

# Stochastic Differential Equations: A Tool for Studying Animal Movement

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**Abstract.** Stochastic differential equations (SDE) have been used to analyze data from such areas as quantum physics, economics, control engineering, and epidemiology. In this presentation we discuss the use of SDE's to characterize the direction and speed of an animal's movements and to study the effects of explanatory variables (e.g., habitat characteristics) on movement patterns. Analyses of animal movements demand the use of complex models and computationally intense techniques. The use of these techniques is demonstrated by two examples. In the first example the tracks of female bark beetles are studied as they orient and move toward a point source emitting male pheromones. In the second example the trajectories of radio-collared elk and deer are studied as they forage in a 9000 ha fenced experimental forest in Oregon.

## 1 Introduction

Some of the first examples of the use of stochastic models to describe environmental systems are those concerning movements of species [1]. Stochastic models were used to characterize the random process  $Y = \{Y(t), t \in T\}$ , where  $Y(t)$  is the location of a particle (or an organism) at time  $t$ . More recently, environmental scientists use stochastic models to characterize movements of and study environmental effects on populations of organism.

Most movement models involve some form of differential equations. For example, the deterministic partial differential equation

$$\frac{\partial u(x, t)}{\partial t} = -\frac{\partial}{\partial x}(\beta_1 u(x, t)) + \frac{\partial^2}{\partial x^2}(\beta_2 u(x, t)) \quad (1)$$

has been used to characterize the steady state probability density,  $u(x, t)$ , of beetles [2], coyote [3] and other free ranging animal population [4], [5].

A univariate stochastic differential equation (SDE) is defined by

$$dY(t) = \mu(Y, t, \theta)dt + \sigma(Y, t, \theta)dB(t) \quad (2)$$

where  $Y(t)$  is a random variable,  $\{B(t), t \geq 0\}$  is a random process, and  $\theta$  is a set of parameters, some known and some unknown. The parameter  $\mu(Y, t, \theta) = E\{dY(t)/Y(s), s < t\}/dt$  is interpreted as the instantaneous velocity of the individual (drift coefficient), and  $\sigma(Y, t, \theta) = se\{dY(t)/Y(s), s < t\}/dt$  is interpreted as the speed or the diffusion coefficient.

The simplest model for the SDE in (2) is a pure diffusion model where  $\mu(Y,t,\boldsymbol{\theta}) = 0$  and  $B(t)$  is a Brownian process, i.e., each individual's movement is a random walk independent of others. Another special case is the mean-reverting *Ornstein-Uhlenbeck* (O-U) process where  $\mu(Y,t,\boldsymbol{\theta}) = \alpha [Y(t)-a]$  and  $\sigma^2(Y,t,\boldsymbol{\theta}) dt = \sigma^2$ . The O-U process has been used to estimate home ranges of animals where  $a$  is the center of the home range [6], [7].

More complicated animal movement behavior may be studied by modeling the drift and diffusion coefficients as functions of explanatory variables. Bengtsson et al. [8] model the drift term as a function of the distance between individuals in their attempt to characterize dispersal patterns of soil-living invertebrates. In the bark beetle example presented below Preisler and Akers [9] model the drift term as a function of the heading angle between the direction along the path of female beetles and a point source emitting male pheromones. In the second example [10] bivariate SDE's are used to study trajectories of radio-collared elk and deer as they forage in a 9000 ha fenced experimental forest in Oregon.

## 2 Some Estimation Techniques

In statistical practice one is usually interested in estimating the parameters of a process (e.g.,  $\boldsymbol{\theta}$  in equation (2)) given observation at discrete time points  $\mathbf{y} = \{y_{t_1}, y_{t_2}, \dots, y_{t_i}\}$ . Some of the methods that may be used to estimate the parameters in a SDE are described below.

### 2.1 Stochastic difference equations

In cases where the SDE in [2] may be approximated by the difference equation

$$Y(t_i) - Y(t_{i-1}) = \mu(\mathbf{y}; \boldsymbol{\theta})(t_i - t_{i-1}) + \sigma(\mathbf{y}; \boldsymbol{\theta})\varepsilon_i \quad (3)$$

where  $(\varepsilon_i, i=1, \dots, n)$  are independent random noise, such as a standard Gaussian variates, the parameters in  $\boldsymbol{\theta}$  may then be estimated using nonlinear regression techniques. The second example described below uses difference equations and nonparametric regression techniques to estimate effects of a heterogeneous environment on the movements of deer and female elk.

