One size does not fit all: flexible models are required to understand animal movement across scales

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Summary

1. Large data sets containing precise movement data from free-roaming animals are now becoming commonplace. One means of analysing individual movement data is through discrete, random walk–based models.

2. Random walk models are easily modified to incorporate common features of animal movement, and the ways that these modifications affect the scaling of net displacement are well studied. Recently, ecologists have begun to explore more complex statistical models with multiple latent states, each of which are characterized by a distribution of step lengths and have their own unimodal distribution of turning angles centred on one type of turn (e.g. reversals).

3. Here, we introduce the compound wrapped Cauchy distribution, which allows for multimodal distributions of turning angles within a single state. When used as a single state model, the parameters provide a straightforward summary of the relative contributions of different turn types. The compound wrapped Cauchy distribution can also be used to build multiple state models.

4. We hypothesize that a multiple state model with unimodal distributions of turning angles will best describe movement at finer resolutions, while a multiple state model using our multimodal distribution will better describe movement at intermediate temporal resolutions. At coarser temporal resolutions, a single state model using our multimodal distribution should be sufficient. We parameterize and compare the performance of these models at four different temporal resolutions (1, 4, 12 and 24 h) using data from eight individuals of *Loxodonta cyclotis* and find support for our hypotheses.

5. We assess the efficacy of the different models in extrapolating to coarser temporal resolution by comparing properties of data simulated from the different models to the properties of the observed data. At coarser resolutions, simulated data sets recreate many aspects of the observed data; however, only one of the models accurately predicts step length, and all models underestimate the frequency of reversals.

6. The single state model we introduce may be adequate to describe movement data at many resolutions and can be interpreted easily. Multiscalar analyses of movement such as the ones presented here are a useful means of identifying inconsistencies in our understanding of movement.

Key-words: Latent states, model complexity, directional bias, scaling, random walk

Introduction

The details of animal movement decisions can have profound implications for spatial population structure (Kareiva 1990;

Austin, Bowen & McMillan 2004), interspecific interactions such as predation (Mitchell & Lima 2002; Moorcroft, Lewis & Crabtree 2006) and seed dispersal (Russo, Portnoy & Augspurger 2006; Levey, Tewksbury & Bolker 2008; Will & Tackenberg 2008) as well as for the cascading effects of these interactions on habitat structure and ecosystem functions (Wiens *et al*. 1993; Creel *et al*. 2005; Fortin *et al*. 2005; Kremen & Ostfeld 2005; Hollenbeck & Ripple 2008).

Although the importance of movement in ecological processes is increasingly recognized, researchers are only beginning to determine the degree to which conclusions from a single study can be applied more broadly. While simple models can accurately describe movement behaviour over short time periods, the parameters underlying these models often change over time leading to poor predictions over longer time-scales (Morales & Ellner 2002; Gurarie, Andrews & Laidre 2009). Factors such as behavioural complexity and landscape structure complicate modelling of movement and lead to analyses that are specific to the study species and landscape (Yang 2000; Jonsen, Myers & Flemming 2003; Morales *et al.* 2004; Moorcroft & Lewis 2006; Forester *et al.* 2007; Dalziel, Morales & Fryxell 2008; Fryxell *et al.* 2008).

Movement models differ greatly in their details, but they can be grouped into a few classes based on criteria such as their focus (e.g. detailed movement paths of individuals or less frequent relocations from a population of individuals) and whether they treat the movement process as continuous or discrete. Here, we focus on random walk–based models, a popular class of models that is generally applied to detailed movement paths of individuals and treats movement as discrete process. Random walk–based approaches to movement data define the distance between relocations as 'steps' and the difference in bearings between successive steps as 'turning angles'. Distributions of steps and turning angles can then be used to fit random walk–based models that are modified to account for common features of movement paths. The tendency for step bearings to be positively correlated is referred to as *persistence* in step orientation leading to correlated random walk models (Kareiva & Shigesada 1983; Turchin 1998; Bartumeus *et al.* 2008). Another set of modifications include a bias towards either an absolute or relative position (Benhamou 2006). Often models incorporate a bias towards a fixed point in the centre of the home range (Borger, Dalziel & Fryxell 2008), which we refer to as a *centring* component. A third type of modification accounts for a high proportion of reversals in movement paths. *Reversals* may be common when features of the environment act as either physical or behavioural barriers to movement or when species slow down their movement and become involved in movement bouts (Barraquand & Benhamou 2008). Assuming that only one type of movement dominates, we can generally describe it using one parameter, the variance or spread around the orientation that is expected (e.g. 0 for persistence). Alternatively, some researchers refer to the mean and variance in the cosine of the turning angles (Turchin 1998). However, when faced with a histogram that shows evidence of both persistence and reversals, such methods can provide poor summaries (Fig. 1a).

