

Modeling animal movements using stochastic differential equations[‡]

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SUMMARY

We describe the use of bivariate stochastic differential equations (SDE) for modeling movements of 216 radio-collared female Rocky Mountain elk at the Starkey Experimental Forest and Range in northeastern Oregon. Spatially and temporally explicit vector fields were estimated using approximating difference equations and nonparametric regression techniques. Estimated vector fields of movement were mapped onto the project area at selected times of the day to examine spatial patterns of movement in relation to topography. Using the concept of a potential function, we were able to study the influence of roads and grassland foraging areas on elk movements. Doing so we identified broad spatial patterns of elk movements and showed the time dependent effects of habitat features within the habitat mosaic at Starkey. Our analyses quantify the cycles of movements in spring and summer in terms of attraction or repulsion to specific habitat features, and illustrate the magnitude, timing and direction of these movements. An extensive list of references is included. Published in 2004 by John Wiley & Sons, Ltd.

KEY WORDS: *cervus elaphus*; diffusion process; potential functions; random vector field; splines; telemetry data

1. INTRODUCTION

Studies on the movement and foraging behavior of wild ungulates (e.g. elk and deer) provide essential information for wildlife managers. Movements of ungulates have been studied to examine a range of ecological questions related to dispersal, home ranges, foraging strategies, habitat grain, natural disturbance and herbivory (Turner *et al.*, 1993; Gross *et al.*, 1995; Focardi *et al.*, 1996; Lima and Zollner, 1996; Carter and Finn, 1999; Moorcroft *et al.*, 1999; Zollner and Lima, 1999; Bergman *et al.*, 2000; Wu *et al.*, 2000). The broad goal of animal movement studies is to better understand the complex interactions between animal behavior, environmental and human caused disturbances, and animal distributions in space and time. Understanding factors influencing animal movement and dispersal is critical for preserving and rebuilding threatened or endangered populations.

There is a wealth of statistical methodology dealing with monitoring and analysis of wildlife populations; see *Environmetrics* (Special issue, 2002). Modeling animal movements is one of the more challenging aspects of wildlife studies. Existing models for analyzing movements include models

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based on stochastic differential equations (SDEs), and in particular, random walks and diffusion processes. The theory and some of the practice of vector-valued diffusion processes are found in Karlin and Taylor (1981) and Bhattacharya and Waymire (1990). The Ornstein–Uhlenbeck process employed by Dunn and Gipson (1977) and Dunn and Brisbin (1985) is an example of such a process. Brillinger (1997) and Brillinger and Stewart (1998) use SDEs to model elephant-seal migrations. Anderson-Sprecher and Ledolter (1991) and Anderson-Sprecher (1994) use a state-space model to allow for measurement error in locations of individual mule deer (*Odocoileus hemionus*). Newman (1998) also uses a state-space model to describe movement and mortality of Pacific coho salmon (*Oncorhynchus kisutch*). Kendall (1974) developed a variety of results for movement of birds heading to a target. Kareiva and Shigesada (1983), Wagner (1986) and references therein, are concerned with studies of flies moving under the influence of the environment and other flies. Preisler and Akers (1995) are concerned with movement of bark beetles under the influence of pheromones. In an environmental hazard analysis Moore (1985) and Zwiers (1985) model iceberg movements as vector ARIMA processes. Some authors, e.g. Niwa (1996), seek to describe animal movements by variants of Newton's equations of motion. Minta (1992) is concerned with interactions among moving animals. In particular, Minta studies the overlap in home range by observing the presence or absence of the animal in a shared area. White *et al.* (1996) use partial differential equations to model the density of wolf packs and wolf–deer interaction. Mladenoff *et al.* (1999) use a logistical model to describe the effects of road density on probabilities of gray wolves' presence in an area. Clark *et al.* (1993) developed a model based on the Mahalanobis distance statistic to study the effects of spatially explicit habitat characteristics to identify areas of high use by female black bears. Blackwell (1997) uses a generalization of the Ornstein–Uhlenbeck process to accommodate different behavioural or physiological states of the animal. Bengtsson *et al.* (2002) use SDEs where the diffusion terms for different individuals are correlated in an attempt to study the dispersal patterns of soil Collembola in the presence of organisms from the same species. Further references on analyses of animal movements using radio-telemetry are found in Bowyer (2001) and Turchin (1998).

In this article we describe the application of SDEs and the concept of a potential function, first discussed in Brillinger *et al.* (2001a), to model animal movement and estimate spatially and temporally explicit movement parameters. Previous works on this topic include Brillinger *et al.* (2001a,b, 2002) and Preisler *et al.* (1999, 2001). We demonstrate the use of the methods by analyzing a large set of radio-telemetry data collected from female Rocky Mountain elk (*Cervus elaphus nelsoni*) on the Starkey Experimental Forest and Range (hereafter, Starkey) in northeastern Oregon (Rowland *et al.*, 1997). We include habitat covariates (road refugia and grasslands outside refugia used for foraging) that are known to influence elk distributions at Starkey, and examine the changes in movement patterns between two seasons (spring and summer).

2. STUDY AREA

Starkey Experimental Forest and Range is located 35 km southwest of La Grande, Oregon, in the Blue Mountains of northeastern Oregon, USA. This 10 125-ha project area is enclosed by a 2.4-m high fence that prevents immigration or emigration of resident elk and other large mammals (Rowland *et al.*, 1997). Starkey is divided into multiple subunits, the largest being a 7762-ha main study area where data for the current study were obtained (Figure 1a). Starkey is situated at about 1500 m elevation and supports a mosaic of coniferous forests, wet meadows and grasslands that typify summer range habitat for elk in the Blue Mountains. A network of drainages creates a complex and varied topography

