

## SPECIAL FEATURE: STUCK IN MOTION? RECONNECTING QUESTIONS AND TOOLS IN MOVEMENT ECOLOGY

# What is the animal doing? Tools for exploring behavioural structure in animal movements

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## Summary

1. Movement data provide a window – often our only window – into the cognitive, social and biological processes that underlie the behavioural ecology of animals in the wild. Robust methods for identifying and interpreting distinct modes of movement behaviour are of great importance, but complicated by the fact that movement data are complex, multivariate and dependent. Many different approaches to exploratory analysis of movement have been developed to answer similar questions, and practitioners are often at a loss for how to choose an appropriate tool for a specific question.
2. We apply and compare four methodological approaches: first passage time (FPT), Bayesian partitioning of Markov models (BPMM), behavioural change point analysis (BCPA) and a fitted multistate random walk (MRW) to three simulated tracks and two animal trajectories – a sea lamprey (*Petromyzon marinus*) tracked for 12 h and a wolf (*Canis lupus*) tracked for 1 year.
3. The simulations – in which, respectively, velocity, tortuosity and spatial bias change – highlight the sensitivity of all methods to model misspecification. Methods that do not account for autocorrelation in the movement variables lead to spurious change points, while methods that do not account for spatial bias completely miss changes in orientation.
4. When applied to the animal data, the methods broadly agree on the structure of the movement behaviours. Important discrepancies, however, reflect differences in the assumptions and nature of the outputs. Important trade-offs are between the strength of the *a priori* assumptions (low in BCPA, high in MRW), complexity of output (high in the BCPA, low in the BPMM and MRW) and explanatory potential (highest in the MRW).
5. The animal track analysis suggests some general principles for the exploratory analysis of movement data, including ways to exploit the strengths of the various methods. We argue for close and detailed exploratory analysis of movement before fitting complex movement models.

**Key-words:** behavioural change points, hidden Markov models, partitioning, segmentation, state space models, telemetry

## Introduction

A near universal property of animal movements is a high degree of behavioural structure. This structure is linked to

a wide range of phenomena, including habitat use, foraging and predation (Forester *et al.* 2007; Gurarie *et al.* 2011), dispersal and migration (Block *et al.* 2001; Delgado *et al.* 2010), social and territorial behaviours (Blackwell 1997; Moorcroft, Lewis & Crabtree 1999), biological invasions (Morgan *et al.* 2004), the coexistence of competitors

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(Keeling & Grenfell 1997) and community interactions (Kareiva, Mullen & Southwood 1990; Turchin 1991, 1998; Hanski 1998). As collecting movement data has become one of the most common methodologies for studying animals in the wild, there is no shortage of data with which to explore behavioural heterogeneity. Data are increasingly precise, sampled at higher temporal resolutions and collected simultaneously for larger numbers of individuals, and the opportunities to explore the behavioural mechanisms animals use to navigate their environment have never been greater (Cagnacci *et al.* 2010).

We can assign the objectives of animal movement studies into a hierarchy of exploratory, explanatory and predictive questions. The exploratory question related to individual movement is, simply, *What is the animal doing?* This includes both identification and quantification of the structure of the movement track: *Are there distinct behaviours? If so, how many? What distinguishes behaviour A from behaviours B and C? When and where does an animal switch from A to B to C? What spatial and/or temporal patterns are observable in this structure?* The explanatory analysis attempts to explain the behaviours and/or the transitions between behaviours in terms of relevant covariates, such as seasonal patterns, environmental cues or presence of conspecifics, asking *Why is the animal doing what it's doing?* Finally, predictive questions attempt to anticipate the spatial use of an animal based on close analysis of its behaviour, for example to ask *If the environment is modified in a specific way, can we anticipate the movement response of the animal?* The explanatory analysis depends on a good understanding of the properties and structure of the behaviour, and the predictive analysis depends entirely on a believable, well-parameterized behavioural model.

Linking analysis of behaviourally structured movement data to the main questions of interest is a significant

challenge. In contrast to a controlled experiment, where randomization isolates an effect of interest and the statistical models themselves are often straightforward to select and implement, there is little that can be controlled in a free-ranging organism. Potentially influential covariates are difficult to enumerate, and the data models themselves are multidimensional, correlated and heterogeneous within and among individuals. Given this complexity, the analytical approach for the exploratory step is particularly important.

Papers devoted to identifying and classifying behavioural heterogeneity in individual animal tracks have proliferated in step with the available data (a non-exhaustive list is provided in Table 1). Not surprisingly, the lack of a clear and agreed-upon framework for the selection of appropriate analysis tools has led to a wide array of approaches being applied to similar research questions. This methodological ambiguity has led to a crisis of choice where practitioners, particularly those new to the analysis of movement data, face difficulties deciding which tool to use for a given data set and question.

Our primary aim was to apply and contrast a sample of available methodologies for the exploratory analysis of behavioural structure in animal movement data. We selected four methods, chosen because they represent distinct analytical traditions and because they are relatively straightforward to implement using existing computational tools. We apply them to three simulated tracks where we have complete knowledge of the timing and nature of three different kinds of behavioural change: in speed, in tortuosity and in spatial bias. We then apply the methods to two very different animal tracks: an acoustically tracked sea lamprey (*Petromyzon marinus*) and a GPS collared wolf (*Canis lupus*). We look critically at the strengths and weaknesses of each method, paying particular attention to the statistical and biological assumptions, technical aspects of implementation and the complexity of the outcomes. In

**Table 1.** Summary table of four broad categories of behavioural movement analysis methods. The four methods implemented in this paper and the most directly relevant references are bold faced. All of the entries in the last category can be considered multistate random walks, hidden Markov models or state space models

Category	Method	References
Metric-based	Fractal analysis	Fritz, Said & Weimerskirch (2003), Laidre <i>et al.</i> (2004)
	Tortuosity measures	Nams & Bourgeois (2004); Tremblay, Roberts & Costa (2007)
	<b>First passage time (FPT)</b>	Bovet & Benhamou (1988); Benhamou (2004)
	Residence time (RT)	<b>Fauchald &amp; Tveraa (2003)</b>
Classification and segmentation	Penalized contrasts	Barraquand & Benhamou (2008)
	<b>Bayesian partitioning (BPMM)</b>	Lavielle (2005), Calenge (2006)
	k-clustering	<b>Calenge (2006)</b>
	RT (segmentation step)	van Moorter <i>et al.</i> (2010)
Phenomenological time-series analysis	Autocorrelation functions	Barraquand & Benhamou (2008)
	<b>Change point analysis (BCPA)</b>	Boyce <i>et al.</i> (2010)
	Wavelet	<b>Gurarie, Andrews &amp; Laidre (2009), Gurarie (2013)</b>
		Kranstauber <i>et al.</i> (2012)
Mechanistic movement modelling	<b>Multistate random walk (MRW)</b>	Polansky <i>et al.</i> (2010)
	Ignoring location error	<b>Morales <i>et al.</i> (2004)</b>
	Accounting for error	Forester <i>et al.</i> (2007), Langrock <i>et al.</i> (2012)
		Patterson <i>et al.</i> (2008), McClintock <i>et al.</i> (2012)
		Jonsen <i>et al.</i> (2013), Breed <i>et al.</i> (2012)

both of the case studies, the focal individual is one of several dozens or even hundreds of similarly tracked individuals. We therefore also consider the feasibility of applying the analyses to a large number of individuals – necessary for bridging movement ecology with population processes (Morales *et al.* 2010).

## Materials and methods

Movement analysis tools vary widely in the underlying mathematical and statistical methods, the treatment of variables and the nature of the questions they address, making it difficult to classify them with respect to method or application. However, they can be broadly categorized with respect to the analytical traditions they have inherited. Thus, *metric-based methods*, inspired by geometric analyses of one-dimensional curves, include such tools as fractal analysis, first passage time (FPT) and various tortuosity measures, all of which compute a metric of wigginess or intensity of local area use along a track. *Classification methods*, with origins in machine learning, apply clustering algorithms and selection criteria to determine the number of partitions a data set can parsimoniously be subdivided into. *Phenomenological methods*, such as behavioural change point analysis, wavelet and decomposition analyses, identify the structure or periodicity of movement paths adapting techniques with origins in time series and signal processing. *Mechanistic movement models* include the large family of mixed random walk, hidden Markov and state space models that all have as a goal to estimate transitions between states in a statistical framework derived from the generalized mixed modelling tradition. It is worth noting that these analyses are not primarily designed to be exploratory in nature but, by virtue of fitting a full model of movement behaviour, are meant to address explanatory questions. A non-exhaustive list of references for each of these categories is provided in Table 1.

