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Characterizing change points and continuous transitions in movement behaviours using wavelet decomposition

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Summary

1. Individual behaviour, that is, the reaction of an organism to internal state, conspecifics and individuals of other species as well as the environment, is a crucial building block of their ecology. Modern tracking techniques produce high-frequency observations of spatial positions of animals and accompanying speed and tortuosity measurements. However, inferring behavioural modes from movement trajectories remains a challenge.

2. Changes in behavioural modes occur at different temporal and spatial scales and may take two forms: abrupt, representing distinct change points; or continuous, representing smooth transitions between movement modes. The multi-scale nature of these behavioural changes necessitates development of methods that can pinpoint behavioural states across spatial and temporal scales.

3. We propose a novel segmentation method based on the discrete wavelet transform (DWT), where the movement signal is decomposed into low-frequency approximation and high-frequency detail sub-bands to screen for behavioural changes at multiple scales. Approximation sub-bands characterizes broad changes by taking the continuous variations between behavioural modes into account, whereas detail sub-bands are employed to detect abrupt, finer scale change points.

4. We tested the ability of our method to identify behavioural modes in simulated trajectories by comparing it to three state-of-the-art methods from the literature. We further validated the method using an annotated dataset of turkey vultures (*Cathartes aura*) relating extracted segments to the expert knowledge of migratory vs. non-migratory patterns. Our results show that the proposed DWT segmentation is more versatile than other segmentation methods, as it can be applied to different movement parameters, performs better or equally well on the simulated data, and correctly identifies behavioural modes identified by the experts. It is hence a valuable addition to the toolbox of land managers and conservation practitioners to understand the behavioural patterns expressed by animals in natural and human-dominated landscapes.

Key-words: change points, continuous transitions, discrete wavelet transform, movement behaviour, scale, segmentation

Introduction

Inferring behaviour from movement trajectories can be hampered by behavioural heterogeneity, which is a key property of movement processes and results in multiple movement modes in the trajectory of an individual (Gurarie, Andrews & Laidre 2009). For example, the behaviour of an animal is influenced by environmental heterogeneity, such as varying spatial and temporal resources (Giuggioli & Bartumeus 2010; Yackulic *et al*. 2011). Animals therefore usually linger (i.e. move slowly and with short steps and large turning angles) in locations with abundant resources, whereas they move faster and more linearly in locations without resources or when migrating (Schtickzelle *et al*. 2007). Moreover, due to the effect of internal and external factors influencing movement at different spatial and temporal scales, behaviours may result in different patterns at various scales (Nathan *et al*. 2008; Thiebault & Tremblay 2013). Confining the analysis of scale to the original temporal granularity will hence overlook the fact that each movement pattern has a particular scale range at which it is manifested (Laube & Purves 2011; Soleymani *et al*. 2014; de Weerd *et al*. 2015). Importantly, not only the behavioural modes but also the transitions between them are intrinsically multi-scale (Gaucherel 2011). For example, different behaviours in a bird trajectory (i.e. flying, foraging, resting) may occur at different spatial and temporal scales and similarly, the magnitude of variations in a flying mode is at a different scale than the ones in a resting mode. Thus, extracting behavioural states from movement data requires an approach that can act at multiple temporal scales, which not only detects the abrupt changes in behavioural modes but also pinpoints the continuous variations in movement characteristics.

Trajectory segmentation represents a set of methods, where variation in movement parameters (MP) – such as speed,

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tortuosity, etc. – is used to identify segments of homogenous characteristics corresponding to particular behavioural states (Buchin *et al.* 2011). Different segmentation approaches have been employed to identify behaviours in movement trajectories of a range of species. The first approaches were based on simple metrics such as fractal dimension (Fritz, Said & Weimerskirch 2003; Nams 2005; Webb *et al.* 2009) or first-passage time (Fauchald & Tveraa 2003; Pinaud 2008), which can pinpoint different regimes in the movement signal. These methods, however, do not identify change points or segments. More recently, Gurarie, Andrews & Laidre (2009) developed a method for behavioural change point analysis (BCPA) based on likelihood estimation to detect abrupt structural changes in the values of movement parameters. Thiebault & Tremblay (2013) introduced another segmentation method based on the consistency of speed and direction in movement to split trajectories based on breakpoints that correspond to decisions of animals to change their movement. Machine learning approaches have also gained attraction: de Weerd *et al.* (2015) used decision trees to classify high-frequency movement trajectories of cows into fine-grained behaviours of foraging, lying, standing and walking. Finally, the most mechanistic but also technically demanding segmentation approaches are Bayesian state-space models (Jonsen, Myers & Flemming 2003; Morales *et al.* 2004; Jonsen, Flemming & Myers 2005; Patterson *et al.* 2008). They have been shown to correctly classify turning angle and step-length distributions into different behavioural modes (Beyer *et al.* 2013), dealing with observational error and being able to pinpoint important mechanisms in movement variation (Patterson *et al.* 2008). Due to their ability to model underlying processes, state-space models are suitable for predictive modelling, however, they are computationally demanding and hence less suitable for large-scale analyses.

Gurarie *et al.* (2016) illustrate two important limitations of the above methods for behavioural characterization of movement data. First, all approaches rely on a single, given movement parameter (e.g. speed) to detect changes in behaviours. Therefore, they generally have difficulties identifying cases where behavioural states are affecting other parameters (e.g. tortuosity), a problem termed *model misspecification* by Gurarie *et al.* (2016). Model misspecification extends to methods that do not account for autocorrelation in the movement variables, leading to spurious change points and hence false inference. Second, overlooking autocorrelation effects will also cause methods to fail in correctly *determining the magnitude of changes* in movement modes, which is due to their emphasis on detecting abrupt changes and therefore missing the continuous variations in the movement modes (Gurarie *et al.* 2016).

