

## The effectiveness of Bayesian state-space models for estimating behavioural states from movement paths

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### Summary

1. Bayesian state-space movement models have been proposed as a method of inferring behavioural states from movement paths (Morales *et al.* 2004), thereby providing insight into the behavioural processes from which patterns of animal space use arise in heterogeneous environments. It is not clear, however, how effective state-space models are at estimating behavioural states.

2. We use stochastic simulations of two movement models to quantify how behavioural state movement characteristics affect classification error. State-space movement models can be a highly effective approach to estimating behavioural states from movement paths.

3. Classification accuracy was contingent upon the degree of separation between the distributions that characterize the states (e.g. step length and turn angle distributions) and the relative frequency of the behavioural states. In the best case scenarios classification accuracy approached 100%, but was close to 0% when step length and turn angle distributions of each state were similar, or when one state was rare. Mean classification accuracy was uncorrelated with path length, but the variance in classification accuracy was inversely related to path length.

4. Importantly, we find that classification accuracy can be predicted based on the separation between distributions that characterize the movement paths, thereby providing a method of estimating classification accuracy for real movement paths. We demonstrate this approach using radiotelemetry relocation data of 34 moose (*Alces alces*).

5. We conclude that Bayesian state-space models offer powerful new opportunities for inferring behavioural states from relocation data.

**Key-words:** classification accuracy, correlated random walk, global positioning system, mechanistic movement model, telemetry

### Introduction

Patterns of animal distribution and space use arise from a complex interaction between environmental conditions and behavioural responses. Understanding the processes that govern movement, and the evolutionary consequences of movement, is a fundamental research area in ecology (Nathan *et al.* 2008). One of the motivations for monitoring animal space use is to develop an understanding of the behavioural strategies underlying how animals use heterogeneously distributed resources and habitat, and how animals manage risk and competing demands that influence fitness (Rosenzweig 1991; Morris 2003).

Advances in location-monitoring technology, such as global positioning system (GPS) devices, have enhanced our ability to accurately sample space use at high temporal frequencies (Cagnacci *et al.* 2010). There are, however, two issues that must be confronted when using location data to quantify the

link between space use and fitness: the spatial locations lack a behavioural context and they are typically sampled at regular, but behaviourally arbitrary, time intervals. In the absence of knowledge of what the animal is doing at a location, or whether a location corresponds to a transition between behaviours, it can be difficult to quantify the utility of a location to the animal (Beyer *et al.* 2010).

One approach to modelling movement paths are correlated random walks (CRWs) whereby a continuous movement path is approximated as a series of discrete ‘steps’ (two consecutive point locations) characterized by a step length ( $d$ ) and turn angle ( $\theta$ ) representing the change in direction of the current step relative to the previous step (Kareiva & Shigesada 1983; Turchin 1998; Jonsen, Myers & Flemming 2003). Unlike simple isotropic random walks, in which each step is independent of all preceding steps, CRWs take into account directional persistence (a short-term tendency to keep moving in the same direction). Random walks form the basis of the theory of diffusive processes and provide a strong theoretical framework for understanding movement processes (reviewed in Codling,

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Plank & Benhamou 2008). CRWs are generally only reasonable approximations of animal movement paths over short periods of time because they fail to incorporate behavioural or cognitive processes (e.g. site fidelity, memory, intra- or interspecific interactions, etc.) that are important determinants of space use over longer time periods (Börger, Dalziel & Fryxell 2008).

Morales *et al.* (2004) proposed modelling movement paths as a mixture of several CRWs each of which corresponds to a different behavioural 'state' (or movement mode). A behavioural state is defined as a collection of behaviours that have similar movement characteristics. For instance, given a movement path that has been characterized using one or more quantitative metrics (e.g. step lengths, turn angles, etc.), the behavioural states correspond to different modes in a multi-modal distribution or, using a *k*-means clustering analogy, to clusters in multidimensional parameter space. Using a Bayesian state-space modelling framework, Morales *et al.* (2004) demonstrated that elk (*Cervus elaphus*) movement paths could be characterized as a mixture of 'encamped' and 'exploratory' behavioural states. Transitions between states can be modelled as a constant switching probability, or with more complex models based on previous states and other environmental or path covariates (Morales *et al.* 2004). Similarly, Eckert *et al.* (2008) used this approach to model movement paths of loggerhead turtles (*Caretta caretta*), identifying an intensive- and extensive-search behavioural states and relating the probability of being in these states to environmental features. The Morales *et al.* (2004) approach is an important development as it provides a method for estimating the behavioural context of spatial locations.

It is not clear, however, to what extent behavioural states identified using the Morales *et al.* (2004) approach might be meaningful representations of real animal behaviour, or how the characteristics of the CRWs for each state might influence our ability to identify these states. Here, we use stochastic simulations of two movement models to generate movement paths comprised of a mixture of two CRWs, and evaluate the ability of Bayesian state-space models to recover behavioural states and parameter values from the simulated movement paths. Specifically, we evaluate five aspects of state-space model classification accuracy: (1) How is classification accuracy of behavioural states influenced by the degree of overlap of step length and turn angle distributions for each of the two states? How different do the movement characteristics of the behavioural states need to be in order to be reliably estimated using this approach? (2) Is classification accuracy sensitive to the proportion of time spent in these states? If a state is rare, can it still be identified reliably? (3) Is it possible to estimate classification accuracy *a posteriori*-based solely on the distributions that characterize the movement paths? (4) How is classification accuracy influenced by sample size (path length)? and (5) Is classification accuracy influenced by model complexity (the number of covariates upon which state assignments are based)? We then apply what is learned from the simulations to a real-world case study of the analysis of moose telemetry data.

## Materials and methods

### MOVEMENT MODELS

We model movement as a mixture of CRWs corresponding to discrete behavioural states ( $I = 1, \dots, M$ ). Our simulations include two behavioural states (*sensu* Morales *et al.* 2004): an encamped state (*E*) characterized by short step lengths and random (uniform) turn angles, and an exploratory state (*X*) having longer step lengths and greater directional persistence relative to the encamped state. It is straightforward to extend these models to more than two states (see Morales *et al.* 2004; McClintock *et al.* 2012). Each CRW is characterized by gamma-distributed step lengths ( $\Gamma$ , with shape and rate parameters  $a$  and  $b$  respectively) and wrapped Cauchy-distributed turn angles ( $C$ , with mean turn angle  $\mu$  and dispersion parameter  $\rho$ ). The general form of the likelihood function for the movement model is as follows:

$$P(y|a, b, \mu, \rho) = \prod_{t=1}^T \Gamma(d_t|a_t, b_t) C(\theta_t|\mu_t, \rho_t) \quad \text{eqn 1}$$

where  $T$  is the number of observations in the location time series.

