THE USE OF POTENTIAL FUNCTIONS IN MODELLING ANIMAL MOVEMENT

D. R. BRILLINGER, H. K. PREISLER, A. A. AGER, J. G. KIE

Department of Statistics
University of California
Berkeley, CA, 94720-3860

Pacific Southwest Research Station
USDA Forest Service
Albany, CA 94710

Pacific Northwest Research Station
USDA Forest Service
La Grande, OR 97850

Pacific Northwest Research Station
USDA Forest Service
La Grande, OR 97850

SUMMARY

Potential functions are a physical science concept often used in modelling the motion of particles and planets. In the work of this paper potential function based models are considered for the movement of free-ranging elk in a large, fenced experimental forest. Equations of motion are set down and the parameters involved are estimated nonparametrically. The question of whether a potential function is plausible for describing the elk motion is considered. The conclusion is that it is not possible to reject this hypothesis for the data set and estimates considered.

Key Words and Phrases: animal movement, diffusion models, elk, force field, nonparametric regression, potential functions, stochastic differential equations, telemetry data.

1. INTRODUCTION

The problem of interest is the description of the movement of elk, *Cervus elaphus*, in a large free-ranging environment. Models of animal movement are becoming important tools in the study of a variety of ecological problems, especially habitat selection, animal migration and dispersal in heterogeneous landscapes. Specific questions that wildlife biologists have include: How to allocate forage amongst competing species? What is the effect of vehicular traffic? Is change taking place? What is the sequence of habitat use? The physical and biological mechanisms that regulate such movements are clearly complex.

The data available are the locations of M elk, labelled by $m = 1, ..., M$, recorded at times, $t_{mk}, k = 1, ..., K_m$. More specifically the data consist of the locations $\mathbf{r}_{mk} = (X(t_{mk}), Y(t_{mk}))$, corresponding to the UTM (Universal Transverse Mercator) coordinates of the k-th time measurement of the m-th elk. Explanatory variables describing vegetation, topography, and other habitat features (e.g., distance to road, distance to water) known to influence elk movement, are also available.

The approach developed in this work is to assume that the animals are moving in a potential field, $H(\mathbf{r}, t)$, that controls their direction and speed of motion. The potential field may have points, lines or regions of attraction or repulsion and may include barriers. The barriers may represent actual physical constructions (e.g., fences or be natural). Stochastic differential equations (SDEs) are used to include variability in the model such as attractors and repellors not in the potential H. The estimated SDEs may be used to produce estimates of other parameters, eg. speed, to predict spatial and temporal patterns of animal distribution and habitat preferences, to simulate trajectories and to study the directionality of the movement, amongst other possibilities. Later in the paper simulations of the trajectories will be used to estimate the potential function.

The paper begins with a description of both deterministic and stochastic methods for describing the paths followed by particles under the influence of a potential field. Next the experiment in which the elk data were collected is described. Section 4 provides details of the statistical methods employed in the problem. Section 5 presents the results obtained. A key examination of the assumption that a potential function exists is a comparison of second-order partial derivatives taken in the two possible orders, separately for daytime and nighttime data. The final section reviews some of the merits and limitations of employing the potential function to model animal movement.

References describing models for animal movement include: [6, 9, 10, 18, 27]. Reference [18] sets down deterministic differential equations (DDEs) for density functions describing the expected pattern of space use by coyotes being influenced by the accumulation and decay of scent marks, also described by DDEs. This is to be contrasted with the approach in [4, 20] where stochastic equations were set down describing the individual realizations or trajectories, for elephant seals migrating and female bark beetles responding to male pheromones emitted from a point source, respectively.

2. SOME MATHEMATICS OF MOVING PARTICLES

Both deterministic and stochastic approaches are available for describing the trajectories of moving particles.

2.1 *Deterministic case.*

Motion in Newtonian dynamics has often been described by a potential function, $H(\mathbf{r}, t)$, see [19]. Here $\mathbf{r} = (x, y)$ is location and t is time. The equation of motion takes the form

$$d\mathbf{r}(t) = \mathbf{v}(t)dt$$

$$d\mathbf{v}(t) = -\beta\mathbf{v}(t)dt - \beta\nabla H(\mathbf{r}(t), t)dt$$

with $\mathbf{r}(t)$ the particle's location at time t, $\mathbf{v}(t)$ the particle's velocity and $-\beta\nabla H$ the external force field acting on the particle, β being the coefficient of friction, [19]. Here $\nabla = (\partial/\partial x, \ \partial/\partial y)$ is the gradient operator. The function H is seen to control the particle's direction and velocity. For example $H(\mathbf{r}) = |\mathbf{r} - \mathbf{a}|^2$ corresponds is a point of attraction at $\mathbf{a}$ and $H(\mathbf{r}) = 1/|\mathbf{r} - \mathbf{a}|^2$ is a potential function with a point of repulsion at $\mathbf{a}$.

In the case that β is large, the equations are approximately

$$d\mathbf{r}(t) = -\nabla H(\mathbf{r}(t), t)dt \qquad (2.1)$$

and only the location, $\mathbf{r}(t)$, at time t is involved.

There exists considerable mathematical development in the time stationary case. A force field, $\mathbf{F}$, may be given and the question arises whether there exists a real-valued function H, such that $\mathbf{F} = \nabla H$. When it does the field is called *conservative*. Such a field then has the property that line integrals

$$\int_C \mathbf{F} \cdot d\mathbf{r}$$

depend only on the initial and terminal points of the curve C, see [26], and $\cdot$ refers to the fact that a line integral is involved.

In this case the function H may be obtained from its partial derivatives, $\mathbf{F} = (H_x, H_y)$, [25, 26]. Specifically for motion in an open connected region the potential function may be obtained, up to an additive constant, as

$$H(x, y) = \int_{(a,b)}^{(x,y)} \mathbf{F} \cdot d\mathbf{r} \qquad (2.2)$$

where (a, b) is a point in the region. When a potential function exists, the path of the line integral taken from the starting point (a, b) to the terminal point (x, y) will not affect the final result. The function H may also be estimated, given H_x, H_y via simulation experiments as described below.

If $\mathbf{F}$ has components H_x, H_y, then a necessary condition for the existence of a corresponding potential function is that

$$\frac{\partial}{\partial y} H_x = \frac{\partial}{\partial x} H_y \qquad (2.3)$$

[25, 26]. In the case that the region is simply connected, this condition is also sufficient.

