

September 2004

Extracting more out of relocation data: building movement models as mixtures of random walks

Juan Manuel Morales

University of Connecticut, juan.morales@uconn.edu

Daniel T. Haydon

University of Guelph

Jacqui Frair

University of Alberta

Kent E. Holsinger

University of Connecticut, kent.holsinger@uconn.edu

John M. Fryxell

University of Guelph

Follow this and additional works at: http://digitalcommons.uconn.edu/eeb_articles

Recommended Citation

Morales, Juan Manuel; Haydon, Daniel T.; Frair, Jacqui ; Holsinger, Kent E.; and Fryxell, John M., "Extracting more out of relocation data: building movement models as mixtures of random walks" (2004). *EEB Articles*. 4.

http://digitalcommons.uconn.edu/eeb_articles/4

1 Running Head: Random walk mixtures from relocation data

2

3 **Extracting More out of Relocation Data: Building Movement**

4 **Models as Mixtures of Random Walks**

5

6 **Juan Manuel Morales¹**

7 Ecology & Evolutionary Biology, University of Connecticut, 75 North Eagleville Road

8 Storrs, CT 06269 U-43

9 **Daniel T. Haydon**

10 Department of Zoology, University of Guelph, Guelph Ontario, Canada N1G

11 2W1.

12 **Jacqui Frair**

13 Department of Biological Sciences, University of Alberta,

14 Edmonton, Alberta T6G 2E9.

15 **Kent E. Holsinger**

16 Department of Ecology & Evolutionary Biology, University of Connecticut, U-3043,

17 Storrs, CT 06269-3043

18 **John M. Fryxell**

19 Department of Zoology, Rm 268, Axelrod Building, University of Guelph, Guelph

20 Ontario, Canada N1G 2W1.

21

¹ Corresponding author; phone (860) 486 4689, fax (860) 486 6364, email: juan.morales@uconn.edu

1 Abstract

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

18

19 Keywords: elk, landscape, GPS collars, WinBUGS, Bayesian, redistribution, switching
20 behavior, spatial, scale

21

1 **Introduction**

2 Over limited time scales the path of a moving individual can often be characterized by
3 relatively simple mathematical models. Examples of such models include biased random
4 walks and correlated random walks (Okubo 1980, Turchin 1998, Okubo and Levin 2001).
5 Over longer time-scales these models often fail to describe patterns of movement because
6 of the likelihood that individuals change movement behavior (Firle et al. 1998, Morales
7 and Ellner 2002). One way to accommodate these multiple behaviors is to develop
8 different movement models for a number of discrete modes or states of movement
9 (Grünbaum 2000, Skalski and Gilliam 2003). In order to characterize long-term
10 movement of individuals over landscapes it is necessary to estimate both the parameters
11 of the model governing movement in each behavioral state, and the rate of transitions
12 between states. Data from VHF radio-tagging or radio-collars that use Global
13 Positioning Systems (GPS collars) can be used to locate the spatial position of individuals
14 at discrete time intervals and makes possible the reconstruction of movement paths of
15 animals. An important methodological question is how to make inference about different
16 movement behaviors given movement paths. This requires answers to three main
17 questions: 1) how to distinguish different movement states from relocation data; 2) how
18 to parameterize movement models for each different state; and 3) how to model
19 transitions between different states.

20

21 Recent analyses of animal movement data has focused on the distributions of distance
22 moved or movement rate (Viswanathan et al. 1996, Johnson et al. 2002, Viswanathan et
23 al. 2002). Other analyses rely on summary properties of movement paths such as fractal

1 dimension (Nams 1996, Fritz et al. 2003) or first passage times (Fauchald and Tveraa
2 2003). We propose instead to fit mixtures of random walk models directly from observed
3 trajectories. Furthermore, we present ways to incorporate environmental factors into such
4 models.

5

6 Combining relocation data with GIS mapping (Geographic Information System) is a
7 potentially powerful way of deducing the influence of landscape features on movement
8 behavior. For example, we might expect an animal to move quickly through sub-optimal
9 habitat, but slow down on encountering improved habitat. Consider for example an
10 individual performing area-restricted search (Kareiva and Odell 1987, Bell 1991). When
11 in an intensive search state (for example after encountering a habitat patch with abundant
12 food), step lengths will be short, turns will be frequent and turning angles large. In
13 contrast, extensive search states will be characterized by longer step lengths and small
14 and infrequent turning angles (Zollner and Lima 1999).

15

16 Identifying movement states based on location data requires decomposing a single
17 observed bivariate distribution (step lengths and turning angles) into two or more
18 bivariate distributions (one for each behavioral state identified). Using both step length
19 and turning angles to attempt this decomposition is likely to be more powerful than using
20 just one variable. The probability distributions used to characterize step length should be
21 carefully chosen. When an individual is in a behavioral state characterized by small-scale
22 movements, the most common step lengths should be short, (i.e. the mode of the step
23 length distribution will be located relatively close to zero), and when in a behavioral state

1 characterized by larger-scale movements, the most common step lengths should be
2 longer. Consequently the distributions selected to model step length in different
3 behavioral states should have different modes. This is in contrast to the case of multiple
4 exponential distributions used by Johnson et al. (2002) in which the mode of the step
5 length distribution for both small and large-scale movements is the same and very small.

6

7 Here, we use relocation data from GPS collared elk to classify movement into states, a
8 small-scale movement pattern corresponding to elk that are ‘encamped’ (Bailey et al.
9 1996), and larger-scale movements undertaken between camps, which we will refer to as
10 the ‘exploratory’ state. Specifically we attempt to:

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

18 Such an analysis would be extremely difficult using classical methods of analysis and we
19 therefore perform inference with WinBUGS (Bayesian Analysis Using Gibbs Sampler
20 (Spiegelhalter et al. 1999), freely available at <http://www.mrc-bsu.cam.ac.uk/bugs/>) using
21 data from the movement paths of 4 elk re-introduced into east-central Ontario.

22

23

1 **Methods**

2 *The data*

3 GPS collars were fitted to 4 cow elk (*Cervus elaphus*) that were translocated with 116
4 other elk from Elk Island National Park, Alberta to east-central Ontario as part of a
5 provincial re-introduction program. Locations used in this study were the first obtained
6 each day, typically 0200hrs, but sometimes 0000 or 0400hrs depending on fix
7 availability. An average speed of travel was calculated for each approximate 24 hour
8 period by dividing distance between successive locations by the time interval that
9 separated them. Turning angles (in radians) were calculated for each trajectory. GPS
10 paths were overlaid on a classified TM image obtained from the Ontario Land Cover
11 Data Base (Spectranalysis-Inc 1999), with a pixel resolution of 25m. Major habitat types
12 were enumerated as follows: 1) water, 2) swamp, 3) treed wetland, 4) open forest, 5)
13 non-treed wetland, 6) mixed forest, 7) open habitat, 8) dense deciduous forest, 9)
14 coniferous forest, and 10) alvar.

15

16 GPS fixes (obtained with an accuracy of 10-20 m's) from 4 collars (elk-115, 161, 287,
17 and 363) were obtained for 158, 164, 194 and 218 days respectively following release on
18 April 15th 2001, and corresponding net displacements (straight-line distance from release
19 point to the last relocation) were 7.1, 124.7, 89.5 and 92.5 km's respectively. Since all
20 120 released animals were VHF collared we know from their combined trajectories that 3
21 of these individuals were mostly solitary, while elk-115 was within 2km of other collared
22 animals for much of its tracked history. During the duration of the study, there was no

1 snow accumulation at any time, and none of the animals calved. Displacement-time plots
 2 indicated no common effects of season or of the rut (data not shown).

3

4 *Models*

5 We assume that the movement path of an individual is composed of one or more Random
 6 Walks (RWs), each characterized by distributions of step lengths and turning angles.

7 Correlated Random Walks (CRW) occur when turning angles are concentrated around
 8 zero (Turchin 1998). When multiple RWs are considered, we want to classify each
 9 observation as belonging to one of these RWs and obtain the parameters for each of them.

10 Obviously such a formulation may potentially be applied to movement paths from any
 11 species, and as we discuss later may be fitted at the individual and population level.

12

13 The general model structure can be formulated as a latent variable model where each
 14 observation y_t ($t = 1, \dots, T$) is associated with an unobserved (latent) state-indicator
 15 variable $I_t = i$, $i \in \{1, \dots, M\}$ where M is the number of different movement states
 16 considered. In this way, every observation is assigned to only one of M movement states.

17 Observations $y_t = [r_t, \phi_t]$, are pairs of daily average movement rates and turning angles.

18 Conditioned on the i^{th} movement state, each observation is assumed to be independently
 19 drawn from a Weibull distribution (for step length) with parameters a_i , and b_i

20 ($i \in \{1, \dots, M\}$), and wrapped Cauchy distribution (for turning angles) with parameters μ_i

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

$$22 \quad P(y|a, b, \mu, \rho) = \prod_{t=1}^T W(r_t | a_{I_t}, b_{I_t}) C(\phi_t | \mu_{I_t}, \rho_{I_t}) \quad (1)$$

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

$$6 \quad W(x) = abx^{b-1} \exp(-ax^b) \quad (2)$$

7 Note that if $b = 1$ this reduces to an exponential distribution. When $b = 3.6$, the
 8 distribution is similar to a Gaussian. For $b \geq 1$ the distribution has an exponential tail,
 9 and when $b < 1$ the distribution has a fat-tail. A justification for the use of the Weibull
 10 distribution is presented in the Discussion. Wrapped Cauchy distributions are governed
 11 by 2 parameters: μ - the mean direction and ρ - the mean cosine of the angular
 12 distribution. The density function is:

$$13 \quad C(\phi) = \frac{1}{2\pi} \frac{1 - \rho^2}{1 + \rho^2 - 2\rho \cos(\phi - \mu)} \quad 0 \leq \phi \leq 2\pi, \quad 0 \leq \rho \leq 1 \quad (3)$$

14 As ρ goes to zero, the distribution converges to a uniform distribution over the circle. As
 15 ρ goes to 1, the distribution tends to the point distribution concentrated in the direction of
 16 μ (Fisher 1993).