### 2.2 Autoregressive models

When realizations of a random process  $\{Y(t), t > 0\}$  are recorded at equal intervals ( $t=1, 2, 3, \dots$ ) and the relationship between consecutive values of the process is given by

$$Y_t = \rho Y_{t-1} + \eta_t \quad (t = 1, 2, 3, \dots) \quad \eta_t \sim \text{i.i.d} \quad (4)$$

then the relationship is called an autoregressive model of order 1. Equation (4) is a special case of the difference equation in (3) with  $\mu(\mathbf{y}; \boldsymbol{\theta}) = (\rho - 1) y_{t-1}$  and  $\sigma(\mathbf{y}; \boldsymbol{\theta}) = 1$ .

Time series estimation techniques may be used to estimate the parameter in the model (see [11]). Example 1 below describes the use of an autoregressive model to study chemotaxis (orientation in relation to gradients of chemicals) by walking bark beetles.

### 2.3 Maximum likelihood estimates for a diffusion process

Given the SDE in (2) with  $\{B(t), t \geq 0\}$  a Brownian process and  $\boldsymbol{\theta}$  the parameter of interest the log likelihood ratio function of an observed path is given by

$$L(\boldsymbol{\theta}) = \int_0^T \frac{\mu(y(s); \boldsymbol{\theta})}{\sigma^2(y(s))} dy(s) - \frac{1}{2} \int_0^T \frac{\mu^2(y(s); \boldsymbol{\theta})}{\sigma^2(y(s))} ds \quad (6)$$

[12]. The maximum likelihood estimate (MLE) of  $\boldsymbol{\theta}$  may be calculated by setting the derivative of the log likelihood ratio with respect to  $\boldsymbol{\theta}$  to zero and solving for  $\boldsymbol{\theta}$ . For example, to obtain the MLE for  $\alpha$  in the  $O-U$  process with  $\mu(y(t); \boldsymbol{\theta}) = ay(t)$  and  $\sigma(y(t)) = \sigma$ , we solve the equation

$$\frac{\partial}{\partial a} L(a) = \frac{1}{\sigma^2} \int_0^T y(s) dy(s) - \frac{\hat{a}}{\sigma^2} \int_0^T y^2(s) ds = 0 \quad (7)$$

to obtain

$$\hat{a} = \frac{y(T) - y(0)}{\int_0^T y^2(s) ds} . \quad (8)$$

An example of use of the maximum likelihood technique in wildlife biology is given in [13] where the authors estimate speed and other parameters describing the migration paths of elephant seals.

### 3 Two Examples from Ecology

#### 3.1 Bark beetle response to pheromone

Biologists are interested in statistical models to study the response of bark beetles to compounds involved in their chemical communication (i.e., pheromone) system. Pheromone systems are of concern to entomologists because they appear to be promising as nontoxic alternatives to insecticides for insect control. Insect pheromones control the orientation of one individual with respect to another. Chemicals emitted by the male guide the flight of the female to him for the purpose of mating. A useful measure for studying characteristics of an animal track as they orient and move towards a point source is the ‘heading’ angle between the direction toward the source and the direction along the animal’s path.

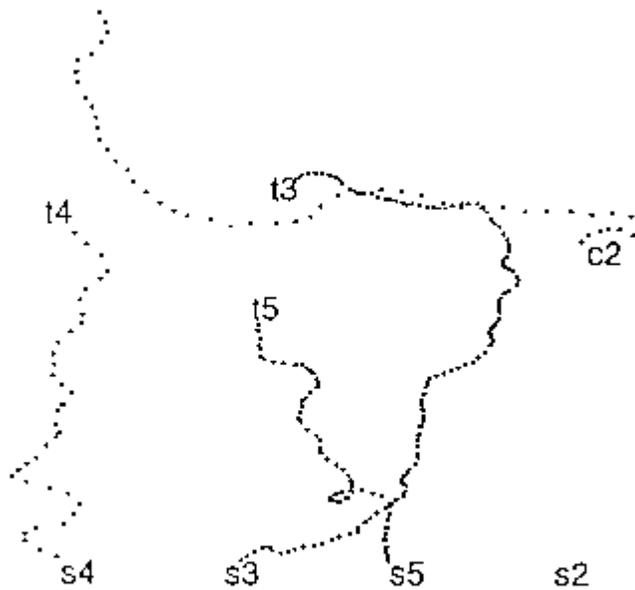
In the study described in [14] and [9] female *Ips paraconfusus* bark beetles were introduced into a small circular arena (36-cm diameter) with a pheromone source at one end. The progress of beetles was tracked by marking their positions at one-second intervals. Figure 1 shows examples of individual tracks from one control (no pheromone emitted from source) and three treatment groups.

