How well can animals navigate? Estimating the circle of confusion from tracking data

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SUMMARY

State-space models have recently been shown to effectively model animal movement. In this paper we illustrate how such models can be used to improve our knowledge of animal navigation ability, something which is poorly understood. This work is of great interest when modeling the behavior of animals that are migrating, often over tremendously large distances. We use the term circle of confusion, first proposed by Kendall (1974), to describe the general inability of an animal to know its location precisely. Our modeling strategy enables us to statistically describe the circle of confusion associated with any animal movements where departure and destination points are known. For illustration, we use ARGOS satellite telemetry of leatherback turtles migrating over a distance of approximately 4000 km in the Atlantic Ocean. Robust features of the model enable one to deal with outlying observations, highly characteristic of these types of data. Although specifically designed for data obtained using satellite telemetry, our approach is generalizable to other common kinds of movement data such as archival tag data. Copyright © 2005 John Wiley & Sons, Ltd.

KEY WORDS: animal migration; state-space models; circle of confusion; satellite telemetry; robust methods

1. INTRODUCTION

A variety of technologies now exist to track animals as they move through their environment. Unfortunately, estimation methods have yet to be developed to the point where they are routine and readily available for biologists wishing to model movement processes. Estimation of these processes as they relate to migration, foraging, and dispersal is vital for understanding the population ecology of any animal species. Given recent concerns regarding population trends of many wide ranging or migratory marine species (Spotila et al., 2000; Baum et al., 2003; Myers and Worm, 2003), biologists urgently need methods that allow quantification of behavior directly from movement data.

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Our work focuses on estimating the navigation ability of organisms as they move through their environment. We make use of the term circle of confusion which was first used by Kendall (1974) to describe the region around a desired target where homing birds become lost. Here we extend this idea to describe the general inability of any animal to know its current location precisely. By examining observed movement pathways we are able to statistically describe the circle of confusion. Those animals with relatively large circles of confusion are considered to have less developed navigation skills.

When modeling animal movement data, we must deal with the dependence among successive observations as well as the uncertainty inherent in both the movement process being modeled and in the observations. State-space models provide a natural context with which to handle such data (Anderson-Sprecher and Ledolter, 1991; Brillinger and Stewart, 1998; Jonsen et al., 2003). They allow us to capture the movement as well as model the two types of errors that are typical of observed movement pathways: (i) that resulting from the animal’s inability to follow the desired course precisely, and (ii) that which is a consequence of our inability to observe the movement pathways exactly. We note that the first type of error quantifies the animal’s circle of confusion while at the same time acknowledging that there are other factors that result in deviations from a desired course. The robust features inherent in our modeling strategy enable us to routinely handle such errors.

Various authors have employed state-space models for modeling animal movement with attention generally focusing on random-walk models. Anderson-Sprecher (1998) and Anderson-Sprecher and Ledolter (1991) examined the movement of mule deer with particular attention to ensuring analyses are robust to gross observation errors. Jonsen et al. (2003) demonstrated how information from individual pathways can be combined. Less attention has been paid to cases in which animals are migrating and simple random-walk models are therefore no longer appropriate. The work of Brillinger and Stewart (1998) is an exception here as they proposed a model for great-circle motion and found it gave reasonable results for the movement of a particular elephant seal in the Northeastern Pacific Ocean.

Our approach builds on the work of Kendall (1974) and Brillinger and Stewart (1998) by (i) specifically focusing on the navigation abilities of the animal of concern and (ii) allowing the progression of the animal along its course to be determined empirically so there is no longer a need to model its speed. This latter feature means that we no longer need to build complex movement models to describe the speed at which the animal moves, something which can be exceedingly difficult. The simplicity of our approach in this regard actually makes it more general. This is particularly desirable as we would ultimately like to compare circle of confusion estimates for a broad range of species.

Details of our modeling approach are provided in Section 2 followed by a discussion of estimation techniques in Section 3. In Section 4 we present an application to real data on several migrating leatherback turtles. Conclusions and future directions are given in Section 5.