17

18 Different movement models can be constructed by fitting different numbers of RW
 19 models – corresponding to different behavioral states – to the data, and by making the
 20 switching rate between these different RWs fixed, or dependent on one or more landscape
 21 features. We present results for 7 models:

- 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_{it}) of being in one or the other movement state.
- 3) “Double with covariates”: same as model (2) but with the probability of being in a movement state being 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.

$$\begin{aligned} \eta_{1t} &= \exp(v_h) / (1 + \exp(v_h)), \quad h = 1, \dots, H \\ \eta_{2t} &= 1 - \eta_{1t} \end{aligned} \quad (4)$$

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 by 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 .

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

$$4 \quad q_{21} = \frac{\exp\left(\beta_1 + \sum_{h=1}^H m_h d_h\right)}{1 + \exp\left(\beta_1 + \sum_{h=1}^H m_h d_h\right)} \quad (5)$$

$$q_{11} = 1 - q_{21}$$

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

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

15 7) “Triple switch”: Three RWs with fixed switching probabilities. A 3-state analogue
 16 of model (4).

17

18 *Priors*

19 The use and choice of priors is probably the most controversial aspect of Bayesian
 20 methods (Dennis 1996). We used vague priors whenever possible (Table 1). However,
 21 due to lack of convergence of some models for some data sets, we chose to be more
 22 “informative” about some prior distributions (see Results).

1

2 The models were fitted using Monte-Carlo Markov-Chain (MCMC) techniques
 3 implemented within the software WinBUGS 1.4 (Spiegelhalter et al. 1999). For each
 4 model we ran four MCMC chains for 20,000 iterations and examined autocorrelations
 5 and convergence to stationary distributions in sample paths of the parameters.

6 Operationally, convergence is reached when the quantiles of interest for the posterior
 7 distributions do not depend on the starting points of the Markov chain simulations.

8 WinBUGS calculates the Gelman-Rubin convergence statistic, as modified by Brooks
 9 and Gelman (1998). This test compares variance between and within several Markov
 10 chains run in parallel and with different initial points. Under convergence the ratio of
 11 pooled to within variances should asymptote to one. We also checked that the width of
 12 the central 80% interval of the pooled runs and the average width of the 80% intervals
 13 within individual runs had stabilized.

14

15 *Model Comparison and Goodness of Fit*

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

22

$$Dev(\theta) = -2 \log P(y|\theta) \quad (6)$$

1 Model complexity is measured by the “effective number of parameters”, p_D , defined as
 2 expected deviance minus deviance evaluated at expectations for the posterior of the set of
 3 parameters, that is, mean deviance minus deviance of the means (see Spiegelhalter et al.
 4 (2002) for the derivation of p_D)

$$5 \quad p_D = \overline{Dev(\theta)} - Dev(\bar{\theta}) \quad (7)$$

6 DIC is defined as

$$7 \quad DIC = Dev(\bar{\theta}) + 2p_D \quad (8)$$

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

11

12 The joint posterior distribution of parameters generated by the MCMC simulation can be
 13 used to check the ability of models to reproduce observed properties of the data. We
 14 asked whether movement paths simulated with model parameters could produce
 15 autocorrelation functions (acfs) for mean daily movement rates similar to those observed
 16 in the data. Autocorrelation in movement rate reflects temporal structure of changes in
 17 movement behavior. For 5000 replicates, we sampled from the joint posterior
 18 distribution of model parameters. A movement path was then simulated with each set of
 19 sampled parameters and we calculated the acf of daily distance moved. In this way we
 20 produced a “posterior predictive distribution” (Brooks and Gelman 1998) for the acf that
 21 can be compared to the observed one. Note that DIC assesses how well a particular
 22 model fits the daily movement rate and turning angles, while by doing the check on the
 23 posterior predictive distribution of the autocorrelation function we are assessing the

1 ability of models to fit a property of whole movement paths that are not explicitly
2 included in the model.

3

4 **Results**

5 Convergence of the Markov chains was usually reached during the first few hundred
6 iterations and autocorrelation was indistinguishable from zero for lags greater than 5. In
7 order to be conservative, we discarded the first 5000 iterations and kept every 10th
8 MCMC sample for posterior estimation. Thus, the posterior distribution of each
9 parameter was estimated from a sample of 4 x 1500 independent MCMC observations.

10 Tables of all estimated parameters (means and 95% credible intervals) are included in the
11 Appendix, *DIC* values for each model and modal step lengths (calculated as

12 $\left[\frac{(b-1)}{ab} \right]^{\frac{1}{b}}$ when $b > 1$ and zero otherwise) for each movement state are reported in

13 Tables 2 and 3.

14

15 Step length distributions derived from fitting a “single” RW were all zero-modal and fat-
16 tailed with mean values ranging from 0.99-1.32 km/day. Mean turning angle for all 4
17 animals was 165° suggesting a high tendency to reverse direction, but the mean cosine of
18 turning angle was low, indicating a high variance around this tendency.

19

20 The “double” model – in which there are two RWs and no model for switching (and
21 therefore no constraints on changing from one movement state to another) – place elk in
22 the encamped state about 60% of the time (range 0.47-0.70). Expected daily movement
23 rates in the encamped state range from 0.14-0.70 km/day, and in the exploratory state

1 from 1.651 – 3.26 km/day. However, the Weibull distributions governing movement in
2 the exploratory state are zero-modal and fat-tailed, indicating that most movement rates
3 in the exploratory state are very close to zero, in contradiction to our interpretation of
4 movement for this behavior. Mean turning angle for all individuals in the encamped state
5 was 172° indicating many reversals but only 20° in the exploratory state.

6
7 The “double with covariates” model, in which the probability of being in any one
8 movement state may be a function of the habitat type that the animal is located in, yielded
9 RWs broadly similar to those of the “double” model described above (except for elk-115
10 for which this model failed to converge). The principal difference was that animals were
11 identified to be in the encamped mode a greater proportion of the time (range 0.81-0.88)
12 relative to the “double” model, and that the step length distribution in the exploratory
13 state tended to have an interior mode – in contrast to the simpler double model, and
14 slightly increased mean. No habitat variables were associated with individuals when in
15 an exploratory state but all individuals were more likely to be in an encamped state when
16 in open habitat. Other habitat types associated with the encamped state were mixed
17 forest and alvar (elk-287); and water, dense deciduous forest, and coniferous forest (elk-
18 363).

19
20 The “double switch” model (in which switching rates between movement rates are
21 estimated from the data) yielded very similar results to the “double” model for step
22 length, turning angles, and time spent in each movement state. Daily switching

1 probabilities from encamped to exploratory states ranged from 0.096 to 0.295, and from
2 exploratory to encamped states from 0.085 to 0.399.

3

4 The “switch with covariates” model (in which switching probability may be a function of
5 distance to various habitat types) generated results similar to the “double with covariates”
6 – that is, a greater proportion of time in the encamped state (0.78-0.91), a longer mean
7 step length in the exploratory mode (3.65-5.53 km/day), and a tendency for the step
8 length distribution to have an interior mode in the exploratory state. However, the
9 switching rates were not related to distance to any habitat type for any of the individuals
10 (no m_i significantly different from zero) except elk-363 for which propensity to switch
11 from exploratory to encamped state increased with distance from open habitat.

12

13 The “switch constrained” model yielded RWs very similar to that of “switch with
14 covariates” and “double with covariates”. Mean values of step length varied from 0.233-
15 0.659 km/day in the encamped state, and 5.23-7.00 km/day in the exploratory state.
16 Modes in the exploratory state varied from 1.78-4.43 km. Daily switching probabilities
17 from encamped to exploratory state ranged from 0.047-0.156, and from exploratory to
18 encamped states from 0.372-0.616. Figure 1 illustrates fitted distributions for turning
19 angles and step length for elk-287 in the two movement states.

20

21 The “triple switch” model, in which 3 RWs are fitted with switching parameters, tends to
22 divide the encamped state into two further states – an almost stationary state where
23 movement rates are very low (0.03-0.11 km/day) and a low movement state (0.33-0.73

1 km/day) – but leaves the parameters for the exploratory state almost unchanged compared
2 to “switch constrained”, “switch with covariates” and “double with covariates”. The
3 proportion of time spent in the exploratory state is almost identical to these other 3
4 models, but the proportions of time spent in the almost stationary and low movement
5 states are variable with individual (ranges 0.10-0.40 and 0.40-0.80 respectively). Figure
6 2 shows the assignment of movement states with all the multiple mixed RW models fitted
7 to elk-163, together with step length data for the movement path of this individual.

8

9 *DIC* values for each model indicated that rank order of performance of these different
10 models varied with individuals (Table 2). Mixed multiple RWs were usually supported
11 by a considerable margin over a single RW. Furthermore, more structured models with
12 explicit “switch” parameters or models that linked movement states to habitat tended to
13 outperform the less structured “double” model in which states were freely assigned.
14 “Single” and “double switch” models were always among the least supported 3 models
15 for all individuals, “triple” and “switch constrained” were always ranked first or second
16 in the level of support.

