

Supplement

March 16, 2006

1 Derivation of the space-use and scent-marking equations

In this section we derive Eq.s (1)-(4) from underlying correlated random walk models of individual movement and scent-marking behavior.

Let $u(\mathbf{x}, t)$ be the two-dimensional probability density function describing the expected location of an individual at time t , where \mathbf{x} is a vector indicating the (x, y) position of the individual. We begin by writing a conservation equation describing change in $u(\mathbf{x}, t)$ as a result of movement by an individual over a single time step τ :

$$u(\mathbf{x}, t + \tau) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} u(\mathbf{x}', t) k(\mathbf{x}', \mathbf{x} - \mathbf{x}', \tau, t) dx' dy', \quad (\text{S1})$$

where $k(\mathbf{x}', \mathbf{x} - \mathbf{x}', \tau, t) d\mathbf{x}' d\mathbf{x}$ is the probability of the individual moving from a small rectangle $d\mathbf{x}'$ located at \mathbf{x}' at time t to a small rectangle $d\mathbf{x}$ located at \mathbf{x} at time $t + \tau$. Taylor expansion of the integrand of Equation (S1) with respect to \mathbf{x}' about the point \mathbf{x} , and then taking the limit as τ becomes small, yields

$$\begin{aligned} \frac{\partial u}{\partial t} + \nabla \cdot [c(\mathbf{x}, t)u] &= \frac{\partial^2 (d_{xx}(\mathbf{x}, t)u)}{\partial x^2} + \frac{\partial^2 (d_{xy}(\mathbf{x}, t)u)}{\partial x \partial y} \\ &+ \frac{\partial^2 (d_{yx}(\mathbf{x}, t)u)}{\partial y \partial x} + \frac{\partial^2 (d_{yy}(\mathbf{x}, t)u)}{\partial y^2}, \end{aligned} \quad (\text{S2})$$

where ∇ denotes $\nabla = (\partial/\partial x, \partial/\partial y)^T$. The advection term

$$\mathbf{c}(\mathbf{x}, t) = \lim_{\tau \rightarrow 0} \frac{1}{\tau} \int (\mathbf{x} - \mathbf{x}') k(\mathbf{x}, \mathbf{x} - \mathbf{x}', \tau, t) d\mathbf{x}', \quad (\text{S3})$$

is a vector and

$$\begin{aligned} d_{xx}(\mathbf{x}, t) &= \lim_{\tau \rightarrow 0} \frac{1}{2\tau} \int (x' - x)^2 k(\mathbf{x}, \mathbf{x} - \mathbf{x}', \tau, t) d\mathbf{x}', \\ d_{xy}(\mathbf{x}, t) &= \lim_{\tau \rightarrow 0} \frac{1}{2\tau} \int (x' - x)(y' - y) k(\mathbf{x}, \mathbf{x} - \mathbf{x}', \tau, t) d\mathbf{x}', \\ d_{yx}(\mathbf{x}, t) &= d_{xy}(\mathbf{x}, t), \\ d_{yy}(\mathbf{x}, t) &= \lim_{\tau \rightarrow 0} \frac{1}{2\tau} \int (y' - y)^2 k(\mathbf{x}, \mathbf{x} - \mathbf{x}', \tau, t) d\mathbf{x}' \end{aligned} \quad (\text{S4})$$

are the diffusion coefficients. Making the standard isotropic diffusion assumption, that the second and third terms in the above equation are both zero and the first and last terms are equal, Eq. (S4) reduces to the following equation for the time-dependent pattern of space use by the individual:

$$\frac{\partial u}{\partial t}(\mathbf{x}, t) = -\nabla \cdot (\mathbf{c}(\mathbf{x}, t)u) + \nabla^2 (d(\mathbf{x}, t)u), \quad (\text{S5})$$

where $\nabla^2 u = \nabla \cdot \nabla u = \partial^2 u / \partial x^2 + \partial^2 u / \partial y^2$. Further details can be found in Bharucha-Reid (1960).