One solution to this problem is to fit models that include mixtures of different random walks (e.g. Morales *et al.* 2004). In the case of persistence, centring and reversals, such a model would have three states (hereafter 3-state model). Not only do these models allow us to account for mixtures of different types of turns, they also can be configured to account for nonindependence between step length and turn-
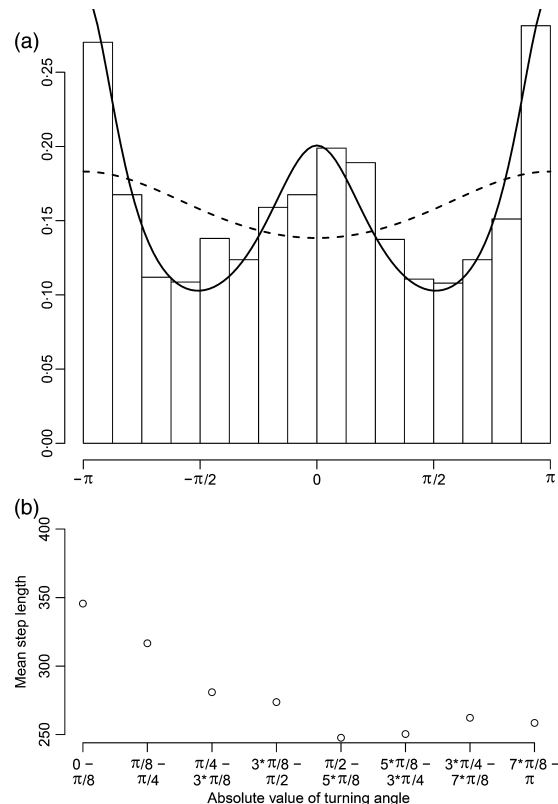

Fig. 1. (a) Histogram of turning angles based on 12-h intervals between relocations showing evidence of reversals (peaks at either end of histogram) and persistence (smaller peak at 0). Dotted line represents the probability distribution function predicted by maximum likelihood assuming a unimodal distribution of turning angles. Solid line represents the probability distribution function assuming a bimodal distribution of turning angles with persistence and reversal components. (b) Average step length is greater when the absolute value of the turning angle is closer to zero (based on 1-h intervals between relocations).

ing angle (Fig. 1b) by allowing persistent movements to have different step lengths than reversals or by linking step length to the turning angle and other covariates. This type of models allows us to accommodate hidden structure in the data (such as the order of turns) that cannot be inferred from histograms.

Here, we develop a second solution, the compound wrapped Cauchy distribution (see Methods), which allows for either a unimodal or a multimodal distributions of turning angles within a single state. When used as a single-state model (hereafter 1-state model), the parameters provide a straightforward summary of the contributions of different movement types (e.g. persistence, centring and reversals). The compound wrapped Cauchy distribution can also be used to build multiple state models in which the relative contributions of persistence, centring and reversals vary by state.

The questions of whether mixture models based on unimodal or multimodal distributions are appropriate or even necessary will vary based on characteristics of the study species and the frequency at which relocations are recorded. Although we know quite a bit about how different theoretical

models scale (e.g. Smouse *et al.* 2010), we know far less about how mixture models scale and the degree to which they are appropriate at different temporal resolutions. We expect that mixture models with unimodal distributions will be most appropriate at finer resolutions. At these resolutions, latent states may be synonymous with behaviours (e.g. foraging, travelling to resting sites). However, if movement path are sampled less frequently, then steps will quickly begin to represent groups of behaviours and mixture models based on multimodal distributions will be more appropriate (Getz & Saltz 2008; Nathan *et al.* 2008). As we consider step measured over still coarser resolutions and maintain a constant temporal extent, we expect that 1-state models with multimodal distribution of turning angles will be sufficient.

Because states in mixture models based on multimodal distributions represent groups of movement types, as opposed to specific movement types, it is possible to assign states at resolutions greater than the single step. (This approach would be nonsensical for a mixture model based on unimodal distributions of turning angles.) Assigning states at the resolution of the step can carry a hefty parameter penalty if models are being compared by an information criterion and may lead to the false conclusion that a multistate model is not appropriate. The use of effective parameters in a Bayesian context lessens but does not entirely eliminate this parameter penalty. If latent states reflect changes in the relative frequency of behaviours, specifying a resolution for states, or a few alternative resolutions, based on biological reasons, represents an *a priori* hypothesis about the temporal resolution at which variation in movement behaviour is expected. For example, if states are defined at a resolution of hours, then it is likely that the diel cycles in activity will be an important factor determining how states are assigned. On the other hand, if seasonal variation linked to changes in mating behaviour or availability of food is the primary driver of variation in movement, then defining states at coarser temporal scales may be more appropriate.

In addition to making predictions about the appropriateness of different model structures at different temporal resolutions, we can also predict how parameter values may change based on findings from past studies (e.g. Bovet & Benhamou 1988; Turchin 1998). Using a 1-state model with a multimodal distribution of turning angles, we would expect that persistent movement would be most common at finer resolutions and that centring and reversals are likely to be more important at coarser resolutions. We also expect that the correlation between turning angle and step length will degrade at coarser resolutions.