In keeping with this categorization, we applied the following methods: FPT (*metric-based* method), Bayesian partitioning of Markov models (BPMM – *classification*), behavioural change point analysis (BCPA – *phenomenological*) and a multistate random walk model (MRW – *mechanistic*). In each case, we stayed as close to possible to the most straightforward implementation. The analyses we implement are purely exploratory and strictly limited to location and time data, focused on the shared goal of identifying times, locations and features of important changes in movement behaviour with no ancillary covariates. We neglect issues of observation error, which are negligible for the data we analyse. We emphasize that each of these methods has been refined and expanded in various actual applications, and in almost no case is the movement-only exploratory implementation we present the most useful endpoint of an analysis.

The estimating routines and data are bundled into a single R package called WADDLE, which depends on ADEHABITATLT (Calenge 2006), the BCPA package (Gurarie 2013) and a package called MRW for post-processing the multistate random walk fitting. The WADDLE and MRW packages are available as online supplements – ADEHABITATLT and BCPA are available on CRAN. Implementing MRW requires computationally intensive MCMC which we coded in JAGS. The MRW package contains the post-processing and results of the analysis, while the estimating routine itself is provided in the Supporting information.

## ANALYSIS METHODS

### *First passage time*

The FPT is a measure of the time it takes for an individual to enter and leave a circle of fixed radius  $r$  drawn around each location (Fauchald & Tveraa 2003), thereby locally quantifying intensity of space use. If a radius is chosen that is greater than the scale of a restricted area, the FPT is much higher within the restricted area and low when the animal is moving. In more advanced applications, the FPT is used to quantify characteristic spatial scales of area restricted behaviour by computing the radius at which the variance of the FPT is maximized (Fauchald & Tveraa 2003). A closely related metric, the residence time (RT), similarly computes the amount of time an animal spends within a given radius, but allows the individual to leave and return within a prescribed time window as well (Barraquand & Benhamou 2008).

There is only one free parameter: the radius  $r$ , which we chose in all cases by inspection. There are no assumptions related to the underlying movement model except that the behaviours of interest are characterized by intensity of spatial use. The FPT is insensitive to irregularly collected data as long as the passage times are generally larger than the sampling interval. The output is simply the FPT at every point along the track: more intense spatial use is reflected as a plateau at higher FPT, whereas more transient movements have smaller and often more variable FPT. The FPT (and related RT) are purely visual tools. Some *post hoc* analysis is required in order to partition the resulting analysis into behavioral phases. In examples below, we implement an *ad hoc* separation of Gaussian models, though much more sophisticated partitioning algorithms can be implemented as well (e.g. Barraquand and Benhamou 2008).

### *Bayesian partitioning of Markov models*

The BPMM is a classification approach originally developed to partition DNA sequences (Guéguen 2001). The method assumes that the movement (or, more precisely, some ordered sequence of data derived from the movement) is composed of a discrete number of homogeneous processes (candidate models) and that the transition between these models is Markovian. The algorithm uses a randomized likelihood-based method to choose the number of candidate models and partitions the time series into a specific sequence of those models (Guéguen 2009). For more details, see (Guéguen 2001, 2009) and the ADEHABITATLT documentation (Calenge 2006).

Applying this segmentation to animal movement data requires several initializing steps: (i) the data need to be regularized via subsampling or imputation of gaps, (ii) a movement variable for analysis needs to be selected (typically, step length) and (iii) the set of candidate models needs to be pre-defined (typically, a set of Gaussian models with a range of means and constant variance). Once an optimal number of models is selected, via the randomized likelihood, the track is partitioned and the index of the model for each partition is reported. An important additional assumption is that the step lengths are independent between observations. To assess the assumptions, we produce diagnostic plots, in which we compare the residuals to a standard normal distribution and inspect their autocorrelation function.

### Behavioural change point analysis

The BCPA identifies changes in movement parameter values across a data set by sweeping an analysis window over the time series and locating the most likely change point within each window according to BIC (Gurarie, Andrews & Laidre 2009). As with the BPMM, a response variable needs to be selected –typically the ‘persistence velocity’, or the product of the estimated speed and the cosine of the turning angle. The response variable is modelled as a continuous-time autoregressive Gaussian process with mean ( $\mu_i$ ), standard deviation ( $\sigma_i$ ) and characteristic time-scale ( $\tau_i$ ) of autocorrelation, that is the time at which the autocorrelation drops to a factor of 1/e (Gurarie & Ovaskainen 2011). Sudden or gradual changes in the parameter values are allowed for and a list of significant change points is reported.

The BCPA is meant to be robust to irregularly sampled data and be free of a priori assumptions about the number of states. The output of the analysis is presented in two ways: the *smooth BCPA* returns the estimated parameters for each data point averaged over all the windows, taking the change points and the change point models into account, while the *flat BCPA* finds the most frequently chosen change points and estimates the parameter values within each phase. The flat BCPA assumes homogeneous behaviour between the change points and produces output directly comparable to the BPMM segmentation. The residuals of BCPA can be diagnosed by comparing to the standard normal distribution. Note, the use of the characteristic time-scale and the flat BCPA are innovations on the original approach that have been implemented in the *bcpa* package (Gurarie 2013) available on CRAN.

There are two important tuning parameters to the BCPA: the sensitivity parameter  $K$  modifies the penalty for extra parameters on the BIC and is selected by inspection, and the window size  $w$ , which should correspond to the temporal scale over which the biologically relevant change point might occur and include  $>20$  points. The clustering width of change points in the flat BCPA also effects the results as a wider range will pool more neighbouring changes into a single change point.

### Multistate random walk

A MRW model assumes that the animal transitions between several discrete states and that each state is associated with unique parameters of a movement model. The transitions between states can be independent, leading to a simple multistate random walk, or they can be modelled as Markov process with probability  $p_{ij}$  of switching at any time between states  $i$  and  $j$ . Note the latter case falls under the general class of hidden Markov models of animal movement (Morales *et al.* 2004; Jonsen, Myers & Flemming 2005; McClintock *et al.* 2012; Langrock *et al.* 2012), including the state space models which also account for error by including an explicit observation term (Patterson *et al.* 2008; Jonsen *et al.* 2013).

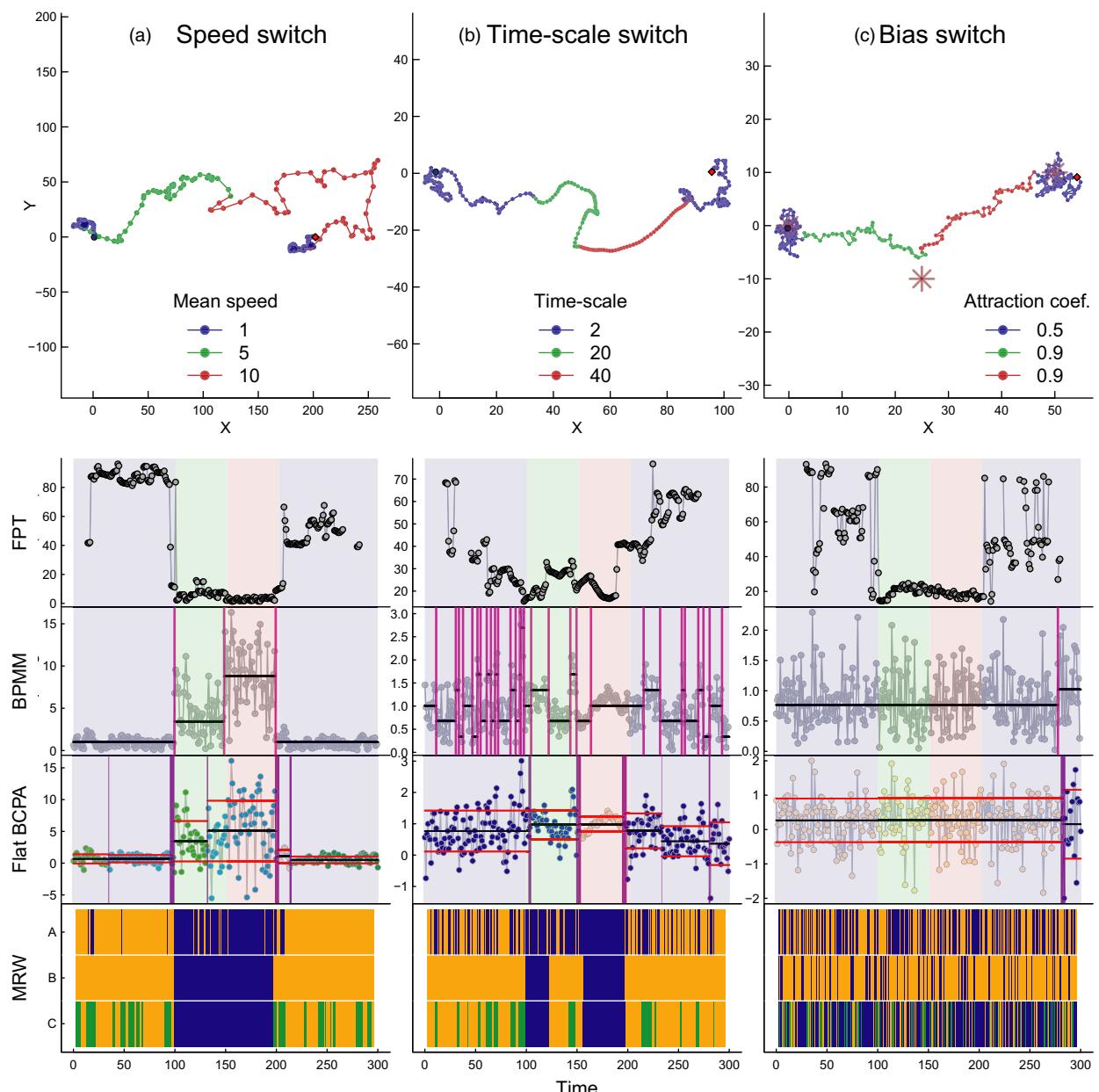
The most commonly used movement model within a given state is the correlated random walk (CRW) in which the turning angles are assumed to be drawn from some circular distribution, and step lengths are assumed to be drawn from some unimodal positive distribution (Kareiva & Shigesada 1983). Following closely the analysis of elk (*Cervus elaphus*) in Morales *et al.* (2004), turning angles were modelled as a wrapped Cauchy distribution with mean 0 and clustering coefficient  $-1 < \kappa < 1$  (where  $\kappa = 0$  corresponds to uncorrelated steps,  $\kappa = 1$  to linear movement in previous direction and  $\kappa = -1$  to perfectly back-and-forth movements); step lengths were assumed to come from a Weibull