2. THE CIRCLE OF CONFUSION MODEL

To begin, the data consist of the position of an animal at particular points in time, $z_0, z_1, \ldots, z_T$ as it moves from an initial position, $z_0$, to a final destination point, $z_T$. These positions are derived from satellite tags and are subject to error. As a result, we assume that this observed time series of location coordinates derives from an unobservable state process $\alpha_0, \ldots, \alpha_T$ describing the true pathway of the animal.
We are specifically interested in animals’ ability to follow a particular route during migration. Here we assume that the animal intends to follow a great circle (GC) route while noting that other presumed routes could easily be used. The true locations $\alpha_t$ can be viewed as representing the animal’s *best guess* at where it is relative to this desired pathway. Note that it is straightforward to superimpose the GC route between any starting point $z_0$ and ending point $z_T$ as it is simply the shortest distance on the earth’s sphere between these two points. We define $a_t$ as the distance from $\alpha_t$ to the nearest point on the GC route. Similarly, $v_t$ is defined as the distance from $\alpha_t$ to the nearest point on the GC route. Both $a_t$ and $v_t$ can be regarded as deviations from the GC route, only the latter of which are observable. Figure 1 illustrates the relationship between these deviations. Note that the difference between the deviations $a_t$ and $v_t$ describes the measurement error of the deviations and can be expressed as $a_t \cos \theta_t$.

If the animal is to one side of the GC route at one particular point in time, it is likely that it will also be on this side of the GC route at the next point in time. This behavior suggests that the $a_t$ are not independently and identically distributed but rather possess some dependence structure. Here we assume that they can be represented by a first order autoregressive process while noting that other dependence structures are possible (ARMA, GARCH, etc.). That is,

$$a_t = \rho a_{t-1} + \eta_t$$

where the $\eta_t$ are independently and identically distributed with mean 0 and unknown variance $\sigma^2$. In summary, we have arrived at a state-space model for the times series $v_t$ consisting of the following two equations:

$$v_t = a_t + r_t \cos \theta_t, \quad \text{for} \quad t = 1, \ldots, T \quad (1)$$

and

$$a_t = \rho a_{t-1} + \eta_t, \quad \text{for} \quad t = 1, \ldots, T \quad (2)$$

where the $r_t \cos \theta_t$ are independently and identically distributed with mean 0 and unknown variance $\tau^2$, and the $\eta_t$ are independently and identically distributed with mean 0 and unknown variance $\sigma^2$. As

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Figure 1. Geometry of relationship between observed deviation $v_t$ and unobserved deviation $a_t$. Note that the corresponding distance along the great circle (GC) route is assumed to be linear as it is so small.

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noted earlier, by modeling the deviations, we allow the movement along the GC route to be determined empirically. Note that if both \( r_t \cos \theta_t \) and \( \eta_t \) are normally distributed then \( v_t \) is in fact an ARMA(1,1) process. See Appendix for further details.

Equations (1) and (2) describe a state-space model with unknown parameters \( \tau \), \( \rho \), and \( \sigma \) to be estimated. Unless \( r_t \cos \theta_t \) and \( \eta_t \) are assumed to be normal, the computation of these estimates can be exceedingly complex.

### 2.1. Robust methods

Regardless of the technology used to track animals, there exists the possibility of extreme location values occurring. For example, the ARGOS satellite system estimates transmitter locations by using the Doppler shift in uplink transmitter frequencies as the satellite passes over the transmitter. Two first guess locations are calculated from the known position of the satellite when the first and last uplinks are received, and the altitude (assumed known) of the transmitter. Latitude, longitude, transmitter frequency, and residual errors are estimated from the Doppler shift data via least squares for each of the two first guess locations. Therefore, a minimum of four uplinks during a satellite pass are required to yield a moderate to high quality location estimate (classes 0–3). When only three uplinks are received, only a location and a transmit frequency are estimated (class A). When only two uplinks are received, the first guess location that is closest to the previous location is selected (class B).

Empirical tests of the accuracy of ARGOS location estimates suggest that errors are non-normal for the poorer-location classes and only approximately normal for the higher-quality classes (Vincent et al., 2002), suggesting a need for robust methods. Furthermore, up to 90% of location estimates for marine animals are of class A or B, due in part to low uplink rates arising from diving behavior, and are typically filtered using ad hoc methods (Vincent et al., 2002) or completely removed prior to analysis (Godley et al., 2002). Therefore, in order to take full advantage of all the data collected, it is important to develop analytical techniques that allow robust information to be derived from the raw data. Ideally, what we would like is a suitable choice for the measurement error distribution that works well if the errors are normal while at the same time lessens the impact of extreme observations on parameter estimates.