17

18 Comparing the autocorrelation structure in the model output and data provides a further
19 means by which model fit to the temporal structure of observed data may be judged. In
20 Figure (3) acfs from observed data are compared with those predicted by the “double
21 switch” and “switch constrained” models applied to the 4 individuals. The “switch
22 constrained” model provides an improved representation of the observed acf for elk-115,
23 163 and 363 compared to the “switch model”. This improvement arises because the

1 constrained model forces a non-zero mode on the step length distribution which is
2 modeled with zero-modal distributions by the unconstrained model. There is no
3 noticeable improvement for elk-287 because the step length distribution is non-zero
4 modal in both versions of the model. In general, only those models that adopted
5 distributions with non-zero modes for the exploratory state were able to faithfully
6 represent the observed structure in the acf.

7

8 **Discussion**

9

10 Identifying behavioral states based on some set of observations is a common
11 methodological problem in behavioral ecology. For example, Sibly *et al.* (1990)
12 developed a method to identify different behavioral states based on the rate of some
13 activity such as the pecking of a feeding bird. They assumed that pecking was a Poisson
14 process (i.e. events arise at random and independently of the timing of any previous
15 event), which means that the time interval between events will be exponentially
16 distributed (Karlin and Taylor 1975). Non-linear curve fitting on log transformed
17 frequencies of waiting times between events can be used to ask whether the observed
18 pecking intervals are best described by one or multiple exponential distributions, each
19 corresponding to a different behavioral process. This approach was modified by Johnson
20 *et al.* (2002) in order to identify scales of movement in caribou. Frequency distributions
21 of rates of movement obtained from animal locations collected using GPS collars were
22 modeled with 1, 2 or 3 exponential distributions. Threshold values (or ‘scale criteria’)
23 were used to differentiate between movement rates corresponding to different categories

1 of movement scale. Other techniques have been developed to identify scale “domains”
2 (Wiens 1989) from movement paths. Changes in the fractal dimension (tortuosity) of
3 movement paths have been interpreted as changes in movement behavior across scales
4 (Nams 1996, Fritz et al. 2003). Similarly, (Fauchald and Tveraa 2003) used changes in
5 the variance of first passage times to measure how much time an animal uses within an
6 area of a given spatial scale.

7

8 We have presented a general and flexible framework by which movement paths may be
9 described and behavioral states of animals inferred. This framework has several
10 advantages over previous approaches: 1) it uses information from both turning angles and
11 step lengths in assigning behavioral states to movement events; 2) it accounts for
12 temporal ordering of the data; 3) it provides a means of directly estimating switching
13 rates between behavioral states; 4) it allows formulation of models in which the habitat
14 that individuals are located in, or the proximity of different habitat types might influence
15 behavioral state; 5) the methods presented lead naturally to formulation of models of
16 movement as opposed to just a classification of movement states or the determination of
17 “scale domains”.

18

19 Given the high accuracy of GPS fixed locations, and the relatively large distances moved
20 each day by these elk we chose to ignore measurement error. However, it is
21 straightforward to incorporate known measurement error in these analyses by specifying
22 informative priors on measured variables (Jonsen et al. 2003). Since we only have data
23 for four animals we have fitted models to each path but it is readily extended to a

1 population level by adding hyper-prior distributions - that is adding prior distributions on
 2 the parameters of prior distributions (Jonsen et al. 2003). Each individual is assumed to
 3 sample its movement parameters (say turning angle variance for encamped mode) from a
 4 common, population-level distribution of individual parameters. Analysis at the
 5 population level may generate more precise estimates of the underlying model parameters
 6 (Jonsen et al. 2003). Moreover, this hierarchical approach would permit assesment of the
 7 degree of individual variability in movement behavior. Further details on hierarchical
 8 Bayesian models can be found in Carlin and Louis (1996) and in the WinBugs user
 9 manual.

10

11 We propose the use of Weibull distributions to model distance moved for the following
 12 reason. Suppose that during the time period between successive GPS fixes the animal
 13 performs an unobserved ‘microscale’ correlated random walk. Given enough time, such
 14 a CRW will converge to normal diffusion, in which displacement distance (r_t) after time t
 15 is given by the probability density function:

$$16 \quad f(r) = \frac{r}{2Dt} \exp\left[-r^2/4Dt\right] \quad (9)$$

17 where D is diffusion rate. Equation (9) is equivalent to the two-parameter Weibull
 18 density (Eq. (2)) with shape parameter $b = 2$ and a scale parameter $a = \frac{1}{4Dt}$ [Cain, 1991
 19 #1059]. Convergence to a simple diffusion and hence to a Weibull distribution with
 20 shape parameter 2 for distance moved is expected even for mixtures of CRWs (Skellam
 21 1973, Morales 2002, Skalski and Gilliam 2003). Of course there is no reason to suppose
 22 that the distribution describing displacement of an individual has converged to a Weibull

1 distribution over the time interval between location fixes (convergence is less likely when
2 this interval is short, or when individuals move little, and presumably more likely when
3 movement rate is higher) but a Weibull distribution (with $b \neq 2$) may be flexible enough
4 to accommodate departures from this convergence. For example, Rudd and McEvoy
5 (1996) found that Weibull distributions provided good fit to observed cinnabar moth
6 displacement. The Weibull distribution not only describes distribution for distance
7 moved under simple diffusion but it also has a very flexible shape, which may
8 approximate distribution of distance moved under other forms of movement. The only
9 drawback of the Weibull is that its density at zero distance is undefined for some
10 combinations of parameters.

11

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

23

1 Visual inspection of movement paths suggested that elk alternate between at least two
2 types of movement and that a single movement model such as a CRW could not
3 adequately represent their behavior. *DIC* values indicate that models with two movement
4 states usually out performed the “single” model indicating that movement of elk is indeed
5 better described as a mixture of movement behaviors rather than a single process, even if
6 we use very flexible distributions for turning angles and distance moved. However, our
7 simplest bi-phasic models (“double” and “switch”) usually fitted fat-tailed and zero-
8 modal distributions to infrequent exploratory moves. This presumably helped to account
9 for variation in small to medium sized steps. We considered the identification of a
10 second state associated with exploratory behavior in which the most common moves
11 were very small to be biologically problematic because by definition we expect the
12 exploratory state to consist of long step lengths. The problem may be overcome in two
13 ways: 1) constrain the second Weibull distribution to have a mode greater than zero, or 2)
14 add a third state that results in sub-division of the encamped state into two states
15 permitting very small and small steps, leaving the exploratory state to be described by a
16 distribution with non-zero mode characteristic of longer step lengths. While it is not clear
17 that this triple-phase model containing the ‘very small steps’ really represents discrete
18 behavioral states, or is biologically informative with respect to larger-scale movement
19 patterns it does provide an improved fit of the model to the data.

20

21 The interpretation of *DIC* requires caution. While *DIC* values for the “switch
22 constrained” model are smaller than the unconstrained “switch” model, only the
23 differences for elk-163 and elk-363 are larger than 10 units. Because the constraint we

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

15

16 The generality and flexibility of methods presented here comes with the cost of
17 computing time and need for careful assessment of MCMC convergence. However,
18 availability of WinBUGS software makes implementation of numerical techniques
19 relatively easy and it also provides useful diagnostic tools. As with any Bayesian
20 method, an explicit quantification of uncertainty in model parameters is given by their
21 posterior distributions. Since we have used very vague priors (Table 1) and have a large
22 number of sample points in each path, we expect that these posterior distributions are

1 largely determined by the data. The use of informative priors in the “switch constrained”
2 model seems justified on biological grounds and on model fit.

3

4 Simple homogenous movement models have succeeded in describing relatively short-
5 term movement paths within homogeneous environments. Describing movement paths in
6 heterogeneous environments and over longer time-scales for large cognitive animals will
7 require more sophisticated models that account for greater behavioral complexity. Fitting
8 these more sophisticated models to data is technically challenging, but the increasing
9 development and use of MCMC methods represents a promising means by which this
10 challenge may be met.

11

12 **Acknowledgements**

13 We thank Peter Turchin and Rob Dunn, two anonymous reviewers and the editor Ottar
14 Bjornstad for useful comments on the manuscript. This work was supported by National
15 Science Foundation grant 0078130.

16

17 **References**

- 18 Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M.
19 Swift, and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing
20 distribution patterns. *Journal of Range Management* **49**:386-400.
- 21 Bell, W. J. 1991. *Searching behavior: the behavioral ecology of finding resources*.
22 Chapman and Hall, London.

- 1 Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of
2 iterative simulations. *Journal of Computational and Graphical Statistics* **7**:434-
3 455.
- 4 Carlin B.P., and Louis, T.A. 1996. Bayes and empirical Bayes methods for data analysis.
5 Vol. 69. Monographs on statistics and applied probability. Chapman and Hall,
6 London.
- 7 Dennis, B. 1996. Discussion: should ecologists become Bayesians. *Ecological*
8 *Applications* **6**:1095-1103.
- 9 Fauchald, P., and T. Tveraa. 2003. Using first-passage time in the analysis of area-
10 restricted search and habitat selection. *Ecology* **84**:282-288.
- 11 Firle, S., R. Bommarco, B. Ekbom, and M. Natielo. 1998. The influence of movement
12 and resting behavior on the range of three carabid beetles. *Ecology* **79**:2113-2122.
- 13 Fisher, N. I. 1993. Statistical analysis of circular data. Cambridge University Press,
14 Cambridge, New York, NY, USA.
- 15 Grünbaum, D. 2000. Advection-diffusion equations for internal state-mediated random
16 walks. *SIAM Journal of Applied Mathematics* **61**:43-73.
- 17 Johnson, C. J., K. L. Parker, D. Heard, C., and M. P. Gillingham. 2002. Movement
18 parameters of ungulates and scale-specific responses to the environment. *Journal*
19 *of Animal Ecology* **71**:225-235.
- 20 Jonsen, I. D., R. A. Myers, and J. M. Flemming. 2003. Meta-analysis of animal
21 movement using state-space models. *Ecology in press*.
- 22 Kareiva, P., and G. Odell. 1987. Swarms of predators exhibit "preytaxis" if individual
23 predators use area-restricted search. *American Naturalist* **130**:233-270.