distribution with shape and scale parameters  $\alpha$  and  $\beta$ . We fitted three models to the data: a two-state (model A), a two-state switching (B) and a three-state switching (C). The models were fitted using Bayesian MCMC implemented with JAGS and R using the *rJAGS* (Plummer 2013) and *R2JAGS* (Su & Yajima 2012) packages. We used a thinned set of two chains and reported the mode of the state attributed to each movement step. The final fitted models were compared using deviance information criteria (DIC).

Fitting this MRW requires a temporal regularization of the data, a strict *a priori* enumeration of the number of states, and specification of the movement model. Because a linear interpolation across a wide gap in the data introduces a series of zero turning angles and constant step lengths, an interpolation interval no smaller than half the largest gap is recommended (Bovet & Benhamou 1988). Alternatively, the missing locations can be integrated over during the fitting of the MRW model (Jonsen, Myers & Flemming 2005). Otherwise there are no tuning parameters, although, as with all Bayesian MCMC model fitting, some diagnostic exploration is required to determine the required length of the MCMC chains, the extent of the thinning and whether the chains have converged. We used the *coda* package (Plummer *et al.* 2006) for post-processing of the JAGS output and include routines for post-processing and visualizing the model output in the *mrw* package and accompanying vignette (see supplementary materials).

**Table 2.** Parameters for the three simulated tracks illustrated in Fig. 1. Simulations I and II are based on the continuous-time correlated velocity movement (CVM) model specified in terms of the mean speed ( $v$ ) and the characteristic time-scale of autocorrelation ( $\tau$ ): smaller values of  $\tau$  indicate more tortuous movements, larger values indicate more linear movements. In the first simulation, the velocity changes from low, to high, to higher, to low again; in the second, the time-scale changes from low, to high, to higher, and back to low. Simulation III is based on a discrete biased correlated random walk (BCRW), where the step-length parameters  $\alpha$  and  $\beta$  are the shape and scale parameters of the Weibull distribution and,  $\kappa$  is the concentration parameter of the wrapped Cauchy turning angle. The bias of the CRW in this simulation is generated by having the expected mean of the turning angle distribution be a weighted average of the direction towards the given attraction point, with the weight given by the attraction strength. In this simulation, the concentration parameter and the step-length parameters are constant throughout, while the attraction strength is greater during the second and third phases. For more details on the simulation algorithms, see Appendix S1A (Supporting information)

Phase (time period)	I (1–100)	II (100–150)	III (150–200)	IV (200–300)
<b>Simulation I: velocity switch CVM</b>				
Tortuosity	$\tau = 2$	–	–	–
Mean speed	$v = 1$	5	10	1
<b>Simulation II: time-scale switch CVM</b>				
Tortuosity	$\tau = 2$	20	40	2
Mean speed	$v = 1$	–	–	–
<b>Simulation III: home-range switch BCRW</b>				
Step lengths	$\alpha = 2, \beta = 1$ (mean = 0.886)	–	–	–
Turning angles	$\kappa = 0.5$	–	–	–
Attraction strength	$A = 0.5$	0.9	0.9	0.5
Attraction point	(0, 0)	(25, -10)	(50, 10)	(50, 10)



**Fig. 1.** Simulated tracks (top panels) and results of change point analyses. In the tracks, dark blue indicates the first and last phase, green and red indicate the second and third phase (see Table 2 for parameter values and further details). The analysis results, top to bottom, refer to first passage time (FPT), Bayesian partitioning of Markov models (BPMM), flat behavioural change point analysis (BCPA) and three fitted multistate random walk (MRW) models. Vertical purple bars represent identified change points (BPMM and BCPA). Horizontal black segments represent the estimated mean for the BPMM, and BCPA, the red lines represent the 95% prediction intervals ( $\hat{\mu} \pm 2\hat{\sigma}$ ); the colours indicate estimates of time-scale  $\tau$ , cooler and warmer colours indicating smaller and larger values, that is more and less tortuous movements, respectively. Tuning parameters are listed in Table 3. The background colours represent the four known phases of the original simulations. In the bottom panel, the three strips (top to bottom) represent (a) a two-state model, (b) a two-state model with Markov switching and (c) a three-state switching model. Orange and blue colours represent the most and least ‘intensive’ (i.e. slow and tortuous) states, while green is an intermediate state.

#### MOVEMENT TRACKS

We applied these four methods to three simulated tracks with known behavioural phases and to two animal tracks.

Each of the simulated tracks (Fig. 1a–c) consisted of 300 observations equally spaced in time. In each simulation, a distinct movement parameter changes several times: the speed (velocity

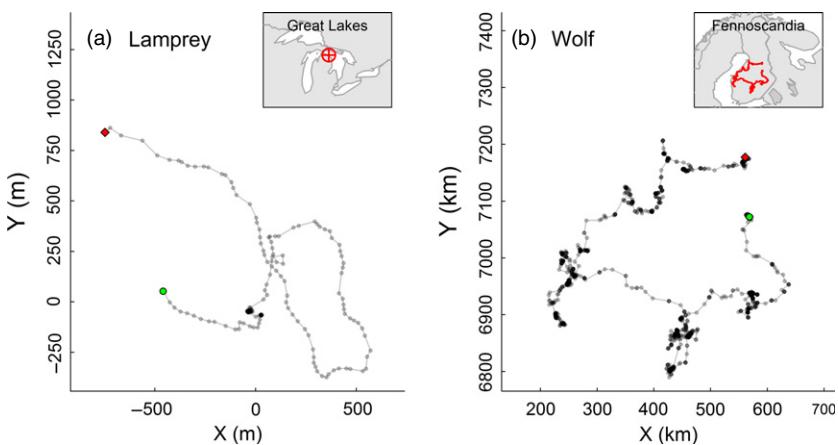
switch model), the tortuosity (time-scale switch model) and the home-ranging behaviour (bias switching model). In all three simulations, the first and fourth phases lasted 100 time units and represented more intensive movement (i.e. slower, more tortuous and strong local attraction, respectively), whereas the middle 100 observations were split between two phases of duration 50 which were more transitional (i.e. faster, less tortuous and strongly

biased, respectively). In all cases, the third phase was less intensive than the second phase. Importantly, the second and third models were generated from processes with constant mean velocity, the first and third models had constant tortuosity regardless of the speed, and the first and second models had no spatial biases. Details on simulating these models are provided in Appendix S1A (Supporting information), parameters are in Table 2, and code to generate the tracks is provided in the WADDLE package with examples in the supplementary material accompanying the package. We performed the analysis on only one, completely arbitrary, realization of each of these processes as an illustrative example, but encourage interested readers to replicate the analyses using the code and examples provided.

The animal tracks (Fig. 2) were well-contrasted by behavioural complexity, spatial and temporal scale, and ecological context. The lamprey acoustic telemetry data (Fig. 2a) consisted of 433 observations over an 11·3 h period, with locations collected approximately once every 1·5 min, with several longer gaps up to 7 min. For all analyses, we performed a simple smoothing of the lamprey data, averaging three subsequent locations. This smoothing was required despite the high precision of the hydroacoustic device used (Meckley *et al.* 2014b), the lamprey spent some of the time essentially immobile, making even small errors significant. The lamprey was a female engaging in a terminal reproductive migration, seeking a spawning stream as it moved along the coastline of Lake Huron near Millersburg, Michigan, USA.

