Modelling particles moving in a potential field with pairwise interactions and an application

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Abstract. Motions of particles in fields characterized by real-valued potential functions, are considered. Three particular expressions for potential functions are studied. One, U, depends on the ith particle's location, $\mathbf{r}_i(t)$ at times t_i. A second, V, depends on particle i's vector distances from others, $\mathbf{r}_i(t) - \mathbf{r}_j(t)$. This function introduces pairwise interactions. A third, W, depends on the Euclidian distances, $\|\mathbf{r}_i(t) - \mathbf{r}_j(t)\|$ between particles at the same times, t. The functions are motivated by classical mechanics.

Taking the gradient of the potential function, and adding a Brownian term one, obtains the stochastic equation of motion

$$d\mathbf{r}_i = -\nabla U(\mathbf{r}_i)\,dt - \sum_{j \neq i} \nabla V(\mathbf{r}_i - \mathbf{r}_j)\,dt + \sigma\,d\mathbf{B}_i$$

in the case that there are additive components U and V. The ∇ denotes the gradient operator. Under conditions the process will be Markov and a diffusion. By estimating U and V at the same time one could address the question of whether both components have an effect and, if yes, how, and in the case of a single particle, one can ask is the motion purely random?

An empirical example is presented based on data describing the motion of elk (*Cervus elaphus*) in a United States Forest Service reserve.

1 Introduction

An analytic method is presented for describing the motion of particles ranging about in a possibly confined region. The motion of a particle is described as possibly being affected by its physical location and also its relative distances to other particles.

The work may be motivated by concepts and methods from physics. Landau and Lifshitz (1969) write, page 1:

> "One of the fundamental concepts of mechanics is that of a particle. By this we mean a body whose dimensions may be neglected in describing its motion."

This work will view elk as particles. Skorokhod (1983, 1993, 1996, 2003) has prepared a sequence of pertinent works concerning gradient systems. In particular Chapter 2 of his 1982 book is titled "Randomly interacting systems of particles".

The research is assisted by the fact that advances in radio-telemetry tracking of animals allow high-frequency and highly accurate monitoring of their movements. These advances provide novel opportunities for development and application of new analytical methods to characterize animal movements and landscape use. References include Brillinger et al. (2001a, 2001b, 2002), Cooke et al. (2004), Coulombe et al. (2006) and Preisler et al. (2004, 2006).

2 Stochastic particle processes

The concern is particle systems, that is collections of particles moving about in some space, for example, R^d. The particles may be interacting perhaps because of others or perhaps due to common influences. Several models and methods will be emphasized in this work having in mind a particular animal biology example.

2.1 Model I

Consider a particle, labeled i, at location $\mathbf{r}_i(t)$ at time t whose motion may be described by

$$d\mathbf{r}_i = -\nabla U(\mathbf{r}_i)\,dt + \Sigma\,d\mathbf{B}_i, \tag{2.1}$$

where $\nabla = (\partial/\partial x, \partial/\partial y)$ is the gradient operator, and $\mathbf{B}_i$ is a standard vector-valued Brownian motion. The potential function U is real-valued which incidentally makes it easier to model directly rather than working with the components of ∇U themselves. Under regularity conditions, for example, Lipschitz ones, the solution of a system of equations like (2.1) for $i = 1, \ldots, I$ will be Markov and be stationary. Further there may be an invariant distribution, sometimes called a Gibbs distribution,

$$C \exp\{-2U(\mathbf{r})\}/\sigma_0^2 \tag{2.2}$$

in the case that Σ in (2.1) is $\sigma_0^2 \mathbf{I}$. There are some results for the case that Σ is not diagonal and depends on $\mathbf{r}$. Specifically Ait-Sahalia (2008) presents conditions under which a process described by

$$d\mathbf{r} = \mu(\mathbf{r})\,dt + \Sigma(\mathbf{r})\,d\mathbf{B}$$

can be transformed into one satisfying

$$d\mathbf{r} = \mu(\mathbf{r})\,dt + d\mathbf{B}$$

by an invertible infinitely differentiable function γ satisfying $\nabla \gamma(\mathbf{r}) = \Sigma^{-1}(\mathbf{r})$. This has the implication that after finding a suitable γ, one can use the simpler form above. In particular this shows the difficulty in simply working directly with empirical density estimates and their hotspots.

The minus sign in (2.1) comes from classical mechanics and is traditional. One notes then that depressions in U correspond to points of attraction, while ridges lead to repulsion at least when formula (2.2) holds. The Ornstein–Uhlenbeck process is a particular case.

2.2 Model II

One assumes that the motion of the particle is described by

$$d\mathbf{r}_i = -\sum_{j \neq i} \nabla V(\mathbf{r}_i - \mathbf{r}_j) \, dt + \Sigma \, d\mathbf{B}_i, \qquad (2.3)$$

that is, that the next small movement depends on the vector distances, $\mathbf{r}_i - \mathbf{r}_j$ from particle i to the others. Here V thereby introduces interactions.

2.3 Model III

One assumes that the V above has the form

$$W(\|\mathbf{r}_i - \mathbf{r}_j\|), \qquad (2.4)$$

with the $\|\mathbf{r}_i(t) - \mathbf{r}_j(t)\|$ the Euclidian distances between the ith and jth particles at time t.

A specific example of this last is provided by the case of gravitation where W is given by

$$-GM_0/\|\mathbf{r}_0 - \mathbf{r}\|$$

with $\mathbf{r}_0$ the location of an attracting object of mass M_0 and $\mathbf{r}$ the location of the particle of concern.

