Computational Ecology and Software, 2011, 1(2):69-85

Article

Wavelet analysis to detect regime shifts in animal movement

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Received 11 March 2011; *Accepted 20 April 2011*; *Published online 15 June 2011*
IAEES

Abstract

Animals most often move in a non-homogeneous way as a long movement path through a heterogeneous landscape that corresponds to a sequence of various behavioural states. Hence, a large majority of movement analyses make the assumption that long movements combine typical behaviours like intensive search or resting which are separated by sharp transitions.

This study aimed at providing an alternative method for identifying intensive search areas using sharp as well as more continuous (smooth) transitions. I proposed analyzing movement data over temporal and spatial scales by the use of the wavelet analysis and drew inferences about the behaviours that shape movements.

I computed a synthetic index built with wavelet time-spectra of turning angle and speed parameters, this method offered a robust and automatic way to characterize movement transitions. The first step was to work on simulated movements to define the confidence levels of detection. The second was to illustrate the use of wavelet analysis on the movements of wandering albatrosses.

As a result, this study outlined two fundamental areas of interest in animal movement analysis: i) it is relevant to select behavioural modes with continuous transitions between them along the animal's movement, as it is done with usual segmentation methods; ii) to suppose that every behaviour and every transition between them is intrinsically multiscale (i.e. with a scaling property) appeared to be an interesting approach to identify and characterize them.

The mathematical robustness and predictive ability of wavelet analysis make it a promising road towards multiscale movement ecology that fuses insights from the study of animal behaviour and environmental properties.

Keywords marine predator; scale; frequency analysis; trajectory; path analysis.

1 Introduction

The study of animal movement is interesting for many reasons: it provides precious information about their behaviour, about the properties of their environment and about the way they perceive it. It has often been advocated that multiscale processes are common in ecology (Halley et al., 2004; Wiens, 1989), i.e. processes that are either scale-dependant or scale-independent in a characteristic way, and that the movements described by a foraging predator may be concerned by scaling too (Benhamou, 2007; Sims et al., 2008; Turchin, 1996). Predators tend to increase their turning rate in a scale-dependant manner once the prey has been captured or predators are likely to forage in a hierarchical patch system in which patches at fine scales are nested in patches at larger scales (Gaucherel, 2009; Kotliar and Wiens, 1990). It is still discussed whether animals move by multiscale Lévy-Walks or Lévy-flights, a special class of random walks whose step lengths are chosen from a probability distribution with a power-law tail, or rather a mixture of more classical Brownian Random Walks (Benhamou, 2007).

A vast majority of movement analysis studies make the assumption that such long composite movements (or trajectories) are approximately homogeneous (i.e. stationary). Yet, most movements are non-homogeneous because animals move through heterogeneous landscapes and because movements combine a series of discrete behaviours ranging from foraging at the best patches, to resting at the safest patches or reaching these patches with more oriented walks. Several methods (called segmentation methods) have been developed to identify the different types of behaviour (Barraquand and Benhamou, 2008; Benhamou, 2004; Jonsen et al., 2005; Morales et al., 2004). A common idea found in movement studies is the concept of intensively used areas. These areas are areas in which predators are expected to increase their search efforts after having detected a prey item because of the high probability of encountering other prey items nearby (a behaviour usually referred to Area Restricted Search (ARS)). Furthermore, such intensive search behaviours are intimately linked to the so-called “organisation level” characteristic of their associated used areas. Characteristic organisation levels have to be differentiated from the (continuous) concept of scale, more related to the successively increasing steps used to measure the signal. That is the reason why various behavioural modes can be characterized at the same scale. Movement analyses usually concern time scales, as they are based on recorded temporal signals, while temporal structures are often correlated with spatial structures.