We assume that the individual's redistribution kernel $k(\mathbf{x}', \mathbf{x} - \mathbf{x}', \tau, t)$ depends upon the jump length $\rho = |\mathbf{x}' - \mathbf{x}|$ and the angle to the home range center $\phi - \phi_H$, and therefore can be described by an equation following form:

$$k(\mathbf{x}', \mathbf{x} - \mathbf{x}', \tau, t) = \underbrace{\frac{1}{\rho} f_\tau(\rho) \cdot K_\tau(\phi - \phi_H)}_{\text{Prob. density for moving from location } \mathbf{x}' \text{ to } \mathbf{x}}$$

where ρ is the distance between the starting point \mathbf{x}' and the finishing point \mathbf{x} , ϕ is the angle of the jump between the starting point \mathbf{x}' and the finishing point \mathbf{x} ($\phi = \tan^{-1}((y - y')/(x - x'))$) and ϕ_H is the direction of a line from the starting point \mathbf{x}' to the home range center \mathbf{x}_H ($\phi_H = \tan^{-1}((y_H - y')/(x_H - x'))$) (Figure S1).¹ $K_\tau(\phi - \phi_H)$ is the probability density for the jump direction and $f_\tau(\rho)$ is the probability density for the jump distance. The $1/\rho$ that precedes $f_\tau(\rho)$ translates the probability of moving a given distance and direction into a probability of moving from one area to another. In the coefficients of the forward Kolmogorov equation (S5), the first argument to the redistribution kernel (starting point \mathbf{x}') is replaced by the point about which the Taylor series is made (finishing point \mathbf{x} , as in equations (S3) and (S4)). In this case,

$$k(\mathbf{x}, \mathbf{x} - \mathbf{x}', \tau, t) = \frac{1}{\rho} f_\tau(\rho) \cdot K_\tau(\phi - \phi_H), \quad (\text{S6})$$

where ϕ_H is the direction from individual's finishing point \mathbf{x} to its home range center \mathbf{x}_H ($\phi_H = \tan^{-1}((y_H - y)/(x_H - x))$) (Figure S1).

To simplify notation, we use $\theta = \phi - \phi_H$ as the argument to K_τ in equation (S6). In general, K_τ and f_τ can have additional variation with the specific location \mathbf{x} and time t .

CA Model:

In the Conspecific Avoidance (CA) model, K_τ is described by a von Mises (circular Normal) distribution

$$K_\tau(\theta, \mathbf{x}, t) = \frac{1}{2\pi I_0(\kappa_\tau)} \exp[\kappa_\tau \cos(\theta)] \quad (\text{S7})$$

where $I_0(\kappa_\tau)$ is a modified Bessel function of the first kind and of zeroth order, and κ_τ is the concentration parameter governing the degree of non-uniformity in the distribution of movement directions. The value κ_τ for individuals in the i^{th} pack depends explicitly on space and time,

¹Here the arctan function is extended from its usual range of $(-\pi/2, \pi/2)$ to $(-\pi, \pi]$, by taking into account which quadrant the point $(x - x', y - y')$ is in.

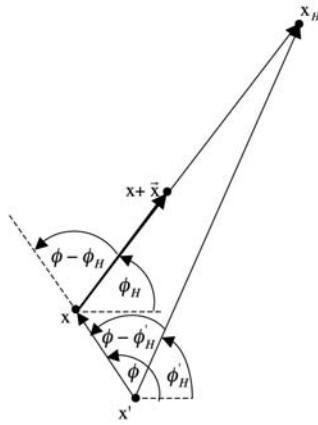


Figure S1: Angles and locations associated with movement from \mathbf{x}' at time t to \mathbf{x} at time $t + \tau$. The den is located at \mathbf{x}_H . The vector $\vec{\mathbf{x}}$ and the angles ϕ , ϕ_H and ϕ'_H are defined in the text.

varying as a function of the density of foreign scent marks encountered by an individual belonging to pack i , i.e.:

$$\kappa_\tau(\mathbf{x}, t) = b\bar{\rho}_\tau \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)}(\mathbf{x}, t), \quad (\text{S8})$$

where $p^{(j)}$ is the density of scent marks of pack j , n_{pack} is the number of packs, $\bar{\rho}_\tau$ is the mean move length over a time step of length τ , and the parameter b is the bias per unit distance moved per unit density of scent marks encountered, which governs the sensitivity of the individual's distribution of movement directions to foreign scent marks.