A second example is developed in the work of Zohdi (2003, 2009). He employs the functional form

$$\alpha_1 \|\mathbf{r}_i - \mathbf{r}_j\|^{\beta_1} - \alpha_2 \|\mathbf{r}_i - \mathbf{r}_j\|^{\beta_2}$$

with the α's and β's to be estimated. This form allows both attraction and repulsion depending on the distances between the particles. Zohdi uses this model to simulate "swarms" of particles.

2.4 Model IV

One considers a hybrid process defined by

$$d\mathbf{r}_i = -\nabla U(\mathbf{r}_i) \, dt - \sum_{j \neq i} \nabla V(\mathbf{r}_i - \mathbf{r}_j) \, dt + \sigma \, d\mathbf{B}_i. \qquad (2.5)$$

The potential here is a sum $U + V$ and this model includes Models I, II and III as particular cases.

There is a substantial theoretical literature on the models just set down. One can mention the papers Skorokhod (1983, 1993, 1996, 2003), Skrypnik (1984), Spohn (1986), Cepa and Lepingle (2000) and Fritz (1987). Often the theoretical work is getting limiting results, laws of large numbers and central limit theorems.

The potential functions might be represented via basis functions as in

$$U(\mathbf{r}) = \sum_j \alpha_j \phi_j(\mathbf{r}) \quad \text{and} \quad V(\mathbf{r} - \mathbf{r}_l) = \sum_k \beta_k \psi_k(\mathbf{r} - \mathbf{r}_l) \qquad (2.6)$$

with $\mathbf{r}_l$ denoting location of the lth elk and the α's and β's parameters to be estimated. The basis functions are given and might be monomials, thinplate splines, cosinusoids or Gaussians densities, for example.

In the work of this paper Models I, II, III will be fit in an animal biology example. In Brillinger et al. (2006) polynomials of orders 2 and 3 in x and y were employed with (x, y) denoting the location of a particle in the plane. There was also a boundary, but this will not be taken specific account of here.

When appropriate one can set down SDEs or their approximations with non-Gaussian and autocorrelated stimulation as well.

3 Inference methods

The Model I will be approximated by

$$\mathbf{r}_i(t_{k+1} - t_k) = -\nabla U\big(\mathbf{r}_i(t_k)(t_{k+1} - t_k)\big) + \Sigma \mathbf{Z}_{ik}, \tag{3.1}$$

$k = 1, 2, \ldots$ in the case of elk i. The $\mathbf{Z}_i$ will be independent standard bivariate normals. This is a form of Euler scheme; see Kloeden and Platen (1995). To begin α and β of (2.6) will be estimated by multiple regression with the response the empirical velocity

$$\big(\mathbf{r}_i(t_{k+1}) - \mathbf{r}_i(t_k)\big)/(t_{k+1} - t_k)$$

and the explanatories partial derivatives of the functions ϕ and ψ. Then, following the Gauss–Markov theorem estimable linear functions may be learned by plugging in estimates $\hat{\alpha}$ and $\hat{\beta}$. The potential function U of (3.1) may be estimated by

$$\hat{U}(\mathbf{r}) = \sum_j \hat{\alpha}_j \phi_j(\mathbf{r}),$$

for example.

Discrete approximations need to be employed for the models I–III as the data are available only at discrete times. These approximations become the models of record.

In some of the paper's work the $\{t_k, \mathbf{r}(t_k)\}$ values need be interpolated to the same equally spaced times for all the animals.

Monnomials will be employed for the basis functions and parameters will be estimated by ordinary least squares. Σ may be chosen to have a variety of forms, but the form $\sigma \mathbf{I}$ will be used in the computations of this paper. Statistical details of this approach are provided in Brillinger et al. (2001b) and Brillinger (2007). Specifically the large sample properties of the least squares estimates may be set down using existing results, making use of the fact that the values

$$r(t_{k+1}) - E\{r(t_{k+1})|F_k\},$$

$k = 0, 1, 2, \ldots$ form a martingale difference series. Here F_k is a pertinent increasing sequence of σ-fields. See Lai and Wei (1982), Lai (1994) and Chang and Lin

(1995) for the case of a finite dimensional parameter. The results look very much like those of generalized least squares estimates in the independent identically distributed case.

4 The Starkey experiment and the data

In a continuing large-scale experiment data are collected to evaluate responses of elk (*Cervus elaphus*) to recreation activities; see Wisdom et al. (2004) and Preisler et al. (2006). Movements were monitored for radio-collared animals in the absence of any human activities during an extended control period in 2005. These are studied in this paper. The data were obtained with the use of telemetry systems that collect values frequently (here time spacings of about 5 minutes) and accurately (location error often less than 10 meters). The high volume and high quality of these data, in the absence of any confounding human activities, provide an opportunity to explore the development of new models and to fit existing ones to certain animal movements.

The data of this research were collected in the period April–October 2005 at the USDA Forest Service Starkey Experimental Forest and Range (Starkey) in Oregon, United States [Rowland et al. (1997); Wisdom et al. (2005)]. The data were for its Northeast Pasture [Wisdom et al. (2005)]. The vegetation there was a mosaic of forests and grasslands. This study area has a tall fence about it whose shape and size are shown in Figures 2 and 3 below. See Rowland et al. (1997), Wisdom et al. (2005) and Preisler et al. (2006) for additional details about the study area and related elk research.

The data were collected via a global positioning system (GPS) with telemetry systems programmed to obtain one location per radio-collared elk about every 5 minutes in the months May through October, 24 hours a day for weekdays.