- 1 Karlin, S., and H. M. Taylor. 1975. A first course in stochastic processes, 2d edition.
2 Academic Press, New York.
- 3 Morales, J. M. 2002. Behavior at habitat boundaries can produce leptokurtic movement
4 distributions. *American Naturalist* **160**:531-538.
- 5 Morales, J. M., and S. P. Ellner. 2002. Scaling up movement in heterogeneous
6 landscapes: the importance of behavior. *Ecology* **83**:2240-2247.
- 7 Okubo, A. 1980. Diffusion and ecological problems : mathematical models. Springer-
8 Verlag, Berlin ; New York.
- 9 Okubo, A., and S. A. Levin. 2001. Diffusion and ecological problems: modern
10 perspectives, second edition. Springer-Verlag.
- 11 Rudd, N. T., and P. B. McEvoy. 1996. Local dispersal by the cinnabar moth *Tyria*
12 *jacobaeae*. *Ecological Applications* **6**:285-297.
- 13 Sibly, R. M., H. M. R. Nott, and D. J. Fletcher. 1990. Splitting behaviour into bouts.
14 *Animal Behaviour* **39**:63-69.
- 15 Skalski, G. T., and J. F. Gilliam. 2003. A diffusion-based theory of organism dispersal in
16 heterogeneous populations. *American Naturalist* **161**:441-458.
- 17 Skellam, J. G. 1973. The formulation and interpretation of mathematical models of
18 diffusory processes in population biology. Pages 63-85 in M. S. Barlett and R.
19 W. Hiorns, editors. *The mathematical theory of the dynamics of biological*
20 *populations*. Academic Press, London.
- 21 Spectranalysis-Inc. 1999. Ontario Land Cover Data Base Revised User's Manual.
22 Unpublished Report to Ontario Ministry of Natural Resources.

- 1 Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. van der Linde. 2002. Bayesian
2 measures of model complexity and fit. *Journal of the Royal Statistical Society B*
3 **64**:583-639.
- 4 Spiegelhalter, D. J., A. Thomas, and N. G. Best. 1999. WinBUGS Version 1.2 User
5 Manual. MRC Biostatistics Unit.
- 6 Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling
7 population redistribution in animals and plants. Sinauer Associates, Sunderland,
8 Massachusetts.
- 9 Viswanathan, G. M., V. Afanasyev, S. V. Buldyrev, E. J. Murphy, P. A. Prince, and H. E.
10 Stanley. 1996. Levy flight search patterns of wandering albatrosses. *Nature*
11 **381**:413-415.
- 12 Viswanathan, G. M., F. Bartumeus, S. V. Buldyrev, J. Catalan, U. L. Fulco, S. Havlin, M.
13 G. E. da Luz, M. L. Lyra, E. P. Raposo, and H. E. Stanley. 2002. Levy flight
14 random searches in biological phenomena. *Physica a-Statistical Mechanics and Its*
15 *Applications* **314**:208-213.
- 16 Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**:385-397.
- 17 Zollner, P. A., and S. L. Lima. 1999. Search strategies for landscape-level interpatch
18 movements. *Ecology* **80**:1019-1030.
- 19

1 **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 ($a_{i+1} = a_i + eps_i$).
b_i	Gamma(0.01, 0.01)	Shape parameter for Weibull distribution describing step length for the i^{th} movement state.
μ_l	Uniform($-\pi, \pi$)	Mean direction for turning angles for the i^{th} movement state.
ρ_l	Uniform(0, 1)	Mean cosine for turning angles for the i^{th} movement state
$\eta_{l,t}$	Uniform(0, 1)	Mixture coefficient for the t^{th} observation –the probability that the t^{th} observation is in movement state 1 ($\eta_{2,t} = 1 - \eta_{1,t}$).
ν_h	Normal(0, σ), $\sigma = 100$	Coefficients in equation (4) relating state of individual to habitat in which it currently resides.
β_l	Normal(0, σ), $\sigma = 100$	Intercept in equation (5) relating probability of switching to distance to open habitat.
m	Normal(0, σ), $\sigma = 100$	Slope in equation (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.

2

1 Table 2. *DIC* values for the 7 models examined.

Model	elk-115		elk-163		elk-287		elk-363	
	<i>DIC</i>	p_D	<i>DIC</i>	p_D	<i>DIC</i>	p_D	<i>DIC</i>	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

2 *NC* – MCMC failed to converge

3

1 Table 3. Modes for different movement states (km/day).

		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

2 *NC* – MCMC failed to converge

1 **Figure legends**

2 Figure 1. Turning angle and step distributions for elk-287 in two behavioral states as
3 inferred using the “switch constrained model”. Turning angles (visualized using polar
4 plots) have Wrapped Cauchy distributions with parameters μ_i and ρ_i corresponding to the
5 mean of their posterior distributions. Step lengths have Weibull distributions with
6 parameters a_i and b_i corresponding to the mean of their posterior distributions.

7

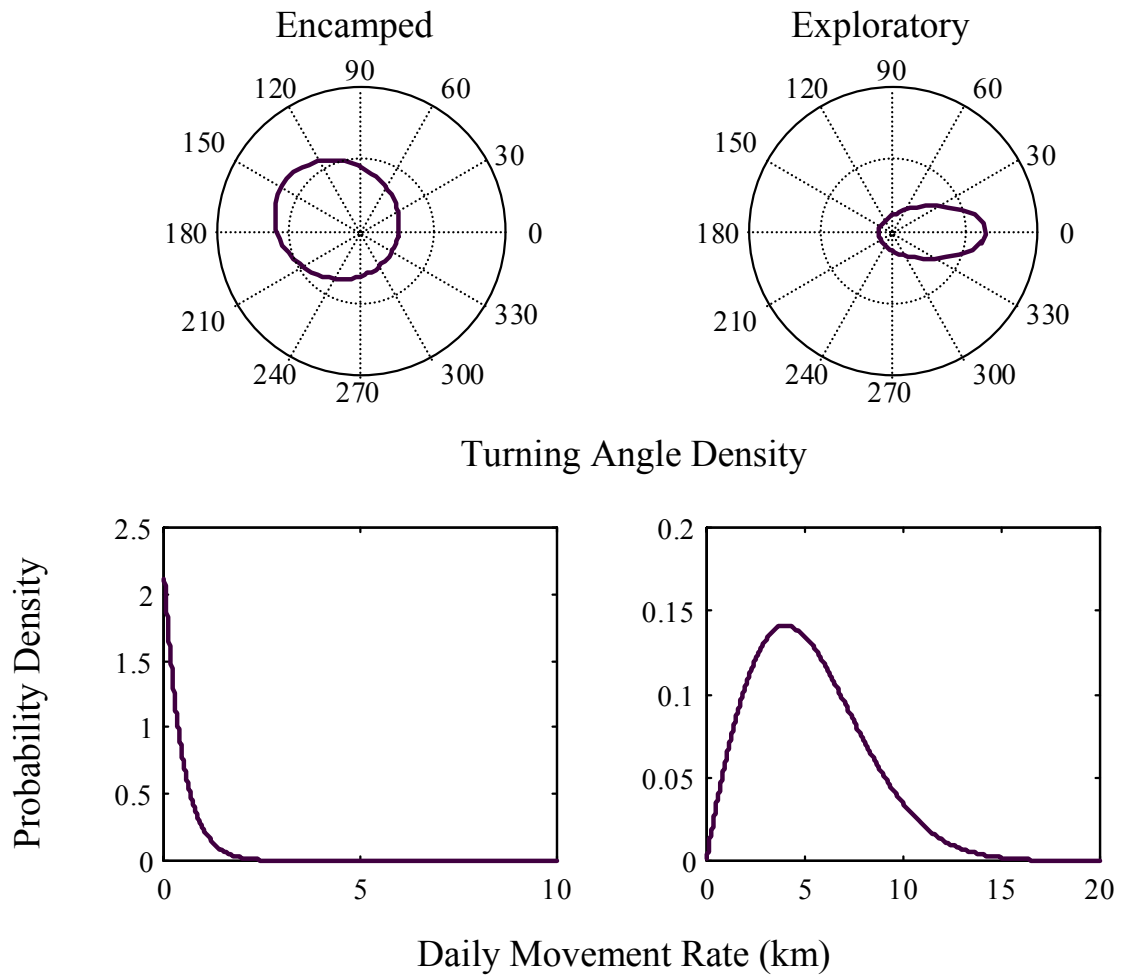
8 Figure 2. Activity bar showing assignment of behavioral states through time for all
9 multiple RW models fitted to elk-163. A: “Double”, B: “Double with covariates”, C:
10 “Double switch”, D: “Switch constrained”, E: “Triple switch”. The dots above the
11 activity bars indicate daily movement rate (on a log scale).

12

13 Figure 3. Autocorrelation functions (acfs) of daily movement rate for observed and
14 modeled elk paths for lags 1-60 for all 4 individuals. The left-hand column has acfs
15 corresponding to the “double switch” model and the right hand column corresponds to
16 acfs from the “switch constrained” model. Thick dotted lines are observed acfs. Thin
17 lines are 95% credibility intervals for the acfs of modeled paths (5000 replicates). Dots
18 are autocorrelation values for modeled paths.

