

HOME RANGE ANALYSIS USING A MECHANISTIC HOME RANGE MODEL

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Abstract. The traditional models used to characterize animal home ranges have no mechanistic basis underlying their descriptions of space use, and as a result, the analysis of animal home ranges has primarily been a descriptive endeavor. In this paper, we characterize coyote (*Canis latrans*) home range patterns using partial differential equations for expected space use that are formally derived from underlying descriptions of individual movement behavior. To our knowledge, this is the first time that mechanistic models have been used to characterize animal home ranges. The results provide empirical support for a model formulation of movement response to scent marks, and suggest that having relocation data for individuals in adjacent groups is necessary to capture the spatial arrangement of home range boundaries. We then show how the model fits can be used to obtain predictions for individual movement and scent marking behavior and to predict changes in home range patterns. More generally, our findings illustrate how mechanistic models permit the development of a predictive theory for the relationship between movement behavior and animal spatial distribution.

Key words: animal movement; *Canis latrans*; Carnivora; carnivore; coyotes; home range analysis; home range models; mechanistic models; scent marking; space use; territoriality.

INTRODUCTION

The analysis and description of home range patterns has been central to understanding the ecology of many mammalian populations. The relationship between patterns of space use and the spatial and temporal distribution of resources (Brown and Orians 1970), as well as the consequences for social organization (Rubenstein, and Wrangham 1986), mating systems (Clutton-Brock 1989) and demography (Clutton-Brock and Albon 1985) have all been subjects of considerable theoretical and empirical interest. Moreover, there is increasing evidence that animal spacing patterns play important roles in determining the spatial distributions of prey and competitors within animal communities (Mech 1977, Paquet 1991, Creel 1996, White et al. 1996b).

Animal home ranges have been traditionally characterized using a variety of statistical models (Macdonald et al. 1980, Worton 1987). The Minimum Convex Polygon model (Odum and Kuenzler 1955, Jennrich and Turner 1969) provides a simple estimate of home range size. Density estimation models, such as the bivariate normal (Jennrich and Turner 1969), harmonic mean (Dixon and Chapman 1980) and kernel (Worton 1989) models, provide more detailed infor-

mation, characterizing the relative intensity of space use in the form of a probability density function (PDF), sometimes referred to as a utilization distribution (UD). While these various statistical methods can provide useful descriptions of home range data, they are of little theoretical or predictive value because they have no mechanistic basis underlying their descriptions of space use.

The development and application of mechanistic home range models offers a promising way to integrate theoretical and empirical home range studies. In contrast to statistical home range models, mechanistic home range models derive patterns of space use from an underlying description of individual movement and interaction behavior. As we hope to show in this paper, fitting mechanistic models to empirical home range data offers two important advantages over traditional approaches to home range analysis. First, the results of the model fits can be used to evaluate hypotheses regarding the factors underlying animal home range patterns. Second, the fitted models can be used to obtain predictions for how home range patterns change following perturbation. In addition, since the parameters reflect the behaviors of individuals, they can be verified from field measurements of individual behavior (Moorcroft 1997).

The origins of mechanistic models for animal movement lie in the mathematical analysis of correlated random walks, in which individual motion is characterized as a sequence of movements at different speeds, orientations, and turning frequencies. The term “corre-

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lated random walk” is used to indicate that the locations of individuals are correlated in time and that movement rules are stochastic, specified in terms of probability distributions of movement speeds, orientation angles, and turning frequencies (Skellam 1951, Skellam 1973, Okubo 1980). The recent development of mechanistic models for foraging (Grunbaum 1996, 1998), aggregation (Guéron and Levin 1994), and home ranges (Lewis and Murray 1993), suggests that mechanistic models are widely applicable in studies of animal movement.

In this paper, we use a mechanistic home range model for carnivores, proposed by Lewis and Murray (1993), to characterize coyote (*Canis latrans*) home ranges in the Hanford Arid Lands Ecological Reserve, Washington, USA. The model formulation reflects observations that scent marking is the dominant, proximate mechanism indicating home range occupation in coyotes (Gese and Ruff 1996) and many other carnivore species (Brown and Macdonald 1985). Earlier analysis showed that the model equations could be derived from two simple rules for individual movement and scent marking behavior: (1) encounters with foreign scent marks increase an individual’s probability of movement toward the center of its home range, and (2) an individual’s rate of scent marking increases after encountering foreign scent marks. Explicit mathematical scaling of these individual rules yielded a partial differential equation (PDE) for each home range, describing the expected pattern of space use, coupled to ordinary differential equations (ODEs) describing the spatial pattern of scent marks (Moorcroft 1997).

Further analysis showed that solutions of the model equations in two spatial dimensions resulted in home range and scent mark distributions that are qualitatively consistent with those observed in empirical studies of carnivores (Lewis and Murray 1993, White et al. 1996a, Moorcroft 1997). Depending on the model parameters and spatial arrangement of home range centers, which for many carnivores corresponds to a den site (or, in other cases, a core foraging area), the expected pattern of space use varies from exclusive, non-overlapping territories to loosely overlapping home ranges. Scent marking patterns also vary, both in density and spatial distribution, from cases where scent marks are found mostly in the interior of the home range to cases where the scent marks are concentrated into peaks along home range boundaries (Moorcroft 1997).