Recognizing the importance of scale, some of the aforementioned methods are capable of multi-scale analysis (i.e. fractal analysis and first-passage time). There are other methodological approaches for computation of MPs at different temporal window sizes (Laube & Purves 2011) or the multi-scale straightness index (Postlethwaite, Brown & Dennis 2012). The wavelet transform has been proposed as another multi-scale approach to link movement patterns (periodic movements) to internal and external factors (e.g. physiological, ecological, contextual; Wittemyer *et al.* 2008). Polansky *et al.* (2010) used the continuous wavelet transform (CWT) to identify temporal dependency (i.e. timing and extension) of behavioural patterns, which are not detected by other frequency-based methods (e.g. Fourier transform). Gaucherel (2011) identified the continuity between transitions of discrete behavioural modes using CWT analysis. Puckett, Ni & Ouellette (2015) employed CWT to extract behavioural modes indicating pairwise interactions in trajectories of swarming midges. The discrete wavelet transform (DWT) on the other hand has been applied in change point detection of bird trajectories (Sur *et al.* 2014) and to extract recurring and periodic behaviours of ciliates (Soleymani *et al.* 2015). CWT is mainly used where a qualitative explanation of movement behaviours is sought by visual exploration of the wavelet coefficients, whereas DWT provides a quantitative approach readily streamlined for change point detection in movement behaviour.

We propose a new segmentation method based on the DWT to infer behavioural states from movement trajectories in a multi-scale manner. The movement signal (formed by the time series of a movement parameter) is decomposed via the DWT into *low-frequency approximation sub-bands* and *high-frequency detail sub-bands* at multiple scales. For the approximation sub-bands, a method based on *peak analysis* is used to detect broad-scale patterns, whereas for the detail sub-bands, thresholding of DWT coefficients is used to identify abrupt change points. To our knowledge, no study so far combined information from detail and approximation components of the DWT for behavioural movement analysis. An implementation of the method in *Matlab R2016a* scripts is provided as supplementary material.

We compare the performance of DWT to state-of-the-art techniques, including first-passage time (FPT), Bayesian partitioning of Markov models (BPMM) and BCPA, using simulations presented in Gurarie *et al.* (2016), to show how the DWT-based segmentation can overcome limitations of those methods. We then validate our method by applying it to long trajectories of migratory turkey vultures (*Cathartes aura*). The results show high correspondence of the segments identified by the DWT and those annotated by experts.

Materials and methods

INTRODUCTION TO SPECTRAL ANALYSIS

Spectral analysis aims to detect periodic variation in a signal, such as the time series of step lengths or turning angles from a movement trajectory of an animal. For spectral analysis, the time series of movement parameters is transformed from the time domain into the frequency domain (frequency = 1/period of the signal). The signal is decomposed by the *Fourier* transform into sine and cosine terms (i.e. representing various frequencies) and then partitioned into all frequencies contributing to the variation in the original time series (Boggess & Narcowich 2009). The partitioning allows to pinpoint the most relevant frequencies and hence periods, however, no information is provided about when in time these frequencies occur. Moreover, an important assumption of the Fourier transform is a stationary signal, that is, the mean and variance of the signal do not change over the sampling period. This often does not hold for movement time series, where behaviour changes along a trajectory. The wavelet transform can overcome these limitations (Daubechies 1990).

WAVELET ANALYSIS

The wavelet transform can detect and localize different forms of changes in time series, by scaling and shifting a single *mother wavelet* function across the time series and quantify the correspondence between them as a wavelet coefficient. Because the wavelet transform uses a finite oscillatory function, it can resolve the temporal location, that is, pinpoint where in the movement signal the correspondence between the signal and the mother wavelet is high, resulting in high values for the associated wavelet coefficients. This is a major distinction to spectral analysis that does not contain information about temporal location. Furthermore, by scaling (i.e. dilating and contracting) the mother wavelet, the wavelet transform allows to zoom into smaller and larger scale variation across the time series and hence to look at variation in the signal at different scales.

The two main types of wavelet transform are the CWT and the DWT. CWT calculates the coefficients at every possible scale, whereas in DWT the shifting and scaling of the mother wavelet function is based on powers of 2 and therefore the signal is partitioned into dyadic blocks. Nevertheless, it is considered to be just as accurate as the CWT (Mallat 1999; Khorrami & Moavenian 2010). The scaling process of DWT can be also represented as a decomposition tree, where the original movement time series S is passed through low-pass and high-pass filters, yielding approximation (A) and detail (D) sub-bands. In its basic form, the decomposition is done based on only the lower resolution component (i.e. approximations) and the high-frequency component is not analysed further. However, the power of DWT can be significantly increased by a level by level transformation of both the low- and high-frequency components (Gokhale & Khanduja 2010). By retaining the length of the approximation and the detail sub-bands the same as the original signal, this will allow an analysis best matched to the signal (Appendix S1, Supporting Information).

Approximation sub-bands that contain the low-frequency components of the signal maintain the general structure of the movement signal. Conversely, the detail sub-bands contain the higher frequencies, enabling to capture the details of variation in the signal. As an example, the approximation sub-bands should retain periodicity due to migration back and forth between breeding and overwintering sites, whereas detail sub-bands should retain daily movement variation between foraging and resting sites.

APPLICATION OF THE DWT-BASED SEGMENTATION METHOD

An overview of the main steps of the DWT workflow is shown in Fig. 1. Movement parameters were computed for each trajectory fix (x, y, t) from the raw movement trajectory, representing the input signal for the wavelet analysis (e.g. the profile of speed over time). We selected a *Daubechies* wavelet of degree 4 as the mother wavelet to detect discontinuities and changes in the signal (Subasi 2007; Sur *et al.* 2014). Other mother wavelet functions are available (e.g. Haar, Morlet, Mexican hat) and their application depends on the response one is interested in. For instance, certain wavelet functions are able to resolve small, abrupt discontinuities, whereas others may better capture linear changes in the movement (Daubechies 1990; Boggess & Narcowich 2009). The movement signal (i.e. speed) will be first decomposed into approximation and detail sub-bands through the DWT (Fig. 2). Peak analysis of approximation sub-bands will be used for broad-scale behavioural segmentation, while thresholding of the detail sub-bands are used to detect more fine-scale change points.