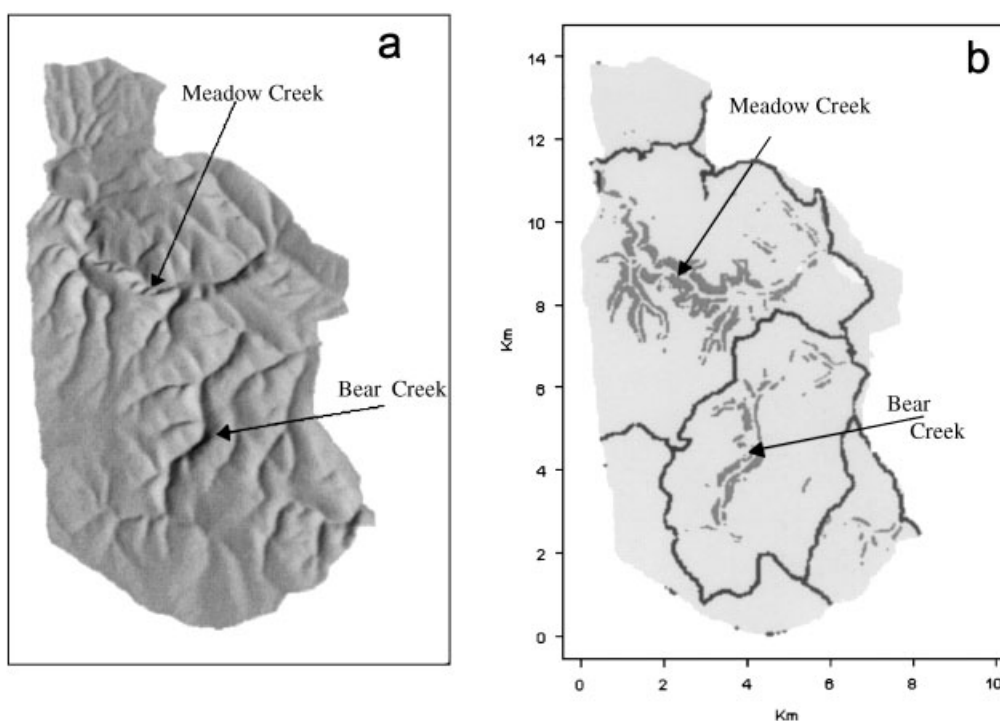


Figure 1. (a) Topography of the main study area at the Starkey Experimental Forest and Range, northeastern Oregon. (b) Locations of roads open to vehicular traffic (black lines) and regions where slope exceeds 40% (gray)

(Figure 1a). Details of the study area and facilities are available elsewhere (Rowland *et al.*, 1997; Johnson *et al.*, 2000).

3. METHODS

3.1. Telemetry data

Elk locations were obtained by an automated telemetry system that uses retransmitted LORAN-C radio navigation signals (Rowland *et al.*, 1997). A subset of the Starkey telemetry data was selected for two intervals, April 15–May 15 (spring) and July 15 to August 15 (summer) for the years 1993, 1995 and 1996. Johnson *et al.* (2000) and Ager *et al.* (in press) have shown large differences in the patterns of habitat use by elk over these two periods.

We used recorded locations from 216 individual elk. The mean elapsed time between locations for each animal averaged 53 min. Locations were assigned habitat information by matching each observation to the closest 30-m $\times$ 30-m pixel. Locations had a mean error of 53 m (Findholt *et al.*, 1996). Calculations of movement were deleted if elapsed time was <5 min or >150 min between successive observations of animals. The Main Study Area at Starkey is 3–4 times larger than typical summer home ranges of elk in the Blue Mountains. This provides elk with large-scale habitat choices commensurate with free-ranging herds. The approximately 30–40 elk per season/year in our study that

were tracked simultaneously were single female elk selected at random out of a total population of 311–386 adult cow elk in Starkey.

3.2. Movement model

Following the work in Brillinger *et al.* (2001b), we used stochastic differential equations to describe the incremental step movement of an animal at time t and location $\mathbf{r}(t) = \{X(t), Y(t)\}'$. Specifically, we used the equations:

$$\begin{bmatrix} dX(t) \\ dY(t) \end{bmatrix} = \begin{bmatrix} \mu_x\{\mathbf{r}(t), t\} \\ \mu_y\{\mathbf{r}(t), t\} \end{bmatrix} dt + \mathbf{D}\{\mathbf{r}(t), t\} \begin{bmatrix} d\Psi_x(t) \\ d\Psi_y(t) \end{bmatrix} \quad (1)$$

Here, $dX(t)$ and $dY(t)$ are the incremental step sizes in the x and y directions; vector $\boldsymbol{\mu} = (\mu_x, \mu_y)'$ is the drift parameter; $\mathbf{D}$, the diffusion matrix, describes the correlation between the steps in the x and y directions and over time; Ψ_x, Ψ_y are random processes with expected values equal 0. In the case that Ψ_x, Ψ_y are independent Brownian processes and $\boldsymbol{\mu}$ and $\mathbf{D}$ are continuous in t , the resulting process is a diffusion process that is Markovian with continuous sample paths. The parameters $\boldsymbol{\mu}$ and $\mathbf{D}$ and the random processes control the direction and speed of the motion. The vector $\boldsymbol{\mu}$ represents the instantaneous velocity of an animal at time t and position $\mathbf{r}$. The random process $\boldsymbol{\Psi} = \{\Psi_x, \Psi_y\}$ introduces variability into the deterministic motion $d\mathbf{r}(t) = d\boldsymbol{\mu}(t)dt$.

Some special cases of (1) are:

1. $\boldsymbol{\mu} = \mathbf{0}$; $\mathbf{D} = \sigma^2\mathbf{I}$, with $\mathbf{I}$ the 2×2 identity matrix and Ψ_x, Ψ_y independent Brownian processes. This corresponds to a continuous *random walk* where animals travel at random with no drift in any particular direction.
2. $\boldsymbol{\mu} = \mathbf{A}$; $\mathbf{D} = \sigma^2\mathbf{I}$; and Ψ_x, Ψ_y are independent Brownian processes. This corresponds to a *biased random walk* where animals drift in the direction of vector $\mathbf{A}$.
3. $\boldsymbol{\mu} = \mathbf{A}[\mathbf{r}(t) - \mathbf{a}]$; $\mathbf{D} = \sigma^2\mathbf{I}$; and Ψ_x, Ψ_y are independent Brownian processes. This corresponds to the mean-reverting *Ornstein–Uhlenbeck* (O-U) process where animals are drifting, i.e. attracted to the central point $\mathbf{a}$.
4. $\boldsymbol{\mu} = \mathbf{0}$; $\mathbf{D} = \sigma^2\mathbf{I}$; and Ψ_x, Ψ_y are processes with positively correlated increments. This corresponds to a *correlated random walk* (CRW) where animals move with persistence in a given direction, i.e. consecutive moves are correlated. In the O-U process, an animal's consecutive moves are also persisting in a given direction; however, the persistence is because of attraction toward a common point such as a food patch or the center of the home range.