In this analysis, we fit the Lewis and Murray (1993) carnivore home range model to radio-tracking observations of individuals belonging to a single coyote pack located at the center of the study area. We compare the fit to that obtained with a simpler, mechanistic home range model (Holgate 1971) in which individuals exhibit a constant bias in movement direction. We then characterize the regional pattern of home ranges at Hanford and show how the model fits can be used to

obtain predictions for movement and scent-marking behavior.

MODELS

Constant bias in movement direction

Holgate (1971) proposed a simple mechanistic home range model in which individuals moved on a square lattice, exhibiting a constant bias in their movement towards a home range center. An equivalent, continuous space formulation can found in Lewis et al. (1997) and Moorcroft (1997). Each home range $i = 1, \dots, n$ (where n is the number of home ranges) is described by the steady-state solution of a PDE for a probability density function $u^{(i)}(x, y)$:

$$\frac{\partial u^{(i)}}{\partial t} = D\nabla^2 u^{(i)} - \nabla \cdot (u^{(i)} c \tilde{\mathbf{x}}_i) = 0 \quad i = 1, \dots, n \tag{1}$$

that describes the expected pattern space use by an individual, or pack of individuals, sharing a common home range. At every point in space (x, y) , the unit vector $\tilde{\mathbf{x}}$ indicates the direction of the home range center, and ∇ indicates spatial derivatives ($\partial/\partial x, \partial/\partial y$). In Eq. 1, D indicates the strength of the random (diffusive) component of movement, relative to c , the directed (advective) component of movement, caused by individuals having an increased probability of turning towards the center of the home range. Note that, as in the original Holgate (1971) model, the magnitude of directional movement c is simply a constant. The formal connection between the two macroscopic parameters D and c and the properties of individual movement are given in Eq. 4 (see *Models: Movement behavior*, below).

Movement in response to foreign scent marks

In the carnivore home range model, first proposed by Lewis and Murray (1993), directional bias in movement arises as a result of encounters with foreign scent marks. Each home range i is described by the steady-state solution of a PDE for a probability density function $u^{(i)}(x, y, t)$ ($i = 1, \dots, n$), that is coupled at each point in space, to ODEs describing the accumulation and decay of scent marks $p^{(i)}(x, y)$ within the region:

$$\frac{\partial u^{(i)}}{\partial t} = D\nabla^2 u^{(i)} - \nabla \cdot \left[u^{(i)} c \tilde{\mathbf{x}}_i \alpha \sum_{j \neq i}^n p^{(j)} \right] = 0 \tag{2}$$

$$i = 1, \dots, n$$

$$\frac{dp^{(i)}}{dt} = u^{(i)} \left[l + m \sum_{j \neq i}^n p^{(j)} \right] - \mu p^{(i)} = 0 \tag{3}$$

$$i = 1, \dots, n$$

where the spatial coordinates (x, y) describe locations within a domain Ω representing the study area. The explicit spatial dependency (x, y) of u and p has been dropped for notational convenience.

In contrast to Eq. 1, where the directed component

of motion is constant, in Eq. 2 the local density of foreign scent marks $\sum p^{(j)}, j \neq i$, governs the strength of directed movement. The coefficient α governs the magnitude of directed movement per unit of scent mark density. Note that Eqs. 2 and 3 are coupled: foreign scent marks j influence the movement direction of individuals in pack i and the resulting space use by individuals in pack i , $u^{(i)}$; furthermore, the density of foreign scent marks $p^{(j)}$ influence the rate at which i individuals deposit scent marks at different locations in space.

The spatial distribution of scent marks for each pack arises from the accumulation and subsequent decay of scent marks, as described by simple first-order kinetics (Eq. 3). The rate of scent mark accumulation depends on extent of space use by individuals in pack i and their rate of scent marking. Individuals mark at a background rate l , and increase their marking, at rate m , in response to the density of foreign scent marks encountered $p^{(j)}, j \neq i$. Deposited scent marks decay at rate μ .

Movement behavior

The parameters D and c in Eqs. 1 and 2 describe the characteristics of individual movement:

$$D = \frac{1}{4} \frac{\int_0^\infty \int_0^\infty c^2 \tau^2 f(c, \tau) dc d\tau}{\int_0^\infty \tau f(c, \tau) d\tau}$$

$$c = \frac{1}{2} \frac{\int_0^\infty \int_0^\infty c \tau f(c, \tau) dc d\tau}{\int_0^\infty \tau f(c, \tau) d\tau} \tag{4}$$

The integrals in the numerators are, respectively, the first and second moments of the joint distribution $f(c, \tau)$ of movement speeds c and times between turns τ . In both cases, the denominator is the mean time between turns (Patlak 1953, Moorcroft 1997).

