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

3

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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

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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/sinuuous 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

1 boar *Sus scrofa* tracked by GPS and investigate the potential suitability of this method for
2 broad application.

3

4 **Materials and methods**

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

7 *Step 1: Segmenting GPS track into meaningful segments based on similar “state”*

8 We apply behavioural change point analysis (BCPA) to automatically segment the
9 complete time-series, in our case a complete GPS track (Gurarie *et al.* 2009). This method
10 converts raw locational data (i.e. including time, latitude and longitudinal positional fixes, e.g.
11 as produced by GPS loggers) into a time-series’ of step length (distance between two
12 consecutive relocations) and turning angle (angle between two consecutive steps, a measure
13 of directional change) and then further transforms these into orthogonal persistence velocity
14 (the magnitude of movement) and turning velocity (tendency toward a particular direction)
15 (Gurarie *et al.* 2009, see Appendix S1). Persistence and turning velocity presents the
16 advantage of being locally stationary and Gaussian, enabling the analysis of this
17 autoregressive process as a time-series process (Gurarie 2008). Any significant change in
18 parameters (either mean, variance or continuous autocorrelation) in this time-series, identified
19 using Bayesian Information Criterion (BIC), is considered as a change in the animal state.
20 BCPA relies on user-defined settings: *response variable* (persistence velocity or turning
21 velocity or combination of both), *moving window size* (within which significant structural
22 shifts between homogenous patterns are assessed), *cluster width* (temporal range over which
23 changing points are observed) and *sensitivity parameter* (K). Since we had no prior
24 information on the effect of these parameterizations, for our case study (see below) we tested

1 the effect of the above-mentioned parameters on the outcome of BCPA prior to implementing
2 final BCPA on our GPS tracks.

3 We then calculate net squared displacement (NSD) separately for each segment (see
4 Papworth *et al.* (2012) for detailed R code). NSD, which is the Euclidian squared distance
5 between the first location of a segment and any consecutive relocations, is an effective
6 method to characterize GPS data because it transforms movement data from 3D (x, y, t) to 2D
7 (x from origin, t) permitting the application of simpler statistical models (Börger & Fryxell
8 2012). NSD is commonly used to model migratory movement of animals at very large scales
9 (Bunnefeld *et al.* 2011; Singh *et al.* 2012; Beatty *et al.* 2013) but can logically be applied to
10 smaller scale movements.

11

12 *Step 2: Defining potential candidate movement modes*

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

1 spatial modes: encamped (i.e. sedentary behavior), round trips (complete and partial), ranging
2 (i.e. rapid directional movement) and wandering (i.e. non-directional movement).

3 Once decided upon, mathematical curve equations that best represent each movement
4 mode are identified. First, users define an expected relationship between NSD and time for
5 each candidate movement mode (e.g. Figure 1). Dummy data are generated for each
6 candidate mode (extracting data points from published sources, or “drawing” the shape of the
7 curve (Fig 1) and extracting the underlying data points). Curve-fitting routines are then used
8 to identify the equation that represents (best fits) the dummy data, translating the expected
9 shape into a mathematical relationship between NSD and time. For example, we used model
10 selection routine `pn.mod.compare()` in *FlexParamCurve*, which provides a simple method for
11 discriminate among non-linear curves (Oswald *et al.* 2012), to identify the specific non-linear
12 equation that best represented each of five movement modes: encamped, round-trips, partial
13 round-trips, wandering and ranging (Table 1, see case study below). The names chosen
14 represent previously reported behaviors translated to small spatiotemporal scales (e.g. ranging
15 is a short-term, small scale version of a dispersal movement mode). We then designated
16 linear models for wandering and encamped behaviours (Table 1).

17

18 *Step 3: Classifying segments into movement modes*

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

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

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

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

17 Each segment is then classified as the movement mode with the highest CC value.
18 Segments with poor fitting values (i.e. above/below a threshold of 0.7, empirically assessed)
19 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*

22 We illustrate our approach using movement data from wild boar, a species with a
23 high spatial plasticity of complex movements strategies (Spitz & Janeau 1990; Janeau et al.

1 1995a; Podgórski et al. 2013). GPS data were collected from three subadult males tracked in
2 an agroecosystem of Southern Belgium (50°25'N, 4°53'E). Animals were caught using 2 x 1
3 m transportable baited (with corn) cage (Jullien 1990) in autumn 2011 and tagged with
4 GPS/GSM Plus 3D collar (Vectronics Aerospace GmbH). To avoid influences of hunting
5 disturbances (McIlroy & Saillard 1989; Keuling et al. 2008), we only used tracking data
6 collected between January 1 and April 31, 2012. During this period, positional fixes were
7 recorded for each tracked individual at an interval of 15 min.