This study aimed at providing an alternative method for identifying intensive search areas related to behaviours with sharp as well as more continuous (i.e. progressive or smooth) transitions between them. Therefore, I will make here two closely related hypotheses: i) most animals move in a succession of behavioural modes with rather continuous transitions between each one of them; and ii) every transition and behavioural mode is intrinsically multiscale (i.e. with properties modulated across a range of continuous scales), this property can be used to improve the interpretation of the movement. The second hypothesis tells nothing about the scaling modulations as this response may depend on the processes involved. A direct consequence of these hypotheses is that every animal movement has a non-stationary and multiscale pattern that may be analyzed by dedicated time-frequency methods such as the wavelet transform (Daubechies, 1990; Grossman and Morlet, 1984; Mallat, 1989b). One study using wavelets recently highlighted the non-stationarity of animal movements (Wittemyer et al., 2008). A few studies have already mentioned the possibility for movements to have multiscale properties (Fritz et al., 2003; Tremblay et al., 2007), but they usually use a self-similar dimension that is unable to explain the animal’s behaviour (Turchin, 1996). A recent study also proposed a simple multiscale approach focused on movement and not behaviour (Wilson et al., 2007).

Wavelet transform appears to be a powerful method for analyzing non-stationary and multiscale animal movements. Firstly, this method benefits from a well-established mathematical formalism that has seen many improvements in the last decade (Mallat, 1989a; Mallat, 1989b; Gaucherel, 2002; Cazelles et al., 2008; Zhang, 2010). Indeed many widely used methods, such as the first-passage time (Fauchald and Tveraa, 2003) used to detect ARS are partly based on visual interpretation which is likely to be submitted to subjective biases (Barraquand and Benhamou, 2008). Mathematical foundation also is the main lack of the none the less interesting study of (Wilson et al., 2007), which aims at determining the movement of marine animals by using dead-reckoning techniques and multiscale analysis, although they did not give it that name. Secondly, wavelet is an easy-to-use method, with simple concepts and user-friendly software. Wavelet coefficient maps are correlation maps allowing easy reading along the length of time scales (in the case of a path) and for the chosen movement parameter (turning angle and speed). In a sense, wavelets are a way to perform massively parallel segmentation computations, with variable parameterizations. Thirdly, another interesting property of wavelets is their ability to reconstruct (to generate) a new signal based on the analyzed signal properties (the wavelet moments) (Cazelles et al., 2008; Mallat, 1989b). This opens the possibility of modelling animal movements with wavelets in a complementary way to already used Lévy-walks, Brownian random walks or state-space models (Benhamou, 2007; Edwards et al., 2007; Jonsen et al., 2005).

The first objective of this study is to test the two hypotheses with the well formalized wavelet analysis. The second objective is to illustrate the use of wavelet analysis on both simulated and observed trajectories. It is expected from the simulations that they show the ability of the method to recover simulated movement properties and to demonstrate its simplicity and its robustness. I illustrated the detection of successive behavioural modes by analysing an observed movement, here a movement of wandering albatrosses observed over the Indian Ocean (Weimerskirch et al., 2007).

2 Methodology

2.1 Wavelet analysis

The wavelet transform achieves a time-scale representation of any temporal phenomenon an alternative to Fourier or other time-frequency decomposition methods (Grossman and Morlet, 1984). In continuous time, but on a finite interval, it is possible to construct a basis with elementary wavelets:

$$\psi_{ab}(x) = \frac{1}{\sqrt{a}}\psi\left(x - \frac{b}{a}\right), \qquad \text{with } a > 0$$

Where $\psi(x)$ is called the “mother wavelet” or “wavelet function”. This two-parameter basis allows a time-scale discrimination of the processes. The definition of the coefficients of the wavelet transform of a square-integral continuous-time signal $f(x)$ is therefore:

$$C_f(a,b) = \int_{-\infty}^{\infty} f(x).\psi^{*}_{ab}(x).dx = \langle f(x), \psi_{ab}(x) \rangle$$

where * corresponds to the complex conjugate operation. The parameter a acts as a dilation factor (i.e. the scale at which the mother wavelet is dilated), while the parameter b corresponds to a temporal translation of the function $\psi_{ab}(x)$, which allows the study of the signal around b. The final wavelet transform of the signal $f(x)$ is the whole set of wavelet coefficients.