Nondimensionalization

Eqs. 1–3 can be nondimensionalized in the following way. We make the following definitions:

$$x^* = \frac{x}{L} \quad y^* = \frac{y}{L} \quad t^* = t\mu \quad D^* = \frac{D}{\mu L^2}$$

$$c^* = \frac{c}{\mu L} \quad \alpha^* = \frac{\alpha l}{\mu} \quad m^* = \frac{m}{\mu} \quad p^{*(i)} = \frac{p^i \mu}{l} \tag{5}$$

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

The time scale for the system is now the rate of decay of scent marks μ . The scent mark density p_i is nondimensionalized by scaling to μ and the low-level scent

marking rate of individuals l . Making the substitutions from Expression 5 into Eqs. 1–3, applying a steady-state condition, and defining

$$\delta^* = \frac{D^*}{c^*} \tag{6a}$$

$$\delta^* = \frac{D^*}{\alpha^* c^*} \tag{6b}$$

for Eqs. 1 and 2, respectively, then dropping the asterisks, we get

$$\frac{\partial u^{(i)}}{\partial t} = \delta \nabla^2 u^{(i)} - \nabla \cdot [u^{(i)} \tilde{\mathbf{x}}_i] = 0 \tag{7}$$

and

$$\frac{\partial u^{(i)}}{\partial t} = \delta \nabla^2 u^{(i)} - \nabla \cdot \left[u^{(i)} \tilde{\mathbf{x}}_i \sum_{j \neq i}^n p^{(j)} \right] = 0 \tag{8}$$

$$\frac{dp^{(i)}}{dt} = u^{(i)} \left[1 + m \sum_{j \neq i}^n p^{(j)} \right] - p^{(i)} = 0. \tag{9}$$

Boundary conditions

Movement Eqs. 7 and 8 have associated boundary conditions that describe the behavior of the solutions at the boundary $\partial\Omega$ of the domain Ω :

$$[\delta \nabla u^{(i)} - u^{(i)} \tilde{\mathbf{x}}_i] \cdot \tilde{\mathbf{n}} = 0 \tag{10}$$

for Eq. 7, and

$$\left[\delta \nabla u^{(i)} - u^{(i)} \tilde{\mathbf{x}}_i \sum_{j \neq i}^n p^{(j)} \right] \cdot \tilde{\mathbf{n}} = 0 \tag{11}$$

for Eq. 8, where $\tilde{\mathbf{n}}$ is the outwardly oriented unit normal to $\partial\Omega$. These are “zero flux” boundary conditions, in both cases indicating movement and interaction in a finite, self-contained region.

ANALYSIS

We performed two separate analyses. In the first analysis, we characterized the home range of a single pack, the centrally located Hopsage Pack at the Hanford Arid Lands Ecosystem Reserve (ALE). We compared the fit of Holgate’s (1971) model, which assumes a constant bias in movement direction (Eq. 7), to the fit obtained using the Lewis and Murray (1993) carnivore home range model (Eqs. 8 and 9), in which directional movement arises from encounters with foreign scent marks.

In the second analysis, we used the Lewis and Murray (1993) carnivore home range model to characterize the regional home range patterns at Hanford ALE, fitting the model to relocation data for six contiguous packs in the region. The results of the regional fit were compared to that obtained in the single-pack fit and then used to predict (1) the expected distribution of scent marks across the region, (2) the spatial pattern of directionality in individual movement, and (3) the effects of pack removal for home range patterns within the region.

Data

For the model fitting, we used observations of coyote home ranges collected at the Hanford ALE. The data comprised radio locations of known individuals belonging to six contiguous coyote packs, in the western portion of the ALE, collected by Crabtree (1989). Weekly relocations were collected during December 1985–June 1987 from high accuracy triangulations (0.5° error), recorded by two fixed monitoring stations that had “line-of-sight” coverage over the entire 150 km² study area; see Crabtree (1989) for details.

Model fitting

The home range models were fitted to the relocation data by maximum likelihood. We used a log-likelihood function $l(\theta)$ to measure goodness-of-fit:

$$l(\theta) = \sum_{i=1}^n \sum_{j=1}^{q_i} \ln u^{(i)}(x_{ij}, y_{ij}) \quad (12)$$

where θ is the vector of model parameters $u^{(i)}(x_{ij}, y_{ij})$ is the height of the probability density function (PDF), for expected space use by pack i at point (x_{ij}, y_{ij}) , given by the steady-state solution of Eq. 7 or Eqs. 8 and 9. (x_{ij}, y_{ij}) are the spatial coordinates of relocations for individuals belonging to pack i ($i = 1, \dots, n, j = 1, \dots, q_i$), where q_i is the total number of relocations for pack i , expressed as Universal Trans-Mercator (UTM) grid (x, y) coordinates. Because information on core denning and foraging areas was not available, we assumed that the centroid of the relocation observations indicated the location of the home center.

The models were fitted to the data by maximizing $l(\theta)$ with respect to the model parameters θ , using an iterative maximization algorithm (Press et al. 1992). For each set of parameter values θ , Eq. 7, or Eqs. 8 and 9, were solved, and the relative goodness-of-fit of the two models were compared, using changes in log-likelihood $\Delta l(\theta)$, which asymptotically follows a half chi-square distribution, the number degrees of freedom being given by the change in the number of model parameters (Edwards 1992).

Solving for patterns of space use and scent marking

For the biologically realistic case of home ranges in two-dimensional space, the home range model Eq. 7 or Eqs. 8 and 9 could not be solved analytically; hence, they were solved by numerical simulation. We used the Method of Lines (Schiesser 1991) to approximate the PDEs given by Eqs. 7 and 8, discretizing the spatial derivative terms to second order, and yielding a large set of spatially coupled ODEs. The scent marking ODEs (Eq. 9) were discretized onto the same spatial grid used to discretize the associated PDEs (Eq. 8). Using this method, all the models could be represented by large systems of coupled ODEs.

