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Extracting More out of Relocation Data: Building Movement Models as Mixtures of Random Walks

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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 include the habitat type that animals are located in. 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 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 formulations of movement models. Analysis of relocation data from elk released in east-central Ontario suggests a bi-phasic movement behavior: elk are either in an ‘encamped’ state in which step lengths are small, and turning angles high, or, in an ‘exploratory’ state, in which daily step lengths are several kilometers, and turning angles small. Animals encamp in open habitat (agricultural fields and opened forest), but the exploratory state is not associated with any particular habitat type.

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

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

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 mapping (Geographic Information System) 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 sub-optimal habitat, but slow down on encountering improved habitat. Consider for example an individual performing area-restricted search (Kareiva and Odell 1987, Bell 1991). When in an intensive search state (for example after encountering a habitat patch with abundant food), 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 and 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 and we therefore perform inference with WinBUGS (Bayesian Analysis Using Gibbs Sampler (Spiegelhalter et al. 1999), freely available at <http://www.mrc-bsu.cam.ac.uk/bugs/>) using data from the movement paths of 4 elk re-introduced into east-central Ontario.

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

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 (Turchin 1998). When multiple RWs are considered, we want to classify each observation as belonging to one of these RWs and obtain the parameters for each of them. Obviously such a formulation may potentially 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_t ($t = 1, \dots, T$) is associated with an unobserved (latent) state-indicator variable $I_t = i$, $i \in \{1, \dots, M\}$ 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 $y_t = [r_t, \phi_t]$, 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 ($i \in \{1, \dots, M\}$). For a given vector of states I the likelihood function is

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

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 unfeasible to evaluate all possible forms of I and Bayesian methods become particularly useful in determining the best fitting combination. The Weibull distribution takes the form:

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

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

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

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

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 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.

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

- 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 .

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

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

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

where β_1 and m_h are parameters, and d_h is distance (km) to habitat h . The rationale behind this model is that elk may be more likely to switch from 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 some other factor but we chose not to include covariates in the determination of this transition probability. Equations (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 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. A 3-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). However, due to lack of convergence of some models for some data sets, we chose to be more “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

$$22 \quad Dev(\theta) = -2 \log P(y | \theta) \quad (6)$$

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

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 x 1500 independent MCMC observations. Tables of all estimated parameters (means and 95% credible intervals) are included in the Appendix, *DIC* values for each model and modal step lengths (calculated as $\left[(b-1)/ab \right]^{\frac{1}{b}}$ when $b > 1$ and zero otherwise) 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 0.99-1.32 km/day. Mean turning angle for all 4 animals was 165° suggesting a high tendency to reverse direction, but the mean cosine of turning angle was low, indicating a high variance around this tendency.

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 about 60% of the time (range 0.47-0.70). Expected daily movement rates in the encamped state range from 0.14-0.70 km/day, and in the exploratory state

from 1.651 – 3.26 km/day. 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. Mean turning angle for all individuals in the encamped state was 172° indicating many reversals but 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 that the animal is located in, yielded RWs broadly similar to those of the “double” model described above (except for elk-115 for which this model failed to converge). The principal difference was that animals were identified to be 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 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 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 the “double with covariates” – that is, 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/day), 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_i significantly different from zero) except elk-363 for which propensity to switch from exploratory to encamped state increased with distance from open habitat.

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

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

km/day) – but leaves the parameters for the exploratory state almost unchanged compared to “switch constrained”, “switch with covariates” and “double with covariates”. The proportion of time spent in the exploratory state is almost identical to these other 3 models, but the proportions of time spent in the almost stationary and low movement states are variable with individual (ranges 0.10-0.40 and 0.40-0.80 respectively). Figure 2 shows the assignment of movement states with all the multiple mixed RW models fitted to elk-163, together with 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 3 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 data provides a further means by which model fit to the temporal structure of observed data may be judged. In Figure (3) acfs from observed data are compared with those predicted by the “double switch” and “switch constrained” models applied to the 4 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

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.

