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Mapping behavioral landscapes for animal movement: a finite mixture modeling approach

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Abstract. Because of its role in many ecological processes, movement of animals in response to landscape features is an important subject in ecology and conservation biology. In this paper, we develop models of animal movement in relation to objects or fields in a landscape. We took a finite mixture modeling approach in which the component densities are conceptually related to different choices for movement in response to a landscape feature, and the mixing proportions are related to the probability of selecting each response as a function of one or more covariates. We combined particle swarm optimization and an expectation-maximization (EM) algorithm to obtain maximum-likelihood estimates of the model parameters. We used this approach to analyze data for movement of three bobcats in relation to urban areas in southern California, USA. A behavioral interpretation of the models revealed similarities and differences in bobcat movement response to urbanization. All three bobcats avoided urbanization by moving either parallel to urban boundaries or toward less urban areas as the proportion of urban land cover in the surrounding area increased. However, one bobcat, a male with a dispersal-like large-scale movement pattern, avoided urbanization at lower densities and responded strictly by moving parallel to the urban edge. The other two bobcats, which were both residents and occupied similar geographic areas, avoided urban areas using a combination of movements parallel to the urban edge and movement toward areas of less urbanization. However, the resident female appeared to exhibit greater repulsion at lower levels of urbanization than the resident male, consistent with empirical observations of bobcats in southern California. Using the parameterized finite mixture models, we mapped behavioral states to geographic space, creating a representation of a behavioral landscape. This approach can provide guidance for conservation planning based on analysis of animal movement data using statistical models, thereby linking connectivity evaluations to empirical data.

Key words: circular data; conservation biology; hierarchical mixture of experts; landscape connectivity; landscape ecology; Lynx rufus; *particle swarm optimization.*

Introduction

Movement of individual animals in response to landscape features plays a role population dynamics, population genetics, disease transmission, and many other ecological processes; therefore, understanding the movement of individual animals in landscapes is of great importance in many areas of ecology and conservation biology (van Vuren 1998, Tracey 2006, Morales et al. 2010). Landscape features may consist of discrete objects or continuous fields. Conceptually, *object orientation* refers to movement in relation to objects in a landscape such as prey items or resource patches (Jander 1975, Lima and Zollner 1996). Further, *taxis* refers to movement in response to continuous fields such as temperature, moisture, or elevation (i.e., gradients; Benhamou and Bovet 1992). Qualitatively, an animal may show attractive, repulsive, or neutral movement responses to these landscape features (Jander 1975, Lima and Zollner 1996). Movement data for individual animals are often collected using field techniques such as radiotelemetry or Global Positioning System (GPS) telemetry. Data on landscape features are often collected via remote sensing, ground measurement using GPS, or other techniques. Due to these technological advances, data required for analyzing movement behavior in response to landscape features are becoming increasingly available.

Over the past decade, great advances have been made in modeling animal movement behavior. This includes the development of a general state-space modeling (SSM) framework for animal movement in which true animal locations are modeled by a process model, while the probability of the data conditional on the true state

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is described by an observation model (Patterson et al. 2008, Schick et al. 2008). The state-space modeling approach has been applied in several movement modeling efforts. Tracey et al. (2005) developed a set of statistical models for the analysis of individual animal movement data in relation to a single type of landscape feature. In these models, the concentration parameter of a von Mises distribution for response angle changes based on the animal's location relative to the location of an object. This approach allows for nonlinear models, but the forms of nonlinearity are restricted to exponential and logistic functions, and the movement response is based on a single probability density. Recently, animal movement models that combine movement, resource selection, and home range of an animal have been developed (e.g., Dalziel et al. 2008, Christ et al. 2008, Johnson et al. 2008, Forester et al. 2009). Most of these models incorporate covariates in a probability density function of bivariate locations rather than turn angles and move length, and it is not always straightforward to assess the effect of landscape features. Furthermore, these models are formulated using techniques such as kernel smoothing, and the statistical inference is often computationally expensive. More recently, Hooten et al. (2010) developed agent-based models for movement in which latent variables for residency and movement were modeled on a lattice as a function of environmental covariates with the same spatial support. This approach is likely to have many useful applications, but it requires space to be discretized and inference about the nature of movement appears to be indirect, mediated through the latent variables. Tracey et al. (2011) developed a semiparametric regression approach using neural networks to relate the movement model parameters of probability distributions to covariates associated with landscape features without having to discretize space. While fully connected feedforward neural networks have proven useful in modeling animal movement (Dalziel et al. 2008, Tracey et al. 2011), neural network parameters are not directly interpretable in terms of animal behavior, so inference can be made only about the relationship between movement and landscape features in terms of the responses produced by the network.

Other network-based approaches to modeling movement behavior are possible. For example, Jacobs et al. (1991) and Jordan and Jacobs (1994) developed mixture of experts (ME) and hierarchical mixture of experts (HME) models in the field of artificial intelligence. In this framework, the model consists of a set of *expert networks*, where each expert network models a response to a vector of inputs. However, some expert networks perform better in some regions of the input space than others. Thus, a second *gating network* controls the selection of expert networks based on the position in input space. From a statistical perspective, these can be viewed as finite mixture models (FMMs). In FMMs, a distribution is formed by a weighted sum of component probability densities (McLachlan and Peel 2000). The weights, referred to as mixing proportions, sum to 1. The mixing proportions can depend on inputs (i.e., covariates; McLachlan and Peel 2000).

We consider finite mixture models as a viable alternative approach for modeling complex movement behavior in relation to a landscape feature consisting of either a continuous field or discrete objects. From a biological perspective, the components are considered to be different behavioral responses that produce the observed move angles, move distances, or both over discrete time intervals. These responses are interpreted as movement patterns with specific functions, as in the *movement phases* described by Nathan et al. (2008) or *behavioral modes* described by Patterson et al. (2008). The mixing proportions, which are the probabilities of selecting each response, describe the selection of a response by an animal with a given local environment and other factors such as an animal's internal state. These factors are described by covariates associated with each observation and are used to model the mixing proportions. For example, if an animal is closer to a particular object, then it may have a higher probability of choosing to avoid the object. Thus, our approach contains many of the elements in the general conceptual framework for modeling animal movement described by Nathan et al. (2008). As a result, the FMMs we describe expand the capabilities of the models presented by Tracey et al. (2005) because they allow movement responses to change in complex ways and they allow for a range of movement responses to be utilized. Furthermore, unlike neural networks, a behavioral interpretation of the finite mixture model parameters is possible.

Lima and Zollner (1996) discussed the need for relating animal behavior and landscape features, and described *information-based* modeling approaches in which animal behavior is dependent on the surrounding landscape. More recently, Bakian et al. (2012) proposed the concept of a *behavioral landscape* in which animal behaviors are mapped by a model to geographic space. They demonstrated their approach for foraging and vocalization behavior of Willow Flycatchers (*Empidonax traillii adastus*). In their study, foraging and vocalization behaviors could be directly observed and associated with the animal's location. However, for studies of movement via biotelemetry, movement behavioral states of a study animal are typically not directly observed. However, using the FMMs, we are able to both group observed movements into behavioral states and characterize movement behavior within the states. Furthermore, these models directly relate movement behavior and the local landscape as described by Lima and Zollner (1996).

Mammalian carnivores such as bobcats (*Lynx rufus*) are sensitive to habitat loss and fragmentation due to urbanization (Crooks 2002, Gehrt et al. 2010), a leading agent of habitat destruction and primary threat to biodiversity (Wilcove et al. 1998, Czech et al. 2000, McKinney 2002, McDonald et al. 2008). These impacts

TABLE 1. Bobcat (*Lynx rufus*) data summary from remote-sensing sources in Orange County, California, USA, in 2003.

Bobcat	Gender	Tracking interval	No. observations	Area of use (km^2)†	Urbanization‡
$LYRU_1$	male	Jan–Jul	184	3.97	0.00–0.45
$LYRU_2$	female	Jan–Jul	142	2.16	0.00–0.36
$LYRU_3$	male	Jan–Mar	195	24.19	0.00–0.14

† Area based on a 95% contour of fixed kernel density.
‡ Range of proportion of urbanization at observed bobcat locations.

are particularly evident in coastal southern California, a hotspot of biodiversity that has experienced rapid urbanization, leading to declines in the distribution and abundance of numerous species (Dobson et al. 1997), including bobcats (Crooks 2002, Tigas et al. 2002, Riley et al. 2003, 2006, 2010). Landscape ecologists have identified functional connectivity, the ability of animals to move among resource patches, as an important characteristic of landscapes (Taylor et al. 1993, Forman 1997, Taylor et al. 2006). Changes in functional connectivity have numerous demographic, genetic, and epidemiological implications for wildlife (Crooks and Sanjayan 2006). One goal of movement analysis is to understand how landscape changes alter functional connectivity for a species. In this paper, we applied the FMM approach to analyze movement of bobcats in an urbanized environment and then used the movement models to visualize behavioral landscapes.