The number of ODEs used to represent Eq. 7 and Eqs. 8 and 9 is governed by the size of the simulation

region and the spatial scale used for discretization. We simulated the model equations in a 12.5×11.0 km domain, encompassing the relocation data, at a spatial resolution of 100×100 m, since fine-scale approximations of the spatial derivatives were necessary for accurate simulation of the PDEs in Eqs. 7 and 8. Due to their flux-conserving nature (Press et al. 1992), we solved for the steady state of Eqs. 7 and 8 by solving the corresponding time-dependent equations. From a prescribed initial condition of uniform space use across the study area by all packs, we iterated the equations to convergence, a procedure known as the Method of False Transients (Ames 1992). The time integration was done using a fully implicit method to solve the system of coupled equations at each time step (Saad and Schultz 1986, Brown et al. 1989, Byrne 1992). Further details of the simulation and fitting methods can be found in Moorcroft (1997).

RESULTS

Characterization of a single home range

Visual inspection of the home range fits shows that the Holgate (1971) constant bias model (Eq. 7) produces a circular home range that gives a relatively poor fit to the observed pattern of relocation data for the Hopsage pack (Fig. 1a). In contrast, the fit of the Lewis and Murray (1993) carnivore home range model matches the spatial distribution of relocations more closely (Fig. 1b). The shape of the contour lines around the home range center indicate that the shape of the probability density function (PDF) for expected space use is influenced by the presence of neighboring home range centers (Fig. 1b). Examination of the likelihood scores for the two models (Table 1) shows that switching from a constant bias in movement direction (Eq. 7) to directional movement, induced by encounters with foreign scent marks (Eq. 8 and 9), significantly improves the goodness-of-fit to the relocation data ($\Delta l = 62.6; p < 0.0001$).

Regional range patterns

Fits of the carnivore home range model (Eqs. 8 and 9), to the relocation data for the six contiguous packs at Hanford ALE are shown in Fig. 2. Compared to the single pack fit (Fig. 1b), the regional fit of the carnivore home range model to the centrally located Hopsage pack suggests a more exclusive pattern of space use (Fig. 2a). The inclusion of the relocations from the surrounding groups into the model fits results in probability density functions (PDFs) for expected space use that show increased platykurtosis, indicating a more uniform intensity of space use within sharply defined home range boundaries, beyond which space use declines more sharply (Fig. 2b).

The carnivore home range model captures the spatial pattern of home ranges across the region well, capturing the location of the boundaries between adjacent

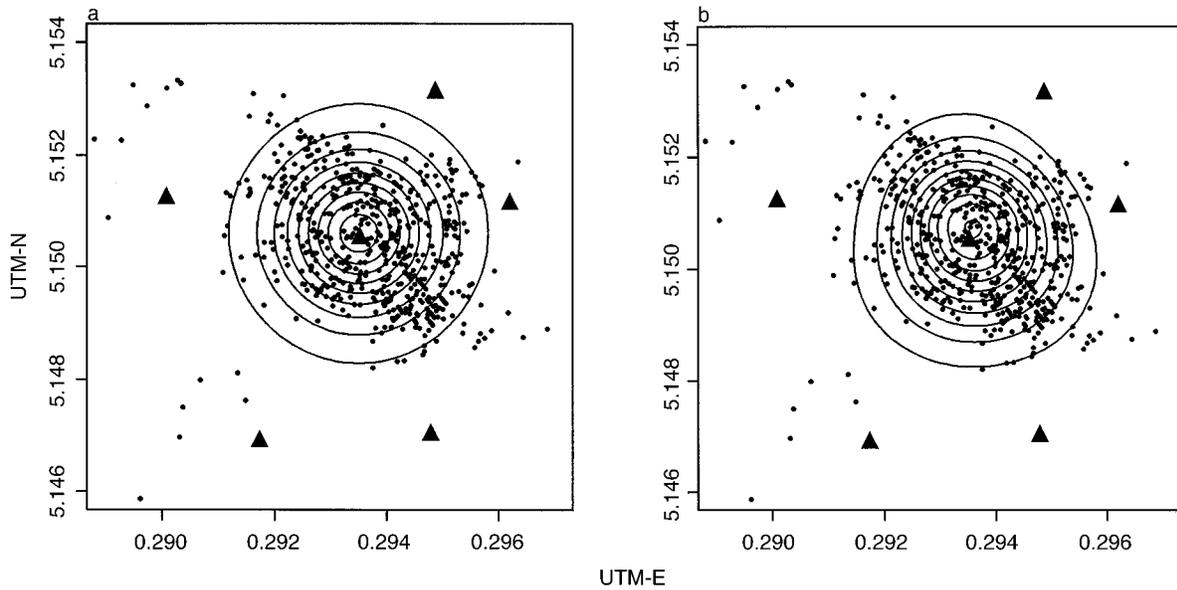


FIG. 1. Contour lines showing the probability density function $u(x, y)$ for the home range of the central Hopsage pack at Hanford ALE obtained by fitting (a) Holgate's (1971) model of constant bias in movement direction (Eq. 7) to relocation data (●) collected by Crabtree (1989). (b) The Lewis and Murray (1993) carnivore home range model, in which directional movement arises from encounters with foreign scent marks and individuals' scent marks in response to encounters with foreign scent marks (Eqs. 8 and 9). The contour interval is 2, in density units, scaled so that both the domain area A and integral of $u(x, y)$ are unity. Home range centers of the Hopsage pack and neighboring packs, as estimated by the centroids of the relocation data for each pack, are shown (▲). The fitting procedure is described in the text (see *Models*), and the maximum likelihood values and parameter estimates for δ and m are given in Table 1. Positions are indicated in Universal Trans-Mercator (UTM) grid coordinates (east, north); axis scale numbers are in terms of millions of meters (i.e., 10^6 m).