For the analyses presented six elk having the same general periods of observation were chosen for the study.

A variety of questions arise. These include: Is the movement of a particular animal associated with distances to the others or to the terrain they are located in at the moment? Are animals moving jointly? Is joint movement driven by presence of other elk or by exogenous variables? Is there an effect of other elk on an elk's location and if yes, at what distance does it appear? Can one characterize elk movement in the absence of disturbances? (The latter is important for use as a baseline control in studies of effects of disturbances, e.g., hikers.)

References to such work include: Dunn and Gipson (1977), Dunn and Brisbin (1985), Brillinger et al. (2004), Preisler et al. (2004), Lasiecki (2006).

5 Some exploratory data analysis

Elementary displays are extremely useful at the beginnings of empirical studies. One concern here was that because of the measurement process employed the time
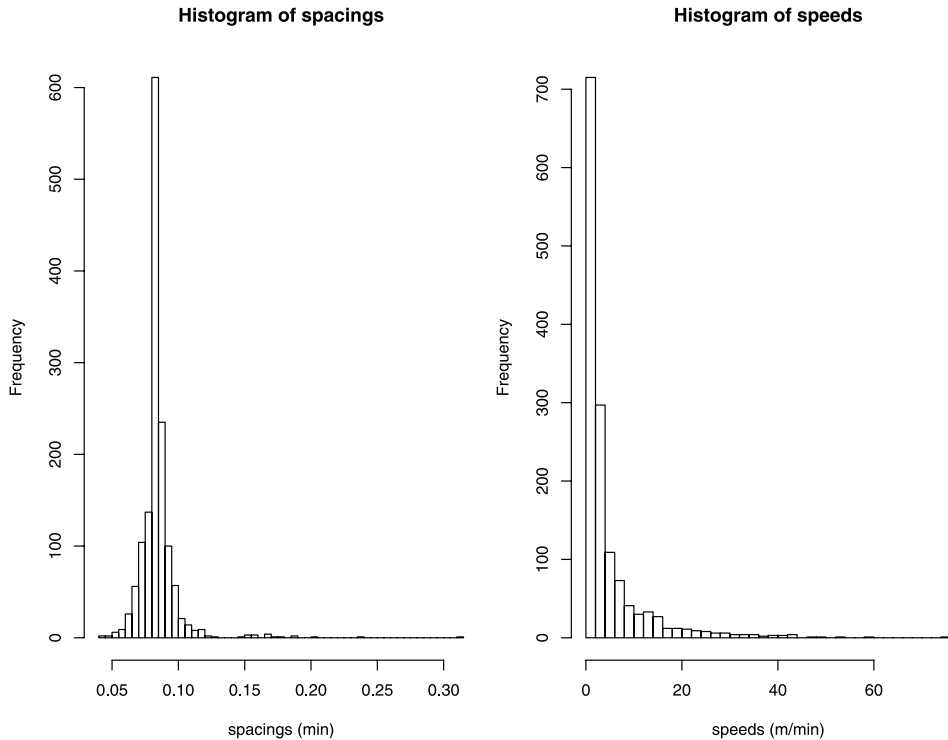
Histogram of spacings   **Histogram of speeds**

Figure 1 *Histogram of the spacings, $t_{k+1} - t_k$, and of the speeds. First week's data.*

intervals $\{t_{i,k+1} - t_{i,k}\}$ between location estimates are not equally spaced. They do vary around 5 minutes. An elementary histogram is useful for learning details of this temporal sampling circumstance and for deciding on appropriate analysis procedures. Figure 1 provides the histogram of all the time intervals and also of the empirical speeds for the first week's data for the group of six animals. There are outliers to the right in each case, so in the computations that follow the cases with the top 1% of the velocities are trimmed out. (A distinction is being made here between speeds and velocities. Briefly, speed is a scalar whereas velocity is a 2-vector.)

Figures 2 and 3 show the tracks of six of the animals during the first week of the experiment. These animals were numbered 280, 281, 395, 396, 397 and 398 by the Starkey researchers. The "o" in the figure denotes the start of the track. Similarities of the paths may be noted, particularly of animals 395 and 396. The particular animals all go to the SE corner at some point in the first week.

Figures 2 and 3 suggested that simple linear interpolation between adjacent time points might suffice. This was done to get estimated locations every 5 minutes exactly, the same times for all the animals. A comparison of the original data paths and the interpolated ones showed little difference.
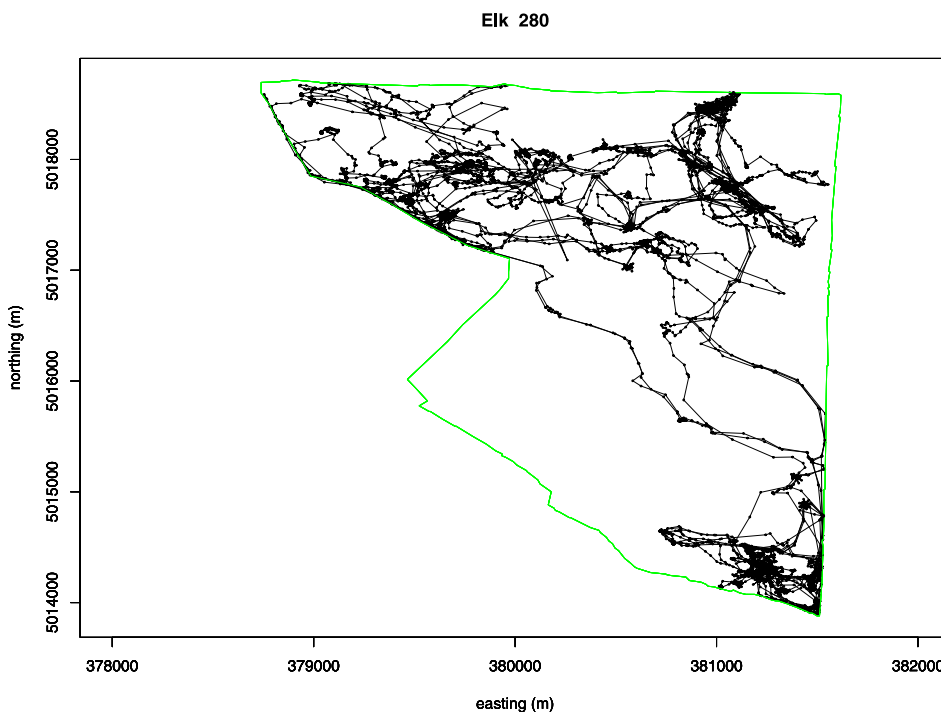
Elk 280