Other more general models may be obtained, for example, by specifying non-Markovian random processes Ψ_x, Ψ_y , or by involving time lags in the modeling of the drift term, $\boldsymbol{\mu}$.

3.3. Estimating the drift term

We calculated estimates of the drift terms as smooth functions of time and space by approximating the SDEs in (1) by the difference equations:

$$\begin{aligned} (X_{i+1} - X_i)/(t_{i+1} - t_i) &= \mu_x(X_i, Y_i, t_i) + \sigma_x \varepsilon_{1i} / \sqrt{t_{i+1} - t_i} \\ (Y_{i+1} - Y_i)/(t_{i+1} - t_i) &= \mu_y(X_i, Y_i, t_i) + \sigma_y \varepsilon_{2i} / \sqrt{t_{i+1} - t_i} \end{aligned} \quad (2)$$

where (X_i, Y_i) , $i = 1, 2, \dots$, is the location of an animal at time t_i , with $t_1 < t_2 < t_3 \dots$; ε_{1i} , ε_{2i} are white noise; and σ_x , σ_y are unknown constants. The model in (2) assumes a diagonal diffusion matrix, **D**. This assumption was partly justified by the negligible correlations between the observed unit step sizes for the spring and summer data (0.021 and -0.068 , respectively). Moreover, a study done using 1994 Starkey elk data (Brillinger *et al.*, 2002) seemed to indicate that when the estimated drift term, $\hat{\boldsymbol{\mu}}$, which representing a common component affecting all elk simultaneously, is removed from the series, the residual series in the x - and y -directions were not correlated in a linear time-invariant manner.

The slopes (km/h) on the left-hand side of (2) from all elk within a season (spring or summer) were analyzed simultaneously. Plots of the estimated vectors $\{\hat{\mu}_x(X, Y, t_o), \hat{\mu}_y(X, Y, t_o)\}$ for a given time t_o at each location (X, Y) display the expected vector fields describing movement patterns of elk at Starkey. Estimates of the drift surfaces were calculated by the nonparametric regression routine LOESS (Cleveland *et al.*, 1992) within the generalized additive model GAM (Hastie, 1992). Preliminary analysis had suggested that elk movements were affected by both location and the time of day. Consequently, the drift terms were modeled as smooth functions of location and hour of the day, henceforth denoted by $\langle t \rangle$ with values between 0 and 24 h. All time values were Pacific Standard Time.

3.4. Including habitat variables

In the previous section we indicated how one could estimate the drift term as a smooth function of location and time of day. In this section we describe how to include local habitat variables in the model and estimate the significance of different explanatory variables on movement. We used the concept of potential functions (Brillinger *et al.*, 2001a) to motivate a form for the drift term as a function of distances to selected habitat covariates. Potential functions have often been used to describe motion in Newtonian dynamics (Goldstein, 1950). Assume there exists an external force field acting on an animal and, hence, controlling the movement. The function, $H(\mathbf{r}(t), t)$, that describes this force field at location $\mathbf{r}$ and time t is referred to as a potential function. When a potential function exists, the relationship between the function and the drift term is given by

$$\boldsymbol{\mu}(\mathbf{r}, t) = -\nabla H(\mathbf{r}, t) \quad (3)$$

where $\nabla = \{\partial/\partial x, \partial/\partial y\}'$ is the gradient operator. For example, $H(\mathbf{r}) = |\mathbf{r} - \mathbf{a}|^2$ corresponds to motion with a point of attraction at $\mathbf{a}$, i.e. the O-U process.

If animals are attracted or repelled from grassland foraging areas or other habitat features at certain times of the day then $H(\mathbf{r})$ might be assumed to depend on distances to the habitat feature. For example, if the shortest distance from an animal at $\mathbf{r}$ to a foraging area is $d(\mathbf{r})$, then $H(\mathbf{r}, t) = h(d(\mathbf{r}), t)$ for some function $h(\cdot)$.

One advantage of the potential function approach is that independent potential functions from a variety of sources may be added to give a description of a combined force field acting on an animal as follows:

$$H(\mathbf{r}, t) = h_1(d_1(\mathbf{r}), t) + h_2(d_2(\mathbf{r}), t) + \dots + h_m(d_m(\mathbf{r}), t) \quad (4)$$

where d_k , $k = 1, \dots, m$, are distances to m points of attraction or repulsion, such as distances to roads, to food, to streams, etc. Using (3), the corresponding drift term will be:

$$\begin{aligned}\mu_x(\mathbf{r}, t) &= 2\{(X - U_1)h'_1 + (X - U_2)h'_2 + \cdots + (X - U_m)h'_m\} \\ \mu_y(\mathbf{r}, t) &= 2\{(Y - V_1)h'_1 + (Y - V_2)h'_2 + \cdots + (Y - V_m)h'_m\}\end{aligned}\quad (5)$$

where (U_k, V_k) is the location of the center of the k th region of attraction or repulsion; h'_k is the partial derivative of h_k with respect to $d_k^2 = (X - U_k)^2 + (Y - V_k)^2$. It is interesting to note that although the potential function (4) was assumed to depend on location only through the distance variables (i.e. a scalar variable with no direction), the drift term (5) is still a vector variable depending on distance and location.

Based on previous work at Starkey and elsewhere, we chose four specific variables to test as explanatory variables in our movement model. The four variables were road refugia, distance to grassland foraging areas outside those refugia, distance to canyons (slopes >40%) and distance to nearest stream. We captured the avoidance to roads by identifying areas where animal's distance to roads is greater than 1.0 km (defined here as road refugia). We excluded road segments at Starkey that were closed to vehicular traffic in the identification of road refugia. Foraging areas were defined as grasslands where tree canopy was less than 5% and outside of road refugia.

