

EXTRACTING MORE OUT OF RELOCATION DATA: BUILDING MOVEMENT MODELS AS MIXTURES OF RANDOM WALKS

JUAN MANUEL MORALES,^{1,4} DANIEL T. HAYDON,² JACQUI FRAIR,³ KENT E. HOLSINGER,¹
AND JOHN M. FRYXELL²

¹*Ecology and Evolutionary Biology, University of Connecticut, 75 North Eagleville Road,
Storrs, Connecticut 06269-3043 USA*

²*Department of Zoology, University of Guelph, Guelph, Ontario, Canada N1G 2W1*

³*Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9*

Abstract. We present a framework for fitting multiple random walks to animal movement paths consisting of ordered sets of step lengths and turning angles. Each step and turn is assigned to one of a number of random walks, each characteristic of a different behavioral state. Behavioral state assignments may be inferred purely from movement data or may include the habitat type in which the animals are located. Switching between different behavioral states may be modeled explicitly using a state transition matrix estimated directly from data, or switching probabilities may take into account the proximity of animals to landscape features. Model fitting is undertaken within a Bayesian framework using the WinBUGS software. These methods allow for identification of different movement states using several properties of observed paths and lead naturally to the formulation of movement models. Analysis of relocation data from elk released in east-central Ontario, Canada, suggests a biphasic movement behavior: elk are either in an “encamped” state in which step lengths are small and turning angles are high, or in an “exploratory” state, in which daily step lengths are several kilometers and turning angles are small. Animals encamp in open habitat (agricultural fields and opened forest), but the exploratory state is not associated with any particular habitat type.

Key words: *Bayesian; Cervus elaphus; GPS collars; landscape; movement models; random walks; redistribution kernel; relocation data; spatial scale; switching behavior; wapiti; WinBUGS.*

INTRODUCTION

Over limited time scales, the path of a moving individual often can be characterized by relatively simple mathematical models. Examples of such models include biased random walks and correlated random walks (Okubo 1980, Turchin 1998, Okubo and Levin 2001). Over longer time scales, these models often fail to describe patterns of movement because of the likelihood that individuals change movement behavior (Firle et al. 1998, Morales and Ellner 2002). One way to accommodate these multiple behaviors is to develop different movement models for a number of discrete modes or states of movement (Grünbaum 2000, Skalski and Gilliam 2003). In order to characterize long-term movement of individuals over landscapes, it is necessary to estimate both the parameters of the model governing movement in each behavioral state and the rate of transitions between states. Data from VHF radio-tagging or radio collars that use Global Positioning Systems (GPS collars) can be used to locate the spatial position of individuals at discrete time intervals and make possible the reconstruction of movement paths of animals. An important methodological question is

how to make inferences about different movement behaviors, given movement paths. This requires answers to three main questions: (1) how to distinguish different movement states from relocation data; (2) how to parameterize movement models for each different state; and (3) how to model transitions between different states.

Recent analyses of animal movement data have focused on the distributions of distance moved or movement rate (Viswanathan et al. 1996, Johnson et al. 2002, Viswanathan et al. 2002). Other analyses rely on summary properties of movement paths, such as fractal dimension (Nams 1996, Fritz et al. 2003) or first passage times (Fauchald and Tveraa 2003). We propose instead to fit mixtures of random walk models directly from observed trajectories. Furthermore, we present ways to incorporate environmental factors into such models.

Combining relocation data with GIS (Geographic Information System) mapping is a potentially powerful way of deducing the influence of landscape features on movement behavior. For example, we might expect an animal to move quickly through suboptimal habitat, but to slow down on encountering improved habitat. Consider, for instance, an individual performing an area-restricted search (Kareiva and Odell 1987, Bell 1991). When it is in an intensive search state (for example after encountering a habitat patch with abundant food),

Manuscript received 22 April 2003; revised 10 November 2003; accepted 8 December 2003; final version received 6 February 2004. Corresponding Editor: O. N. Bjørnstad.

⁴ E-mail: juan.morales@uconn.edu

the animal's step lengths will be short, turns will be frequent, and turning angles large. In contrast, extensive search states will be characterized by longer step lengths and small, infrequent turning angles (Zollner and Lima 1999).

Identifying movement states based on location data requires decomposing a single observed bivariate distribution (step lengths and turning angles) into two or more bivariate distributions (one for each behavioral state identified). Using both step length and turning angles to attempt this decomposition is likely to be more powerful than using just one variable. The probability distributions used to characterize step length should be carefully chosen. When an individual is in a behavioral state characterized by small-scale movements, the most common step lengths should be short, (i.e., the mode of the step length distribution will be located relatively close to zero), and when in a behavioral state characterized by larger scale movements, the most common step lengths should be longer. Consequently, the distributions selected to model step length in different behavioral states should have different modes. This is in contrast to the case of multiple exponential distributions used by Johnson et al. (2002), in which the mode of the step length distribution for both small- and large-scale movements is the same and very small.

Here, we use relocation data from GPS-collared elk to classify movement into states, a small-scale movement pattern corresponding to elk that are "encamped" (Bailey et al. 1996), and larger scale movements undertaken between camps, which we will refer to as the "exploratory" state. Specifically we attempt to:

- 1) devise a statistical basis for partitioning animal movements into multiple states based on ordered series of step lengths and turning angles;
- 2) include in this approach a method for estimating the switching rates between movement states;
- 3) show how landscape data can be integrated into this approach to explore whether certain particular landscape features are associated with movement state transitions.

Such an analysis would be extremely difficult using classical methods of analysis; therefore we perform inference with WinBUGS (Bayesian Analysis Using Gibbs Sampler (Spiegelhalter et al. 1999; freely available online)⁵ using data from the movement paths of four elk reintroduced into east-central Ontario.