Figure 2 *Superposed paths of six animals for the first week.*

Even before Figures 2 and 3 were examined there was interest in whether these animals moved about in groups. The results of two exploratory methods follow. The methods employed were: studying the paths plotted, hierarchical clustering and coherence analysis. The analyses presented in Figure 4 and Tables 1 and 2 are for the first week of data.

As may be seen in Figure 3 the animals' range has changed for the second week. The modelling will need to take note of this.

5.1 Example A

A cluster analysis of the vectors $\mathbf{r}_i$; $i = 1, \ldots, 6$ was carried out employing the R/Cran function hclust(method = "single") for the week's data. The resulting dendrogram is displayed in Figure 4. One sees the triplet (395, 396, 398) standing out for consideration as co-movers as does the pair (281, 397). Tracks similarities are also apparent in Figure 3 showing the second week's data.

5.2 Example B

In coherence analysis one creates a setup involving complex-valued quantities. This was done earlier in Arato, Kolmogorov and Sinai (1962) who were studying the path of the Earth's North Pole as the earth wobbled.
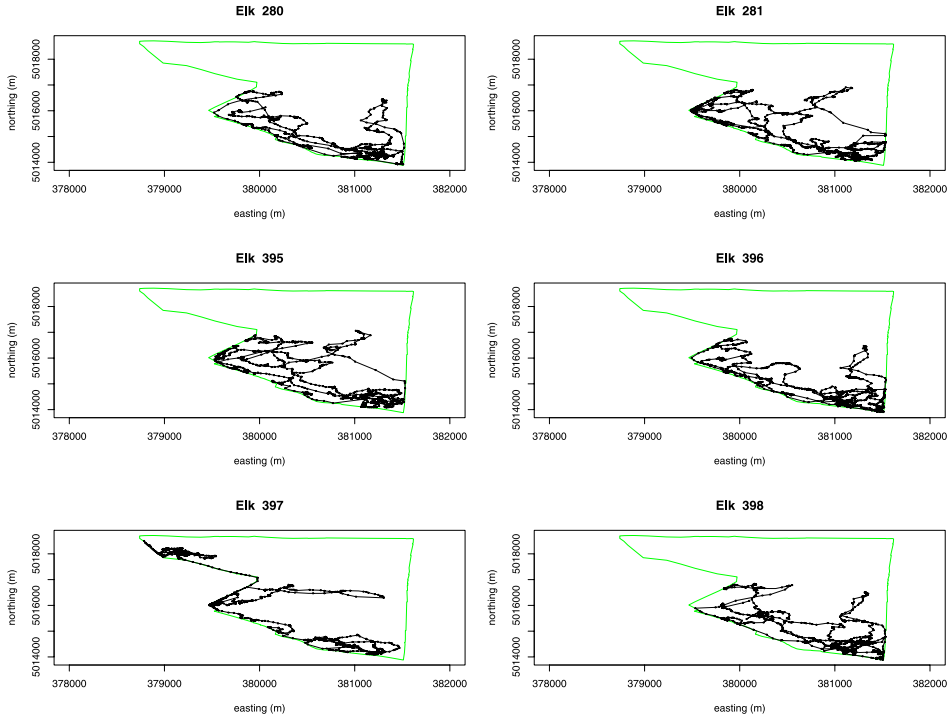
Figure 3 *Individual paths of six animals for the second week.*

To begin one replaces $\mathbf{r}(t) = (x(t), y(t))$ by

$$z(t) = x(t) + iy(t)$$

with $i = \sqrt{-1}$.

Basic definitions are needed. When z_1 and z_2 are complex-valued random variables with mean 0 it is convenient to define their covariance as $\mathrm{cov}\{z_1, z_2\} = E\{z_1\bar{z}_2\}$ and their variances by $\mathrm{var}(z) = E\{|z|^2\}$. Their coherence is also defined as

$$|R_{12}|^2 = |\mathrm{cov}\{z_1, z_2\}|^2/[\mathrm{var}\{z_1\}\,\mathrm{var}\{z_2\}].$$

Estimates of the values of the quantities are given in the two tables that follow. The first table is based on week one's data and the second on all 14 weeks.