The statistical model that well described the observed heading angle,  $\theta_t$ , of a beetle between times  $t-1$  and  $t$ , given the history of the beetle’s movements up to time  $t-1$ , was a second order autoregressive-type

$$Y_t = \beta_1 \gamma_{t-1} + \beta_2 (Y_{t-1} - \gamma_{t-2}) + \varepsilon \pmod{2\pi} \quad \text{with } \varepsilon \sim VM(0, \kappa_t) \quad (9)$$

where  $Y_t$  is a random angular variate ranging between  $-\pi$  and  $\pi$ ;  $VM$  is the von Mises distribution [15];  $\kappa_t = e^{\alpha_0 + \alpha_1 \cos(Y_{t-1})}$ ;  $\gamma_{t-1}$  is the heading angle of a beetle traveling in a

straight line between time  $t-2$  and  $t$ ;  $\{\beta_1, \beta_2, \alpha_0, \alpha_1\}$  a set of unknown parameters.



**Fig. 1.** Tracks of 4 female bark beetles. Location c2 is the starting point of a beetle in the control group (no pheromone emitted at the source located at s2). The locations t3, t4, t5 are the starting points of 3 beetles in the treatment groups with pheromone sources at s3, s4, and s5 respectively. Points on the tracks indicate locations of beetles at on second intervals.

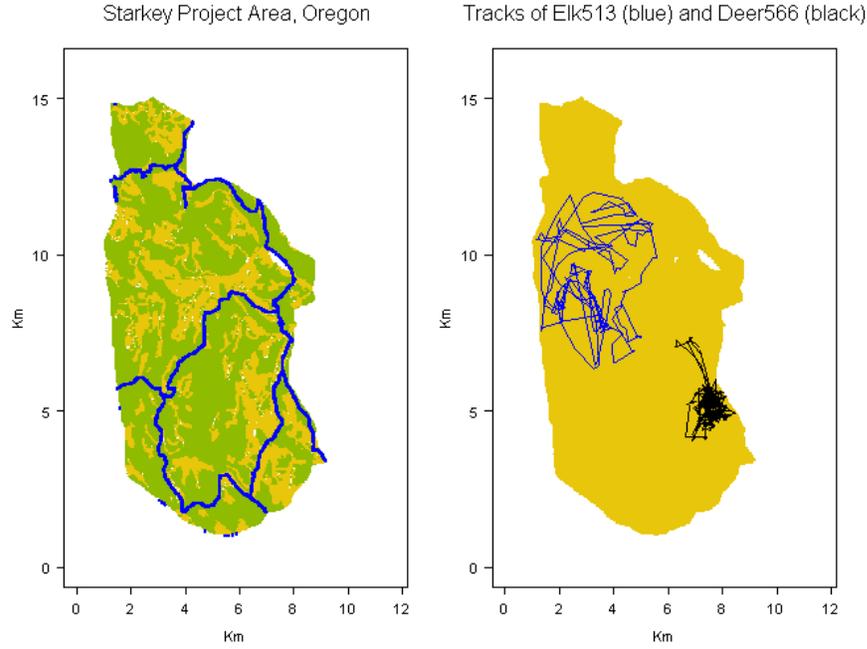
When the concentration parameter  $\kappa = 0$  the model in (9) corresponds to a random walk with no mean direction. If  $\kappa \rightarrow \infty$ ,  $0 < \beta_1 < 1$ , and  $\beta_2 = 0$  the beetle will approach the source S along an arc.

One interesting result of the analysis was the fact that the concentration parameter,  $\kappa$ , was a function of the heading angle at time  $t-1$  rather than the distance to the source. It also appeared that when the absolute value of the heading angle was large (i.e., when a beetle is heading away from a pheromone source) the fluctuation around the mean direction was larger than when a beetle is heading toward the source.