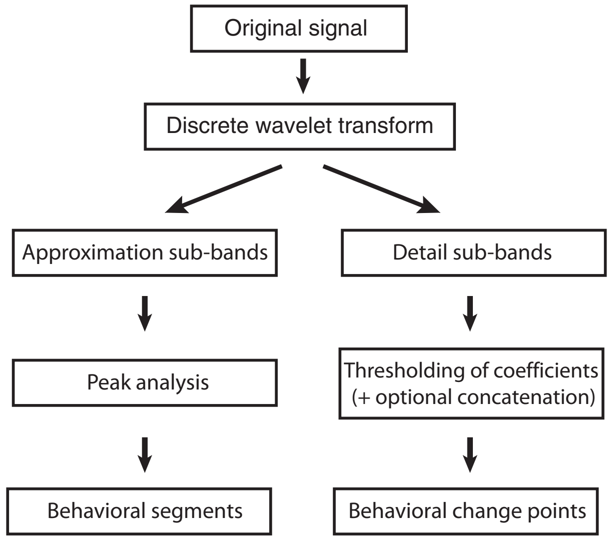

Fig. 1. Flowchart of the discrete wavelet transform (DWT)-based segmentation method. After the signal is decomposed by the DWT two major paths can be followed to extract behavioural segments via peak analysis (left side) or behavioural change points via coefficient thresholding (right side).

PEAK ANALYSIS OF APPROXIMATION SUB-BANDS

Approximation sub-bands will smooth the movement signal due to the locally adaptive property of DWT, where the effect of frequency localization becomes stronger at deeper levels of decomposition, by accounting for the values of neighbouring fixes (Daubechies 1990; Mallat 1999). Multiple approximation sub-bands result from the DWT transform and the appropriate decomposition level needs to be selected at which the signal can be divided into distinct segments. This step requires judgement by the analyst in terms of the target behaviour (e.g. migration vs. monthly or daily variation), but results are generally robust as long as the approximately correct decomposition level is selected. Next, *peak analysis* is performed on the selected approximation sub-band to differentiate between behavioural segments. Peak analysis has been widely used in different areas including genomic data analysis (Wilbanks & Facciotti 2010; Hocking, Hocking & Mcgill 2015) and moment segmentation of heart sound patterns (Sun *et al.* 2014). In this study, the peak *height*, that is, distance to the baseline (black vertical bars in Fig. 2) is used to distinguish between behavioural phases and the peak *width* (orange horizontal bars in Fig. 2) indicates the magnitude of the segments. To determine the width of the peak, the peak *prominence* (red vertical bars in Fig. 2) is used. The prominence of a peak is the minimum vertical distance to the local minima on either side of the peak, before reaching a higher peak or the signal endpoints. The width is then computed as the distance between two points on either side of the peak, where the signal intercepts the horizontal line through the mid-point of the prominence.

Thresholds for the height of the peaks are used to differentiate between behaviours (Fig. 2). A threshold can be selected to differentiate the heights of peaks A and C from peak B (Fig. 2). Depending on the number of target behaviours, the method is flexible to incorporate multiple behavioural phases by employing multiple thresholds for the heights of the peaks. Our method is designed such that all the adjacent

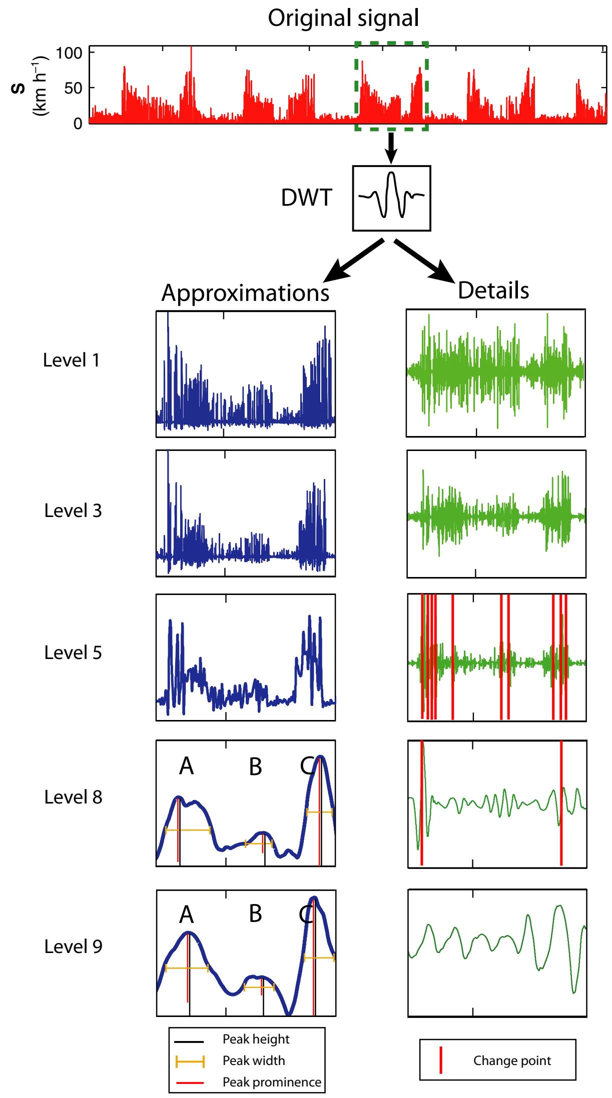

Fig. 2. A movement signal (i.e. speed profile of a bird trajectory) and the resulting discrete wavelet transform (DWT) sub-bands. The inset in the original signal highlights a part including migratory and non-migratory behaviours. After DWT decomposition, the resulting approximation sub-bands are shown on the left and the detail sub-bands on the right. The approximations contain lower frequencies and the general structure of the signal, while the details contain higher frequencies indicating abrupt changes and fine-scale structure of the signal. The approximations will show increasing smoothness with increasing level and ideally a level is reached where distinct segments become apparent. After peak analysis, the resulting peaks at the 8th level of approximation sub-band are a good estimator of differences between migratory (A and C) and non-migratory phases (B). In the detail sub-bands, a level where finer scale behaviours can be distinguished should be chosen, simultaneously making sure noise (e.g. tracking error) is not leading to too many false positives. In this example, thresholding on Level 5 seems indicative of such changes and would allow to further explore the fine-scale changes within migratory and non-migratory phases.

peaks below a certain threshold will represent the same segment and a new segment is only started if the adjacent peak exceeds the threshold. The magnitude of the segment is then calculated by summation of all the peaks within a threshold range. More detail, on setting these parameters, is given in the Section 'Parameterizing the decomposition levels and the thresholds' below.