2.2 *Stochastic case.*

A pertinent probabilistic concept for dynamic situations is a stochastic differential equation (SDE), see [3, 16]. Such equations lead to Markov processes and take the form

$$d\mathbf{r}(t) = \boldsymbol{\mu}(\mathbf{r}(t), t)\, dt + \boldsymbol{\Sigma}(\mathbf{r}, t)\, d\mathbf{B}(t) \qquad (2.4)$$

with $\boldsymbol{\mu}$ the drift parameter, $\boldsymbol{\Sigma}$ the variance or diffusion parameter and $\mathbf{B}$ bivariate Brownian motion. Here $\mathbf{r}$, $\boldsymbol{\mu}$, $\mathbf{B}$ are vectors while $\boldsymbol{\Sigma}$ is a matrix.

The parameters have the interpretations

$$E\{d\mathbf{r}(t)|\mathcal{H}_t\} \;=\; \boldsymbol{\mu}(\mathbf{r}(t), t)\,dt$$

$$var\{d\mathbf{r}(t)|\mathcal{H}_t\} \;=\; \boldsymbol{\Sigma}(\mathbf{r}(t), t)\,dt$$

with $\mathcal{H}_t$ representing the time history of the process. Since the process is Markov, these conditional parameters depend only on the previous position, as indicated.

Many properties are known concerning solutions of SDEs, for example in the present context when H does not depend on t and $\boldsymbol{\Sigma} = \sigma_0^2\mathbf{I}$, there may be an invariant density

$$\pi(\mathbf{r}) \;=\; c\; exp\{-2H(\mathbf{r})/\sigma_0^2\} \tag{2.5}$$

representing the longrun density of locations the particle visits, [3]. Thus, by modelling movements, population distributions may be estimated. At the same time given $\boldsymbol{\mu} = (-H_{\boldsymbol{x}}, -H_{\boldsymbol{y}})$ and a σ_0, realizations of the process (2.4) may be generated, from which the density $\pi(\mathbf{r})$ may be estimated from the realizations and then (2.5) inverted to obtain an estimate of H.

There may be barriers restraining the motion. Also the stimulus, here represented by $\boldsymbol{\Sigma}(\mathbf{r}, t)\,d\mathbf{B}(t)$, may have periodic properties in t.

A particular case of an SDE is provided by the mean-reverting $Ornstein-Uhlenbeck$ (O-U) process where

$$\boldsymbol{\mu}(\mathbf{r}, t) \;=\; \mathbf{A}(\mathbf{a} \;-\; \mathbf{r}(t))$$

$$\boldsymbol{\Sigma}(\mathbf{r}, t) \;=\; \boldsymbol{\Sigma}$$

and the mean is $\mathbf{a}$. The papers [9, 10] propose the O-U process as a model for animal motion and develop maximum likelihod estimates of the parameters. The O-U process becomes the *random walk* when $\mathbf{A} = \mathbf{0}$, i.e., when the drift term, $\boldsymbol{\mu}(\mathbf{r}, t)$, is $\mathbf{0}$.

If $\mathbf{A}$ is symmetric, the potential function corresponding to an O-U process is

$$H(\mathbf{r}, t) = (\mathbf{a} - \mathbf{r})^\tau \mathbf{A}(\mathbf{a} - \mathbf{r})/2$$

Its invariant distribution is multivariate normal, $N(\mathbf{a}, \boldsymbol{\Psi})$, where

$$\boldsymbol{\Psi} = \int_0^\infty e^{-\mathbf{A}u} \boldsymbol{\Sigma}\boldsymbol{\Sigma}^\tau e^{-\mathbf{A}u} du$$

see [3], p. 597. If $\boldsymbol{\Sigma} = \sigma_0^2 \mathbf{I}$, then $\boldsymbol{\Psi} = \sigma_0^2 \mathbf{A}^{-1}/2$.

The situation of a particle being affected by the force field of a potential function is conveniently visualized by picturing a ball rolling around in the interior of a perspective plot of the potential function. Some simulations are provided below.

To derive simulated paths on can proceed as follows. Consider a one-dimensional process $dx(t) = \mu(x, t)dt + \sigma(x, t)dB(t)$. Suppose that at time t the particle is at location $x(t) = x$. Now for the location at time $t + dt$ take

$$x(t + dt) = x \pm \sigma(x, t)\sqrt{dt} \;\; with\ prob \;\; \frac{1}{2} \pm \frac{\mu(x, t)}{2\sigma(x, t)}\sqrt{dt}$$

See [17, 22]. In the bivariate case one generates x and y processes.

Figure 1 presents examples of such simulations in the case of the process

$$d\mathbf{r}(t) = -\nabla H(\mathbf{r})dt + d\mathbf{B}(t)$$

and two particular potential functions. In the first example $H(\mathbf{r}, t) = \mathbf{r}^\tau \mathbf{r}$, i.e. the process is Ornstein-Uhlenbeck reverting to the origin. The trajectory is seen to meander around the origin and one can imagine a ball rolling around in the interior of the parabaloid in the left column of the Figure 1.

In the second example a mound has been added at the origin. Now the trajectory is seen to circle around the mound staying in the groove of the bottom of H.

Keeping in mind these examples one can visualize the motion of particles given particular potential functions.

2.3 *Random potential/environment.*

The discussion above provides a means of interpreting the drift term of a bivariate SDE. It is also important to have an understanding of what phenomena can lead to the variance/diffusion term.

Suppose that at time t there are other particles and that they are at random positions $\mathbf{r}_j(t)$. These particles might be attracted towards each other following the existence of a potential function

$$H(\mathbf{r},t) = \alpha(\mathbf{r})\sum_{j=1}^{J}|\mathbf{r} - \mathbf{r}_j(t)|^2$$

for some pertinent function $\alpha(.)$. Following equation (2.1)

$$d\mathbf{r}(t) = -\nabla H(\mathbf{r},t)dt$$

with $\nabla H(\mathbf{r},t)$ approximately normal for large J via some Central Limit Theorem. One has, approximately, an SDE such as (2.4) with no drift term.

The concept of other particles in the field might be used to portray the attraction among elk traveling together in a herd for example. Conversely, it could be used to portray repulsion between two different species of animals where, because of social interactions, individuals of one species are avoiding individuals of the other species.