We test the above predictions by parameterizing four movement models (Fig. 2) with movement data from *Loxodonta cyclotis* (Matschie, 1900; forest elephants). Our data set includes relocations from eight individuals collected at four different temporal resolutions (1, 4, 12 and 24 h). We use model comparison to evaluate the fit of these models to observed data. After using these models to understand movement patterns at different temporal resolutions, we simulate data using parameters estimated at the finest resolution (1 h)
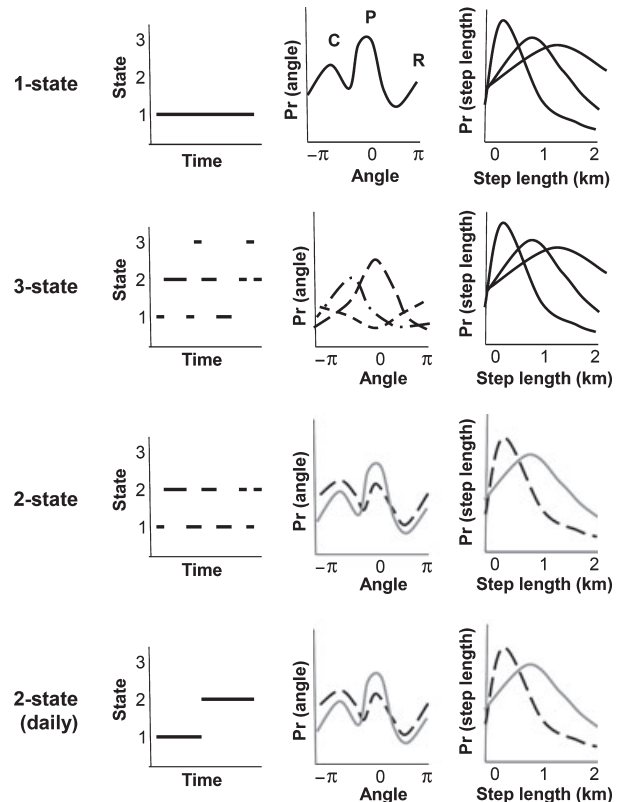

Fig. 2. Schematic representation of four different models being compared. The first column illustrates how many latent states are considered according to the model structure and the resolution at which they are assigned. The second column illustrates how step orientation is modelled. For this figure, the centre of the home range is at an angle of approximately $3\pi/4$, corresponding to the peak in the first row labelled C. Also labelled are the peaks corresponding to reversals (R) and persistence (P). Curves with different shading and hash mark signify the different probability distributions for each latent state. The final column illustrates how step length is modelled. Note that in the first two rows of the third column, the different curves are all solid, to reflect differences as a result of the covariates; in the bottom rows, the dashed curves illustrate that differences in latent states determine both step orientation and step length.

to determine the relative efficacy of the suite of models in reproducing movement observed at coarser temporal resolutions. Comparing simulated data with observed data is an important way to evaluate models and provides a useful compliment to model comparison techniques, which only provide information on relative performance (Gelman & Hill 2007; Uriarte & Yackulic 2009).

Materials and methods

DATA SOURCES

Our analyses focus on the movement paths of *L. cyclotis*. *L. cyclotis* spends most of its day moving at relatively fast speeds, meaning that there is a high signal-to-noise ratio in successive GPS relocations, even at a temporal resolution as fine as 1 h. There is extreme variation among the movement paths of the eight individuals in our data set, which gives us an opportunity to test the generality of different

models across individuals. Animals were fitted with GPS collars under supervision from the Field Veterinary Program of the Wildlife Conservation Society following methods described by Blake, Douglas-Hamilton & Karesh (2001). Individuals were tracked for an average of 319 days during the period of 2000–2005. These eight individuals were chosen from a larger data set based on their superior coverage at 1-, 4-, 12- and 24-h temporal resolutions (Appendix S2, Blake *et al.* 2008). The collars on all individuals were set to take measurements at time intervals of 1-h or less for some portion of the study and at 4-h intervals at least for the rest of the study. All animals were adults and were drawn from three protected areas, three from Lopé National Park (Gabon), one from Ivindo National Park (Gabon) and four from Nouabalé-Ndoki National Park (Congo), and included both sexes (six females; two males).

DATA PROCESSING

To determine how temporal resolution influences model selection, the data were resampled at 1, 4, 12, and 24-h resolutions. The original data set included a series of relocations distributed throughout time at semi-regular intervals. This semi-regularity was the result of intended changes in sampling frequency as well as missed relocations (Appendix S2). While the 4-, 12- and 24-h resolution data sets cover the entire data sets, the 1-h data have more gaps. For each individual, the median latitude and longitude of all relocations were calculated and used as a proxy for the centre of the individual's home or foraging range. To prepare the original data for analysis at fixed temporal resolution, the coordinates at 1-, 4-, 12- and 24-h intervals were calculated to create data sets of fixed time lengths. If coordinates were not available at a given time, that point was excluded from further analysis. For all points where the coordinates of the next interval were available, the step length and orientation were determined; otherwise, the point was ignored in our analyses. If the orientation of the last step was also available, the turning angle was calculated as the difference in the orientations of the successive steps. For all data points where the orientation of the last data step was missing, the missing data values were modelled using imputation (see Appendix S3).