In the *Methods*, we describe bobcat data collected by GPS telemetry and the urban land cover data. We present the general structure of finite mixture models for move angles and the specific models we applied to the bobcat GPS telemetry data and urban land cover data. We also describe an optimization procedure for obtaining parameters estimates and standard errors, and inference using the models. Finally, we describe how to use the models to relate locations in geographic space to bobcat movement behaviors. In the *Results*, we describe the results of the analysis of bobcat movement in relation to urban development and give an example of a behavioral landscape generated from a model from one of the bobcats. In the *Discussion*, we provide an ecological interpretation of the results and discuss future research directions. By mapping movement behavioral states on the landscape, we can better understand movement of animals in their environment, identify areas that might enhance or inhibit functional connectivity, and identify areas that pose higher risks to animals.

METHODS

Movement and landscape data

We used data from a bobcat GPS telemetry study that was conducted to better understand bobcat home range, habitat use, movement response to roads, and the effects of habitat fragmentation due to urban development in Orange County, California, USA (Lyren et al. 2006; see Plate 1). Bobcat locations were collected at 15- or 30-min time intervals using a collar with a GPS receiver and data logger placed on each study animal. Locations were only collected during night, between the hours of 22:00 and 01:00, several nights per week.

In order to better understand bobcat movement responses to urbanization, we applied the FMM models to GPS telemetry data for three bobcats (a number we deemed sufficient to assess our finite mixture modeling approach) identified as $LYRU_1$, $LYRU_2$, and $LYRU_3$. These animals were selected for this analysis from a larger set of 16 animals based on (1) if a 15-min relocation time interval was used for the animals, (2) the number of observations per animal, and (3) how many locations were in proximity to urban areas. During exploratory data analysis, we evaluated temporal autocorrelation in move angles by conducting Rayleigh tests for the uniformity of the turn angle distributions for each bobcat. For $LYRU_1$ we rejected the null ($\chi^2 = 18.383$, $P = 0.0001$), while for $LYRU_2$ ($\chi^2 = 0.3855$, $P = 0.825$) and $LYRU_3$ ($\chi^2 = 1.4780$, $P = 0.478$), we failed to reject the null. Although temporal autocorrelation in move angles appears to be present for $LYRU_1$, the models we present do not assume that move angles are identically independently distributed (iid). Rather, the models assume that move angles are independent after conditioning on the landscape (or other) covariates used in the model. Often, programmed location acquisition by the GPS receivers fails due to terrain, vegetation cover, or lack of satellite availability. However, the missing observations can be ignored in the analysis. Additionally, if two consecutive locations were co-located, then the move distance is 0.0 and the move angle is undefined. In these cases, we omitted such observations from the analysis. Properties of the data for the three selected bobcats are summarized in Table 1. Note that the movement paths of $LYRU_1$ and $LYRU_2$ partially overlapped, while $LYRU_3$ had a larger area of activity that did not overlap with the others (Fig. 1).

Spatial data for 30-m resolution urban land use were developed using impervious surface data from the National Land Cover Database (NLCD; Homer et al. 2004) and land use from the Southern California Association of Governments (SCAG). Areas identified as urban, residential, or industrial use by the SCAG or having greater than 15% impervious surface in the NLCD data were classified as urban. This raster was developed for a 5971.2-km^2 area that covered the entire extent of Orange County and parts of Los Angeles County, California. Within the area where bobcats were GPS tracked (shown in Fig. 1), raster cells classified as

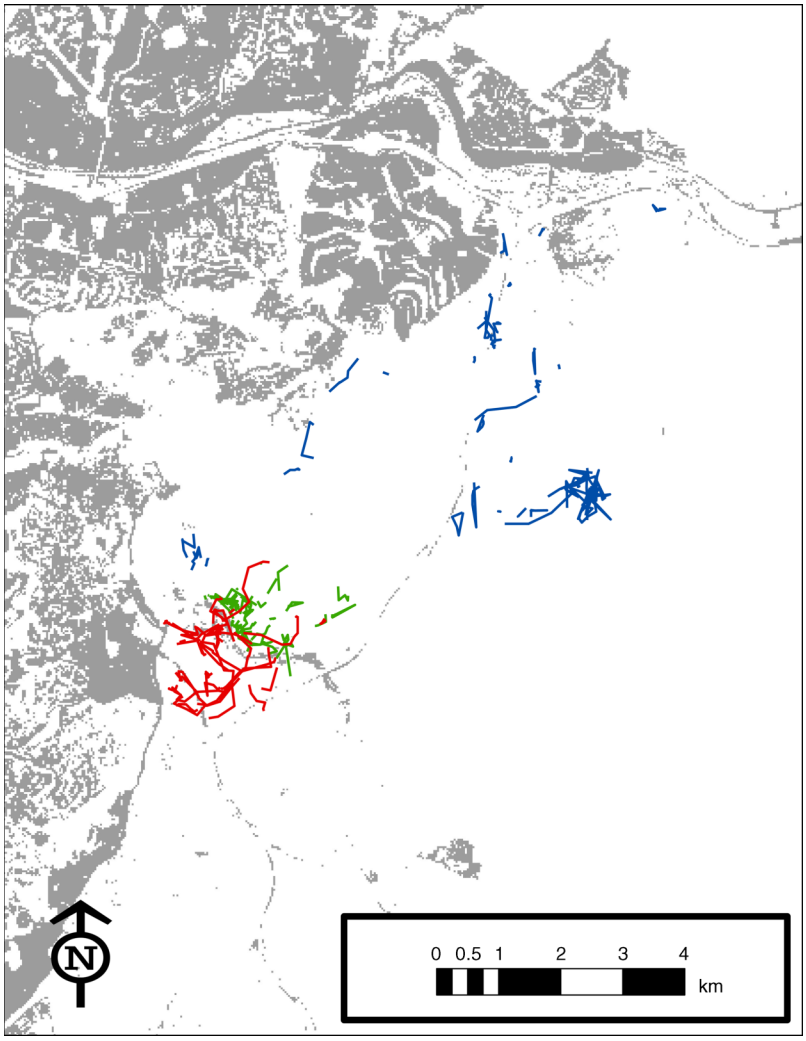

FIG. 1. Bobcat (*Lynx rufus*) location data were collected by Global Positioning System (GPS) telemetry, and landscape data were compiled from remote-sensing sources in Orange County, California, USA. The map shows urban land cover in gray. Observed move steps for bobcat $LYRU_1$ are shown in red, those for bobcat $LYRU_2$ are shown in green, and those for bobcat $LYRU_3$ are shown in blue.

urban were compared to U.S. Geological Survey Digital Orthoimagery Quarter Quadrangles (DOQQ) imagery (*available online*)[7] and corrected where large discrepancies were found. The final urban land cover data raster cells held an integer corresponding to a land cover category (0 = not urban, 1 = urban; Fig. 1). Using this categorical raster, we computed the proportion of cells classified as urban within moving windows centered on the raster cells with a radius 200 m. We refer to this quantity as X_{urb} and use it as a covariate in the functions for component mixing proportions. At each bobcat location, we calculated the direction of increasing urbanization using the raster of X_{urb} values. If this raster had no slope in the first-order neighborhood around a bobcat location, we set this direction to 0.0 radians, which resulted in a von Mises distribution being fit to the bobcat move angles when no urbanization is present. The range of X_{urb} values at the observed bobcat locations is given in Table 1.

[7] http://nationalmap.gov

Finite mixture model for move angles

Movement data notation.—Here we describe the notation for the data used in the model formulations. Let $i = 1, \ldots, I$ index observations for a particular animal. For the ith observation, we let $\mathbf{s}_i = (s_{i,1}, s_{i,2})'$ denote an observed location of an animal, where $I + 1$ locations at approximately regular time intervals have been observed. These data are becoming common for many species with increased use of GPS telemetry. Let $D_i = ||;\mathbf{s}_i - \mathbf{s}_{i+1}||^2$ denote the move distance between animal locations $\mathbf{s}_i$ and $\mathbf{s}_{i+1}$ and let $Y_i = \text{atan2}(s_{i+1,2} - s_{i,2}, s_{i+1,1} - s_{i,1})$ denote the move angle between animal

locations. Note that this angle is undefined if $\boldsymbol{s}_i = \boldsymbol{s}_{i+1}$; therefore, we omit any zero-length move steps from the analysis. Thus, the ith move can be modeled as

$$\mathbf{s}_{i+1} = \mathbf{s}_i + D_i \times \Big(\cos(Y_i), \sin(Y_i)\Big)' \tag{1}$$

where $i = 1, \ldots, I$.