3. THE EXPERIMENT

The main study area at Starkey Experimental Forest and Range consists of 7,762 ha in the Blue Mountains of northeastern Oregon [23]. It was enclosed with a gameproof fence in 1988 and radio-telemetry studies were initiated. Each spring a sample of the resident population of elk and mule deer (*Odocoileus hemionus*) are fitted with collars containing Loran-C receivers. A sample of the domestic cattle herd brought to Starkey Forest each summer is also fitted with collars. The collars are instructed at regular intervals to intercept Loran-C broadcsts and relay these signals to a central receiver. Locations are then computed from the Loran-C time delay. They have a mean error about 50 m [12]. The telemetry system attempts to locate some animal every 20 seconds, and thus cycles through approximately 190 collared elk, deer, and cattle in about 60-65 minutes. The study area is also managed for a variety of public uses such as recreation, hunting, forest management, cattle grazing, and other activities. An extensive database was built describing vegetation, topography, and location of roads, streams and other features relevant to the study of elk [23]. The data used in the work of this paper were collected from the analyses in 1994 and involve 53 female elk. Observations were omitted from the analysis for 30 days when hunting of elk by rifle occurred in the forest, and also when time intervals between successive locations were greater than 1.5 hours. This was done in an attempt to make the situation more uniform and reduce the difficulties of interpreting widely spaced observations. Figure 2 illustrates the successive movements for two typical elk during 1994. Two small game-proof exclosures within the study area are shown in white. Elk 43 is seen to spend much of its time below the larger fenced off area on the right. The trajectory plotted is a sequence of straight line segments and jagged. This discreteness results from the fact that location estimates are available but every 1-4 hours.

Turning to Elk 42, it is seen to spend most of the time in the northern part of the forest. The implications of the time sampling are particularly apparent in this case in the upper right corner. It is not that the elk is jumping the fence, rather the locations are at time points an hour or so apart. Elk 42 does stay within the Starkey Forest (at least as far as is known).

Figure 3 shows separately the daytime and nighttime locations visited by all 53 elk, but restricting the points plotted to those less than 1.5 hours apart and excluding the days with hunting.

The points plotted have been jittered to make their apparent density clearer. A variety of heavily used and and also sparsely used regions may be seen. When a detailed map is consulted it can be seen that some of these regions relate to the locations of roads and other habitat features. This circumstance will be addressed in later research. There is also an apparent difference between day and night distributions, which is no surprise because the animals forage at dawn and dusk and rest in the daytime.

4. THE STATISTICAL METHODS USED

Kernel methods, [14], may be employed to form an estimate of the longrun density of elk locations. Estimates take the form

$$\hat{\pi}(\mathbf{r}) \;=\; \sum_{m,k} K(\mathbf{r} \;-\; \mathbf{r}(t_{mk})) \;/\; \sum_{m,k} 1 \qquad (4.1)$$

for some kernel function $K(.)$. Such an estimate will be employed later in the paper, together with the realtion (2.5), to obtain an estimated of the (assumed to exist) potential function.

Turning to the SDE (2.4) its solution may be approximated by

$$(\mathbf{r}(t_{l+1}) - \mathbf{r}(t_l))/(t_{l+1} - t_l) \approx \boldsymbol{\mu}(\mathbf{r}(t_l), t_l) + \boldsymbol{\Sigma}(\mathbf{r}(t_l), t_l)\mathbf{Z}/\sqrt{t_{l+1} - t_l}$$

$l = 1, 2, ...$ with $t_1 < t_2 < t_3 < ...$ sampling times and with $\mathbf{Z}$ a bivariate standard normal. In terms of the individual components of $\mathbf{r}$ one can write

$$\frac{\Delta X(t)}{\Delta t} = \mu_1(X, Y) + noise$$

$$\frac{\Delta Y(t)}{\Delta t} = \mu_2(X, Y) + noise$$

further assuming time invariance. If the drift functions, μ_1, μ_2, are smooth, one has a nonparametric regression problem. The functions μ_1, μ_2 may be estimated via loess(.), [7], or by a kernel method, [14].

Acting as if H exists, from estimates of μ_1, μ_2 one has an estimate of H's gradient $(\hat{H}_x, \hat{H}_y) = -(\hat{\mu}_1, \hat{\mu}_2)$. The function H itself may then be estimated following (2.2), specifically one could employ

$$\sum_i \hat{H}_x(x_i, y_i)\triangle x_i + \sum_i \hat{H}_y(x_i, y_i)\triangle y_i$$

for some path of points (x_i, y_i), $i = 0, 1, 2, ...$ from (a, b) to (x, y) staying within the region having taken some starting point (a, b) in the region, i.e. standardized the estimate by $\hat{H}(a, b) = 0$. Depending on the character of the region complex paths may be needed. This is the case for the region of this paper.

References to inferential methods for diffusion processes include: [1, 2, 5, 8, 13, 15, 24].

5. RESULTS

The results of the model fitting and assessment are provided in Figures 4-7.

Following expression (2.5), and under assumptions leading to its existence, the potential function may be estimated up to an additive constant by

$$-log\ \hat{\pi}(\mathbf{r}) \tag{5.1}$$

with $\hat{\pi}(.)$ the density estimate, usin gthe kernel estimate. The results are given in Figure 5 separately for days and nights. The hotspots of Figures 3 go over into the depressions, i.e. coldspots, of Figure 4.

Figure 5 provides $\hat{H}$ as estimated by simulation following the method described in Section 2.2 having used loess(.) to estimate the gradient of H. In the estimate provided the starting point was taken to be the center point of the region. The value of σ_0 was 20 pixel units, to be sure the trajectory roamed around the region widely. The points of the trajectory were picked to remain within the outer boundary of Starkey by resampling an increment if it led to a point outside of the region.

In both Figures 4 and 5 the hotspots (lighter areas) are in the north of Starkey in daytime and in the south in nightime. One sees the main attractors. The extent of agreement relates in part to the question of whether a potential function actually exists, for this assumption underlies the computations leading to Figure 5. If a potential function does not exist then one needs a different method of estimating $\pi(\mathbf{r})$ because one cannot simply integrate up. The question of statistical uncertainty will be addressed below.

Expression (2.3) suggests one way to address the question of the existence of a potential function. Figure 6 takes $\hat{H}_x$, $\hat{H}_y$ and further computes $\Delta_y \hat{H}_x$ and $\Delta_x \hat{H}_y$. (Here Δ_x, Δ_y are the x and y difference operators.) There is some agreement. The daytime plots are on the same grey scale, as are the nighttime plots.

It is clear that some discussion of sampling uncertainty is needed in order to make plausible inferences. In the work the jackknife, [11], was employed to examine the hypothesis of the existence of a potential function. In its implimentation 50 of the elk tracks were used, 5 tracks were dropped each time in the evaluations of the 10 pseudo estimates.