### 3.1 Movement patterns of free-ranging elk and deer

Studies on the movement of free-ranging animals can provide valuable information to wildlife managers, conservation biologists, and population and landscape ecologists.

In the study described in [16], a telemetry system was used to monitor the locations of radio-collared female elk and deer foraging in a 9000 ha fenced region of the Starkey experimental forest in Oregon. Figure 2a gives the fenced region of the experimental forest and the locations of cover areas, meadows, and roads. Figure 2b shows the locations along the trajectory of an elk and a deer for a period of 30 days in the spring. Observations on the locations of each animal were recorded once every 0.1-2.5 hours.



**Fig. 2. (a)** Fenced region of Starkey experimental forest and the location of forest (light regions), meadows (darker regions) and open roads (blue curves). **(b)** The locations are given along the trajectory of one elk (upper left) and one deer (lower right) for a 30-day period in the spring. The forest regions above are possible areas of elk hiding cover, canopy > 40%.

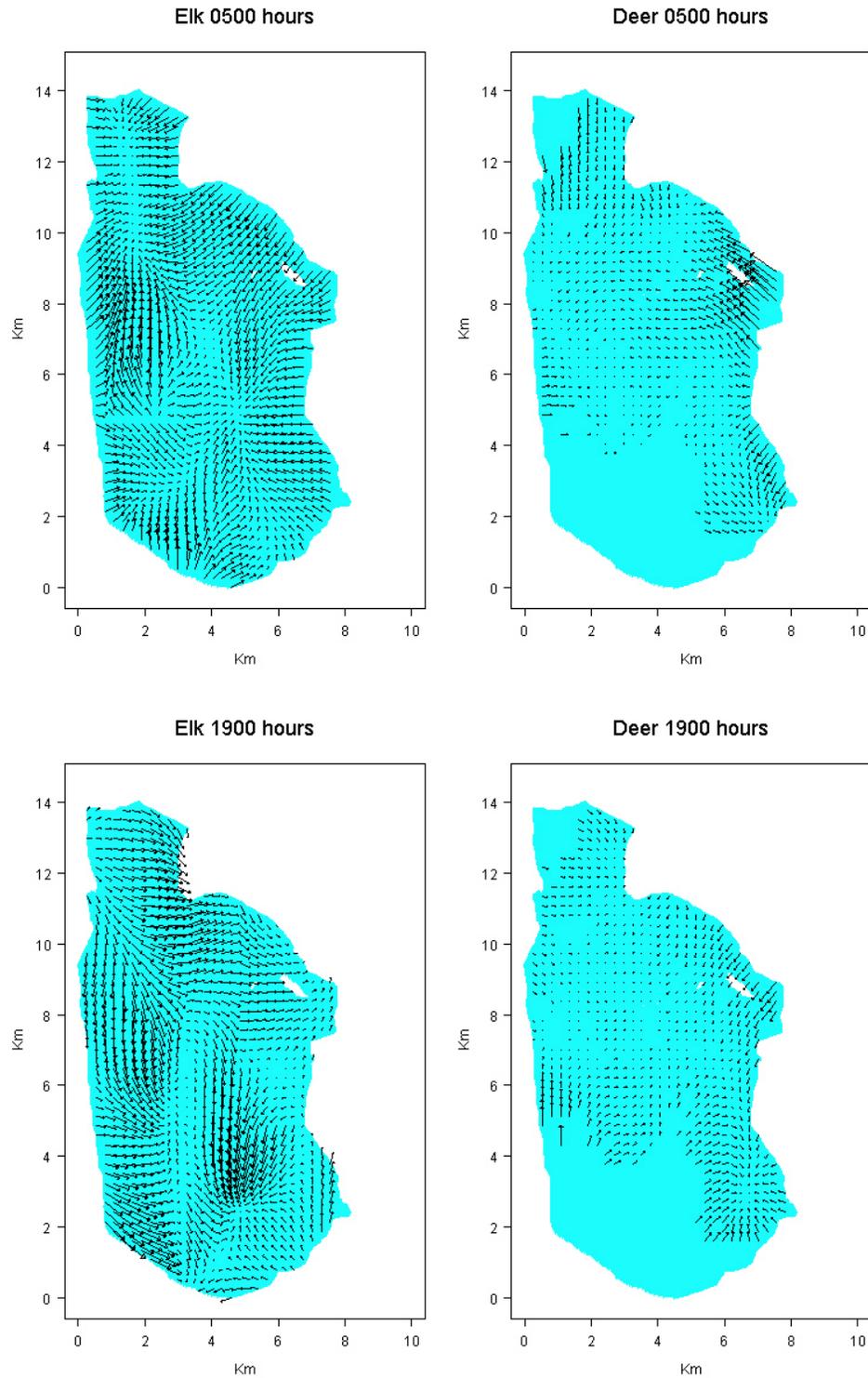
Ninety-six elk tracks and 48 deer tracks observed for 30 days in the springs of three years (1993, 1995, 1996) were analyzed in this study. The analysis was done using the statistical model developed in [10]. In the analysis it was assumed that an animal moves in accordance with the bivariate stochastic differential equation

