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From animal tracks to fine-scale movement modes: a straightforward approach for identifying multiple spatial movement patterns

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Summary

1. Thanks to developments in animal tracking technology, detailed data on the movement tracks of individual animals are now attainable for many species. However, straightforward methods to decompose individual tracks into high-resolution, spatial modes are lacking but are essential to understand what an animal is doing.

2. We developed an analytical approach that combines separately validated methods into a straightforward tool for converting animal GPS tracks into short-range movement modes. Our three-step analytical process comprises: (i) decomposing data into separate movement segments using behavioural change point analysis; (ii) defining candidate movement modes and translating them into nonlinear or linear equations between net squared displacement (NSD) and time and (iii) fitting each candidate equation to NSD segments and determining the best-fitting modes using Concordance Criteria, Akaike's Information Criteria and other fine-scale segment characteristics. We illustrate our approach for three sub-adults, male wild boar *Sus scrofa* tracked at 15-min intervals over 4 months using GPS collars. We defined five candidate movement modes based on previously published studies of short-term movements: encamped, ranging, round trips (complete and partial) and wandering.

3. Our approach successfully classified over 80% of the tracks into these movement modes lasting between 5 and 54 h and covering between 300 m to 20 km. Repeated analyses of GPS data resampled at different rates indicated that one positional fix every 3–4 h was sufficient for >70% classification success. Classified modes were consistent with published observations of wild boar movement, further validating our method.

4. The proposed approach advances the status quo by permitting classification into multiple movement modes (where these are adequately discernable from spatial fixes) facilitating analyses at high temporal and spatial resolutions, and is straightforward, largely objective, and without restrictive assumptions, necessary parameterizations or visual interpretation. Thus, it should capture the complexity and variability of tracked animal movement mode for a variety of taxa across a wide range of spatial and temporal scales.

Key-words: behavioural change point analysis, fine-scale movement, FlexParamCurve, GPS tracks, net squared displacement, spatial patterns, wild boar

Introduction

Tracking animal movements are broadly utilized by many disciplines to solve various ecological problems, from developing effective conservation efforts for endangered species (Cooke 2008) to defining appropriate control measures for pest species (Adams *et al.* 2013). Recent technological advances make it possible to collect vast time series of animal spatial and temporal locations in conjunction with physiological measurements (e.g. through add-on sensors), enabling a better understanding of animal spatial ecology and behaviour (Cagnacci *et al.* 2010). However, understanding animal movement is contingent on accessible methods that permit comprehensive analysis of long-term, high-resolution time series, or 'tracks'. As short-term behaviours such as feeding, dispersing, exploring, mating or escaping (Fryxell *et al.* 2008; Singh *et al.* 2012) determine fitness of individuals and influence animal distributions (Getz & Saltz 2008; Hawkes 2009), classifying long-term tracks into movement behaviours within short spatial and temporal scales has recently emerged as a critical research agenda within movement ecology (Fryxell *et al.* 2008; Gurarie *et al.* 2015).

Classifying movement data is a complex task because behaviours are dependent on a large number of internal and external factors (Nathan *et al.* 2008) and can vary according to the spatial and temporal scales considered (Morales & Ellner 2002). Integrated analysis of an animal movement path requires an exploratory phase where tracks are segmented and classified into animal paths according to changes in behaviour (Gurarie *et al.* 2015). For this phase, the absence of a standardized analytical framework to decipher the behavioural

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structure of animal tracks has produced a number of diverse approaches to classify animal tracks into shorter spatial and temporal movement modes. All existing methods are fundamentally similar in that they try to group segments of the track that represent similar movement patterns. Thus, all methods are subject to the assumptions that sequential locational fixes can be translated into detectable movement modes and are also subject to possible errors arising from subsetting tracks into time series that include either multiple movement modes (too long) or partial movement modes (too short). For an exhaustive review of existing methods on detecting changes in animal movement patterns, we refer the readers to Edelhoff, Signer & Balkenhol (2016).

Although existing methods improve our understanding of animal spatial behaviour, there are many drawbacks that prevent their widespread application. These include: (i) that they usually only provide a binary classification of what the animal is doing, e.g. fast/slow and straight/sinuous segments (Thiebault & Tremblay 2013), foraging/travelling (Fauchald & Tveraa 2003) and intensive/extensive searching (Knell & Codling 2011); (ii) the statistical models are relatively complex and include restrictive assumptions; (iii) they require extensive computer processing capacity (Nams 2014); (iv) they require tracks recorded at high temporal resolution (that are not always available because of limits of battery life) and (v) they require laborious visual interpretation (e.g. Allen *et al*. 2014).

Here, we propose a user-friendly analytical approach combining separately validated methods to develop a powerful tool for segmenting and classifying animal tracks into multiple movement modes over short spatial and temporal scales. Our analysis comprises three steps: (i) the entire animal track is split into segments using behavioural change point analysis (BCPA) (Gurarie, Andrews & Laidre 2009) and converting movement data into net squared displacement (NSD); (ii) a set of potential candidate movement modes is defined and represented by linear or nonlinear equations (Bunnefeld *et al*. 2011; Oswald *et al*. 2012) and (iii) each segment is then classified by assessing the relative fit of these equations to NSD segments. We illustrate the strength of this approach using movement track data from wild boar *Sus scrofa* tracked by GPS and investigate the potential suitability of this method for broad application.