THRESHOLDING OF THE DETAIL SUB-BANDS

Abrupt change points are detected with the help of the detail sub-bands (D), which in contrast to the approximation sub-bands (A) have better frequency resolution with each level of decomposition. As for the approximation sub-bands, first a decomposition level in the detail sub-bands is selected, where discontinuities suggestive of distinct behavioural modes become apparent. The change points are detected by measuring the difference between the detail coefficients of two subsequent points. If the difference to the previous point is higher than a defined threshold, they are marked as change points. We illustrate this by a time series in which two migratory phases are divided by a non-migratory phase (Fig. 2). The red points indicate change points, where the threshold value to the preceding fix is exceeded. In the next section, more detail is given on setting these parameters.

Measurement error and behavioural heterogeneity of movement data can lead to variable detail sub-bands. Therefore, using only the difference between detail coefficients will often result in excessive numbers of change points. In order to compensate, a shortest length constraint for the extracted segments can be specified, concatenating all the fixes (or a collection of fixes) in between and hence resulting in longer segments. By changing the shortest length constraint, the sensitivity to detect fine-scale behaviours is adjusted.

PARAMETERIZING THE DECOMPOSITION LEVELS AND THE THRESHOLDS

The method requires specifying a number of user inputs, which are informed by a minimum of domain knowledge about the expected behaviour. For both the approximation and the detail sub-bands, the selection of appropriate decomposition levels is done by visual inspection of the sub-bands (*approx_band* or *detail_band*). This can be done in a supervised fashion by comparing to the known behaviours in annotated datasets, or in an unsupervised fashion by spotting the appearance of distinct segments that the analyst would expect *a priori*, given the knowledge about his/her study organism. The selected decomposition levels will hence vary depending on the chosen movement parameter and the data used.

The thresholds for the peak height (*peak_threshold*) are selected by visual inspection, that is, by selecting the values of lower peaks as thresholds to detect the segments of higher peaks. Definition of sub-bands and thresholds should be carefully justified by the biology of the study organism and the expected behaviour. We provide examples and a step-by-step guideline for the implementation of the method in Appendix S2.

SIMULATED DATA

We used R code provided in Gurarie *et al.* (2016) to simulate tracks with switches in the speed and the tortuosity values (Appendix S3). In each simulation, one movement parameter is changing: speed in the first track and tortuosity in the second track. The behavioural modes are known in both simulations: the first and the fourth modes include 1000 fixes indicating intensive movement (i.e. low speed and high tortuosity) (shown in dark blue), whereas the second and third modes last 500 fixes, representing higher speed and less tortuous tracks (shown in green). The third mode represents movement with highest speed and least tortuosity (shown in red).

To compare the performance of the DWT segmentation to the segmentation methods presented in Gurarie *et al.* (2016), we count the number of extracted segments on the simulated data for each of the methods (Table 2). For detailed investigations of the performance of each of these methods except the DWT, the reader is referred to Gurarie *et al.* (2016). We exclude the multi-state random walk (MRW) model, since it assigns behavioural states to fixes rather than segments and hence cannot be compared. Since MRW performed rather poorly compared to the other methods presented in Gurarie *et al.* (2016), our comparisons remain representative. Speed for the first simulation and tortuosity (product of estimated velocity and the cosine of turning angles as calculated by the BCPA) for the second simulation were generated as the relevant MP signals for wavelet analysis.

In a second set of simulations, we compare whether the different segmentation methods can detect more continuous transitions (Appendix S4). We modified the speed simulation, such that there was a stepwise, gradual increase in the speed values (5 steps). Although this does not represent perfectly continuous transitions, it covers the middle ground between abrupt transitions and continuous transitions. In all the simulation cases, DWT segmentation was applied on the 6th level of approximation sub-bands.

EMPIRICAL DATA: TURKEY VULTURES

We use four GPS tracks of turkey vultures (*C. aura*) from the interior North America population to illustrate the segmentation method on real data. As shown in Fig. 3, the migration path extends from Canada to South America across central regions of North America. These birds show several states during their annual migrations: (i) breeding areas in North America, (ii) outbound migration in the Fall from breeding areas to wintering grounds, (iii) tropical wintering grounds in South America, and (iv) return migration to breeding grounds in the Spring. The data were manually classified into the above-mentioned behavioural states (four segments) by domain experts as discussed in Dodge *et al.* (2014). Although such annotated behaviour is valuable information to parameterize the analysis, this can as well be done by domain knowledge about the target behaviour, or in an exploratory fashion. To illustrate two of these cases, we used the track of the individual *Leo*. For validation purposes, three annotated trajectories of individuals *Mac*, *Steamhouse 1* and *Steamhouse 2* were used for validation (Table 1 and Appendix S5). The data of *Leo* and *Mac* were down sampled to 3 h (from the original 1 h), in order to be able to use the same decomposition level for all the individuals.

We first applied the segmentation approach based on the approximation sub-bands on the speed profiles of turkey vultures to illustrate the ability to recover behavioural annotation by expert knowledge. Level 8 of the approximation sub-bands was selected for segmentation based on the data of *Leo* (but see Appendix S6 for an illustration that the adjacent decomposition levels provide similar answers). The threshold for the height of the peaks was selected based on the highest peak in the non-migratory segments of the *Leo* track.

Second, we used the detail sub-bands to explore the more fine-scale behaviours. We show this by investigation of level 5 of the detail sub-bands of *Leo*. Here, we define a change point as a fix with a difference in the coefficient value >1 unit from its preceding fix. The shortest length constraint was selected as the appropriate length for the occurrence of migratory patterns in the data and set to concatenate sub-trajectories shorter than 500 fixes (i.e. ~20 days) between two change points.