To achieve our goal of robustness, we assume that the measurement errors \( r_t \cos \theta_t \) are distributed as \((1/\tau) \phi(r_t \cos \theta_t / \tau)\) where \( \phi \) may be either a \( t \) distribution with three degrees of freedom (\( t_3 \)) or Huber’s least favorable distribution for scale, that is:

\[
\phi(z) = \phi^H(z) = \begin{cases} 
\frac{1-z^2}{\sqrt{2\pi}} \exp\left(-\frac{z^2}{2}\right) & \text{if } |z| \leq k \\
\frac{1-\epsilon}{\sqrt{2\pi}} \exp\left(-\frac{k^2}{2}\right) & \text{if } |z| > k 
\end{cases}
\]

Huber’s least favorable distribution for scale is normal in the middle, behaves like a \( t \) distribution with \( k \) degrees of freedom in the tails, and consequently downweights the influence of extremes. It does so by allowing longer tails which is a usual type of deviation. This makes outliers less unlikely under the model so that their effect on the parameter estimates is reduced. Choices for \( \epsilon \), \( k \) pairs are given in Huber (1981). A reasonably efficient choice is \( \epsilon = 0.005 \) and \( k = 2.46 \). Note that one might also consider \( \phi \) to be a mixture distribution of normals where the mixing proportion and ratio of the variances are assumed known apriori.

We next consider the errors \( \eta_t \). Having taken into account the dependence at successive locations, these errors capture the discrepancy between where the animal is at time \( t \) and where it intends to be at
time $t$. As mentioned previously, it is likely that in some instances the animal will be required to
deveiate from its course, not due to limitations in navigation but for other reasons such as the need to
forage. It is important that our model be robust to such errors so that our resulting estimates are not
inflated by such behavior. In order to do so we can again let $\phi$ be either a $t_3$ distribution or Huber’s least
favorable distribution for scale (with $\epsilon = 0.005$ and $k = 2.46$) and assume that the $\eta_t$ are distributed as
$(1/\sigma)\phi(\eta_t/\sigma)$. With the distributions for $r_t \cos \theta_t$ and $\eta_t$ now well defined, our state-space formulation
given by Equations (1) and (2) is complete.

The overall variance of the autoregressive model encapsulated in our state-space model (see
Equation 2) is $\sigma^2/(1 - \rho)^2$. This quantity is not only interpretatable from a statistical perspective but
also from a biological one as we can view this quantity as a measure of how good the animal is at
determining its location. We define $r_{coc} = \sigma/\sqrt{(1 - \rho)^2}$ and interpret this as describing the circle of
confusion: a circle with radius $r_{coc}$ drawn about the animal’s location within which it is unable to
determine its location precisely. Therefore, the smaller the $r_{coc}$, the better the navigation ability.

3. ESTIMATION

The state-space model, as described by Equations (1) and (2) of the previous section, can be fitted to
data using the general Kalman-Filter recursions. Essentially this is a recursive estimation procedure
which allows us to predict the true path of the animal and estimate the parameters of the movement
process, $\rho$ and $\sigma$, and the measurement error, $\tau$. We note that in some situations it may be reasonable to
take $\tau$ as known. The recursion is conducted from the initial known position $z_0$ (e.g., where the animal
was tagged).