METHODS

The data

GPS collars were fitted to four cow elk (*Cervus elaphus*) that were translocated with 116 other elk from Elk Island National Park, Alberta to east-central Ontario, Canada as part of a provincial reintroduction pro-

gram. Locations used in this study were the first obtained each day, typically at 02:00, but sometimes at 00:00 or 04:00 hours, depending on fix availability. An average speed of travel was calculated for each approximate 24-h period by dividing the distance between successive locations by the time interval that separated them. Turning angles (in radians) were calculated for each trajectory. GPS paths were overlaid on a classified Landsat TM (Thematic Mapper) image obtained from the Ontario Land Cover Data Base (Spectranalysis-Inc. 1999), with a pixel resolution of 25 m. Major habitat types were enumerated as follows: (1) water, (2) swamp, (3) treed wetland, (4) open forest, (5) non-treed wetland, (6) mixed forest, (7) open habitat, (8) dense deciduous forest, (9) coniferous forest, and (10) alvar (dwarf shrubs and limestone grasslands).

GPS fixes (obtained with an accuracy of 10–20 m) from four collars (elk-115, 161, 287, and 363) were obtained for 158, 164, 194, and 218 days, respectively, following release on 15 April 2001. Corresponding net displacements (straight-line distance from release point to the last relocation) were 7.1, 124.7, 89.5, and 92.5 km, respectively. Because all 120 released animals were VHF-collared we know from their combined trajectories that three of these individuals were mostly solitary, whereas elk-115 was within 2 km of other collared animals for much of its tracked history. During the duration of the study, there was no snow accumulation at any time, and none of the animals calved. Displacement–time plots indicated no common effects of season or of the rut (data not shown).

Models

We assume that the movement path of an individual is composed of one or more random walks (RWs), each characterized by distributions of step lengths and turning angles. Correlated random walks (CRW) occur when turning angles are concentrated around zero (Turcotte 1998). When multiple RWs are considered, we want to classify each observation as belonging to one of these RWs and to obtain the parameters for each of them. Obviously such a formulation potentially may be applied to movement paths from any species and, as we discuss later, may be fitted at the individual and population level.

The general model structure can be formulated as a latent variable model where each observation y_i ($t = 1, \dots, T$) is associated with an unobserved (latent) state-indicator variable $I_i = i$, $i \in \{1, \dots, M\}$ where M is the number of different movement states considered. In this way, every observation is assigned to only one of M movement states. Observations $y_i = [r_i, \phi_i]$, are pairs of daily average movement rates and turning angles. Conditioned on the i th movement state, each observation is assumed to be independently drawn from a Weibull distribution (for step length) with parameters a_i and b_i ($i \in \{1, \dots, M\}$), and wrapped Cauchy distribution (for turning angles) with parameters μ_i and ρ_i .

⁵ (<http://www.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml>)

($i \in \{1, \dots, M\}$). For a given vector of states I , the likelihood function is

$$P(y|a, b, \mu, \rho) = \prod_{i=1}^T W(r_i|a_i, b_i)C(\phi_i|\mu_i, \rho_i) \quad (1)$$

where W and C denote Weibull and wrapped Cauchy distributions, respectively. Part of the analysis involves finding the best combination for the elements in I . As the number of observations and behavioral states increases, it becomes infeasible to evaluate all possible forms of I , and Bayesian methods become particularly useful in determining the best fitting combination. The Weibull distribution takes the following form:

$$W(x) = abx^{b-1}\exp(-ax^b). \quad (2)$$

Note that if $b = 1$, this reduces to an exponential distribution. For $b \geq 1$, the distribution has an exponential tail, and when $b < 1$, the distribution has a fat tail. The mode of the Weibull distribution is $[(b-1)/ab]^{1/b}$ when $b > 1$, and is zero otherwise. A justification for the use of the Weibull distribution is presented in the *Discussion*. Wrapped Cauchy distributions are governed by two parameters: μ , the mean direction; and ρ , the mean cosine of the angular distribution. The density function (Fisher 1993) is

$$C(\phi) = \frac{1}{2\pi} \frac{1 - \rho^2}{1 + \rho^2 - 2\rho \cos(\phi - \mu)} \\ 0 \leq \phi \leq 2\pi \quad 0 \leq \rho \leq 1. \quad (3)$$

As ρ goes to zero, the distribution converges to a uniform distribution over the circle. As ρ goes to one, the distribution tends to one the point distribution concentrated in the direction of μ .

Different movement models can be constructed by fitting different numbers of RW models (corresponding to different behavioral states) to the data and by making the switching rate between these different RWs fixed, or dependent on one or more landscape features. We present results for seven models (WinBUGS code is provided in the Supplement):

1) “Single,” a single RW. The entire movement path is assumed to be generated within a single movement state, and we estimate parameters for step length distribution (a and b) and turning angle distribution (μ and ρ) for this state.

2) “Double,” a mixture of two RWs with no model for switching. Each observation is assigned to one movement state independently of previous states. For this model we need to estimate parameters for step length and turning angles in each state. In addition, for every observation we need estimates for the probability (η_i) of being in one or the other movement state.

3) “Double with covariates.” The same as model (2), but the probability of being in a movement state is related to habitat type h in which the individual is currently located (out of H possible habitat types) via a

logit link with v_h parameters estimated directly from the data:

$$\eta_{1t} = \exp(v_h)/[1 + \exp(v_h)] \quad h = 1, \dots, H \\ \eta_{2t} = 1 - \eta_{1t} \quad (4)$$

where η_{it} is the mixture coefficient for the t th observation and determines the probability that the individual was in the i th movement state.