Materials and methods

Our new analytical approach uses a straightforward, three-step process to decompose the GPS track.

STEP 1: SEGMENTING GPS TRACK INTO MEANINGFUL SEGMENTS BASED ON SIMILAR ‘STATE’

We apply BCPA to automatically segment the complete time series, in our case a complete GPS track (Gurarie, Andrews & Laidre 2009). This method converts raw locational data (i.e. including time, latitude and longitudinal positional fixes, e.g. as produced by GPS loggers) into a time-series of step length (distance between two consecutive relocations) and turning angle (angle between two consecutive steps, a measure of directional change) and then further transforms these into orthogonal persistence velocity (the magnitude of movement) and turning velocity (tendency towards a particular direction) (Gurarie, Andrews & Laidre 2009; see Appendix S1, Supporting Information). Persistence and turning velocity presents the advantage of being locally stationary and Gaussian, enabling the analysis of this autoregressive process as a time-series process (Gurarie 2008). Any significant change in parameters (mean, variance or continuous autocorrelation) in this time series, identified using Bayesian Information Criterion (BIC), is considered as a change in the animal state. BCPA relies on user-defined settings: *response variable* (persistence velocity or turning velocity or combination of both), *moving window size* (within which significant structural shifts between homogenous patterns are assessed), *cluster width* (temporal range over which changing points are observed) and *sensitivity parameter* (*K*). As we had no prior information on the effect of these parameterizations, for our case study (see below) we tested the effect of the above-mentioned parameters on the outcome of BCPA prior to implementing final BCPA on our GPS tracks.

We then calculate net squared displacement (NSD) separately for each segment [see Papworth *et al*. (2012) for detailed R code]. NSD, which is the Euclidian squared distance between the first location of a segment and any consecutive relocations, is an effective method to characterize GPS data because it transforms movement data from 3D (x, y, t) to 2D (x from origin, t) permitting the application of simpler statistical models (Börger & Fryxell 2012). NSD is commonly used to model migratory movement of animals at very large scales (Bunnefeld *et al*. 2011; Singh *et al*. 2012; Beatty *et al*. 2013), but can logically be applied to smaller-scale movements.

STEP 2: DEFINING POTENTIAL CANDIDATE MOVEMENT MODES

One originality of our approach is the *a priori* definition of several candidate movement modes, taking advantage of existing knowledge or expectation about spatial behaviour of the focal species. To classify segments (see Step 3) correctly, the set of candidate movement modes must be ecologically appropriate movement strategies and should be as comprehensive as possible. The set of candidates can be defined either using expert opinion or existing literature, but if such information is not available, the approach can still be used ‘blindly’ by testing all imaginable potential candidate movement behaviours. As in Information Theoretic model selection (Burnham & Anderson 2004), correct and comprehensive selection of candidate models is vital to ensure that segments are correctly classified (Papworth *et al*. 2012). If a strategy is omitted from the candidate set it obviously cannot be identified by subsequent model selection (Step 3), thus preventing complete classification of movement mode. In our case study (see below), we identified five candidate spatial modes: encamped (i.e. sedentary behaviour), round trips (complete and partial), ranging (i.e. rapid directional movement) and wandering (i.e. non-directional movement).

Once decided upon, mathematical curve equations that best represent each movement mode are identified. First, users define an expected relationship between NSD and time for each candidate movement mode (e.g. Fig. 1). Dummy data are generated for each candidate mode (extracting data points from published sources, or ‘drawing’ the shape of the curve (Fig. 1) and extracting the underlying data points). Curve-fitting routines are then used to identify the equation that represents (best fits) the dummy data, translating the expected shape into a mathematical relationship between NSD and time. For example, we used model selection routine pn.mod.compare() in *FlexParamCurve*, which provides a simple method to discriminate among nonlinear curves (Oswald *et al*. 2012), to identify the specific nonlinear

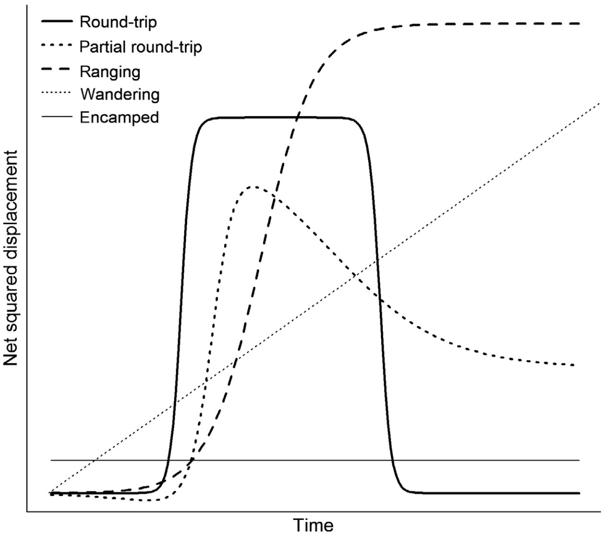


Fig. 1. Defined candidate movement modes for illustrative case study of sub-adult male wild boar. See text for description of the different modes.

equation that best represented each of five movement modes: encamped, round trips, partial round trips, wandering and ranging (Table 1, see case study below). The names chosen represent previously reported behaviours translated to small spatiotemporal scales (e.g. ranging is a short-term, small-scale version of a dispersal movement mode). We further designated linear models to represent wandering and encamped modes (Table 1).