The main property of wavelet analysis is to provide a time-scale localisation of processes, which derives from the fact that its basic function is not extended (i.e. narrow). This contrasts with the classical (infinite supports) trigonometric functions of Fourier analysis (for more details see (Cazelles et al., 2008; Mallat, 1989b; Zhang, 2010)). The principle of wavelet analysis is to search for correlations between the signal (here temporal, Fig. 1c) and a family of curves with similar shapes (the mother wavelet, Fig. 1a). This calculation is done at different dilation scales a (y-axis) and locally around time b (x-axis). The result is a wavelet coefficient map (Fig. 1b) in which the greyscale indicates the correlation intensity for different times and dilation scales. The dark spots (or bumps) on top come from very short fluctuations all along the signal’s duration; the two bigger spots at the beginning of the signal are interpreted as intermediate scale modulations; the two intense spots at the bottom of the map are explained by the smoothed trends of the high and low values of the signal; finally, the white or dashed lines indicate one of the two main transitions and may be accurately identified by wavelet phases (Fig. 1b-d). Indeed, the wavelets have both real and imaginary parts allowing separation of the amplitude and phase of the studied signal. Finally, the wavelet analysis acts as a “mathematical zoom”. The greyscale, combined with the absolute values, has been chosen to discriminate features of this wavelet map.

Theoretically, mother wavelets are conditioned by some strict mathematical conditions and should be carefully chosen, even though they sometimes have little influence on the final results. The first conditions are called “admissibility conditions”. They establish that to locally study the signal the mother wavelet’s values must be located around the origin of time and frequency:

$$\int_{-\infty}^{\infty} \psi(x).dx = 0 , \qquad \text{and} \qquad \int_{-\infty}^{\infty} \frac{\|\hat{\psi}(\omega)\|^2}{|\omega|}.d\omega = K_{\psi} < \infty$$

where ^ is the Fourier transformation of a function. These conditions ensure a rapid decrease around the null time and frequency. In case the signal is the mother wavelet itself, the mother wavelet has to be normalised ($\|\psi\| = 1$, where $\| . \|$ is the norm).

It is possible to reconstruct the signal using the wavelet coefficients, although it was not explored in this study. In order to obtain a reconstruction formula for the studied signal, it is necessary to add “regularity conditions” to the previous ones:

$$\int_{-\infty}^{\infty} x^k \psi(x).dx = 0 , \qquad \text{where } k = 1,\ldots, n-1$$

that is to say, high-order moments of the mother wavelet are null or nearly so:

$$f(t) = \frac{1}{K_{\psi}} \int_{0}^{\infty} \int_{-\infty}^{\infty} C_f(a,b).\psi_{ab}(t).\frac{da}{a^2}.db$$

Several mother wavelets that fulfil, more or less, the previous conditions are presented in the literature. The main disadvantage of these non-orthogonal wavelets is that the continuous wavelet transform of the signal is characterised by a redundancy of information among the wavelet coefficients. This redundancy (intrinsic to this wavelet basis and not to the signal) can be reduced by the chosen projection basis. It can even be avoided with an orthonormal continuous time-wavelet basis. Hence, the wavelet coefficient interpretation is strongly dependant on the chosen projection basis.

The simple and commonly used “Mexican hat” mother wavelet was finally chosen in this study, for easier interpretations. The reason is that although it gives a poor resolution for the frequency, the “Mexican hat” provides a good resolution for the time, unlike other mother wavelets. As we will see, the main features of movements have to be precisely localised in time, instead of scale, while another choice might be relevant too (Gaucherel, 2002). Only continuous wavelet transform theory has been used here. A discrete-time approach has been imagined to remove the information redundancy in the wavelet coefficients and to help discriminate the signal processes in a more proper manner (Daubechies, 1990). Nevertheless, it was not our objective to study the combination of processes that lead to the movement signal. For that the continuous wavelet transform, simpler to implement, would have been suitable.