The gamma distribution is useful for modelling movement distance because it is bounded at 0 and has a flexible, right-skewed shape that is often a good fit to observed animal step length distributions. The Weibull distribution has similar properties and has also been used to model step length distributions (e.g. Morales *et al.* 2004), but is less suitable in our application because its density is undefined for some combinations of parameter values, making it more problematic to fit. The von Mises distribution may be a suitable alternative to the wrapped Cauchy distribution, but is harder to implement because the probability density function includes a Bessel function.

We evaluated two movement models with different mechanisms governing state transitions. In the 'double' model Morales *et al.* 2004 there is a fixed probability ( $\gamma_i$ ) of being in behavioural state  $i$ , and where  $\sum_i^M \gamma_i = 1$ . Behavioural states are, therefore, independent of the previous state or any environmental conditions. To examine whether the scarcity of the behavioural state influences classification accuracy we evaluated three levels of  $\gamma_2$ , the probability of being in the exploratory state, of 0.5, 0.3 and 0.1.

We also define a 'patch' model in which the probability of switching between behavioural states depended on the time spent in that state and the habitat class (here, patch or matrix) in which a location occurs. The rationale behind the patch model is that habitat may often be an important determinant of behavioural state, and states may often be temporally autocorrelated. The encamped and exploratory states are more strongly associated with habitat patches and matrix respectively. Specifically, the matrix of switching probabilities ( $W$ ) is modelled as:

$$W = \begin{pmatrix} e^{-\lambda_{(s,h)}t} & 1 - e^{-\lambda_{(s,h)}t} \\ 1 - e^{-\lambda_{(s,h)}t} & e^{-\lambda_{(s,h)}t} \end{pmatrix} \quad \text{eqn 2}$$

where  $s$  is an index of the current state,  $h$  is an index of the habitat class and  $t$  is the time since the last state transition. In the patch model there are two states and two habitat classes such that  $\lambda$  is a  $2 \times 2$  matrix, the values of which determine how the probability of switching from one state to another (or staying in a state) changes as a function of  $t$ . We used an exponential form to describe this relationship because of its simplicity, although any asymptotic function that scales values to the range  $[0, 1]$  could be used (e.g. logit, Gompertz function). The probability of switching states increases monotonically as  $t$  increases and, conversely, the probability of remaining in a given state decreases monotonically as  $t$  increases. This formulation is useful for

representing temporal autocorrelation in states, and helps to resolve the problem that the temporal sampling interval of the telemetry data may be finer than the temporal frequency of behavioural state transitions.

#### SIMULATION ANALYSIS

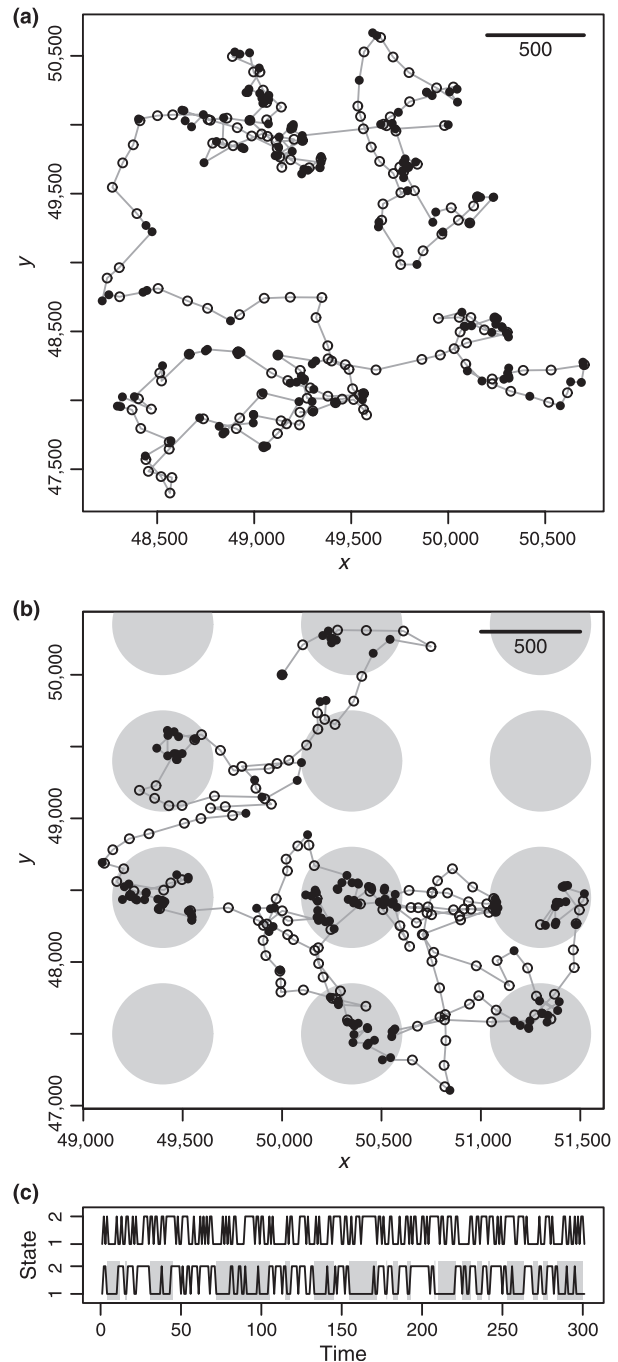
We investigated the determinants of classification accuracy (our five objectives) by simulating movement paths using the double or patch models (Fig. 1; Appendix S1) to generate paths with known behavioural states, and then attempted to recover both the movement model parameters and the behavioural states by fitting the model to these simulated data. The choice of model and the combination of parameters used to simulate a path depended on the question being addressed. Using these known and estimated paths we quantified classification accuracy of behavioural states using the Kappa statistic ( $\hat{\kappa}$ ), which is a measure of agreement between observed and expected values that takes into account chance agreement (Congalton 1991) and ranges from 0 (chance agreement) to 1 (perfect agreement).

The parameterization of the encamped state was the same among all simulations, with step lengths drawn from an exponential distribution (a gamma distribution where  $a = 1$ ) with a mean and standard deviation of 50 (the distances are unitless, but could be conceptualized as metres), and with turn angles drawn from a wrapped Cauchy distribution with mean and dispersion of 0 (equivalent to a uniform distribution in the range  $0-2\pi$ ). The exploratory state was parameterized to vary the degree of separation between the encamped and exploratory distributions (Table 1, Fig. 2a and b).

The degree of separation between step length and turn angle distributions ( $\Delta d$  and  $\Delta\theta$  respectively) was calculated based on frequency distributions (with  $B = 30$  bins) derived from 10000 random samples from each distribution using  $\Delta = \sum_i^B |f_{E,i} - f_{X,i}| / \sum_i^B (f_{E,i} + f_{X,i})$ , where  $f_{E,i}$  and  $f_{X,i}$  are the frequencies in bin  $i$  of the encamped and exploratory states respectively. Values of  $\Delta$  can range from 0 (the distributions are identical) to 1 (no overlap between distributions). This metric is a close empirical approximation of the Kolmogorov–Smirnov  $\hat{D}$  statistic, but unlike  $\hat{D}$  it can be applied to circular distributions. As the number of bins is arbitrary, we used 30 bins to ensure that the difference between  $\Delta d$  and  $\hat{D}$  was less than 0.01.