STEP 3: CLASSIFYING SEGMENTS INTO MOVEMENT MODES

For each of the candidate movement modes from Step 2, we then fit the corresponding nonlinear or linear mathematical curve equations separately to NSD data from each segment. In each case, NSD is predicted as a function of time (Table 1, Fig. 1). The R package *FlexParamCurve* (Oswald *et al.* 2012) allows up to 32 different nonlinear curve equations, each a reduction of the 8-parameter double Richards curve:

$$\mathrm{NSD} = \frac{A}{1 + m \cdot \exp\left(-k(t-i)\right)^{1/m}} + \frac{A'}{1 + m' \cdot \exp(-k'(t-i'))}$$

where A is the asymptote, t the time since start of the trip, k the rate parameter, i is the inflection point, m the shape parameter for the first portion of the curve and A', k' and i' are their equivalent parameters for the subsequent portion of the curve. This package permits modelling of a much wider range of time–NSD relationships than previous large-scale approaches (e.g. Bunnefeld *et al.* 2011). We use the function SSposnegRichards() to generate appropriate starting parameters values for nonlinear least squares fitting in nls() of these curve equations in R. Linear equations are fitted by least squares regression in R.

Finally, we use Concordance Criterion (CC) to evaluate the relative goodness-of-fit (Huang, Meng & Yang 2009; Singh *et al.* 2012) for candidate movement behaviours for each segment. CC outperforms traditional goodness-of-fit measures in the case of nonlinear models. Values fall between −1 (perfect negative fit) and 1 (perfect positive fit) for the concordance between observed data and predicted values. If convergence fails for any nonlinear model it is assigned a CC value of 0. As CC is not applicable for the intercept model (NSD = c, Table 1), Akaike Information Criterion (AIC) is subsequently used to assess goodness-of-fit of encamped mode (see case study below).

Each segment is then classified as the movement mode with the highest CC value. Segments with poor fitting values (i.e. above/below a threshold of 0·7, empirically assessed) were classified as encamped mode if the intercept model has the lowest observed AIC.

CASE STUDY: ANALYTICAL APPROACH ILLUSTRATED USING WILD BOAR GPS TRACKS

We illustrate our approach using movement data from wild boar, a species with a high spatial plasticity of complex movements strategies (Spitz & Janeau 1990; Janeau *et al.* 1995a; Podgórski *et al.* 2013). GPS data were collected from three sub-adult males tracked in an agroecosystem of Southern Belgium (50°25′N, 4°53′E). Animals were caught using 2 × 1 m transportable baited (with corn) cage (Jullien 1990) in autumn 2011 and tagged with GPS/GSM Plus 3D collar (Vectronics Aerospace GmbH, Berlin, Germany). To avoid influences of hunting disturbances (McIlroy & Saillard 1989; Keuling, Stier & Roth 2008), we only used tracking data collected between January 1 and April 31, 2012. During this period, positional fixes were recorded for each tracked individual at an interval of 15 min.

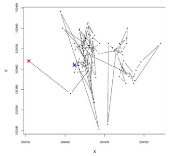
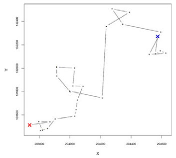
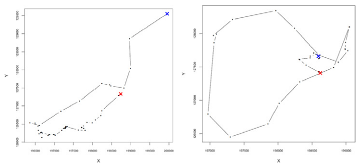
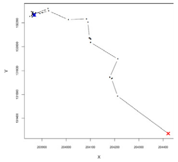
Raw GPS data were ‘cleaned’ by removal of extreme locations, i.e. presenting unlikely speeds (distances moved within the sampling interval) and turning angles associated with outgoing and incoming movement (Bjørneraas *et al.* 2010). We specified these parameters as follows: maximum moved distance to 10 km, speed to 1·5 m s^{-1} and angle spike to 180°. Deleted locations composed 0·1% of all locations. Tracks were then decomposed into movement segments using BCPA (Gurarie, Andrews & Laidre 2009).

Before classifying consequent segments into movement modes, we classified segments as stationary, those segment with a maximum NSD < mean error around positional locations, estimated from the literature at a value of 25 m (Orio, Callas & Schaefer 2003). In total, across the three observed individuals, 13·6% of segments were stationary. These segments were not included in subsequent analyses. For the remaining segments, movement data were converted into NSD.

We tested the following candidate set of movement modes based on (i) adapted movement modes observed at annual scale (Bunnefeld *et al.* 2011) and (ii) published results from previous studies of wild boar spatial strategies: encamped (i.e. residency behaviour) (Suselbeek *et al.* 2014), round and partially round trip (Spitz & Janeau 1990), wandering (Spitz & Janeau 1990; Scillitani, Monaco & Toso 2010) and ranging (Markov, Neifel’d & Estaf’ev 2004; Keuling *et al.* 2010; Prevot & Licoppe 2013) (Fig. 1). More specifically we defined encamped mode as movement performed within the vicinity (c. 200 m radius) of the starting point, possibly including short, outside excursions (Spitz & Janeau 1990). Round and partially round trips modes are longer movements away from the bedding site followed by a complete (i.e. round) or incomplete (i.e. partially round) return (Orians & Pearson 1979). In both wandering and ranging animals move away from a starting point with no return. Wandering animals gradually (i.e. linearly) increase their distance from the starting point, whereas ranging animals exhibit fast, directed movements, followed or preceded by slow movements (Clobert *et al.* 2012) (Fig. 1). We further subset ranging mode into three separate categories based on distance travelled: short (<3 km), medium (3–6 km) and long range (>6 km).