$$d\mathbf{r}(t) = \boldsymbol{\mu}(\mathbf{r}(t), t)dt + \Sigma(\mathbf{r}(t), t)d\mathbf{B}(t) \quad (10)$$

Here,  $\mathbf{r}(t) = (x(t), y(t))'$  is the location of an animal at time  $t$ ;  $\mathbf{B}(t)$  is a bivariate Brownian process;  $\boldsymbol{\mu}(\mathbf{r}, t)$  is the velocity in some direction (drift).

The drift term  $\boldsymbol{\mu}(\mathbf{r}, t)$  was first modeled as a function of location  $\mathbf{r}(t)$  and the time of day at time  $t$ , henceforth denoted by  $\langle t \rangle$  ( $0 \leq \langle t \rangle < 24$ ). The estimation was done using the difference equations described in (3) and nonparametric locally weighted regression function (*loess*, [17]) within a generalized additive model [18]. The response variables were the speeds (Km/hr) in the x and y directions, namely,  $[x(t_i) - x(t_{i-1})] / (t_i - t_{i-1})$  and  $[y(t_i) - y(t_{i-1})] / (t_i - t_{i-1})$ , and the variance was proportional to  $(t_i - t_{i-1})^{-1}$ . Figure 3 is a plot of the resulting estimated vector field,  $\hat{\boldsymbol{\mu}}$ . It describes the expected movements of elk and deer at 0500 and 1900 hours.

The idea of potential functions [10] may be used to motivate a form for the drift term as a function of other explanatory variables such as distance to road or distance between deer and elk. It is assumed that a potential function  $H(\mathbf{r}(t), t)$  exists that controls the movement of animals at location  $\mathbf{r}(t)$  at time  $t$  such that  $\boldsymbol{\mu}(\mathbf{r}, t) = -\nabla H(\mathbf{r}(t), t)$  and

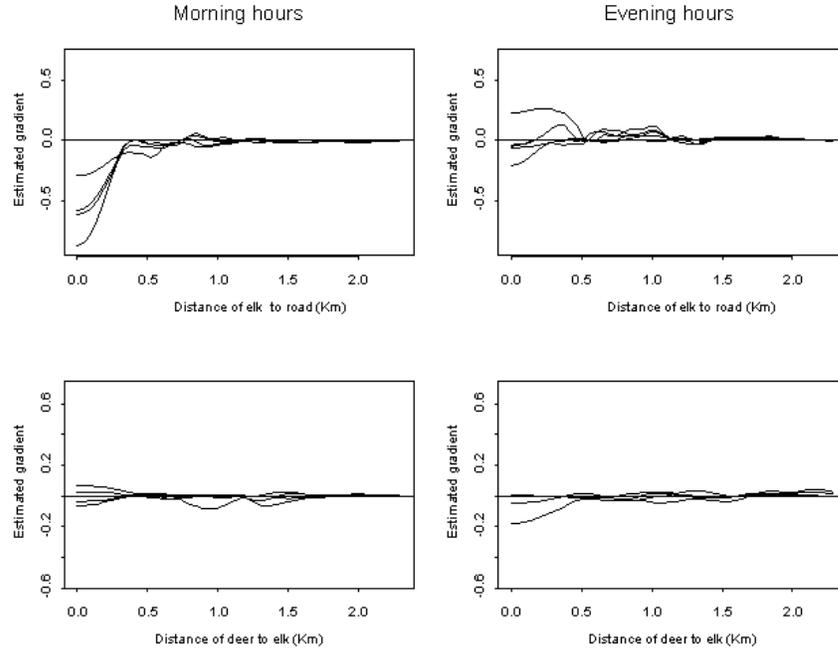


**Fig. 3.** Plots of the estimated vector fields describing the expected movements of elk and deer in the experimental forest. Ninety-six elk tracks and 48 deer tracks were used to estimate the vector fields describing movement during 30 days in the spring.

