flying housefly. *Philos. Trans. Roy. Soc. London Ser. B*, 312, 581–595.

Wehner, R., Michel, B., and Antonsen, P. (1996). Visual navigation in insects: Coupling of egocentric and geocentric information. *J. Exp. Biol.* 199, 129–140.

Wehrhahn, C., Poggio, T., and Bulthoff, H. (1982). Tracking and chasing in houseflies. *Biol. Cybernet.* 45, 123–130.

Weindler, P., Wiltschko, R., and Wiltschko, W. (1996). Magnetic information affects the stellar orientation of young birds. *Nature*, 383, 158–160.

Wiltschko, W., and Wiltschko, R. (1996). Magnetic orientation in birds. *J. Exp. Biol*, 199, 29–38.

Yosida, K. (1949). Brownian motion on the surface of the 3-sphere. *Ann. Math. Statis.*, 20, 292–296.

Zwiers, F.W. (1985). Estimating the probability of collision between an iceberg and a fixed marine structure. *Canad. J. Statist.*, 13, 94–105.

Received 11 December 1996
Revised 21 June 1997
Accepted 10 July 1997

Department of Statistics
University of California
Berkeley, California
U.S.A. 94720

email: brill@stat.berkeley.edu

Boalt Hall School of Law
University of California
Berkeley, California
U.S.A.