We then generated dummy data for each candidate movement mode and used all model selection [function pn.mod.compare()] in *FlexParamCurve* (Oswald *et al.* 2012) to identify the appropriate nonlinear equation to describe each. Ranging mode was best represented by a logistic equation (*modno* = 32) and round and partially round were best modelled using 7- and 6-parameter, non-monotonic curves

Table 1. Defined candidate movement behaviours for illustrative case study of sub-adult male wild boar, their corresponding linear or nonlinear mathematical equations and an illustrative example of the corresponding movement path (the blue cross indicating the starting point of the trip and the red cross the ending point)

Strategy	FlexParamCurve model	Equation	Example of the movement path
Encamped		$\text{NSD} = c$	
Wandering		$\text{NSD} = a{\cdot}t$	
Round trip and partial round trip	2	$\text{NSD} = \frac{A}{1+m\cdot\exp\left(-k(t-i)\right)^{1/m}} + \frac{A'}{1+\exp(-k'(t-i'))}$	
	22	$\text{NSD} = \frac{A}{1+\exp\left(-k(t-i)\right)} + \frac{A'}{1+\exp(-k'(t-i'))}$	
Ranging	12	$\text{NSD} = \frac{A}{1+m\cdot\exp\left(-k(t-i)\right)^{1/m}}$	
	32	$\text{NSD} = \frac{A}{1+\exp\left(-k(t-i)\right)}$	

Parameters description: t time since departure, a slope, A first curve plateau, A' difference between second and first curve plateaus, k rate of change between initial y value and first plateau, k' rate of change between first and second plateaus, i inflection point of first curve, i' inflection point of second curve, m shape parameter (changes the inflection point and rate of change) of first curve and m' shape parameter (changes the inflection point and rate of change) of second curve (Oswald *et al.* 2012).

(*modno* = 2 and 22), respectively (Oswald *et al.* 2012) (Appendix S1, Table S1.1). Wandering was best fit by the linear equation $\mathrm{NSD} = at$, where t = time since departure and a = slope, and encamped mode was described by a constant value: $\mathrm{NSD} = c$.

Once nonlinear curves representing candidate strategies had been determined, we generated initial starting parameter estimates and bounds for each NSD segment using modpar() in *FlexParamCurve*. Each candidate curve was then separately fitted using SSposnegRichards() from the same R package to generate equation-specific starting parameters with a call to nls(). For strategies best represented by linear equations, i.e. encamped and wandering mode (Fig. 1), linear regression was performed (with and without a slope parameter, respectively; Table 1) using lm() in the *stats* package in R.

Concordance Criteria and the AIC were used to discriminate among the fit of the different nonlinear and linear models. Because ranging events can occur at various spatial scales in wild boar (Prevot & Licoppe 2013; Jerina, Pokorny & Stergar 2014), we classified these into short-, medium- or long-ranging movements by calculating the minimum total within-cluster variance using Ward's minimum variance hierarchical clustering (Ward 1963) implemented in *hclust()* in R (Maechler *et al.* 2015). For round-trip movement, we discriminated between round and partially round movement by comparing NSD value at the first inflection point to the net change in NSD from the start to end of the segment. $\mathrm{NSD}_{\mathrm{Infl}} > \mathrm{NSD}_{\mathrm{net}}$ indicated round-trip movement, otherwise movement was classified as partial trip.

EVALUATING THE NEW APPROACH

To validate our classification, we compared our results with those obtained by Spitz & Janeau (1990) for classified spatial movement patterns of radio-tracked sub-adult, male wild boar. For comparison, we measured the total distance travelled (TDT) and the total activity duration (AD) using the move package (Kranstauber & Smolla 2015) for each movement mode. We also calculated the average radius (AVR), i.e. the mean of the distances between relocations and centre of activity (Calhoun & Casby 1958) for each.

We assessed the generality of our approach for different temporal scales by resampling our data at different rates (varying from one location every 15 min to one location every 24 h) and repeating our approach on each resampled dataset.

Results

Parameter settings in BCPA had little impact on the number of segments detected in each track (Appendix S1, Fig. S1.2), suggesting robust identification of changes in behavioural mode. As final settings, we used a window size of 30, a sensitivity K of 2 and used a cluster width of 2. These value of settings produced 143, 155 and 143 segments for each of the three wild boar (Boars #1, #2 and #3), respectively. Across all animal tracks, 72 stationary segments were identified, representing 11·5%, 16·9% and 12·6% of total tracking time of Boars #1, #2 and #3, respectively. From the remaining 369 segments, 81·0 (±6) % were successfully classified into candidate movement behaviours (having $|\mathrm{CC}| > |0{\cdot}7|$ or lowest AIC for encamped strategy). Although classified segments varied in duration from 5 to 54·2 h, mean duration was 10·4 (±4·7) h, corresponding to half-day behavioural activity. Classified movement modes displayed diagnostic movement patterns, ranging from behaviours that usually occurred over a few hundred metres, to those that commonly involved 15 km of travel (Table 2).