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

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) the methods presented lead naturally to formulation of models of movement as opposed to just a classification of movement states or the determination of “scale domains”.

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 (Jonsen et al. 2003). Since we only have data for four animals we have fitted models to each path but it is readily extended to a

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

We propose the use of Weibull distributions to model 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_t) after time t is given by the probability density function:

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

where D is diffusion rate. Equation (9) is equivalent to the two-parameter Weibull density (Eq. (2)) with shape parameter $b = 2$ and a scale parameter $a = \frac{1}{4Dt}$ [Cain, 1991 #1059]. Convergence to a simple diffusion and hence to a Weibull distribution with shape parameter 2 for 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 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 more likely when movement rate is higher) but 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 displacement. The Weibull distribution not only describes distribution for distance moved under simple diffusion but it also has a very flexible shape, which may approximate 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.

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 multi-phasic: 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 lower (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 (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 out performed 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 sub-division of the encamped state into two states permitting very small and small steps, leaving the exploratory state to be described by a distribution with non-zero mode characteristic of longer step lengths. While 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. While *DIC* values for the “switch constrained” model are smaller than the unconstrained “switch” model, only the 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

largely determined 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 sophisticated 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.

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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($-\pi$, π)	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.

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

	elk-115		elk-163		elk-287		elk-363	
Model	<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

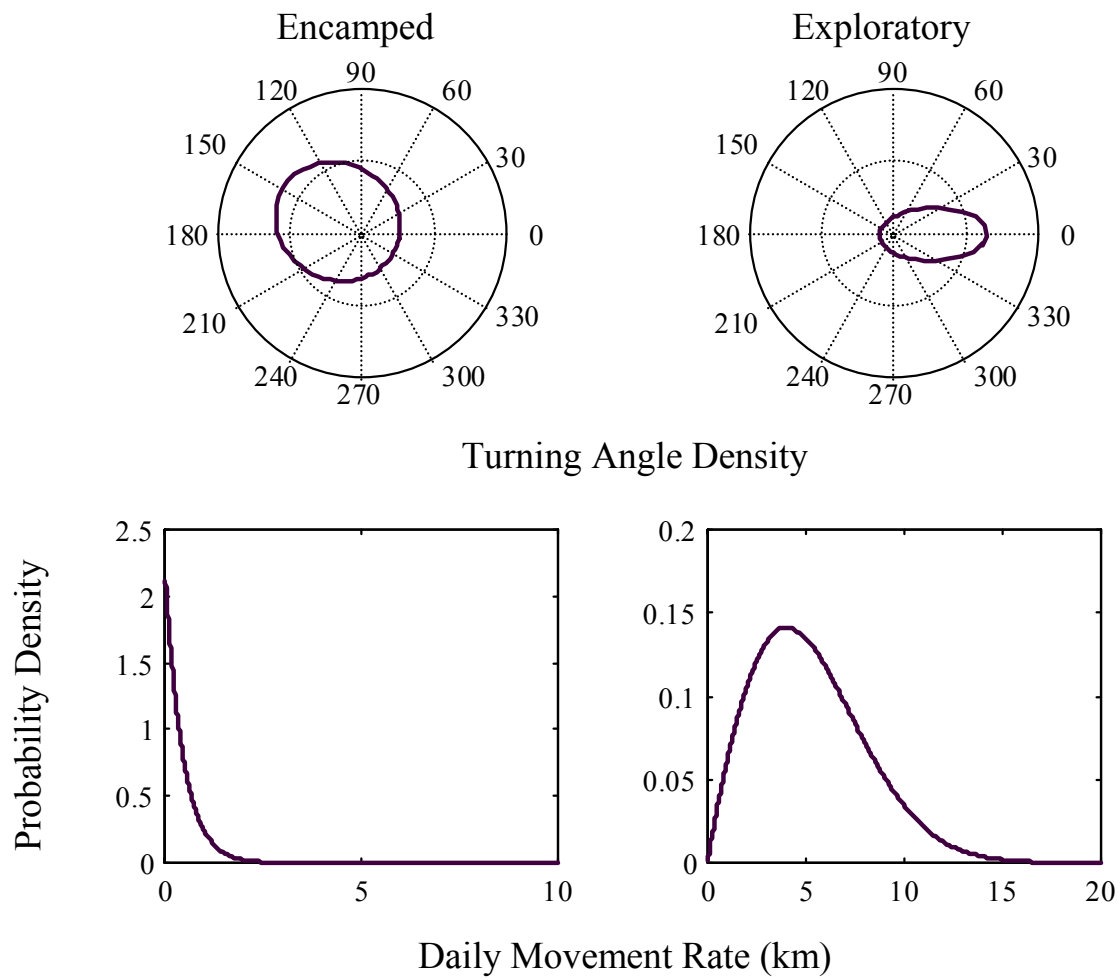
8 Figure 2. Activity bar showing assignment of behavioral states through time for all
9 multiple RW models fitted to elk-163. A: “Double”, B: “Double with covariates”, C:
10 “Double switch”, D: “Switch constrained”, E: “Triple switch”. The dots above the
11 activity bars indicate daily movement rate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