We now consider the case where the turning kernel K_τ is oriented with respect to the home range center so that it is an even function of $\theta = \phi - \phi_H$. We start by evaluating coefficients \mathbf{c} , d_{xx} , d_{xy} and d_{yy} from Eq.s (S3) and (S4). For notational simplicity, we drop the explicit space, time and pack dependencies of K_τ and κ_τ until Eq. (S21). The coefficients are

$$\mathbf{c} = \lim_{\tau \rightarrow 0} \frac{1}{\tau} \int_0^{2\pi} \int_0^\infty (\mathbf{x} - \mathbf{x}') f_\tau(\rho) K_\tau(\theta) d\rho d\theta, \quad (\text{S9})$$

and

$$\begin{aligned} d_{xx} &= \lim_{\tau \rightarrow 0} \frac{1}{2\tau} \int_0^{2\pi} \int_0^\infty (x' - x)^2 f_\tau(\rho) K_\tau(\theta) d\rho d\theta, \\ d_{xy} = d_{yx} &= \lim_{\tau \rightarrow 0} \frac{1}{2\tau} \int_0^{2\pi} \int_0^\infty (x' - x)(y' - y) f_\tau(\rho) K_\tau(\theta) d\rho d\theta, \\ d_{yy} &= \lim_{\tau \rightarrow 0} \frac{1}{2\tau} \int_0^{2\pi} \int_0^\infty (y' - y)^2 f_\tau(\rho) K_\tau(\theta) d\rho d\theta. \end{aligned} \quad (\text{S10})$$

Taking the vector dot product of Eq. (S9) with the vector pointing towards the den site, $\vec{\mathbf{x}} = (\mathbf{x}_H - \mathbf{x})/|\mathbf{x}_H - \mathbf{x}| = (\cos(\phi_H), \sin(\phi_H))^T$ (Figure S1), yields:

$$|\mathbf{c}| = \mathbf{c} \cdot \vec{\mathbf{x}} = \lim_{\tau \rightarrow 0} \frac{1}{\tau} \int_0^\infty \rho f(\rho) d\rho \int_0^{2\pi} \cos(\theta) K_\tau(\theta) d\theta, \quad (\text{S11})$$

once the identity $\mathbf{x} - \mathbf{x}' = \rho(\cos(\phi), \sin(\phi))^T$, and the double angle formula expansion for $\cos(\theta) = \cos(\phi - \phi_H)$ are used. Multiplying Eq. (S9) by a unit vector perpendicular to $\vec{\mathbf{x}}$, $(-y_H + y, x_H - x)^T/|\vec{\mathbf{x}}|$ yields a similar formula, but with $\cos(\theta)$ replaced by $\sin(\theta)$ in the integrand of (S11). The even form of K_τ with respect to its argument $\theta = \phi - \phi_H$ causes the associated integral to equal zero, and implies that no advection occurs in directions perpendicular to the direction of the den site. Hence $\mathbf{c} = |\mathbf{c}|\vec{\mathbf{x}}$ points directly towards the den site, and $|\mathbf{c}|$ is the signed advection speed.