For the ith observation, A_i is an observed angular covariate related to the object or field to which we are modeling the animal movement response. In our analysis, A_i is the direction of a gradient in the density of urbanization around the ith bobcat location; however, this covariate could be the angle from the ith location to a vector-based feature such as the nearest point on a road or the aspect of a continuous surface represented by a raster. Further, let, $j = 0, \ldots, J$ index covariates and $\mathbf{X}_i = (X_{0,i}, \ldots, X_{J,i})$ be a vector of covariates related to the movement response where $X_{0,i} = 1$ corresponds to the constant in the regression model. In our analysis, the covariate $X_{1,i}$ is the density of urbanization within 200 m of each bobcat location, which we will refer to as X_{urb} when discussing the specific models applied in this paper. We define the *response angle* as $R_i = (Y_i - \mathrm{A}_i)\text{mod}(-\pi, \pi]$, which is the offset angle between Y_i and A_i.

General model formulation.—Let $g = 1, \ldots, G$ index finite mixture model components. The components are interpreted as movement behavior states of the animal, and we typically use the term *component* when discussing the model itself and *movement behavior state* (or simply *behavioral state*) when interpreting the meaning of a specific model. We model the ith move angle Y_i, given the angular covariate A_i as a mixture of von Mises distributions, as follows:

$$f(Y_i \,|\, \mathbf{X}_i, A_i; \boldsymbol{\beta}, \eta) = \sum_{g=1}^{G} p_g(\mathbf{X}_i, \boldsymbol{\beta}) f_g(Y_i \,|\, A_i; \eta_g). \tag{2}$$

In Eq. 2, we use the multiple logit model for the mixing proportions. The gth mixing proportion is

$$p_g(\mathbf{X}_i, \boldsymbol{\beta}) = \exp(\boldsymbol{\beta}_g' \mathbf{X}'_i) \left\{ \sum_{g=1}^{G} \exp(\boldsymbol{\beta}_g' \mathrm{X}_i') \right\}^{-1} \tag{3}$$

where $\mathbf{X}_i$ is a vector of covariates related to the ith observation and $\beta = (\boldsymbol{\beta}_1', \ldots, \boldsymbol{\beta}_G')'$ is a vector of parameters. The first category ($g = 1$) is established as our reference category by setting $\boldsymbol{\beta}_1 = 0$ to ensure identifiability and $\boldsymbol{\beta}_g = (\beta_{g,0}, \ldots, \beta_{g,J})'$ when $g > 1$. Note that $\sum_g p_g(\mathbf{X}_i; \beta) = 1$. In essence, the choice to move in an angle described by a component distribution is a multicategory logistic function of covariates $\mathbf{X}_i$ associated with the animal at location $\mathbf{s}_i$. Moreover, the gth component density,

$$f_g(Y_i; A_i, \boldsymbol{\eta}_g) = \left\{2\pi I_0(\kappa_g)\right\}^{-1} \exp\Big\{\kappa_g \cos(Y_i - \mu_g - A_i)\Big\} \tag{4}$$

is a von Mises probability density function (pdf), where $\boldsymbol{\eta}_g = (\mu_g, \kappa_g)'$, $\mu_g \in (-\pi, \pi]$ is the mean response angle, and $\kappa_g \geq 0$ is the concentration parameter. Furthermore, $\{2\pi I_0(\kappa_g)\}$ is a normalizing constant, and $I_0(\kappa_g)$ is a modified Bessell function of the first kind and zero order.

More complicated distributions for response angles to landscape features may be multimodal. To accommodate this situation, each mixture component g may in turn be a mixture of $s_g > 0$ subcomponents as follows:

$$f_g(Y_i \,|\, A_i;\ \boldsymbol{\eta}_g) = \sum_{k=1}^{s_g} q_k(\phi_g) f_{g,k}(Y_i \,|\, A_i; \mu_{g,k}, \kappa_{g,k}) \tag{5}$$

and

$$q_k(\phi_g) = \exp(\phi_k) \left\{ \sum_{k=1_g}^{s_g} \exp(\phi_k) \right\}^{-1}. \tag{6}$$

Thus, the component pdf in Eq. 5 has parameters $\boldsymbol{\eta} = (\boldsymbol{\eta}_1', \ldots, \boldsymbol{\eta}_G')'$, where $\boldsymbol{\eta}_g = (\boldsymbol{\mu}_g', \boldsymbol{\kappa}_g', \phi_g')'$, $\boldsymbol{\mu}_g = (\mu_{g,1}, \ldots, \mu_{g,s_g})'$, $\boldsymbol{\kappa}_g = (\kappa_{g,1}, \ldots, \kappa_{g,s_g})'$ and $\phi_g = (\phi_{g,1}, \ldots, \kappa_{g,s_g})'$. All elements of $\boldsymbol{\mu}_g$ are on $(-\pi, \pi]$, all elements of $\boldsymbol{\kappa}_g \geq 0$, and all elements of $\phi_g \in \Re$. We let $\phi_{g,1} = 0$ to ensure identifiability. The behavioral motivation for incorporating subcomponents is that once an animal has selected a response based on the covariates, the distribution for the response variable may still be multimodal, and hence, better modeled as a mixture of subcomponent distributions. An example of this case is when an animal exhibits repulsion to a landscape feature; it may avoid it by moving with response angle of $\pm\pi/2$ radians in an effort to circumvent it. This FMM approach is in the spirit of the hierarchical mixture of experts (HME) approach taken by Jordan and Jacobs (1994), and reflects hierarchical decision making by an animal. The total number of parameters in a move angle model is $(J + 1)(G - 1) + 3\sum_{g=1}^{G} s_g - G$, where J is the number of covariates, G is the number of components, and s_g is the number of subcomponents in the gth component. Additional models that include move distance response are described in online Appendix A.

Candidate models.—Following from the general model formulation, we considered 11 alternative move angle models in our analysis of the bobcat data. In the first two models (A and B; Table 2), no covariates were used in the functions for the mixing proportions; that is, the mixing proportions were constant. Model A had one component and model B had two components. These two models permitted move angle responses to the angular covariates, but did not incorporate responses to the landscape with respect to the mixing proportions. Therefore, we used them for comparison to the remaining nine models (C–K; Fig. 2 and Table 2) that do incorporate mixing proportions as a function of landscape covariates. In these models, the mixing proportions were a function of a single covariate (X_{urb}), the proportion of urbanization within 200 m of a bobcat

TABLE 2. Summary of specific models used in the examples.

Model (m)	Components	sub1	sub2	sub3	sub4	Parameters
A	1	1	0	0	0	2
B	1	2	0	0	0	5
C	2	1	1	0	0	6
D	2	2	1	0	0	9
E	2	2	2	0	0	12
F	3	1	1	1	0	10
G	3	2	1	1	0	13
H	3	2	2	1	0	16
I	4	1	1	1	1	14
J	4	2	1	1	1	17
K	4	2	2	1	1	20

Notes: The network structure for models C–K is shown in Fig. 2. Also shown are the number of components in the model; the number of subcomponents in the first, second, third, and fourth components, sub1, sub2, sub3, and sub4, respectively; and the number of parameters in the model.

location, although the general formulation can handle multiple covariates. The nine models can be illustrated as a network of choices (i.e., gating networks in hierarchical mixture of experts) terminating with a component (or subcomponent) of the finite mixture model (Fig. 2). For example, in model D, the animal may choose from two components for a movement response. One component (left) is a mixture of two subcomponents, so the response distribution could be bimodal. The other component (right) has only one subcomponent, so the response would be unimodal. If the proportion of urbanization surface is flat within the 200-m neighborhood about an animal location, we set the angle covariate to 0.0 and fit a von Mises distribution to the animal move angle.