4) “Double-switch,” two RWs with fixed switching probabilities. Switching behavior between movement states is explicitly modeled. At each time step, an individual can decide to change from the current movement state to a different one with fixed probability. For two possible movement states, we have a 2×2 matrix that defines the probabilities q_{ij} of being in movement state i at time $t + 1$ given that the individual is in state j at time t .

5) “Switch with covariates.” The same as model (4), but with switching probability from the exploratory to the encamped movement state (q_{21}) being a function of distance to open sites:

$$q_{21} = \frac{\exp\left(\beta_1 + \sum_{h=1}^H m_h d_h\right)}{1 + \exp\left(\beta_1 + \sum_{h=1}^H m_h d_h\right)} \\ q_{11} = 1 - q_{21} \quad (5)$$

where β_1 and m_h are parameters, and d_h is distance (in kilometers) to habitat h . The rationale behind this model is that elk may be more likely to switch from the exploratory state to encamped movement when they are close to habitats in which they can obtain forage. A switch from encamped to exploratory state could be related to the internal state of the individual or to some other factor, but we chose not to include covariates in the determination of this transition probability. Eqs. 4 and 5 are “logit” links to transform the real covariates to the $[0, 1]$ responses.

6) “Switch-constrained.” This model is identical to model (4) except that the mode in the exploratory step length distribution is forced (by constraining the prior distribution) to have a mode greater than zero (i.e., $b_2 > 1$).

7) “Triple-switch,” three RWs with fixed switching probabilities. This is a three-state analogue of model (4).

Priors

The use and choice of priors is probably the most controversial aspect of Bayesian methods (Dennis 1996). We used vague priors whenever possible (Table 1), except for the “Switch-constrained” model, as previously indicated.

The models were fitted using Monte Carlo Markov-Chain (MCMC) techniques implemented within the

TABLE 1. Prior distributions.

| Parameter | Prior distribution | Interpretation |
|----------------|--------------------------------------|---|
| a_i | gamma(0.01, 0.01) | Scale parameter for Weibull distribution describing step length for the i th movement state. |
| eps_i | gamma(0.01, 0.01) | Difference between a_i and a_{i+1} when multiple walks fitted ($a_{i+1} = a_i + \text{eps}_i$). |
| b_i | gamma(0.01, 0.01) | Shape parameter for Weibull distribution describing step length for the i th movement state. |
| μ_i | uniform($-\pi$, π) | Mean direction for turning angles for the i th movement state. |
| ρ_i | uniform(0, 1) | Mean cosine for turning angles for the i th movement state. |
| $\eta_{1,i}$ | uniform(0, 1) | Mixture coefficient for the i th observation: the probability that the i th observation is in movement state 1 ($\eta_{2,i} = 1 - \eta_{1,i}$). |
| v_h | normal(0, σ), $\sigma = 100$ | Coefficients in Eq. 4 relating state of individual to habitat in which it currently resides. |
| β_1 | normal(0, σ), $\sigma = 100$ | Intercept in Eq. 5 relating probability of switching to distance to open habitat. |
| m_h | normal(0, σ), $\sigma = 100$ | Slope in Eq. 5 relating probability of switching to distance to open habitat. |
| q_{ij} | uniform(0, 1) | Transition probability from the i th to the j th movement state. |

software WinBUGS 1.4 (Spiegelhalter et al. 1999). For each model we ran four MCMC chains for 20 000 iterations and examined autocorrelations and convergence to stationary distributions in sample paths of the parameters. Operationally, convergence is reached when the quantiles of interest for the posterior distributions do not depend on the starting points of the Markov chain simulations. WinBUGS calculates the Gelman-Rubin convergence statistic, as modified by Brooks and Gelman (1998). This test compares variance between and within several Markov chains run in parallel and with different initial points. Under convergence, the ratio of pooled to within variances should asymptote to one. We also checked that the width of the central 80% interval of the pooled runs and the average width of the 80% intervals within individual runs had stabilized.

Model comparison and goodness of fit

Spiegelhalter et al. (2002) proposed a “Deviance Information Criterion” (DIC) as a natural generalization of Akaike’s Information Criterion (AIC). As in AIC and other model comparison tools, DIC consists of two terms, one representing goodness of fit and the other a penalty for increasing model complexity. Model fit is summarized by the expectation of the posterior distribution of the “Bayesian Deviance” (Dev), which is calculated from the posterior distributions of the set of parameters θ as follows:

$$\text{Dev}(\theta) = -2 \log P(y|\theta). \quad (6)$$

Model complexity is measured by the “effective number of parameters,” p_D , defined as expected deviance minus deviance evaluated at expectations for the posterior of the set of parameters, that is, mean deviance minus deviance of the means (see Spiegelhalter et al. [2002] for the derivation of p_D):

$$p_D = \overline{\text{Dev}(\theta)} - \text{Dev}(\bar{\theta}). \quad (7)$$

DIC is defined as follows:

$$\text{DIC} = \text{Dev}(\bar{\theta}) + 2p_D. \quad (8)$$

We do not use DIC as a strict criterion for model choice; rather we use it as a method for screening alternative formulations in order to produce a set of candidate models for further consideration.