We used thin plate spline functions (Hastie *et al.*, 2001) as the functional forms for the individual potential functions $h_k(d_k, <t>)$ for $k = 1, 2, 3, 4$. Thin plate spline functions are a generalization of one-dimensional smoothing splines to two or more dimensions (see Appendix). We found these functions useful here because they allow the fitting of complicated smooth curves and surfaces but at the same time they are parametrically simple enough so that their derivatives are tractable (see Appendix). Derivatives were needed because we wished to fit the drift terms in (5) which involve the derivatives of the individual potential functions. The required modules for fitting thin plate splines within S-PLUS were downloaded from the web (Geophysical Statistical Project, 2002).

We used likelihood ratio test statistics to evaluate the significance of each of the terms in (5), and consequently the significance of the four chosen distance covariates on the potential function describing elk movement.

3.5. Comparison of deterministic and random components in movements of elk

Effects of spatial location and time of day on the variance, i.e. the diagonal terms in the matrix **D**, were studied by fitting the model

$$\log(|\hat{e}_{ik}|) = \alpha_k + f(X, Y, <t>) + \tau\epsilon_{ik} \quad k = 1, 2 \quad (6)$$

where $\hat{e}$ are the residuals in the x -direction when $k = 1$ and in the y -direction when $k = 2$; $f(X, Y, <t>)$ is a smooth function of location and time in day; α and τ are unknown parameters and the ϵ s are independent standardized errors. The function f was estimated using the generalized additive model function `gam()` in S-PLUS (2001).

The drift and variance terms of SDEs offer different insights on movement. The drift measures strategic moves over longer time periods, such as movements that lead to habitat shifts during early morning and evenings. In the temporal scale of our data (~ 1 h) these moves are the daily shifts between grassland foraging areas and areas distant from roads. The variance term measures the shorter temporal moves of animals, possibly resulting from sudden reactions to anthropogenic disturbance, topography, and other habitat features that we did not consider. The latter fine-grain movements are what motivate the random component in the model. The probability of an animal moving in a given

direction with a given step size is a function of the ratio of these long- and short-term movements (ratio of drift to standard deviation).

In our model, the error term represents the random portion of movement in addition to measurement error due to inaccuracies in the telemetry system. The ratios $\hat{\mu}_x/\hat{\sigma}_x$ and $\hat{\mu}_y/\hat{\sigma}_y$ were computed to estimate the fraction of total variability in movement that is not due to random walk or to measurement error.

The ratio of drift to diffusion is also useful for building simulation models of animal movements. When the random error processes, Ψ_x , Ψ_y , in (1) are Brownian, i.e. movements are approximated with a diffusion model with drift, animal tracks may be simulated using the following equations. Consider an animal at location (x, y) at time t . In the next small time interval Δt the animal moves to location $(x \pm \sigma_x \sqrt{\Delta t}, y \pm \sigma_y \sqrt{\Delta t})$ with probabilities

$$\frac{1}{2} \left(1 \pm \frac{\mu_x}{\sigma_x} \sqrt{\Delta t} \right) \quad \text{and} \quad \frac{1}{2} \left(1 \pm \frac{\mu_y}{\sigma_y} \sqrt{\Delta t} \right)$$

for moves in the x - and y - directions, respectively (Prohorov and Rozanov, 1969). The approximation is reasonable when Δt is small. Simulated animal paths, using estimates of the drift and diffusion terms computed from observed paths, may be useful for estimating animal density, calculating bootstrap standard errors, and testing hypotheses about animal movements across heterogeneous landscapes. Brillinger (2003) discusses methods for simulating diffusion processes when the movements are in a restricted region, such as the fenced area of Starkey.

4. RESULTS

4.1. Movement vector fields

We observed a significant drift in the movement patterns of elk in both the spring and summer data sets. Both the spatial location and time of day had significant effects on the drift vector μ (P -value $< 10^{-8}$). The temporal dependence can be anticipated in animal movements because of the circadian (24-h period) cycles between foraging and resting areas. Estimated vector fields $\hat{\mu}$ for spring showed the strongest movement vectors during the crepuscular twilight periods (Figures 2 and 3) and revealed spatial patterns of movement between grassland foraging area and road refugia at Starkey. The estimated drift terms were largely nonsignificant for most other time periods, especially during midday and midnight. The latter suggests that at those hours observed elk movements were not significantly different from random walk.

The vector fields revealed the strong influence of terrain on the landscape patterns of movements. Starkey is divided by Meadow Creek, a 300 m deep canyon that dissects the project area from west to east, and Bear Creek, which runs north and south (Figure 1a,b). The drainages appeared to split the spatial pattern of movements (Figure 2b) into three fairly distinct regions (northeast, west and east). The effect of Meadow Creek canyon on movement vectors can be seen in Figure 4, where no vectors appear to be crossing the canyon. Bear Creek had similar effects (Figure 2b) although a road parallels the drainage and may have confounded this comparison.

We found qualitative changes in estimated vector fields between spring and summer (Figure 5). Estimated drifts were markedly diminished in the summer, although there still was some evidence of the elk's avoidance of steep terrain. Most notably absent was the zone of strong movements at