We assume here that the observed times series ($V_t$) derives from the unobservable state process ($A_t$)
where their joint distribution is specified by the assumptions:

- $A_0, A_1, A_2,$ is a Markov Chain with $A_0 \sim p_0(a)da$ and

  $$a_t|a_{t-1} = a_{t-1} \sim p_t(a|a_{t-1})da$$

- The $V_t$’s are conditionally independent given $A_0, A_1, A_2, \ldots$ and each $V_t$ is conditionally
  independent of $A_s$, $s \neq t$, given $A_t$ with

  $$V_t|A_t = a_t \sim q_t(v|a_t)dv$$

We let $V_t^s$ represent the observed deviations up to and including time $s$, and denote the conditional
density of $A_t$ given $V_t^s = v_t^s$ by $f_{t|s}(a|v_t^s)$. We can obtain $f_{t|t-1}$ and $f_{t|t}$ according to the following general
Kalman recursions:

$$f_{t|t-1}(a|v_t^{s-1}) = \int p_t(a|a_{t-1})f_{t-1|t-1}(a_{t-1}|v_t^{s-1})da_{t-1}$$

(3)

$$f_{t|t}(a|v_t^s) = \frac{q_t(v_t|a_t)f_{t|t-1}(a|v_t^{s-1})}{\int q_t(v_t|a_t)f_{t|t-1}(a|v_t^{s-1})da_t}$$

(4)
The recursion is started with \( f_{00}(a) = p_0(a) \). In practice exact computations are not possible except when both the measurement errors and circle of confusion errors are normal. In such a case one can then use the usual Kalman filter. In practically all other cases one has to rely on some approximations.

Note that the densities given above are key for likelihood estimation because the joint density of \( V_T^T \) is

\[
p(V_T^T) = \prod_{t=1}^{T} \int q_t(v_t|a)f_{t-1}(a|v_{t-1}^T)da
\]  

(5)

In order to obtain the above likelihood we utilize the Monte Carlo approximations recently proposed by Hurzeler and Kunsch (1998) for the densities given in Equations (3) and (4). Their direct method (see Equations (3.1) and (3.2) of Hurzeler and Kunsch (1998)) essentially amounts to recursively generating samples for which we can approximate moments and quantiles by using averages instead of integrals. This procedure leads to an approximate likelihood (Equation 5) for a particular set of parameter values. One must then maximize this likelihood in order to obtain maximum likelihood estimates of the parameters, that is, \( \hat{\rho} \), \( \hat{\sigma} \), and \( \hat{\tau} \). We were successful in using Splus' `nlminb` for this purpose. We hereafter refer to this approach as our HK implementation. One might also choose to use a global search procedure in order to maximize the likelihood.

4. APPLICATION

The movement of a large variety of terrestrial and aquatic vertebrates is studied using data obtained from the ARGOS satellite system. This system uses transmitters that periodically send a short radio signal, termed an uplink, to polar-orbiting satellites (Hays et al., 2001). See Subsection 2.1 for further details.

In order to fit our proposed model to data obtained with the ARGOS system, we require measurements made at equally spaced points in time. To obtain this data, hereafter referred to as regularized, we define a `stepsize` of 24 h which is reasonable given that we are modeling migratory pathways that span approximately 3 months. This stepsize results in a series of 1-day windows within each of which we must then obtain a two-dimensional estimate of location. We choose to utilize the minimum covariance determinant (MCD) estimator proposed by Rousseeuw (1984, 1985) which results in a robust location estimate for each window that is not highly influenced by outlying locations due to limitations of ARGOS. In cases where we have less than four locations within a window, and hence the MCD is not computable, we take the median (also robust) as our estimate of location. Alternatively, one might increase the window size so that each window has a minimum of four locations or use an iterative approach that utilizes information on locations from the windows prior and following the current window. Note that one could also include the data quality measures provided by ARGOS along with each location estimate (Vincent et al., 2002). However, at present we believe that the reported standard errors for each location class are in need of refinement (cf. Vincent et al., 2002).

We consider here data on leatherback turtles obtained via the ARGOS system. Leatherback turtles are the largest of sea turtles and undertake the most extensive migrations (Hays et al., 2004a; Ferraroli et al., 2004). These migrations occur between tropical nesting beaches (Hays et al., 2004b) and northern foraging areas where the turtles feed on jellyfish (James and Herman, 2001).
We examine three different tracks as shown in Figure 2. Each turtle track was initially represented by a time series of ARGOS location data. These data were then regularized (as discussed above) to obtain three tracks of equally spaced daily observations. For illustration, both the original track (comprised of 803 observations) and the regularized track (comprised of 101 observations) are shown in Figure 3 for turtle A. It is clear that the regularized track captures the underlying behavior of this turtle. Plots were similar for turtles B and C. The endpoint of all three tracks was taken to be on or about 25° N latitude. This is the point at which diving behavior suggests that they are switching behavior from migrating to foraging. The corresponding GC route is also shown in Figure 3.