The joint posterior distribution of parameters generated by the MCMC simulation can be used to check the ability of models to reproduce observed properties of the data. We asked whether movement paths simulated with model parameters could produce autocorrelation functions (acf’s) for mean daily movement rates similar to those observed in the data. Autocorrelation in movement rate reflects the temporal structure of changes in movement behavior. For 5000 replicates, we sampled from the joint posterior distribution of model parameters. A movement path was then simulated with each set of sampled parameters, and we calculated the acf of daily distance moved. In this way, we produced a “posterior predictive distribution” (Brooks and Gelman 1998) for the acf that can be compared to the observed one. Note that DIC assesses how well a particular model fits the daily movement rate and turning angles, whereas by doing the check on the posterior predictive distribution of the autocorrelation function, we are assessing the ability of models to fit a property of whole movement paths that are not explicitly included in the model.

RESULTS

Convergence of the Markov chains was usually reached during the first few hundred iterations and autocorrelation was indistinguishable from zero for lags greater than 5. In order to be conservative, we discarded the first 5000 iterations and kept every 10th MCMC sample for posterior estimation. Thus, the posterior distribution of each parameter was estimated from a sample of 4×1500 independent MCMC observations. Tables of all estimated parameters (means and 95% credible intervals) are included in Appendix A; DIC

TABLE 2. DIC (deviance information criterion) values for the seven models examined, with the effective number of parameters, p_D .

| Model | Elk-115 | | Elk-163 | | Elk-287 | | Elk-363 | |
|------------------------|---------|-------|---------|-------|---------|-------|---------|-------|
| | DIC | p_D | DIC | p_D | DIC | p_D | DIC | p_D |
| Single | 1083 | 4 | 804 | 4 | 902 | 4 | 1138 | 4 |
| Double | 1054 | 91 | 738 | 65 | 807 | 59 | 1056 | 76 |
| Double with covariates | NC | NC | 695 | 30 | 801 | 60 | 1040 | 32 |
| Double switch | 991 | 10 | 688 | 6 | 699 | 18 | 1033 | 47 |
| Switch with covariates | 1195 | 23 | NC | NC | 724 | 16 | 1320 | 15 |
| Switch constrained | 984 | 8 | 644 | 16 | 689 | 17 | 945 | 19 |
| Triple switch | 896 | 19 | 641 | 23 | 626 | 16 | 960 | 54 |

Note: NC indicates that MCMC failed to converge.

values for each model and modal step lengths for each movement state are reported in Tables 2 and 3.

Step length distributions derived from fitting a “single” RW were all zero-modal and fat-tailed, with mean values ranging from 0.99 to 1.32 km/d. The mean turning angle for all four animals was 165° , suggesting a high tendency to reverse direction, but the mean cosine of the turning angle was low, indicating a high variance around this tendency (all turning angle means reported are circular means; Fisher [1993]).

The “double” model, in which there are two RWs and no model for switching (and therefore no constraints on changing from one movement state to another), place elk in the encamped state $\sim 60\%$ of the time (range 0.47–0.70). Expected daily movement rates in the encamped state range from 0.14 to 0.70 km/d, and in the exploratory state from 1.651 to 3.26 km/d. However, the Weibull distributions governing movement in the exploratory state are zero-modal and fat-tailed, indicating that most movement rates in the exploratory state are very close to zero, in contradiction to our interpretation of movement for this behavior. The mean turning angle for all individuals in the encamped state was 172° , indicating many reversals, but was only 20° in the exploratory state.

The “double with covariates” model, in which the probability of being in any one movement state may be a function of the habitat type in which the animal is located, yielded RWs broadly similar to those of the “double” model previously described (except for elk-115, for which this model failed to converge). The principal difference was that animals were identified as being in the encamped mode a greater proportion of the time (range 0.81–0.88) relative to the “double” model, and that the step length distribution in the exploratory state tended to have an interior mode (in contrast to the simpler double model) and a slightly increased mean. No habitat variables were associated with individuals when in an exploratory state, but all individuals were more likely to be in an encamped state when in open habitat. Other habitat types associated with the encamped state were mixed forest and alvar (elk-287); and water, dense deciduous forest, and coniferous forest (elk-363).

The “double switch” model (in which switching rates between movement rates are estimated from the data) yielded very similar results to the “double” model for step length, turning angles, and time spent in each movement state. Daily switching probabilities from encamped to exploratory states ranged from 0.096

TABLE 3. Modes for different movement states (all values have units of km/day).

| State and elk | Single | Double | Double with covariates | Switch | Switch with covariates | Switch constrained | Triple switch |
|---------------|--------|--------|------------------------|--------|------------------------|--------------------|---------------|
| State 1 | | | | | | | |
| Elk-115 | 0.000 | 0.331 | NC | 0.293 | 0.000 | 0.000 | 0.000 |
| Elk-163 | 0.000 | 0.008 | 0.000 | 0.010 | NC | 0.000 | 0.019 |
| Elk-287 | 0.000 | 0.061 | 0.024 | 0.017 | 0.021 | 0.015 | 0.050 |
| Elk-363 | 0.000 | 0.082 | 0.088 | 0.073 | 0.000 | 0.006 | 0.000 |
| State 2 | | | | | | | |
| Elk-115 | | 0.000 | NC | 0.000 | 3.927 | 3.538 | 0.146 |
| Elk-163 | | 0.000 | 0.000 | 0.000 | NC | 4.429 | 0.000 |
| Elk-287 | | 0.000 | 1.910 | 0.940 | 0.000 | 1.783 | 0.190 |
| Elk-363 | | 0.000 | 2.912 | 0.000 | 1.846 | 4.004 | 0.079 |
| State 3 | | | | | | | |
| Elk-115 | | | | | | | 2.784 |
| Elk-163 | | | | | | | 0.590 |
| Elk-287 | | | | | | | 0.682 |
| Elk-363 | | | | | | | 0.000 |

Notes: NC indicates that MCMC failed to converge. Models are defined in *Methods: Models*.

