

This is the peer reviewed version of the following article: Morelle, K., Bunnefeld, N., Lejeune, P. and Oswald, S. A. (2017), From animal tracks to fine-scale movement modes: a straightforward approach for identifying multiple spatial movement patterns. *Methods Ecol Evol*, 8: 1488–1498, which has been published in final form at <https://doi.org/10.1111/2041-210X.12787>. This article may be used for non-commercial purposes in accordance With Wiley Terms and Conditions for self-archiving.

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

4    **running title:** Decomposing GPS tracks into movement patterns

5    **word count:** 6933

7    Kevin Morelle\*, BIOSE Department, Gembloux Agro-Bio Tech, University of Liège, passage des  
8    déportés 2, 5030 Gembloux, Belgium.

9    Nils Bunnefeld, Biological and Environmental Sciences, School of Natural Sciences, University of  
10    Stirling, Stirling, FK9 4LA, UK.

11    Philippe Lejeune, Gembloux Agro-Bio Tech, University of Liège, passage des déportés 2, 5030  
12    Gembloux, Belgium.

13    Stephen Oswald, Division of Science, Penn State University, Berks Campus, Reading, PA 19610,  
14    USA.

16    \*correspondence author. Email: [morelle.k@gmail.com](mailto:morelle.k@gmail.com)

19    Accepted for publication in *Methods in Ecology and Evolution* published by Wiley-  
20    Blackwell.

## 1 Abstract

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

6 2. We developed an analytical approach that combines separately-validated methods  
7 into a straightforward tool for converting animal GPS tracks to short-range movement modes.  
8 Our three-step analytical process comprises: (1) decomposing data into separate movement  
9 segments using behavioural change point analysis; (2) defining candidate movement modes  
10 and translating them into non-linear or linear equations between net squared displacement  
11 (NSD) and time; and (3) fitting each candidate equation to NSD segments and determining  
12 the best-fitting modes using Concordance Criteria, Akaike's Information Criteria and other  
13 fine-scale segment characteristics. We illustrate our approach for three sub-adults, male wild  
14 boar *Sus scrofa* tracked at 15 min intervals over 4 months using GPS collars. We defined five  
15 candidate movement modes based on previously published studies of short-term movements:  
16 encamped, ranging, round trips (complete and partial), and wandering.

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

22 4. The proposed approach advances the status quo by permitting classification into  
23 multiple movement modes (where these are adequately discernable from spatial fixes)  
24 facilitating analyses at high temporal and spatial resolutions, and is straightforward, largely

1 objective, and without restrictive assumptions, necessary parameterizations or visual  
2 interpretation. Thus, it should capture the complexity and variability of tracked animal  
3 movement mode for a variety of taxa across a wide range of spatial and temporal scales.

4 **Keywords:** behavioural change point analysis, fine scale movement, FlexParamCurve, GPS  
5 tracks, net squared displacement, spatial pattern, wild boar

6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20

## 1    **Introduction**

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

15            Classifying movement data is a complex task because behaviours are dependent on a  
16    large number of internal and external factors (Nathan *et al.* 2008) and can vary according to  
17    the spatial and temporal scales considered (Morales & Ellner 2002). Integrated analysis of an  
18    animal movement path requires an exploratory phase where tracks are segmented and  
19    classified into animal paths according to changes in behaviour (Gurarie *et al.* 2015). For this  
20    phase, the absence of a standardized analytical framework to decipher the behavioural  
21    structure of animal tracks has produced a number of diverse approaches to classify animal  
22    tracks into shorter spatial and temporal movement modes. All existing methods are  
23    fundamentally similar in that they try to group segments of the track that represent similar

1 movement patterns. Thus, all methods are subject to the assumptions that sequential  
2 locational fixes can be translated into detectable movement modes and are also subject to  
3 possible errors arising from subsetting tracks into time-series that include either multiple  
4 movement modes (too long) or partial movement modes (too short). For an exhaustive  
5 review of existing methods on detecting changes in animal movement patterns, we refer the  
6 readers to (Edelhoff *et al.* 2016).

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

16        Here, we propose a user-friendly analytical approach combining separately-validated  
17 methods to develop a powerful tool for segmenting and classifying animal tracks into  
18 multiple movement modes over short spatial and temporal scales. Our analysis comprises  
19 three steps: (1) the entire animal track is split into segments using behavioural change point  
20 analysis (BCPA) (Gurarie *et al.* 2009) and converting movement data to net-squared  
21 displacement (NSD), (2) a set of potential candidate movement modes is defined and  
22 represented by linear or non-linear equations (Bunnefeld *et al.* 2011; Oswald *et al.* 2012), and  
23 (3) each segment is then classified by assessing the relative fit of these equations to NSD  
24 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 behavioural change point analysis (BCPA) to automatically segment the complete time-series, in our case a complete GPS track (Gurarie *et al.* 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 toward a particular direction) (Gurarie *et al.* 2009, see Appendix S1). 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 (either 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* ( $K$ ). Since 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 behavior), 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. Figure 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 for discriminate among non-linear curves (Oswald *et al.* 2012), to identify the specific non-linear 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 behaviors translated to small spatiotemporal scales (e.g. ranging is a short-term, small scale version of a dispersal movement mode). We then designated linear models for wandering and encamped behaviours (Table 1).

### *Step 3: Classifying segments into movement modes*

For each of the candidate movement modes from Step 2, we then fit the corresponding non-linear 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, Figure 1). The R package *FlexParamCurve* (Oswald *et al.* 2012) allows up to 32 different non-linear curve equations, each a reduction of the 8-parameter double Richards curve:

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

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 non-linear 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 *et al.* 2009; Singh *et al.* 2012) for candidate movement behaviours for each segment. CC outperforms traditional goodness-of-fit measures in the case of non-linear 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 non-linear model it is assigned a CC value of 0. Since 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.

20

#### 21 *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 subadult males tracked in an agroecosystem of Southern Belgium (50°25'N, 4°53'E). Animals were caught using 2 x 1 m transportable baited (with corn) cage (Jullien 1990) in autumn 2011 and tagged with GPS/GSM Plus 3D collar (Vectronics Aerospace GmbH). To avoid influences of hunting disturbances (McIlroy & Saillard 1989; Keuling *et al.* 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 and angle spike to 180°. Deleted locations composed 0.1% of all locations. Tracks were then decomposed into movement segments using BCPA (Gurarie *et al.* 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 *et al.* 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.