Model fitting and inference

We adopted a maximum-likelihood approach for statistical inference. However, optimization to obtain the maximum-likelihood estimates for FMMs can be very difficult because numerous local optima often exist. The expectation-maximization (EM) algorithm typically used with mixture models is prone to becoming trapped by local optima (McLachlan and Peel 2000). To overcome this difficulty, we employed particle swarm optimization (PSO), a stochastic optimization algorithm originally inspired by flocking behavior of birds, to search for the general area of the global optimum (Poli et al. 2007). Application of the PSO was followed by an EM algorithm to converge on the maximum-likelihood estimates (MLEs) for the model parameters. We provide details of this approach in Appendix B, and examples of fitting models to simulated data are given in Appendix C. The optimization code was implemented in R (R Development Core Team 2010). For the PSO step of the procedure, we used the canonical PSO implemented in the psoptim function (Bendtsen 2011). In the EM algorithm, we consider each observation to be augmented with a label that identifies the model component that generated the observation. The observed data plus the unobserved component labels constitutes the complete data. Each iteration of the optimization procedure consists of an expectation step (E-step) in which the component labels are set to their expected values and a maximization step (M-step) in which the complete data log-likelihood is optimized. We used the R function nlm to optimize the complete data log-likelihood in the M-step. We obtained standard errors based on the asymptotic variance calculated from the inverse of the numerically computed Hessian matrix returned by the R numDeriv package using the hessian function call on the observed negative log-likelihood function (Gilbert 2011). Bootstrap procedures are also available for

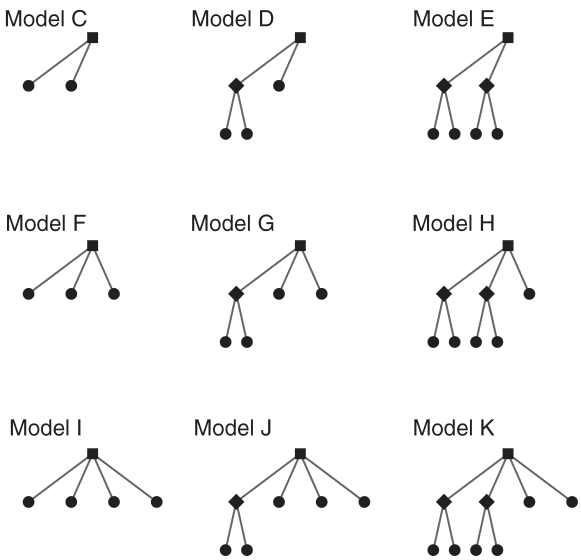

FIG. 2. An illustration of the gating network structure for finite mixture models C–K. Each row, from top to bottom, corresponds to models with an increasing number of components. Each column, from left to right, corresponds to models with an increasing number of model components with two subcomponents. Given sufficient data, any number of components and subcomponents may be specified. Nodes at the root of the trees shown as squares represent multiple logit functions, nodes shown as diamonds represent logistic functions for subcomponent selection, and leaf (terminal) nodes shown as circles represent von Mises distributions. Additional details for the models are given in Table 2.

estimating the standard errors for the model parameters (see, e.g., McLachlan and Peel 2000), but they tend to be more computationally intensive.

We used an information-theoretic approach to model selection (Burnham and Anderson 2002). For each model from A to J, we computed the incomplete data negative log-likelihood value, the small sample variant of Akaike's information criterion, AIC_c, ΔAIC_c values, the rank of each model based on ΔAIC_c, and the Akaike weight, W, for each model. Akaike's information criterion (AIC) is interpreted as the relative expected Kullback-Leibler distance between a model and the true process that generated the data; thus, the model with the lowest AIC_c is estimated to be the model that best approximates this unknown process. The ΔAIC_c value for a model is calculated as its AIC_c minus the AIC_c of the best model. Thus, for the best model $\Delta AIC_c = 0$. The models are then ranked relative to each other based on ΔAIC_c in ascending order. The model probability, or Akaike weight, for a model is computed as $W = \exp\{-(1/2)\Delta AIC_c\}/\Sigma\exp\{-(1/2)\Delta AIC_c\}$. We can consider the weight of evidence for all models or perform multi-model inference, but here we focus our presentation and interpretation of the results on the model with the lowest AIC_c.

Mapping behaviors to the landscape

Producing the behavioral landscapes for each bobcat from the finite mixture models consisted of two steps. First, based on the component (i.e., movement behavior state) probability density functions for response angle in Eq. 4, we were able to quantitatively and qualitatively describe the movement response associated with each state. The attractive, repulsive, and neutral qualitative movement responses can be interpreted via the fitted movement models. In the models we have considered here, a neutral response occurs when the distribution of the response angle is fairly uniform; that is, it has a low concentration parameter. Attraction occurs when the mean angle of the response distribution is near 0.0 and increases with the concentration parameter. A repulsive response can take two forms. The animal may show repulsion by moving away from the landscape feature if the mean response angle is near $\pm\pi$. The strength of the repulsion will increase with the concentration parameter of the response angle distribution. Alternatively, an animal may show a repulsive response by moving perpendicular to the angle of a landscape feature. In this case, the mean response angle will be near $\pm\pi/2$ and the repulsion will increase with the concentration parameter. In our example, the landscape features are areas classified as urban development, and our covariate related to this feature is X_{urb}. This response then relates to movement toward areas of roughly the same amount of urbanization around the bobcat; that is, parallel to the edge of the urban area. Therefore, we refer to this as a *parallel* response. An animal can engage in a parallel response by turning approximately $\pi/2$ radians to the left or right. We hypothesize that an animal will assume this response in order to avoid a landscape feature when it interferes with movement toward another goal. These different qualitative responses may occur over different ranges of the covariate(s) used to model the mixing proportions.

In the second step, we applied the parameterized multiple logit model for mixing proportions given by Eq. 3 to the raster for the urban covariate X_{urb}, which yields the probability of each behavioral state at each raster cell. These probability surfaces for each behavioral state were combined into a single map by assigning the component number (g) for the most probable state to each cell in a categorical raster. Taken together, we were able to identify the most probable behavioral response to urban development at each point in space and describe the nature of that response.

From these maps, we can make predictions about the permeability of different areas of a landscape or evaluate the functional connectivity of movement corridors. For example, some corridors may be dominated by an urban avoidance response (Fig. 3A). This may occur if a corridor is too narrow. Others might be strongly influenced by a tendency to move parallel to the urban edge, which may actually enhance connectivity by directing movement through the corridor (Fig. 3B). If a corridor is wide enough, movement in the interior may be similar to movements where there is no influence of urbanization (Fig. 3C). In this case, movement may actually be slower through these areas because of a lack of strong directionality to the movement and potentially higher residency due to the availability of resources. Thus, in this approach, connectivity is dictated by landscape structure and movement behavior, which is perfectly consistent with definitions of functional connectivity (Taylor et al. 1993, 2006).

Results

Parameter estimation and model selection

The resident male bobcat $LYRU_1$ showed little response when the proportion of urbanization (X_{urb}) was low, but then transitioned through movement parallel to the urban edge to strong movement away from urbanization as X_{urb} increased. The best approximating model for $LYRU_1$ was model H (Table 3). Parameters and standard errors for this model are given in Table 4. All other models had $\Delta AIC_c \geq 2.0$, and four models had $\Delta AIC_c \geq 10.0$ (Table 3). Model H had three components (Fig. 2). The first and second components had two subcomponents each, and the third component had one subcomponent. The mixing proportion for the first component was near 0.0 when $X_{urb} = 0.0$, increased to a peak of about 0.7 when $X_{urb} \simeq 0.18$, and then declined back to near 0.0 as X_{urb} increased to its maximum observed value of 0.45 (Fig. 4). The first component had one subcomponent that produced strong movement parallel to the urban edge (to the left) and a second subcomponent that produced movement

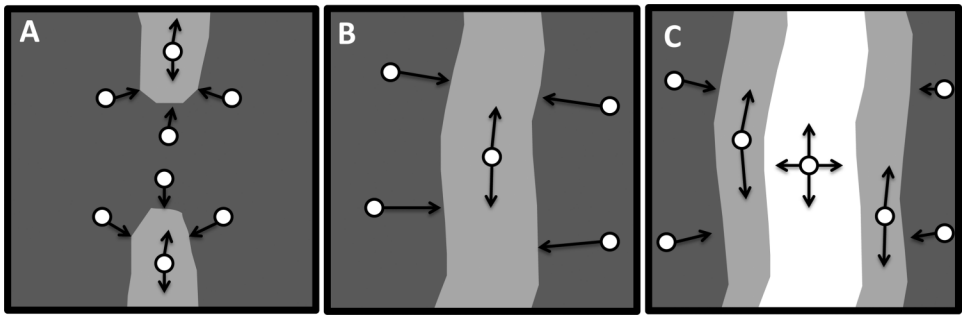

FIG. 3. A conceptual illustration of the application of a behavioral landscape to evaluating functional connectivity through an urbanized area. Dark gray areas are those where an animal shows strong avoidance of the landscape. Light gray shows areas where the animal most likely moves parallel to the landscape features it avoids. White areas are those where the animal responds in a neutral or attractive manner. The white-filled points with arrows show animal response to different parts of the landscape. In panel (A), movement through the corridor is unlikely because of the avoidance response that dominates the central part of the area. In panel (B), movement through the area is likely; in this case, the animal may actually move rapidly through the area because of its parallel response to the urban edge. In panel (C), the corridor is intact; however, movement may be less directional because the weak movement response to urbanization in the interior area is less likely to direct movement through it. In this case, movement through the area may be slower than in panel (B).