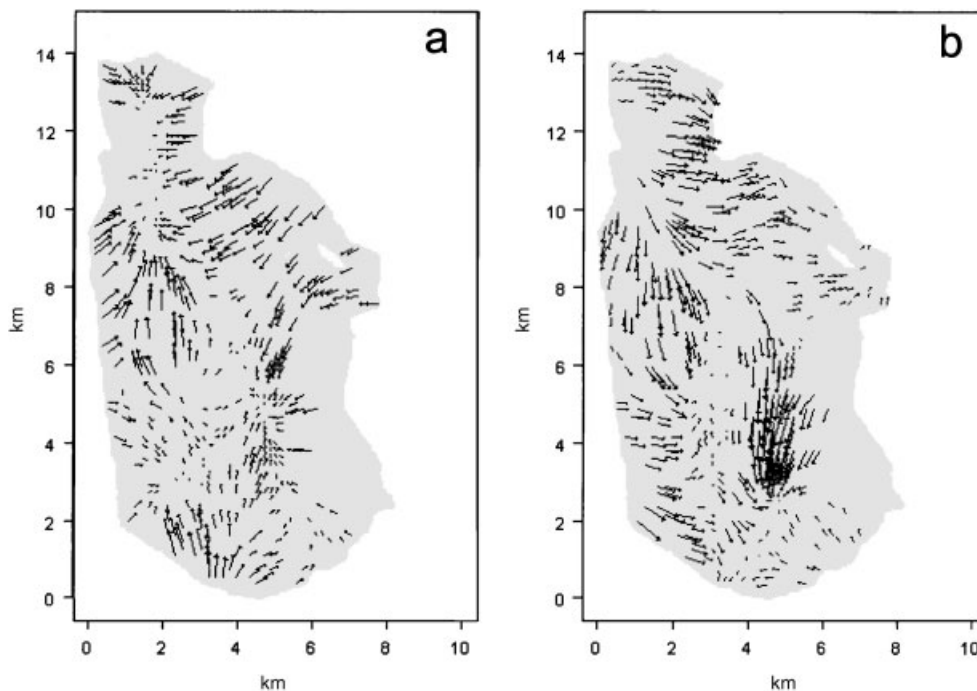


Figure 2. Gradient vector fields for 0500 (a) and 1900 (b) hours estimated from the spring telemetry data. Arrows were plotted where at least one elk was observed. The unit vector corresponds to 0.8 km/h. The plots illustrate the crepuscular transitions between areas used for resting and ruminating during the day, and foraging from dusk to dawn

1900 hours on the southeast side of Starkey. The same is true for the network of meadows on the west midsection of Starkey that attract elk earlier in the season. A combination of early forage maturation and previous foraging in the spring reduces both the biomass and protein content of the bunchgrass meadows in summer at Starkey, and elk concentrate their foraging under forest canopy where more mesic (wet) conditions sustain the growth of herbaceous species.

4.2. Potential functions for habitat features

We used the potential function approach to quantify the effects of specific habitat features on movement. We found all four distance covariates—i.e. distance to road refugia, food patches, canyons and streams—to have significant effects on the potential function for elk movement. Plots of estimated individual potential curves for two of the covariates (Figure 6) demonstrate the attraction at dawn during spring to road refugia and at dusk to food patches (imagine a ball rolling along the contour lines). The estimated potential surfaces combining the effects of all four sources of attraction/repulsion for dawn and dusk in the spring are given in Plates 1 and 2. These surfaces are compared with the stationary kernel density estimates of the elk a few hours later, i.e. around midday and midnight when elk appear to have reached hiding or foraging areas (drifts vectors are mostly zero). If during dawn and dusk elk are attracted to regions of low potential then we expect to see a high density of elk in those regions around noon and midnight when most elk appear to reach their destinations. Plates 1 and 2 seem to confirm our expectations. Most of the areas of low potential (attraction regions) appear to

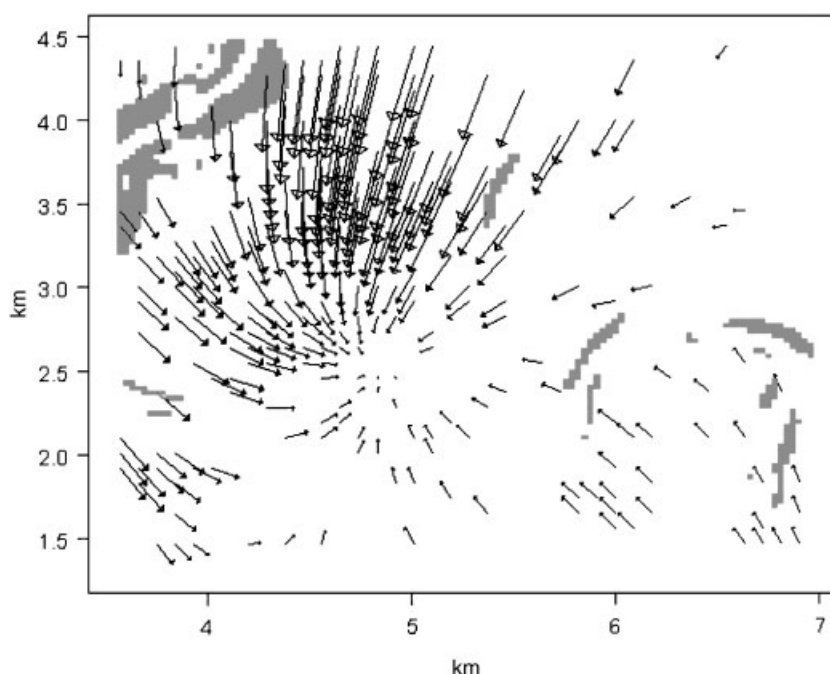


Figure 3. Estimated gradient vector field for the lower center region of Figure 3(b) (Bear Creek area) showing finer scale movement vectors of elk to intensely grazed grassland at Starkey. Gray areas indicate canyon side slopes that exceed 40%. The unit vector corresponds to 0.5 km/h

correspond with the regions of high density a few hours later. The four distance variables picked to be included in the movement model appear to describe many of the features of the stationary distribution of elk.

4.3. Comparison of deterministic and random components in movements of elk

Ratios of the deterministic to random components of movements, $\hat{\mu}/\hat{\sigma}$, smoothed over time of day, were computed for the x - and y -directions. For both spring and summer, the deterministic to random ratio showed maxima during the dawn and, except for the summer, dusk hours (Figure 7). In spring, the ratio for the y -direction approached 1.0, implying that deterministic and random movements were, on average, of equal magnitude. Interestingly, the ratios for spring were higher in the y -direction than in the x -direction. In other words, there was more random error in the data in the E-W direction. Two factors that may have contributed to the observed differences: landscape use of forage and road refugia involved a stronger N-S component than E-W; there is more measurement error in the data in the E-W direction compared to the N-S direction (Findholt *et al.*, 1996). From the vector plots (Figure 2) it can be seen that many of the dominant spring movement vectors are oriented north-south, suggesting higher drift in this direction.