Adapted from movement strategies observed at annual scale (Bunnefeld *et al.* 2011), we tested whether our method was able to detect movement modes observed at the local in wild boar. To this aim, we defined the following candidate set of five 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.

1 residency behavior) (Suselbeek *et al.* 2014), round and partially-round trip (Spitz & Janeau  
 2 1990), wandering (Spitz & Janeau 1990; Scillitani *et al.* 2010), and ranging (Markov *et al.*  
 3 2004; Keuling *et al.* 2010; Prevot & Licoppe 2013) (Figure 1). We defined encamped mode  
 4 as movement performed within the vicinity (~200 m radius) of the starting point, possibly  
 5 including short, outside excursions (Spitz & Janeau 1990). Round and partially-round-trips  
 6 movements are longer movements away from the bedding site followed by a complete (i.e.  
 7 round) or incomplete (i.e. partially-round) return (Orians & Pearson 1979). In both wandering  
 8 and ranging animals move away from a starting point with no return but wandering animals  
 9 gradually (linear) increase their distance from the starting point whereas exploring animals  
 10 exhibit a fast, directed movement, followed or preceded by slow movements (Clobert *et al.*  
 11 2012) (Figure 1). We subset exploring into three separate categories based on distance  
 12 travelled: short- (<3 km), medium (3 - 6km) and long-range (> 6 km).

13 We then generated dummy data for each candidate movement mode and used all  
 14 model selection [function `pn.mod.compare()`] in *FlexParamCurve* (Oswald *et al.* 2012) to  
 15 identify the appropriate non-linear equation to describe each. Ranging mode was best  
 16 represented by a logistic equation (*modno* = 32) and round and partially-round were best  
 17 modelled using 7- and 6-parameter, nonmonotonic curves (*modno* = 2 and 22), respectively  
 18 (Oswald *et al.* 2012) (Appendix S1, Table S1.1). Wandering was best fit by the linear  
 19 equation  $NSD = at$ , where  $t$  = time since departure and  $a$  = slope, and encamped mode was  
 20 described by a constant value:  $NSD = c$ .

21 Once nonlinear curves representing candidate strategies had been determined, we  
 22 generated initial starting parameter estimates and bounds for each NSD segment using  
 23 `modpar()` in *FlexParamCurve*. Each candidate curve was then separately fitted using  
 24 `SSposnesgRichards()` 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 (Figure 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 Akaike Information Criteria were used to discriminate among the fit of the different non-linear and linear models. Because ranging events can occur at various spatial scales in wild boar (Prevot & Licoppe 2013; Jerina *et al.* 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.  $NSD_{\text{infl}} > NSD_{\text{net}}$  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 behaviour. We also calculated the average radius (AVR), i.e. the mean of the distances between relocations and center 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 1 location every 15 minutes to 1 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, Figure S1.2), suggesting robust identification of changes in animal behaviour. As final settings, we used a window size of 30, a sensitivity  $K$  of 2 and used a cluster width of 2. These values of settings produced 143, 155 and 143 segments for each of the three wild boar (Boars #1, #2, #3), respectively. Across all animal tracks, 72 stationary segments were identified and excluded, representing 11.5%, 16.9% and 12.6% of total tracking time of Boars #1, #2, #3, respectively. From the remaining 369 segments, 81.0 ( $\pm 6$ ) % were successfully classified into candidate movement behaviours (having  $|CC| > |0.7|$  or lowest AIC for encamped strategy). Though classified segments varied in duration from 5 to 54.2 h, mean duration was 10.4 ( $\pm 4.7$ ) h, corresponding to half-day behavioural durations. Classified movement behaviours displayed diagnostic movement patterns, ranging from behaviours that usually occurred over a few hundred meters, to those that commonly involved 15 km of travel (Table 3).

The three individual sub-adult, male boar engaged in the seven defined movement behaviours to a strikingly similar degree, spending most time in short-distance ( $1.5 \pm 0.8$  km) ranging (43%) followed by either encamped, round or partially-round-trip modes (Figure 2). Movements other than long-range ( $> 6$  km) and medium-range ranging were 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  $\sim 1\%$  was long-range ranging mode. Total distance travelled (TDT) and speed reached their minima and maxima in the encamped (1.2 km and 0.04 m/s) and long-distance ranging (21.9 km and 0.76 m/s), respectively (Figure 3). Some individual differences between individuals were evident, with Boar #1 generally

moving much shorter distances than the other two, and Boar #2 undergoing long-distance nomadic wanderings, up to 6 km in distance (Figure 3).

Our study animals exhibited similar patterns in the TDT, activity duration and the average radius to those reported by Spitz & Janeau (1990) (Table 3). 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 (Figure 4). Temporal and spatial scales of classified behaviours from resampled datasets were relatively constant until sampling rate dropped below one relocation every 4h, after which both became biased towards larger values (Figure 5).

## Discussion

Our straightforward analytical framework combines existing, validated segmentation and classification techniques to convert 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 meters to > 15 km and lasted between 5 and 50 hours. 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 ~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

1 & Janeau 1990) and confirmed previous findings on the spatial strategies of sub-adult, wild  
2 boar at the daily scale, including large distances traveled (Russo *et al.* 1997), diurnal activity  
3 and movement patterns (Janeau *et al.* 1995a; Podgórski *et al.* 2013), and use of multiple  
4 resting sites within a home range (predominance of partially round-trip over round-trip mode,  
5 Figure 3) (Janeau *et al.* 1995b; Spitz & Janeau 1995). These results validate the use of our  
6 approach for decomposing animal tracks into meaningful, movement modes across high  
7 resolution temporal and spatial scales.

8       Our approach has the advantage of combining two established methods: BCPA  
9 (Gurarie *et al.* 2009) and the modelling of NSD using non-linear equations (Börger & Fryxell  
10 2012). BCPA is easily implemented (see *bcpa* package, Gurarie 2014), computationally  
11 efficient, and robust to gaps and errors in the movement data and issues of autocorrelation  
12 (Gurarie *et al.* 2009). Although the method requires user-defined parameters (sensitivity *K*,  
13 window size, cluster width), it is straightforward to test the effect of varying parameter values  
14 and we found our track segmentation to be robust to such variation (Appendix S1, Figure  
15 S1.2). Secondly, modelling NSD objectively discriminates among movement patterns, detects  
16 inter- and intra-individual variability in patterns, and is robust to low sampling rates and  
17 variable sampling intervals. This makes the method easily expandable to a wide range of  
18 animal taxa (Bunnefeld *et al.* 2011, Börger & Fryxell 2012) and our results indicate that it  
19 works well for movement of animal occurring at the daily scale.