Using similar methods, the diffusion coefficients (Eq. S10) can be calculated as

$$\begin{aligned} d_{xx} &= \lim_{\tau \rightarrow 0} \frac{1}{4\tau} \int_0^\infty \rho^2 f_\tau(\rho) d\rho \\ &\quad \left(1 + \frac{x_1^2 - x_2^2}{|\mathbf{x}|} \int_0^{2\pi} \cos(2\theta) K_\tau(\theta) d\theta \right), \\ d_{xy} &= d_{yx} = 0, \\ d_{yy} &= \lim_{\tau \rightarrow 0} \frac{1}{4\tau} \int_0^\infty \rho^2 f_\tau(\rho) d\rho \\ &\quad \left(1 + \frac{x_2^2 - x_1^2}{|\mathbf{x}|} \int_0^{2\pi} \cos(2\theta) K_\tau(\theta) d\theta \right). \end{aligned} \quad (\text{S12})$$

We evaluate the advection speed Eq. (S11) and diffusion coefficients Eq. (S12) using Eq. (S7) for K_τ , and assuming that f_τ and κ_τ approach zero as τ becomes small. We define the first two moments of the probability density function for jump distances $f_\tau(\rho)$ as

$$\overline{\rho_\tau} = \int_0^\infty \rho f_\tau(\rho) d\rho, \quad (\text{S13})$$

and

$$\overline{\rho_\tau^2} = \int_0^\infty \rho^2 f_\tau(\rho) d\rho. \quad (\text{S14})$$

We use the identity

$$\int_0^{2\pi} \cos(n\theta) K_\tau(\theta) d\theta = \frac{I_n(\kappa_\tau)}{I_0(\kappa_\tau)} \quad (\text{S15})$$

and series expansions for the modified Bessel functions

$$I_0(\kappa) = 1 + \frac{1}{4}\kappa^2 + \text{h.o.t.}, \quad (\text{S16})$$

$$I_1(\kappa) = \frac{1}{2}\kappa + \text{h.o.t.}, \quad (\text{S17})$$

$$I_2(\kappa) = \frac{1}{8}\kappa^2 + \text{h.o.t.}, \quad (\text{S18})$$

to evaluate Eq. (S11), retaining terms to leading order, as

$$|c| = \lim_{\tau \rightarrow 0} \frac{\overline{\rho_\tau \kappa_\tau}}{2\tau}, \quad (\text{S19})$$

and Eq. (S12) as

$$d_{xx} = d_{yy} = d = \lim_{\tau \rightarrow 0} \frac{\overline{\rho_\tau^2}}{4\tau}. \quad (\text{S20})$$

Inserting (S19 and S20) into (S11) and (S12) and then inserting the resulting expressions into (S5) yields

$$\frac{\partial u^{(i)}}{\partial t}(\mathbf{x}, t) = \underbrace{d\nabla^2 u^{(i)}}_{\text{random motion}} - \underbrace{\nabla \cdot (c\bar{\mathbf{x}}u^{(i)} \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)}(\mathbf{x}, t))}_{\text{scent mark avoidance}} \quad (\text{S21})$$

where

$$c = \lim_{\tau \rightarrow 0} \frac{b\overline{\rho_\tau^2}}{2\tau}, \quad (\text{S22})$$

Scent-Marking Equations: The CA model is completed by equations expressing how the spatial distribution of scent marks change as a result of scent marking by individuals. Suppose that in the absence of foreign scent-marks individuals scent mark at a rate l , and that the marks decay as a result of aging at rate μ . Suppose further that consistent with observation (ii) (see main paper), encounters with foreign scent marks causes individuals to increase their marking rate by an amount proportional to the local density of foreign scent marks encountered. Recalling that $p^{(i)}(\mathbf{x}, t)$ is the

expected density of scent marks for pack i , we can write equations describing the rate of change of $p^{(i)}$ at each point in space $\mathbf{x} = (x, y)$:

$$\frac{\partial p^{(i)}}{\partial t}(\mathbf{x}, t) = Nu^{(i)}(\mathbf{x}, t)(l + m \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)}(\mathbf{x}, t)) - \mu p^{(i)}(\mathbf{x}, t), \quad (\text{S23})$$

where m denotes the sensitivity of the marking response to foreign scent marks and N is the number of individuals in each pack.