The second track is of a GPS collared wolf from Finland followed over a 316-day period in 2005. The raw GPS data were sampled at 4-h intervals, but because the key ecological questions had to do with the annually scaled transitions between dispersive and settled behaviours (see Discussion), we were not interested in the strong diel patterns of wolf activity. We therefore averaged daily locations in all analyses. The wolf was a wide-ranging disperser that left its natal pack in March and followed an irregular loop with an approximately 410 km maximum extent east–west and north–south (Fig. 2b). At several locations along its track, the wolf appeared to settle into spatially constrained behaviours we refer to as ‘pseudo-territorial’ modes before switching back to a ‘dispersive’ behaviour.

Additional details on the ecological and management context and methods of data collection for lamprey and wolf data are provided in Appendix S1B (Supporting information). See also (Vrieze, Bergstedt & Sorensen 2011; Meckley *et al.* 2014a) for details on the lamprey migration study and (Kojola *et al.* 2006) for aspects of the wolf dispersal study.



User settings for all analyses were selected by informed inspection, as discussed in the Results and Discussion sections below and, in greater detail, in the supplementary materials, with the final selected values are listed in Table 3. A post hoc segmentation of the FPT results was obtained by visual inspection in the more trivial lamprey case. In the wolf case, we segmented the FPT by fitting a Gaussian mixture model (McLachlan & Peel 2000), using a bootstrapped likelihood to select the number of models, and segmenting the final FPT time series whenever it transitioned from one mode to another. This segmentation was performed using the MIXTOOL package in R (Benaglia *et al.* 2009).

## Results

Because of the complexity of the results and the intrinsic differences in the output, the results of the analyses are best compared visually: as parallel time series (Figs 1, 3 and 4) and as colour-coded path plots (Fig. 5). Additional details, including diagnostic plots, summary tables and reproducible examples of the analyses, are included in the supplementary materials.

### SIMULATION STUDY

Each of the methods did an excellent job of identifying the change between low and high velocities in the first simulation (Fig. 1, left panels). Notably, the BPMM (applied to the log of velocity) picked out the four phases exactly at the true break points – the only method among all simulations to score ‘perfectly’. The BCPA did a poorer job of capturing the more subtle middle transition, likely because the persistence velocity at a relatively high tortuosity dilutes some of the difference in the speeds. It also, characteristically, picked up some more subtle changes within the slower phases. The MRW, similarly, very clearly separates the two intensive phases (orange vs. blue colours in Fig. 1), with the two-state switching model (B). However, the three-state switching model (C), which was most similar to the ‘correct’ model, did not pick out the difference between the two intermediate fast phases, but rather structured the slower phases with additional transitions, similar to the BCPA. The lowest DIC was for the

**Fig. 2.** Tracks analysed for the paper: (a) lamprey in the Lake Huron (see inset) and (b) wolf in Finland (see inset). Green circles and red diamonds indicate the beginning and end of each track.

**Table 3.** User choices and settings for each of four methods and five data sets.  $s$  refers to step length,  $|v|$  refers to estimated speed (step length divided by time interval), and  $\theta$  to turning angles

Method	Setting	Data		
		Simulations	Lamprey	Wolf
First passage time	Radius ( $r$ )	10	20 m	10 km
Bayesian partitioning of Markov models	Response variable	log ( $s$ )	$s$	log ( $s$ )
	n models	10	10	20
	SD per model	0.5	0.125 m	1 km
Behavioural change point analysis	Response variable		$ v  \cos (\theta)$	
	Window size	30	30	20
	Sensitivity ( $K$ )	1	0.5	1
	Cluster width	3	3 min	3 days
Multistate random walk	Regularization	—	2 min	1 day

two-state switching model (5003), compared to 5034 for the three-state switching and the 5323 for the two-state model.

In the second simulation (Fig. 1, middle panels), the FPT is fairly uninformative, and the BPMM is incapable of picking out the correct changes. It is notable that in selecting the total number of segments with these data (where the mean velocity did not change), the BPMM ended up trying to fit far too many (over 20) short segments. The BCPA accurately detected the change points for all three major transitions, as expected, since it explicitly makes use of autocorrelation information. The MRW did somewhat worse than for the first simulation; the two-state model alternating too often between the states, and the two-state switching model mainly identifying the most directionally persistent phase and splitting the intermediate phase, providing the ‘tidiest’ result in this case, and the three-state switch again missing the nature of the intermediate state. Again, this can largely be attributed to the intrinsic autocorrelation in this model, not just in the step lengths but also in the turning angles. Once again, the two-state switch model had the lowest DIC (4219) compared to 4287 and 4485 for the three-state switching and two-state model, respectively.

The third simulation (Fig. 1, right panels) was specifically designed to foil the BPMM, BCPA and MRW by having a model where speeds and tortuosity remain constant. Indeed, none of the velocity- or step-length-based methods reveal any intrinsic structure. Only the FPT separates, roughly, the home-ranging phases. Note that the BPMM suggested only one break (compared to the 20 in the time-scale simulation). This is a consequence of the fact that the actual step lengths here were drawn independently, whereas the second simulation used an intrinsically autocorrelated model for speeds.

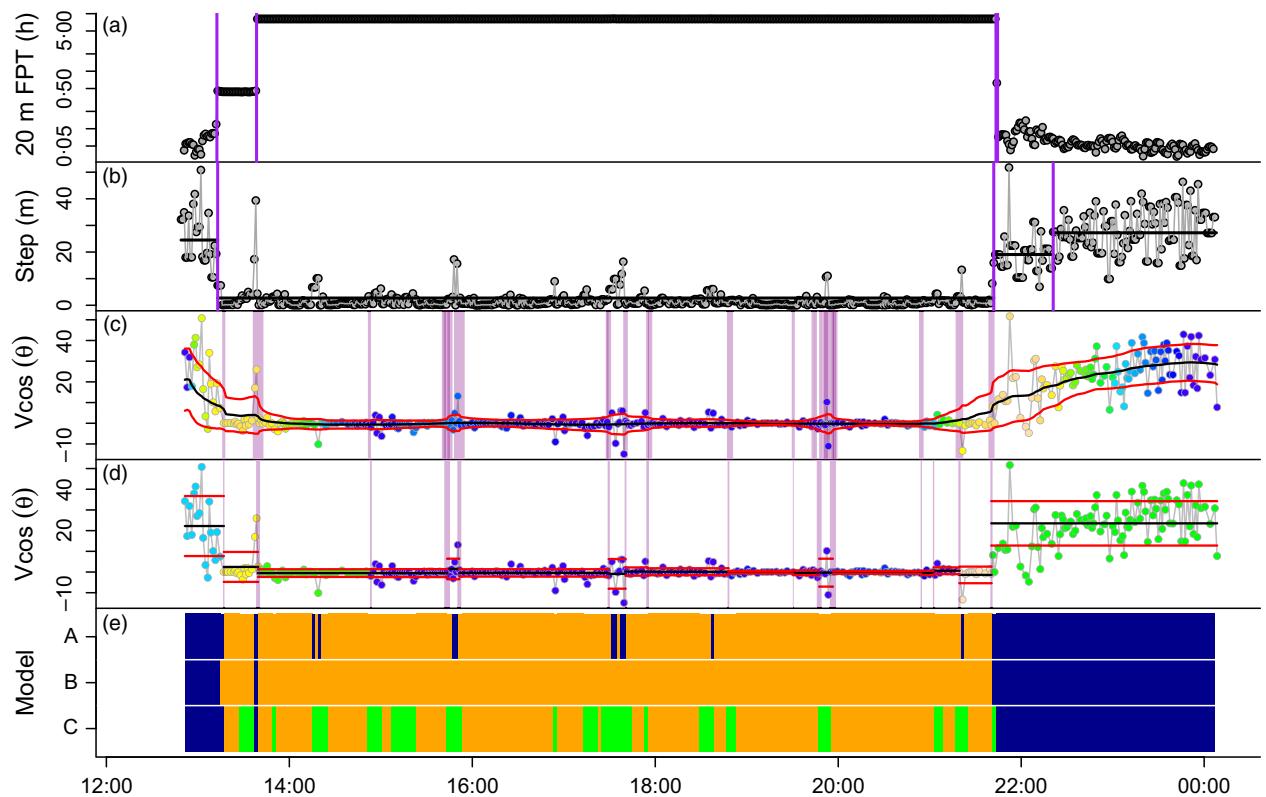
#### LAMPREY

The lamprey’s movement phases were consistently summarized by all four methods (Fig. 3). The lamprey settled within an hour of being released at 12:50, spent the

daylight hours at the water bottom in a ‘settled’ state and started swimming again at 21:42. The transition from being settled to swimming was identified exactly and identically by all methods. The 20 m FPT analysis (see supplementary material for results of the FPT for other radii) suggested an intermediate ‘settling’ phase between 13:13 and 13:38 (Fig. 3a), thus four phases in total. The BPMM also suggested four partitions, but rather than pick out the ‘settling’, identified an intermediate ‘rising’ phase between 21:42 and 22:21 (Fig. 3b). It should be noted that in the application of the BPMM, the equivariance normality assumption on the distance steps was violated (see diagnostic plots in supplementary materials).