8 Raw GPS data were “cleaned” by removal of extreme locations, i.e. presenting
9 unlikely speeds (distances moved within the sampling interval) and turning angles associated
10 with outgoing and incoming movement (Bjørneraas *et al.* 2010). We specified these
11 parameters as follows: maximum moved distance to 10 km, speed to 1.5 m/s and angle spike
12 to 180°. Deleted locations composed 0.1% of all locations. Tracks were then decomposed into
13 movement segments using BCPA (Gurarie *et al.* 2009).

14 Before classifying consequent segments into movement modes, we classified
15 segments as stationary those segment with a maximum NSD < mean error around positional
16 locations, estimated from the literature at a value of 25 m (Orio *et al.* 2003). In total, across
17 the three observed individuals, 13.6% of segments were stationary. These segments were not
18 included in subsequent analyses. For the remaining segments, movement data were converted
19 into NSD.

20 Adapted from movement strategies observed at annual scale (Bunnefeld *et al.* 2011),
21 we tested whether our method was able to detect movement modes observed at the local in
22 wild boar. To this aim, we defined the following candidate set of five movement modes based
23 on i) adapted movement modes observed at annual scale (Bunnefeld *et al.* 2011) and ii)
24 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

1 parameters with a call to `nls()`. For strategies best represented by linear equations, i.e.
2 encamped and wandering mode (Figure 1), linear regression was performed (with and
3 without a slope parameter, respectively; Table 1) using `lm()` in the *stats* package in R.

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

14

15 *Evaluating the new approach*

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

22 We assessed the generality of our approach for different temporal scales by
23 resampling our data at different rates (varying from 1 location every 15 minutes to 1 location
24 every 24 h) and repeating our approach on each resampled dataset.

25

1 Results

2 Parameter settings in BCPA had little impact on the number of segments detected in
3 each track (Appendix S1, Figure S1.2), suggesting robust identification of changes in animal
4 behaviour. As final settings, we used a window size of 30, a sensitivity K of 2 and used a
5 cluster width of 2. These values of settings produced 143, 155 and 143 segments for each of
6 the three wild boar (Boars #1, #2, #3), respectively. Across all animal tracks, 72 stationary
7 segments were identified and excluded, representing 11.5%, 16.9% and 12.6% of total
8 tracking time of Boars #1, #2, #3, respectively. From the remaining 369 segments, 81.0 (± 6)
9 % were successfully classified into candidate movement behaviours (having $|CC| > |0.7|$ or
10 lowest AIC for encamped strategy). Though classified segments varied in duration from 5 to
11 54.2 h, mean duration was 10.4 (± 4.7) h, corresponding to half-day behavioural durations.
12 Classified movement behaviours displayed diagnostic movement patterns, ranging from
13 behaviours that usually occurred over a few hundred meters, to those that commonly involved
14 15 km of travel (Table 3).

15 The three individual sub-adult, male boar engaged in the seven defined movement
16 behaviours to a strikingly similar degree, spending most time in short-distance (1.5 ± 0.8 km)
17 ranging (43%) followed by either encamped, round or partially-round-trip modes (Figure 2).
18 Movements other than long-range (> 6 km) and medium-range ranging were generally over
19 small spatial scales (< 3.5 km, Fig 3). Longer range movements were relatively rare; only an
20 average of 6% of segments was medium-range and $\sim 1\%$ was long-range ranging mode. Total
21 distance travelled (TDT) and speed reached their minima and maxima in the encamped (1.2
22 km and 0.04 m/s) and long-distance ranging (21.9 km and 0.76 m/s), respectively (Figure 3).
23 Some individual differences between individuals were evident, with Boar #1 generally

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

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

10

11 **Discussion**

12 Our straightforward analytical framework combines existing, validated segmentation
13 and classification techniques to convert animal GPS tracks into multiple, high resolution
14 movement behaviours. Using field data for wild boar we show that our approach easily
15 accommodates behaviours that incorporate movements from a few hundred meters to > 15
16 km and lasted between 5 and 50 hours. Over 80 % of segmented GPS tracks were
17 successfully classified into predefined movement modes for data logged from wild boar at 15
18 min intervals. Resampling of these data indicated that classification success rates exceeding
19 ~70% were easily achievable as long as logging intervals were under 3 h and that bias in the
20 duration and spatial extent of classified modes was minimal when logging intervals remained
21 below 4 h. A minimum of six relocations could thus be used to model daily animal
22 movements, a resolution often achieved by studies tracking terrestrial mammals for seasonal
23 and multi-year information on habitat use. Furthermore, movement characteristics of the
24 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 (Bunnfeld *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 $2 * \text{peak}$) 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