Given estimates of the variances of the quantities graphed in Figure 6, they may be compared by taking the difference and dividing by the estimate of the standard deviation of the difference, point by point and separately for day and night. Figure 7 graphs the locations where the absolute values of t-statistics obtained exceed the 95 percent point of the Student-t distribution with 9 degrees of freedom. There are not a lot, the proportions of point exceedances are .036 and .026, for day and night respectively to be contrasted with the nominal .05 . One doesn't notice much structure in where the exeedances are located.

The conclusion of the analysis is that with the data set and estimates considered, it is not possible to reject the hypothesis that a potential function exists that may be used to describe the motion of the elk.

6. DISCUSSION AND SUMMARY

A basic advantage of working with a potential function, H, is that H is scalar-valued, as opposed to the bivariate $\boldsymbol{\mu}$ of (2.4). That is one has to model but a single real-valued function. The function can include individual effects, eg. attraction, repulsion, barriers, and this will be done in future work. The estimates computed here are nonparametric. In practice the results obtained can be expected to sometimes suggest particular explanatories to include in parametric forms.

A disadvantage of the work is that such an H may not exist. In such a case one needs an alternate method of estimating $\pi(.)$ given estimates of the parameters of the SDE. The concept of potential comes from the "much simpler" physical sciences. The motion of complex biological entities is surely many times more complicated than that of a falling ball, for example. A further difficulty arises in the drawing of conclusions. An elk's locations are available at successive time points, but they are 1-4 hours apart. The elk can be many different places between the times at which locations are estimated. This complication showed itself in Figure 2, where the track plotted would suggest that Elk 42 jumped some fences.

The assumption of a potential function led to the setting down of a stochastic differential equation for a diffusion process. Such an SDE assumption was needed both in motivating the estimates computed and in estimating the potential function itself. But diffusion processes are Markov, whereas more realistic equations would involve time lags and the process therefore not be Markov.

Some related results are presented in [21]. In current work the SDE approach is being further developed as a convenient way to include covariates in the models.

ACKNOWLEDGEMENT

This paper is dedicated to Don Fraser. But for DASF one of us (DRB) would almost certainly not be a statistician. Don's force field gently deflected DRB from the road towards actuarial science. The research we present concerns the movement of wildlife. From his cottages by Lake Temagami and Georgian Bay, Don has certainly watched lots of wildlife in motion. He has surely constructed some effective models for movement, albethey involving loons and nonanalytic.

Moe Hirsch and George Oster made some comments that helped this research along. The Referee's comments improved the discussion and presentation.

This research is supported in part by the National Science Foundation Grant DMS-9704739.

REFERENCES

[1] Banon, G. and Nguyen, H. T. (1981). Recursive estimation in diffusion model. *SIAM J. Control and Optimization* **19** 676-685.

[2] Bertrand, P. (1998). Comparison de l'erreur quadratique moyenne intégrée pour différents estimateurs du coefficient de diffusion d'un processus. *C. R. Acad. Sci. Paris* **327** 399-404.

[3] Bhattacharya, R. N. and Waymire, E. (1990). *Stochastic Processes with Applications.* Wiley, New York.

[4] Brillinger, D. R. and Stewart, B. S. (1998). Elephant seal movements: modelling migration. *Canadian J. Statistics* **26** 431-443.

[5] Burgière, P. (1993). Théorème de limite centrale pour un estimateur non paramétrique de la variance d'un processus diffusion multidimensionelle. *Annales de l'Institut Henri Poincaré, Section B, Calcul des Probabilities et Statistique* **29** 357-389.

[6] Clark, J. D., Dunn, J. E., Smith, K. G. (1993). A multivariate model of female

black bear habitat use for geographic information system. *Jour. Wild. Manage.* **57** 519-526.

[7] Cleveland, W. S., Grosse, E. and Shyu, W. M. (1992). Local regression models. Pp. 309-376 in *Statistical Models in S* (Eds. J. M. Chambers and T. J. Hastie). Pacific Grove, Wadsworth.

[8] Dohnal, G. (1987). On estimating the diffusion coefficient *Journal of Applied Probability* **24** 105-114.

[9] 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.]. Elsevier Science Publishers B.V. North-Holland. 181-205.

[10] Dunn, J. E. and Gipson, P. S. (1977). Analysis of radio telemetry data in studies of home range. *Biometrics* **33** 85-101.

[11] Efron,B. and Tibshirani, R. J. (1993). *An Introduction to the Bootstrap.* Chapman and Hall, New York.

[12] Findholdt, S. L., Johnson, B. K., Bryant, L. D. and Thomas, J. W. (1996). Corrections for position bias of a LORAN-C radio-telemetry system using DGPS. *Northwest Science* **70** 273-280.

[13] Genon-Catalot, V., Laredo, C., Picard, D. (1992). Nonparametric estimation of the diffusion coefficient by wavelets methods. *Scandinavian Journal of Statistics* **19** 317-335.

[14] Hastie, T. J. and Tibshirani, R. J. (1990). *Generalized Linear Models.* Chapman and Hall, London.

[15] Heyde, C.C. (1994). A quasi-likelihood approach to estimating parameters in diffusion-type processes. Essays in Honour of Takacs. *Journal of Applied Probability,* **31A** 283-290.

[16] Karlin, S. and Taylor, H.M. (1981). *A Second Course in Stochastic Processes.* Academic, New York.

[17] Kloeden, P. E. and Platen, E. (1995). *Numerical Solution of Stochastic Differential Equations.* Springer, New York.

[18] Moorcroft, P. R., Lewis, M. A. and Crabtree, R. L. (1999). Home range analysis using a mechanistic home range model. *Ecology* **80** 1656-1665.

[19] Nelson, E. (1967). *Dynamical Theories of Brownian Motion.* Princeton U. Press, Princeton.

[20] Preisler, H. K. and Akers, P. (1995). Autoregressive-type models for the analysis of bark beetle tracks. *Biometrics* **51** 259-267.

[21] Preisler, H. K., Brillinger, D. R., Ager, A. A. and Kie, J. G. (1999). Analysis of animal movement using telemetry and GIS data. *Proc. ASA Section on Statistics and the Environment.*

[22] Prohorov, Yu. V. and Rozanov, Yu. A. (1969). *Probability Theory.* Springer-Verlag, New York.

[23] Rowland, M. M., Bryant, L. D., Johnson, B. K., Noyes, J. H., Wisdom, M. J. and Thomas, J. W. (1997). *The Starkey Project: History, Facilities, and Data Collection Methods for Ungulate Research.* Technical Report PNW-GTR-396, Forest Service, USDA.

