ELEPHANT SEAL MOVEMENTS: MODELLING MIGRATION*

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Key words and phrases: Animal migration, Diffusion process, Drift, Elephant seal, Great circle route, Likelihood, Spherical motion, Stochastic differential equation.

AMS 1991 subject classification: Primary 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

*The work of DRB supported by the Office of Naval Research Grant N00014-94-1-0042 and the National Science Foundation Grant DMS-9625774. Elephant seal dive data were collected in previous studies with partial support of a contract to BSS from the Space and Missile Command, U.S. Department of the Air Force.

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

Les éléphants de mer du nord ...

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)). 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 and dive behavior for one seal during the post-breading season migration. This figure here 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 a the particle heading towards a particular destination. Section 4 fouses 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 being an examination of the hypothesis that the motion is a great circle. The 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 recording the data.

2. MODELS FOR PARTICLE MOVEMENT

Various authors have employed random walk models for particle movement. Some particular cases follow. Okubo (1980) devotes a chapter to the topic. Kareiva and Shigesada (1983) study butterflies and caterpillers. A general reference is Levin (1986). McCulloch and Cain (1989) who study swallowtails, butterflies and goldenrod may be mentioned. 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, eg. Hadeler et al. (1980), Niwa (1996), sought to describe animal 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 towards a source. Malik et al (1994) investigate 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 huricane tracks, considered a state space model with a randomly varying drift.

An original term for "stochastic process" is "trajectory" so it is interesting to return to the roots of the subject. Stochastic differential equations (SDEs) are a powerful tool for conceptualizing processes and investigating trajectories. These equations have 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 motion. Letting (X_t, Y_t) represent a particle's location at time t, the SDE for the motion may be written

$$dX_t = \sigma dU_t \qquad (1)$$
$$dY_t = \sigma dV_t \qquad (2)$$

with $\{U_t\}$ and $\{V_t\}$ independent standard univariate Brownians. 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 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 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 righthand 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 δdt towards the target, then was subject to random Gaussian disturbance, of amount σdU_t towards the target and amount σdV_t at right angles to the path. Here U_t and V_t are independent standard Brownian motions and σ^2 their common variance. 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 were given in Yosida (1949). Following directly from the infinitesimal generator are the Itô SDEs

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

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

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 anlogy with the model of Kendall (1974) the following Itô differential equations are set down in Brillinger (1997)

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

$$d\phi_t = \frac{\sigma}{\sin\,\theta_t} dV_t \qquad (9)$$

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 analagous 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 .005 radians.

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

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

4. ESTIMATION

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

$$\frac{1}{\sigma^2}[(-\delta)\int_0^T d\theta_s - \frac{1}{2}\int_0^T (-\frac{2\delta\sigma^2}{\tan\,\theta_s} + \delta^2) ds] \qquad (11)$$

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

$$\hat{\delta} = \frac{1}{T}[(\theta_0 - \theta_T) + \sigma^2 \int_0^T \frac{1}{\tan\,\theta_s} ds] \qquad (12)$$

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

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 θ_s, $0 \le s \le T$, and it is assumed that there exists $\varepsilon > 0$ such that $|\sin\theta_s| \ge \varepsilon$. The curve $\tilde{\phi}_t$ refers to a continuous curve obtained from the curve ϕ_t by either patching together continuous segments or by reflecting ϕ_t whenever it reaches the barriers $\phi = 0, \pi$. (It is assumed that $0 < \phi_0 < 2\pi$.)

When working in practice the data will be available at discrete time points and the above likelihood ratio (11) is not available. However, if one has an expression for the transition density, then that can be used to obtain the likelihood function and estimates of the parameters obtained. 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 great circle course and that is followed for a day. The next day the navigator determines the ship's new position, then the great circle course based on that position. The latter is followed for a 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 transition density by a succession of planar motions with different headings.

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

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

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

$t = 0, 1, 2, \cdots$ 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 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. The minus twice the loglikelihood is

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

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 post-breeding 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, 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 (1997) carry out some frequency domain studies of the series of depth values recorded during this particular migration.

6. RESULTS OF SOME ANALYSES

To begin, consider the path of top graph of Figure 1. Figure 3 provides a corresponding smoothed path. This smooth path was determined via the procedure loess of Cleveland, Grosse and Shyu (1992). 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 fit to the outbound and inbound daily positions, merged appropriately, by minimizing the minus twice the loglikelihood (16). The estimates obtained are

$$\begin{aligned} \hat{\delta} &= -.0113 \; radians/day = -72.0 \; km/day \\ \hat{\sigma} &= .00805 \; radians = 51.3 \; km/day \end{aligned} \tag{16}$$

The estimated standard error of $\hat{\delta}$ is .0011 .

Figure 4 plots the values

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

for $t = 0,1, \cdots$, 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 reasonable then. In the case of the outbound trip the destination was taken as the average of the two 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

$$\begin{aligned} \theta_t' &= \theta_t + \varepsilon_t' \\ \phi_t' &= \phi_t + \eta_t' \end{aligned} \tag{18}$$

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 analysis may be employed to develop a full likelihood and corresponding estimates. The Kalman filter is employed with wildlife data in Anderson-Sprecher (1994) and Anderson-Sprecher and Ledolter (1991).

8. DISCUSSION

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

A 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 viable 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 extent in a variety of other animal taxa (eg. Able (1996), Dittman and Quinn (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' relatively 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 mostly travel 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 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 are 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 (eg. 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.

ACKNOWLEDGEMENT

We thank Haiganoush Preisler for some helpful comments.

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APPENDICES

Appendix A. The change of coordinates

A transformation $(\phi,\theta) \rightarrow (\tilde{\phi},\tilde{\theta})$ 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) becomes the great circle $(0,\tilde{\theta})$. The required change of variables may be derived to be

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

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

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

Figure legends

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.

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

Figure 3. Smoothed track of seal 91510.

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.

Appendix B. The data

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			