$\nabla = (\partial/\partial x, \partial/\partial y)$  is the gradient operator. For example,  $H(\mathbf{r}) = |\mathbf{r} - \mathbf{a}|^2$  corresponds to motion with a point of attraction at  $\mathbf{a}$ . This model leads to the  $O-U$  process described above. If animals are expected to be attracted or repelled from roads at certain times of the day then  $H$  might be assumed to depend on say distance to nearest road,  $d_r$ , in a natural way. Specifically,  $H(\langle t \rangle, \mathbf{r}) = g(\langle t \rangle, d_r^2)$  for some function  $g$  with  $d_r^2 = (x - x_o)^2 + (y - y_o)^2$ , and  $(x_o, y_o) = (x_o(x, y), y_o(x, y))$  the nearest point on a road to  $(x, y)$ . Under this model, the drift term will be given by

$$\boldsymbol{\mu}(\mathbf{r}, t) = -\nabla H(\langle t \rangle, d_r^2) = - \begin{bmatrix} g_2(\langle t \rangle, d_r^2) \frac{\partial d_r^2}{\partial x} \\ g_2(\langle t \rangle, d_r^2) \frac{\partial d_r^2}{\partial y} \end{bmatrix} \quad (11)$$

where  $g_2$  is the partial derivative with respect to the second argument. An important point to note about equation (11) is that even when the potential function  $H$  is assumed to depend on location only through the variable distance to road, this is not the case for the drift term. Specifically, locations relative to nearest road point (i.e.,  $x - x_o$  and  $y - y_o$ ) are seen to play an important role through the derivatives  $\partial d_r^2 / \partial x$  and  $\partial d_r^2 / \partial y$ . In this study



**Fig. 4.** Estimated values of  $g_2$  for various times of day plotted against distances of elk from nearest open road (top panels) and distances of deer from nearest elk (bottom panels). The curves for the morning were for 0500, 0600, 1000, and 1100 hours and the evening were for 1800, 1900, 20,00 and 2100 hours. Negative values are interpreted as repulsion and positive values as attraction.

estimates for  $g_2$  were calculated by using as the response variable the observed local speed (Km/hr) divided by the respective derivatives,  $\partial d_r^2 / \partial x$  and  $\partial d_r^2 / \partial y$ , also calculated using differences. Locally weighted regression routines were again employed to obtain estimated functions of time of day and distance to road as values for  $g_2$ . The top two panels of figure 4 are plots of the estimated values of the  $g_2$  function for the elk data

for various hours of the day. Both time of day and distance to road were significant. The estimated values for distances close to road (<0.5 Km.) were negative in the morning hours. This might be reflecting motions by elk away from roads (or avoidance of roads) during the day when traffic is the highest. No avoidance of roads was apparent in the evening and nighttime hours (estimates were positive or zero for the evening hours). The bottom two panels of figure 4 give similar plots for a potential function describing the movements of deer as a function of time of day and distance to nearest elk. Although there appeared to be some evidence of deer avoiding elk at the landscape level (see arrows in figure 3), the data showed no significant effects of distance to nearest elk on the movements of deer. This latter might be due to the fact that elapsed times between two consecutive observations on the same animal were > 30 minutes in 98% of the cases. Reactions of individual deer to elk sightings are probably occurring at much smaller time scales.

## Conclusions

Analyses of animal movements demand the use of complex models and computationally intense techniques. Stochastic differential equations are one useful tool for describing movement with physically interpretable parameters. SDE's have been used to analyze data from such areas as quantum physics, economics, control engineering, and epidemiology. The use of SDE's to model animal movements, however, has been limited to a few papers on the use of the Ornstein-Uhlenbeck process (a special case of and SDE) to study and estimate the home range of free-ranging animals.

Other methods crucial to the analysis of animal movements are powerful graphical procedures that are flexible and interactive for displaying movements, landscape features, and model outputs, among other things. Additionally, computationally intensive statistical techniques are required. Such techniques include iterative methods for estimating nonlinear functions (including nonparametric functions), jackknife procedures for estimating standard errors, and cross-validation methods for assessing the fit of models.

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