TABLE 3. Results of fitting 11 alternative models to move angle data for three bobcats.

Bobcat and model	$-\ell(\beta, \eta)$	AIC_c	ΔAIC_c	Rank	W
$LYRU_1$					
A	334.62	673.32	10.76	8	0.00
B	332.51	675.36	12.81	9	0.00
C	331.89	676.26	13.71	11	0.00
D	326.02	671.07	8.52	6	0.01
E	324.77	675.36	12.81	10	0.00
F	324.99	671.26	8.71	7	0.01
G	319.09	666.32	3.77	3	0.09
H	313.65	662.55	0.00	1	0.62
I	319.25	668.98	6.43	5	0.02
J	313.62	664.92	2.37	2	0.19
K	311.10	667.36	4.81	4	0.06
$LYRU_2$					
A	258.12	520.33	7.94	10	0.01
B	256.14	522.72	10.33	11	0.00
C	250.83	514.28	1.90	4	0.13
D	248.08	515.53	3.14	6	0.07
E	246.82	520.06	7.68	9	0.01
F	245.91	513.50	1.11	2	0.19
G	241.77	512.38	0.00	1	0.34
H	239.52	515.39	3.00	5	0.08
I	241.48	514.26	1.87	3	0.13
J	239.47	517.89	5.50	8	0.02
K	235.28	517.50	5.12	7	0.03
$LYRU_3$					
A	358.38	720.83	20.34	11	0.00
B	348.60	707.51	7.02	8	0.02
C	348.38	709.21	8.71	9	0.01
D	343.88	706.73	6.24	6	0.02
E	338.37	702.45	1.96	2	0.20
F	343.02	707.23	6.73	7	0.02
G	336.24	700.49	0.00	1	0.52
H	335.61	706.28	5.78	5	0.03
I	341.08	712.50	12.00	10	0.00
J	333.59	704.65	4.15	4	0.07
K	329.28	703.38	2.89	3	0.12

Notes: The fitted response angle density for the model with the lowest AIC_c for each bobcat is shown in Fig. 4. The negative log-likelihood for each model is shown by $-\ell(\boldsymbol{\beta},\boldsymbol{\eta})$; AIC_c is the small-sample adjusted AIC; ΔAIC_c is the difference between the model AIC_c and the smallest AIC_c; and W is the model weight. Rank shows the rank of the model according to AIC_c in ascending order.

TABLE 4. Parameter estimates via maximum likelihood and standard errors (SE) for the top-ranked model H for bobcat $LYRU_1$, model G for bobcat $LYRU_2$, and model G for bobcat $LYRU_3$.

		$LYRU_1$		$LYRU_2$		$LYRU_3$	
Component	Parameter	Estimate	SE	Estimate	SE	Estimate	SE
1	$\mu_{1,1}$	1.98	0.07	−1.41	0.03	1.26	0.35
1	$\mu_{1,2}$	−0.37	0.13	−2.40	0.12	−1.55	0.05
1	$\ln(\kappa_{1,1})$	3.20	0.56	5.07	0.56	−1.09	0.40
1	$\ln(\kappa_{1,2})$	2.75	0.68	1.60	0.50	4.32	0.72
1	$\phi_{1,2}$	−0.35	0.50	1.28	0.53	−2.34	0.40
2	$\beta_{2,0}$	−8.61	4.59	−6.94	4.58	−4.17	1.58
2	$\beta_{2,1}$	38.80	19.92	37.31	20.12	48.65	21.33
2	$\mu_{2,1}$	2.69	0.03	2.45	0.07	−1.22	0.15
2	$\mu_{2,2}$	−1.11	0.61	...	...	...	...
2	$\ln(\kappa_{2,1})$	5.13	0.53	4.03	0.72	2.81	0.85
2	$\ln(\kappa_{2,2})$	−0.80	0.67	...	...	...	...
2	$\phi_{2,2}$	1.43	0.46	...	...	...	...
3	$\beta_{3,0}$	6.41	2.96	0.38	0.39	−9.79	4.73
3	$\beta_{3,1}$	−48.96	22.18	8.67	5.55	94.76	44.43
3	$\mu_{3,1}$	2.11	0.40	1.18	0.40	1.63	0.04
3	$\ln(\kappa_{3,1})$	−1.11	0.42	−0.77	0.60	5.38	0.88

Notes: Parameters are as follows: $\mu_{g,k}$ is the mean angle of the von Mises distribution for component g, subcomponent k; $\kappa_{g,k}$ is the concentration parameter of the von Mises distribution for component g, subcomponent k; $\phi_{g,k}$ is the mixing proportion for component g, subcomponent k; $\beta_{g,j}$ is the regression parameter for the component g, covariate j. This parameter is used in the multi-category logistic function used to compute the mixing proportion for component g as a function of X_{urb}. Ellipses (...) indicate that the parameter was not part of the model.

toward areas with more urbanization. The mixing proportion for the second component started at near 0.0 when $X_{\text{urb}} = 0.0$ and increased to near 1.0 as X_{urb} increased to 0.45, and had an inflection point at approximately 0.225 (Fig. 4). The second component had one subcomponent that produced strong movement away from urban areas, and a second subcomponent that was roughly uniform. The mixing proportion for the third component started at near 1.0 when $X_{\text{urb}} = 0.0$, declined to near 0.0 when X_{urb} reached 0.2, and had an inflection point at approximately $X_{\text{urb}} = 0.125$ (Fig. 4). The third component produced a response angle distribution that was roughly uniform. In summary, the model predicts movement roughly at random relative to the direction of increasing urbanization, transitioning to movement either toward areas of increasing urbanization or parallel to the urban edge, and then finally movement away from urbanized areas as the degree of urbanization increases (Fig. 4).

The resident female bobcat $LYRU_2$ had a similar response to $LYRU_1$ at high levels of X_{urb}, but showed more of a tendency to move parallel to the urban edge at lower levels of X_{urb}. The best approximating model for $LYRU_2$ was model G (Table 3). Parameters and standard errors for this model are given in Table 4. Seven of the models (A, B, D, E, H, J, and K) had $\Delta AIC_c \geq 2.0$, and model B had $\Delta AIC_c \geq 10.0$. Model G had three components. The first component had two subcomponents, and the second and third components had one subcomponent each (Fig. 2, Table 3). The mixing proportion for the first component was codominant with component 3 when $X_{\text{urb}} = 0.0$ and declined gradually, in a nearly linear fashion, as X_{urb} increased (Fig. 4). The first component had one subcomponent that produced a strong parallel (to the right) response and a second subcomponent that produced moderately strong movement away from areas of higher urbanization. The mixing proportion for the second component was small when $X_{\text{urb}} = 0.0$ and abruptly increased with increasing X_{urb} (Fig. 4). The mixing proportion function had an inflection point at approximately $X_{\text{urb}} = 0.25$ and approached a value of 1.0 when X_{urb} reach the maximum observed value of 0.36 (Fig. 4). The second component produced a strong movement response away from increasing urbanization. The mixing proportion for the third component was codominant with component 1 when $X_{\text{urb}} = 0.0$, reached its peak at about $X_{\text{urb}} = 0.16$, and then declined as X_{urb} increased further. This third component produced a roughly uniform response angle distribution. In summary, the model predicts movement parallel to or away from the urban boundary and then transition to movement away from urbanized areas as the proportion of urbanization within 200 m increases (Fig. 4).