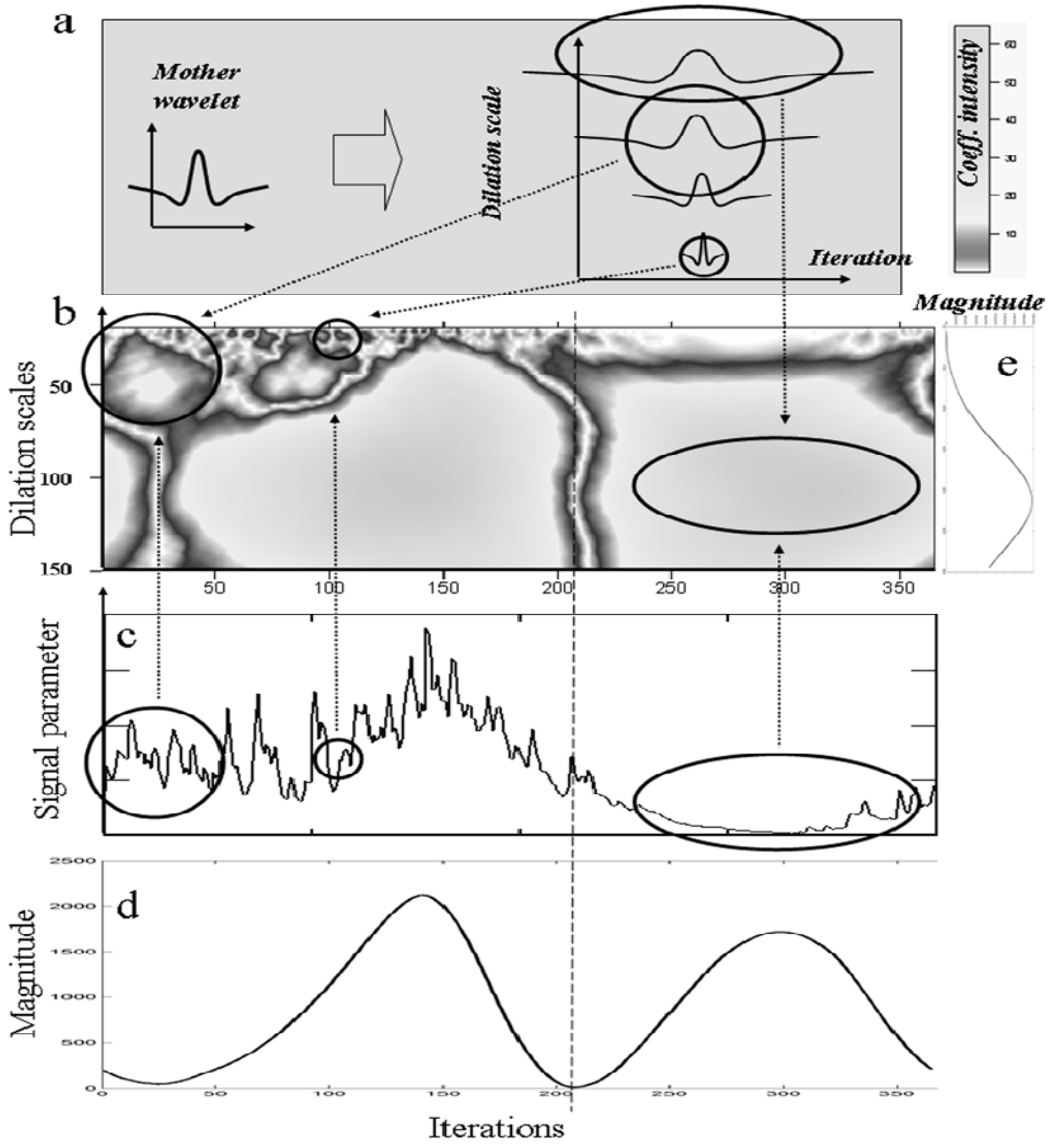

Figure 1

Fig. 1 Illustration of the wavelet analysis method. The principle is to search for correlations between the signal (c) and a family of curves with similar shapes (a, right) given by the “mother wavelet” (a, left). These curves are related to “dilation” scales (y-axis) and are translated along the signal axis (here the time, x-axis) for the computation of the correlation. The computations lead to a wavelet coefficient map (b) on which the greyscale indicates the correlation intensity at different times and dilation scales. Fine, intermediate and large scale structures in the signal are featured with ellipse and dotted arrows respectively. Here, the greyscale has been chosen to discriminate the features of the wavelet map. Further, it is often convenient to work with time- (d) or dilation-spectra (e) computed as the sum of wavelet coefficient norms (i.e. absolute values) along the columns (y-axis) or lines (x-axis) respectively. The spectra quantify the magnitudes of the studied signal at each date and at each scale.