The three individual sub-adult, male boar engaged in the *a priori* defined movement modes to a strikingly similar degree, spending most time in short-distance (1·5 ± 0·8 km) ranging (43%) followed by either encamped, round- or partially round-trip modes (Fig. 2). Movements other than long-range (>6 km) and medium-range ranging occurred generally over small spatial scales (<3·5 km, Fig. 3). Longer-range movements were relatively rare; only an average of 6% of segments was medium-range and c. 1% was long-range ranging mode. Total distance travelled and speed reached their minima and maxima in the encamped (1·2 km and 0·04 m s^{-1}) and long-distance ranging (21·9 km and 0·76 m s^{-1}), respectively (Fig. 3). Some differences between individuals were evident, with Boar #1 generally moving much shorter distances than the other two, and Boar #2 and #3 undergoing long-distance nomadic wanderings, above 6 km in distance (Fig. 3).

Our study animals exhibited similar patterns in the TDT, AD and the AVR to those reported by Spitz & Janeau (1990) (Table 2). Varying the resampling rate had little effect on classification success (maintained above 70%) until more than 3 h between successive relocations, after which classification success rates dropped linearly (Fig. 4). Temporal and spatial scales of classified behaviours from resampled datasets were relatively constant until sampling rate dropped below one relocation every 4 h, after which both became biased towards larger values (Fig. 5).

Discussion

Our straightforward analytical framework combines existing, validated segmentation and classification techniques to convert

Table 2. Central tendency and variability (mean ± SD) for a range of descriptive statistics for each of the tested movement strategies

Strategy	*N*	Duration (h)	Speed (km h^{-1})	Total travelled distance (m)	Average radius (m)	Net displacement (ND) (m)	Maximum ND (m)
Encamped	50	16·5 ± 7·1	0·3 ± 0·3	4845·8 ± 4740·1	294 ± 459	789·5 ± 1035·8	635·5 ± 655·1
Wandering	26	15·1 ± 5·5	0·5 ± 0·5	6191·2 ± 3576·6	614·4 ± 588·8	1874·3 ± 1775·8	1758·8 ± 1555·3
Round trip	42	14·1 ± 5·1	0·4 ± 0·2	4982·4 ± 2467·6	481·6 ± 274·9	556·6 ± 481	1408·5 ± 843·6
Part. Round trip	54	15·6 ± 6·4	0·5 ± 0·5	6193·7 ± 4263·1	607·4 ± 467·2	1144·7 ± 977·4	1953·1 ± 1482·1
Ranging– short	148	14·7 ± 5·6	0·3 ± 0·2	4017·5 ± 2215·7	430·5 ± 319·9	1462·2 ± 797·6	1472·2 ± 762·6
Ranging– medium	33	13·8 ± 6·2	0·7 ± 0·3	9096·2 ± 4188·7	1455 ± 535·9	4530·8 ± 1263·9	4480·9 ± 1245·8
Ranging– long	10	19·2 ± 13·5	1 ± 0·4	14 378·4 ± 4408·8	2511·9 ± 993·7	8281·3 ± 1671·1	8058·3 ± 1468·3

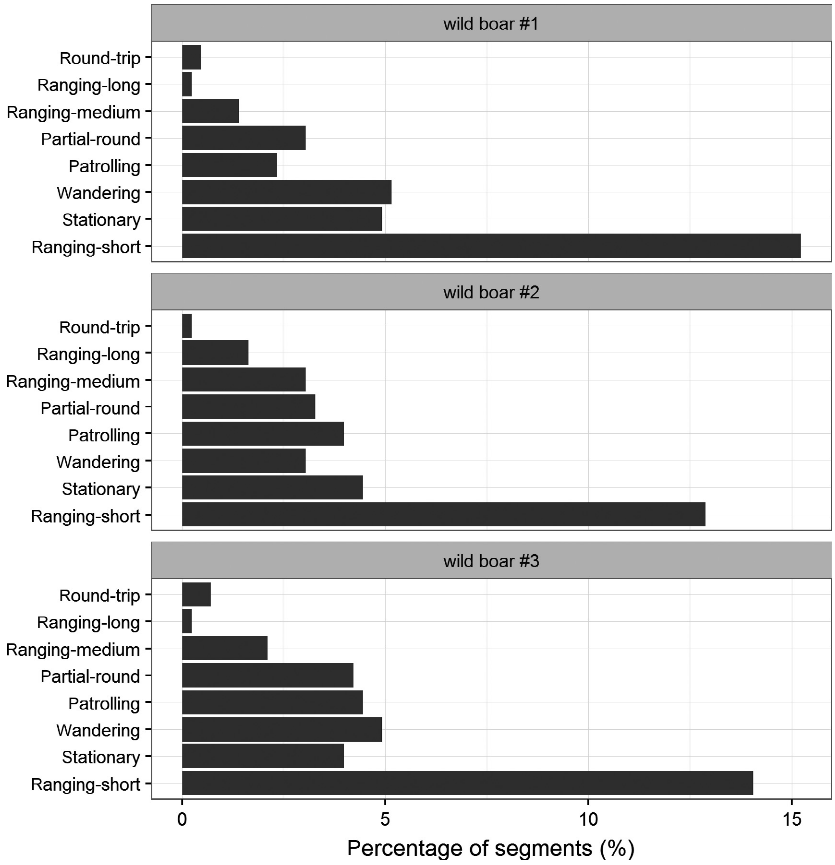


Fig. 2. Percentage of segments classified as specific movement modes for the three GPS-tracked sub-adult, male wild boar.