[24] Sorensen, M. (1997). Estimating functions for discretely observed diffusions: a review. Pp. 305-326 in *Selected Proceedings of the Symposium on Estimating Functions.* Eds. Basawa, I. V, Godambe, V. P. and Taylor, R. L. Vol. 32 Lecture Notes. Institute of Mathematical Statistics, Hayward.

[25] Spivak, M. (1965). *Calculus on Manifolds.* Benjamin, New York.

[26] Stewart, J. (1991). *Calculus, Early Transcendentals.* Brooks/Cole, Pacific Grove.

[27] Turchin, P. (1998). *Quantitative Analysis of Movement.* Sinauer, Sunderland, MA.

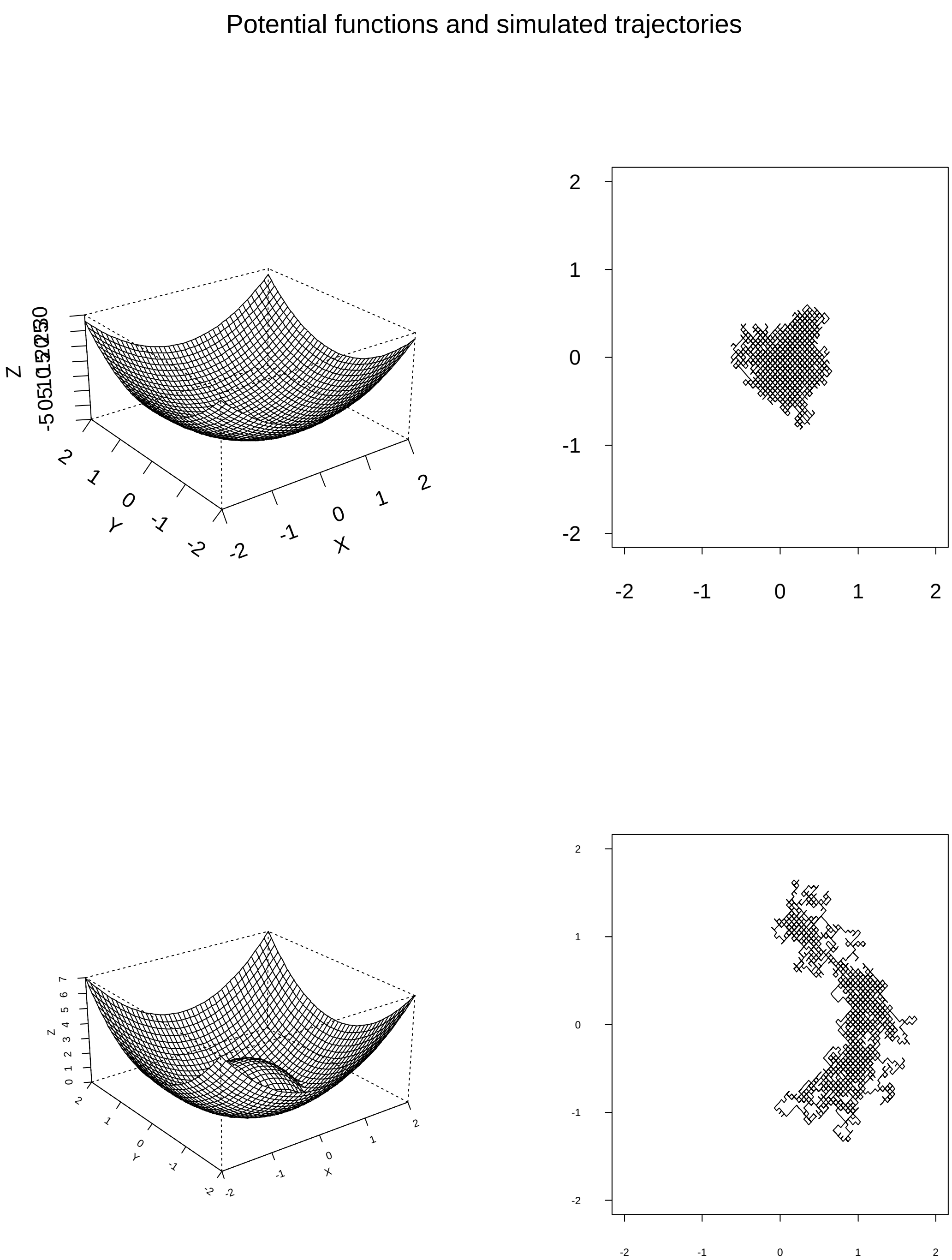

FIG. 1. *Examples of trajectories corresponding to the potential functions of the lefthand column.*