home ranges (Fig. 2b). The degree of overlap between neighboring packs appears to vary; the central Hopsage pack home range has sharper boundaries where the neighboring home range centers are in close proximity

(in the northeast section of the study area), while those between more distant neighbors tend to be more overlapping (Figure 2b). Note, however, that the ability of the model to describe observed patterns of space use at the periphery of the region is limited. This is a result of the exterior home range boundaries being set by the "zero-flux" boundary conditions for the edges of the domain (Eq. 11), rather than as a result of interactions with foreign scent marks of adjacent packs (Fig. 2b).

TABLE 1. Details of the home range model fits (Figs. 1 and 2) to relocation data collected Hanford ALE.

	Constant bias	Single home range	Regional fit
No. of packs (n)	1	1	6
Equations	7	8 and 9	8 and 9
Parameter			
δ	0.081	0.178	1.829
m	...	0.083	0.131
$l(\theta)$	741.9	801.3	3106
		$q_{total} = 480$	$q_{total} = 2325$

Notes: Parameter values and likelihood scores are given for the fit of the Holgate (1971) constant bias model, Eq. 7, and the Lewis and Murray (1993) carnivore home range model (Eqs. 8 and 9). The single home range fits used relocations collected on individuals belonging to the Hopsage pack. In the regional fit, the Lewis and Murray (1993) home range model was fitted to relocation data for the six contiguous pack home ranges in Hanford ALE study area: q_{total} is the total number of data points used in each model fit $q_{total} = \sum_{i=1}^n q_i$ (Eq. 12). In Eq. 7, δ indicates the ratio of nondirected movement D to directed movement c (Eq. 6a). In Eqs. 8 and 9, δ indicates the ratio of nondirected movement D relative to the strength of directed movement c and the sensitivity of directed movement to foreign scent mark density α (Eq. 6b).

Model predictions

Since the spatial pattern of home ranges in the carnivore home range model arises from interactions between individuals and scent marks, the fits provide information about the expected distribution of scent marks across the region (Fig. 3). The results of the regional fit (Fig. 2b) suggest that, in the interior of the domain, elevated concentrations of scent marks should occur along the boundaries between neighboring home ranges. In particular, high scent mark concentrations are expected in the northeast section of the domain, where three home range centers lie in close proximity (Fig. 3). The absence of any high concentrations at the periphery of the domain can be attributed to the absence of interacting packs along these home range boundaries, which are governed by the boundary conditions (Eq. 11).