Finally, the wavelet spectrum is defined as the average of the modulus (i.e. norm, occasionally signed with the wavelet coefficient signs) of the wavelet coefficients, either for the time or for the scale dimension. While the time average synthesises the distribution of the signal's variance between the scales (called frequency-spectrum or dilation-spectrum, y-axis), the scale average allows the temporal identification (time-spectrum, x-axis) of a particular component of the signal. The wavelet spectrum averaged over time is qualitatively similar to the Fourier spectrum, but can give new quantitative information on the studied process.

2.2 Simulated movements with continuous transitions

This work is based on the assumption that a continuous animal movement in two dimensional space can be reliably represented as a discrete, ordered set of locations and associated times (x_i, y_i, t_i), with $0 \le i \le n$. In this context, any step $\vec{l_i}$ with $1 \le i \le n$ is defined as the movement between two successive locations (x_{i-1}, y_{i-1}, t_{i-1}) and (x_i, y_i, t_i), with length $l_i = \left[(x_i - x_{i-1})^2 + (y_i - y_{i-1})^2\right]^{0.5}$, orientation (i.e. moving direction) $\theta_i = \arctan(y_i - y_{i-1}, x_i - x_{i-1})$, and duration $d_i = t_i - t_{i-1}$, from which other series of variables can be obtained such as speeds $s_i = l_i / d_i$ and turning angles (i.e. rotation) $\alpha_i = \theta_{i+1} - \theta_i$. Movements are often initially recorded at constant time intervals, that is with a constant step duration *d* (in the case of this study), although it may sometimes be useful, for analytical purposes, to re-discretize the path through a linear interpolation (Benhamou, 2004).

Following (Barraquand and Benhamou, 2008), I modified the Correlated Random Walks (CRW) to simulate walks with modulations (i.e. variations) on speed as well as on turning angle. The simulated walk was made of steps with a constant length *l* serving as distance unit totalling a path length of n = 10000 *l*. Initially, turns were drawn from a wrapped normal distribution with a null mean and standard deviation σ. Speeds were drawn from a log-normal distribution whose mean value μ and variation coefficient were equal to unity. Contrary to the previous authors, I modulated speed and turning angle by sinusoidal functions with different periods to represent continuous transitions and to illustrate the ability for wavelets to recover them. Turning angle period was chosen so that the movement was composed of eight maxima (i.e. larger turns, every 1300 *l*) corresponding to eight intensive modes. The speed period was chosen so that the movement was composed of 15 minima (i.e. lower speeds) corresponding to 11 intensive modes (every 1300 *l*) in the first half and four intensive modes (every 433 *l*) in the second half of the movement. Multiplying by three this speed period after 5000 steps should illustrate the ability of wavelets not only to quantify any change (in scale) of a non-stationary signal, but also to locate this change in time.

$\sigma = \frac{1}{2}\sin\left(\frac{2\pi.i}{T_a}\right) + 1$; $\mu = \frac{1}{2}\sin\left(\frac{2\pi.i}{T_s}\right) + 1$; with $T_a = 0.03$, and $T_s = 0.09$ if $1 \le i \le \frac{n}{2}$ and $T_s = 0.03$ if $\frac{n}{2} < i \le n$. By using this method, speed and turning angle are not correlated and should be detected separately in the wavelet analysis, while it is not possible to detect such modulations solely with the angle analysis. With pure angle analysis the intensive modes would correspond to the coincidence of turning angle maxima and speed minima in time. This single noise level has been compared to a hundred walks without any modulation (i.e. without sinusoidal weights on turns and speeds), thus defining 95 % and 99 % confidence levels.