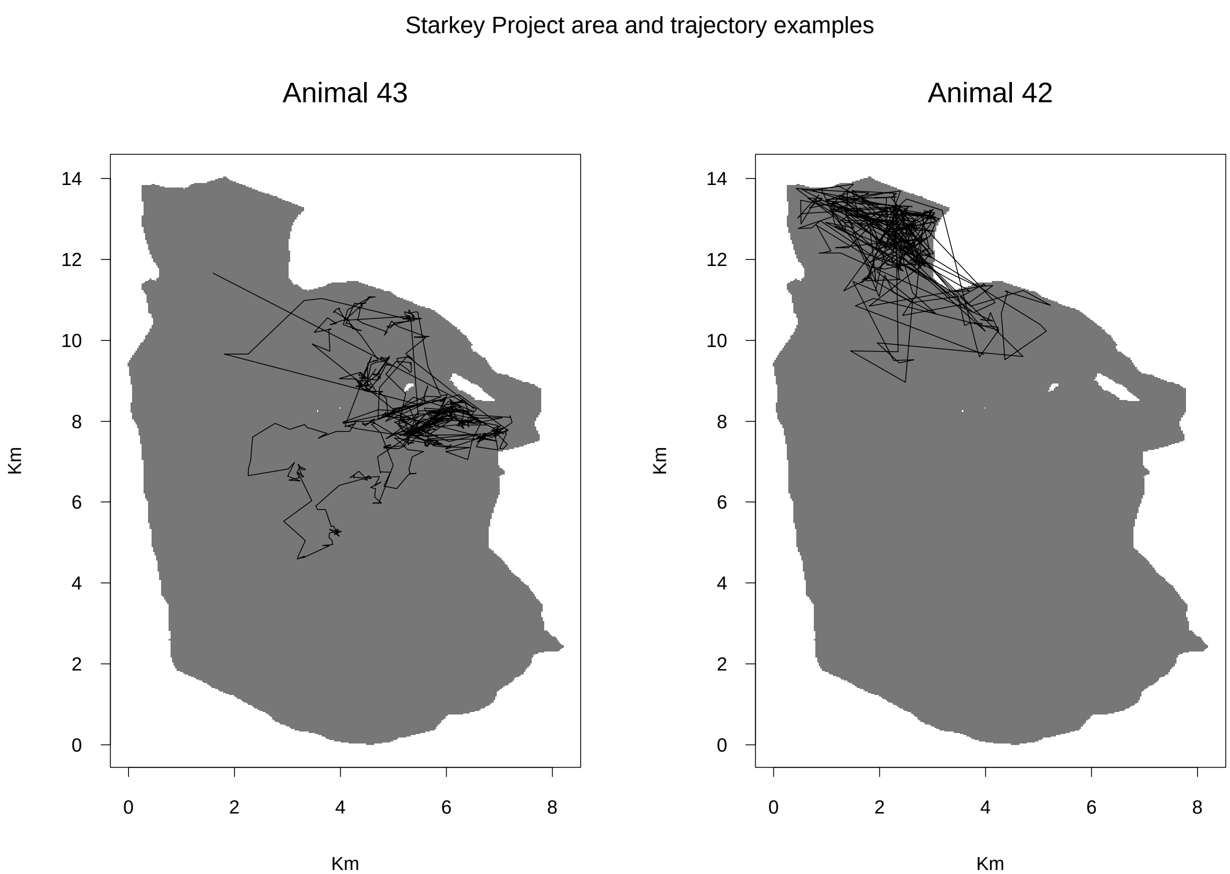

FIG. 2. *Points along the trajectories of two elk.*

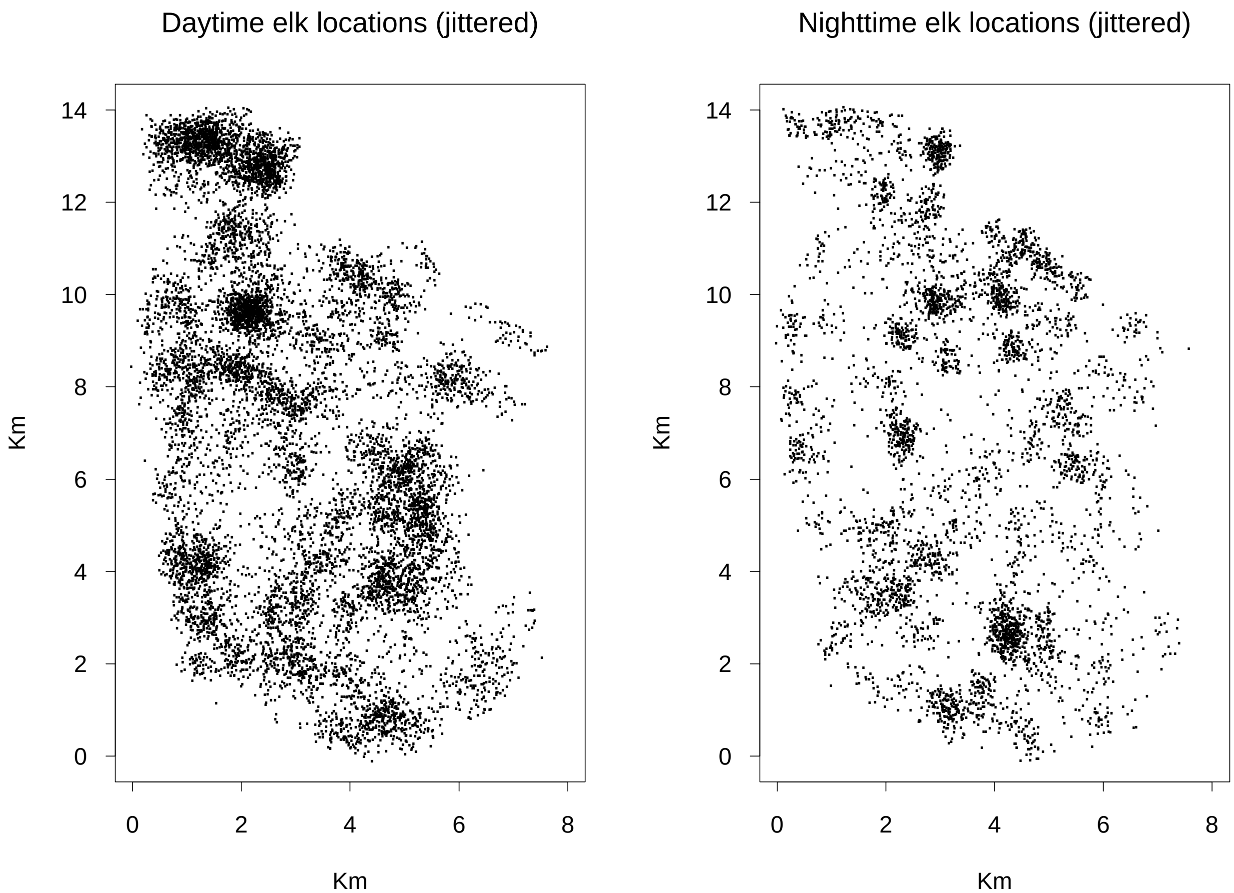

FIG. 3. *Locations visited by all 53 collared elk.*

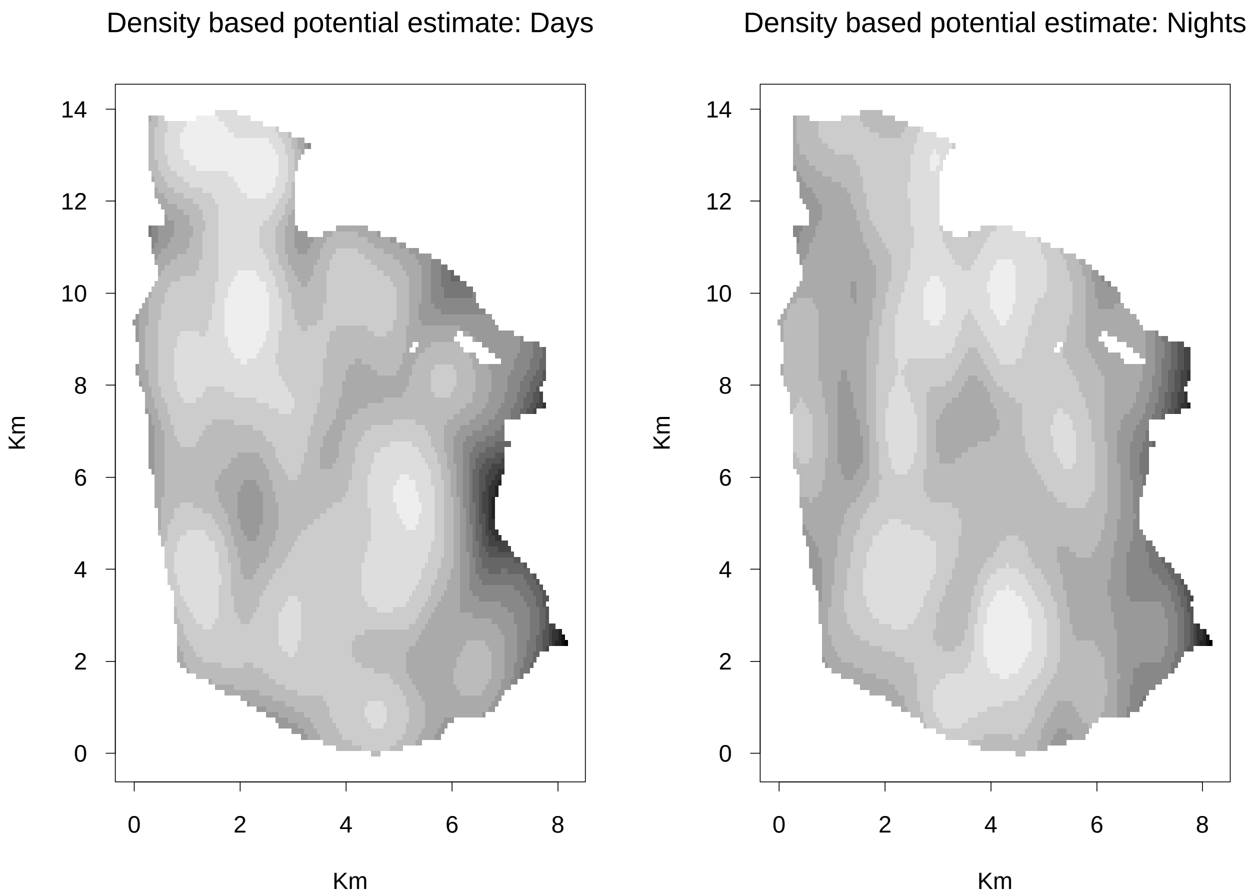