The mechanistic nature of the home range models

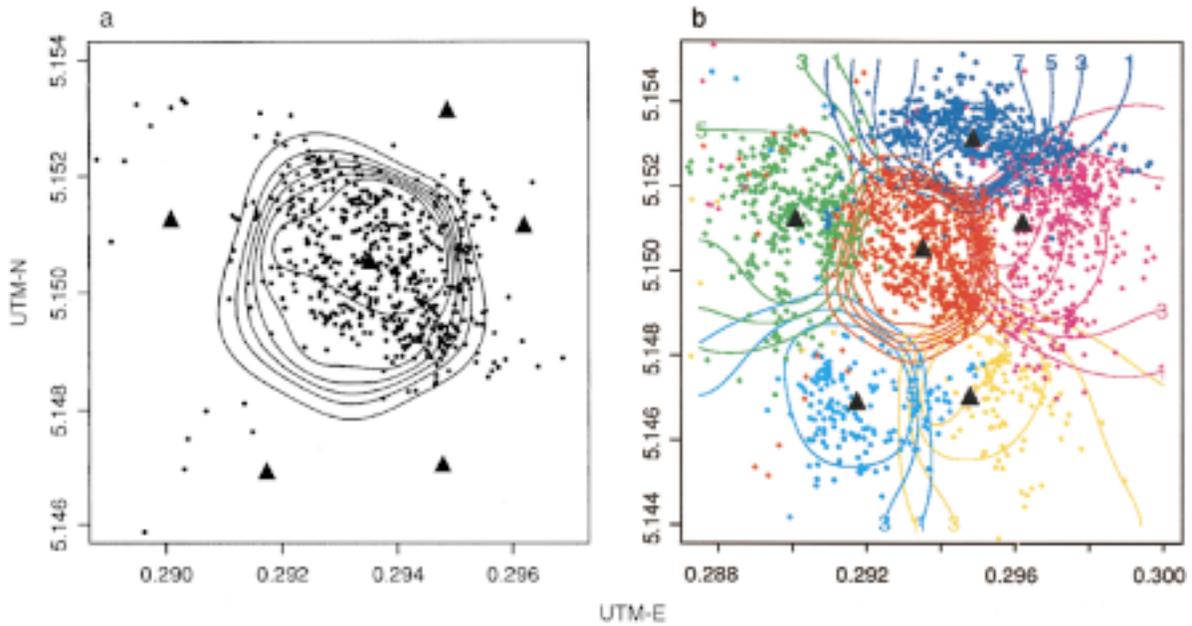


FIG. 2. Contour lines showing fit of the Lewis and Murray (1993) carnivore home range model (Eqs. 8 and 9) to relocation data (●) for six groups at Hanford ALE collected by Crabtree (1989). As in Fig. 1, the contour interval for $u(x, y)$ is 2, and the home range centers for each pack are shown (▲). The axis scales are in terms of millions of meters (i.e., 10^6 m). (a) Home range of the central Hopsage pack. (b) Regional fit showing home ranges for all six groups in the study region (packs are indicated by different colors). Maximum likelihood values and estimates for δ and m are given in Table 1.

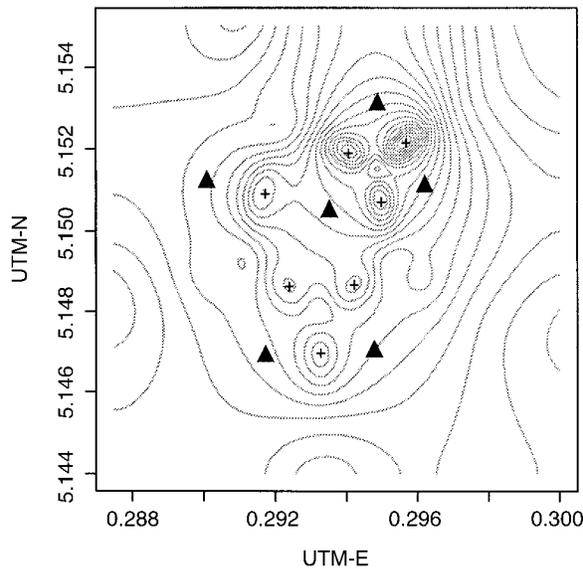


FIG. 3. Contour lines showing the expected regional pattern of total scent mark density $\sum_{j=1}^n p^{(j)}$ within Hanford ALE study area, obtained from the fit of the Lewis and Murray (1993) carnivore home range model (Eqs. 8 and 9) shown in Fig. 2b. The axis scales are in terms of millions of meters. Peaks in scent mark density are indicated (+). Scent mark densities across the domain vary in the range 1.1–22.1 in rescaled units (Eq. 9), as shown using a contour interval of 1.

used in this analysis means that the model parameters (Table 1), reflect the behavior of individuals that can be verified with measurements obtained on movement and scent-marking behavior. For example, in the Lewis and Murray (1993) model, directionality in individual movement is caused by encounters with foreign scent marks. From this, we can calculate distributions of expected movement directions in different regions of the study area. Earlier analysis (Moorcroft 1997) showed that the distribution of turning angles $K(\phi, x, y)$ is given by

$$K(\phi, x, y) \approx \frac{1}{2\pi} \left[1 + \alpha \sum_{j \neq i}^n p^{(j)}(x, y) \cos \hat{\phi} \cos \phi + \alpha \sum_{j \neq i}^n p^{(j)}(x, y) \sin \hat{\phi} \sin \phi \right] \quad (13)$$

where $\hat{\phi}$ is the direction of the home range center, and α is the sensitivity of movement direction to foreign scent mark density, $\sum_{j \neq i}^n p^{(j)}(x, y)$, both in nondimensional form. The model fit provides the values of the scent mark density for each pack (see Eq. 9 and Fig. 3). The value of α , the sensitivity of movement direction to foreign scent marks, depends on δ and the ratio D/c (Eq. 6b). The value of δ is estimated as part of the model-fitting procedure (see Table 1), and an estimate for D/c is provided by the single-pack fit of Eq. 1 in which $\delta = D/c$ (Eq. 6b). Alternatively, D/c can be obtained from observed statistics of individual movement using Eq. 4. Resolving the density of scent marks