**Table 1.** Parameterization of six step length and turn angle distributions used to simulate movement paths using gamma (with shape parameter  $a$ , rate parameter  $b$  and mean step length  $\bar{d}$ ) and wrapped Cauchy distributions (with mean turn angle  $\mu$  and dispersion  $\rho$ ) respectively. The first distributions (id 1) were used to simulate the encamped state in all models. The exploratory state was based on one of the other distributions (id 2–6) of increasing mean step length and increasing directional persistence. The variance of all six step length distributions was held constant (50). The degree of separation of the exploratory and encamped step length distributions ( $\Delta d$ ) and turn angle distributions ( $\Delta\theta$ ) ranged from 0.07 (a high degree of overlap) to 0.94 (almost no overlap)

id	$a$	$b$	$\bar{d}$	SD	$\Delta d$	$\mu$	$\rho$	$\Delta\theta$
1	1	0.02	50	50	–	0	0	–
2	2.25	0.03	75	50	0.29	0	0.1	0.07
3	4	0.04	100	50	0.50	0	0.3	0.19
4	9	0.06	150	50	0.75	0	0.5	0.33
5	16	0.08	200	50	0.87	0	0.7	0.50
6	25	0.1	250	50	0.94	0	0.9	0.72



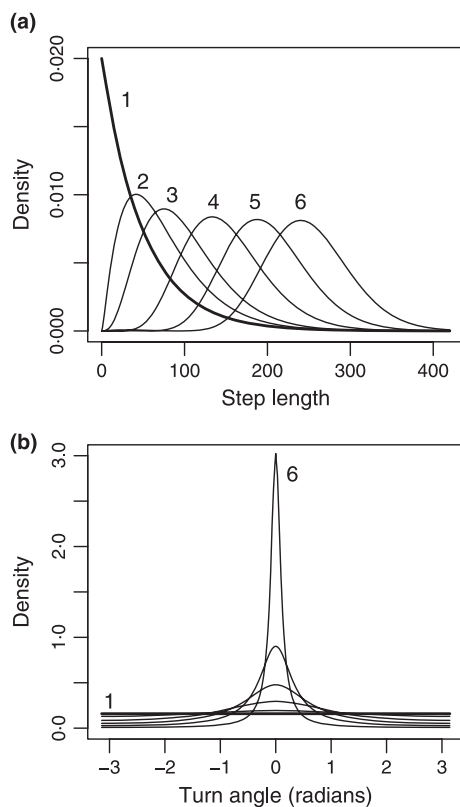
**Figure 1.** Examples of movement paths generated using two movement models (a, b), each consisting of a mixture of random walks corresponding to an encamped (filled circle) or exploratory (open circle) behavioural state. In the ‘double’ model (a) behavioural states are independent, resulting in frequent switching between the states (c; top). In the ‘patch’ model switching probabilities vary according to habitat and the time since the last state transition, resulting in less frequent switching (c; bottom). Light grey corresponds to the patch habitat and white is the matrix (b, c).

To investigate how classification accuracy was influenced by the separation between distributions (objective 1) and the rarity of a state (objective 2), 10 replicates of movement paths (of length 300 steps) using the double model were generated using all 75 possible combinations of the three levels of  $\gamma_2$  (0.5, 0.3, 0.1) and the five step length and five turn angle distributions for the exploratory state (Table 1), for a

total of 750 simulated paths. We fit a linear regression to quantify the relationship between classification accuracy ( $\hat{\kappa}$ ) and the separation between the step length ( $\Delta d$ ) and turn angle ( $\Delta\theta$ ) distributions of the behavioural states, the relative frequency of the movement states ( $\gamma_2$ ) as a three-level factor and including all-way interaction terms among these variables. This linear model was used as the basis for establishing a predictive relationship between the separation of the distributions and classification accuracy (objective 3).

To quantify the influence of sample size (path length) on classification accuracy (objective 4) we restricted our analysis to a single combination of movement parameters for the double model because of processing time constraints. The exploratory state was simulated using the fourth step length distribution and the fifth turn angle distribution (Table 1), which were selected because they provide enough separation ( $\Delta d$  and  $\Delta\theta$ ) to ensure that the two states could be distinguished but not so much separation that classification accuracy was universally high. Ten replicates of movement paths were generated for the three levels of  $\gamma_2$ , with path lengths ranging from  $T = 100$  to 1500 in intervals of 100. We quantified how classification accuracy and the variation in classification accuracy changed as a function of sample size using linear regression models.

We qualitatively contrast results from the double and patch model to investigate how model complexity influenced classification accuracy (objective 5). For the patch model, habitat patches were simulated as regularly spaced circles of radius 250 units (Fig. 1b). The relative frequency of encamped and exploratory states is determined by the



**Figure 2.** Distributions of step lengths (a) and turn angles (b) used to generate simulated movement paths based on an encamped state with short step lengths and random turns (distribution 1 in a and b, bold lines), and an exploratory state with longer step lengths (a; lines 2–6) and greater directional persistence (b; lines 2–6). The ability to recover behavioural state and movement model parameters using state-space models was quantified as a function of the degree of overlap between the encamped and exploratory distributions.

interaction between the matrix  $\lambda$ , the step length and turn angle distributions and the distribution of habitat. To facilitate comparison, the spacing among habitat patch centres was adjusted to ensure the mean proportion of encamped locations was 0.4–0.5 among all patch models (patches constituted 21.8% of the landscape). Ten replicates of movement paths of length 300 steps were generated using all 25 possible combinations of the five step length and five turn angle distributions for the exploratory state (Table 1). All simulation and statistical analyses were implemented in R (R Core Development Team 2010).

State-space models were used to estimate parameter values and behavioural states from the simulated data. Models were fit using Monte Carlo Markov chain (MCMC) techniques implemented in the software JAGS (Plummer 2010) with a burn-in period of 5000 samples, which were discarded, followed by 25 000 samples that were thinned to retain every 25th sample resulting in 1000 independent samples from the posterior distribution of each parameter. Behavioural state variable estimates were based on a further 2500 samples (also thinned to retain every 25th sample, resulting in 100 samples). Behavioural states were sampled separately from the other parameters because of processing constraints (behavioural states involve monitoring  $2T$  latent variables, which is computationally demanding). Every replicate was checked for convergence to a stationary distribution using the Gelman-Rubin convergence statistic ( $\hat{R}_c$ ; Gelman & Rubin 1992) and by visually examining plots of the chains and autocorrelation plots for each chain. MCMC chain convergence is improved under the assumption that the exploratory state is characterized by steps that, on average, have longer step lengths and greater directional persistence than those of the encamped state. Vague priors were specified for all parameters (Appendix S1), but the parameters were constrained to reflect these *a priori* assumptions.