20       Compared to existing methods, our approach has the advantage of increasing the  
21 number of behavioural classes ('behavioural states', Nams 2014) from typically binary  
22 categories (Thiebault & Tremblay 2013) to, conceivably, as many as desired. The maximum  
23 limit is only constrained by the mathematical capacity to discriminate between proposed  
24 NSD-time relationships and prior knowledge of the species. Furthermore, when such prior  
25 knowledge is lacking, hypothetical movement behaviours and their associated mathematical



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

15         Although the approach we describe requires very little user-parameterization, apart  
16 from deciding on the candidate movement behaviours and their mathematical curve  
17 equations, we strongly recommend the user to review the output at each step (Mysterud *et al.*  
18 2011). We initially faced some challenges discriminating among curve equations that  
19 represented similar shape patterns (see Figure 1 of Oswald *et al.* 2012). For example, models  
20 2 and 22 from *FlexParamCurve* successfully fit both round-trip and partial round-trip modes  
21 (Figure 1) so that directly discriminating among strategies from model fit was not possible. In  
22 this situation, we used a simple metric (when distance between start and end segment >  
23 2\*peak) to differentiate between the two behaviours. In some cases, ranging strategies were  
24 successfully modelled by both monotonic (as anticipated) but also nonmonotonic curves. To  
25 overcome this issue, we verified if the last predicted value was also the maximum value of

1 NSD (reflecting a ranging mode) or not (reflecting either a round or partially-round mode).  
 2 We implemented both of these fixes in our R code and so processing times were not  
 3 adversely affected. With greater numbers of candidate behaviours and when behaviours are  
 4 predicted to have similar mathematical descriptions it is essential to develop such  
 5 discriminatory criteria for post-processing after curve-fitting.

6 A few caveats should be considered when designing a field study or considering  
 7 applying our approach to existing tracking data since animal tracks are made of movement  
 8 mechanisms and patterns operating at multiple spatiotemporal scales (Nathan et al. 2008).  
 9 Naturally, if activities of interest do not show unique, detectable movement signals, then they  
 10 will not be discriminable by our approach. This may potentially be overcome using  
 11 biologgers (Rutz & Hays 2009). Simultaneously measuring acceleration or animal state (e.g.  
 12 heart rate) should help to further decompose a spatial strategy on its multiple activity  
 13 components (e.g. Halsey *et al.* 2009), enabling a better understanding of finer spatial  
 14 behaviour. A further important consideration is that if activities occur at spatial and temporal  
 15 (i.e. sampling) scales below the discrimination of the tracking device (i.e. due to tracking  
 16 device error margins) and chosen sampling rate (e.g. de Weerd et al. (2015)) these will not be  
 17 detectable using our approach. Although our NSD modelling approach is scale-independent  
 18 (Bunnefeld et al. 2011), bcpa analysis brings scale-dependency into our approach (Gurarie et  
 19 al. 2009). Thus, results of BCPA analysis applied for very different time scales are not  
 20 directly comparable and may highlight different types of behaviour. Within a particular  
 21 spatial behaviour, multiple types of smaller-scale movement activity may occur (e.g. feeding,  
 22 rooting, and walking; Blasetti et al. 1988). Therefore, it is important to correctly define the  
 23 timescale of interest prior to analysis. A strength of our approach is that it can easily be  
 24 tailored to accommodate multiple scales of movement behavior, by running the process (from  
 25 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 not detected when run over the whole whole track, but 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 behaviours 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 analyzing 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.

## **Author contribution**

KM, NB, PL and SO conceived the ideas and designed methodology; KM collected the data; KM, NB and SO analysed the data; KM, NB and SO led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## **Acknowledgements**

We are grateful to Coralie Mengal for her help in the data collection. We also would like to thank the anonymous reviewers for their insightful comments which helped to improve the quality of the manuscript. This research was supported by the Belgian Fund for Research

Training in Industry and Agriculture (F.N.R.S-F.R.I.A.). The authors declare they have no conflict of interest.

### Data Accessibility

R script is uploaded as online supporting information and dataset containing the three individual wild boar tracks are deposited in the MOVEBANK repository.

### References

Adams, A.L., Recio, M.R., Robertson, B.C., Dickinson, K.J.M. & Heezik, Y. van. (2013). Understanding home range behaviour and resource selection of invasive common brushtail possums (*Trichosurus vulpecula*) in urban environments. *Biological Invasions*, **16**, 1791–1804.

Allen, A.M., Månsson, J., Jarnemo, A. & Bunnefeld, N. (2014). The impacts of landscape structure on the winter movements and habitat selection of female red deer. *European Journal of Wildlife Research*, **60**, 411–421.

Beatty, W.S., Kesler, D.C., Webb, E.B., Raedeke, A.H., Naylor, L.W. & Humburg, D.D. (2013). Quantitative and qualitative approaches to identifying migration chronology in a continental migrant. *PLoS ONE*, **8**, e75673.

Bjørneraas, K., Van Moorter, B., Rolandsen, C.M. & Herfindal, I. (2010). Screening global positioning system location data for errors using animal movement characteristics. *The Journal of Wildlife Management*, **74**, 1361–1366.

Blasetti, A., Boitani, L., Riviello, M.C. & Visalberghi, E. (1988). Activity budgets and use of enclosed space by wild boars (*Sus scrofa*) in captivity. *Zoo Biology*, **7**, 69–79.