animal GPS tracks into multiple, high-resolution movement behaviours. Using field data for wild boar we show that our approach easily accommodates behaviours that incorporate movements from a few hundred metres to >15 km and lasted between 5 and 50 h. Over 80% of segmented GPS tracks were successfully classified into predefined movement modes for data logged from wild boar at 15 min intervals. Resampling of these data indicated that classification success rates exceeding c. 70% were easily achievable as long as logging intervals were under 3 h and that bias in the duration and spatial extent of classified modes was minimal when logging intervals remained below 4 h. A minimum of six relocations could thus be used to model daily animal movements, a resolution often achieved by studies tracking terrestrial mammals for seasonal and multi-year information on habitat use. Furthermore, movement characteristics of the classified modes for our wild boar were very similar to those reported in the literature (Spitz & Janeau 1990) and confirmed previous findings on the spatial strategies of sub-adult, wild boar at the daily scale, including large distances travelled (Russo, Massei & Genov 1997), diurnal activity and movement patterns (Janeau *et al.* 1995a; Podgórski *et al.* 2013), and use of multiple resting sites within a home range (predominance of partially round-trip over round-trip mode, Fig. 2) (Janeau *et al.* 1995b; Spitz & Janeau 1995). These results validate the use of our approach for decomposing animal tracks into meaningful, movement modes across high-resolution temporal and spatial scales.

Our approach has the advantage of combining two established methods: BCPA (Gurarie, Andrews & Laidre 2009) and the modelling of NSD using nonlinear equations (Börger & Fryxell 2012). BCPA is easily implemented (see bcpa package, Gurarie 2014), computationally efficient and robust to gaps and errors in the movement data and issues of autocorrelation (Gurarie, Andrews & Laidre 2009). Although the method requires user-defined parameters (sensitivity K, window size and cluster width), it is straightforward to test the effect of varying parameter values and we found our track segmentation to be robust to such variation (Appendix S1, Fig. S1.2). Secondly, modelling NSD objectively discriminates among movement patterns, detects inter- and intra-individual variability in patterns and is robust to low sampling rates and variable sampling intervals. This makes the method easily expandable to a wide range of animal taxa (Bunnefeld *et al.* 2011; Börger & Fryxell 2012) and our results indicate that it works well for movement of animal occurring at the daily scale.

Compared to existing methods, our approach has the advantage of increasing the number of behavioural classes (‘behavioural states’, Nams 2014) from typically binary categories (Thiebault & Tremblay 2013) to, conceivably, as many as desired. The maximum limit is only constrained by the mathematical capacity to discriminate between proposed NSD–time relationships and prior knowledge of the species. Furthermore, when such prior knowledge is

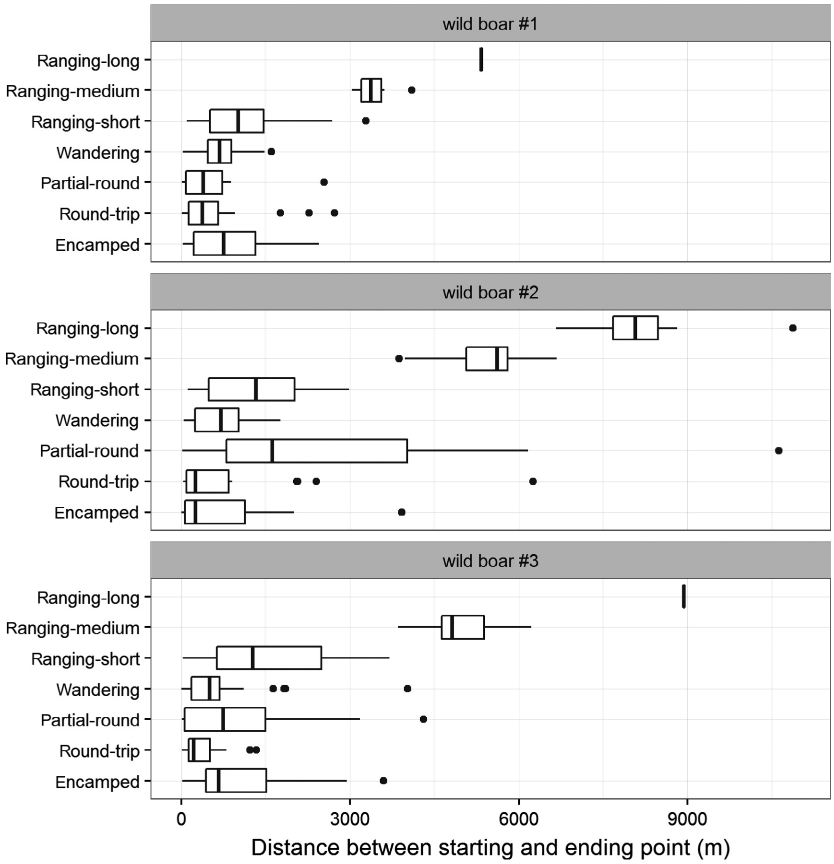


Fig. 3. Comparison of the different classified movement modes according to the net displacement between the starting and ending points.