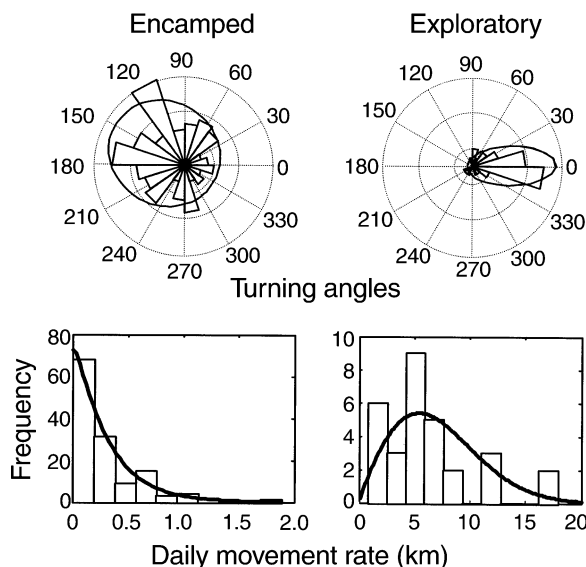


FIG. 1. Turning angles and step distributions for elk-287 in two behavioral states as inferred using the “switch-constrained model.” Turning angles (visualized using polar plots) have Wrapped Cauchy distributions with parameters μ_i and ρ_i corresponding to the mean of their posterior distributions. Step lengths have Weibull distributions with parameters a_i and b_i corresponding to the mean of their posterior distributions. Bars are observed frequencies of movements (km/d).

to 0.295, and from exploratory to encamped states from 0.085 to 0.399.

The “switch with covariates” model (in which switching probability may be a function of distance to various habitat types) generated results similar to those of the “double with covariates,” i.e., a greater proportion of time in the encamped state (0.78–0.91), a longer mean step length in the exploratory mode (3.65–

5.53 km/d), and a tendency for the step length distribution to have an interior mode in the exploratory state. However, the switching rates were not related to distance to any habitat type for any of the individuals (no m_h significantly different from zero) except for elk-363, for which the propensity to switch from exploratory to encamped state increased with distance from open habitat.

The “switch constrained” model yielded RWs very similar to those of “switch with covariates” and “double with covariates.” Mean values of step length varied from 0.233 to 0.659 km/d in the encamped state, and from 5.23 to 7.00 km/d in the exploratory state. Modes in the exploratory state varied from 1.78 to 4.43 km. Daily switching probabilities from encamped to exploratory state ranged from 0.047 to 0.156, and switching from exploratory to encamped states ranged from 0.372 to 0.616. Fig. 1 illustrates fitted distributions for turning angles and step length for elk-287 in the two movement states.

The “triple switch” model, in which three RWs are fitted with switching parameters, tends to divide the encamped state into two further states: an almost stationary state in which movement rates are very low (0.03–0.11 km/d) and a low movement state (0.33–0.73 km/d). However, it leaves the parameters for the exploratory state almost unchanged compared to those of “switch constrained,” “switch with covariates,” and “double with covariates” models. The proportion of time spent in the exploratory state is almost identical to that of these other three models, but the proportions of time spent in the almost stationary and low-movement states are variable with the individual (ranges 0.10–0.40 and 0.40–0.80, respectively). Fig. 2 shows the assignment of movement states with all of the multiple mixed RW models fitted to elk-163, together with

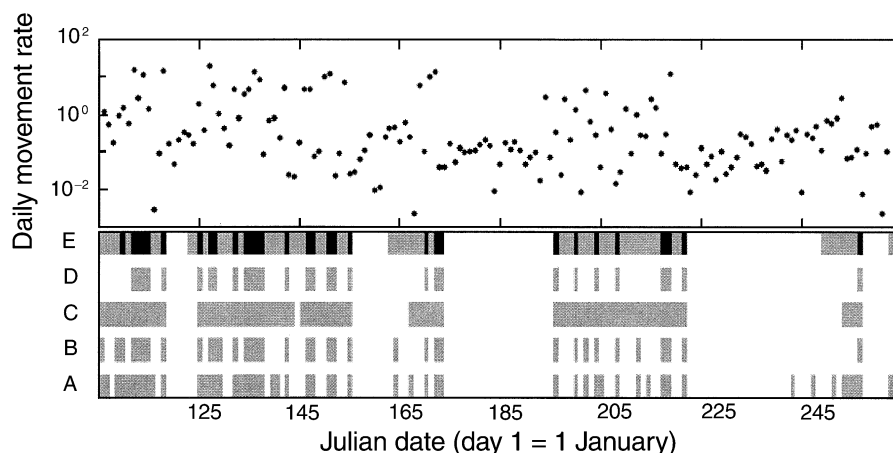


FIG. 2. Activity bar showing the assignment of behavioral states through time for all multiple RW (random walk) models fitted to elk-163: A, “Double”; B, “Double with covariates”; C, “Double switch”; D, “Switch constrained”; E, “Triple switch.” Gray bars correspond to the exploratory state, white bars to the encamped state, and black bars to the fastest movement state in the “Triple switch” model. Dots above the activity bars indicate daily movement rate on log scale. Models are defined in *Methods: Models*.