For illustration we initially assume normal distributions for both the measurement and circle of confusion errors. These assumptions allow us to fit the model using the standard Kalman Filter, recently implemented in the S+Finmetrics module available with Splus 6.0. We begin by analyzing turtle track A as shown in Figure 3. We obtain \( \hat{\rho} = 0.98, \hat{\sigma} = 15 \text{ km, and } \hat{\tau} = 0 \text{ km} \) with corresponding circle of confusion estimate \( \hat{r}_{coc} = 75 \text{ km} \). What is striking here is the zero estimate for the measurement error variance. Such an estimate implies that the location estimates were observed without error, something which we know not to be true in practice. What is also interesting is that with our HK implementation we are unable to converge to a solution. To investigate further we simulated...
some data with $\tau$ small, and $\rho$ and $\sigma$ as above. We were able to obtain matching results with both methods. The fact that we cannot do this with the real data seems to suggest that a problem exists. It is also insightful to look at the normal probability plot shown in the top of Figure 4. If the normal distributional assumptions are correct then the quantities $v_t - \hat{\rho}v_{t-1}$ should be approximately normal. However the plot suggests this is not the case. The bending down on the left and bending up on the right suggest the data has longer tails. We decided to try using a $t_3$ distribution for the errors as it is often a sensible robust alternative to the normal distribution in our experience. The quantile-quantile plot for the $t_3$ distribution shown in the second plot of Figure 4 illustrates that in this case the $t_3$ distribution is a more reasonable model for the deviation errors.

As discussed in Subsection 2.1, there are a number of reasons to expect the need for robustness in our proposed model. The analyses discussed in the previous paragraph support this notion.

We now fit our robust model by assuming both the measurement and circle of confusion errors follow a $t_3$ distribution. S+Finmetrics does not possess the flexibility to fit such a model so we rely on our HK implementation. We find that the model converges to a solution and yields estimates $\hat{\rho} = 0.97$, $\hat{\sigma} = 9$ km, and $\hat{r} = 2$ km. Note that we have averaged results over five different runs to compensate for any Monte Carlo variation present in our approximations. Given that the turtle is traveling approximately 4000 km, our estimate for the circle of confusion error $\hat{r}_{coc} = 36$ (se = 17) km suggests that it is doing a good job of navigating. Recent experiments suggest that Green turtles use geomagnetic cues for long-range navigation toward specific destinations (Lohmann et al., 2004), it is possible that leatherback turtles utilize a similar mechanism. The high value for $\rho$ (bounded between 0 and 1) indicates that the turtle’s deviations from course are highly correlated. This might suggest that the turtle periodically is updating the optimal GC route, an hypothesis that we test with an alternative model (below). Alternatively, the high value for $\rho$ may simply reflect a trade-off in favor of minimizing energy expenditure on course corrections, rather than remaining close to the desired course. Finally, for comparison we took the mean of the measurement error estimates (68 percentile, non-filtered) over
the six location classes each for latitude and longitude as reported in Table 1 of Vincent et al. (2002), and found our measurement error estimate to be the same, 2 km.

We went on to repeat the above analyses for the other two turtle tracks. For turtle B we obtained $\hat{r}_{coc} = 40 \ (se = 6) \text{ km}$ and for turtle C $\hat{r}_{coc} = 38 \ (se = 7) \text{ km}$. From a biological perspective this indicates that, at least for the three turtles under consideration, navigation errors are highly consistent among individual leatherback turtles. The circle of confusion estimates are all within one standard error of each other. Note that we again averaged results over five different runs to compensate for any Monte Carlo variation.

4.1. Alternative biological models

In the analysis just presented we assume that if an animal moves off track, correction takes the form of it going back to its original course. It is natural to suspect that such animals may behave more like a
ship’s navigator. That is, occasionally an animal will update its course and head along a new GC route directed at its final destination. This idea is similar in spirit to that discussed on p. 367 of Kendall (1974). In an effort to test this hypothesis we have proposed two alternative model formulations and fitted them to the original data, details of which are given below.