#### CASE STUDY: MOOSE MOVEMENT

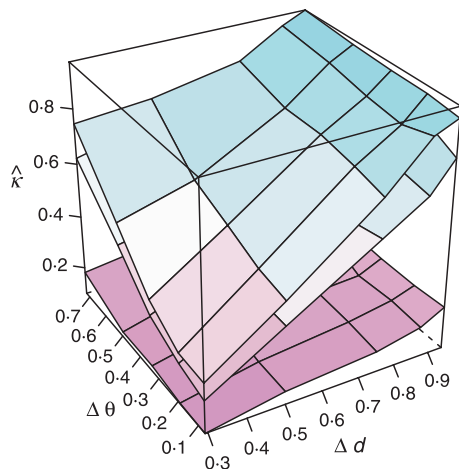
We demonstrate the application of the double model to GPS telemetry data collected from 34 moose in southern Ontario, Canada. Telemetry collars (GPS 3300; Lotek Wireless Inc., Newmarket, Ontario, Canada) were fit to adult, female moose in January 2006 and February 2007. See Lowe, Patterson & Schaefer (2010) for a description of the study area and the methods used to capture and collar moose. Spatial locations were collected at 2 h intervals until March 2008, or until the animal died or the collar failed. Success rates for acquiring locations were generally high (mean 97.9% among all moose). Twelve locations were deleted from the data set because they represented unrealistic or obviously erroneous movements, such as movement distances greater than 6 km in a 2 h interval followed by a return to the vicinity of the previous location.

We restrict our analysis to summer movements from May to August 2007 inclusive (mean 1437 telemetry locations per moose; range: 1374–1465). Step lengths were expressed as movement rates ( $\text{mh}^{-1}$ ) because movement rates are less sensitive to occasional missing locations than are step lengths. The double model was fit to each animal independently as described above. The classification accuracy of moose behavioural states (encamped or exploratory) cannot be quantified directly because the true states are unknown. Instead, we estimate the classification accuracy by simulating movement paths using the fitted parameter estimates, and use these simulated paths as the known states that we then attempt to estimate using the approach described above for the simulation analysis. Specifically, for each moose movement path we simulated 10 movement paths using the maximum density parameter values from the posterior distributions with the same number of steps as the observed path. The double model was then fit to each of these simulated paths, and the mean classification accuracy among the 10 simulated paths quantified for each animal (as described above).

## Results

Not all replicates converged. An attempt was made to refit models that did not converge, but if they failed to converge again then they were excluded from the analysis. Failure to converge in the double model was most common when the probability of being in one of the movement states was rare (5, 8 and 22 of 250 replicates of the double model were excluded for  $\gamma = 0.5, 0.3$  and  $0.1$  respectively). Failure to converge in the patch model occurred in 6 of 250 replicates.

Classification accuracy ( $\hat{\kappa}$ ) of behavioural states using the double model was positively associated with the separation of the step length ( $\Delta d$ ) and turn angle ( $\Delta\theta$ ) distributions that characterize each state, and was highest when the two behavioural states were present in equal proportions (Fig. 3; Table 2). For instance, when  $\gamma_2 = 0.5$ ,  $\hat{\kappa}$  ranged from 96.3% when there was little overlap between the distributions, to only 28.2% when there was most overlap between the distributions (Fig. 3).  $\hat{\kappa}$  decreased by approximately 16% when  $\gamma_2 = 0.3$  except for the replicates with strongly dissimilar distributions where  $\hat{\kappa}$  remained high (up to 93.6%). However, when  $\gamma_2 = 0.1$ ,  $\hat{\kappa}$  was low (mean 19.4%) and increased little as the separation of the step length and turn angle distributions increased ( $\hat{\kappa}$  was 9.6% for the most similar distributions and only increased to 28.3% for the most dissimilar distributions). There were strong interaction effects between  $\Delta d$ ,  $\Delta\theta$  and  $\gamma_2$  (Table 2), indicating that the problem of low classification accuracy was compounded when there was poor separation of both the step length and turn angle distribution, and this effect was exacerbated as the second behavioural state became rarer. Conversely, good separation of the step length and turn angle distributions and an equal frequency of states combined to result in good classification accuracy.



**Figure 3.** Classification accuracy ( $\hat{\kappa}$ ) of behavioural states using state-space movement models to recover movement model parameters and states based on simulated movement paths of 300 steps in length. Classification accuracy varies as a function of the degree of separation between distributions that characterize the states for both step lengths ( $\Delta d$ ) and turn angles ( $\Delta\theta$ ). Classification accuracy decreases when one movement state becomes rare: the three planes from top to bottom represent a 50, 30 and 10% frequency of the exploratory state.

**Table 2.** Coefficients and standard errors of linear models relating classification accuracy of encamped and exploratory behavioural states to the separation between the step length ( $\Delta d$ ) and turn angle ( $\Delta\theta$ ) distributions of these states. The double model (top panel) also includes the relative frequency of the movement states ( $\gamma_2$ ) as a three-level factor (see text for details), but this value was held near constant by design in the patch model (bottom panel) and hence was omitted. All-way interaction terms among variables were evaluated for both models.

Coefficients	Estimate	SE	<i>t</i> value
Intercept	0.015	0.0202	0.74
$\Delta d$	0.224	0.0281	7.98*
$\Delta\theta$	0.149	0.0471	3.16*
$\gamma_2$ (0.3)	-0.172	0.0281	-6.12*
$\gamma_2$ (0.5)	-0.182	0.0279	-6.50*
$\Delta d:\Delta\theta$	-0.101	0.0653	-1.54
$\Delta d:\gamma_2$ (0.3)	0.731	0.0396	18.5*
$\Delta d:\gamma_2$ (0.5)	0.946	0.0390	24.2*
$\Delta\theta:\gamma_2$ (0.3)	0.659	0.0655	10.1*
$\Delta\theta:\gamma_2$ (0.5)	0.875	0.0652	13.4*
$\Delta d:\Delta\theta:\gamma_2$ (0.3)	-0.555	0.0920	-6.04*
$\Delta d:\Delta\theta:\gamma_2$ (0.5)	-0.982	0.0911	-10.8*
Intercept	-0.019	0.0039	-4.79*
$\Delta d$	0.149	0.0065	22.9*
$\Delta\theta$	0.924	0.1379	6.70*
$\Delta d:\Delta\theta$	-3.02	0.2549	-11.9*