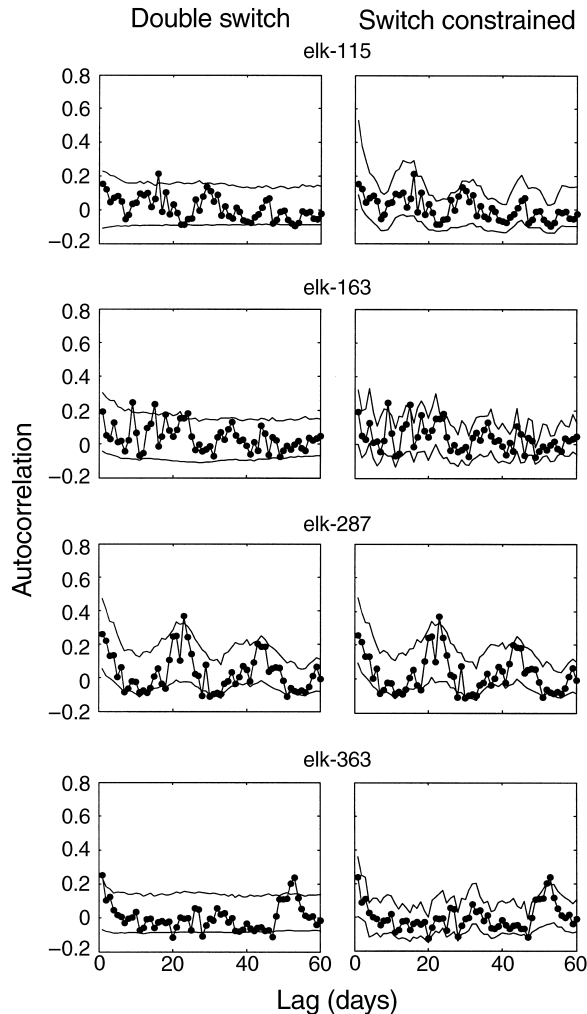


FIG. 3. Autocorrelation functions (acf's) of daily movement rate for observed and modeled elk paths for lags 1–60 for all four individuals. The left-hand column has acf's corresponding to the “double-switch” model, and the right-hand column corresponds to acf's from the “switch-constrained” model. Lines connecting solid circles (data points) are observed acf's. Thin lines are 95% credibility intervals for the acf's of modeled paths (5000 replicates).

step length data for the movement path of this individual.

DIC values for each model indicated that rank order of performance of these different models varied with individuals (Table 2). Mixed multiple RWs were usually supported by a considerable margin over a single RW. Furthermore, more structured models with explicit “switch” parameters or models that linked movement states to habitat tended to outperform the less structured “double” model in which states were freely assigned. “Single” and “double-switch” models were always among the least supported three models for all individuals; “triple” and “switch-constrained” were always ranked first or second in the level of support.

Comparing the autocorrelation structure in the model output and the data provides a further means by which model fit to the temporal structure of observed data may be judged. In Fig. 3, acf's from observed data are compared with those predicted by the “double-switch” and “switch-constrained” models applied to the four individuals. The “switch-constrained” model provides an improved representation of the observed acf for elk-115, 163, and 363 compared to the “switch model.” This improvement arises because the constrained model forces a nonzero mode on the step length distribution, which is modeled with zero-modal distributions by the unconstrained model. There is no noticeable improvement for elk-287 because the step length distribution is nonzero modal in both versions of the model. In general, only those models that adopted distributions with nonzero modes for the exploratory state were able to faithfully represent the observed structure in the acf.

DISCUSSION

Identifying behavioral states based on some set of observations is a common methodological problem in behavioral ecology. For example, Sibly et al. (1990) developed a method to identify different behavioral states based on the rate of some activity such as the pecking of a feeding bird. They assumed that pecking is a Poisson process (i.e., events arise at random and independently of the timing of any previous event), which means that the time interval between events will be exponentially distributed (Karlin and Taylor 1975). Nonlinear curve fitting on log-transformed frequencies of waiting times between events can be used to ask whether the observed pecking intervals are best described by one or multiple exponential distributions, each corresponding to a different behavioral process. This approach was modified by Johnson et al. (2002) in order to identify scales of movement in caribou. Frequency distributions of rates of movement obtained from animal locations collected using GPS collars were modeled with one, two, or three exponential distributions. Threshold values (or “scale criteria”) were used to differentiate between movement rates corresponding to different categories of movement scale. Other techniques have been developed to identify scale “domains” (Wiens 1989) from movement paths. Changes in the fractal dimension (tortuosity) of movement paths have been interpreted as changes in movement behavior across scales (Nams 1996, Fritz et al. 2003). Similarly, Fauchald and Tveraa (2003) used changes in the variance of first passage times to measure how much time an animal uses within an area of a given spatial scale.

We have presented a general and flexible framework by which movement paths may be described and behavioral states of animals inferred. This framework has several advantages over previous approaches: (1) it uses information from both turning angles and step lengths in assigning behavioral states to movement

events; (2) it accounts for temporal ordering of the data; (3) it provides a means of directly estimating switching rates between behavioral states; (4) it allows formulation of models in which the habitat that individuals are located in, or the proximity of different habitat types, might influence behavioral state; (5) it leads naturally to the formulation of models of movement as opposed to just a classification of movement states or the determination of scale domains.