- 1 Börger, L. & Fryxell, J. (2012). Quantifying individual differences in dispersal using net  
2 squared displacement. *Dispersal Ecology and Evolution* (eds J. Clobert, M. Baguette, T.G.  
3 Benton & J.M. Bullock), pp. 222–230. Oxford University Press.
- 4 Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C.M., Dettki, H., Solberg, E.J. &  
5 Ericsson, G. (2011). A model-driven approach to quantify migration patterns: individual,  
6 regional and yearly differences. *Journal of Animal Ecology*, **80**, 466–476.
- 7 Burnham, K.P. & Anderson, D.R. (Eds.). (2004). *Model Selection and Multimodel Inference*.  
8 Springer New York, New York, NY.
- 9 Cagnacci, F., Boitani, L., Powell, R.A. & Boyce, M.S. (2010). Animal ecology meets GPS-  
10 based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical  
11 Transactions of the Royal Society of London B: Biological Sciences*, **365**, 2157–2162.
- 12 Calhoun, J.B. & Casby, J.U. (1958). Calculation of home range and density of small  
13 mammals. *Public Health Reports*, **73**, 1143–1145.
- 14 Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M. (Eds.). (2012). *Dispersal Ecology  
15 and Evolution*. Oxford University Press.
- 16 Cooke, S.J. (2008). Biotelemetry and biologging in endangered species research and animal  
17 conservation: Relevance to regional, national, and IUCN Red List threat assessments.  
18 *Endangered Species Research*, **4**, 165–185.
- 19 Edelhoff, H., Signer, J. & Balkenhol, N. (2016). Path segmentation for beginners: an  
20 overview of current methods for detecting changes in animal movement patterns. *Movement  
21 Ecology*, **4**, 21.
- 22 Fauchald, P. & Tveraa, T. (2003). Using first-passage time in the analysis of area-restricted  
23 search and habitat selection. *Ecology*, **84**, 282–288.

- 1 Fryxell, J.M., Hazell, M., Börger, L., Dalziel, B.D., Haydon, D.T., Morales, J.M., McIntosh,  
2 T. & Rosatte, R.C. (2008). Multiple movement modes by large herbivores at multiple  
3 spatiotemporal scales. *Proceedings of the National Academy of Sciences*, **105**, 19114–19119.
- 4 Getz, W.M. & Saltz, D. (2008). A framework for generating and analyzing movement paths  
5 on ecological landscapes. *Proceedings of the National Academy of Sciences*, **105**, 19066–  
6 19071.
- 7 Gurarie, E. (2014). *bcpa: Behavioral change point analysis of animal movement*. R package  
8 version 1.1. <http://CRAN.R-project.org/package=bcpa>.
- 9 Gurarie, E. (2008). *Models and analysis of animal movements: From individual tracks to*  
10 *mass dispersal*. PhD thesis thesis, University of Washington.
- 11 Gurarie, E., Andrews, R.D. & Laidre, K.L. (2009). A novel method for identifying  
12 behavioural changes in animal movement data. *Ecology Letters*, **12**, 395–408.
- 13 Gurarie, E., Bracis, C., Delgado, M., Meckley, T.D., Kojola, I. & Wagner, C.M. (2015).  
14 What is the animal doing? Tools for exploring behavioural structure in animal movements.  
15 *Journal of Animal Ecology*, **85**, 69–84.
- 16 Halsey, L.G., Portugal, S.J., Smith, J.A., Murn, C.P. & Wilson, R.P. (2009). Recording raptor  
17 behavior on the wing via accelerometry. *Journal of Field Ornithology*, **80**, 171–177.
- 18 Hawkes, C. (2009). Linking movement behaviour, dispersal and population processes: is  
19 individual variation a key? *Journal of Animal Ecology*, **78**, 894–906.
- 20 Huang, S., Meng, S.X. & Yang, Y. (2009). Assessing the goodness of fit of forest models  
21 estimated by nonlinear mixed-model methods. *Canadian Journal of Forest Research*, **39**,  
22 2418–2436.
- 23 Janeau, G., Cargnelutti, B., Cousse, S., Hewison, M. & Spitz, F. (1995a). Daily movement  
24 pattern variations in wild boar (*Sus scrofa* L.). *Journal of Mountain Ecology*, **3**, 98–101.

- 1 Janeau, G., Cousse, S., Cargnelutti, B. & SPITZ, F. (1995b). Role of daily movements in the  
2 socio-spatial organization of wild boar populations (*Sus scrofa* L.). *Revue d'Ecologie (La*  
3 *Terre et la Vie)*, **50**, 35–48.
- 4 Jerina, K., Pokorny, B. & Stergar, M. (2014). First evidence of long-distance dispersal of  
5 adult female wild boar (*Sus scrofa*) with piglets. *European Journal of Wildlife Research*, **60**,  
6 367–370.
- 7 Jullien, J.M. (1990). Sélectivité de cinq modes de piégeage pour le sanglier. *Proceedings of*  
8 *the Symposium on Techniques de capture et de marquage des ongulés sauvages*, pp. 95–101.
- 9 Dubray D. Montpellier: FDC; 1990, Meze-Hérault.
- 10 Keuling, O., Lauterbach, K., Stier, N. & Roth, M. (2010). Hunter feedback of individually  
11 marked wild boar *Sus scrofa* L.: Dispersal and efficiency of hunting in northeastern Germany.  
12 *European Journal of Wildlife Research*, **56**, 159–167.
- 13 Keuling, O., Stier, N. & Roth, M. (2008). How does hunting influence activity and spatial  
14 usage in wild boar *Sus scrofa* L.? *European Journal of Wildlife Research*, **54**, 729–737.
- 15 Knell, A.S. & Codling, E.A. (2011). Classifying area-restricted search (ARS) using a partial  
16 sum approach. *Theoretical Ecology*, **5**, 325–339.
- 17 Kranstauber, B. & Smolla, M. (2015). *move: Visualizing and Analyzing Animal Track Data*.  
18 *R package version 1.5.514*. <http://CRAN.R-project.org/package=move>.
- 19 Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M. & Hornik, K. (2015). *cluster: Cluster*  
20 *Analysis Basics and Extensions*. *R package version 2.0.3*.
- 21 Markov, N.I., Neifel'd, N.D. & Estaf'ev, A.A. (2004). Ecological aspects of dispersal of the  
22 wild boar, *Sus scrofa* L., 1758, in the Northeast of European Russia. *Russian Journal of*  
23 *Ecology*, **35**, 131–134.