One notes some very high coherences values in Table 1, namely 0.997, 0.995, 0.994 and 0.897. They involve elk 396, 397 and 398. When all 14 weeks of data are studied, Table 2, the highest values are: 0.689, 0.452, 0.438 and 0.422. Such a drop could have been anticipated given the length of the time period.
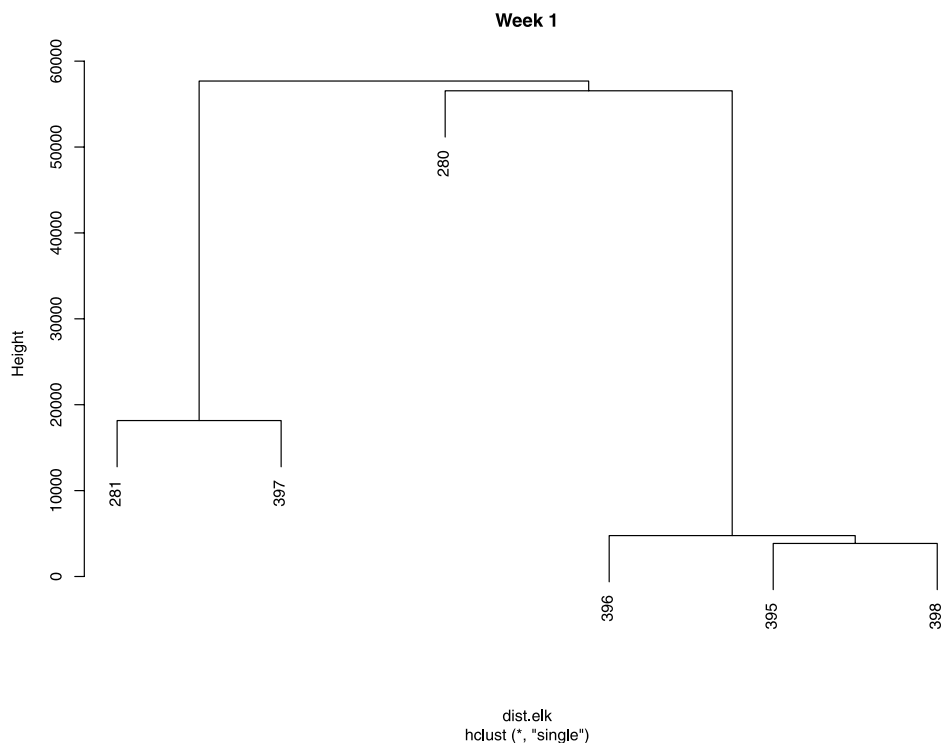
Week 1

Figure 4 *Result of the hierarchical clustering analysis. First week's data for the six animals.*

Table 1 *Coherence estimates for first week of data*

elk	280	281	395	396	397	398
280	1	0.416	0.466	0.472	0.471	0.477
281	0.416	1	0.343	0.349	0.897	0.356
395	0.466	0.343	1	0.995	0.415	0.997
396	0.472	0.349	0.995	1	0.424	0.994
397	0.471	0.897	0.415	0.424	1	0.427
398	0.477	0.356	0.997	0.994	0.427	1

Table 2 *Coherence estimates for 14 weeks of data*

elk	280	281	395	396	397	398
280	1	0.308	0.26	0.438	0.265	0.345
281	0.308	1	0.337	0.42	0.253	0.339
395	0.26	0.337	1	0.422	0.092	0.452
396	0.438	0.42	0.422	1	0.199	0.689
397	0.265	0.253	0.092	0.199	1	0.119
398	0.345	0.339	0.452	0.689	0.119	1

6 Model fitting

The gradient models of Section 2 detail how an animal, given its location, and those of other animals at time t, might move in the next small time interval.

The potential function form employed in the computations to be presented is

$$\beta_1 x + \beta_2 y + \beta_3 x^2 + \beta_4 xy + \beta_5 y^2 + \beta_6 x^3 + \beta_7 x^2 y + \beta_8 xy^2 + \beta_9 y^3$$

with (x, y) denoting location. The gradient is

$$\begin{pmatrix} 1 & 0 & 2x & y & 0 & 3x^2 & 2xy & y^2 & 0 \\ 0 & 1 & 0 & x & 2y & 0 & x^2 & 2xy & 4y^2 \end{pmatrix}$$

matrix multiplied by the transpose of the row vector

$$(\beta_1 \quad \beta_2 \quad \beta_3 \quad \beta_4 \quad \beta_5 \quad \beta_6 \quad \beta_7 \quad \beta_8 \quad \beta_9).$$

The result is linear in the β's. Because of this linearity simple multiple regression may be employed to obtain estimates. The steps of the analysis were described in Sections 2 and 3.

7 Results

7.1 Model I results

The animals 395 and 398 will be studied principally, and the first two weeks of data analyzed. To handle outliers in the empirical velocity the top 5% of cases are trimmed off. The results are in Figure 5.

The model fit is

$$d\mathbf{r} = -\nabla U(\mathbf{r})\, dt + \mathbf{\Sigma}\, d\mathbf{B}$$

with $\mathbf{\Sigma} = \sigma \mathbf{I}$. In this situation the elk's change in location is dependent on its current location, up to noise.

In Figure 5 one notes the low (darker) values to the right in the top two panels. These have the implication that when the animal is there generally speaking it will be staying and if it is not on the right it will be moving in that direction.

Some formal statistical conclusions need to be stated. One can consider the null hypothesis that the potential function is constant, that is, the animal is moving around purely randomly. An F test of this hypothesis may be carried out. The result is $F = 2.879$ with degrees of freedom 9 and 5533, and p-value 0.00215. The large sample validity of these results may be based on work of Lai (1994) and Brillinger (2007). In particular the p-value approximation is based on an assumption of independent innovations.