Our approach is similar to that of Blackwell (1997) and Jonsen et al. (2003). However, both of their studies used Gaussian distributions to model the distance moved in each dimension of a plane, instead of modeling step length and turning angles. We propose the use of Weibull distributions to model the distance moved for the following reason. Suppose that during the time period between successive GPS fixes, the animal performs an unobserved “microscale” correlated random walk. Given enough time, such a CRW will converge to normal diffusion, in which displacement distance (r) after time t is given by the probability density function:

$$f(r) = \frac{r}{2Dt} \exp\left(-\frac{r^2}{4Dt}\right) \quad (9)$$

where D is the diffusion rate. Eq. (9) is equivalent to the two-parameter Weibull density (Eq. 2) with shape parameter $b = 2$ and a scale parameter $a = 1/4Dt$ (Cain 1991). Convergence to a simple diffusion and, hence, to a Weibull distribution with shape parameter 2 for the distance moved is expected even for mixtures of CRWs (Skellam 1973, Morales 2002, Skalski and Gilliam 2003). Of course, there is no reason to suppose that the distribution describing the displacement of an individual has converged to a Weibull distribution over the time interval between location fixes (convergence is less likely when this interval is short, or when individuals move little, and presumably is more likely when movement rate is higher). However, a Weibull distribution (with $b \neq 2$) may be flexible enough to accommodate departures from this convergence. For example, Rudd and McEvoy (1996) found that Weibull distributions provided good fit to observed cinnabar moth (*Tyria jacobaeae*) displacement. The Weibull distribution not only describes the distribution for distance moved under simple diffusion, but also it has a very flexible shape, which may approximate the distribution of distance moved under other forms of movement. The only drawback of the Weibull is that its density at zero distance is undefined for some combinations of parameters.

Given the high accuracy of GPS fixed locations, and the relatively large distances moved each day by these elk, we chose to ignore measurement error. However, it is straightforward to incorporate known measurement error in these analyses by specifying informative priors on measured variables (e.g., Jonsen et al. 2003). Be-

cause we only have data for four animals, we have fitted models to each path, but our models can be extended to include a population level by adding hyper-prior distributions; i.e., adding prior distributions for the parameters of prior distributions (Jonsen et al. 2003). Each individual is assumed to sample its movement parameters (for example, the mean cosine of turning angles for the encamped mode) from a common, population-level distribution of individual parameters. A hierarchical approach would also permit an assessment of the degree of individual variability in movement behavior. In Appendix B, we provide an example of such a hierarchical approach applied to data simulated using a switching model with parameters similar to those found for our four elk. Further details on hierarchical Bayesian models can be found in Wikle (2003) and in the WinBUGS user manual (Spiegelhalter et al. 1999).

Elk are complex, cognitive animals, and it would be naïve to assume that their movement paths could be fully described by simple memory-less models of the type described here. Inevitably such models will only succeed in characterizing certain aspects of their movement paths. However, our analysis suggests that, at least over the period of a few months, elk movement may be thought of as multiphasic: elk spend the majority of their time in an encamped state (in which step lengths are of the order of hundreds of meters, and turning angles tend to be very high), or in an exploratory state (in which daily step lengths are several kilometers, and turning angles are lower; see Fig. 1). Application of the “double with covariates” model consistently reveals that animals are likely to encamp in open habitat (agricultural fields and opened forest), but finds no habitat associations in the exploratory state (Appendix A, Table A3).

Visual inspection of movement paths suggested that elk alternate between at least two types of movement and that a single movement model such as a CRW could not adequately represent their behavior. DIC values indicate that models with two movement states usually outperformed the “single” model, indicating that movement of elk is indeed better described as a mixture of movement behaviors rather than a single process, even if we use very flexible distributions for turning angles and distance moved. However, our simplest bi-phasic models (“double” and “switch”) usually fitted fat-tailed and zero-modal distributions to infrequent exploratory moves. This presumably helped to account for variation in small- to medium-sized steps. We considered the identification of a second state associated with exploratory behavior, in which the most common moves were very small to be biologically problematic because, by definition, we expect the exploratory state to consist of long step lengths. The problem may be overcome in two ways: (1) constrain the second Weibull distribution to have a mode greater than zero, or (2) add a third state that results in subdivision of the

encamped state into two states permitting very small and small steps, leaving the exploratory state to be described by a distribution with nonzero mode characteristic of longer step lengths. Although it is not clear that this triple-phase model containing the “very small steps” really represents discrete behavioral states, or is biologically informative with respect to larger scale movement patterns, it does provide an improved fit of the model to the data.

The interpretation of DIC requires caution. Although DIC values for the “switch-constrained” model are smaller than those of the unconstrained “switch” model, only the differences for elk-163 and elk-363 are larger than 10 units. Because the constraint that we imposed corresponds to putting a very strong prior on movement length in the exploratory state, which will have a large effect on DIC, we do not regard DIC as an appropriate criterion for choosing between these models. Thus a more sophisticated assessment of model adequacy is required to compare models in which parameter values are constrained. Rather than looking for the smallest DIC value, we suggest that it is important to consider the ability of models to fit different aspects of data, especially those that have not been explicitly modeled. For example, our insistence on having non-zero modes for the exploratory state is justified by the fact that only in those cases in which the exploratory state had a mode away from zero were we able to simulate autocorrelation functions similar to those observed for elk (Fig. 3). We interpret the apparent cyclicity in observed autocorrelation in the rate of movement as being a consequence of individuals moving at a similar rate while in a particular movement state, acting in conjunction with switching between movement states that results in a characteristic time spent in each state (see also Fig. 2).

The generality and flexibility of methods presented here comes with the cost of computing time and need for careful assessment of MCMC convergence. However, the availability of WinBUGS software makes implementation of numerical techniques relatively easy and it also provides useful diagnostic tools. As with any Bayesian method, an explicit quantification of uncertainty in model parameters is given by their posterior distributions. Because we have used very vague priors (Table 1) and have a large number of sample points in each path, we expect that these posterior distributions will be determined largely by the data. The use of informative priors in the “switch-constrained” model seems justified on biological grounds and on model fit.

Simple, homogenous movement models have succeeded in describing relatively short-term movement paths within homogeneous environments. Describing movement paths in heterogeneous environments and over longer time scales for large cognitive animals will require more sophisticated models that account for greater behavioral complexity. Fitting these more so-

phisticated models to data is technically challenging, but the increasing development and use of MCMC methods represents a promising means by which this challenge may be met.