- 1 McIlroy, J. & Saillard, R. (1989). The effect of hunting with dogs on the numbers and  
2 movements of feral pigs, *Sus scrofa*, and the subsequent success of poisoning exercises in  
3 Namadgi-National-Park, A.C.T. *Wildlife Research*, **16**, 353–363.
- 4 Morales, J.M. & Ellner, S.P. (2002). Scaling up animal movements in heterogeneous  
5 landscapes: the importance of behavior. *Ecology*, **83**, 2240–2247.
- 6 Mostello, C.S., Nisbet, I.C.T., Oswald, S.A. & Fox, J. (2014). Non-breeding season  
7 movements of six North American Roseate Terns *Sterna dougallii* tracked with geolocators.  
8 *Seabird*, **27**, 1–21.
- 9 Mysterud, A., Loe, L.E., Zimmermann, B., Bischof, R., Veiberg, V. & Meisingset, E. (2011).  
10 Partial migration in expanding red deer populations at northern latitudes – a role for density  
11 dependence? *Oikos*, **120**, 1817–1825.
- 12 Nams, V.O. (2014). Combining animal movements and behavioural data to detect  
13 behavioural states. *Ecology Letters*, **17**, 1228–1237.
- 14 Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E.  
15 (2008). A movement ecology paradigm for unifying organismal movement research.  
16 *Proceedings of the National Academy of Sciences*, **105**, 19052–19059.
- 17 Nisbet, I.C.T., Mostello, C.S., Veit, R.R., Fox, J.W. & Afanasyev, V. (2011). Migrations and  
18 winter quarters of five common terns tracked using geolocators. *Waterbirds*, **34**, 32–39.
- 19 Orians, G.H. & Pearson, N.E. (1979). On the theory of central place foraging. *Analysis of*  
20 *Ecological Systems*, 154–177.
- 21 Orio, A.P.D., Callas, R. & Schaefer, R.J. (2003). Performance of two GPS telemetry collars  
22 under different habitat conditions. *Wildlife Society Bulletin*, **31**, 372–379.
- 23 Oswald, S.A., Nisbet, I.C.T., Chiaradia, A. & Arnold, J.M. (2012). FlexParamCurve: R  
24 package for flexible fitting of nonlinear parametric curves. *Methods in Ecology and Evolution*,  
25 **3**, 1073–1077.



- 1 Papworth, S.K., Bunnefeld, N., Slocombe, K. & Milner-Gulland, E.J. (2012). Movement  
2 ecology of human resource users: using net squared displacement, biased random bridges and  
3 resource utilization functions to quantify hunter and gatherer behaviour. *Methods in Ecology*  
4 *and Evolution*, **3**, 584–594.
- 5 Podgórski, T., Baś, G., Jędrzejewska, B., Sönnichsen, L., Śnieżko, S., Jędrzejewski, W. &  
6 Okarma, H. (2013). Spatiotemporal behavioral plasticity of wild boar (*Sus scrofa*) under  
7 contrasting conditions of human pressure: primeval forest and metropolitan area. *Journal of*  
8 *Mammalogy*, **94**, 109–119.
- 9 Prevot, C. & Licoppe, A. (2013). Comparing red deer (*Cervus elaphus* L.) and wild boar (*Sus*  
10 *scrofa* L.) dispersal patterns in southern Belgium. *European Journal of Wildlife Research*, **59**,  
11 795–803.
- 12 Russo, L., Massei, G. & Genov, P.V. (1997). Daily home range and activity of wild boar in a  
13 Mediterranean area free from hunting. *Ethology Ecology & Evolution*, **9**, 287–294.
- 14 Rutz, C. & Hays, G.C. (2009). New frontiers in biologging science. *Biology Letters*, **5**, 289–  
15 292.
- 16 Scillitani, L., Monaco, A. & Toso, S. (2010). Do intensive drive hunts affect wild boar (*Sus*  
17 *scrofa*) spatial behaviour in Italy? Some evidences and management implications. *European*  
18 *Journal of Wildlife Research*, **56**, 307–318.
- 19 Singh, N.J., Börger, L., Dettki, H., Bunnefeld, N. & Ericsson, G. (2012). From migration to  
20 nomadism: movement variability in a northern ungulate across its latitudinal range.  
21 *Ecological Applications*, **22**, 2007–2020.
- 22 Spitz, F. & Janeau, G. (1995). Daily selection of habitat in wild boar (*Sus scrofa*). *Journal of*  
23 *Zoology*, **237**, 423–434.
- 24 Spitz, F. & Janeau, G. (1990). Spatial strategies; an attempt to classify daily movement of  
25 wild boar. *Acta Theriologica*, **35**, 129–149.

1    Suselbeek, L., Adamczyk, V.M.A.P., Bongers, F., Nolet, B.A., Prins, H.H.T., van Wieren,  
2    S.E. & Jansen, P.A. (2014). Scatter hoarding and cache pilferage by superior competitors: an  
3    experiment with wild boar, *Sus scrofa*. *Animal Behaviour*, **96**, 107–115.  
4    Thiebault, A. & Tremblay, Y. (2013). Splitting animal trajectories into fine-scale  
5    behaviorally consistent movement units: breaking points relate to external stimuli in a  
6    foraging seabird. *Behavioral Ecology and Sociobiology*, **67**, 1013–1026.  
7    Ward, J.H. (1963). Hierarchical grouping to optimize an objective function. *Journal of the*  
8    *American Statistical Association*, **58**, 236–244.

9

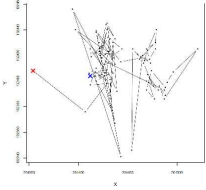
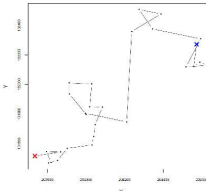
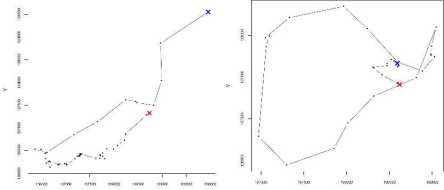
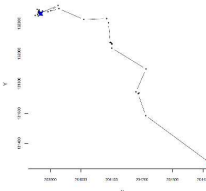
10    **Supporting Information**

11    Details of electronic Supporting Information are provided below.

12    **Appendix S1.** Outcome of the BCPA analysis (Figure S1.1, S1.2) and of the models’  
13    comparison procedure of FlexParamCurve (Table S.1.1).