Non-dimensionalization: Equations (S21) and (S23) can be nondimensionalized by introducing the following variables:

$$\begin{aligned} x^* &= \frac{x}{L}, & y^* &= \frac{y}{L}, & t^* &= t\mu, & u^* &= L^2u, \\ v^* &= L^2v, & p^* &= \frac{L^2\mu p}{Nl}, & q^* &= \frac{L^2\mu q}{Nl}, \\ d^* &= \frac{d}{\mu L^2}, & c^* &= \frac{cN}{\mu^2 L^3}, & m^* &= \frac{mN}{\mu L^2}, \end{aligned} \quad (\text{S24})$$

where L is a characteristic length scale that is related to the area A ($L = A^{\frac{1}{2}}$), of the domain Ω over which the equations are to be solved (the study area).

Making the above substitutions into Equations (S21) and (S23), and then dropping the asterisks for notational simplicity, gives:

$$\frac{\partial u^{(i)}}{\partial t} = d\nabla^2 u^{(i)} - c\nabla \cdot \left[u^{(i)} \vec{\mathbf{x}}_i \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)} \right], \quad (\text{S25})$$

$$\frac{\partial p^{(i)}}{\partial t} = u^{(i)}(1 + m \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)}) - p^{(i)}, \quad (\text{S26})$$

The home ranges of each pack are assumed to correspond to time-independent solutions of the above equations. Applying a steady-state condition to Eq.s (S25–S26) yields the following system of equations:

$$0 = \nabla^2 u^{(i)} - \beta \nabla \cdot \left[u^{(i)} \vec{\mathbf{x}}_i \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)} \right], \quad (\text{S27})$$

$$0 = u^{(i)}(1 + m \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)}) - p^{(i)}, \quad (\text{S28})$$

where $\beta = \frac{c}{d}$. These are Eq.s (1) and (2).

Eq. (S27) is solved subject to ‘zero flux’ boundary conditions indicating that movements and interactions remain in a finite, self-contained region corresponding to the study area:

$$\left[\nabla u^{(i)} - \beta u^{(i)} \vec{\mathbf{x}}_i \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)} \right] \cdot \vec{\mathbf{n}} = 0, \quad (\text{S29})$$

$$(\text{S30})$$

where $\vec{\mathbf{n}}$ is the outwardly oriented unit vector normal to the edge of the domain $\partial\Omega$. Since $u^{(i)}$ is a probability density function, Eq.(S27) is also subject to the following integral constraint

$$\int_{\Omega} u^{(i)} dx = 1. \quad (\text{S31})$$

We refer to this as the pack conservation condition.

The STA+CA model

In the Steep Terrain Avoidance plus Conspecific Avoidance (STA+CA) model (Eq. 3), an individual's distribution of movement directions is a weighted sum of two separate, non-uniform circular distributions that respectively represent the influence of foreign scent-marks and terrain steepness on an individual's probability of moving in a particular direction, yielding the following redistribution kernel for an individual from pack i :

$$\begin{aligned} k(\mathbf{x}, \mathbf{x} - \mathbf{x}', \tau, t) &= \frac{1}{\rho} f_{\tau}(\rho) (\psi K_{\tau}^P(\phi - \phi_H, \mathbf{x}, t) \\ &+ (1 - \psi) K_{\tau}^S(\phi, -\phi_z, \mathbf{x})). \end{aligned} \quad (\text{S32})$$

The kernels K_{τ}^P and K_{τ}^S are again taken to be Von-Mises distributions (Eq. S7), but with concentration parameters

$$\kappa_{\tau}^P(\mathbf{x}, t) = b\bar{\rho}_{\tau} \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)}(\mathbf{x}, t), \quad (\text{S33})$$

$$\kappa_{\tau}^S(\mathbf{x}) = a\bar{\rho}_{\tau} |\nabla z(\mathbf{x})|. \quad (\text{S34})$$