1 to analysis (e.g., whole track, weekly, daily, hourly) and running it independently on all
2 chunks. In our case study, applying BCPA over only round-trip bouts, we found break points
3 not detected when run over the whole whole track, but to be anticipated considering that a
4 round-trip movement is made of at least two different spatial movements.

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

16 **Author contribution**

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

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2 conflict of interest.

3 **Data Accessibility**

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

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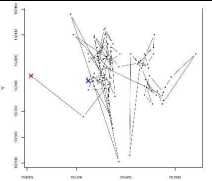
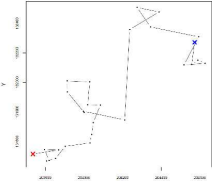
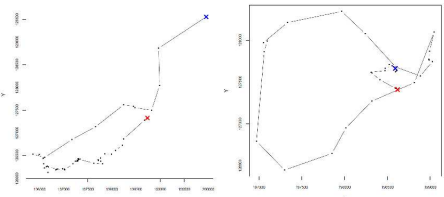
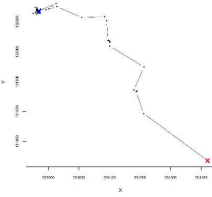
10 **Supporting Information**

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

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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 (hours)	Speed (km/h)	Total travelled distance (m)	Average radius (m)	Net displacement (ND) (m)	Maximum 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

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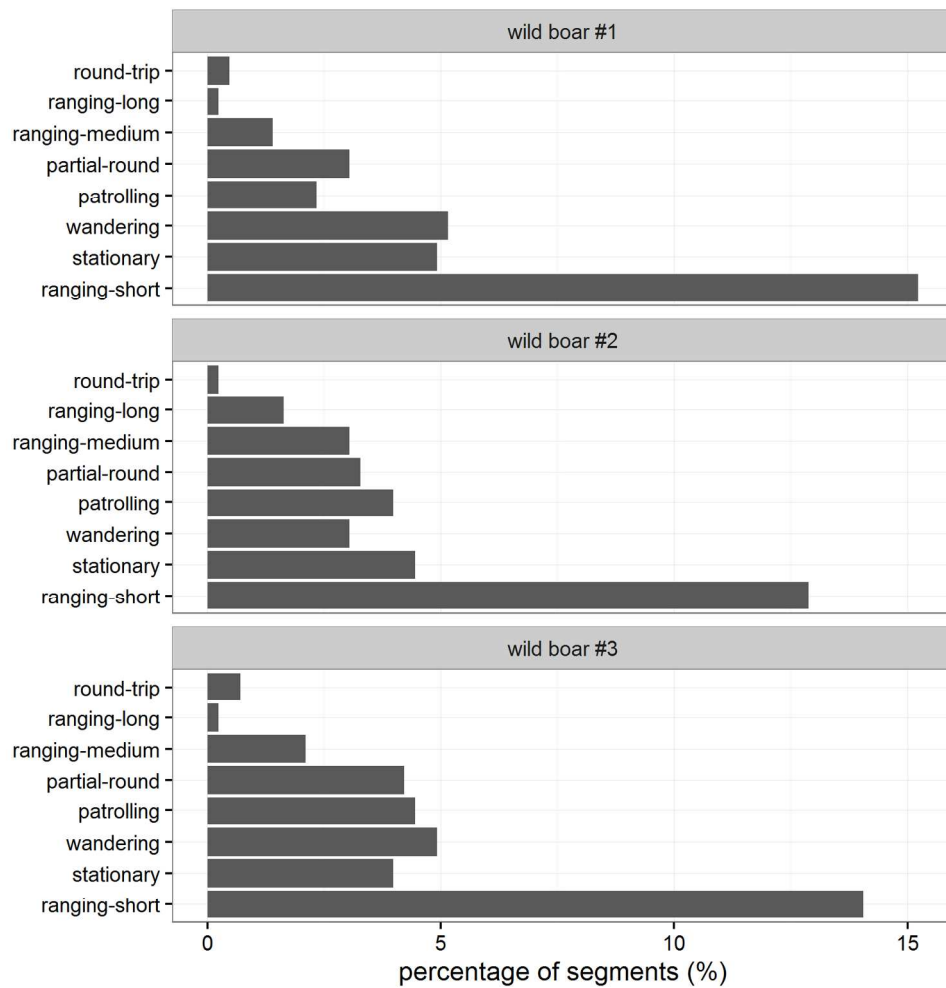


Figure 2. Percentage of segments classified as specific movement modes for the three GPS-tracked sub-adult, male wild boar.