MODEL COMPONENTS

The goal of this study was to evaluate the efficacy of different model structures in reproducing movement data collected at different temporal resolutions. To this end, a compound wrapped Cauchy distribution was developed to characterize latent-state modes. This model structure allows for the simultaneous estimation of the importance of reversals, centring and persistence in explaining movement orientation. This distribution is used to build four movement models (Fig. 2) for the eight individuals and at the four selected temporal resolutions (1, 4, 12 and 24 h).

The compound wrapped Cauchy distribution builds on the simple wrapped Cauchy distribution, which takes the following form:

$$C(\phi|\psi,\rho) = \frac{1-\rho^2}{2\pi(1+\rho^2 - 2\rho\cos(\phi-\psi))} \qquad \text{eqn 1}$$

where ϕ is the observed step orientation, ψ is the predicted step orientation and ρ is a measure of the movement concentration around the expectation. ρ is usually restricted to lie between zero and one, with $\rho = 0$ indicating that ϕ is equally likely to take any value between $-\pi$ and π (or between 0 and $2*\pi$), increasing values of ρ indicating higher concentration around ψ, and $\rho = 1$ indicating that the distribution has all its mass on ψ. If we were seeking to model only directed persistent motion, ψ would be the orientation of the previous step. For

reversals, ψ would be equal to the orientation of the previous movement plus or minus π. For centring, ψ would be the orientation to the centre.

Generalizing from the wrapped Cauchy, the compound wrapped Cauchy is defined as follows:

$$CC(\phi|N,\varphi_N,\rho_N) = \frac{\sum\limits_{i=1}^{N} C(\phi|\psi_i,\rho_i)}{N} \qquad \text{eqn 2}$$

where N is the number of components included (e.g. centring, persistence and reversals), ψ_i is the predicted angle for the ith component and ρ_i is the concentration parameter for that component. (*N.B.* ρ's cannot be directly compared between models where N differs.)

In all models, step lengths were assumed to be drawn from a 2-parameter Weibull distribution, which takes the following form:

$$W(x|\upsilon,\lambda) = \upsilon\lambda x^{\upsilon-1}\exp(-\lambda x^{\upsilon}); \quad x > 0 \qquad \text{eqn 3}$$

where x are the observed step lengths and λ and υ are the estimated parameters. υ is referred to as the shape parameter for the distribution, while $1/\lambda$ is often referred to as the scale parameter. The expectation of the Weibull distribution is given by $\Gamma(1 + 1/\upsilon)/\lambda$, where Γ is the gamma function. A linear model of the covariates was linked to λ via a log link. For the purposes of this analysis, the absolute value of the turning angle (on the interval $[-\pi, \pi]$) was used as covariate. Inclusion of the absolute value of the turning angle allows for a relationship between movement length and orientation, as has been observed in past studies (Morales *et al.* 2004).

MODELS

In the 1-state model, all steps for an individual are described by one set of parameters. Step orientation is modelled using the compound Cauchy distribution as a function of persistence, reversals and centring. Step length is modelled using turning angle. The assumptions underlying this model are that parameters governing step orientation are the same throughout the sampling period (i.e. there are not identifiable discrete states) and that turning angle is negatively related to step length – either because individuals are actually moving slower when making turns or because sampling introduces this effect.

In the second model, the 3-state model, each of the three components of step orientation (persistence, reversals and centring) is given a separate latent state with a compound Cauchy distribution where the ρ's for the other two components are set to zero. The assumption in this model is that individual turns can actually be classified in terms of the three components. The 3-state model shares the same structure for determining step length as the 1-state model, and the parameters governing step length do not vary between states.

Our third model, hereafter the 2-state model, has 2 latent states, one of which is forced to have larger average step length. Each state also has its own parameters determining the degree of persistence, reversals and centring, and each step is assigned to one of the two states. This model represents coarser variation in the frequency of different turn types.

The fourth model, the 2-state (daily) model, is the same as in the 2-state model except that latent states are assigned daily (i.e. all steps on any given day belong to the same state). This model allows us to ignore diel cycles in behaviour and focus only on variation at resolutions > 24 h, like those driven by seasonal variation in food availability. It is possible that an even coarser resolution than daily is optimal for assigning states; however, in this study, we were interested in determining whether assigning states at a resolution greater than diel cycles was advantageous in scaling up movement, not in determining

the optimal resolution for assigning latent states. In each of the three multistate models, the state in each time step was modelled as being independent of the state in the previous time step (i.e. switching probabilities were not estimated).