Fig. 4. *Potential function estimate based on density estimate.*

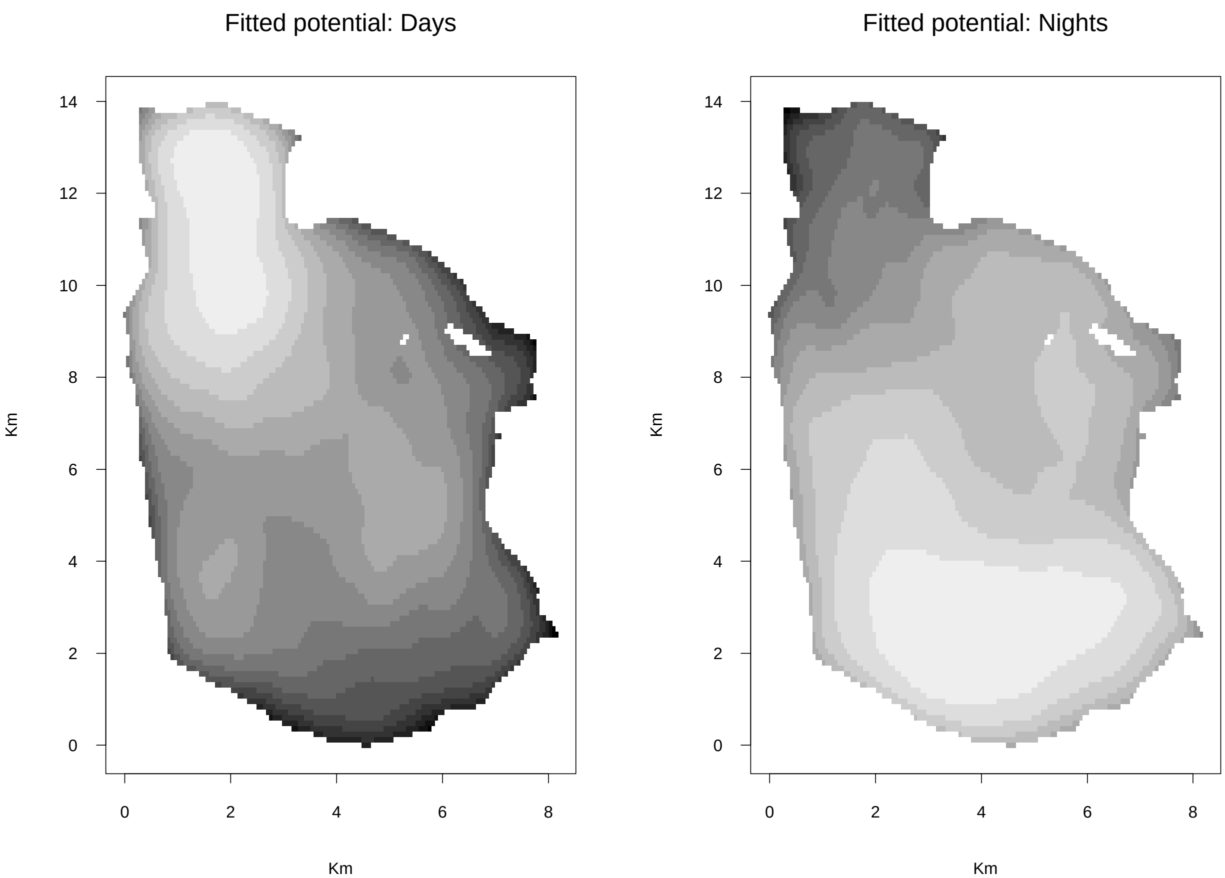

FIG. 5. *Potential function estimate obtained by simulating realizations using* $\hat{H}_x, \hat{H}_y$.