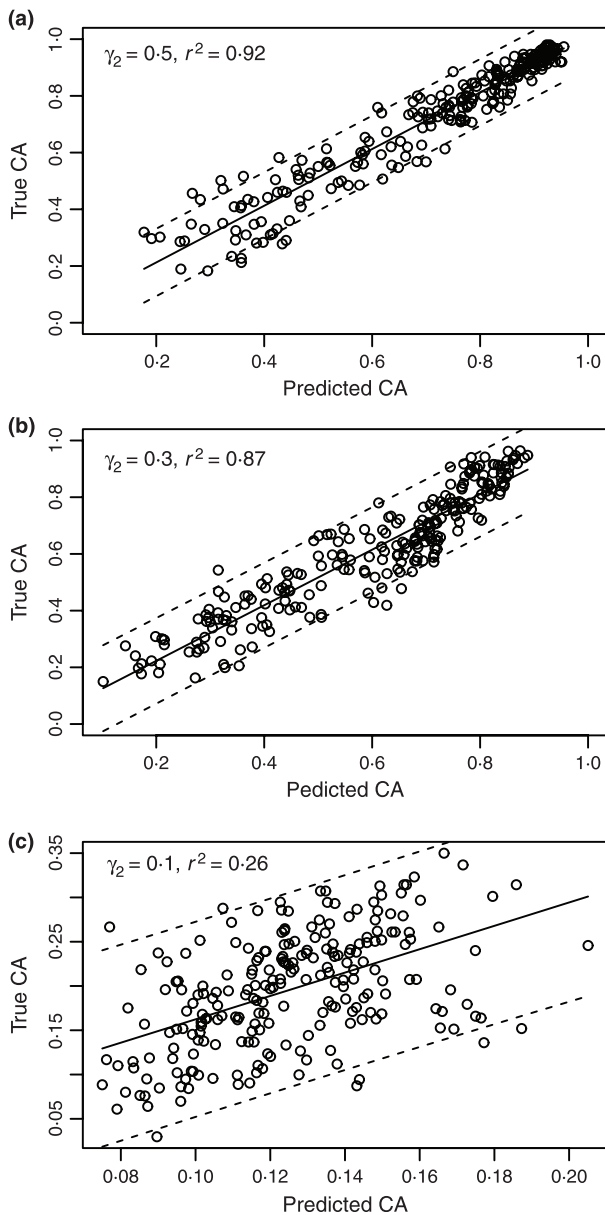
\* $P < 0.01$ .

This linear regression model was used to predict  $\hat{\kappa}$  based on the maximum likelihood estimates of the parameters of the step length and turn angle distributions for each of the simulated movement paths. There was a strong positive linear correlation between predicted and true  $\hat{\kappa}$  when  $\gamma_2 = 0.5$  or  $0.3$ , and a weak but positive correlation when  $\gamma_2 = 0.1$  (Fig. 4;  $\hat{\kappa}_{obs} = \beta_0 + \beta_1 \hat{\kappa}_{pred}$ ,  $\gamma = 0.5$ :  $\beta_0 = 0.012 \pm 0.014$  SE,  $\beta_1 = 1.00 \pm 0.018$  SE;  $\gamma = 0.3$ :  $\beta_0 = 0.027 \pm 0.015$  SE,  $\beta_1 = 0.980 \pm 0.024$  SE;  $\gamma = 0.1$ :  $\beta_0 = 0.030 \pm 0.019$  SE,  $\beta_1 = 1.31 \pm 0.148$  SE).

For the double model, mean  $\hat{\kappa}$  was uncorrelated with path length (linear regression,  $\hat{\kappa} = \beta_0 + \beta_1 T$ ;  $|\beta_1| < 1 \times 10^{-5}$  for all three levels of  $\gamma$ ), but the variance in  $\hat{\kappa}$  declined as a function of length (Fig. 5). The coefficient of variation of  $\hat{\kappa}$  was highest for short path lengths, and when one behavioural state was rare ( $cv_{\gamma_2=0.5} < cv_{\gamma_2=0.3} < cv_{\gamma_2=0.1}$ ). Linear models reveal a significant decline in  $cv$  as a function of path length ( $cv = \beta_0 + \beta_1 T$ ,  $\gamma = 0.5$ :  $\beta_0 = 0.062 \pm 8.2 \times 10^{-2}$  SE,  $\beta_1 = -3.55 \times 10^{-5} \pm 9.0 \times 10^{-6}$  SE;  $\gamma = 0.3$ :  $\beta_0 = 0.11 \pm 1.0 \times 10^{-2}$  SE,  $\beta_1 = -5.96 \times 10^{-5} \pm 1.1 \times 10^{-5}$  SE;  $\gamma = 0.1$ :  $\beta_0 = 0.23 \pm 2.3 \times 10^{-2}$  SE,  $\beta_1 = -1.23 \times 10^{-4} \pm 2.6 \times 10^{-5}$  SE).

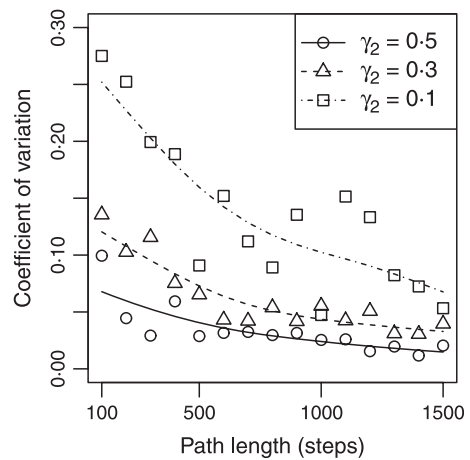
The  $\hat{\kappa}$  of behavioural states using the patch model was also positively associated with the separation of the step length ( $\Delta d$ ) and turn angle ( $\Delta\theta$ ) distributions (Fig. 6), but was uncorrelated with the relative frequency of states (which were in approximately equal proportions with little variability by design). When the separation between distributions was low,  $\hat{\kappa}$  was 10–15% higher for the patch model compared with the corresponding double model ( $\gamma_2 = 0.5$ ), although both models achieved high  $\hat{\kappa}$  when the separation was greatest.