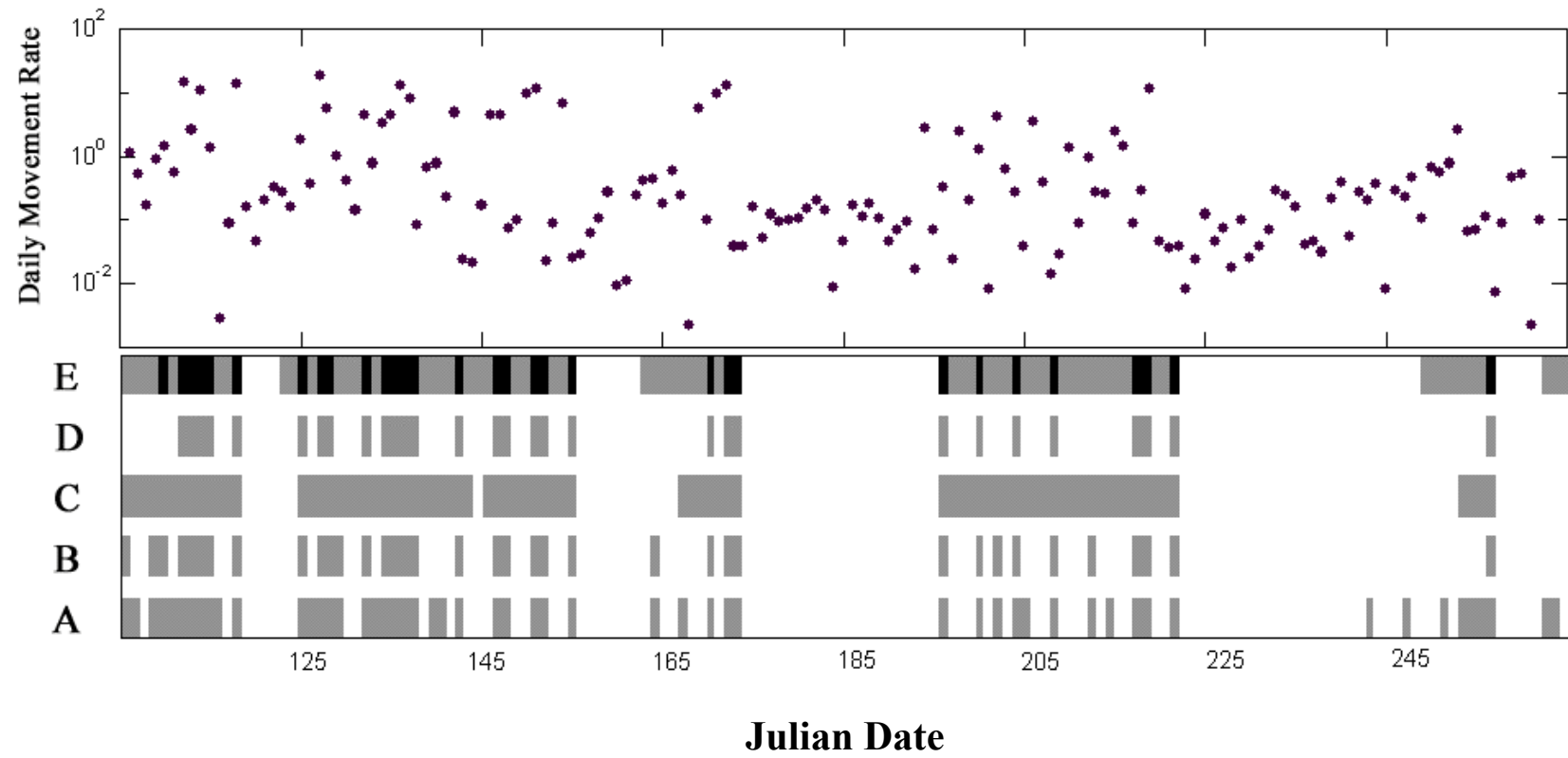
19

1 Figure 1.



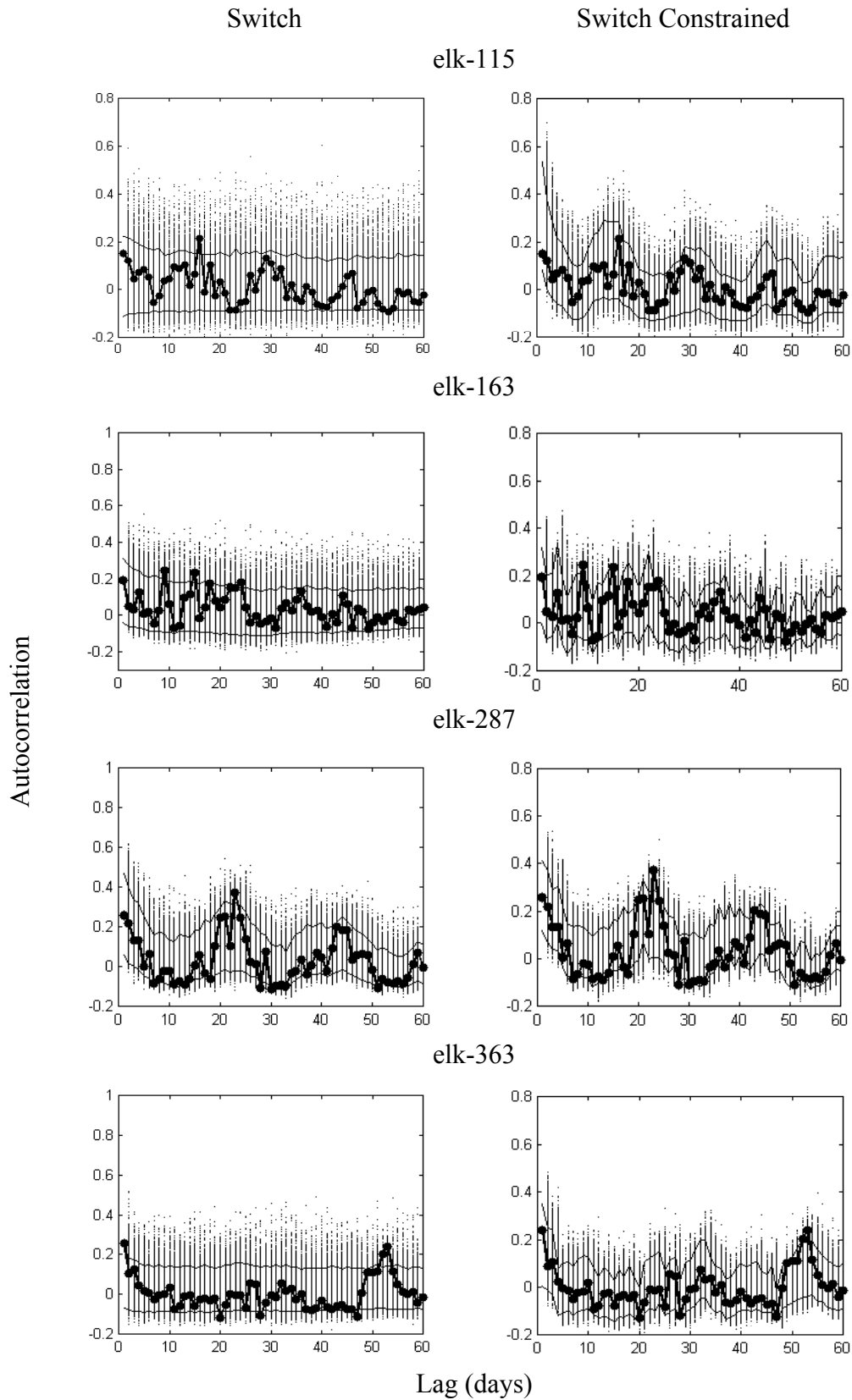
2

1 Figure 2.



2

1 Figure 3.



2

1 Appendix 1.

2

3 Mean and 95 credible intervals for the posterior distributions of model parameters

4

5 A.1. Single model

	elk-115	elk-163	elk-287	elk-363
a	1.066 (0.919, 1.225)	1.233 (1.047, 1.437)	1.154 (0.978, 1.350)	1.256 (1.091, 1.431)
b	0.692 (0.620, 0.767)	0.499 (0.444, 0.558)	0.576 (0.512, 0.641)	0.627 (0.566, 0.688)
μ	3.198 (2.857, 3.564)	3.194 (2.798, 3.591)	2.115 (0.598, 5.138)	2.994 (2.104, 3.952)
ρ	0.261 (0.156, 0.363)	0.263 (0.147, 0.375)	0.089 (0.005, 0.200)	0.124 (0.019, 0.229)

6

7 A.2. Double model

	elk-115	elk-163	elk-287	elk-363
a_1	1.462 (1.089, 1.990)	7.990 (4.558, 13.530)	5.255 (3.343, 9.251)	3.873 (2.560, 5.711)
a_2	1.028 (0.821, 1.245)	0.672 (0.445, 0.916)	0.654 (0.431, 0.895)	0.913 (0.715, 1.129)
b_1	1.430 (1.011, 1.942)	1.052 (0.838, 1.303)	1.215 (0.992, 1.494)	1.223 (0.972, 1.501)
b_2	0.543 (0.452, 0.640)	0.590 (0.469, 0.738)	0.615 (0.489, 0.767)	0.578 (0.485, 0.679)
μ_1	3.171 (-3.131, 3.138)	3.176 (-3.112, 3.105)	2.710 (-3.068, 3.089)	2.966 (2.701, 3.129)
μ_2	0.638 (-2.926, 2.947)	3.141 (-3.127, 3.129)	0.277 (-0.519, 1.284)	6.055 (-1.264, 0.751)
ρ_1	0.564 (0.391, 0.705)	0.179 (0.010, 0.408)	0.283 (0.092, 0.442)	0.477 (0.314, 0.614)
ρ_2	0.077 (0.003, 0.216)	0.341 (0.074, 0.550)	0.300 (0.047, 0.513)	0.205 (0.027, 0.369)