Results

SIMULATED DATA

Discrete wavelet transform segmentation correctly extracted the four behavioural phases in the first two simulations (Table 2 and Appendix S3). In the speed-switch simulation, BPMM correctly detects all the four behavioural phases, while FPT (three segments) and BCPA (six segments) fail to capture the intermediate transitions. In the time-switch simulation, BCPA detects all the four phases accurately, whereas FPT remains uninformative about the intermediate transitions (three segments) and BPMM detects far too many segments (13). Regarding the case where transitions are increasingly continuous, only DWT was able to recover the five incremental speed steps, whereas the other methods identified excessive numbers of segments (Appendix S4 for visual performance of the methods).

TURKEY VULTURE DATA

Extraction of long migratory patterns using approximation sub-bands

All the annotated segments are retrieved accurately for *Leo*, except for a very short migration season at the end of the track (Fig. 4c,d). This is also the case for *Mac*, where a redundant segment is found on the edge (Appendix S5a). This is not the case for the DWT segmentation results on *Steamhouse 2* and *Steamhouse 1*, where all the behavioural segments are correctly identified (Table 3). Appendix S5 illustrates the application of the DWT segmentation method on these tracks.

The average temporal difference in the change points between the extracted segments and annotations is ~7 days among the four individual trajectories (Fig. 5), a good precision compared to the length of migratory segments (range approx. 45–80 days). As expected, the differences are lowest for *Leo*, since it was used as training data. The high differences for *Mac* might be due to highly heterogeneous and unevenly distributed migration seasons compared to the other individuals. For *Steamhouse 1* and *2*, the results are overall reasonable (Appendix S5b,c).

Extraction of fine-scale behaviours using detail sub-bands

Considering the high level of heterogeneity in the variation of detail coefficients (Fig. 6a), the thresholding of detail coefficients resulted in 162 change points shown in Fig. 6b. Careful investigation of the change points has the potential to identify behavioural states *within* the migratory/non-migratory phases and mine movement trajectories for cryptic behaviours. After applying the shortest length constraint (i.e. by concatenating the sub-trajectories shorter than 500 fixes between two change points) the segmentation result is shown in Fig. 6c. Many of the change points are filtered out by the concatenation. Most of the extracted segments now largely resemble the number and position of the annotated segments. However, some interesting differences are apparent within the non-breeding grounds in the years 2009, 2010 and 2011. These differences may reflect real fine-scale behavioural differences in the non-breeding grounds and only can be detected in the detail sub-bands.

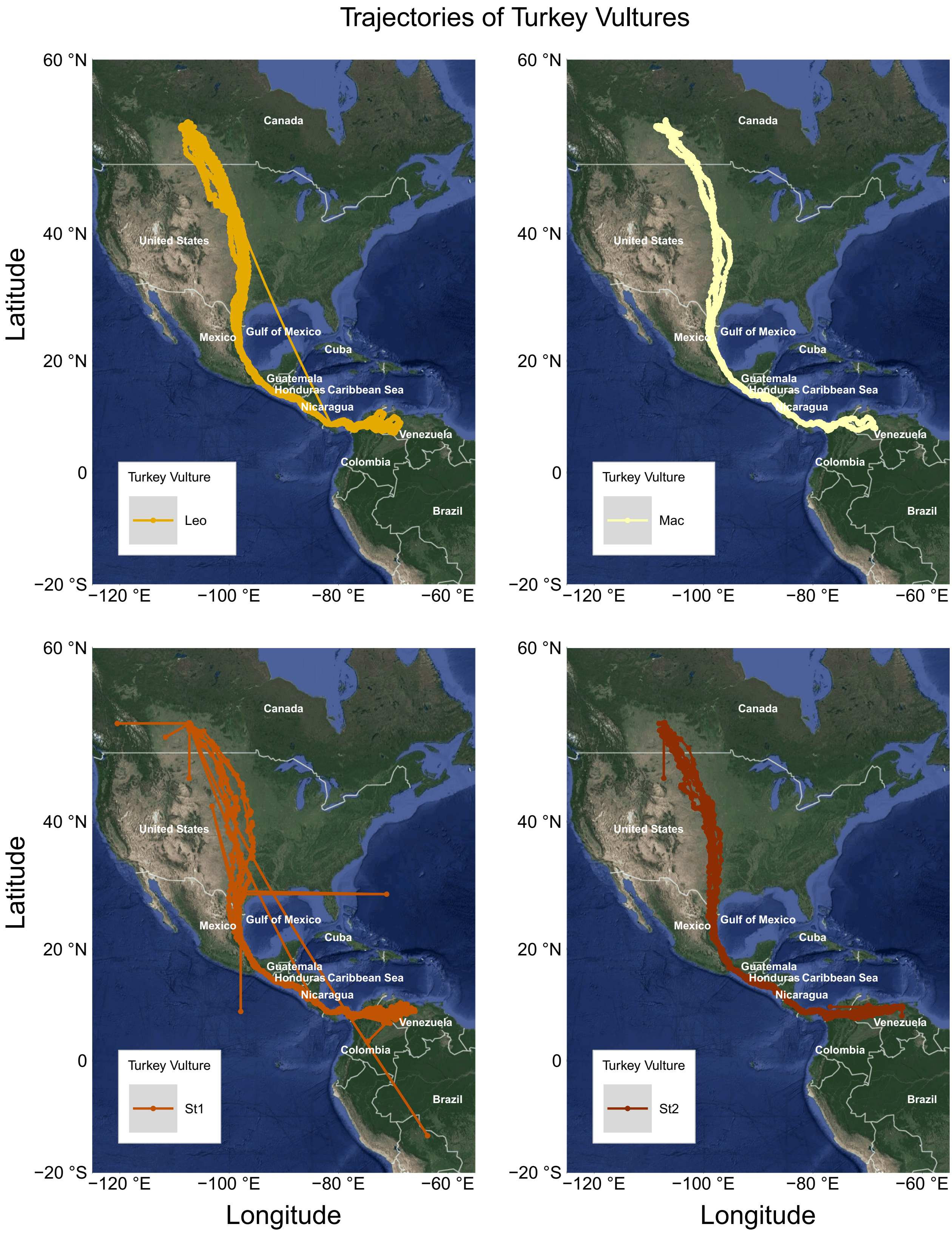

Fig. 3. The trajectories of the four turkey vulture individuals studied. The migration starts from Canada to South America, pathing through central regions of the United States and Central America, and reverse. Some outliers (especially in the case of Steamhouse 1) are evident, however, they were deliberately kept to assess the robustness of the proposed method.