Recovery of parameters was deemed successful if the 95% credible intervals of the posterior distributions contained the

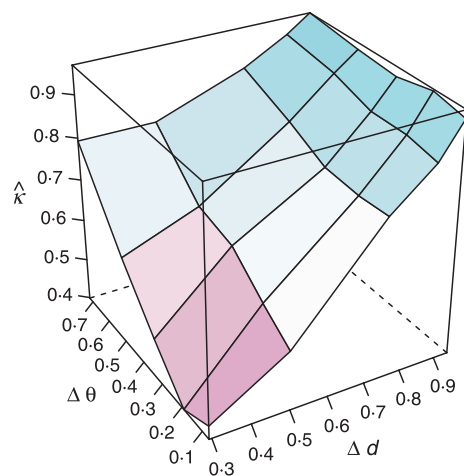


**Figure 4.** The correlation between true and predicted classification accuracy based on the separation between fitted step length and turn angle distributions (see Methods). Movement paths were simulated as a mixture of two random walks corresponding to an encamped and exploratory states with relative frequencies of 50:50 (a), 70:30 (b) or 90:10 (c). When the relative frequency of states is roughly equal (a, b), predicted classification accuracy is a good predictor of the true classification accuracy. When one of the states is rare (c), classification accuracy is universally low.

original value of the parameter. Failure to recover parameters was rare. When this did occur, it was often related to the fact that different combinations of parameter values for the gamma distribution could result in similar distributions. For instance, three of ten replicates of simulations characterized by a mean exploratory state step length of 250 failed to recover parameter values ( $a_2, b_2$ ), but the mean step length of these gamma distributions was 240, 259 and 238, similar to the mean of the original distribution. Thus, failure to recover parameter values was



**Figure 5.** Simulated movement path length has little relationship to the mean classification accuracy of the state-space models, but the variance in classification accuracy is highest for short path lengths. Movement paths were simulated as a mixture of two random walks corresponding to an encamped and exploratory states. The relative frequency of the movement states was 50:50 ( $\gamma_2 = 0.5$ ), 70:30 ( $\gamma_2 = 0.3$ ) or 90:10 ( $\gamma_2 = 0.1$ ). Variance in classification accuracy also increased as one of the movement states become rarer.



**Figure 6.** Classification accuracy ( $\hat{\kappa}$ ) of behavioural states using state-space movement models to recover movement model parameters and states based on simulated movement paths of 300 steps in length using a patch-based model (see Methods). Classification accuracy varies as a function of the degree of separation between distributions that characterize the states for both step lengths ( $\Delta d$ ) and turn angles ( $\Delta\theta$ ).

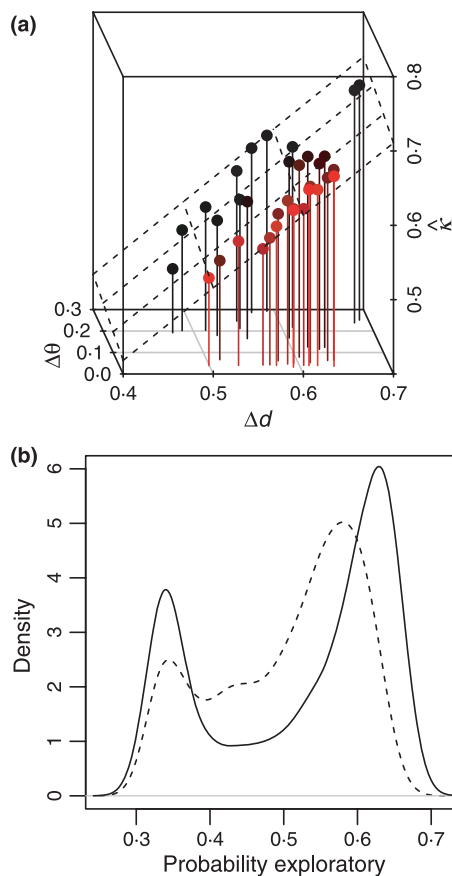
not an important aspect of fitting success compared with the failure of the MCMC chains to converge or classification error, both of which were more problematic when the separation between distributions ( $\Delta d$  and  $\Delta\theta$ ) was small.

#### CASE STUDY: MOOSE MOVEMENT

All models converged. The maximum density values of the fitted parameters for each animal, and the separation between distributions, were generally consistent among animals (Table S1). The mean movement rate ( $\pm$ SD) in the encamped

and exploratory states among all animals was  $30.2 \pm 7.6 \text{ mh}^{-1}$  and  $150 \pm 28 \text{ mh}^{-1}$  respectively. Turn angle distributions were unimodal with a circular mean of  $-3.1$  radians for the encamped state, but were bimodal for the exploratory state with 16 animals tending towards a mean of 0, and 18 animals tending towards a mean of  $\pi$  radians (e.g. Figure S1). Turn angles were more dispersed in the encamped state ( $\rho_1 = 0.12 \pm 0.05$  SD) than the exploratory state ( $\rho_2 = 0.18 \pm 0.06$ ; paired  $t$ -test,  $t = -4.65$ , d.f. = 33,  $P < 0.001$ ). The mean proportion of telemetry locations assigned to the encamped state was  $0.38$  ( $\pm 0.03$  SD; range:  $0.33$ – $0.44$ ).

Estimates of overall classification accuracy for each moose movement path ranged from  $0.49$  to  $0.72$  (mean  $0.61$ ). The estimated classification accuracy ( $\hat{\kappa}$ ) among moose was strongly correlated with the separation between the movement rate ( $\Delta d$ ;  $0.91 \pm 0.034$  SE) and turn angle ( $\Delta\theta$ ;  $0.09 \pm 0.021$  SE) distributions (Fig. 7a), and the proportion of locations in the encamped state ( $\gamma_2$ ;  $-0.19 \pm 0.069$  SE). The number of steps



**Figure 7.** Application of the double model to summer GPS telemetry locations of 34 moose. (a) The estimated classification accuracy ( $\hat{\kappa}$ ) among the models was strongly correlated with the separation between the movement rate ( $\Delta d$ ) and turn angle ( $\Delta\theta$ ) distributions of the encamped and exploratory states (linear regression:  $\hat{\kappa} = -0.01 + 0.91\Delta d + 0.09\Delta\theta - 0.19\gamma_2$ ). The colour gradient of the points is in relation to  $\Delta\theta$ . (b) Within a movement path, the probabilities of each location being in the exploratory state were bimodally distributed, although much more so for the paths with the highest classification accuracy (solid line) compared with the paths with the lowest (dashed line).

in each path was not a significant predictor of  $\hat{\kappa}$  for the moose case study, possibly because of the narrow range of these value. The distributions of probabilities of being in the exploratory state for each location within a telemetry path were bimodal, although much more so for the paths with the highest classification accuracy compared with the paths with the lowest (Fig. 7b). Thus, when the ability to discriminate states is high this is reflected by a strongly bimodal distribution of probabilities; conversely, when the ability to discriminate states is low the uncertainty in classification of states results in a greater number of intermediate probability values.

## Discussion

This work demonstrates that state-space movement models can be highly effective for estimating behavioural states from movement paths. The success of this technique is contingent upon the degree of separation between the distributions that characterize the behavioural states (step length and turn angle distributions in our examples), and the relative frequency of the behavioural states. When the distributions are dissimilar, and the behavioural states occur in approximately equal proportions, classification accuracy ( $\hat{\kappa}$ ) approaches 100%. Conversely, when the distributions are similar and/or one state is rare,  $\hat{\kappa}$  approaches 0%.