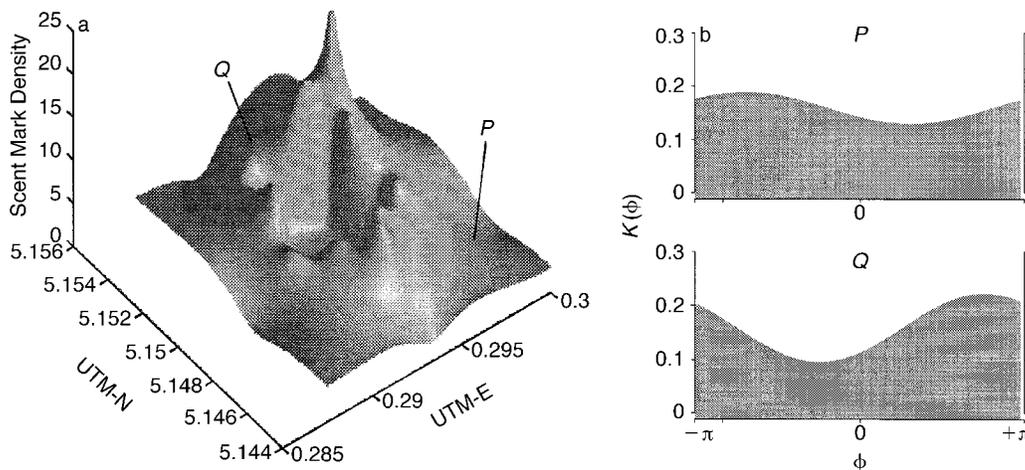


FIG. 4. (a) Surface height indicates the predicted spatial variation in the density of foreign scent marks $\sum_{j \neq i}^n p^{(j)}$ encountered by members of the Hopsage pack in the Hanford ALE study region. The axis scales are in terms of millions of meters. (b) Predicted distribution of turning angles $K(\phi)$ in the regions around points P and Q labeled in Fig. 4a: ϕ indicates movement direction relative to UTM grid north. Around P , the turning distribution is relatively uniform, indicating that movement is relatively nondirectional (isotropic). Around Q , the turning distribution is less uniform, indicating that movement is more directional (nonisotropic). $K(\phi)$ was calculated using the relationship between the density of foreign scent marks, $\sum_{j \neq i}^n p^{(j)}$, and the distribution of turning angles (Eq. 13), using the value of 0.46 for α obtained using Eq. 6 and the values of δ obtained from the fits of Eqs. 7–9.

“foreign” to a particular pack, $\sum_{j \neq i}^n p^{(j)}(x, y)$ (Fig. 4a), then substituting into Eq. 13 along with the estimate of α obtained from the single-pack fit, yields predictions for the direction and magnitude of bias in movement direction across the domain, expressed as distributions of expected movement directions in different regions of the study area (Fig. 4b).

In addition, as a result of the home range boundaries being determined by packs responding to the presence of foreign scent marks, the regional Lewis and Murray (1993) model fit can be used to predict the consequences of removing and introducing packs into a region. For example, before their removal, the central Hopsage pack at Hanford had almost exclusive use of the center of the domain (Fig. 2b). However, following their removal, neighboring packs expanded their home ranges into the unoccupied central region (Fig. 5a). In addition, due to the reduction in the density of packs in the study region, the home ranges of the remaining pack became more overlapping (Fig. 5a). Accompanying these changes in patterns of space use are changes in the spatial distribution of scent marks (Fig. 5b). Following the removal, the peaks in scent mark density present between the Hopsage pack and each of its neighbors (Fig. 3) disappear; the scent mark peaks between the remaining packs alter in shape and size as patterns of space use by the remaining groups shift in response to the removal (Fig. 5b). This is particularly evident in the northeast region where the three ridges of high scent mark density present before the removal (Fig. 3) are replaced by a single ridge between two remaining packs (Fig. 5b). In a similar manner to these predictions following a removal, if the location of the

denning area of a newly introduced pack is known or can be predicted, the model fits can be used to predict the new arrangement of home ranges and patterns of scent marks.

DISCUSSION

We have shown how a mechanistic model for carnivore home ranges, derived from simple individual movement rules, can be directly related to coyote *Canis latrans* home range relocation data. To our knowledge, this is the first time a mechanistic, rather than a statistical, model has been used to characterize animal home ranges. Our previous work had shown that the carnivore home range model reflects the macroscopic pattern of home ranges obtained by scaling two simple rules describing individual movement and scent marking behavior (Moorcroft 1997). Furthermore, the solution of the model equations produces home range and scent mark patterns consistent with those observed in empirical studies of carnivores (Lewis and Murray 1993, Moorcroft 1997). In this paper, we have shown that the carnivore home range model can also be used both to characterize empirical home range patterns and to obtain predictions for individual movement and scent marking behavior.

The results of fitting the model to the central pack at Hanford provides empirical support for the characteristic behavioral rules underlying the Lewis and Murray (1993) carnivore home range model. In particular, the results of the likelihood analysis provide support for a formulation in which foreign scent marks influence the movement behavior of individuals (Eqs. 8 and 9). This formulation provides a better fit to observed