Substituting these into Equation (S5), and following procedures similar to those used to derive the CA model, we obtain the following non-dimensionalized equation for the expected steady-state pattern of space-use:

$$0 = \underbrace{\nabla^2 u^{(i)}}_{\text{random motion}} - \underbrace{\nabla \cdot \left[\beta \vec{\mathbf{x}}_i u^{(i)} \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)} \right]}_{\text{scent-mark avoidance}} \quad (\text{S35})$$

$$+ \underbrace{\nabla \cdot \left[\alpha_z u^{(i)} \nabla z \right]}_{\text{avoidance of steep terrain}}, \quad (\text{S36})$$

where β is the strength of the scent-mark avoidance relative to the random component of motion, and α_z is the strength of the steep terrain avoidance relative to the random component of motion. This is Eq. (3). A nondimensionalization similar to that for the previous model yields an unchanged form for Eq. (S36), but with the pack conservation equation (S31), and Eq. (S28) for the steady state scent mark. Finally, the model formulation requires zero-flux boundary conditions for Eq. (S36).

The PA+CA Model

In the Prey Availability plus Conspecific Avoidance (PA+CA) model (Eq. 4), the distance between relocations, ρ_τ , is a decreasing function of local resource density $h(\mathbf{x})$. Substituting $\rho_\tau(h(\mathbf{x}))$ into Eq. (S21) we obtain the following equations for expected space use:

$$0 = \underbrace{\nabla^2 [d(\mathbf{x})u^{(i)}]}_{\text{foraging response}} - \underbrace{\nabla \cdot \left[c_P(\mathbf{x})\vec{\mathbf{x}}_i u^{(i)} \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)} \right]}_{\text{scent-mark avoidance}}, \quad (\text{S37})$$

where

$$d(\mathbf{x}) = \overline{\rho_\tau^2(h(\mathbf{x}))} / (4\tau) \quad \text{and} \quad c_P(\mathbf{x}) = \overline{b\rho_\tau(h(\mathbf{x}))^2} / (2\tau). \quad (\text{S38})$$

The first term in Eq. (S37) can be expanded to yield

$$0 = \underbrace{\nabla \cdot [d(\mathbf{x})\nabla u^{(i)}]}_{\text{random motion}} - \underbrace{\nabla \cdot \left[c_P(\mathbf{x})\vec{\mathbf{x}}_i u^{(i)} \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)} \right]}_{\text{scent-mark avoidance}} + \underbrace{\nabla \cdot [u^{(i)}\nabla d]}_{\text{directed movement toward areas of high resource density}}, \quad (\text{S39})$$

indicating that the increased turning frequency that occurs in response to increasing resource density results in a directed component of motion towards areas of high resource density. The equations for scent-marking (S23) remain unchanged.

If, as is commonly observed, the distribution of step lengths is exponential with mean $\overline{\rho_\tau}$, we can relate the first and second moments $\overline{\rho_\tau^2} = 2\overline{\rho_\tau}^2$. Assuming that the relationship between mean step length $\overline{\rho_\tau(h(\mathbf{x}))}$ and prey density $h(\mathbf{x})$ is also exponential, i.e.

$$\overline{\rho_\tau(h(\mathbf{x}))} = \sqrt{\tau}\rho_0 \exp(-\rho_1 h(\mathbf{x})), \quad (\text{S40})$$

then substitution of Eq. (S40) into the above definitions for $d(\mathbf{x})$ and $c_P(\mathbf{x})$ yields a simplified version of Eq. (S39):

$$0 = \underbrace{\nabla \cdot [e^{-\alpha_r h(\mathbf{x})}\nabla u^{(i)}]}_{\text{random motion}} - \underbrace{\nabla \cdot \left[e^{-\alpha_r h(\mathbf{x})} c_P(\mathbf{x})\vec{\mathbf{x}}_i u^{(i)} \sum_{j \neq i}^{n_{\text{pack}}} p^{(j)} \right]}_{\text{scent-mark avoidance}} - \underbrace{\nabla \cdot [e^{-\alpha_r h(\mathbf{x})} u^{(i)}\nabla h]}_{\text{directed movement toward areas of high resource density}}, \quad (\text{S41})$$