Confidence levels were applied on both time- and frequency-spectra in order to detect significant differences from such null-hypothesis. Spectrum values were normally distributed.

2.3 Species and field study illustration

I illustrated the wavelet method on wandering albatrosses, large (8-12 kg) seabirds that breed on sub-Antarctic islands. During the breeding season, they are able to forage thousands of kilometres from the colonies by using gliding flight that extensively reduces flight costs (Weimerskirch et al., 2000). They feed mainly on a wide variety of squids that they capture or find dead on the sea surface. The study was carried out on Possession Island (46°S, 51°E), Crozet Islands, south-western Indian Ocean (Fig. 3a), during the brooding periods of 2002-2005. The movement used here was recorded simultaneously with a GPS tag and a stomach temperature transmitter to estimate the length of prey ingestion and the mass of the prey. The GPS tags (New Behaviour, Zurich; 45 g; see (Steiner et al., 2000)) were programmed to give a location (± 5 m) every 10 s (Weimerskirch et al., 2007). Hence, the movement has a constant time step. The duration of this trip (62.47 hours) is common and suggested that there was little effect from the stomach temperature logger or the GPS tag on the performance. GPS locations were used to study the movement's patterns and the sinuosity of the foraging tracks, as well as the time spent on the water. The birds were considered to be sitting on the water when their movement speed between three consecutive locations (i.e. 30 s) was lower than 10 km/h, because birds cannot stay aloft at that speed (Weimerskirch et al., 2007). Environmental data (i.e. winds, currents, bathymetry…) associated to locations and feeding events were not available for this study.

2.4 General methodology

The use of wavelet transform for animal movement analysis was illustrated in this study with coefficient maps and time-spectrum intensities (i.e. magnitudes) only, in order to reduce the paper length. Frequency-spectra (i.e. scale-spectra) and wavelet phases were not shown and were shortly discussed at the end of the paper. Maximum dilation computed in this study was 512 time steps (approximately 1.4 hours), corresponding to a 128 maximum scale on map due to the mother wavelet symmetries. Coefficient maps and time-spectra were successively computed on turning angle and speed parameters for each analyzed movement. Wavelet coefficient intensities have to be interpreted relatively to the time steps or the scales. Spectra were systematically plotted with their 99 % confidence levels. Confidence levels are sometimes weak enough to disappear.

By definition, it is hereafter convenient to call "mode" every homogeneous behaviour (resting, ballistic and intensive search flights), and "regime" every period larger than a hundred time steps (approx. a quarter of an hour) characterized on average either by positive or negative uniform wavelet coefficient values at all scales. Hence, it is necessary to detect wavelet regimes on speed and turning angle signals to conclude that they define intensive search modes having a real biological meaning. The shape of the Mexican hat mother-wavelet is roughly convex and responded positively with a convex signal shape (i.e. increasing, then decreasing parameter values), and negatively for concave signal. Considering the mother wavelet's shape, we expect an intensive search mode and its associated regimes to be characterized by positive wavelet magnitudes at almost all scales.

With the aim of identifying intensive search areas and their smooth transitions, I computed a simple intensive search detection index by combining turning angle and speed time-spectra, in a way close to a cross-wavelet analysis. The usual hypothesis states that intensive searches are associated to higher turning angles and lower speeds than other flying modes (Barraquand and Benhamou, 2008; Benhamou, 2004). Indeed, this hypothesis was the one used for simulated movements, analyzed by multiplying (date by date) negative speed magnitudes by positive turning angle magnitudes. Yet, it was not relevant to proceed similarly with observed movements.

The difference between resting modes and flying modes is that resting modes exhibit high wavelet magnitudes at large scales, thus hiding the intensive search speed reduction. As a consequence, it was not always possible with wavelets to dissociate low speed (intensive search) regimes from resting regimes on the albatross' movement. Therefore, I proceeded as follows. First, in the final intensive search index I simply proposed to multiply positive speed magnitudes by positive turning angle magnitudes. Indeed, it only supposed here that the speeds during intensive search were higher than during resting regimes. Turning angles were then used to discriminate between intensive search and more ballistic flights. The corresponding hypothesis, to be further discussed, is that intensive search modes suppose higher turning angles than other flying modes and higher speeds than resting modes. This modified hypothesis tested on simulated movements led to very similar results to those obtained with the initial hypothesis (not shown). Then I removed the time periods corresponding to the resting modes after the wavelet analysis, which is roughly equivalent to removing negative values from the signed speed time-spectra. Removing resting modes before the wavelet analysis would create artificial temporal autocorrelations and would thus lead to the detection of non-existing features.