ACKNOWLEDGMENTS

We thank Peter Turchin, Steve Ellner, Rob Dunn, and two anonymous reviewers for useful comments on the manuscript. This work was supported by National Science Foundation grant 0078130.

LITERATURE CITED

- Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* **49**:386–400.
- Bell, W. J. 1991. Searching behavior: the behavioral ecology of finding resources. Chapman and Hall, London, UK.
- Blackwell, P. G. 1997. Random diffusion models for animal movement. *Ecological Modelling* **100**:87–102.
- Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* **7**:434–455.
- Cain, M. L. 1991. When do treatment differences in movement behaviors produce observable differences in long-term displacements? *Ecology* **72**:2137–2142.
- Dennis, B. 1996. Discussion: should ecologists become Bayesians? *Ecological Applications* **6**:1095–1103.
- Fauchald, P., and T. Tveraa. 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* **84**:282–288.
- Firle, S., R. Bommarco, B. Ekbom, and M. Natielo. 1998. The influence of movement and resting behavior on the range of three carabid beetles. *Ecology* **79**:2113–2122.
- Fisher, N. I. 1993. Statistical analysis of circular data. Cambridge University Press, Cambridge, UK.
- Fritz, H., S. Said, and H. Weimerskirch. 2003. Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. *Proceedings of the Royal Society of London Series B, Biological Sciences* **270**:1143–1148.
- Grünbaum, D. 2000. Advection–diffusion equations for internal state-mediated random walks. *SIAM (Society for Industrial and Applied Mathematics) Journal of Applied Mathematics* **61**:43–73.
- Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002. Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology* **71**:225–235.
- Jonsen, I. D., R. A. Myers, and J. M. Flemming. 2003. Meta-analysis of animal movement using state-space models. *Ecology* **84**:3055–3063.
- Kareiva, P., and G. Odell. 1987. Swarms of predators exhibit “preytaxis” if individual predators use area-restricted search. *American Naturalist* **130**:233–270.
- Karlin, S., and H. M. Taylor. 1975. A first course in stochastic processes. Second edition. Academic Press, New York, New York, USA.
- Morales, J. M. 2002. Behavior at habitat boundaries can produce leptokurtic movement distributions. *American Naturalist* **160**:531–538.
- Morales, J. M., and S. P. Ellner. 2002. Scaling up movement in heterogeneous landscapes: the importance of behavior. *Ecology* **83**:2240–2247.
- Nams, V. O. 1996. The VFractal: a new estimator for fractal dimension of animal movement paths. *Landscape Ecology* **11**:289–297.
- Okubo, A. 1980. Diffusion and ecological problems: mathematical models. Springer-Verlag, New York, New York, USA.

- Okubo, A., and S. A. Levin. 2001. Diffusion and ecological problems: modern perspectives. Second edition. Springer-Verlag, New York, New York, USA.
- Rudd, N. T., and P. B. McEvoy. 1996. Local dispersal by the cinnabar moth *Tyria jacobaeae*. *Ecological Applications* **6**: 285–297.
- Sibly, R. M., H. M. R. Nott, and D. J. Fletcher. 1990. Splitting behaviour into bouts. *Animal Behaviour* **39**:63–69.
- Skalski, G. T., and J. F. Gilliam. 2003. A diffusion-based theory of organism dispersal in heterogeneous populations. *American Naturalist* **161**:441–458.
- Skellam, J. G. 1973. The formulation and interpretation of mathematical models of diffusionary processes in population biology. Pages 63–85 in R. W. Hiorns, editor. *The mathematical theory of the dynamics of biological populations*. Academic Press, London, UK.
- Spectranalysis-Inc. 1999. Ontario Land Cover Data Base. Revised user's manual. Unpublished report to Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada.
- Spiegelhalter, D. J., N. G. Best, B. R. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society Series B, Statistical Methodology* **64**:583–616.
- Spiegelhalter, D. J., A. Thomas, and N. G. Best. 1999. WinBUGS Version 1.2. User Manual. MRC Biostatistics Unit, Medical Research Council, Cambridge, UK.
- Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, Massachusetts, USA.
- Viswanathan, G. M., V. Afanasyev, S. V. Buldyrev, E. J. Murphy, P. A. Prince, and H. E. Stanley. 1996. Lévy flight search patterns of wandering albatrosses. *Nature* **381**:413–415.
- Viswanathan, G. M., F. Bartumeus, S. V. Buldyrev, J. Catalan, U. L. Fulco, S. Havlin, M. G. E. da Luz, M. L. Lyra, E. P. Raposo, and H. E. Stanley. 2002. Lévy flight random searches in biological phenomena. *Physica A: Statistical Mechanics and Its Applications* **314**:208–213.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**:385–397.
- Wikle, C. K. 2003. Hierarchical Bayesian models for predicting the spread of ecological processes. *Ecology* **84**: 1382–1394.
- Zollner, P. A., and S. L. Lima. 1999. Search strategies for landscape-level interpatch movements. *Ecology* **80**:1019–1030.

APPENDIX A

Mean and 95% credibility intervals for the posterior distributions of model parameters are available in ESA's Electronic Data Archive: *Ecological Archives* E085-072-A1.

APPENDIX B

A hierarchical analysis of simulated movement data is available in ESA's Electronic Data Archive: *Ecological Archives* E085-072-A2.

SUPPLEMENT

The WinBUGS code for analysis of movement paths is available in ESA's Electronic Data Archive: *Ecological Archives* E085-072-S1.