Models for all eight individuals were fit separately at the four different temporal resolutions using WinBUGS. All parameters were given weakly informative or uninformative priors (see Appendix S3 for sample code including priors). Weakly informative priors were chosen for some parameters to avoid portions of parameter space which created errors in WinBUGS. For example, ρ's very close to 1 were found to create problems so we constrained all ρ's to values between 0 and 0·95. We also used weakly informative parameters to constrain the parameters associated with step length to areas of parameter space that made sense based on summary statistics. Given the large amount of data available and the weak nature of the information content in these priors, it is unlikely that priors had much influence on our parameter estimates. For each model, we initially ran three chains for 20 000 iterations. If models had not converged, models were rerun at 50 000 and then 100 000 iterations. We deemed models to have converged when *r*-hat estimates for all parameters were < 1·1. Model results were compared using deviance information criterion (DIC) values (Spiegelhalter *et al.* 2002; Gelman *et al.* 2004).

For the 1-state model, we were interested in calculating population-level estimates for each parameter at each resolution. To accomplish this, we conducted meta-analyses where the parameter estimate (and associated uncertainty) for each individual was treated as a random effect drawn from a distribution defined by the population mean and variance. Although it is possible to calculate the population mean and variance directly using hyperpriors in models that consider all individuals at once, we chose to fit models for each individual separately for two reasons. First, because these models are novel and we wanted to be sure that hyperpriors did not bias our inferences at the individual level by obscuring differences between individuals. Secondly, fitting models for individuals independently is much quicker because multiple WinBUGS models can be run concurrently. Using parameter estimates from each individual in a meta-analysis should provide similar values to hyperpriors. Meta-analyses were conducted using R statistical software (R Development Team 2008 – package rmeta for meta-analyses).

To assess the efficacy of each model in reproducing movement patterns at coarser temporal scales, data from all four models [1-state, 3-state, 2-state and 2-state (daily)] were simulated. For each individual, we drew 30 sets of parameter values from the posterior distributions of each of the fitted model for that individual at a 1-h resolution and used these parameter values to simulate a new movement path. Thus, for each individual, we simulated 120 new paths (30 based on each of the models) and we repeated this process for all eight individuals. Detailed R code for simulations is given in Appendix S4. These simulated data were subsampled to create 4-, 12- and 24-h data sets. For each data set, we then removed any values that were missing in the original data set so that all simulated data sets were of the exact same length as the original data. Each set of simulated data was then used to fit the 1-state model for all eight individuals at four temporal resolutions (1, 4, 12 and 24 h).We fit the 1-state model to these simulated data, because parameters in the 1-state model are easily interpreted and provide the most straightforward summary of step length and turning angles.

For each individual and model at each resolution, we summarized the 30 simulations by combining the mean parameter estimates for each simulation and determining the 2·5% and 97·5% quantiles, as well as the mean and standard deviations. We calculated population-level estimates for parameters for each model and resolution by combining the mean and standard deviations estimated derived from the 30 simulations for each individual into a meta-analysis.

Results

As we predicted, the single-state model with a multimodal distribution (1-state model) was favoured at the coarsest temporal resolutions (12 and 24 h; Table 1, Appendix S1). Of the two mixture models, we expected the mixture model based on unimodal distributions (3-state model) to be favoured at the finest temporal resolutions, and the mixture model based on multimodal distributions to be favoured at intermediate resolutions (2-state model). We found equal support for the 2-state and 3-state models at the 1-h resolution and slightly greater support for the 2-state model at the 4-h resolution supporting these predictions. The fact that the 1-state model was preferred at coarser resolutions and more complex models were preferred at finer resolutions is independent of sample size. For example, at 12-and 24-h resolutions, individuals 2 and 4 had greater sample sizes than most of the other individuals at 1- and 4-h resolution (Appendix S2), yet in the former case the simpler model was preferred and in the later instance more complex models were preferred.

We included both 2-state and 2-state (daily) models to test whether changes in the relative frequency of different movement types occurred mostly at resolutions > 24 h. The 2-state (daily) model was preferred over the 2-state model for all individuals at all temporal resolutions (excluding 24 h where they are the same model). Even though the 2-state model offered more flexibility for grouping steps into states than the 2-state (daily) model, the added cost of the additional effective parameters necessary to estimate a state at each step was not justified. In other words, although the 2-state model always had a lower deviance, the drop in deviance was not justified by the increased number of effective parameters (pD, see Appendix S1). Future research should focus on determining whether this conclusion is general or conditional on the absence of switching probabilities to explain transitions between states.