Step lengths and turn angles are, however, just two of many possible metrics that could be used to describe movement paths. Incorporating other path metrics into state-space movement models may improve their ability to differentiate among behavioural states. For instance, cervid space use and movement is influenced by habitat (Boyce *et al.* 2003; Morales *et al.* 2004), time of day (Forester *et al.* 2007), proximity and direction to features such as roads (Frair *et al.* 2008) or human activity (Hebblewhite *et al.* 2005), conspecifics/herd size (Haydon *et al.* 2008; Fortin *et al.* 2009), predation risk (Fortin *et al.* 2005; Frair *et al.* 2005; Hebblewhite *et al.* 2005) and forage (Fortin *et al.* 2005; Forester *et al.* 2007). These effects can be quantified using a variety of spatial descriptors, such as containment (is the animal within a given habitat?), proximity (what is the distance to a feature/habitat?), visibility (is another entity or place visible from a location?), crossing (is a feature crossed when moving between consecutive locations?) and adjacency (do two features touch?). The combination of effect and summary statistic that is most relevant for distinguishing among behavioural states will depend on the biology of the animal and the set of other states considered. Thus, the addition of descriptor variables may increase both classification accuracy and the number of behavioural states that can be distinguished.

Importantly, this work demonstrates that the classification accuracy of behavioural states can be estimated based on the separation between the fitted step length and turn angle distributions. This is useful because independent behavioural validation data rarely exist to quantify classification accuracy. When applying state-space movement models to real data, such as the moose telemetry data in our case study, stochastic simulations of the best fit model can be performed to quantify

the relationship between classification accuracy, separation of the distributions and the relative frequency of the states. As demonstrated here, these relationships can then be used to estimate both overall classification accuracy and the classification accuracy of individual locations, which could then be used as weightings in subsequent analyses such as resource preference analyses.

A corollary of this work is that, when applied to real animal data, the behavioural states quantified by these state-space models will not necessarily correspond to specific behaviours, but rather to collections of behaviours that have similar movement characteristics. The encamped state, for instance, may reflect several behaviours that occur when animals are moving little (foraging, resting, etc.). Furthermore, animal behaviour occurs across a wide range of temporal scales and although state-space models can be used to infer behaviours occurring on coarser temporal scales than the sampling interval (McClintock *et al.* 2012), they will not be able to distinguish among behaviours occurring on finer temporal scales than the location sampling interval. Thus, caution must be exercised when interpreting modelled behavioural states in the context of real animal behaviour. In some cases modelled behavioural states may be closely linked to real behaviours, but this is likely to vary widely among individuals and species, and as a function of the location sampling interval. When designing a telemetry study it is important to consider the temporal scale at which animal behaviours that are relevant to the questions motivating the study are expressed; if the telemetry sampling interval is too coarse there will be limited scope to make inferences regarding these behaviours.

If classification accuracies are low (perhaps  $\hat{\kappa} < 0.5$ ) then limited confidence could be placed on inferences based on the behavioural state classifications. In our case study, we found that classification accuracies were moderately high (mean 0.61), implying that the simple two-state model provides a reasonable fit to these moose movement paths for many of the animals. It is likely, however, that a more ecologically realistic movement model incorporating habitat and behavioural effects would provide a better fit to the data and more valuable insight into moose space use. The variation in classification accuracy we observed among individuals (range 0.49–0.72) may reflect differences in individual movement strategies. Fitting a suite of competing models that are ranked using DIC would provide useful insight into these individual strategies and is likely to improve classification accuracy (but see comments on model selection below). Understanding variation in space use strategies among individuals in the context of differences in habitat and experience (e.g. memory, site fidelity) is an important goal for future research.

We made two assumptions that may imply this analysis is a best case scenario. First, we assumed there is no spatial error or missing locations in the movement path. Although location-monitoring technology often records locations with seemingly high accuracy, it is the positional error relative to the step length of the animal over the time interval of the relocations that is important in movement models (Jerde & Visscher 2005). For many mammals, for instance, positional error in

locations may be negligible relative to the movement rate of the animal, although this needs to be evaluated on a case-by-case basis. High frequencies of missed locations, however, are problematic for movement models, especially when they are associated with particular habitats (e.g. forest) or behaviours (e.g. resting) as this can lead to bias (Frair *et al.* 2004, 2010). State-space models provide a framework for estimating missed locations (Patterson *et al.* 2010), although this may be of limited value when a high proportion of locations are missing. If positional error is deemed important, however, it can be explicitly incorporated into the state-space modelling framework (Jonsen, Flenning & Myers 2005; Eckert *et al.* 2008).

The second assumption we made is that model selection is perfect because in this study the model used to generate the simulated paths is subsequently fit to these paths. In reality, model selection may introduce considerable error into classification accuracy of behavioural states. More work is needed to evaluate the effectiveness of Bayesian model selection techniques such as Bayes factors (Kass & Raftery 1995) and DIC (Spiegelhalter *et al.* 2002; Plummer 2008) for evaluating the relative strength of evidence of competing models.

We found that constraining the step length and turn angle probability distributions in a way that reflects specific hypotheses about the behavioural states improved our ability to fit the state-space models. For instance, the exploratory state was constrained to have a longer mean step length and a less dispersed distribution of turn angles than the encamped state. This helped to prevent the MCMC chains ‘flipping’ between states, which we observed was one important obstacle to chain convergence. The use of these mild constraints in the model formulation can facilitate the fitting of these models. Constraining models can have important consequences for parameter estimation and inferences derived from models, however, and care is required to ensure that any constraints are appropriate for any particular analysis.

State-space models provide a rigorous method for converting location data that are collected at regular intervals (but at biologically arbitrary times) and that lack a behavioural context into more biologically relevant ‘moves’ (sensu Turchin 1998) that can then be used as a basis for further ecological investigation. For instance, if the encamped state corresponds primarily to within-patch foraging behaviour and the exploratory state to inter-patch movements, then this provides a basis for quantifying foraging strategies (by quantifying patch residency time and inter-patch movements). These behavioural states may help to bridge the knowledge gap between observing the location of an animal in space, and understanding the utility of that location to the animal, i.e. the link between space use and fitness (Beyer *et al.* 2010). The state-space framework can also be used to model the influence of higher order movement processes such as memory and site fidelity on movement and space use (Börger, Dalziel & Fryxell 2008; Dalziel, Morales & Fryxell 2008; Patterson *et al.* 2008; Van Moorter *et al.* 2009). Mechanistic movement models provide exciting new opportunities for understanding how animals use resources, how animals might respond to environmental change (such as anthropogenic disturbance and climate change) and, ultimately, how



animals may optimize fitness in dynamic and heterogeneous environments.