162x162mm (300 x 300 DPI)

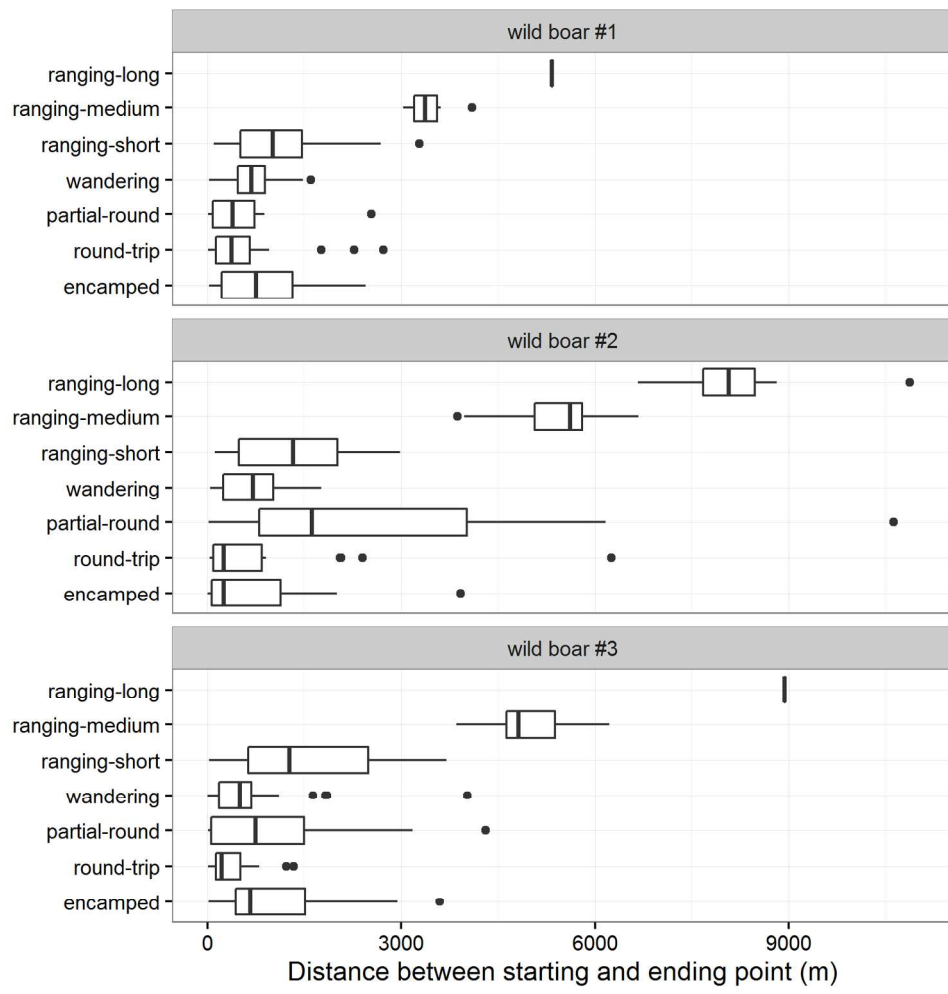


Figure 3. Comparison of the different classified movement modes according to the net displacement between the starting and ending points.

162x162mm (300 x 300 DPI)