The smooth and flat BCPA analyses (Fig. 3c,d) also pointed out a ‘settling’ phase but no ‘rising’ phase; however, the smooth BCPA suggested that the speed change is somewhat gradual while settling and rising. The BCPA additionally indicated that the changes were significant in mean and standard deviation, but not time-scale. It is notable that the BCPA once again articulated finer structure in the change points during the settled phase that neither the FPT nor the BPMM identified. A phase plot of the BCPA (Fig. S1) suggests that the transitions from swimming to settling and from settled to swimming follow a very similar trajectory, with a period of highly correlated movement and moderate speed. At some point, while elevating to swim, the lamprey began a faster and more tortuous behaviour than at the beginning of the track, which may have been related to a searching or sampling behaviour before selecting a direction to swim.

The fits of the three MRW models are presented as colour-coded horizontal bars (Fig. 3e, values in Appendix S1C, Supporting information). The two-state model (A) picked out several apparent bouts of activity during the settled phase at times similar to the BCPA, whereas the two-state switching model (B) assigned the entire settled period (13:14 to 21:40) to a single state with one brief exception (13:36 to 13:38). The three-way switching model identifies an active swimming phase and two phases within the settled phase, also largely agreeing with the



**Fig. 3.** Results of (a) first passage time (FPT), (b) Bayesian partitioning of Markov models (BPMM), (c) smooth behavioural change point analysis (BCPA), (d) flat BCPA and (e) multistate random walk (MRW) analysis for the lamprey. Vertical purple bars represent selected change points (a–d). Horizontal black lines represents the estimated mean (b–d), in (c) and (d) red lines represent the 95% prediction intervals ( $\hat{\mu} \pm 2\hat{\sigma}$ ); colours as in Fig. 1. In (e), as in Fig. 1, orange, green and blue are the slowest, intermediate and fastest states, respectively.

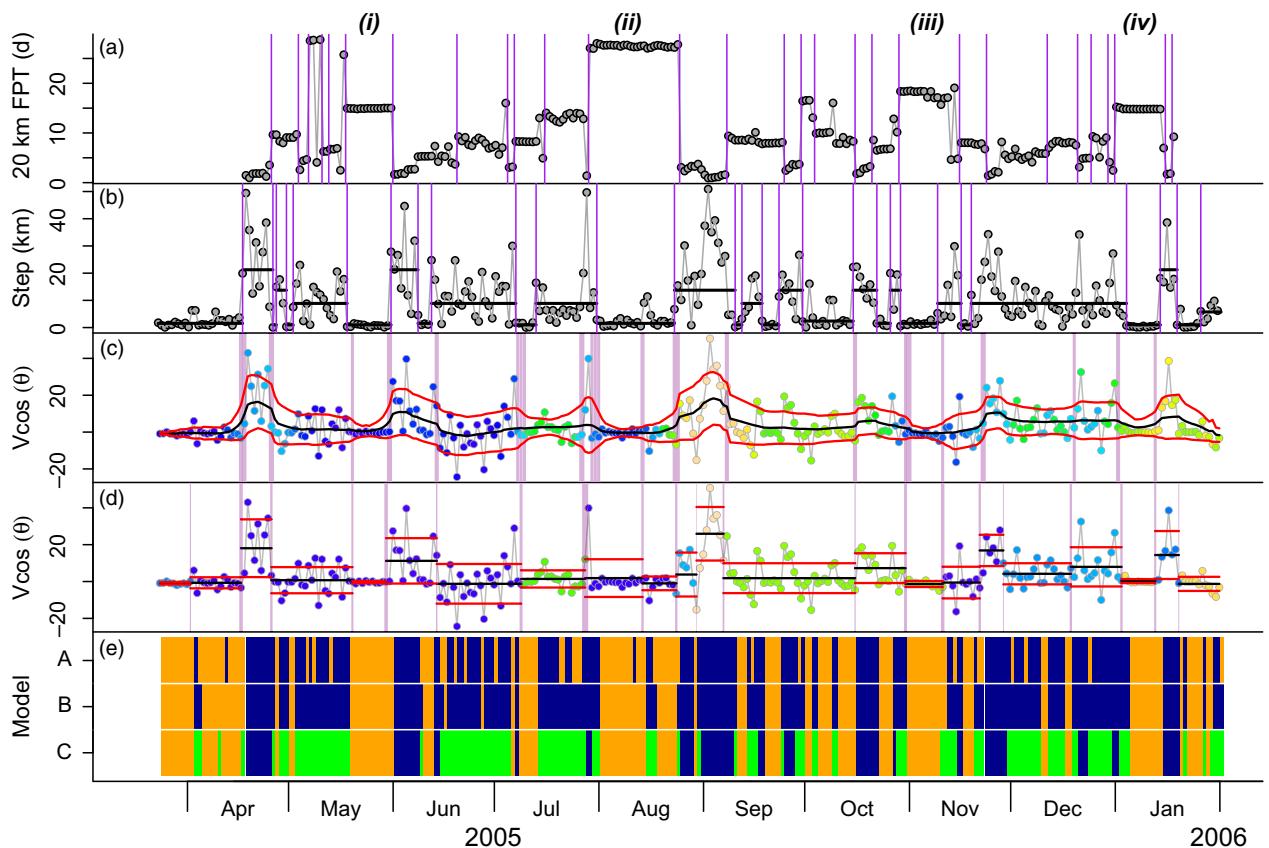
BCPA. The three-state switching model had the lowest DIC (6569, compared to 6607 and 6772 for models B and A, respectively).

#### WOLF

We selected a radius of 20 km for the wolf FPT (Figs 4a and 5a), consistent with the observation that typical wolf territories in Finland are 40 km in diameter (Gurarie *et al.* 2011). The magnitude of the 20 km FPT ranged from 0.92 to 29 days with several clear plateaus, suggesting discrete transitions between more and less intense space use. The parametric bootstrap of Gaussian mixtures suggested a four component mixture with means  $\hat{\mu} = \{3.5, 8.2, 15.3, 27.6\}$ , standard deviations:  $\hat{\sigma} = \{1.7, 1.0, 1.8, 0.54\}$  and weights  $\hat{\lambda} = \{0.32, 0.33, 0.23, 0.11\}$ . We used these modes to obtain breaks at 6.5, 11 and 24.5 FPT and used these as cut-offs to identify shifts between the four possible phases (vertical lines in Fig. 4a). The final analysis identified 30 partitions, including several area-intensive plateaus corresponding to a spatially more intensive phase. The longest plateau was in August (labelled *iii* in Fig. 5), while three other roughly 2 week bouts between May 19 – Jun 1, Oct 31 – Nov 16 and Jan 2 – Jan 16 (labelled *i*, *iii* and *iv*) are

also identifiable. Several shorter (roughly 1 week) plateaus are interspersed, as well as more clearly transitory movements. Of the 276 days, 84 could be considered dispersive based on the modal classification of states. Note that the FPT excluded the first 26 observations and the last 14 observations because the track began and ended with spatially constrained phases and the FPT cannot compute the passage time out of locations before the beginning and after the end of the observations.

The BPMM (Figs 4b and 5b) subdivided the wolf data into 29 partitions (similar to the FPT), each associated with one of eight different means (labelled M1–M8) for daily step length, ranging from 5 to 50 km. For example, the initial territorial phase of the wolf's movement was classified as M1 for 27 days, until it switched on April 17 to M8, for 10 days, corresponding to the initial dispersal from the home territory. Throughout, there was close corroboration between the FPT plateaus and the selection of M1 and M2, corresponding to the enumerated bouts (*i*–*iv*). Conversely when the FPT is lower, higher mean step lengths were typically selected. The FPT identified more structure within many of the dispersive phases, picking out mixed dispersals of longer steps, some very short bouts of long distance movement separating otherwise highly area restricted movements. For example, the



**Fig. 4.** Analysis results for wolf data (see Fig. 3).

extended clusters *i* and *ii* contain short transitions between the centrally area-intensive locations identified in the FPT.