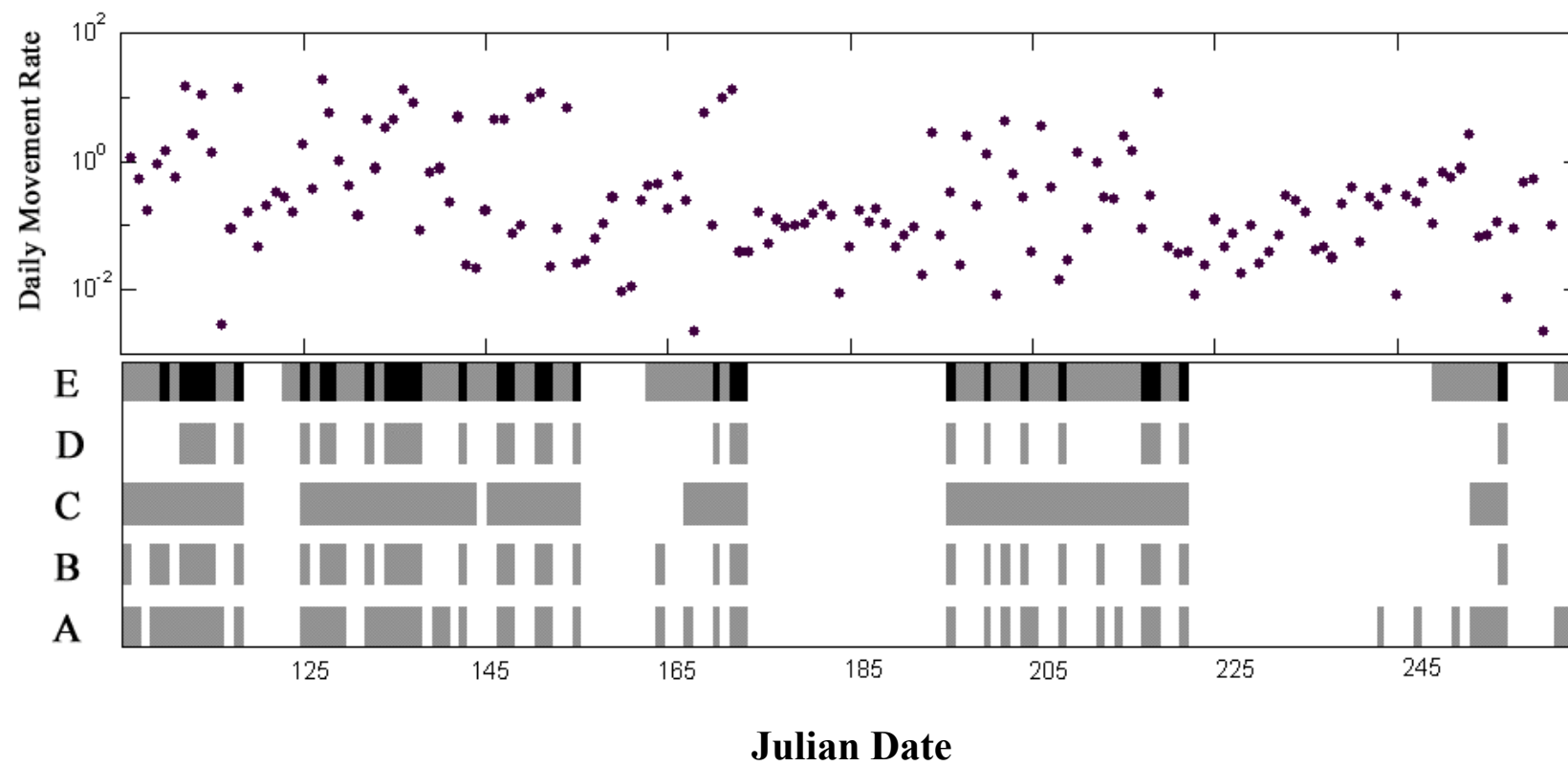
19

1 Figure 1.



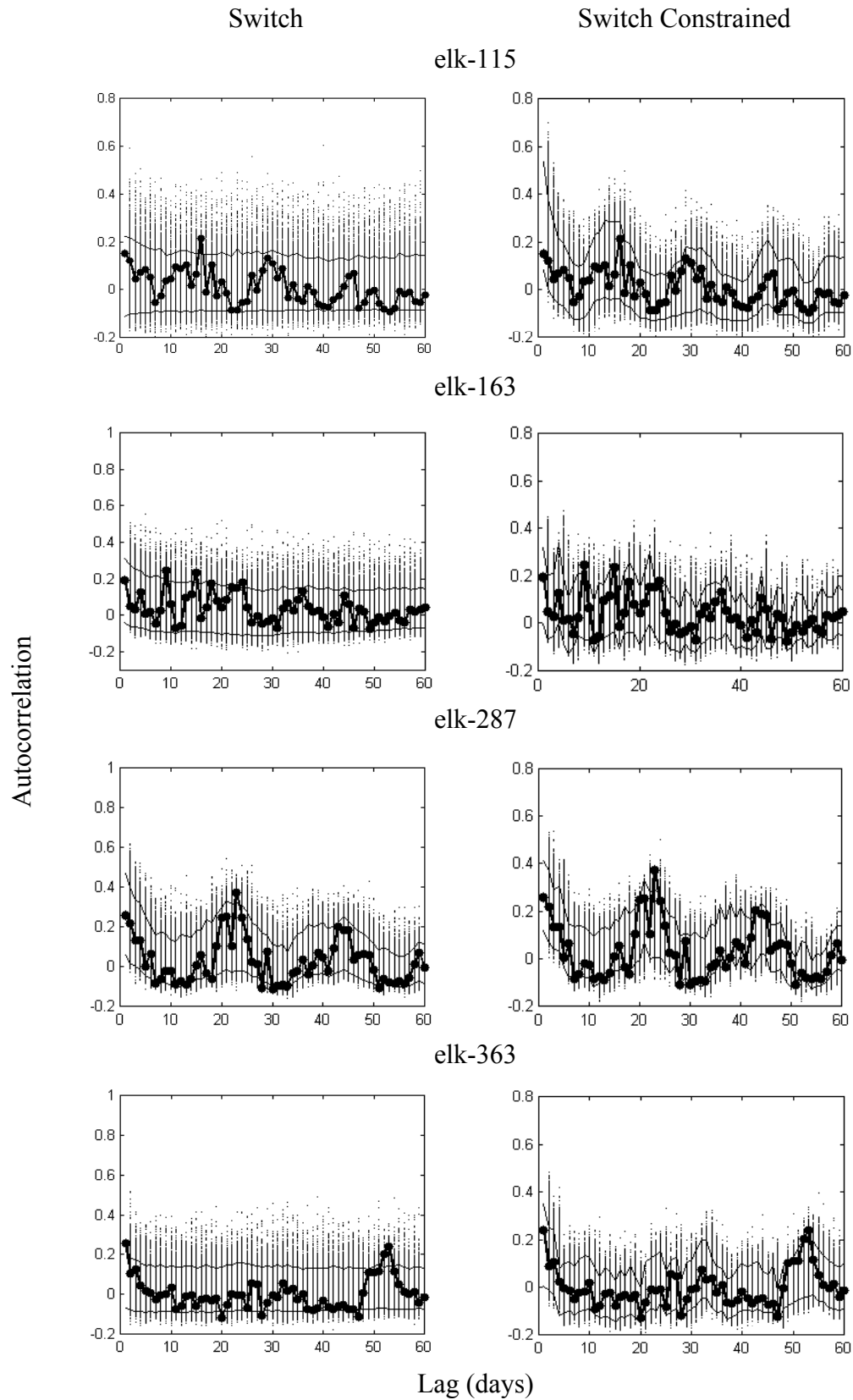
2

1 Figure 2.



2

1 Figure 3.



Appendix 1.

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

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)

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)

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)

ν_1	0.122 (-19.360, 19.990)	-7.717 (-22.390, 2.075)	8.588 (-0.694, 22.920)
ν_2	4.161 (1.402, 12.610)	5.825 (3.615, 8.969)	3.346 (1.568, 5.730)
ν_3	-7.595 (-23.270, 2.222)	-0.174 (-13.840, 5.243)	9.275 (1.318, 23.140)
ν_4	-0.053 (-19.420, 19.400)	1.538 (-0.853, 4.206)	-0.211 (-19.670, 19.310)
ν_5	-5.975 (-21.040, 3.268)	0.088 (-5.404, 3.617)	1.337 (-4.349, 14.250)
ν_6	-0.138 (-19.800, 19.740)	-0.053 (-19.930, 19.580)	0.230 (-19.510, 20.000)
ν_7	1.194 (-0.395, 2.491)	2.136 (1.205, 3.094)	3.206 (2.130, 4.618)
ν_8	-0.923 (-13.130, 2.392)	0.160 (-2.650, 3.039)	2.358 (0.305, 4.641)