8

9 A.3. Double with Covariates

	elk-163	elk-287	elk3-63
a_1	4.802 (2.477, 8.434)	3.739 (2.893, 4.719)	2.141 (1.561, 2.788)
a_2	0.292 (0.018, 0.750)	0.106 (0.019, 0.350)	0.066 (0.004, 0.200)
b_1	0.892 (0.691, 1.110)	1.073 (0.924, 1.232)	0.844 (0.706, 0.980)
b_2	0.962 (0.532, 1.854)	1.338 (0.757, 1.931)	1.732 (1.134, 2.736)
μ_1	6.256 (-2.978, 2.986)	-0.013 (-3.007, 2.950)	1.645 (-2.981, 2.986)
μ_2	2.511 (-2.987, 2.951)	-0.022 (-2.992, 2.952)	6.142 (-2.966, 2.990)
ρ_1	0.018 (0.000, 0.066)	0.017 (0.000, 0.061)	0.013 (0.000, 0.047)
ρ_2	0.037 (0.001, 0.138)	0.606 (0.403, 0.761)	0.359 (0.068, 0.633)

v_1	0.122 (-19.360, 19.990)	-7.717 (-22.390, 2.075)	8.588 (-0.694, 22.920)
v_2	4.161 (1.402, 12.610)	5.825 (3.615, 8.969)	3.346 (1.568, 5.730)
v_3	-7.595 (-23.270, 2.222)	-0.174 (-13.840, 5.243)	9.275 (1.318, 23.140)
v_4	-0.053 (-19.420, 19.400)	1.538 (-0.853, 4.206)	-0.211 (-19.670, 19.310)
v_5	-5.975 (-21.040, 3.268)	0.088 (-5.404, 3.617)	1.337 (-4.349, 14.250)
v_6	-0.138 (-19.800, 19.740)	-0.053 (-19.930, 19.580)	0.230 (-19.510, 20.000)
v_7	1.194 (-0.395, 2.491)	2.136 (1.205, 3.094)	3.206 (2.130, 4.618)
v_8	-0.923 (-13.130, 2.392)	0.160 (-2.650, 3.039)	2.358 (0.305, 4.641)
v_9	-1.178 (-15.030, 4.273)	-0.530 (-3.285, 2.088)	8.758 (1.410, 23.330)
v_{10}	0.127 (-19.820, 18.970)	9.797 (1.766, 23.560)	2.607 (-1.013, 9.293)

1

2 A.4. Switch model

	elk-115	elk-163	elk-287	elk-363
a_1	1.262 (1.063, 1.495)	8.314 (4.433, 14.990)	3.606 (2.853, 4.536)	3.672 (1.998, 6.522)
a_2	1.164 (0.973, 1.364)	0.689 (0.168, 0.993)	0.154 (0.031, 0.413)	0.881 (0.496, 1.161)
b_1	0.442 (0.340, 0.560)	1.064 (0.844, 1.321)	1.051 (0.907, 1.207)	1.193 (0.838, 1.592)
b_2	1.306 (1.081, 1.717)	0.602 (0.462, 1.042)	1.167 (0.692, 1.729)	0.588 (0.464, 0.758)
μ_1	2.999 (-3.046, 3.047)	3.205 (-3.127, 3.125)	2.620 (2.059, 3.196)	2.971 (2.622, 3.247)
μ_2	3.160 (-3.133, 3.135)	3.136 (-3.115, 3.117)	0.118 (0.005, 0.370)	5.962 (0.036, 6.247)
ρ_1	0.089 (0.004, 0.245)	0.313 (0.119, 0.482)	0.226 (0.101, 0.347)	0.427 (0.231, 0.619)
ρ_2	0.408 (0.267, 0.589)	0.183 (0.011, 0.422)	0.582 (0.383, 0.741)	0.217 (0.019, 0.506)
$q_{1,2}$	0.086 (0.023, 0.249)	0.173 (0.036, 0.575)	0.349 (0.151, 0.557)	0.329 (0.148, 0.554)
$q_{2,1}$	0.136 (0.036, 0.288)	0.142 (0.041, 0.294)	0.096 (0.045, 0.158)	0.295 (0.097, 0.526)

3

4 A.5. Switch with Covariates

	elk-115	elk-287	elk-363
--	---------	---------	---------

a_1	1.544 (1.311, 1.811)	3.668 (2.846, 4.679)	2.151 (1.616, 2.803)
a_2	0.038 (0.005, 0.093)	0.248 (0.049, 0.674)	0.129 (0.010, 0.495)
b_1	0.887 (0.779, 1.000)	1.064 (0.911, 1.245)	0.842 (0.711, 0.976)
b_2	1.786 (1.273, 2.531)	0.979 (0.544, 1.545)	1.466 (0.743, 2.325)
μ_1	-1.462 (-3.129, 3.130)	2.312 (-3.030, 3.056)	2.378 (-3.092, 3.121)
μ_2	0.942 (-1.873, 2.583)	0.036 (-0.263, 0.389)	-0.461 (-1.057, 0.068)
ρ_1	0.311 (0.207, 0.411)	0.232 (0.106, 0.354)	0.226 (0.113, 0.349)
ρ_2	0.291 (0.017, 0.619)	0.538 (0.299, 0.730)	0.459 (0.157, 0.705)
β_1	3.070 (2.282, 4.026)	2.425 (1.690, 3.409)	2.292 (1.405, 3.416)
β_2	-0.531 (-6.742, 5.587)	-2.977 (-8.109, 2.076)	-1.140 (-6.019, 3.655)
$m_{2,1}$	-0.041 (-6.236, 6.155)	-0.121 (-6.096, 6.056)	-0.191 (-6.174, 5.921)
$m_{2,2}$	-0.281 (-5.308, 4.987)	0.168 (-3.119, 2.492)	0.042 (-3.520, 3.577)
$m_{2,3}$	0.764 (-5.338, 6.792)	-0.338 (-6.399, 5.713)	1.626 (-4.367, 7.318)
$m_{2,4}$	-3.210 (-7.945, 1.420)	1.276 (-0.363, 2.959)	1.302 (-0.519, 3.508)
$m_{2,5}$	4.025 (-0.927, 9.281)	2.139 (-1.506, 5.685)	3.151 (-0.383, 6.941)
$m_{2,6}$	-0.015 (-6.209, 6.230)	0.054 (-6.171, 6.190)	-0.135 (-6.086, 5.961)
$m_{2,7}$	2.705 (-0.651, 6.312)	0.283 (-4.908, 5.502)	5.062 (0.277, 9.706)
$m_{2,8}$	-0.342 (-6.480, 5.935)	-1.060 (-7.121, 4.852)	-0.331 (-6.104, 5.724)
$m_{2,9}$	0.654 (-5.753, 6.709)	-1.383 (-7.147, 4.443)	-0.235 (-5.995, 5.706)
$m_{2,10}$	-0.712 (-4.079, 2.544)	-0.248 (-1.928, 1.359)	-0.950 (-3.217, 1.268)

1

2 A.6. Triple Switch

	elk-115	elk-163	elk-287	elk-363
a_1	24.06 (12.52, 37.09)	12.43 (5.70, 25.44)	19.41 (9.72, 31.22)	11.05 (3.84, 23.56)

a_2	1.354 (1.124, 1.632)	3.292 (0.858, 11.530)	3.538 (2.589, 4.667)	3.582 (2.098, 5.736)
a_3	0.073 (0.007, 0.251)	0.239 (0.012, 0.827)	0.165 (0.057, 0.346)	0.432 (0.071, 0.793)
b_1	0.895 (0.851, 1.000)	1.150 (0.889, 1.441)	1.406 (1.131, 1.670)	0.519 (0.324, 0.734)
b_2	1.167 (1.014, 1.341)	0.947 (0.529, 2.386)	1.458 (1.158, 1.926)	1.203 (0.968, 1.475)
b_3	1.572 (0.923, 2.407)	1.150 (0.501, 1.960)	1.120 (0.772, 1.515)	0.933 (0.642, 1.593)
μ_1	4.156 (-3.037, 3.005)	-0.750 (-3.125, 3.123)	2.148 (-3.011, 3.006)	1.126 (-2.806, 2.850)
μ_2	3.117 (-3.114, 3.138)	0.101 (-3.089, 3.093)	2.753 (2.241, 3.112)	3.056 (-3.136, 3.108)
μ_3	1.080 (-1.523, 2.501)	0.243 (-3.121, 3.120)	0.067 (-0.201, 0.372)	5.721 (-1.754, 0.409)
ρ_1	0.148 (0.005, 0.405)	0.329 (0.111, 0.511)	0.129 (0.007, 0.328)	0.236 (0.011, 0.564)
ρ_2	0.349 (0.228, 0.464)	0.180 (0.006, 0.617)	0.318 (0.152, 0.478)	0.330 (0.160, 0.506)
ρ_3	0.316 (0.022, 0.642)	0.291 (0.018, 0.653)	0.561 (0.374, 0.719)	0.270 (0.035, 0.536)
$q_{1,1}$	0.724 (0.480, 0.815)	0.839 (0.544, 0.904)	0.689 (0.543, 0.739)	0.870 (0.593, 0.955)
$q_{1,2}$	0.041 (0.008, 0.054)	0.077 (0.001, 0.084)	0.044 (0.001, 0.057)	0.018 (0.001, 0.022)
$q_{1,3}$	0.069 (0.002, 0.097)	0.241 (0.034, 0.331)	0.367 (0.190, 0.429)	0.042 (0.001, 0.039)
$q_{2,1}$	0.094 (0.004, 0.131)	0.095 (0.009, 0.122)	0.053 (0.003, 0.074)	0.067 (0.000, 0.094)
$q_{2,2}$	0.926 (0.847, 0.951)	0.603 (0.103, 0.762)	0.938 (0.801, 0.972)	0.769 (0.598, 0.822)
$q_{2,3}$	0.328 (0.070, 0.411)	0.309 (0.015, 0.424)	0.044 (0.002, 0.062)	0.424 (0.063, 0.517)
$q_{3,1}$	0.181 (0.024, 0.247)	0.066 (0.003, 0.088)	0.258 (0.132, 0.305)	0.064 (0.001, 0.091)
$q_{3,2}$	0.034 (0.001, 0.046)	0.320 (0.061, 0.417)	0.018 (0.001, 0.024)	0.214 (0.057, 0.264)
$q_{3,3}$	0.603 (0.360, 0.685)	0.449 (0.155, 0.565)	0.589 (0.410, 0.654)	0.534 (0.280, 0.615)