Coefficient maps, time-spectra and intensive search index have been computed on both simulated and observed movements. First, time-spectra of turning angle and speed parameters were computed over the whole simulated movement previously described. Then the intensive search index was computed in order to synthesize this movement information and to focus on the relevant modes and transitions between modes only. Secondly, similar computations were performed on the albatross' observed movement. Wavelet coefficient maps provided additional multiscale information discussed in detail. Thirdly, a zoom on this movement (2000 l with a ten second time step, approximately 5.55 hours) was extracted and analyzed in depth to illustrate the smooth transitions between distinct behavioural modes. Wavelet coefficient maps were computed on the turning angle and speed parameters. Finally, intensive search modes identified by the index were qualitatively compared to ARS computed by the first passage time method (Fauchald and Tveraa, 2003) and to the prey captures identified by stomach records (Weimerskirch et al., 2007).

3 Results

3.1 Simulated movement

Noisy Turning Angle (TA, Fig. 2a) and Speed (S, Fig. 2b) series were modulated as expected. TA series exhibited eight visible intensive modes among which were all significantly detected by the corresponding time-spectra (higher values, Fig. 2c). Yet, the first and last modes were very weak due to a lack of information at higher scales because of the uncorrected edge effects, amplified at those higher scales. It is worth noting that maxima as well as minima are detected by the wavelet time-spectra magnitudes. This observation is linked to the shape of the mother wavelet (here, the Mexican hat) broadly having a convex shape, but also allowing concave shape detections with computed anti-correlations. Convex (respectively concave) shapes indeed correspond to increasing then decreasing (resp. decreasing then increasing) parameter values. Finally, eight maxima plus seven minima, minus two edge-hidden maxima, leaded to 13 time-spectra peaks detected with the index (Fig. 2c).