ν_9	-1.178 (-15.030, 4.273)	-0.530 (-3.285, 2.088)	8.758 (1.410, 23.330)
ν_{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
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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 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

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

WinBUGS code for “single” model

```

model{
  for (t in 1:npts) {
    # likelihood for steps
    l[t] ~ dweib(b[t], a[t])      # Weibull distribution for step length

    a[t] <- nu                    # scale parameter
    b[t] <- lambda                # shape parameter

    # likelihood for turns. We use the “ones” trick to sample from the
    # Wrapped Cauchy distribution (see WinBUGS manual)

    ones[t] <- 1
    ones[t] ~ dbern(wc[t])
    wc[t] <- (1/(2*Pi)*(1-rho[t]*rho[t])/(1+rho[t]*rho[t]-2*rho[t]*cos(theta[t]-
mu.t[t])))/ 300 # Density function for Wrapped Cauchy distribution

    rho[t] <- lambda.t           # mean cosine for the circular distribution
    mu.t[t] <- nu.t              # mean direction for turns
  }

  ##### priors on movement parameters

  nu ~ dgamma(0.01, 0.01)      # prior distribution for the scale parameter
  lambda ~ dgamma(0.01,0.01) # prior distribution for shape parameter

  ##### priors for mean direction of turns

  nu.t ~ dunif(-3.14159265359, 3.14159265359)
  lambda.t ~ dunif(0,1) # prior for mean cosine of circular distribution

  Pi <- 3.14159265359 # define  $\pi$ 
}

```

WinBUGS code for “Double” model

```

model{
  for (t in 1:npts) {

```



```

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**

(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**

(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  hac1 = plot(x,ac(5000-125,:), 'k'); set(hac1,'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 distribuibution**

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 nargout == 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

```