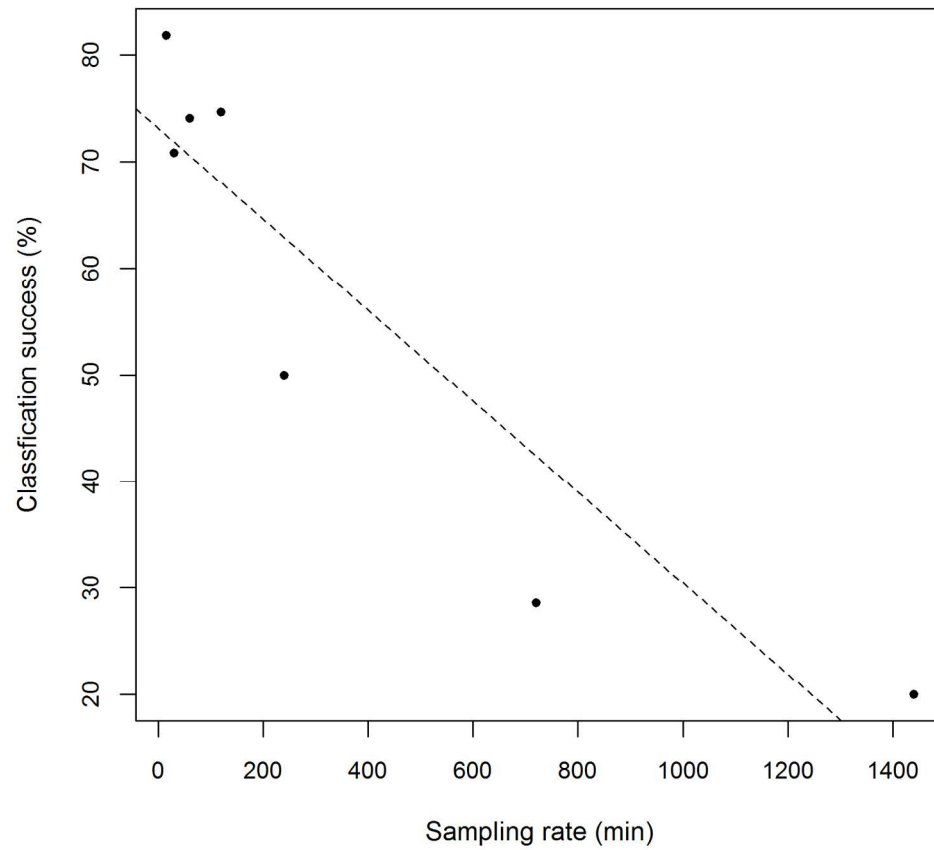


Figure 4. Effect of the sampling rate on the classification success of segments into a candidate movement mode.

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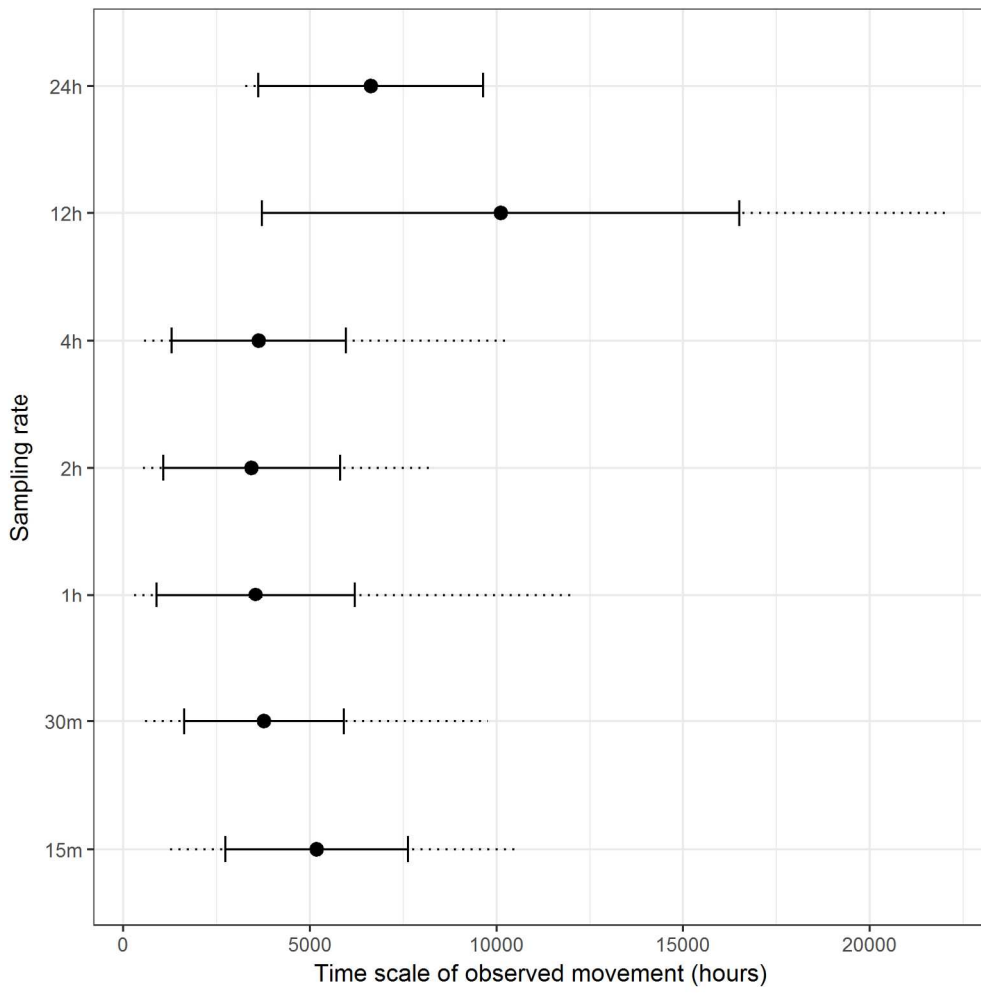