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

1 Table 1. Defined candidate movement behaviours for illustrative case study of sub-adult male wild boar, their corresponding linear or non-linear  
2 mathematical equations and an illustrative example of the corresponding movement path. See also Fig 1.

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

3 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  
4 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  
5 inflection point and rate of change) of first curve,  $m'$  shape parameter (changes the inflection point and rate of change) of second curve (Oswald *et al.* 2012).

1 Table 2. Characteristics of spatial movements of wild boar as classified by our new approach  
2 in comparison to those described by Spitz and Janeau (1990).

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

3  
4  
  
5  
  
6  
  
7  
  
8  
  
9  
  
10  
  
11  
  
12  
  
13  
  
14

1 Table 3. Central tendency and variability (mean  $\pm$  SD) for a range of descriptive statistics for each of the tested movement strategies.

Strategy	N	Duration	Speed	Total travelled distance	Average radius	Net displacement	Maximum ND (m)
		(hours)	(km/h)	(m)	(m)	(ND) (m)	
Encamped	50	16.5 $\pm$ 7.1	0.3 $\pm$ 0.3	4845.8 $\pm$ 4740.1	294 $\pm$ 459	789.5 $\pm$ 1035.8	635.5 $\pm$ 655.1
Wandering	26	15.1 $\pm$ 5.5	0.5 $\pm$ 0.5	6191.2 $\pm$ 3576.6	614.4 $\pm$ 588.8	1874.3 $\pm$ 1775.8	1758.8 $\pm$ 1555.3
Round-trip	42	14.1 $\pm$ 5.1	0.4 $\pm$ 0.2	4982.4 $\pm$ 2467.6	481.6 $\pm$ 274.9	556.6 $\pm$ 481	1408.5 $\pm$ 843.6
Part. Round-trip	54	15.6 $\pm$ 6.4	0.5 $\pm$ 0.5	6193.7 $\pm$ 4263.1	607.4 $\pm$ 467.2	1144.7 $\pm$ 977.4	1953.1 $\pm$ 1482.1
ranging-short	148	14.7 $\pm$ 5.6	0.3 $\pm$ 0.2	4017.5 $\pm$ 2215.7	430.5 $\pm$ 319.9	1462.2 $\pm$ 797.6	1472.2 $\pm$ 762.6
Ranging-medium	33	13.8 $\pm$ 6.2	0.7 $\pm$ 0.3	9096.2 $\pm$ 4188.7	1455 $\pm$ 535.9	4530.8 $\pm$ 1263.9	4480.9 $\pm$ 1245.8
Ranging-long	10	19.2 $\pm$ 13.5	1 $\pm$ 0.4	14378.4 $\pm$ 4408.8	2511.9 $\pm$ 993.7	8281.3 $\pm$ 1671.1	8058.3 $\pm$ 1468.3

1

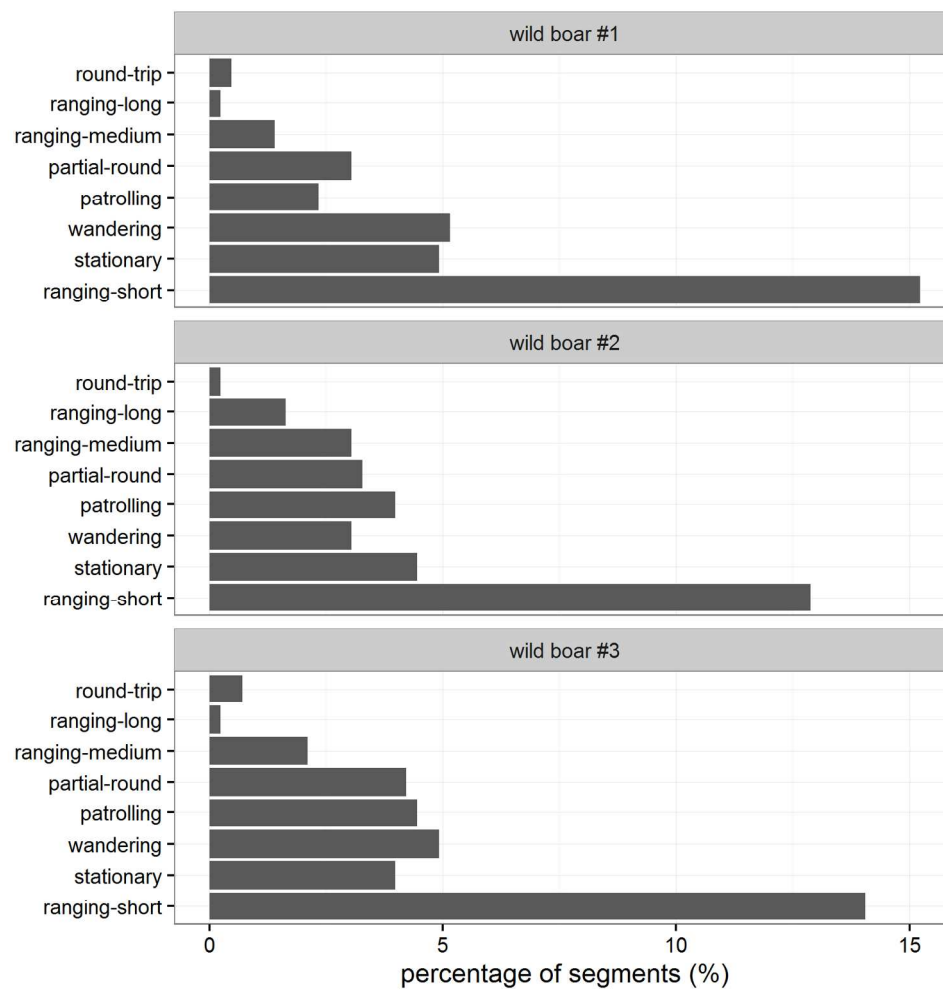


Figure 2. Percentage of segments classified as specific movement modes for the three GPS-tracked sub-adult, male wild boar.