Comparison between spring and summer suggested that the deterministic to random ratios for the summer were considerably smaller, and most movements were composed largely of random noise rather than drift. Perhaps additional habitat covariates could explain more of the deterministic

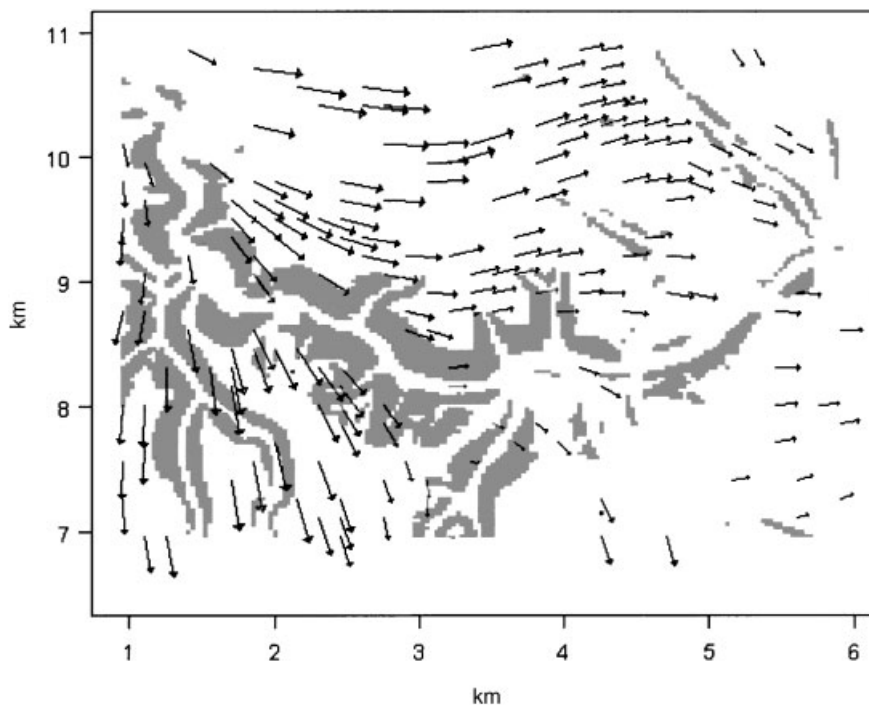


Figure 4. Estimated gradient vector field for the Meadow Creek canyon (see Figure 1) indicating how elk movements are influenced by topography. The unit vector corresponds to 0.5 km/h. Gray areas indicate canyon side slopes that exceed 40%. Elk movements avoid steep topography and either avoid the canyon or cross it using finger ridges. The canyon creates two alternative movement corridors for the dawn transition to grassland foraging areas

movements. In both seasons, the drift term is smaller in the dusk period compared to dawn, suggesting that attractions towards road refugia are perhaps stronger than movements towards foraging patches.

5. DISCUSSION AND CONCLUSIONS

Our work presents a flexible framework for modeling animal movement given discretely observed animal tracks and habitat variables. Nonparametric smoothing techniques together with SDEs enabled us to see patterns even when the signal to noise ratio was low. One of the advantages of the technique is that we were able to estimate movement parameters, such as direction and size of displacement, for each location that an animal visited. It was apparent that spatially and temporally explicit parameters are needed to describe movement. Home range models with one center of attraction will not be adequate for describing the complex movement of animals in heterogeneous terrain such as Starkey. Another advantage of the nonparametric model was that no preconceived functional form beyond smoothness was needed to model the drift. The method allows us to let the data suggest the form of relationships between explanatory variables and the drift.

The potential function framework was another useful tool. In preliminary studies we tried to model the drift term using nonparametric functions of distances and time of day (i.e. ignoring location). We were not successful in finding any meaningful patterns. It was only after we set down the potential

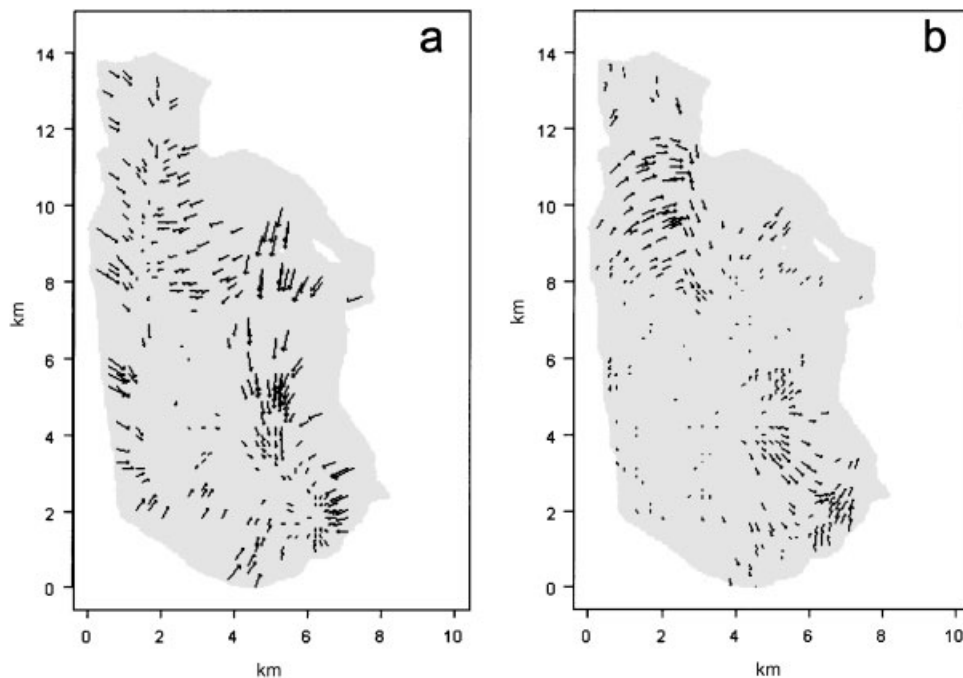


Figure 5. Estimated vector fields for summer telemetry data at 0500 (a) and 1900 (b) hours. The unit vector corresponds to 0.8 km/h. Movement vectors show markedly diminished movement velocities in summer as compared to spring, and qualitatively different movement patterns (cf. Figure 2)

function framework that we realized even when the force field (or potential function) is location independent; for example, in the O-U model the drift terms depends on the direction of approach, and hence, location. Work still remains to develop estimation techniques for more complicated, i.e. non-Markovian, random processes. However, the framework of SDEs set down here will still be applicable. For example, non-Markovian processes may be modeled by including time lags in the drift term. A random group effect may be included in the variance term to extend the estimation to grouped data. Methods for simulating estimated random process might also be of interest. In Brillinger (2003), methods for simulating diffusion processes in restricted domains are described. This is of particular interest when studying movement in restricted regions such as the fenced area of Starkey.