Table 1. Summary of the turkey vulture track

Individual	Tracking period (from–to)	Number of fixes	Temporal resolution	Usage
Leo	16.06.2007–19.03.2013	11 752	3 h	Parameter setting of DWT method
Mac	17.06.2007–12.03.2008	3963	3 h	Validation
Steamhouse 1	22.05.2009–18.03.2012	6545	3 h	Validation
Steamhouse 2	23.05.2009–19.03.2013	10 472	3 h	Validation

Table 2. Number of segments extracted by discrete wavelet transform (DWT) compared to three state-of-the-art methods presented in Gurarie *et al.* (2016). Only the DWT was able to extract the correct number of segments in both simulations

Model	Speed-switch	Time-switch	Continuous simulation
FPT	3	3	>30
BPMM	4	13	30
BCPA	6	4	11
DWT	4	4	5
True number of segments	4	4	5

Behavioural change point analysis, BCPA; first-passage time, FPT; Bayesian partitioning of Markov models, BPMM.

Discussion

The high complexity and multi-scale nature of movement behaviours hampers the identification of homogeneous sub-trajectories indicative of behavioural modes. Here, we have shown that the DWT compares favourably against state-of-the-art methods in automatic behavioural segmentation of simulated trajectories, as well as on real movement trajectories of turkey vultures annotated by domain experts. In the following sections, we address the specific advantages of the DWT, such as overcoming model misspecification, scalability to large numbers of trajectories and detection of multi-scale behaviours.

CIRCUMVENTING THE MODEL MISSPECIFICATION PROBLEM

Discrete wavelet transform proved successful in relating wavelet coefficients at different scales (i.e. the sub-bands) to multiple behavioural modes. All four behavioural segments in both simulations were precisely detected using the appropriate approximation sub-bands. Importantly, only DWT was able to pinpoint segments when speed increased in a step-wise fashion,

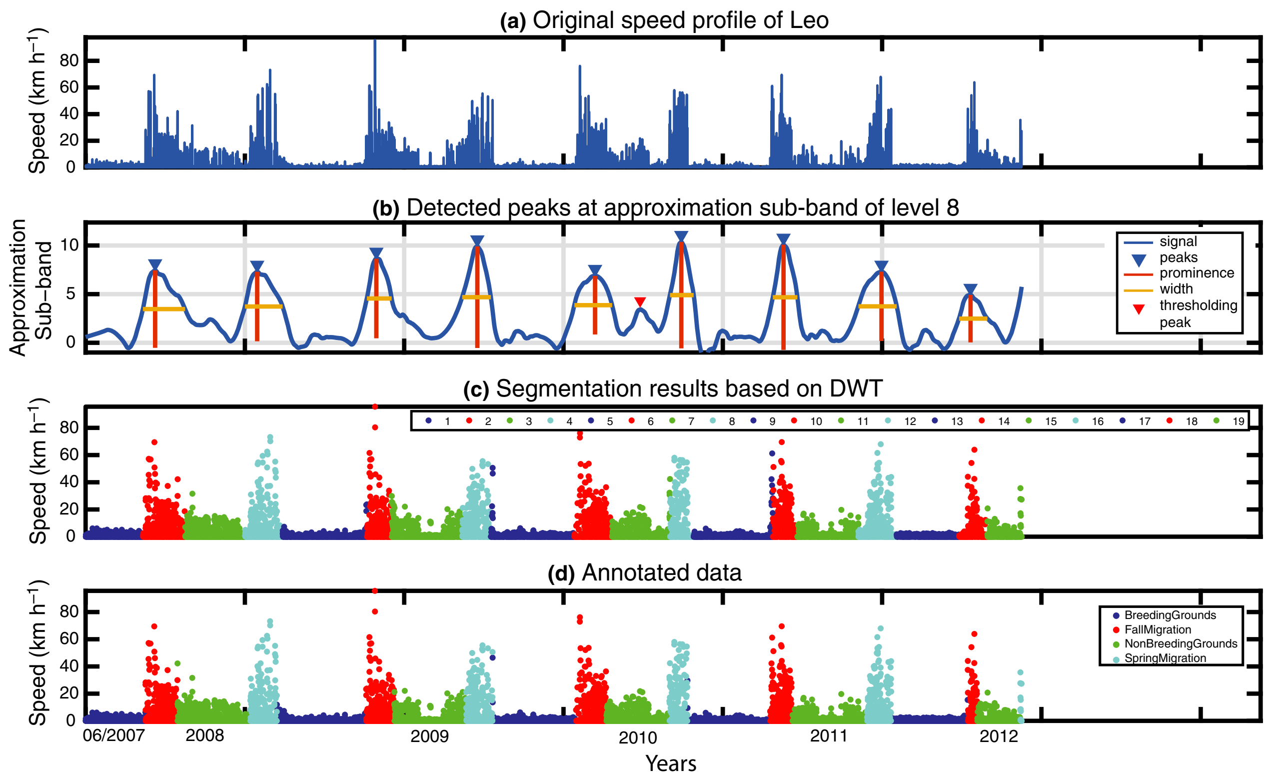

Fig. 4. Applying the proposed segmentation method on data of Leo. (a) Speed profile of Leo as the input signal for wavelet analysis. (b) Detected peaks in approximation level 8 by thresholding the height of the peaks, in order to distinguish between migratory and non-migratory seasons. (c) Segmentation results based on the width of the extracted peaks. The resulting 19 segments are closely representing the annotated data (shown in d).