However, correlation and spectrum analyses of the residuals suggest this is not the case. One could correct the degrees of freedom in an attempt to deal with the autocorrelation, but the fact that the current potentials are linear in the parameters
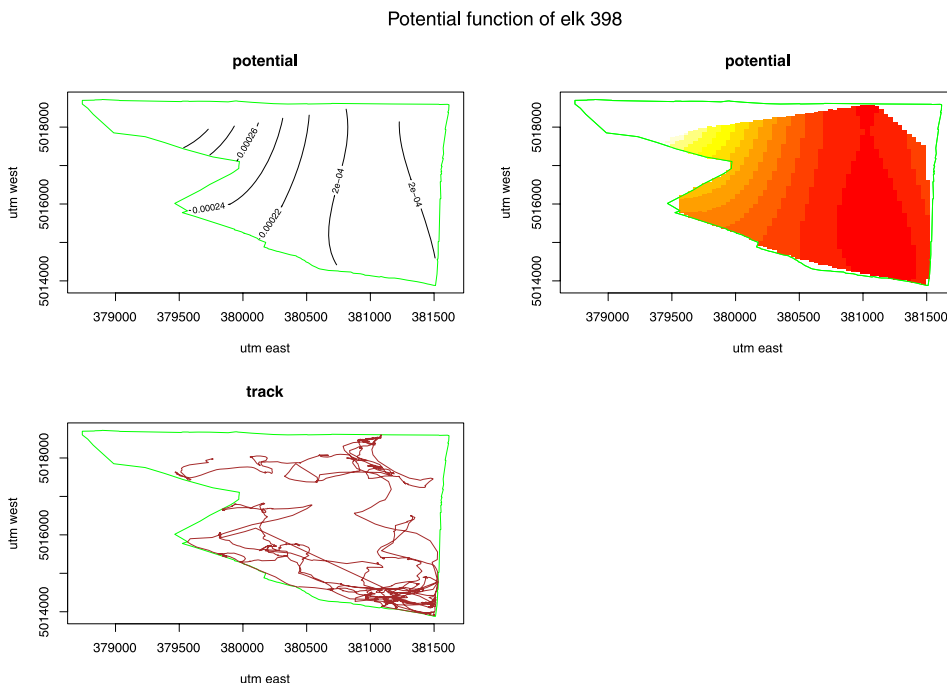
Potential function of elk 398

Figure 5 *The top row is the estimated potential for elk* 398 *in contour and image form. Bottom row provides the animal's trajectory for the first two weeks.*

allows an armax models to be fit directly. This will be done when the full dataset is being analyzed. There are known sources of variability that need to be introduced formally. These include the time of day, the week of the year, the terrain.

A related issue is that one would like a measure of the uncertainty of the potential function estimate. One can get an estimate of the variance covariance matrix of the estimated β's, but there is evidence that these values are not to be trusted; see, for example, Wood (2006). Fitting an armax model might handle this circumstance.

7.2 Model II results

The model is now

$$d\mathbf{r}_i = -\sum_{j \neq i} \nabla V(\mathbf{r}_i - \mathbf{r}_j)\, dt + \sigma\, d\mathbf{B}_i.$$

It will be used to study elk 398's motion dependence on the location of elk 395. The function V of the model has been estimated. The analysis results are shown in Figure 6.

From the top row of Figure 6 one sees that the next relative motion of elk 398, and elk 395 will when their relative distance is in the band running from the NW
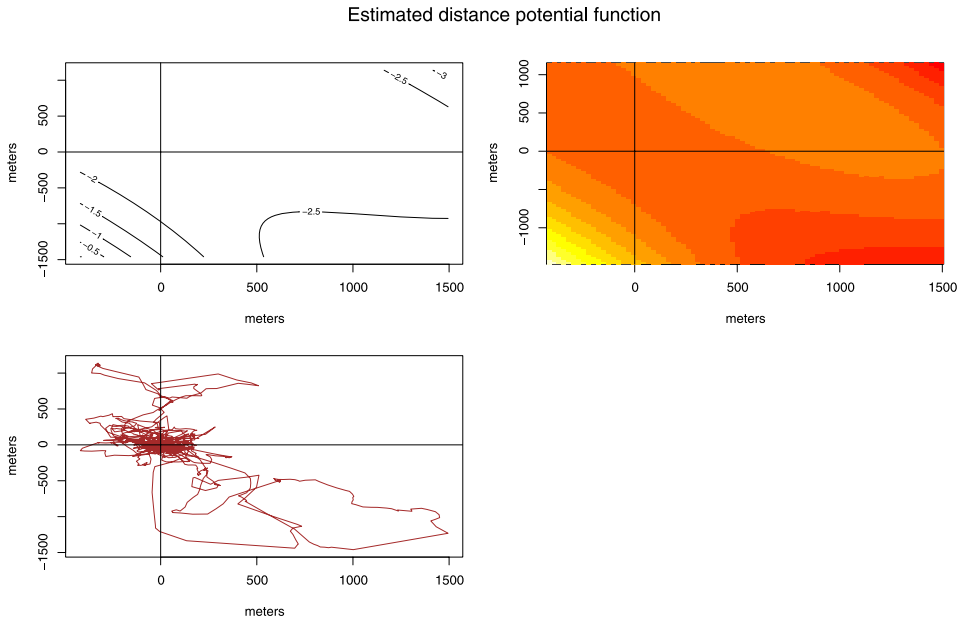
Estimated distance potential function

Figure 6   *Elk* 398*'s movement with respect to elk* 395.

to the SE generally stay in the trough. When that point is outside the trough it will tend to move into it.