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## References

- Beyer, H.L., Haydon, D.T., Morales, J.M., Frair, J.L., Hebblewhite, M., Mitchell, M. & Matthiopoulos, J. (2010) The interpretation of habitat preference metrics under use-availability designs. *Philosophical Transactions of the Royal Society B*, **365**, 2245–2254. doi: 10.1098/rstb.2010.0083.
- Börger, L., Dalziel, B.D. & Fryxell, J.M. (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, **11**, 637–650.
- Boyce, M.S., Mao, J.S., Merrill, E.H., Fortin, D., Turner, M.G., Fryxell, J. & Turchin, P. (2003) Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience*, **10**, 421–431.
- Cagnacci, F., Boitani, L., Powell, R.A. & Boyce, M. (2010) Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B*, **365**, 2157–2162.
- Codling, E.A., Plank, M.J. & Benhamou, S. (2008) Random walk models in biology. *Journal of the Royal Society Interface*, **5**, 813–834. doi: 10.1098/rsif.2008.0014.
- Congalton, R.G. (1991) A review of assessing the accuracy of classifications of remotely sensed data. *Remote Sensing of Environment*, **37**, 35–46.
- Dalziel, B.D., Morales, J.M. & Fryxell, J.M. (2008) Fitting probability distributions to animal movement trajectories: using artificial neural networks to link distance, resources, and memory. *American Naturalist*, **172**, 248–258. doi:10.1086/589448.
- Eckert, S.A., Moore, J.E., Dunn, D.C., van Buiten, R.S., Eckert, K.L. & Halpin, P.N. (2008) Modeling loggerhead turtle movement in the Mediterranean: importance of body size and oceanography. *Ecological Applications*, **18**, 290–308. doi:10.1890/06-2107.1.
- Forester, J.D., Ives, A.R., Turner, M.G., Anderson, D.P., Fortin, D., Beyer, H.L., Smith, D.W. & Boyce, M.S. (2007) State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. *Ecological Monographs*, **77**, 285–299. doi:10.1890/06-0534.
- Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, **86**, 1320–1330. doi:10.1890/04-0953.
- Fortin, D., Fortin, M.E., Beyer, H.L., Duchesne, T., Courant, S. & Dancose, K. (2009) Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. *Ecology*, **90**, 2480–2490. doi:10.1890/08-0345.1.
- Frair, J.L., Nielsen, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H.M., Stenhouse, G.B. & Beyer, H.L. (2004) Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology*, **41**, 201–212. doi:10.1111/j.0021-8901.2004.00902.x.
- Frair, J.L., Merrill, E.H., Visscher, D.R., Fortin, D., Beyer, H.L. & Morales, J.M. (2005) Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology*, **20**, 273–287.
- Frair, J.L., Merrill, E.H., Beyer, H.L. & Morales, J.M. (2008) Thresholds in landscape connectivity and mortality risks in response to growing road networks. *Journal of Applied Ecology*, **45**, 1504–1513.
- Frair, J.L., Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, N.J. & Pedrotti, L. (2010) Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society B*, **365**, 2187–2200. doi:10.1098/rstb.2010.0084.
- Gelman, A. & Rubin, D.B. (1992) Inference from iterative simulation using multiple sequences. *Statistical Science*, **7**, 457–472.
- Haydon, D.T., Morales, J.M., Yott, A., Jenkins, D.A., Rosatte, R. & Fryxell, J.M. (2008) Socially informed random walks: incorporating group dynamics into models of population spread and growth. *Proceedings Of The Royal Society B-Biological Sciences*, **275**, 1101–1109.
- Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E. & Paquet, P.C. (2005) Human activity mediates a trophic cascade caused by wolves. *Ecology*, **86**, 2135–2144.
- Jerde, C.L. & Visscher, D.R. (2005) Gps measurement error influences on movement model parameterization. *Ecological Applications*, **15**, 806–810.
- Jonsen, I.D., Flenning, J.M. & Myers, R.A. (2005) Robust state-space modeling of animal movement data. *Ecology*, **86**, 2874–2880. doi:10.1890/04-1852.
- Jonsen, I.D., Myers, R.A. & Flenning, J.M. (2003) Meta-analysis of animal movement using state-space models. *Ecology*, **84**, 3055–3063. doi:10.1890/02-0670.
- Kareiva, P.M. & Shigesada, N. (1983) Analyzing insect movement as a correlated random-walk. *Oecologia*, **56**, 234–238. doi:10.1007/BF00379695.
- Kass, R.E. & Raftery, A.E. (1995) Bayes factors. *Journal of the American Statistical Association*, **90**, 773–795.
- Lowe, S.J., Patterson, B.R. & Schaefer, J.A. (2010) Lack of behavioral responses of moose (*Alces alces*) to high ambient temperatures near the southern periphery of their range. *Canadian Journal of Zoology-Revue Canadienne de Zoologie*, **88**, 1032–1041.
- McClintock, B.T., King, R., Thomas, L., Matthiopoulos, J., McConnell, B.J. & Morales, J.M. (2012) A general discrete-time modeling framework for animal movement using multistate random walks. *Ecological Monographs*, **82**, 335–349. doi:10.1890/11-0326.1.
- Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E. & Fryxell, J.M. (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology*, **85**, 2436–2445. doi:10.1890/03-0269.
- Morris, D.W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, **136**, 1–13. doi:10.1007/s00442-003-1241-4.
- Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 19052–19059. doi:10.1073/pnas.0800375105.
- Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O. & Matthiopoulos, J. (2008) State-space models of individual animal movement. *Trends in Ecology & Evolution*, **23**, 87–94. doi:10.1016/j.tree.2007.10.009.
- Patterson, T.A., McConnell, B.J., Fedak, M.A., Bravington, M.V. & Hindell, M.A. (2010) Using GPS data to evaluate the accuracy of state-space methods for correction of Argos satellite telemetry error. *Ecology*, **91**, 273–285.
- Plummer, M. (2008) Penalized loss functions for bayesian model comparison. *Biostatistics*, **9**, 523–539. doi:10.1093/biostatistics/kxm049.
- Plummer, M. (2010) JAGS: just another Gibbs sampler. Version 2.2.0. URL <http://www.fis.iarc.fr/martyn/software/jags/>.
- R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>. ISBN 3-900051-07-0.
- Rosenzweig, M.L. (1991) Habitat selection and population interactions – the search for mechanism. *American Naturalist*, **137**, S5–S28. doi:10.1086/285137.
- Spiegelhalter, D.J., Best, N.G., Carlin, B.R. & van der Linde, A. (2002) Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society Series B-Statistical Methodology*, **64**, 583–616. doi:10.1111/1467-9868.00353.
- Turchin, P. (1998) *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates.
- Van Moorter, B., Visscher, D., Benhamou, S., Boerger, L., Boyce, M.S. & Gaillard, J.M. (2009) Memory keeps you at home: a mechanistic model for home range emergence. *Oikos*, **118**, 641–652. doi:10.1111/j.1600-0706.2008.17003.x.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** R code for simulation of movement paths, JAGS code for the fitting of movement models, and further information pertaining to the moose case study.

**Figure S1.** Example of the empirical (grey histograms) and fitted (blue lines) movement rate and turn angle distributions for the exploratory and encamped state for one moose.

**Table S1.** Fitted parameters for the double model for each of 34 moose paths.