The male bobcat $LYRU_3$ had a large-scale movement pattern that was different from the other bobcats and more consistent with dispersal behavior. Likewise, its response to urbanization based on the best approximating model G (Table 3) was qualitatively different. Parameters and standard errors for this model are given in Table 4. Nine of the models (A, B, C, D, F, H, I, J, and K) had $\Delta AIC_c \geq 2.0$, and two models (A and I) had $\Delta AIC_c \geq 10.0$. Again, model G had three components as described in the previous paragraph for $LYRU_2$. The mixing proportion for the first component started at nearly 0.0 when $X_{\text{urb}} = 0.0$, increased to near 1.0 as X_{urb} increased to its maximum observed value of 0.14, and had an inflection point at approximately $X_{\text{urb}} = 0.075$ (Fig. 4). This component had one subcomponent that produced strong parallel (to the right) movement and a

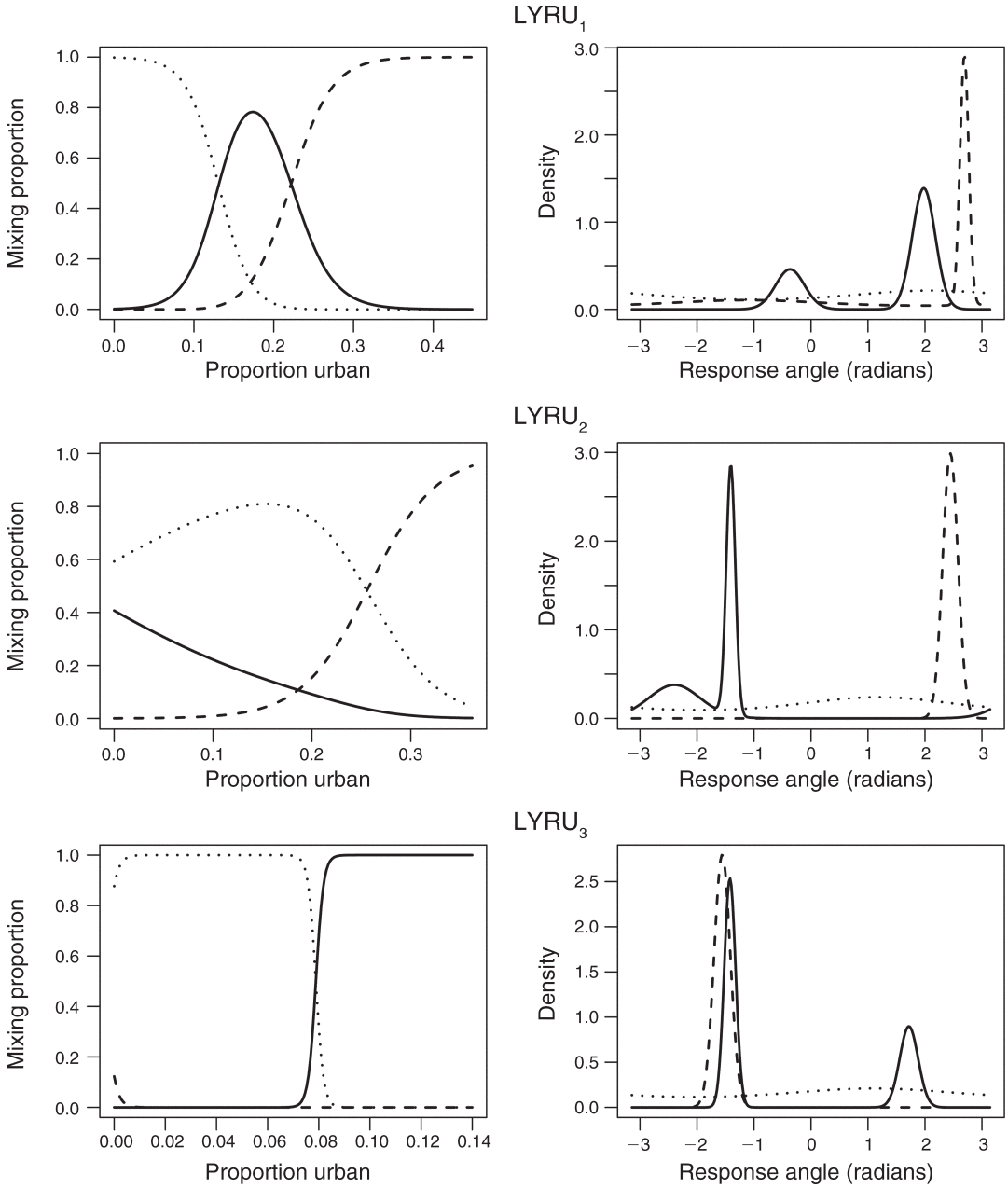

FIG. 4. Plots for mixing proportions (left column) and response angle probability density functions (right column) for each bobcat ($LYRU_1$, $LYRU_2$, and $LYRU_3$). The mixing proportions are a function of X_{urb}, the proportion of urban land cover within a 200-m radius of the bobcat locations. The response angle densities describe movement angles in relation to the angle of an increasing proportion of urbanization. Thus, a response angle of 0 radians corresponds to movement toward more urbanized areas, $\pm\pi$ radians corresponds to movement away from urban areas, and $\pm\pi/2$ corresponds to movement roughly parallel to the urban edge. Plots for bobcat $LYRU_1$ are shown in the top row, those for $LYRU_2$ are shown in the middle row, and those for $LYRU_3$ are shown in the bottom row. Functions for component 1 are shown as a solid line, component 2 as a dashed line, and component 3 as a dotted line.

second subcomponent that produced strong parallel (to the left) movement. The mixing proportion for the second component was approximately 0.15 when $X_{urb} = 0.0$ and then immediately declined to 0.0 as X_{urb} increased (Fig. 4). The second component produced a strong parallel (to the right) movement response to the urban boundary. The mixing proportion for the third component was near 1.0 when $X_{urb} = 0.0$, decreased abruptly to ~0.0 when X_{urb} reached 0.14, and had an inflection point at about $X_{urb} = 0.08$ (Fig. 4). This component had a response angle distribution that was approximately uniform. In summary, the model predicts roughly random movement in relation to urbanization and then transition to movement parallel to the urban

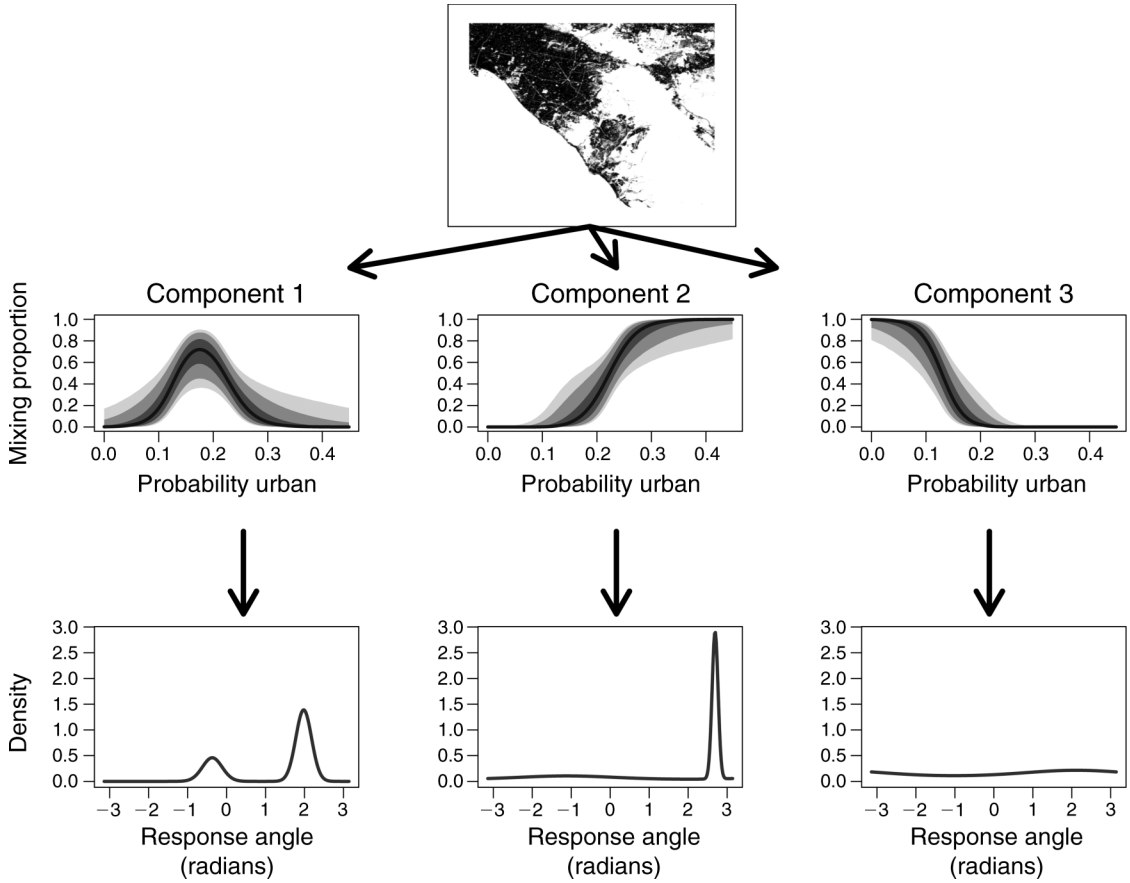

FIG. 5. The process of mapping movement behaviors in geographic space using the finite mixture models. Model H, fitted to data from bobcat $LYRU_1$, is used as an example. The raster of the proportion of urbanization within 200 m (X_{urb}) is used as input to the model (top). Each raster cell is assigned a probability that a movement behavior response will occur there by the mixing proportion functions of the finite mixture models (FMM; middle). The quantiles of the mixing proportions as a function of X_{urb}, based on 20 000 Monte Carlo samples, are shown as shaded bands, from outer to inner, for the intervals of 0.05–0.95, 0.10–0.90, and 0.25–0.75. The black line shows the median value for the mixing proportion. Finally, the move angle responses for each movement behavior state characterize the effect of urbanization on bobcat behavior (bottom), based on probability density functions. In this case, component (behavioral state) 1 corresponds to movement parallel to the urban boundary or slightly toward it, component 2 corresponds to strong avoidance of urban areas, and component 3 corresponds to a very weak response to urbanization.

edge in either the left or right direction as the degree of urbanization increases (Fig. 4).