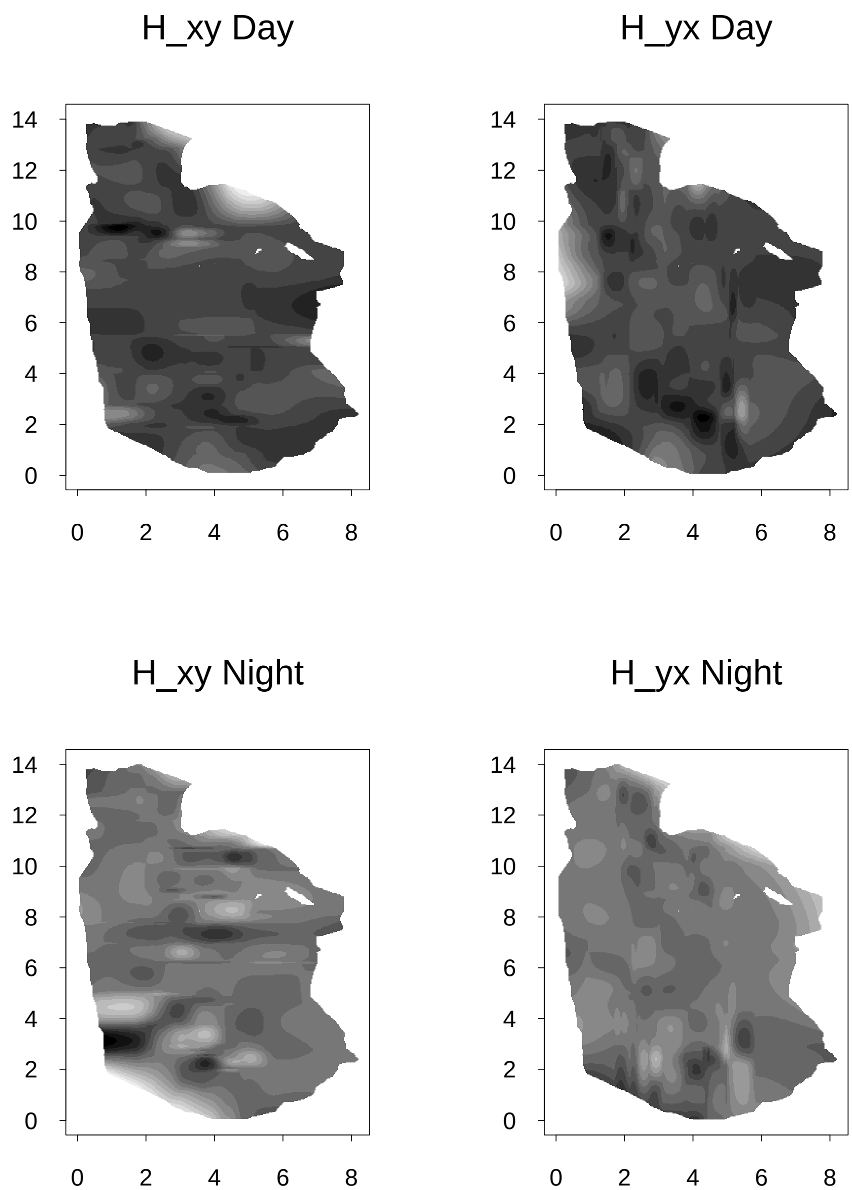

Fig. 6. *Estimates of the second-order mixed partial derivatives.*

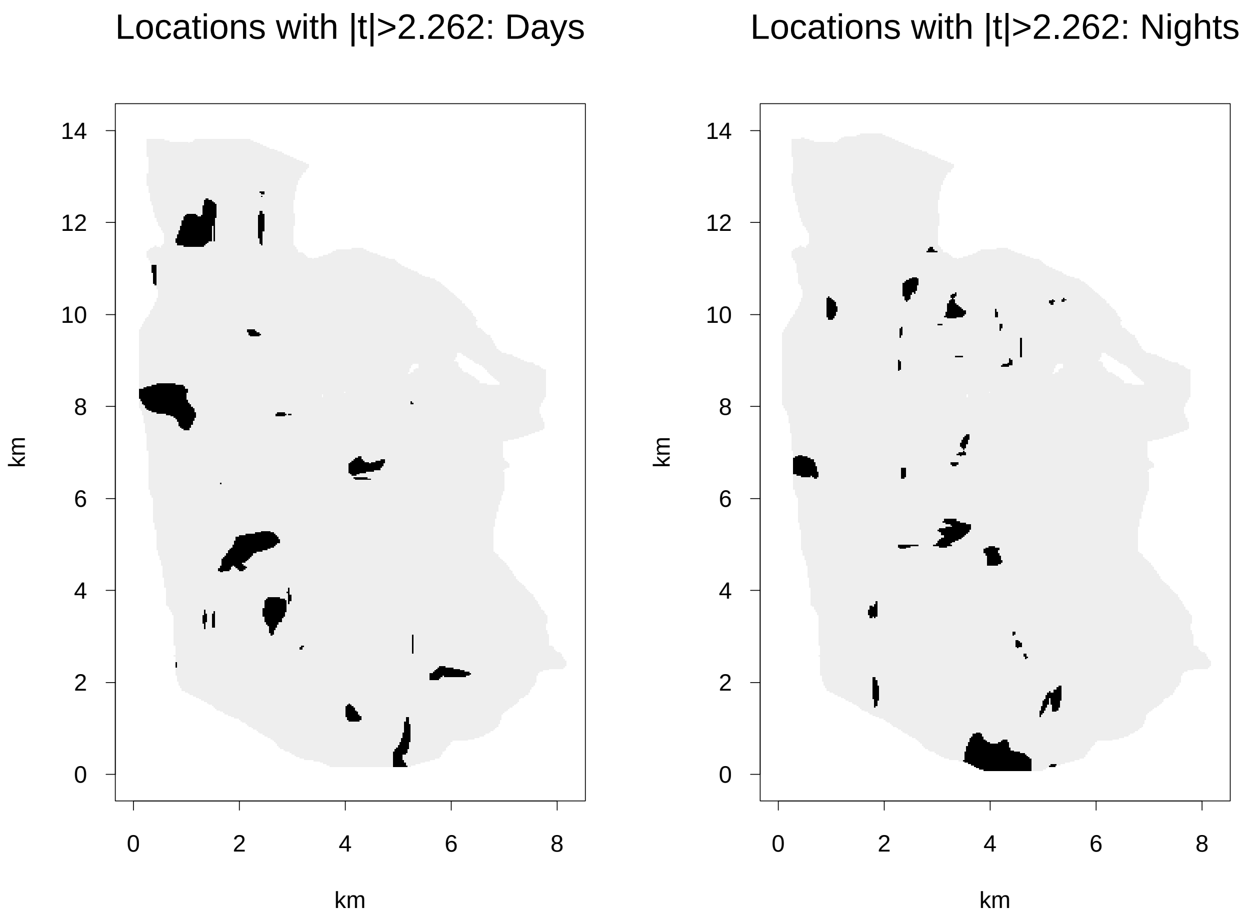

FIG. 7. *Locations where the t-statistic exceeds the 95 percent null value*