162x162mm (300 x 300 DPI)

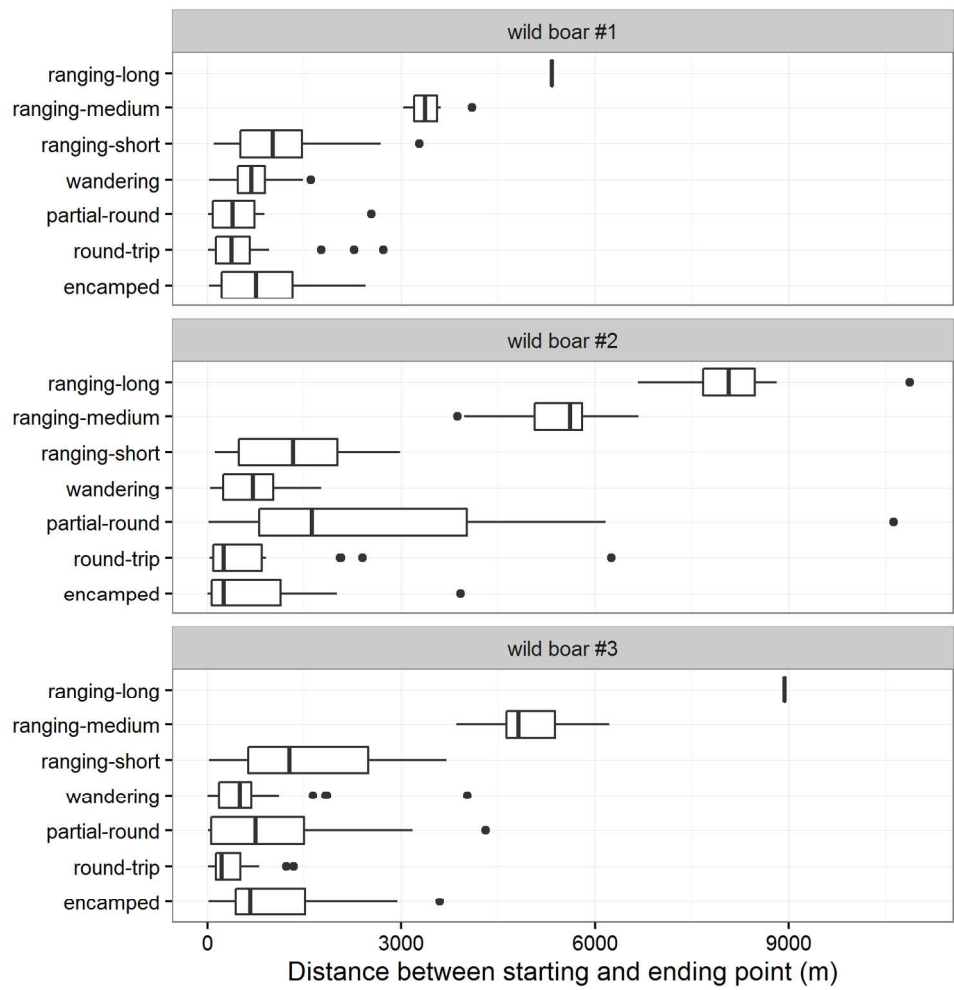


Figure 3. Comparison of the different classified movement modes according to the net displacement between the starting and ending points.

162x162mm (300 x 300 DPI)



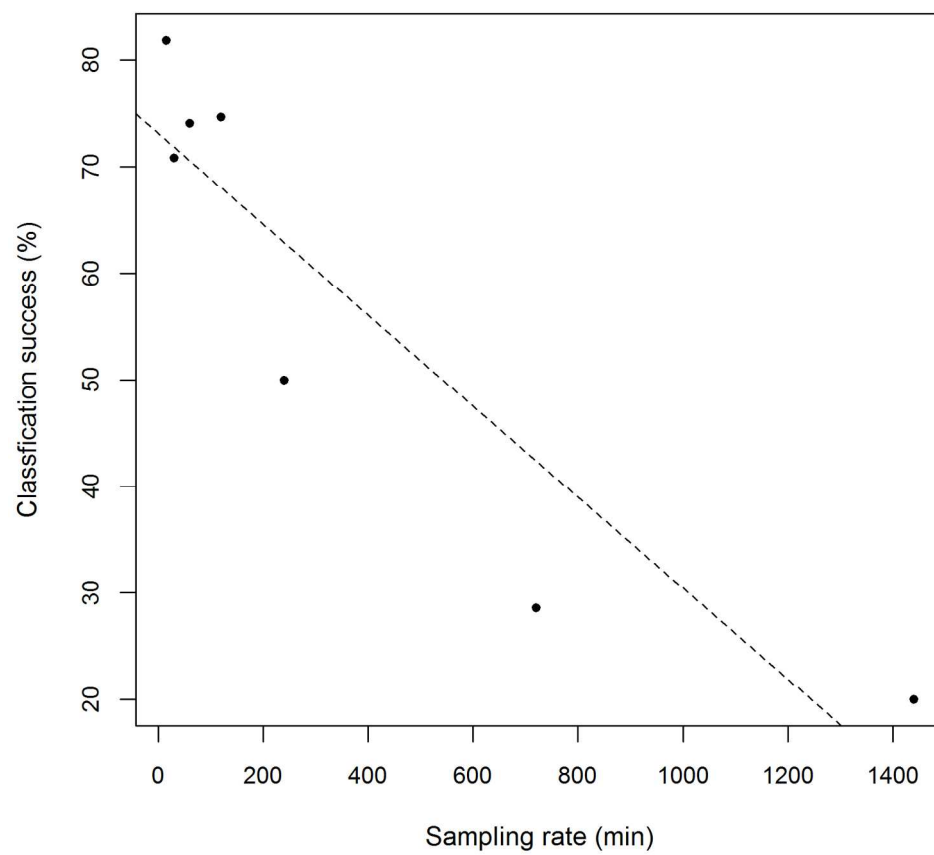


Figure 4. Effect of the sampling rate on the classification success of segments into a candidate movement mode.