Application

Overall, all three bobcats showed avoidance responses to the direction of increasing proportion of urbanization within 200 m of the observed locations. Bobcats $LYRU_1$ and $LYRU_2$ tended to move away with increasing urbanization (X_{urb}), whereas $LYRU_3$, which ranged more widely, had fewer locations in areas of high urbanization and tended to move parallel to the urban areas. For all three bobcats, the response angle densities were most concentrated at high values of X_{urb}. At low values of X_{urb}, $LYRU_1$ and $LYRU_3$ had response angle distributions were nearly uniform, while $LYRU_2$ had a concentrated response angle distribution that produced parallel (to the right) to the urban edge.

The locations where these movement behaviors occurred were visualized with maps of the behavioral landscape by applying the mixing proportion functions from model H for $LYRU_1$ to a raster of X_{urb} (Fig. 5). This process produced three rasters, one for the probability of each behavioral state occurring across the landscape (see Appendix D). From these rasters we produced a single categorical raster for the most probable behavioral response at each point in space (Fig. 6). Some areas could not be assigned a probability because either the gradient of the proportion of urbanized surface was zero (hence, flat) and so the direction of increasing urbanization was undefined, or the proportion of urbanization exceeded levels at the observed locations for $LYRU_1$ (i.e., 0.45). However, if the proportion of urbanization exceeded 0.45, it is reasonable to assume that $LYRU_1$ would also show strong avoidance for these areas. Similarly, if the

proportion of urbanization is 0.0, it is reasonable to assume that $LYRU_1$ would also show a weak (or null) response to urban because it did so at low proportions of urbanization. Where $0 < X_{urb} \leq 0.45$, we can assign a behavioral state from the FMM for $LYRU_1$. In this case, the first component of the FMM corresponded to a moderately strong tendency to move perpendicular to the direction of increasing urbanization (yellow areas in Fig. 6), the second component corresponded to a strong tendency to avoid urbanization (red areas in Fig. 6), and the third component corresponded essentially to a lack of response to urbanization (green areas in Fig. 6). Areas where component 2 dominates are unlikely to be permeable because the bobcat tended to avoid them. In areas where component 1 dominates, connectivity may actually be enhanced because of the strong directionality parallel to the urban edge associated with that behavioral state. For $LYRU_1$, all three cases for landscape connectivity illustrated in Fig. 3 are present in the behavioral landscape map shown in Fig. 6. However, for $LYRU_2$ strong avoidance of urban was the primary response, while for $LYRU_3$ movement parallel to the urban edge was the primary response as X_{urb} increased. Thus, behavioral landscapes for these individuals differed, even though all three individuals showed avoidance of urban at the high values of X_{urb} at observed locations and a weak response at low values of X_{urb}. Behavioral maps for $LYRU_2$ and $LYRU_3$, along with probability surfaces and additional examples for all bobcats, are given as an online Appendix D.

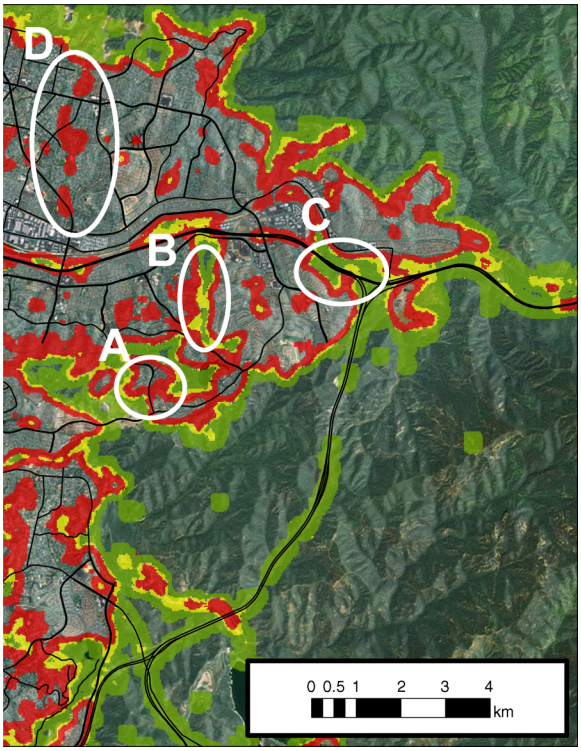

FIG. 6. An example of a behavioral landscape for movement of $LYRU_1$ (refer to the urban areas in Fig. 1). Red areas indicate where response component 2, which corresponds to strong avoidance of urban areas, is most probable. Yellow areas indicate where response component 1, movement perpendicular to the direction of the increasing urbanization (i.e., roughly parallel to the urban edge), is most probable. Green areas indicate where response component 3, which corresponds to a very weak response to urban areas, is most probable. Areas that are not colored are either dominated by nonurban or have a proportion of urbanization that exceed that used by bobcat $LYRU_1$. The letters A, B, C, and D indicate areas with different permeabilities based on the behavioral landscape map. A, B, and C correspond to the cases in the conceptual illustration in Fig. 3. Over much of the area in D, the proportion of urbanization exceeds that observed to be used by the bobcat and is therefore assumed to be of even lower permeability. Remote-sensing imagery and roads in black lines are shown for geographic context.

DISCUSSION

In this paper, we developed a finite mixture model approach for move angle response to landscape features. The models can accommodate multiple covariates that influence the selection of a component of the mixture, analogous to a movement behavior state. We fit 11 specific models to data sets from three bobcats that were tracked by GPS telemetry in Orange County, California, for response to urbanization and assessed the relative empirical support for the models using an information-theoretic approach. Using the best approximating model for each animal, we interpreted the behavioral response of each bobcat to urbanization in qualitative terms and produced behavioral landscape maps for each bobcat.

The top-ranked models for $LYRU_1$, $LYRU_2$, and $LYRU_3$ (models H, G, and G, respectively) were similar in structure, differing in having one (G) or two (H) subcomponents in the second component. The fitted response angle densities vs. X_{urb} showed a good correspondence between the observed data and the top-ranked models (see Appendix D). The second-ranked models had density surfaces similar to the top-ranked models. The difference usually involved the commission or omission of one additional type of movement response. The models without response to urbanization with respect to the mixing proportions (models A and B) were among the lowest ranked models. All three individuals showed avoidance of urban at the high values of X_{urb} at observed bobcat locations and a weak response at low values of X_{urb}. However, for each bobcat these models had specific differences in the responses they produced at different degrees of urbanization.

All three bobcats avoided urban areas by either moving toward areas with lower urban density, moving parallel to the urban edge, or both; however, there were some interesting differences in movement responses between bobcats. $LYRU_1$ and $LYRU_2$ occupied the same general area and showed movement behavior consistent with home range residency. Both of these bobcats avoided urban areas, according to the models with the lowest AIC_C, by moving away from the