where $\beta = b$ and $\alpha_r = 2\rho_1$. The effect of prey density on movement behavior is reflected in the exponential terms and the last term of the equation, which is a classic ‘prey taxis’ term (Kareiva and Odell 1987). A nondimensionalization similar to that for the previous model yields an unchanged form for Eq. (S41), but with the pack conservation equation (S31), and Eq. (S28) for the steady state scent mark. Finally, the model formulation requires zero-flux boundary conditions for Eq. (S41).

2 Model Fitting

The mechanistic home range models were fitted to the relocation datasets using the method of maximum likelihood. The log-likelihood l of obtaining the observed set of relocations is:

$$l(\theta) = \sum_{i=1}^n \sum_{j=1}^{n_{r_i}} \ln u^{(i)}(x_{ij}, y_{ij}), \quad (\text{S42})$$

where θ is a vector of model parameters whose values are to be maximized; $u^{(i)}(x_{ij}, y_{ij})$ is the height of the probability density function for expected space-use by pack i at point (x_{ij}, y_{ij}) , given by the steady-state solutions of the mechanistic home range model; (x_{ij}, y_{ij}) are the spatial coordinates of relocations for individuals belonging to pack i ($i = 1 \dots n$, where n is the number of packs, and $j = 1 \dots n_{r_i}$, where n_{r_i} is the total number of relocations for pack i); and k is an additive constant.

For the CA model, $\theta = [\beta, m]$, and $u^{(i)}(x_{ij}, y_{ij})$ is given by the solution of Equation (1); for the STA+CA model, $\theta = [\beta, m, \alpha_z]$, and $u^{(i)}(x_{ij}, y_{ij})$ is given by the solution of Equation (3); and for the PA+CA model, $\theta = [\beta, m, \alpha_r]$, and $u^{(i)}(x_{ij}, y_{ij})$ is given by the solution of Equation (4).

Equation (S42) was maximized with respect to the model parameters using a numerical maximization algorithm, solving the space-use equations numerically for each set of parameter values. For further information on numerical maximization methods see Press et al. (1992), or Press et al. (1992b). For further details on the method of maximum likelihood see Edwards (1992).

3 Estimates of Small Mammal Biomass

Densities of the primary coyote small mammal prey species—mice (*microtus*), pocket gophers, ground squirrels and voles—were estimated in six different habitat types found within Lamar Valley (see Table 1). Density estimates for each habitat type were obtained by mini-grid trapping (Crabtree and Harter unpubl.). The total small mammal biomass density in each habitat was then calculated by multiplying the habitat-specific density estimate for each species by the species' mean body weight, and summing the resulting numbers (see Table 1). The spatial distribution of total small mammal biomass density (Figure 1b) was then calculated by combining the biomass density estimates for each habitat with the spatial distribution of habitat types obtained from the National Park Service Geographic Information System.

References

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Habitat	Density (# per ha)			
	Mice (<i>Microtus</i>)	Ground Squirrels	Pocket Gophers	Red-backed Voles
Mesic Grass	79.76	0.0	15.02	0.0
Xeric Grassland	8.95	0.83	26.7	0.0
Sagebrush	8.13	0.17	8.48	0.0
Burned Sagebrush	4.47	1.82	10.8	0.0
Forest	0.0	0.0	8.53	8.33
Burned Forest	0.9	0.0	9.41	3.13
Mean weight (g)	50	250	100	20

Table 1: Estimates of small mammal density in the different habitats found in Lamar Valley and surrounding areas. Density estimates for each species were estimated from mini-grid trapping (Crabtree and Harter unpubl.).