The 1-state model provides a relatively straight forward summary and allows us to test additional predictions. Based on previous studies (e.g. Bovet & Benhamou 1988; Turchin 1998), we predicted that both the strength of persistence and the correlation between step length and turn angle would

Table 1. Summary of model comparison results for eight individuals. Each cell contains the number of individuals for which the corresponding model had the lowest DIC value (was most favoured by the data) of the four models at each temporal resolution

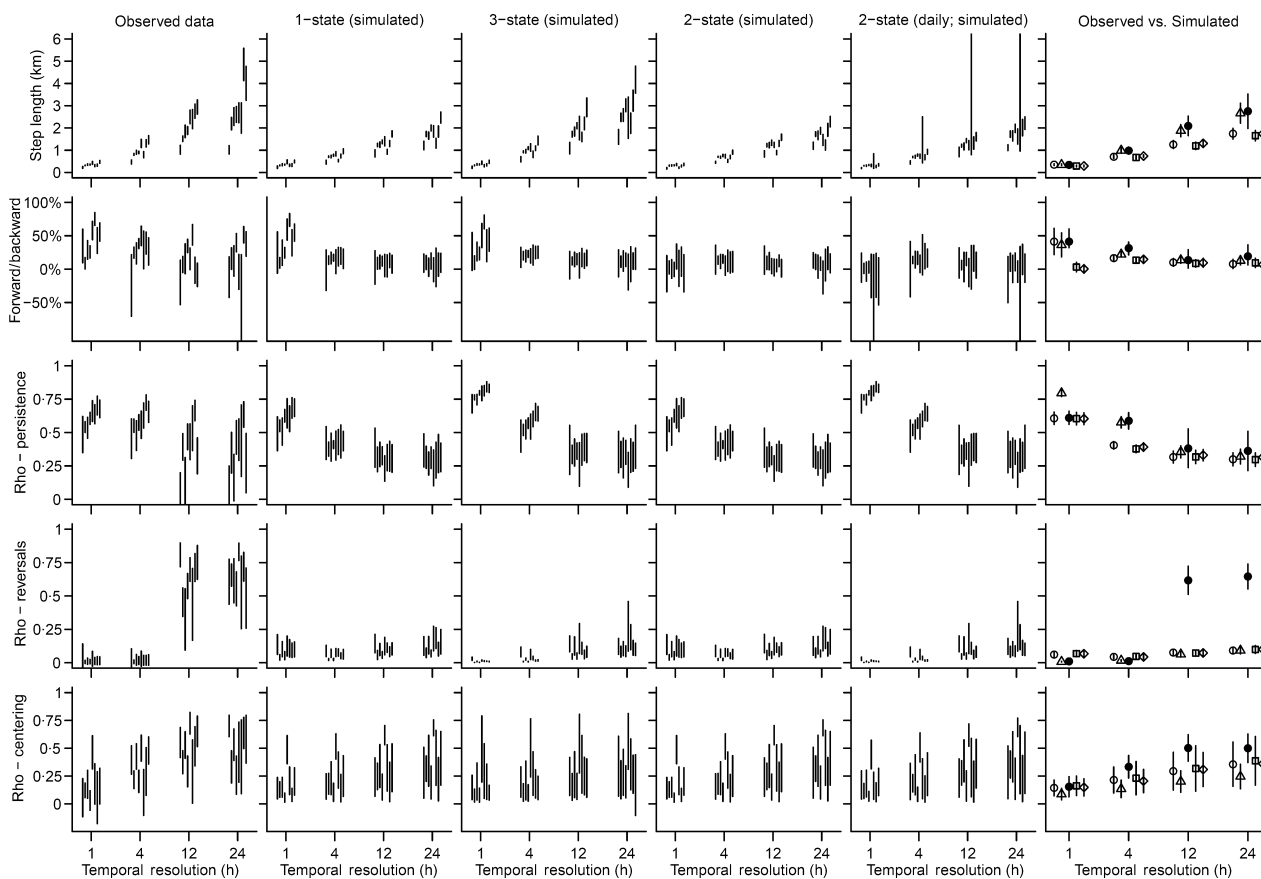|	1-state	3-state	2-state	2-state (daily)
1 h	0	4	0	4
4 h	1	3	0	4
12 h	6	0	0	2
24 h	8	0	0	0

Fig. 3. Comparison of simulated data sets with actual data. In the first column, black lines represent the 95% confidence intervals of the parameter estimates for the eight individuals at the four temporal resolutions. In the second through fifth column, black lines represent the 5% and 95% quantiles of the 30 parameter estimates derived from independent simulated data sets. In the final column, population-level means and 95% confidence intervals from the simulated data sets are compared with the population-level means and 95% confidence intervals for the observed data. Population-level parameter estimates derived from observed data are indicated by closed circles. Open shapes indicate population-level parameter estimates based on data that were simulated from the 1-state (circle), 3-state (triangles), 2-state (diamonds) or 2-state (daily; squares) models.

degrade as we considered coarser temporal resolutions and that the ρ's associated with centring and reversals would increase. All four predictions were supported in the parameter estimates for individuals and in the overall population estimates (Fig. 3, columns 1 and 6). We also found that step length increased with resolution, which is expected based on previous research (e.g. Bovet & Benhamou 1988; Turchin 1998).