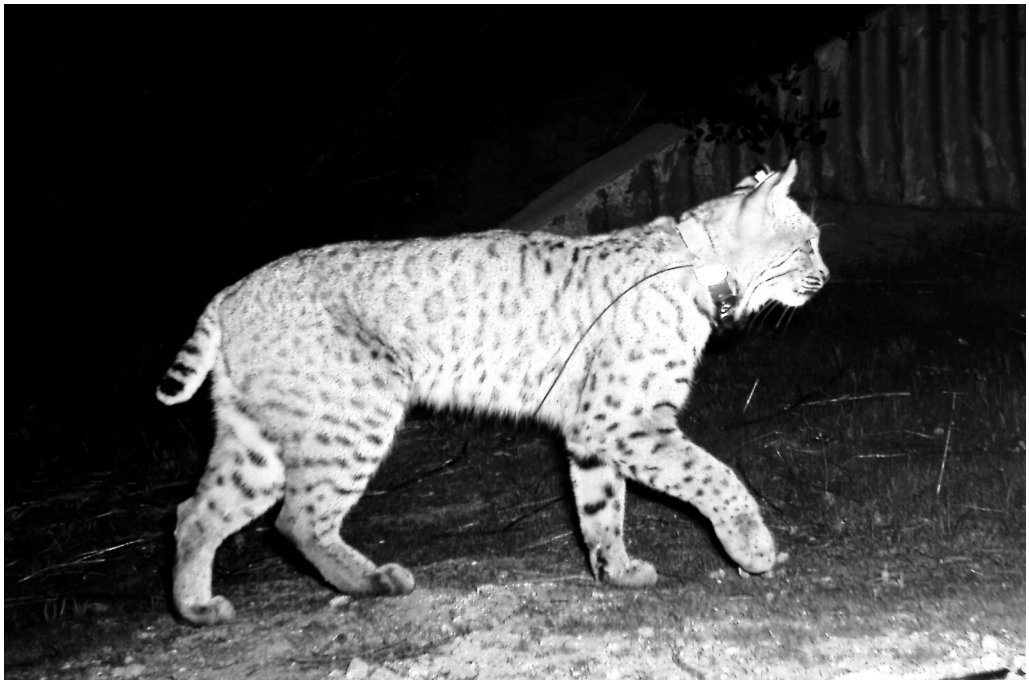

PLATE 1. This bobcat, which was tracked via GPS telemetry, was photographed by a motion-triggered camera as it passed through a highway underpass. The collar features an automatic drop-off mechanism and VHF transmitter that can be used to locate the bobcat with a directional antenna. Once the collar is retrieved, the time and location data collected from the on-board GPS receiver are uploaded for analysis. Photo credit: E. Boydston and L. Lyren.

direction of increasing urbanization. They both transitioned to this behavior as the proportion of urbanization around their locations increased from 0.2 to 0.3. In contrast, $LYRU_3$ had an area of use an order of magnitude larger than the other bobcats, and its movement behavior appeared to be more dispersal-like. Its avoidance of urban areas consisted exclusively of moving parallel to the urban edge. This avoidance response started abruptly, according to model G, when the proportion of urbanization reached 0.08. Also, the proportion of urbanization at $LYRU_3$ locations did not exceed 0.14, less than half of the maximum observed values of the other bobcats. Our results suggest a difference in movement response to urbanization for resident bobcats vs. those engaged in more wide-ranging behavior.

There is reason to expect differences in male vs. female encounter rates with urban edges and movement responses to urbanization. Male bobcats tend to have larger home ranges, move longer distances during the process of dispersal, and exhibit greater competition for space, which makes encounters with roads and urban areas more likely (Sandell 1989, Sunquist and Sunquist 1989, Janecka et al. 2006, Tucker et al. 2008, Riley et al. 2010). Studies of bobcat behavior in California suggest that there is either no difference in male vs. female bobcat use of urbanized areas or that females cross roads and use urbanized areas less than males (Riley et al. 2010). The models for resident male ($LYRU_1$) and female ($LYRU_2$), in addition to the similarities in urban response, also have some differences suggesting that the female bobcat showed greater avoidance of urbanization. At intermediate levels of urbanization, male $LYRU_1$ had a response that consisted of a mixture of moving parallel to the urban edge and moving toward urbanization. In contrast, female $LYRU_2$ showed avoidance of urbanization by moving parallel to the urban edge at low levels of urbanization. Indeed, $LYRU_1$ spent more time in closer proximity to urban areas. It is possible that these results reflect a general pattern in which female bobcat show greater avoidance of urban areas, and should be addressed in future investigations.

In our study, we tracked bobcats at night (22:00–01:00). Some studies suggest that bobcats venture farther into urban areas at night (Riley et al. 2010), so the responses in our observed data may represent the weakest responses to urbanization. Movement responses to urbanization may depend on visibility, urban light and noise, and human activity levels. Future studies can examine responses of bobcats to urbanization during different times of day, using time of day as a covariate in the models. Also, data for the internal state of the bobcats were not available, although an animal's internal state is considered important to movement behavior (Bell 1990, Nathan et al. 2008). Animals with low energy reserves or that are attempting to escape from an unfavorable social environment may be more risk prone (Krebs and Davies 1993). Thus, response to

urbanization may differ depending on the internal state of the individual. Further, bobcats may be responding to landscape features or familiar places in their home ranges that are related to the degree of urbanization, rather than responding directly to the degree of urbanization itself. However, in this example, all three bobcats consistently showed increasing avoidance behavior as the degree of urbanization increased, raising our confidence in our interpretation of the results.

The finite mixture modeling approach has several useful features. First, it is computationally practical compared to many other movement modeling methods currently available. Second, hierarchically structured decision-making allows the complexity of a model to be varied by replacing components (i.e., experts) with a more detailed HME sub-model or collapsing a sub-model in the existing HME into a simplified component. Third, FMMs can be used to perform an unsupervised classification of movement behaviors, which we exploited to create behavioral landscapes. This approach can be useful for inferring distinct patterns of movement, which have been referred to as *behavioral modes* or *movement phases* (Nathan et al. 2008, Patterson et al. 2008), when direct observation of such states is not possible.

In the behavioral landscapes created for Willow Flycatchers by Bakian et al. (2012), they were able to directly observe animals in different behaviors; in our case, however, we had to use the FMM approach to classify movement behaviors based on movement data. In addition, their application focused on foraging and vocalization behavior, which is related to survival and reproduction. We created behavioral landscapes for bobcat movement behavior (Fig. 6; Appendix D), which are related to critical processes such as landscape connectivity, immigration and emigration among populations, and gene flow. These maps are complimentary to those of (Bakian et al. (2012). The behavioral landscape maps we created took urban development into account. However, we can include other landscape features by passing additional covariates to the mixing proportion functions. For example, including the proportion of riparian habitat around a bobcat location may alter its response to urban development. We use these behavioral landscapes to assess connectivity between habitat patches. Such connectivity assessments can be used to prioritize conservation activities, identify areas for further study and provide a priori predictions for those studies, and predict connectivity under future land use scenarios. These areas might then be targeted for further study or management efforts to conserve functional connectivity. In addition, landscape connectivity identified by the behavioral landscapes can be explored in greater depth by using the FMMs to simulate movement across the landscape in an agent-based model.

Objectives for animal movement modeling include improving our understanding of movement behavior itself, better understanding the role of movement behavior at higher levels of biological organization (such as populations, communities, and disease dynamics), and guiding conservation and management. To achieve these ends, we must continually improve both our conceptual and quantitative models of animal movement. With the finite mixture movement models specifically, future versions can incorporate time dependency, modeling response angles to multiple landscape features, influence of large-scale movement patterns, and dependency on internal state. Our results suggest possible movement patterns in response to urbanization based on individual differences in large-scale movement patterns and gender. As the finite mixture models and other movement models are applied to more data, the range of movement responses and how they relate to sex, life history stage, internal state, external (including social) environment, and other factors will become clearer. Agent-based models (ABMs) are useful for understanding how properties of and interactions among individuals result in behavior at higher levels, such as populations (Grimm et al. 2005). ABMs may be useful in developing an understanding of the consequences of behavioral and physiological constraints at the individual level, how they relate to movement decisions, and consequences at the population level (Revilla and Wiegand 2008, Melbourne and Hastings 2009, Morales et al. 2010).

While population models depend on rates of movement across space, conservation applications such as reserve design are also concerned with where movement occurs between habitat patches. In this paper, we visualized the predictions of movement models in geographic space based on the concept of a behavioral landscape. The use of move step or move path data is underrepresented in analysis of landscape connectivity that employ least cost path algorithms (Zeller et al. 2012). More work needs to be done to integrate data-driven movement models into other tools for evaluating connectivity, including least cost path analysis (Theobald 2006), agent-based models (Tracey 2006), and circuit-theoretic models (McRae et al. 2008). We believe the finite mixture movement modeling approach will aid ecological modelers, conservation biologists, and landscape ecologists in understanding animal movement behavior on landscapes, and maps such as the behavioral landscapes we developed will provide meaningful recommendations for conservation and management.

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Supplemental Material

Appendix A

Formulations for extensions of the models that include movement distance (*Ecological Archives* A023-031-A1).

Appendix B

Likelihood-based inference using particle swarm optimization and expectation-maximization (EM) algorithm (*Ecological Archives* A023-031-A2).

Appendix C

A demonstration of parameter estimation using simulated data *Ecological Archives* A023-031-A3).

Appendix D

Additional behavioral landscape maps and examples of applications to several areas in Orange County, California, USA (*Ecological Archives* A023-031-A4).