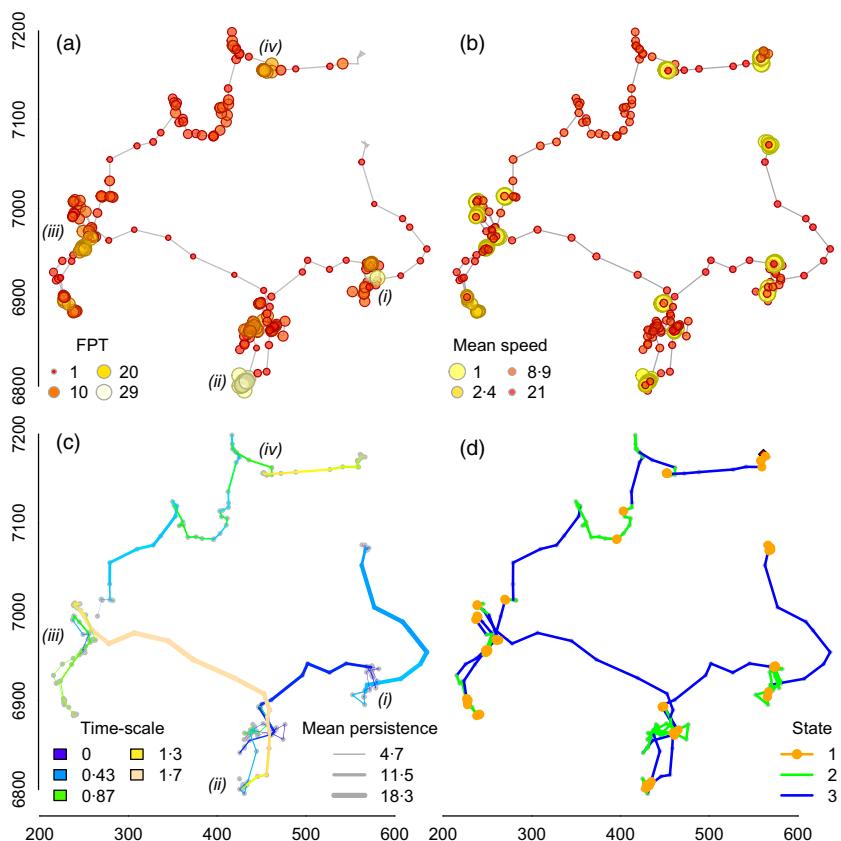
Both the smooth BCPA (Figs 4c and 5c) and flat BCPA (Fig. 4d) partitioned the wolf movement with 20–22 partitions, somewhat fewer than the FPT and BPMM, though this was, in part, a consequence of the selected settings. The intensive area use clusters were clearly marked out as having low mean persistence velocity and variance. For example, the four bouts *i*–*iv* had mean persistence speeds between  $-1.3$  and  $0.2 \text{ km day}^{-1}$ , compared to an overall mean persistence speed (weighted by duration of the phase) of  $3.64 \text{ km day}^{-1}$ , with a maximum peak up to  $25.9 \text{ km day}^{-1}$  in the first week of September. The BCPA partitions were at times less finely resolved than the BPMM, for example a single period in the BCPA covering most of September and October (in green) contained several active and inactive bouts in the BPMM. In a few places, differences were picked out that other methods missed, for example in the transitional period between *iii* and *iv*. The added dimension of characteristic time-scale (cooler colours) indicated transitional phases that were much more correlated than others, for example the rapid linear transition between cluster *ii* and *iii*, but also the much slower but highly correlated transition between cluster *iv* and the final location.

Many of the state switches identified by the MRW were consistent between models as well as with other analysis

methods (Figs 4e and 5d, see also Appendix S1C, Supporting information). All three MRW models identified the first territorial period at cluster *i* as the least active state. The September–October activity switched from high to low several times, with the three-state switching model (C) assigning a subset of these to the intermediate third state. These demarcations aligned most closely to the BPMM partitioning. The two-state switch model had the lowest DIC (6514 compared to 6599 and 6688 for three-state switching and simple two-state, respectively). The mean daily displacement for the three wolf states were  $1.2$ ,  $9.1$  and  $21.1 \text{ km}$ , while the  $\kappa$  values were  $0.4$ ,  $0.1$  and  $0.6$ , respectively (Table 4 in Appendix S1C, Supporting information), suggesting that state 2 was qualitatively quite different from the high-speed-directed dispersal: of intermediate step length, but much less correlated than even the slowest state.

## Discussion

The ability to identify behavioural changes in a movement track based purely on location and time coordinates can be of great utility when first exploring animal movement data. The analyses here point to various advantages and potential pitfalls of several of the more accessible and commonly used tools. Below, we compare the methods broadly, encouraging the interested reader to replicate the



**Fig. 5.** Path plots for wolf analyses: (a) first passage time (FPT) – with larger and paler circles representing higher FPTs, (b) Bayesian partitioning of Markov models (BPMM) – with larger and paler circles representing slower mean velocities, (c) smooth behavioural change point analysis (BCPA), pale colours are higher characteristic time-scales and thicker lines are higher mean persistence velocity, and (d) three-state switching multistate random walk (MRW), the slowest state is denoted with orange dots and the two movement states in blue and green segments. The letters (i–iv) denote the locations of the four spatially intensive (pseudo-territorial) phases referred to in the text and Fig. 4.

analyses with the help of the supplementary materials. We discuss the reasons for failures in the simulation study, link the results of the animal track analyses to relevant ecological questions and conclude with general comments on combining strategies and tools for exploratory analysis.

#### RISKS OF MISSPECIFICATION

The analysis of the simulated data raised several red flags with respect to appropriate use of the methods. Most importantly, it underlined the importance of being aware of what variable each method analyses, the effect of model misspecification and the importance of diagnosing and examining the assumptions.

It is unsurprising that all methods performed admirably in the velocity change simulation. The FPT measures the time it takes to leave a radius – that is a speed – and the other three methods model organism-centric variables related to velocity. The BPMM in particular, which only analyses speed, identified the exact partitioning along with a correct calculation of the number of phases. In both of the other simulations, however, the BPMM failed utterly. In the time-scale shift simulation, the BPMM selected far too many phases. This was due to the fact that in a correlated movement process, the speeds tend to vary over subsequent observations, violating the underlying assumption of independent step lengths between observations. This is analogous to the type II error when estimating linear

models with non-independent data. For the last model, where all step lengths were explicitly drawn from the same serially uncorrelated independent Weibull distribution, the BPMM detected no changes, a result that is ‘correct’ for the speeds, but completely failing to detect the home-ranging behaviour.

The two-state MRWs were, obviously, not able to fit the three-state process of the simulation. However, we expected the three-state MRW to correctly identify the changes in the first two simulations since the process that generated the tracks (the continuous correlated velocity movement) was similar to the discrete correlated random walk that the MRW estimates. In fact, the three-state model failed to identify the intermediate switch in the velocity model completely and made poor assignments in the time-scale switch model, preferring in both cases to assign intermediate states to fluctuations in the slow phase. This is mostly explained by the effect of autocorrelation in the velocities, which leads to greater relative fluctuations at slow speeds. We note that the state space model of Jonsen, Myers & Flemming (2005), which fits a discrete correlated random walk in similar contexts, does account for autocorrelation in the step lengths and turning angles.

The BCPA outperformed all other methods in the time-scale simulation by explicitly including autocorrelation in its determination of behavioural changes, underlining the importance of accounting for autocorrelation.

Models that assume independence are highly susceptible to false inference (e.g. the BPMM and MRW), an issue compounded by the increasingly high temporal resolutions at which modern movement data collection occurs. It is straightforward to assess whether a step length or turning angle is autocorrelated; it suffices to inspect an empirical autocorrelation function of these variables (as illustrated in the supplementary materials). Additionally, the time-scale estimated by a method like the BCPA provides a direct estimate of the temporal scale of the autocorrelation. For example, the time-scale of the wolf's movements range from 0.025 to 1.8 days (median 0.52, IQR 0.23–0.91), for data sampled once daily. Thus, there can be some concern about spurious changes detected when applying those methods. In contrast, the lamprey track exhibited estimated time-scales (median 0.26 min, IQR 0.016–0.83) that were generally smaller than the principal time interval of 1.5 min and therefore less likely to cause spurious change point assignments.

Most striking, though not surprising, all three velocity-based methods fail completely in the third simulation (home-ranging), where the behavioural switch is defined not in terms of the parameters of velocity but in terms of absolute spatial biases. Spatial awareness and memory is a fundamental property of movement (Fagan *et al.* 2013), perhaps the clearest example of this is seasonal migration where seasonally constrained behaviour turns into a long-range directed behaviour. The FPT is the lone method which quantifies intensity of absolute space use regardless of mechanism and is therefore the only one of these tools which picks up behavioural changes which are determined with respect to absolute spatial quantities. Clearly, the lack of absolute spatial information is crippling to the purely relative velocity-based methods. Some correctives include estimation of biased correlated random walks Benhamou (2006) and quasi-mechanistic models of migration via mean squared displacement (Borger & Fryxell 2012). Most relevantly, estimation of unknown centres of attraction in context similar to one we used for the simulation here was developed and demonstrated by McClintock *et al.* (2012).