Table 3. Characteristics of spatial movements of wild boar as classified by our new approach in comparison to those described by Spitz & Janeau (1990)

	This study	Spitz & Janeau (1990)
Total travelled distance (m)	5470 ± 3969	8185 ± 3472
Ranging	5437 ± 3972	7351 ± 3223
Wandering (zigzag)	5679 ± 3577	8351 ± 3117
Round trip (loop)	4518 ± 2467	4346 ± 833
Activity duration (min)	904 ± 378	709 ± 197
Average radius (m)		
Ranging	716 ± 709	944
Wandering (zigzag)	614 ± 589	536
Round trip (loop)	481 ± 275	455

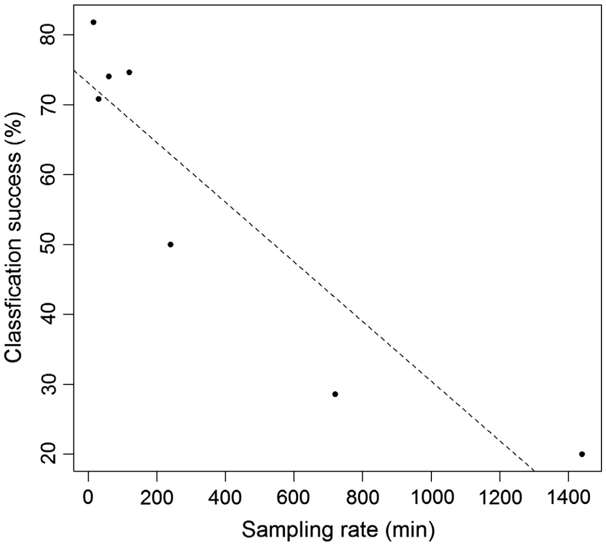


Fig. 4. Effect of the sampling rate on the classification success of segments into a candidate movement mode.

lacking, hypothetical movement behaviours and their associated mathematical descriptions can be proposed and tested using our approach. Our approach is able to describe very high-resolution movements, facilitating a better understanding of local and daily movement of individuals, and simultaneously accommodating datasets that do not incorporate full-yearly coverage (often occurring due to battery failure or loss of the tracking device, e.g. Mostello *et al.* 2014). Our approach also uses established methods, implemented in R, without restrictive assumptions, extensive parameterizations or the need for visual interpretation. Thus, it is straightforward, easily accessible, simple to implement on large datasets from multiple individuals and largely objective. As the choice of candidate modes is based on prior knowledge or proposed relationships, it is implicitly suitable for testing hypotheses about animal movement behaviours. As it does not rely on arbitrarily fixed starting/ending times of movements (e.g. segmentation of night/day, dawn/dusk; e.g. Nisbet *et al.* 2011) it also allows the data to inform when the animal changes behaviour, preventing