Table 3. Comparison of the extracted and annotated behavioural segments for the four turkey vulture individuals. Individual *Leo* was used for parameter tuning and validation, the remaining individuals for external validation

Track	No. of annotated segments	No. of extracted segments	Remarks
Leo (training)	20	19	1 missed segment (due to edge effects)
Mac	6	7	1 redundant segment (due to edge effects)
Steamhouse 1	11	11	All segments comply to annotations
Steamhouse 2	15	15	All segments comply to annotations

highlighting its power to detect increasingly smooth transitions. This stands as a valuable contribution for the identification of continuous changes, that is, the intervals where the behaviour is in flux. This is due to the ability of DWT to account for autocorrelation effects and therefore precisely detect different magnitude of changes (i.e. continuous vs. abrupt) in movement (Gurarie *et al.* 2016). While we showed that the method is insensitive across a range of neighbouring sub-band levels (Appendix S6), careful selection of levels is crucial as very high or very low levels result in inappropriate degrees of autocorrelation and hence blur the behavioural signal.

By choosing the *relevant* univariate MPs in the two simulations – speed and tortuosity, respectively, – the four modes were efficiently distinguished. This addresses the *model misspecification* problem mentioned by Gurarie *et al.* (2016). Since the method is not dependent on any *given* movement parameter, different univariate MPs may be utilized according to their biological plausibility. In contrast, the other segmentation methods only performed well if changes in the behavioural phases were captured by their default movement parameter used for extracting behavioural states (e.g. BCPA usually is applied to the persistence velocity, which describes the tendency and magnitude of movement to persist in a given direction (Gurarie, Andrews & Laidre 2009)).

DWT TO QUANTIFY AND INFER BEHAVIOUR FROM GPS TRAJECTORIES

In the case of the turkey vulture data, the approximation sub-bands successfully identified the broad-scale patterns (migratory vs. non-migratory) lasting over a long time period. By emphasizing the effects of seasonal patterns, the *approximation sub-bands* allow to distinguish the migratory patterns from non-migratory patterns. The *detail sub-bands* in contrast highlighted more segments in the breeding seasons of 2009, 2010 and 2011. Although these segments are not matching the annotated data, they may be explained by larger breeding grounds in warmer seasons, where turkey vultures have to move longer distances to forage (Dodge *et al.* 2014). Detail sub-bands and the concatenation approach hence have the potential of detecting cryptic behaviour. The extracted segments representing migration seasons were also clearly narrower than the ones generated from the approximation sub-bands, referring back to the power of DWT to detect more abrupt changes through detail components, as well as more broad-scale continuous changes through the approximation sub-bands.

Successful recovery of behaviours identified by experts clearly illustrates the power of the DWT approach to work on noisy (see outliers in Fig. 3) and partly irregular data (including gaps). Hence, we suggest that the method can be employed for a multitude of study systems in which such data are collected. A major advantage of DWT is its computational efficiency, providing the scalability to apply the method to large numbers of trajectories in those domains.

We have shown how the parameters of the method were set and validated using the annotated data. We did so to illustrate the power of the method to recover behaviour identified by experts. However, the method can be equally applied in cases where no annotation is available. Domain knowledge about the target behaviour should then be used for the selection of parameters. Although ground truth data about annotation of selected trajectories is valuable for parameter setting and

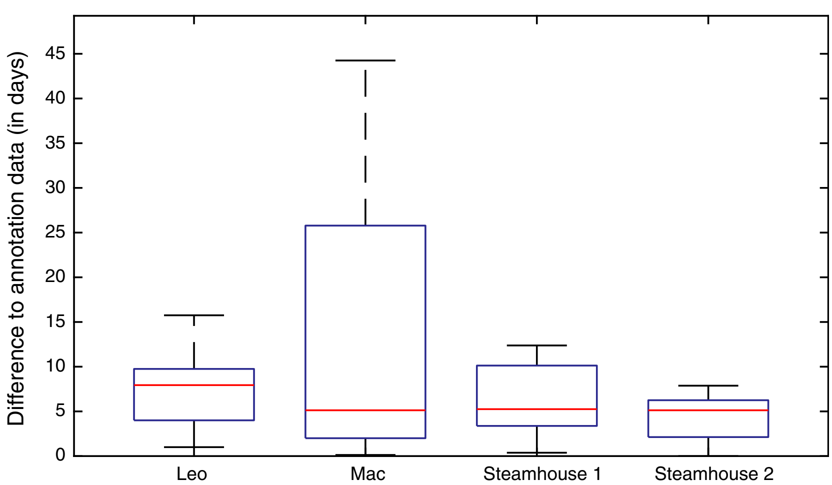

Fig. 5. Temporal difference between extracted and annotated segments in the turkey vulture tracks.