Each of the three simulations were, by design, simplified caricatures of movements observed in nature. In reality, the three attributes of interest (speed, tortuosity and spatial bias) are often closely related. Slower movements are typically also less autocorrelated, as can be seen in the BCPA phase plots of the animal data (Fig. S1). Strongly biased movements, for example during migration, are often more autocorrelated and can be faster. Nonetheless, these cases vividly illustrate the kinds of false inference any method is susceptible to when underlying models are misspecified.

While we highlight model misspecification as the primary culprit in these methods' failings, another potential factor to consider in change point analysis, as for any statistical method that separates signal from noise, is the

magnitude of the changes that are being detected. Beyer *et al.* (2013) thoroughly analyse the ability of Bayesian state space (MRW-type) methods to correctly classify turning angle and step-length distributions with varying degrees of overlap, and many of their general conclusions are applicable to the other methods discussed here. With specific reference to our simulations that the differences between the medium and fast correlated velocity movements (middle two phases) were not sufficiently different to be detected by the MRW method, but a method that does account for the autocorrelation would have no problem detecting those differences. Thus, a more correct movement model will be more likely to detect differences which might otherwise be swamped by the greater net variation associated with autocorrelated processes.

The obverse risk in change point analysis is the risk of detecting spurious changes, i.e. false positives. These can, also, be related to model misspecification, for example in the very large number of phases predicted by the velocity BPMM for the time-change shifting simulation. On the other hand, a method like the BCPA intrinsically comes with several 'knobs' that effect the sensitivity of the results. There is no single, automated way to know what that sensitivity should be as many of those decisions have to do with the scale of the structure of interest and should be guided by biological considerations, as we discuss below. But settings can be experimented with to bring out the behavioural profile of greatest interest, much as one sets the focal length, exposure and sensitivity on a camera.

#### UNIFYING METHODS

It bears reiterating that each of the methods that we have presented here represent the most simple applications, mainly reflecting the way in which they were first presented in the literature, and, consequently, that are most convenient for out-of-the-box implementation. In fact, the BPMM, BCPA and MRW are all based on an underlying likelihood that can be adapted to accommodate process-based models. We have stated that the MRW is the only one of these methods that estimates a mechanistic movement model or that can incorporate covariates. But both the BPMM and BCPA, in principle, can combine two or more dimensional time series into a single likelihood, including the same discrete CRW that underlies the MRW, and add additional parameters that include dependencies on covariates. Similarly, the direct estimation of autocorrelation that is built into the BCPA can be included in the BPMM or MRW framework. Thus, the flexibility of the chosen approach may be an important feature when selecting an exploratory technique, especially if subsequent and highly related analyses are anticipated.

An important goal of future method development should be to adapt these tools to movement models that (a) incorporate auto- and cross-correlation in the movement variables, or, better yet, that are intrinsically continuous and

thus robust to sampling as in Johnson *et al.* (2008), Gurarie & Ovaskainen (2011), Fleming *et al.* (2014), and (b) incorporate absolute spatial information, for example centres of attraction and advective biases, as in McClintock *et al.* (2012). Accounting for both sudden and smooth variation in parameter values, as in the BCPA, is another desirable quantity. A final very important aspect of movement behaviour that we have not touched on in this paper is the near universal diel and seasonal variation in activity observed in animals (Polansky *et al.* 2010). Most of the fundamental methodological groundwork for more sophisticated mechanistic movement models has been done, and these are, in principle, applicable within the framework of any of these methods. Unfortunately, for the time being, these features have not been implemented or integrated jointly in ways that are accessible to practitioners lacking advanced statistical programming skills.

The fundamental difference between these three methods, then, is not in the underlying movement models but in the way in which the changes in the underlying models are inferred. We might draw a line from the FPT, which is descriptive in a way that is essentially divorced from process; to the BCPA, which is descriptive in a more detailed and process-oriented way, but based on a very local sweeping-window analysis; to the BPMM, which assesses the entire track simultaneously to suggest a fixed number of modes and a fixed number of phases; and to the MRW which, while drastically fixing the number of modes, assigns a full probabilistic process to the transitions. In this sequence, the methods are decreasingly descriptive and increasingly ‘modelled’, that is potentially predictive.

Moving from behavioural exploration to actual *predictive modelling* for movement is, however, the most tenuous and difficult step. A fully parameterized movement model, as described above, is minimally required. The ability to explicitly incorporate absolutely spatial information is an extremely important innovation (McClintock *et al.* 2012), as is the incorporation of continuous-time autocorrelation (Johnson *et al.* 2008). However, it should be clear that even a very well parameterized and behaviourally sophisticated model will still necessarily be naive and perhaps most useful as a null-model against which to explore higher order effects such as interactions among individuals (Delgado *et al.* 2014) or spatial memory (Fagan *et al.* 2013).

#### LINKING QUESTIONS TO METHODS

The extent to which a particular tool is appropriate for answering the broad *What is the animal doing?* question depends on the specifics and goals of a given project. We advocate an approach to movement analysis that is adaptive, iterative and contains a relatively high exploratory component, vs. prescriptive and relying on a large number of *a priori* assumptions. In our experience, it is only in the exploration of the deep structure of movement data that

appropriate models and tools can be identified for the testing of hypotheses by fitting models. To illustrate this process, we look closely at the specific insights provided by the analysis of the two animal data sets and discuss the further analyses they inspire.

#### Lamprey analysis

An overarching question motivating the Lake Huron lamprey study is whether their reproductive migrations can be manipulated with pheromonal input into the stream, with the explicit management goal of reducing the productivity of a non-native species that is considered harmful (Meckley *et al.* 2014a). The movement data used here were collected as part of a large-scale experiment in which pheromones were released, with the idea of tracking closely the lampreys’ response. In order to understand the mechanisms by which the pheromones influence behaviour, it is necessary to understand as fully as possible the baseline structure of lamprey movements, including quantifying the diel patterns of settling and swimming. This most basic question of *When are lampreys active?* can be answered by any of the presented methods, though the best suited are the FPT, which is the fastest and the most appropriate for the spatial definition of the ‘settled’ state, and the BPMM can efficiently parse any moving and non-moving phases, especially if it is constrained to just two modes. An objective – and quick – identification of the times and locations of settling and swimming for all the tagged individuals provides data that can be analysed with respect to date, individual and pheromone treatment in a mixed modelling framework.

A higher order question is *What are the behavioural modes of a swimming lamprey as it approaches a potential spawning river?* Modified BCPA-style analysis of the movement has quantified several modes, including a circular sweeping movement, a vertical casting and a directed movement to shore (Meckley *et al.* 2014a, Meckley, pers. comm.). Even in the brief excerpt of the single lamprey analysed here, the BCPA phase plot (Fig. S1) reveals both an uncanny symmetry in the transition to and from the settled state, but also a substantial difference between the swimming mode after (faster, less variable, more correlated) than before the settling. These deeper movement structures reveal signatures that correspond to exploratory vs. directed behaviours that, in turn, can be related to bathymetry, temperature and flow and, ultimately, to the probability and timing of the lamprey attaining the mouth of the spawning stream. It should be noted that the lamprey data, as with much acoustic data on fishes, also come with a *z*-component of depth, the inclusion of which contributes important additional information on movement behaviours.

Once a comprehensive understanding of the movement is obtained, and the patterns are assessed across many individuals, any effect of the treatment of interest (i.e. the pheromone) will be easier to identify. Fitting a process-based model in an MRW-type framework can,

eventually, provide an avenue to testing and comparing the responses of the individual to different cues, but only after the fundamental attributes of the lamprey's behaviour are well understood.

### *Wolf analysis*

The research questions for the wolves are related to the mechanisms and consequences of dispersal. As with the lamprey study, there are many ( $n > 30$ ) other individuals in a larger data set of wolves that have dispersed from their natal territories in Finland. The wolf track has considerably more structure than the lamprey track, though it contains a similar amount of location data points. In particular, it transitioned between dispersive movement and more spatially constrained movement several times, with unique signatures each time and in ways that were more ambiguous to identify than in the lamprey. This complexity is, incidentally, quantified in the MRW transition probabilities: the two-state switching model estimated transition probabilities of 0.22 from slow to fast and 0.15 from fast to slow for the wolf (compared to 0.03 and 0.01 for the lamprey, see Table S1, Supporting Information).