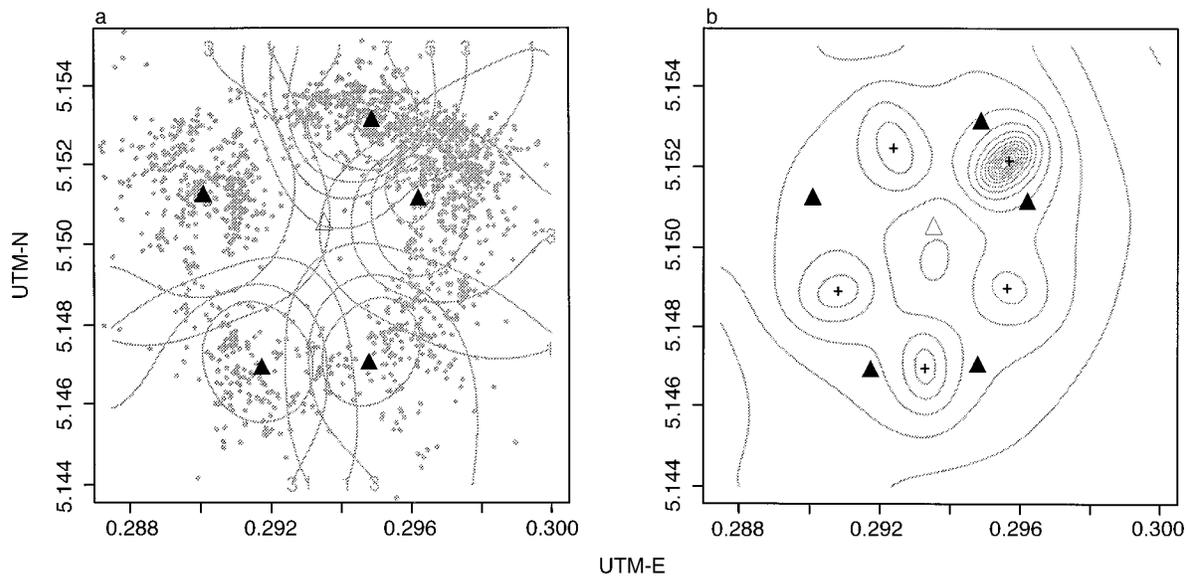


FIG. 5. (a) Contour lines show the predicted home range pattern at Hanford ALE following removal of the Hopsage pack. The patterns of space use prior to removal are shown by the fitted probability density functions in Fig. 2b and the relocation data (\bullet) (this figure). The location of the former home range center of Hopsage pack (Δ) and the locations of the home range centers of the remaining packs (\blacktriangle) are also shown. (b) Contour lines showing the expected new pattern of total scent mark density following the removal of the Hopsage pack (the pattern of scent mark density prior to removal is shown in Fig. 3). Peaks in scent mark density are indicated (+). Scent mark densities across the domain vary in the range 0.9–15.1, in rescaled units (Eq. 9), shown using a contour interval of 1. Axis scales are in terms of millions of meters.

relocation patterns than Eq. 7, in which individuals exhibit a constant bias in movement direction (Table 1).

The underlying formulation of the Lewis and Murray (1993) carnivore home range model of movement in response to the scent marks of neighboring packs results in home ranges whose size and shape are influenced by the location of neighboring home ranges. This effect, particularly apparent in the regional home range fit at Hanford (Fig. 3b), contrasts with the biologically unrealistic property of statistical home range models and the constant-bias mechanistic home range model (Holgate 1971), where home ranges are completely uninfluenced by the presence of neighboring ranges. The mutual interdependency in home range size and shape of neighboring packs captured by this formulation enables the model fits to be used to predict the consequences of pack introduction or removal (Fig. 5).

The shape of the probability density functions for the regional fit at Hanford indicates uniform space use by packs in the home range interior and well-defined home range boundaries. Their shape implies relatively exclusive territories, differing markedly from the typical distributions obtained using statistical home range models, which are often inappropriately peaked and have unrealistically long tails (Schoener 1981). Comparing the fits for the six contiguous packs (Fig. 2a) to that obtained from fitting to a single group (Fig. 1b) suggests that simultaneously fitting the model to relocation data collected on adjacent groups results in a

much better characterization of home range boundaries, capturing variation in the degree of exclusivity in space use along different boundaries.

The ability of the carnivore home range model to accurately represent home range patterns at the periphery of the study area was limited, due to the influence of the boundary conditions. If home ranges are located in a restricted area, such as a steep sided valley, specifying zero-flux boundary conditions (Eq. 11) around an appropriately shaped domain will accurately represent how these natural barriers to movement affect home range patterns within the region. In cases such as those presented here, where there are no apparent landscape boundaries, the artificial influence of the boundary conditions on home range patterns can be mitigated by simulating the home ranges of adjacent packs in addition to the home range(s) of interest. As shown in Fig. 1b, it is not necessary to have relocation data for peripheral packs. Simply specifying the locations of neighboring home range centers, and using the model to simulate the movement and scent-marking behavior of individuals in these packs, provides a method of predicting the position and shape of the home range boundaries between the packs of interest and the adjoining packs.

Just two parameters were used to describe the movement scent marking behavior of individuals in all six packs. The home range model (Eqs. 8 and 9), can be modified to include other relevant details of home range behavior, such as variation in group size, and the effects

of additional orientation cues on individual movement, such as resource availability and landscape heterogeneity (Moorcroft 1997). These more detailed implementations increase the numerical cost of model fitting however, because the maximum likelihood fitting procedure (Eq. 12) involves repeated numerical simulation of Eqs. 8 and 9 in two-dimensional (x, y) space for different parameter combinations. For the simple two-parameter model implementations presented here, it was possible to solve the equations by the simple and robust, though computationally intensive, procedure of solving the corresponding time-dependent problem. Further progress with more detailed implementations of the model will require more sophisticated numerical methods to solve the steady-state Eqs. 8 and 9 directly.

More generally, our analysis shows that a mechanistic framework for home range analysis provides a method for directly integrating theoretical and empirical studies of animal home range patterns. Formulating and applying models, in which predicted patterns of space use are formally scaled from an individual-level description of movement and interaction behavior, in contrast to earlier descriptive approaches, provides a methodology for directly testing hypotheses regarding the factors governing home range patterns. This, in conjunction with an ability to make predictions for individual behavior and changes in home range patterns following perturbation, allows for the development of a quantitative, reductionist understanding of animal home range patterns.

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