To determine the relative efficacy of the suite of models in reproducing movement observed at coarser temporal resolutions, we used the parameter estimates for all four models at the 1-h resolution to simulate movement trajectories and then used the 1-state model to summarize the simulated movement paths at all four temporal resolutions (1, 4, 12 and 24 h). All four simulated data sets adequately recreated observed patterns in three of the five parameters considered: the effect of turning angle on step length, the ρ associated with persistence and the ρ associated with centring (Fig. 3). However, only one of the four simulated data sets, the 3-state model, accurately estimated mean step length at coarser temporal resolutions, and the simulated data sets did a poor job of predicting the magnitude of the increase in the ρ associated with rever-

sals. For example, at both the 12 and 24 h, none of 960 simulated data sets had mean estimated ρ's as great as the population mean derived from the observed data, and only 3 of 960 simulated data sets had estimates of ρ that were greater than the individual with the lowest estimated ρ.

Discussion

We have introduced a novel means of quantifying the relative roles of different components of step orientation (e.g. reversals, persistence and centring). The compound wrapped Cauchy distribution allows us to fit multimodal distributions of turning angles without the aid of multiple latent states and provides straightforward summary statistics. The compound wrapped Cauchy distribution can also be used to build mixture models. These models differ from mixture models based on unimodal distributions of turning angles in their interpretation and in the temporal scales at which they can be appropriately applied. We expected that a mixture model based on unimodal distributions (3-state model) would be more useful when steps are measured at finer temporal resolutions and that a mixture model based on multimodal distributions

would be more appropriate at coarser resolutions (2-state or 2-state (daily) models). The 3-state and 2-state (daily) models found roughly equal support at the 1- and 4-h resolutions; however, the 2-state (daily) model was the best model for two individuals at the 12-h resolution as compared with zero individuals for the 3-state model (Table 1). It would be interesting to compare the two mixture models at even finer resolutions to determine whether 3-state models were favoured as intervals became finer. At coarser resolutions, we expected that 1-state models would be more useful. We found strong evidence that 1-state models are sufficient to describe movement in *L. cyclotis* when relocation events are separated by 12 or 24 h.

Getz & Saltz (2008) provide a useful conceptual framework to interpret our results. They define three components: fundamental movement elements (e.g. a lunge, a turn or a step), activities (e.g. foraging versus directed movements) and canonical activity modes (CAMs) (mixtures of fundamental movement elements). Mixture models based on unimodal distributions are most analogous to activities, while mixture models based on multimodal distributions are a better representation of CAMs. Because CAMs are themselves heterogeneous groupings of fundamental movement elements which include both steps and turns, it is necessary that states allow for multimodal distributions of step orientation. Like Getz & Saltz (2008), we argue that most studies are conducted at too coarse a resolution to characterize fundamental movement elements and therefore CAMs are the focus of studies. In our study, when steps were measured at finer resolutions, the CAMs were more distinct and states were useful for grouping them; however, at coarser resolutions, CAMs become more indistinguishable and states were no longer necessary.

Finer temporal resolution of steps favours multistate models, but coarser resolution was preferred in the 2-state/2-state (daily) comparison. This result could be interpreted as evidence that changes in behaviour at coarser temporal resolutions (e.g. in response to the fruiting season) underlie the need for latent states to describe movement of *L. cyclotis*. Because our models assigned states independently, it would be interesting to test whether our results generalize to the case where starts are assigned based on switching probabilities. Our results suggest that researchers should not assume that defining latent states at the same resolution as steps is appropriate and should consider the biology of the species being modelled in defining *a priori* hypotheses about the resolution at which important behavioural changes occur. Recent reviews (e.g. Nathan *et al.* 2008) have begun to address the issue of the temporal resolution of states by emphasizing that movement paths are structured at multiple temporal scales. Our study provides some important lessons for researchers applying movement models to various animal taxa. If we had assumed that latent states should be defined at the same resolution as steps, we would have concluded that the 2-state structure did not adequately represent movement in *L. cyclotis*. However, because we considered the probable resolution of variation (larger than days), we found that the 2-state

(daily) model did provide a good representation at finer resolutions.

Past studies have detailed the ways in which net displacement increases over time in different theoretical models and compared these predictions with observed data (e.g. Turchin 1998), however, much less emphasis has been placed on understanding how the characteristics of step orientation change with increasing temporal resolution (however, see Bovet & Benhamou 1988; Benhamou 2004). We predicted that the ρ associated with persistence would dominate at the finest resolutions and decrease in importance with increasing temporal resolution. Despite substantial individual variation (Fig. 3, row 3 column 1) in the strength of this decline, the decline in the persistence ρ is clear in the population level trends (Fig. 3 column 6). We also predicted that the ρ's associated with centring and reversals would increase at coarser temporal resolutions. Both ρ's associated with centring and those associated with reversals did in fact increase; however, the ρ associated with centring exhibited a gradual increase, whereas the ρ associated with reversals increased dramatically between 4 and 12 h (Fig. 3 rows 4 and 5). Our final prediction that the correlation between step length and turn angle would degrade as we considered coarser temporal resolutions was also supported.