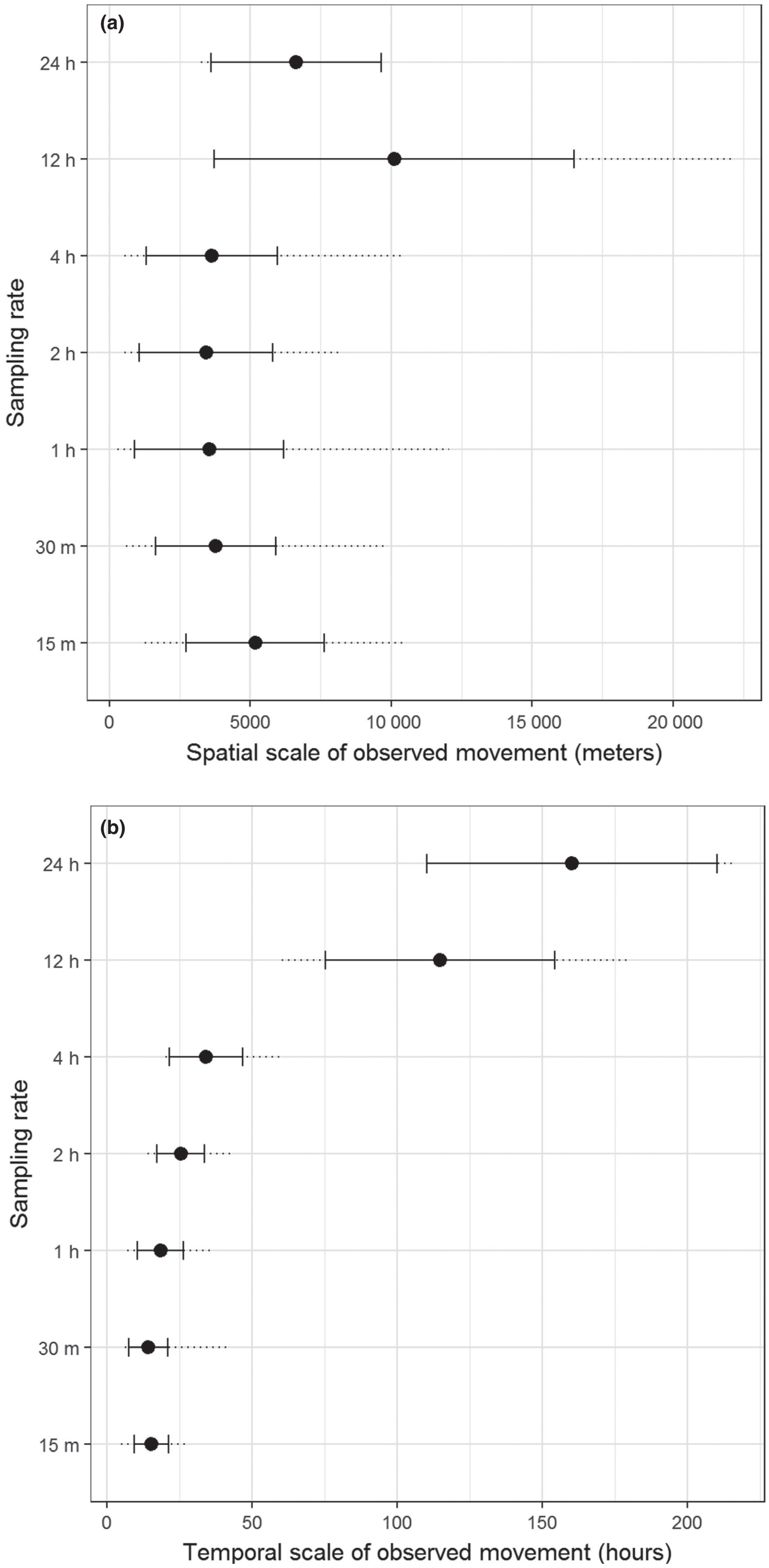


Fig. 5. The effect of varying the resampling rate on the correct identification of spatial (a) and temporal (b) scales of all classified movement behaviours. Mean (black dot), standard deviation (vertical bar) and range (dotted line) are indicated.

the exclusion of unexpected behaviours (e.g. large diurnal movements for nocturnal species, e.g. Jerina, Pokorny & Stergar (2014)).

Although the approach we describe requires very little user parameterization, apart from deciding on the candidate movement behaviours and their mathematical curve equations, we strongly recommend the user to review the output at each step (Mysterud *et al.* 2011). We initially faced some challenges discriminating among curve equations that represented similar shape patterns (see Fig. 1 of Oswald *et al.* 2012). For example, models 2 and 22 from *FlexParamCurve* successfully fit both round-trip and partial round-trip modes (Fig. 1), so that directly discriminating among strategies from model fit was not possible. In this situation, we used a simple metric (comparing NSD value at the inflection point) to differentiate between the two modes. In some cases, ranging modes were successfully modelled by both monotonic (as anticipated) but also non-monotonic curves. To overcome this issue, we verified if the last predicted value was also the maximum value of NSD (reflecting a ranging mode) or not (reflecting either a round or partially round mode). We implemented both of these fixes in our R code and so processing times were not adversely affected. With greater numbers of candidate behaviours and when behaviours are predicted to have similar mathematical descriptions, it is essential to develop such discriminatory criteria for post-processing after curve fitting.

A few caveats should be considered when designing a field study or considering applying our approach to existing tracking data as animal tracks are made of movement mechanisms and patterns operating at multiple spatiotemporal scales (Nathan *et al.* 2008). Naturally, if activities of interest do not show unique, detectable movement signals, then they will not be discriminable by our approach. This may potentially be overcome using biologgers (Rutz & Hays 2009). Simultaneously measuring acceleration or animal state (e.g. heart rate) should help to further decompose a spatial strategy on its multiple activity components (e.g. Halsey *et al.* 2009), enabling a better understanding of finer spatial behaviour. A further important consideration is that if activities occur at spatial and temporal (i.e. sampling) scales below the discrimination of the tracking device (i.e. due to tracking device error margins) and chosen sampling rate (e.g. de Weerd *et al.* 2015), these will not be detectable using our approach. Although our NSD modelling approach is scale independent (Bunnefeld *et al.* 2011), BCPA brings scale dependency into our approach (Gurarie, Andrews & Laidre 2009). Thus, results of BCPA analysis applied for very different time-scales are not directly comparable and may highlight different types of behaviour. Within a particular spatial mode, multiple types of smaller-scale movement activity may occur (e.g. feeding, rooting and walking; Blasetti *et al.* 1988). Therefore, it is important to correctly define the time-scale of interest prior to analysis. A strength of our approach is that it can easily be tailored to accommodate multiple scales of movement mode, by running the process (from BCPA to classification) multiple times, each time splitting the data into smaller chunks prior to analysis (e.g., whole track, weekly, daily, hourly) and running it independently on all chunks. In our case study, applying BCPA over only round-trip bouts, we found break points were not detected when run over the whole track, but this was to be anticipated considering that a round-trip movement is made of at least two different spatial movements.

We have demonstrated that our new approach to decomposing logged animal track data into fine-scale, biologically meaningful movement modes has several characteristics that advance the status quo to help to explore and explain what an animal is doing. These are accommodating more than two behavioural states, facilitating analyses at high temporal and spatial resolutions, and objectively classifying based on established behaviours while avoiding restrictive assumptions, complex parameterizations and visual interpretation. Future development of tracking devices will increase their longevity and resolution allowing finer-scale tracking of animals and greater choice of sampling scheme to answer research questions. Our approach is suitable for analysing such large, high-resolution datasets and is well placed to distinguish between multiple hypotheses on animal movement behaviour and accommodate future developments in tracking technologies.

Authors' contributions

K.M., N.B., P.L. and S.A.O. conceived the ideas and designed methodology; K.M. collected the data; K.M., N.B. and S.A.O. analysed the data; K.M., N.B. and S.A.O. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

R script is uploaded as online supporting information (Appendix S2) and dataset containing the three individual wild boar tracks is deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.pq622 (Morelle *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Outcome of the BCPA analysis (Fig. S1.1, S1.2) and of the models' comparison procedure of FlexParamCurve (Table S.1.1).

Appendix S2. Example R script to perform the analysis on an individual wild boar.