1
2

1 A.7. Switch Constrained

	elk-115	elk-163	elk-287	elk-363
a_1	1.525 (1.272, 1.790)	3.630 (2.475, 5.023)	3.455 (2.824, 4.509)	2.262 (1.715, 3.005)
a_2	0.046 (0.004, 0.171)	0.034 (0.009, 0.049)	0.019 (0.028, 0.208)	0.034 (0.009, 0.049)
b_1	0.883 (0.769, 0.996)	0.829 (0.687, 0.976)	1.034 (0.896, 1.195)	1.012 (0.865, 1.183)
b_2	1.771 (1.084, 2.687)	1.645 (1.391, 2.105)	1.903 (1.015, 1.764)	1.911 (1.609, 2.429)
μ_1	3.190 (-3.116, 3.138)	-0.607 (-3.126, 3.126)	2.613 (-3.011, 3.060)	1.751 (-3.115, 3.130)
μ_2	1.101 (-2.057, 2.575)	0.256 (-3.115, 3.117)	0.027 (-0.228, 0.300)	-0.455 (-1.123, 0.134)
ρ_1	0.310 (0.207, 0.414)	0.248 (0.114, 0.373)	0.209 (0.106, 0.339)	0.234 (0.116, 0.345)
ρ_2	0.292 (0.018, 0.642)	0.265 (0.017, 0.545)	0.616 (0.406, 0.759)	0.426 (0.126, 0.673)
$q_{1,2}$	0.047 (0.019, 0.093)	0.157 (0.087, 0.238)	0.099 (0.051, 0.161)	0.115 (0.057, 0.185)
$q_{2,1}$	0.421 (0.204, 0.666)	0.616 (0.427, 0.790)	0.372 (0.184, 0.567)	0.635 (0.422, 0.820)

2

3

1 Supplementary Material for “Extracting More out of Relocation Data: Building
2 Movement Models as Mixtures of Correlated Random Walks”

3

4 **WinBUGS code for “single” model**

5

```
6 model{
7     for (t in 1:npts) {
8         # likelihood for steps
9         l[t] ~ dweib(b[t], a[t])      # Weibull distribution for step length
10
11         a[t] <- nu                    # scale parameter
12         b[t] <- lambda                # shape parameter
13
14         # likelihood for turns. We use the “ones” trick to sample from the
15         # Wrapped Cauchy distribution (see WinBUGS manual)
16
17         ones[t] <- 1
18         ones[t] ~ dbern(wc[t])
19         wc[t] <- (1/(2*Pi)*(1-rho[t]*rho[t])/(1+rho[t]*rho[t]-2*rho[t]*cos(theta[t]-
20 mu.t[t])))/ 300 # Density function for Wrapped Cauchy distribution
21
22         rho[t] <- lambda.t            # mean cosine for the circular distribution
23         mu.t[t] <- nu.t               # mean direction for turns
24     }
25
26     ##### priors on movement parameters
27
28     nu ~ dgamma(0.01, 0.01)          # prior distribution for the scale parameter
29     lambda ~ dgamma(0.01,0.01) # prior distribution for shape parameter
30
31     ##### priors for mean direction of turns
32
33     nu.t ~ dunif(-3.14159265359, 3.14159265359)
34     lambda.t ~ dunif(0,1) # prior for mean cosine of circular distribution
35
36     Pi <- 3.14159265359 # define  $\pi$ 
37 }
38
39
```

40 **WinBUGS code for “Double” model**

41

```
42 model{
43     for (t in 1:npts) {
44
```

44


```

1      ##### likelihood for steps
2      l[t] ~ dweib(b[t], a[t])      # Weibull distriution for step length
3
4      a[t] <- nu[idx[t]]           # scale parameter
5      b[t] <- lambda[idx[t]]      # shape parameter
6
7      ##### likelihood for turns.
8      #
9      # We use the “ones” trick to sample from the Wrapped Cauchy
10     # (see WinBUGS manual)
11
12     ones[t] <- 1
13     ones[t] ~ dbern(wc[t])
14     wc[t] <- (1/(2*Pi)*(1-rho[t]*rho[t])/(1+rho[t]*rho[t]-2*rho[t]*cos(theta[t]-
15     mu.t[t])))/ 300 # Probability Density Function for Wrapped Cauchy distribution
16
17     rho[t] <- lambda.t[idx[t]]    # mean cosine for the circular distribution
18     mu.t[t] <- nu.t[idx[t]]      # mean direction of turns
19
20     # idx is the latent variable and the parameter index
21     idx[t] ~ dcat(p[t,])
22
23     p[t,1] ~ dunif(0,1)          # priors on p[t,1], the probability that the t-th
24     # observation corresponds to movement state 1.
25     p[t,2] <- 1 - p[t,1]
26 }
27
28 ##### priors on movement parameters
29
30 nu[2] ~ dgamma(0.01, 0.01) # prior distribution for the scale parameter in
31 # “exploratory” movement state
32
33 eps ~ dgamma(0.01, 0.01) # make a nonnegative variate
34 nu[1] <- nu[2] + eps      # this is to make the scale parameter in one of the
35 # distributions larger than the other.
36
37 ##### prior distributions for shape parameters
38 lambda[1] ~ dgamma(0.01,0.01)
39 lambda[2] ~ dgamma(0.01,0.01)
40
41 ##### priors for mean direction of turns
42 nu.t[1] ~ dunif(-3.14159265359, 3.14159265359)
43 nu.t[2] ~ dunif(-3.14159265359, 3.14159265359)
44
45 ##### priors for mean cosine of circular distribution
46 lambda.t[1] ~ dunif(0,1)

```

```

1      lambda.t[2] ~ dunif(0,1)
2
3      ##### define  $\pi$ 
4      Pi <- 3.14159265359
5  }
6

```

7 WinBUGS code for “Double with covariates” model

8 (only those sections that are different from “Double” are reported)

```

9
10      idx[t] ~ dcat(p[t,])
11
12      # probability of being in movement type 1
13      logit.q[t] ~ dnorm(mu.type[t], tau.q)
14      mu.type[t] <- mu.phi[typ[t]]
15      q[t] <- exp(logit.q[t])/(1 + exp(logit.q[t]))
16      p[t,1] <- q[t]
17      p[t,2] <- 1 - q[t]
18  }
19
20      # priors on movement parameters
21
22      # phi[i] is the probability of being in movement type 1 when in habitat i
23      for (i in 1:10) {
24      mu.phi[i] ~ dnorm(0.0, 0.01)
25      }
26  }
27
28

```

29 WinBUGS code for “Switch” model

30 (only those sections that are different from “Double” are reported)

```

31
32      idx[t] ~ dcat(p[t,]) # idx is the latent variable and the parameter index
33
34      p[t,1] <- q[idx[t-1]] # p[t,1] is the probability that the t-th observation
35                          # corresponds to movement state 1.
36      p[t,2] <- 1-q[idx[t-1]]
37
38  }
39
40      ##### priors on movement parameters
41      ##### priors for transition probabilities
42      q[1] ~ dunif(0,1)
43      q[2] ~ dunif(0,1)
44

```

```

1      ##### prior for the state of the first observation
2      idx[1] ~ dcat(phi[])
3  }
4

```

5 **WinBUGS code for “Switch with covariates” model**

6 (only those sections that are different from “Double” are reported)

```

7
8      # the probability of being in movement type 1
9      idx[t] ~ dcat(p[t,])
10     p[t,1] <- q[t]
11     p[t,2] <- 1 - q[t]
12     q[t] <- logit.q[t]/(1 + logit.q[t])
13
14     logit.q[t] <- exp(a[idx[t-1]]+m[idx[t-1],1]*water[t]+m[idx[t-
15     1],2]*swamp[t]+m[idx[t-1],3]*otw[t]+m[idx[t-1],4]*openfor[t]+m[idx[t-
16     1],5]*ntw[t]+m[idx[t-1],6]*mixfor[t]+m[idx[t-1],7]*dev[t]+m[idx[t-
17     1],8]*ddf[t]+m[idx[t-1],9]*conif[t]+m[idx[t-1],10]*alvar[t])
18
19     }
20
21     # priors on movement parameters
22     for(i in 1:10){
23         for(j in 1:2){
24             m[j,i] ~ dnorm(0,0.1)
25         }
26     }
27
28     for (i in 1:10){
29         m[1,i] <- 0
30     }
31
32
33     a[1]~dnorm(0,0.1)
34     a[2]~dnorm(0,0.1)
35
36     }
37

```

38 **WinBUGS code for “Triple switch” model**

39 (only those sections that are different from “Double” are reported)

```

40
41     # the probability of being in movement type 1
42     p[t,1] <- q[idx[t-1]]
43     p[t,2] <- (1 - q [idx[t-1]] ) * qq[idx[t-1]]
44     p[t,3] <- (1 - q [idx[t-1]] ) * (1-qq[idx[t-1]] )