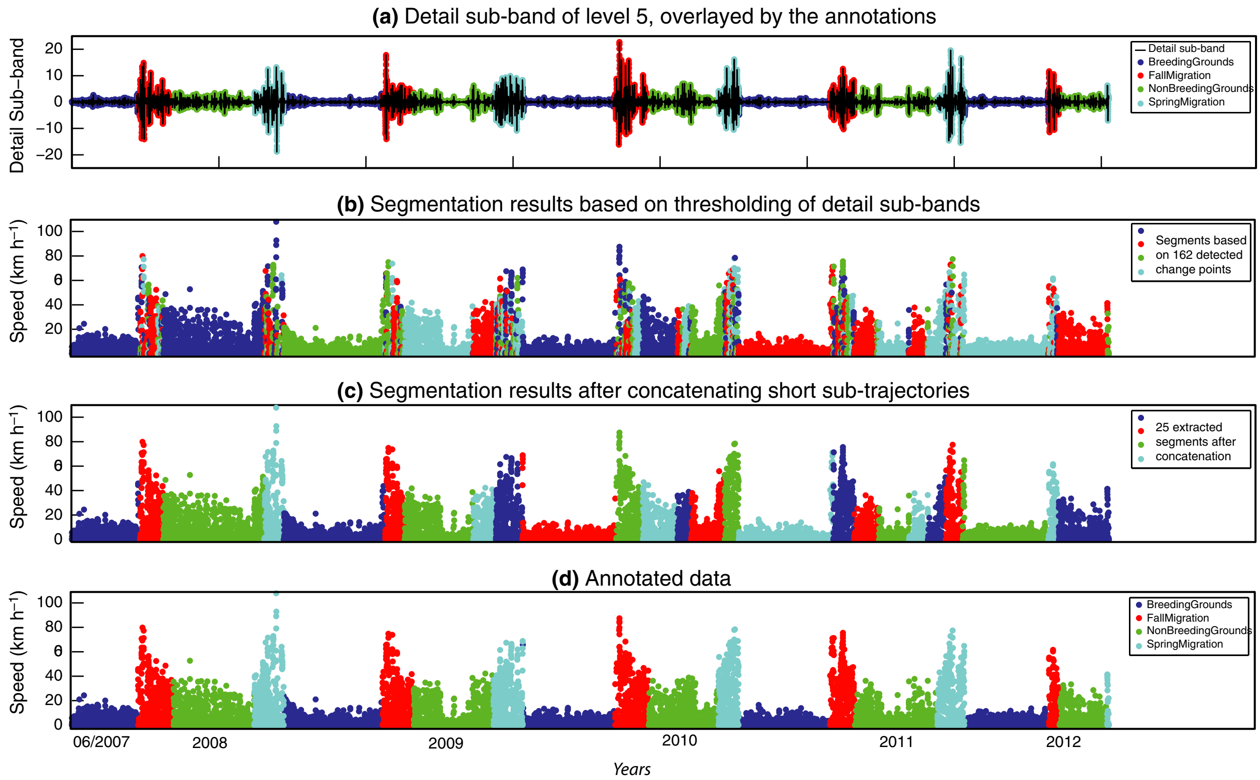

Fig. 6. (a) Overlaying the detail sub-band at level 5 over the annotation data. (b) Detecting change points by thresholding the detail coefficients. High heterogeneity of detail coefficients results in numerous change points and therefore segments. This is particularly visible in the non-migratory seasons, where the variation in the high-frequency content of the signal is higher. (c) After concatenating short sub-trajectories, segmentation results in 25 segments. This is an improved result compared to Fig. 6b, but some redundant segments still remain compared to the annotated data [shown in (d)].

validation, it is not a pre-requisite of the method; nevertheless, the costs and efforts to collect such data may be compensated when the procedure can be applied subsequently to hundreds of trajectories.

Our method takes two control parameters (i.e. sub-band level and threshold), which is less or equal to the number of parameters required to tune the other segmentation methods discussed in Gurarie *et al.* (2016). Moreover, the parameter settings of our algorithm are biologically intuitive, which according to Gurarie *et al.* (2016) is an important factor when fine-tuning the analysis. Doing so, we strike the balance between subjectivity and flexibility, where we integrate the biological knowledge for parameter setting to avoid at face, results by a fully automated method.

However, the method is not without downsides, as shown by the boundary effects in the trajectory of *Leo*. As the length of the wavelet may exceed the length of the final section when shifted along the time series, coefficients obtained from the end of the time series are unreliable. This is also referred to as the 'cone of influence' (Cazelles *et al.* 2008). We recommend discarding segments or parts of the segments affected by the cone of influence, or at least interpret these with great care. Another downside may be that wavelet analysis is also quite demanding in terms of sampling frequency and length of the movement profile. However, the ever-increasing performance of modern GPS tags is likely to compensate for these data requirements.

PREVIOUS WORK USING DWT AND CWT FOR BEHAVIOURAL SEGMENTATION

A similar application of DWT in trajectory segmentation was introduced by (Sur *et al.* 2014). In their work, the *Z*-scores of detail coefficients at a certain wavelet decomposition level are assumed to follow a normal distribution and thresholds are based on the 3-sigma rule. There are, however, certain limitations to this approach: (i) *Z*-scores may not follow the normal distribution (as was the case in our dataset); (ii) thresholds based on n-sigma classes are arbitrary because they lack a link to different movement modes; (iii) it is unclear how to extract more than three movement modes based on the n-sigma rule; (iv) using only the detail sub-bands is susceptible to noise and generally leads to an excessive number of segments. Our approach, in contrast, makes no hypothesis about the distribution of the wavelet coefficients and the semi-automatic thresholding can detect more than three behaviours. Moreover, the full information content of the wavelet decomposition is exploited by using both approximation and detail sub-bands.

Another study by Gaucherel (2011) used the CWT as a powerful tool for investigating the continuous transitions between the behavioural modes. However, the CWT has limitations in inferring the processes underlying movement by building the continuous wavelet map as the summation of the details at all decomposition levels plus the approximation at the final level. Therefore, the map is highly affected by the presence of the detail components and there is also no possibility to relate different frequency bands to different target behaviours. DWT helps discriminating behavioural modes in a more quantitative manner and relating the analysis scale to the multiple scales of expressed behaviours can contribute to our understanding of movement processes across scales.

Conclusion

The high level of variability and the multi-scale nature of movement complicate inferring movement behaviours from trajectories. We believe that the proposed segmentation method is an important step forward to extract movement behaviour from movement trajectories, overcoming some of the limitations of previous methods. Methods that are flexible enough to exploit different movement parameters as well as able to pinpoint not only behavioural segments but also the smooth transitions in between are urgently needed to exploit the full information content in the increasing number of movement trajectories available. Relating movement behaviours across scales to external and internal factors of focal individuals is one of the goals of the movement ecology paradigm (Nathan *et al*. 2008) and the DWT has the potential to uncover some of these links.

Authors' contributions

A.S., F.P. and R.W. conceived the ideas and designed methodology; A.S. and S.D. designed the experiments and processed the data; A.S., F.P. and R.W. analysed the data; A.S., F.P., S.D. and R.W. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

The trajectory data of turkey vulture individuals are available on Movebank (http://www.movebank.org) and are published in the Movebank Data Repository (doi:10.5441/001/1.46ft1k05).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Example of decomposition of movement signal using DWT transform.

Appendix S2. Step-by-step guideline for the application of the DWT-based segmentation method.

Appendix S3. Simulated tracks and the results of applying the DWT-based method.

Appendix S4. Comparison of the DWT-based method to the state-of-the-art segmentation methods to detect continuous transitions in movement.

Appendix S5. Results of applying the proposed DWT-based method on the movement tracks of turkey vulture individuals *Mac*, *Steamhouse 1* and *Steamhouse 2*.

Appendix S6. Sensitivity analysis of the DWT-based segmentation method.

Appendix S7. Matlab and R codes used for implementation of the DWT-based method.