We begin by allowing a turtle to update its course every 10 days. At each of the update points the turtle recalculates its route to its final destination and subsequently follows the corresponding GC route. Under this scenario, if the turtle is indeed updating its course, we would expect the resulting $\hat{r}_{coc}$ to be smaller than that obtained with our original model. However, upon doing so, we obtain a circle of confusion estimate which is not significantly different than that obtained previously, suggesting that our original model formulation is adequate. To investigate further we decided to allow a turtle to update its course after it crosses the gulf stream. If the turtle does behave in this manner we should again obtain a smaller $\hat{r}_{coc}$. This crossing is particularly apparent for turtle track A. Upon performing the analysis we obtain a larger estimate of $\hat{r}_{coc}$, granting us confidence in our original model formulation. That is, if pushed off course, a turtle will tend to return to its original course rather than recalculate before continuing migration.

Our original model formulation could also be brought into question because it can be, at least in some sense, regarded as a random walk tied down at both ends. In an effort to determine whether this feature really did significantly influence our analysis we ignored the first and last five observations for a particular track. We found that parameter estimates do not change significantly. In the circumstances for which this model is designed, situations where an animal’s circle of confusion is small relative to the distance it is traveling, we therefore expect our model to be entirely suitable in its original form.

5. CONCLUSIONS

We have presented a method for successfully modeling a migrating leatherback turtle which allows us to quantify both the measurement error inherent in the data as well as the turtle’s navigation ability. The results are both reasonable and exciting as they open up a new realm of possibilities for analysis. Robustness features grant us additional confidence in our model in being able to deal with sources of error typical of such data.

There exist a variety of possible extensions to our model along with the capability to compare circle of confusion estimates both within and between species. This is a direct result of the generality of our approach. At present we are building functionality into our model so that we can capture an animal’s change of behavior from one state to another (e.g., foraging to migrating or vice versa). In addition, we are investigating other dependence structures for the movement process. We would also like to assume heterogeneity of variance for the measurement errors. This would allow us to build in the possibility of having sequences of very good (or very bad) location estimates from ARGOS depending upon the location of the animal.

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APPENDIX

We wish to show that Equations (1) and (2) together with normality assumptions for the errors can be represented as an ARMA(1,1) process. We have that

\[ v_t = -\frac{\sigma^2 \theta}{\rho} + z_t + \theta z_{t-1} \]

where

\[ z_t \sim N(0, \sigma_z^2), \]

\[ \rho = \frac{\sigma^2}{\frac{1}{\sigma_z^2} + \sigma_z^2}. \]

The proof follows:

\[ v_t = a_t + r_t \cos \theta_t \]
\[ = (\rho a_{t-1} + \eta_t) + r_t \cos \theta_t \]
\[ = \rho a_{t-1} + \eta_t + r_t \cos \theta_t + \rho r_{t-1} \cos \theta_{t-1} - \rho r_{t-1} \cos \theta_{t-1} \]
\[ = \rho (a_{t-1} + r_{t-1} \cos \theta_{t-1}) + \eta_t + r_t \cos \theta_t - \rho r_{t-1} \cos \theta_{t-1}. \]

Denoting \( \zeta_t = \eta_t + r_t \cos \theta_t - \rho r_{t-1} \cos \theta_{t-1} \), we have \( v_t - \rho v_{t-1} = \zeta_t \) where \( E(\zeta_t) = 0 \),

\[ \text{Var}(\zeta_t) = \sigma^2 + (1 + \rho^2) \tau^2 \]

and

\[ \text{Cov}(\zeta_t, \zeta_{t-1}) = -\rho \tau^2. \]

In addition we notice that \( \zeta_t \) is a stationary one-correlated times series with mean 0, and hence can be represented as an MA(1) process, say \( z_t + \theta z_{t-1} \). Then

\[ \text{Var}(\zeta_t) = (1 + \theta^2) \sigma_z^2 \]

and

\[ \text{Cov}(\zeta_t, \zeta_{t-1}) = \theta \sigma_z^2 \]

Equating like terms gives the expressions found above.

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