```

```

1      }
2
3      # priors on movement parameters
4
5      eps1 ~ dgamma(0.01, 0.01)
6      eps2 ~ dgamma(0.01, 0.01)
7
8      nu[3] ~ dgamma(0.01, 0.01)
9      nu[2] <- nu[3] + eps1
10     nu[1] <- nu[2] + eps2
11
12     qq[1] ~ dunif(0,1)
13     qq[2] ~ dunif(0,1)
14     qq[3] ~ dunif(0,1)
15
16     # priors for the pr of switching from anything to 1
17     q[1] ~ dunif(0,1)
18     q[2] ~ dunif(0,1)
19     q[3] ~ dunif(0,1)
20
21 }
22

```

23 **MATLAB code for calculation of DIC and posterior predictive** 24 **check on step length autocorrelation**

```

25
26 % load output files from WinBUGS as saved for the CODA
27 % S-Plus diagnostic package.
28 % Each MCMC chain is in a separate file showing the
29 % iteration number and value
30
31 load out-1.txt;
32 load out-2.txt;
33 load out-3.txt;
34 load out-4.txt;
35
36 load indkey; % this file contains a description of which
37 % lines of the outup file correspond to
38 % which variable - this is the CODA .ind
39 % file.
40
41 load elkdata % an ascii file with observed steps and
42 turning
43 % angles
44

```

```

1  nreps = 5000; % number of replicates for the posterior
2  predictive
3          % check
4  elk = elkdata;
5  n = length(elk); % size of movement path
6  sim = []; % empty array to hold the values from the MCMC samples
7
8  % read MCMC samples
9  for k = 1:4
10     simi = [];
11     if k == 1
12         a = out-1;
13     elseif k==2
14         a = out-2;
15     elseif k==3
16         a = out-3;
17     else
18         a = out-4;
19     end
20
21     for i = 1:length(key)
22         simi = [simi a(key(i,1):key(i,2),2)];
23     end
24
25     sim = [sim; simi];
26 end
27
28 s = size(sim); % size of the MCMC samples (all chains)
29 % samples are in rows and variables in
30 columns
31
32 % create some variables to hold results
33 sqd = ones(nreps,1).*NaN;
34 L = sqd;
35 LW = L;
36 LWC = L;
37 AC = [];
38 X = [];
39 Y = [];
40
41 hh = waitbar(0,'Please wait...');
42 for j = 1:nreps
43
44     waitbar(j/nreps, hh)
45
46     i = ceil(rand*s(1)); % choose a MCMC chain at random
47

```

```

1     camp = find(sim(i,1:n)==1);      % find observations
2     classified as
3                                     % "encamped"
4     expl = find(sim(i,1:n)==2);     % find observations
5     classified as
6                                     % "exploratory"
7
8     % set some values to zero
9     sqdev = 0;
10    sqdeve = 0;
11    lWc = 0;
12    lWe = 0;
13    lWCc = 0;
14    lWce = 0;
15    simdatal = zeros(n,1);
16    simdatat = zeros(n,1);
17
18    if ~isempty(camp)
19
20        % likelihoods (wcauchylike and weiblike return
21        negative log
22        % likelihoods)
23        lWCc = 2 .* wcauchylike([sim(i,n+7)
24        sim(i,n+3)],elk(camp,2));
25        lWc = 2 .* WEIBLIKE([sim(i,n+5)
26        sim(i,n+1)],elk(camp,1));
27
28        % simulate values for step and turs using parameters
29        from the
30        % MCMC chain
31        lpred =
32        weibrnd(sim(i,n+5),sim(i,n+1),length(camp),1);
33        tpred =
34        wcauchy(sim(i,n+7),sim(i,n+3),length(camp),1);
35        % squared deviations
36        sqdev = (elk(camp,1)-lpred).^2+(elk(camp,2)-
37        tpred).^2;
38        simdatal(camp') = lpred;
39        simdatat(camp') = tpred;
40
41    end
42
43    % do the same for exploratory state
44    if ~isempty(expl)
45
46        lWce = 2 .* wcauchylike([sim(i,n+8)
47        sim(i,n+4)],elk(expl,2));

```

```

1         lWe = 2 .* WEIBLIKE([sim(i,n+6)
2 sim(i,n+2)], elk(expl,1));
3         lprede =
4 weibrnd(sim(i,n+6), sim(i,n+2), length(expl), 1);
5         tprede =
6 wcauchy(sim(i,n+8), sim(i,n+4), length(expl), 1);
7         sqdeve = (elk(expl,1)-lprede).^2+(elk(expl,2)-
8 tprede).^2;
9         simdatal(expl') = lprede;
10        simdatat(expl') = tprede;
11
12        end
13
14        % build simulated movement paths
15        x = zeros(n,1);
16        y = x;
17        dir = rand*2*pi;
18        x(2) = cos(dir).*simdatal(1);
19        y(2) = sin(dir).*simdatal(1);
20
21        for k = 2:n
22            x(k+1) = x(k) + cos(simdatat(k-1) + dir) .*
23 simdatal(k);
24            y(k+1) = y(k) + sin(simdatat(k-1) + dir) .*
25 simdatal(k);
26            dir = dir + simdatat(k-1);
27        end
28
29        % calculate and save the autocorrelation function
30        AC = [AC; acf(simdatal)];
31        X = [X x];
32        Y = [Y y];
33
34        % total squared deviations and likelihoods
35        sqd(j) = sum(sum(sqdev)) + sum(sum(sqdeve));
36        LWC(j) = sum(sum(LWCc)) + sum(sum(LWCe));
37        LW(j) = sum(sum(LWc)) + sum(sum(LWe));
38        L(j) = LW(j)+LWC(j);
39
40    end
41    close(hh)
42
43    % calculate Deviance for tetha hat
44    indi = median(sim(:,1:n));
45
46    camp = find(indi == 1);
47    expl = find(indi == 2);

```

```

1
2 lWc = 2 .* WEIBLIKE([mean(sim(:,n+5))
3 mean(sim(:,n+1))], elk(camp,1));
4 lWe = 2 .* WEIBLIKE([mean(sim(:,n+6))
5 mean(sim(:,n+2))], elk(expl,1));
6 lWCc = 2 .* wcauchylike([meandirection(sim(:,n+7))
7 mean(sim(:,n+3))], elk(camp,2));
8 lWce = 2 .* wcauchylike([meandirection(sim(:,n+8))
9 mean(sim(:,n+4))], elk(expl,2));
10
11
12 Dtetha = lWc + lWe + lWCc + lWce;
13
14 % calculate expected Deviance
15 Dbar = mean(L);
16
17 DIC = Dtetha + 2 * (Dbar - Dtetha);
18
19 % display Deviance results
20 [Dbar Dtetha Dbar-Dtetha DIC]
21
22 % plot the acf
23 figure
24
25 x = 0:1:n-1;
26 x = x';
27 aca = acf(elk(:,1));
28 aca(1) = NaN;
29 ac = sort(AC);
30 ha=plot(x,aca,'.-k');
31 set(ha,'MarkerSize',20,'LineWidth',2);
32
33 hold on
34 ac(:,1) = NaN;
35 hacl = plot(x,ac(5000-125,:), 'k'); set(hacl,'LineWidth',1)
36 hacu = plot(x,ac(125,:), 'k'); set(hacu,'LineWidth',1)
37
38 AC(:,1) = NaN;
39 h = plot(AC', '.k'); set(h, 'MarkerSize', 3);
40 AXIS([0 60 -.2 0.8]);
41
42 percentilAC = [ac(125,:) ac(5000-125,:)];
43
44 % save results
45 save DICelk L LWC LW lWc lWe lWCc lWce DIC Dbar Dtetha
46 percentilAC
47

```



```

1
2 MATLAB function to simulate pseudo random numbers with
3 Wrapped Cauchy distribuion
4
5 function [t] = wcauchy(mu,p,M,N)
6
7 % [t] = wcauchy(mu,p,M,N)
8 % pseudo-random number generation of the wrapped cauchy
9 distribution with mean m and
10 % mean resultant lenght p.
11 % wcauchy(mu,p) returns a single value
12 % wcauchy(mu,p,M,N) returns a M by N array
13 % The circular dispersion is
14 %  $(1-p^2)/(2p^2)$ 
15 % circular variance  $v = 1-p$ 
16 % from Fisher(1993) Statistical analysis of circular data
17
18 if nargin == 2
19     u = rand;
20     V = cos(2*pi*u);
21     c = 2*p/(1+p^2);
22
23     t = sign(rand - .5) * acos((V+c)/(1+c.*V)) + mu;
24     t = mod(t,2*pi);
25
26 elseif nargin == 4
27
28     u = rand(M,N);
29     V = cos(2.*pi.*u);
30     c = 2 .* p ./ (1 + p.^2);
31
32     t = sign(rand(M,N) - 0.5) .* acos((V+c)./(1+c.*V)) + mu;
33     t = mod(t,2*pi);
34
35 end
36
37 MATLAB code for negative log likelihood of Wrapped Cauchy
38
39 function logL = wcauchylike(params,data)
40 % logL = wcauchylike(params,data)
41 % log likelihood for wrapped Cauchy distribution
42
43 if nargin < 2,
44     error('Requires at least two input arguments');

```

```
1 end
2
3 [n, m] = size(data);
4
5 if nargin == 2 & max(m,n) == 1
6     error('To compute the 2nd output, the 2nd input must
7 have at least two elements.');
```

```
8 end
9
10 if n == 1
11     data = data';
12     n = m;
13 end
14
15 rho = params(2);
16 mu = params(1);
17
18 rho = rho(ones(n,1),:);
19
20 mu = mu(ones(n,1),:);
21
22 x = (1/(2*pi)) .* (1 - rho.^2)./(1+rho.^2 -
23 2.*rho.*cos(data-mu)) + eps;
24
25 logL = -sum(log(x));
26
```