One of the motivations for our study was to determine whether models parameterized at fine temporal resolution could recreate patterns of animal movement at coarser resolutions. The ability to scale up from short, fine-scale data to longer extents and coarser resolutions is a critical issue in the study of animal movement. For this reason, we simulated data sets using the appropriate model structures and 1-h resolution parameter estimates of the 1-state, 2-state (daily) and 3-state models. When we compared these simulated data with the observed data, we found that the data simulated from the 1-state, 2-state, and 2-state (daily) models significantly underestimated mean step length at the 12- and 24-h resolution. On the other hand, data simulated from the 3-state model did adequately replicate the magnitude of the mean step length at 12- and 24-h resolution in the observed data set. The combination of the failure of the 1-state model and the success of the 3-state model is interesting because the 1-state and 3-state models shared exactly the same structure for determining step length. This suggests that step orientation is playing an important role in determining displacement over longer time-scales. The 2-state (daily) also failed to predict step length at coarser temporal scales, providing evidence that step orientation and not latent states *per se.* is integral to accurately predicting step length at coarser temporal scales. The results of this examination of mean step length in simulated data sets at coarser temporal resolutions suggest that we should be focusing more on step orientation if we hope to understand how mean displacement varies over different temporal resolutions. The difference in mean step length between the data simulated from the different models also suggests why simulating from fine-scale observations to test the ability of models to capture coarser scale movement can illustrate

key differences between models that are not obvious from model comparison at a given temporal scale. By providing a means with which to compare models back to data, our simulations served a similar role to the probes discussed in Dalziel, Morales & Fryxell (2008).

Another important distinction between the simulated data sets and the observed data was all four simulated data sets grossly underestimated the magnitude of the increase in reversals at 12- and 24-h resolutions. One explanation for the sudden rise in reversals is that it represents a fundamental aspect of the habitat structure of *L. cyclotis* which is not included in our models. At the Nouabalé-Ndoki park, individuals have been observed congregating at the same forest clearings (bais) on consecutive nights, leaving bais early in the morning and returning to them in the evening (Blake 2002). Given these facts, we might expect a rise in reversals at the 12-h resolution because measurements were centred on noon and midnight and at this resolution, individuals would move from bais and then reverse their path back to return to the same locations. However, this would not explain why reversals remained a prominent feature of movement paths at the 24-h resolution. In addition, the sudden rise in reversals was also found in individuals from the Lopé park, where bais are not believed to have an important role in structuring *L. cyclotis* behaviour.

A second nonexclusive explanation is that we are ignoring higher-order autocorrelation in step orientation. Although we account for first-order autocorrelation, the increased likelihood that a step will have the same orientation as the previous step, we do not account for second-order autocorrelation, the increased likelihood that a right-hand turn will be preceded by another right-hand turn (or vice versa). At 10- to 20-min temporal resolutions, the movement of *Loxodonta africana* (Blumenbach, 1797; savanna elephants) exhibits evidence of second-order autocorrelation leading to looping behaviour (Dai *et al.* 2007). It seems plausible that this looping behaviour is occurring over longer intervals in *L. cyclotis*. To our knowledge, very little effort has been devoted to incorporating second-order autocorrelation into movement models even though its potential importance to our understating of animal movement has been noted elsewhere (Turchin 1998; Fischhoff *et al.* 2007). It is also possible that analysing movement as a continuous, rather than a discrete process, and focusing on velocity rather than step length and turning angles may better address these autocorrelation issues (Gurarie, Andrews & Laidre 2009).

The last few decades have seen an explosion in the amount of attention given to studies of animal movement that couple observational data with statistical models (Holyoak *et al.* 2008; Nathan *et al.* 2008). There has been a corresponding increase in model complexity coupled with attempts to apply parameters of animal movement estimated from field data to other areas in ecology, including the study of biotic interactions (e.g. seed dispersal and pollination) and spatial population structure. In all these applications, the ability of models to adequately represent patterns not only at the scale at which they are fitted but also over larger temporal scales is an important consideration (Johnson *et al.* 1992; Turchin 1998). Here, we have shown that the choice of temporal resolution determines which model structures are preferred. We have also illustrated the existence of important gaps in our understanding and interpretation of animal movement data by comparing the data structure of simulated data with observed data. We are only beginning to explore how latent states should be defined and interpreted, how the choice of latent states affects our understanding of step length and how animal movement decisions can be scaled up. The study of these questions across a broad range of animal taxa should offer important insights into our understanding of animal movement.

Acknowledgements

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Supporting Information

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

Appendix S1. More detailed summary of model comparison results.

Appendix S2. Coverage of different individuals at different temporal resolutions.

Appendix S3. Winbugs code for four models.

Appendix S4. R code used for simulating movement paths from the four models.

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