The lower graph shows $\mathbf{r}_i - \mathbf{r}_j$ as a function of t with i referring to elk 398 and j to elk 395. One sees a concentration of points, a so-called hotspot, near $(0, 0)$. The animals are often close together.

Next consider the null hypothesis that V is constant. One has $F = 4.75$ with degrees of freedom 9 and 5263, and p-value 0.000235.

7.3 Model III results

The model is now

$$d\mathbf{r}_i = -\sum_{j \neq i} \nabla W(\|\mathbf{r}_i - \mathbf{r}_j\|)\, dt + \sigma\, d\mathbf{B}_{ij}$$

for some real-valued function W of real values.

The top two panels of Figure 7 provide estimates of the function $W(d)$, with d Euclidian distance. One would expect the vector $\mathbf{r}_i - \mathbf{r}_j$ to stay under the main diagonal once it got there and if it wasn't to move over there. One notes the rotational invariance. The bottom left panel again provides the trace of the $\mathbf{r}_i - \mathbf{r}_j$ time series.

The analysis of variance results here are: $F = 3.88$ with degrees of freedom 9 and 5263 and the p-value 0.00263. If one believed the p-value one would be led to reject the hypothesis of flatness, as would be the case for purely random motion.
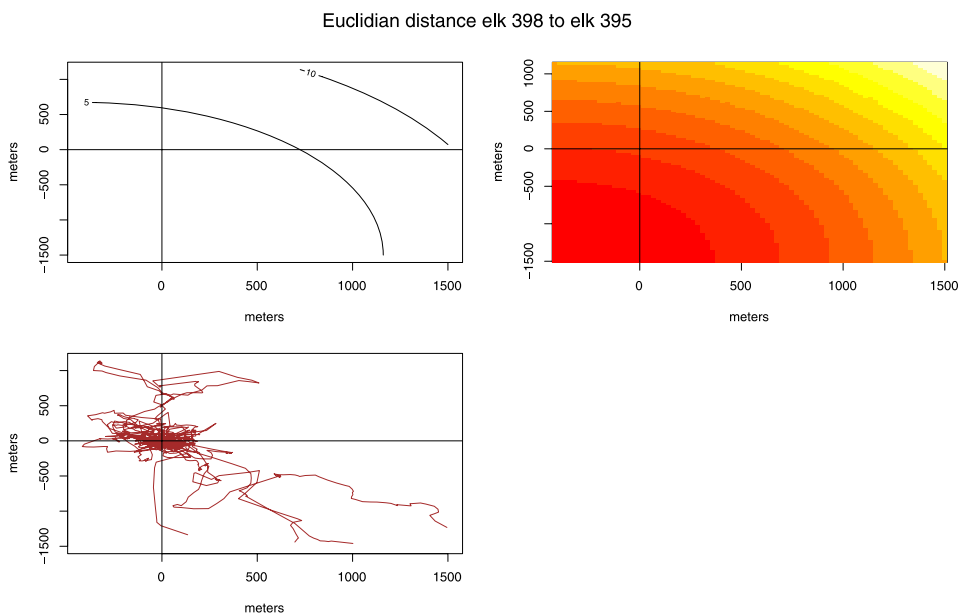
Euclidian distance elk 398 to elk 395

Figure 7 *The results of fitting Model III with elk* 398 *dependent and* 395 *explanatory.*

8 Discussion and summary

The work has been motivated by models of classical mechanics. Stochastic differential equations have been employed to motivate the discrete time models actually used.

In particular the following general model

$$d\mathbf{r}_i(t) = -\nabla U_i(\mathbf{r}_i(t))\,dt - \sum_{j \neq i} \nabla V_{ij}\big(\mathbf{r}_i(t) - \mathbf{r}_j(t)\big)\,dt + \sigma\,d\mathbf{B}_i(t)$$

was set out. Three particular cases of it have been fit to trajectories of a single elk, and then of two elks relative distance to each other. The trajectories have been used to help interpret the estimated potential function in each case.

The use of a potential function simplifies the fitting of a trajectory model since it is real valued. A further simplification results when the function is linear in the parameters as was the case for the examples of the paper. What is less usual here is manipulating the linear regression model to another model and plugging in the parameter estimates. This meant that one couldn't use contemporary linear model programs directly.

Fitting was tried with other basis functions, for example, Gaussian and thinplate splines, but ultimately at this stage in the research it was simpler to stick with monomials.

There were difficulties. For example, the unequally spaced observation times and their differing values for the various elk. This was addressed by simple interpolation.

Since the model is additive in the basic variables, explanatories may be included quite directly. Pertinent explanatories include: time of day, topography and location of a moving attractor/repellor.

One might choose to include time lags as occur in stochastic functional differential equations. In another step one might assume that the innovations come from an ARMA process in the fitting. As the parameters in the potential are linear there are a variety of programs for carrying out this step. One might take specific note of the presence of a boundary, here a fence, see Brillinger (2003). One might derive better approximations to the distribution of the statistics needed in drawing inferences.

Acknowledgments

References

Ait-Sahalia, Y. (2008). Closed-form likelihood expansions for multivariate diffusions. *Ann. Statist.* **36**, 906–937. MR2396819

Arato, M., Kolmogorov, A. N. and Sinai, J. G. (1962). Evaluation of the parameters of a complex stationary Gauss-Markov process. *Soviet Mathematics* **3**, 1368–1371.

Brillinger, D. R. (2003). Simulating constrained animal motion using stochastic differential equations. *Lecture Notes in Statistics* **41** 35–48. New York: Springer. MR1999413

Brillinger, D. R. (2007). Learning a potential function from a trajectory. *Signal Processing Letters* **14**, 867–870.