In previous studies, elk activity patterns have been broadly described as circadian cycles between foraging and secure resting habitat with crepuscular transitions. Our analyses quantify the cycles of movements in spring and summer in terms of attraction or repulsion to specific habitat features, and illustrate the magnitude, timing and direction of these movements. The estimation of time-specific movement vectors at Starkey adds a dynamic dimension to previous studies of habitat use in this area by linking distributions at different times of the day (via a potential function) to the continuous process of elk movements (drift terms).

The SDE framework we describe can represent multi-scale animal movements by the use of multiple, additive potential functions corresponding to the attraction or repulsion to landscape features of different spatial grain. The surface of one or more potential functions can be analyzed with spatial metrics (connectivity, fragmentation, corridors, patch size), allowing the analysis of animal movement behavior in a framework of landscape ecology (Kie *et al.*, 2002).

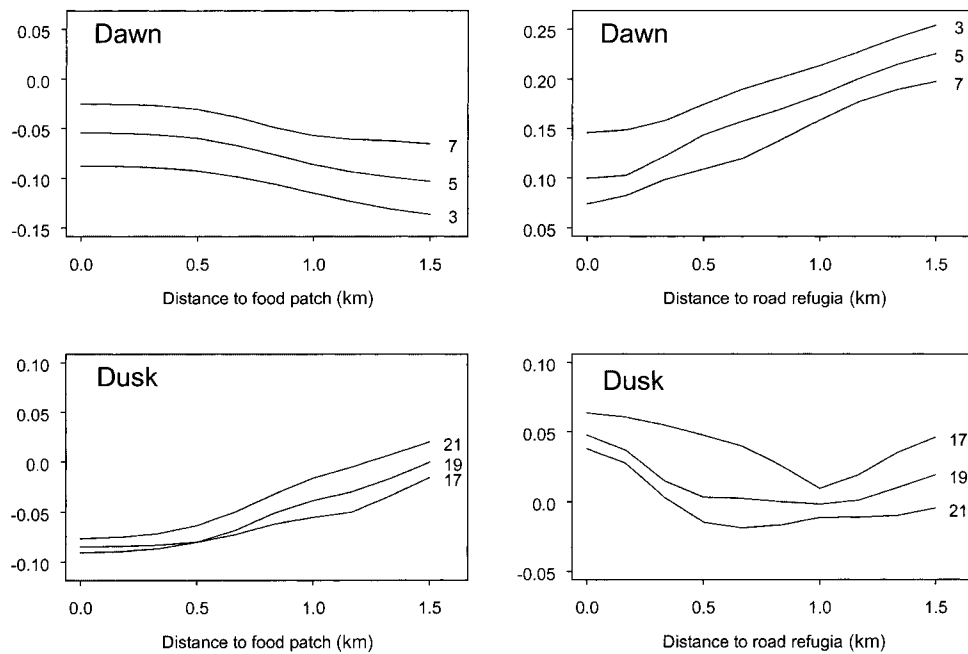


Figure 6. Estimated individual potential curves for 3 dawn hours and 3 dusk hours during spring. According to the contours, elk leave food patches and are attracted to areas of road refugia at dawn (imagine a ball rolling along the contour lines). At dusk, elk leave the road refugia and move towards food patches

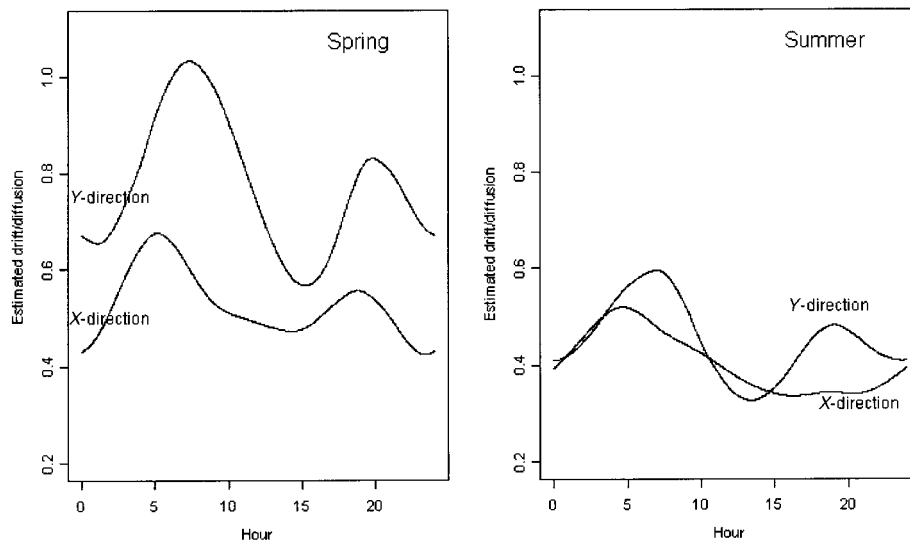


Figure 7. Smoothed estimates of the ratio of deterministic (drift) to random (standard deviation) terms. The ratios appear to be highest at dawn (0500 hours) and dusk (2000 hours)

In the current work, the potential functions represented larger-scale movements controlled mainly by cognitive navigation at hourly time steps. The hourly time interval of the telemetry data precluded the inclusion of additional terms for finer scale foraging movements. These movements were represented as a random walk in the diffusion terms of the model. Our methods could be used to model these finer scales of movements if data were collected at shorter time intervals.