Figure 5a. The effect of varying the resampling rate on the correct identification of spatial (a) and temporal (b) scales of all classified movement behaviours. Mean (black dot), standard deviation (vertical bar) and range (dotted line) are indicated.

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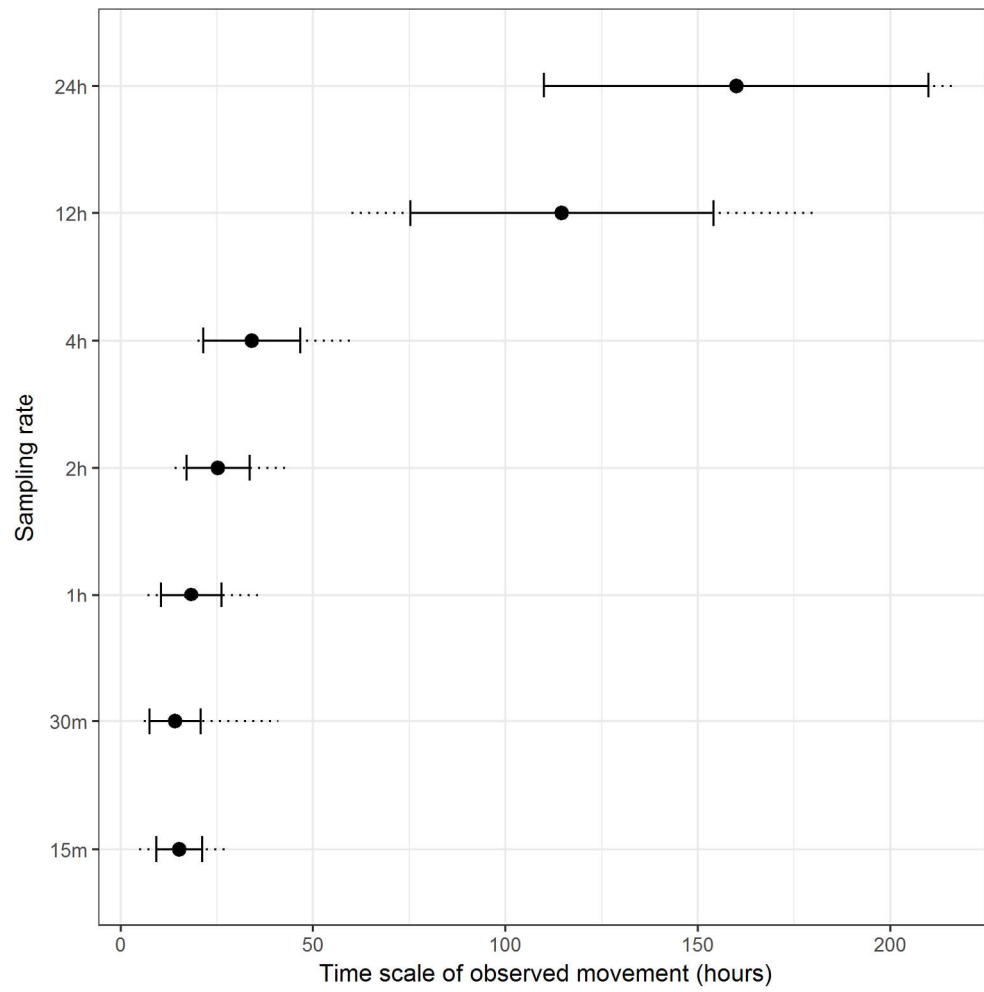


Figure 5b.

162x162mm (300 x 300 DPI)