Brillinger, D. R., Preisler, H. K., Ager, A. A., Kie, J. and Stewart, B. S. (2001a). Modelling movements of free-ranging animals. UCB Statistics Department Technical Report. Available at www.stat.Berkeley.edu/~brill/Preprints/610.pdf.

Brillinger, D. R., Preisler, H. K., Ager, A. A. and Kie, J. (2001b). The use of potential functions in modelling animal movement. *Data Analysis From Statistical Foundations* 369–386. New York: Nova. MR2034526

Brillinger, D. R., Preisler, H. K., Ager, A. A., Kie, J. G. and Stewart, B. S. (2002). Employing stochastic differential equations to model wildlife motion. *Bull. Bras. Math. Soc. New Series* **33**, 385–408. MR1978835

Brillinger, D. R., Preisler, H. K., Ager, A. A. and Wisdom, M. J. (2004). Stochastic differential equations in the analysis of wildlife motion. In *2004 ASA Proceedings, Section on Statistics and the Environment* 2899–2908. Alexandria, VA: American Statistical Association.

Brillinger, D. R., Stewart, B. S. and Littnan, C. L. (2006). A meandering hylje. In Festschrift for Tarmo Pukkila 79–92. Finland: Univ. Tampere. MR2412952

Cepa, E. and Lepingle, D. (2000). Interacting particles with strong repulsion. Available at http://Citeseer.ist.psu.edu/576486.html.

Chang, D.-S. and Lin, G.-C. (1995). Stochastic regression model with heteroscedastic disturbance. *Ann. Inst. Stat. Math.* **47**, 301–309. MR1345428

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G. and Butler, P. J. (2004). Biotelemetry: A mechanistic approach to ecology. *Trends in Ecology and Evolution* **19**, 334–343.

Coulombe, M.-L., Massé, A. and Cote, S. D. (2006). Quantification and accuracy of activity data measured with VHF and GPS telemetry. *Wildlife Society Bulletin* **34**, 81–92.

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.) 181–205. Amsterdam: North-Holland. MR0792315

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

Fritz, J. (1987). Gradient dynamics of infinite point systems. *Ann. Probab.* **15**, 478–514. MR0885128

Kloeden, P. E. and Platen, E. (1995). *Numerical Solution of Stochastic Differential Equations*. Berlin: Springer.

Lai, T. L. and Wei, C. Z. (1982). Least squares estimation in stochastic regression models. *Ann. Statist.* **10**, 1917–1930. MR0642726

Lai, T. L. (1994). Asymptotic properties of nonlinear least squares estimates in stochastic regression models. *Ann. Statist.* **22**, 1917–1930. MR1329175

Landau, L. D. and E. M. Lifshitz (1969). *Mechanics*, 2nd ed. Oxford: Pergamon. MR0475051

Lasiecki, P. (2006). Assessment of stochastic differential equations and Markov chain models in time series. Ph.D. thesis. Berkeley: Univ. California. MR2709936

Preisler, H. K., Ager, A. A., Johnson, B. K. and Kie, J. G. (2004). Modelling animal movements using stochastic differential equations. *Environmetrics* **15**, 643–657.

Preisler, H. K., Ager, A. A. and Wisdom, M. J. (2006). Statistical methods for analyzing responses of wildlife to human disturbance. *Journal of Applied Ecology* **43**, 164–172.

Rowland, M. M., Bryant, L., Johnson, B., Noyes, J., Wisdom, M. J. and Thomas, J. W. (1997). The Starkey Project: History, facility and data collection methods for ungulate research. U.S. Forest Service General Technical Report PNW-GTR- 396, La Grande, Oregon, USA.

Skorokhod, A. V. (1983). *Stochastic Equations for Complex Systems*. Dordrect: Reidel.

Skorokhod, A. V. (1993). Infinite systems of randomly interacting particles. *Random Operators and Stochastic Equations* **1**, 1–14. MR1254170

Skorokhod, A. V. (1996). On the regularity of many-particle dynamical systems perturbed by white noise. *J. Appl. Math. Stoch. Anal.* **9**, 427–437. MR1429265

Skorokhod, A. V. (2003). Quasistable gradient and Hamiltonian systems with a pairwise interaction randomly perturbed by Weiner processes. *J. Appl. Math. Stoch. Anal.* **16**, 45–67. MR1973078

Skrypnik, W. L. (1984). Correlation functions of infinite system of interacting Brownian particles: Local in time evolution close to equilibrium. *J. Stat. Physics* **35**, 587–602. MR0749839

Spohn, H. (1986). Equilibrium fluctuations for interacting Brownian particles. *Commun. Math. Physics* **103**, 1–33. MR0826856

Wisdom, M. J., Ager, A. A., Preisler, H. K., Cimon, J. and Johnson, B. K. (2004). Effects of off-road recreation on mule deer and elk. *Transactions of the North American Wildlife and Natural Resources Conference* **69**, 67–80.

Wisdom, M. J. et al. (2005). The Starkey Project: A synthesis of long-term studies of elk and mule deer. Alliance Communications.

Wood, S. N. (2006). *Generalized Additive Models*. Boca Raton: Chapman and Hall. MR2206355

Zohdi, T. L. (2003). Computational design of swarms. *Int. J. Numer. Methods Engrg.* **57**, 2205–2219. MR1992791

Zohdi, T. L. (2009). Mechanistic modeling of swarms. *Comput. Methods Appl. Mech. Engrg.* **198**, 2039–2051. MR2517953

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