162x162mm (300 x 300 DPI)

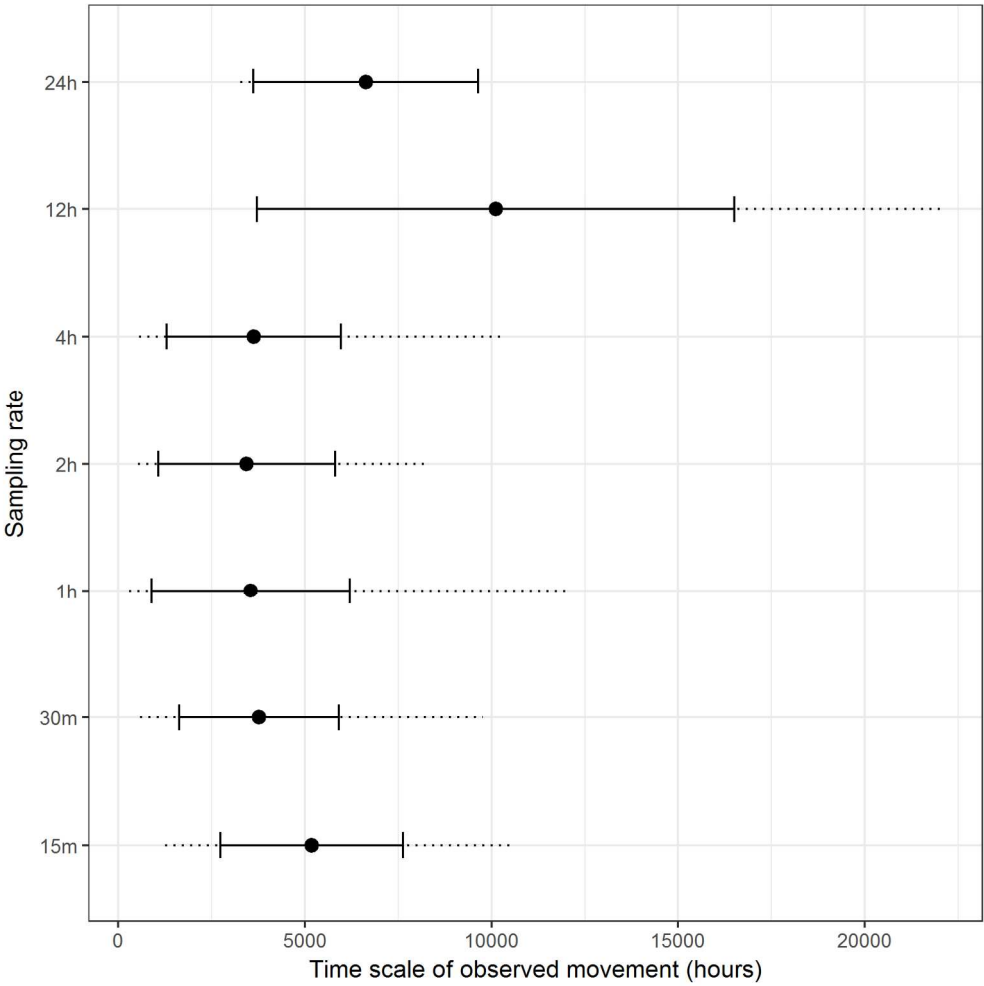


Figure 5a. The effect of varying the resampling rate on the correct identification of spatial (a) and temporal (b) scales of all classified movement behaviours. Mean (black dot), standard deviation (vertical bar) and range (dotted line) are indicated.

162x162mm (300 x 300 DPI)

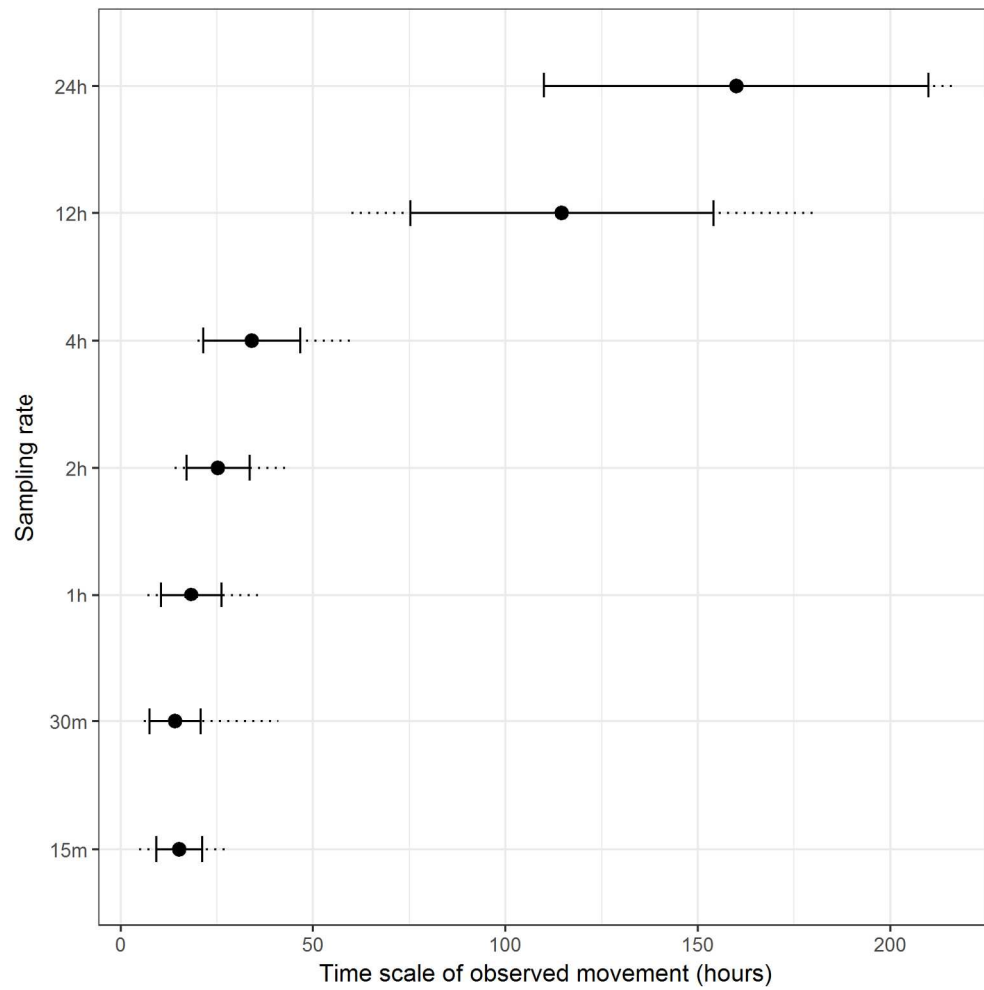


Figure 5b.

162x162mm (300 x 300 DPI)