The first order question is *When is the wolf dispersing (or behaving in a 'dispersive' way)?* An *a priori* assigning of two states, as in the MRW models, unfortunately, does not provide a clear separation, suggesting close to 30 transitions even in the more conservative two-state switching model. The clearest signal (as with the lamprey) is derived from the FPT. Based on visual inspection (aided by our somewhat *ad hoc* FPT classification), we might propose a definition of 'pseudo-territorial behaviour' as those portions of the trajectory which remain within a 20 km radius for at least 2 weeks (i.e. the four plateaus identified in Fig. 4, the mean FPT values of which are 15.7, 27.5, 17.8 and 14.9 days, respectively). This functional definition is satisfyingly simple and motivated partially by the biology of the animal. This result can be applied more or less indiscriminately to other dispersing wolves in the data base, and the properties of the areas which are selected for pseudo-territorial behaviour analysed with respect to the other available habitat in Finland, for example with respect to forest types and human land use.

The higher order question of characterizing the transitional (i.e. non-pseudo-territorial) movements relies on interpreting the more organism-specific metrics. Here certain patterns appear consistently, especially in the BCPA profile. For example, after a pseudo-territorial phase, there was typically a transition to a high persistence speed, followed by a period of less correlated and lower persistence speed movement, followed by the subsequent pseudo-territorial phase. This three-step signature, which we might describe as *dispersive* to *exploratory* to *pseudo-territorial* was visible in the sequence of shifts from mid-April to the end of April (dispersive), through May 20 (exploratory), to the end of May (pseudo-territory *i*). It was visible (again, mostly in the BCPA) in each of the

sets of sequences leading up to pseudo-territory *ii* (with an extended exploratory phase), very clearly in the prolonged sequence through September and October preceding *iii* and to a lesser extent preceding *iv*. This exploratory analysis suggests that a mechanistic partitioning might be made that distinguished these three phases, for example in three-state MRW-type framework, but one that better captures the main features of this behavioural mode, for example by a spatially aware movement model. The transitions within a model might then be modelled with relevant covariates and *a priori* hypotheses in mind.

It is important when exploring behavioural changes to compare the time series of analysis output with path plots of the animal movement. When comparing the smooth-BCPA path plot of the wolf (Fig. 5c) to the output time series, it is clear that the putative 'exploratory phases' often involved returning to a previously, recently visited region (note the hairpin turns around *i*, *iii* and *iv*, and the return behaviour after the pseudo-territoriality of *iii*). This signal suggests a cognitive (and game theoretic) trade-off between the risks of further exploring unknown areas or returning to a known quantity. Identifying, exploring and, perhaps, explaining this behaviour in other data sets could yield some insights into the actual cognitive processes underlying dispersal.

### PRACTICAL SUGGESTIONS

Keeping in mind that the goals of movement analysis are very diverse and difficult to generalize, we nonetheless propose several broad principles for exploratory analysis of behavioural changes. Though there are methodological needs, as described above, the following principles are intended for biologists who collect or have access to movement data and have ecological questions, rather than modellers developing novel techniques.

#### *Trust biological intuition*

When fine-tuning an analysis, choosing criteria for classifying behavioural states, or formulating hypotheses based on exploratory analysis, it is important to trust biological intuition. Setting the parameters of an analysis is not an exact science, but a matter of detecting the most interesting patterns to motivate further exploration, much like a photographer selects the zoom, focal length and shutter speed necessary to produce the most informative image. This principle applies as well to the pre-processing of the data, especially in selecting the scale of subsampling and filtering. For example, if changes are occurring on weekly or monthly scale, a daily average of locations (as we used for the wolf data) will be sufficient.

#### *Be aware of the structure of the data*

Perhaps the most important step in movement analysis is thorough, iterative exploration and visualization of the

data with the relevant question in mind. Important concerns specific to movement data include: Are the data highly autocorrelated and/or irregularly sampled? If so, use a method that is robust or accounts for those issues (BCPA), or, if feasible, subsample and regularize the data to minimize autocorrelation and irregularity. Is there significant error in the measurements? If so, consider smoothing, filtering, or extracting the signal via a single-state state space model. Is there unanticipated structure in the behavioural states, or is a simple two- or three-state model appropriate? Inspect these with something like a behavioural phase plot. Are there seasonal patterns? A simple boxplot of activity against time of day or month of year can be highly illuminating (see Polansky *et al.* 2010 for more sophisticated analyses). Plots of simple movement metrics like step lengths against covariates of interest are likely to suggest testable hypothesis at later stages.

#### *Consider feasibility*

Do packages or software tools already exist for implementing an analysis? Spend some time looking for and experimenting with existing tools and exploring the rapidly expanding literature for case studies relevant or similar to your interest. Consider the complexity, utility and computational intensity of any analysis tool. If there are many individuals, the speed and ease of implementation are at an even higher premium. Be parsimonious, and try the simplest techniques (e.g. FPT) first. Attempt complex full-model fitting exercises only with access to good programmers, powerful computers, well-tested assumptions and plenty of time. As a general rule, if feasible, it is much faster to deal with measurement error, for example via smoothing, filtering or averaging, in a pre-processing stage than to estimate the errors while fitting, though this may not be feasible with very large (e.g. ARGOS) errors.

#### *Build your analysis off focal individuals*

If there are many individuals that you would like to study, take a few individuals with high-quality data (i.e. long-time series, good contrasts, few gaps). Fine-tune your behavioural analysis on those individuals, determine the analysis parameter settings that are most informative and use those as a basis for analysing the rest of the population. Hierarchical modelling of multistate movement behaviours for populations is increasingly feasible (Langrock *et al.* 2012; McClintock *et al.* 2013), though, for the time being, only for relatively simple models and small population sizes ( $n < 20$  in both cited examples). For large numbers of individuals, a fast, consistent descriptive summarization of the behavioural structure followed by a comprehensive *post hoc* analysis is the most straightforward strategy for yielding population-level inference.

#### *Be aware of and test assumptions*

Every statistical method comes with certain assumptions, whether distributional or structural. Parametric methods (BPMM, BCPA, MRW) provide a fitted model, and the best way to test distributional assumptions is to examine the residuals. Spurious results are a common consequence of poor agreement to assumptions, as illustrated in the simulation study. For example, fat tails in an assumed Gaussian distribution and autocorrelation in the residuals (in a method that does not take autocorrelation into account) will both lead to proliferation of type I (false positive) errors. Structural assumptions should be explored empirically. For example, to determine the number of states to fit explore the behavioural phase space, or to test a functional relationship between some covariate and a parameter, visualize those potential relationships graphically. Analysis of movement data seems to be a subfield where assumptions are rarely assessed rigorously. For example, in the nearly half-century pedigree of correlated random walk models in ecological literature, we are aware of only one study in which autocorrelation within and between turning angles or step lengths are assessed (Nams 2013).

#### *Assess via simulation*

If there is concern with respect to lack of sensitivity to specific changes (type I error), identification of spurious changes (type II error), robustness to measurement error, or the effect of subsampling or smoothing, it can be useful to simulate a movement process (e.g. building off the templates used in our simulations) that shares some properties (approximate durations, scales, distances and intervals between observations) of the data to be analysed and to assess the respective sensitivity and robustness of the different tools.

#### *Combine tools*

It can often be useful to explore data using different tools, both to see whether the main results are sufficiently robust and to see whether some patterns emerge in an analysis that are obscured in another one. In the wolf example, a spatial analysis of FPT coarsely identifies resident and transient phases, while the closer analysis of the BCPA revealed additional structure. Alternatively, a segmentation or change point analysis can be applied directly to the output of an index-based analysis like the FPT. A good understanding of the assumptions underlying the methods, and the meaning of their outputs, can lead to creative and insightful hybrid analyses.

Getting the most out of movement data requires creativity and persistence. It is hoped that biologists confronted by the wealth of available methodologies will benefit from this discussion of approaches. As complex and at times frustrating as movement data can be to

analyse, the reward is often deep insight into the behaviour of animals in the wild that is obtainable in no other way.

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## Data accessibility

All relevant code is provided in the supplementary materials, and the data used in these analyses made available in the attached R packages (WADDLE, MRW).

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## Supporting Information

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

**Appendix S1.** Additional details on the various simulations and analysis: (A) details on the simulation algorithms used to generate the tracks in Fig. 1, (B) additional background material on the lamprey and wolf studies, and (C) results of the multistate random walk (MRW) analysis of the lamprey and wolf data.

**Appendix S2.** Examples and overview of using the waddle package (the ‘waddle’ vignette) for replication of analysis and results.

**Data S1.** The ‘waddle’ R package source bundle, including functions and data for replicating the simulation and data analyses presented here.

**Data S2.** The ‘mrw’ R package bundles functions for the post-processing and visualization of the JAGS fit to the multistate random walk fits, includes the completed chains for the real and simulated data analysed in the manuscript.

**Table S1.** Parameter estimate means (and standard deviations) for all three multi-state random walk model fits, applied to the two datasets.

**Fig. S1.** Phase plots of smooth behavioural change point analysis (BCPA) for (a) lamprey and (b) wolf.