An analogous application of SDEs arises with the attraction/repulsion with respect to conspecifics or individuals of other species such as predators or competitors (Kie and Bowyer, 1999; Coe *et al.*, 2001). For instance, suppose that at time t there are predators at random locations $r_j(t)$. The attraction/repulsion between predator and prey might be described by a potential function $H(r, t) = \alpha(r) \sum_{j=1}^J |r - r_j(t)|^2$ for some pertinent function $\alpha(\cdot)$. This approach might be used to model other similar phenomena such as avoidance of motorized vehicles by elk (Rowland *et al.*, 2000).

The need for empirical methods like those we describe will grow as the rapid advances in automated telemetry systems materialize, and large telemetry data sets are generated. Telemetry data with sub-meter accuracy collected at very frequent time intervals coupled with high-resolution satellite imagery will allow for parameterization of empirical models that span a broad scale of animal behaviors. These models may provide for a more holistic assessment of how foraging movement and search rules affect forage consumption rates and ultimately landscape process and pattern.

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APPENDIX: THIN PLATE SPLINE SURFACE AND DERIVATIVES

A two dimensional function, such as the potential function $H(s, t)$, may be approximated by a linear combination of *basis functions* as follows:

$$H(s, t) = \alpha + \sum_{j=1}^J \delta_j u_j \log u_j \quad (7)$$

where $u_j = (s - s_j^o)^2 + (t - t_j^o)^2$, $s_j^o, t_j^o, j = 1, \dots, J$, are J knots on a grid around s and t , respectively, and δ_j are parameters to be estimated.

For the elk data, s is taken to be the distance of an elk, at location (x, y) time t , from a point of attraction/repulsion at coordinates (X, Y) , i.e. $s = (x - X)^2 + (y - Y)^2$.

The partial derivatives of (7) with respect to x and y are:

$$\begin{aligned} \frac{\partial H(s, t)}{\partial x} &= \sum_j \delta_j \frac{\partial(u_j \log u_j)}{\partial u_j} \frac{\partial u_j}{\partial s} \frac{\partial s}{\partial x} \\ &= 4 \sum_j \delta_j (\log u_j + 1) (s - s_j^o) (x - X) \\ \frac{\partial H(s, t)}{\partial y} &= 4 \sum_j \delta_j (\log u_j + 1) (s - s_j^o) (y - Y) \end{aligned} \quad (8)$$

The equations in (8) with the basis functions $4(\log u + 1)(s - s^o)(x - X)$ and $4(\log u + 1)(s - s^o)(y - Y)$ were used in (5) to estimate the parameters δ_j . Estimates of the potential function, up to a constant, were next obtained by substituting values of $\hat{\delta}_j$ in (7) above.

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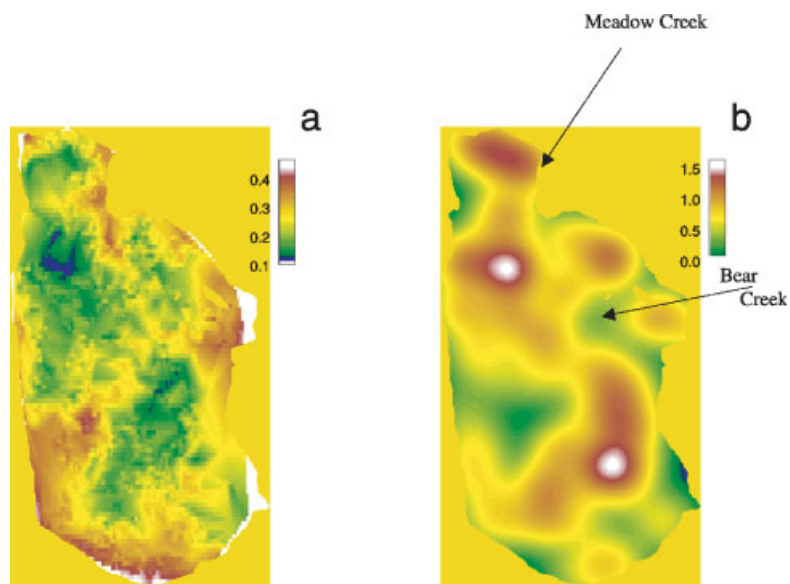


Plate 1. (a) Estimated potential surface for 0500 hours during spring. (b) Kernel density estimate (elk/km²) for observed elk locations between the hours of 1000 and 1300. Most of the areas of low potential (attraction regions) at dawn correspond with regions of high elk density around noon

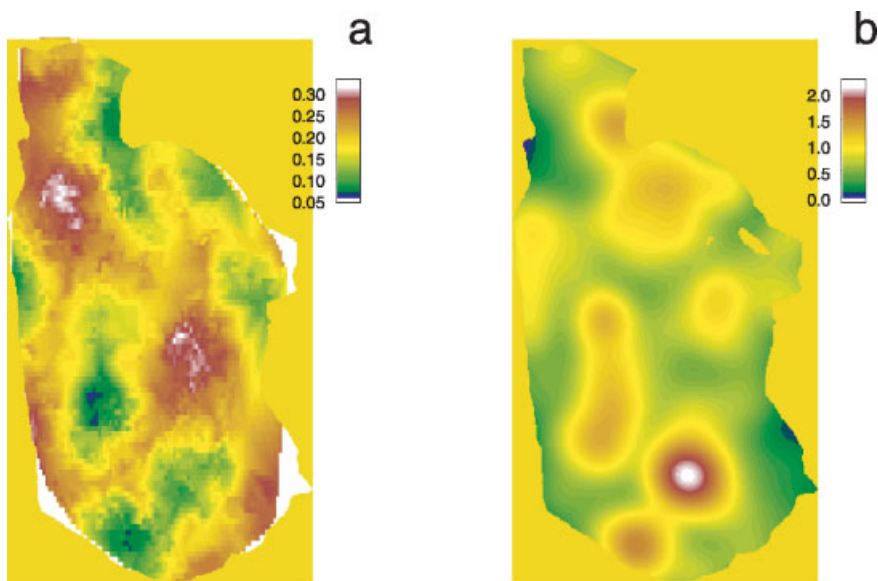


Plate 2. (a) Estimated potential surface for 1900 hours during spring. (b) Kernel density estimate (elk/km²) for observed elk locations between the hours of 2200 and 0100. Areas of low potential (attraction regions) at dusk correspond with regions of high elk density around midnight

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