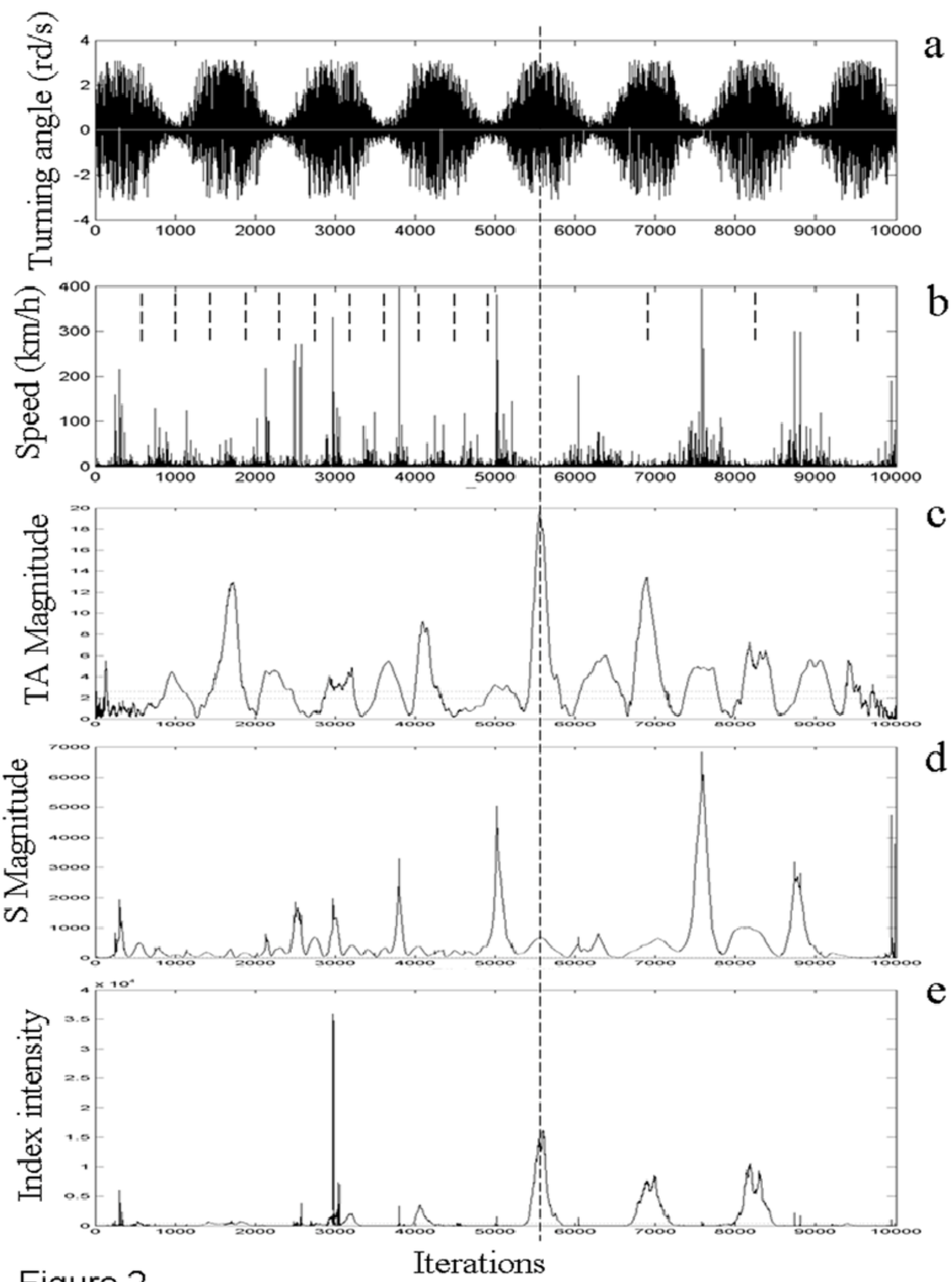

Figure 2

Fig. 2 Example of a simulated movement. A Correlated Random Walk characterized by its wrapped normal distribution turning angle (a) and log-normal distribution speed (b). These distributions have been modulated by sinusoidal functions with different periods over 10000 time steps. The turning angle (c) and speed (d) time-spectra, and their associated confidence levels were computed in order to detect significant “regimes”. The synchronisation between some turning angles and speed regimes (e.g. dashed line) is enhanced by using the intensive search index (e) built by multiplying these two spectra.

Speed series exhibited 11 + 4 intensive modes (Fig. 2b), all successfully detected by the corresponding time-spectra (significant values, Fig. 2d). The 99 % confidence level is much lower than the computed magnitudes due to a high signal to noise ratio, which means that all S time-spectra peaks are significant. The same reasoning as for the TA parameter leaded to 29 peaks. Signals were built so that only the four last modes were synchronous for the S and TA parameters. The minima of the first half of the S series may be synchronous with some maxima of the TA series by chance. Yet, such temporal coincidence for the extremes of the time series remained exceptional; this was due to the added noise and always occurred for short time. This was confirmed by the computation of the index that emphasized the intensive modes (Fig. 2e). Seven of the eleven speed decreases were detected in the first half of the movement. They were significant (99 % CL) although very weak, and even lower than other isolated peaks. The width of these remaining peaks appeared to be very small and may indicate irrelevant parameter coincidences, i.e. obtained by chance. The four last intensive modes were correctly detected and were highly significant (Fig. 2, the dashed line features the first intensive mode), except maybe for the last one that was very close to the 99 % confidence level due to uncorrected edge effects.

3.2 Observed movement

The first observed movement was a closed loop starting from Crozet Island (Fig. 3a). Wavelet coefficient maps of Turning Angle (TA, Fig. 3b) and speed (S, Fig. 3c) showed positive (in red) and negative (blue) intensities across dilation scales (y-axis) and along time (x-axis). The TA time-spectrum approximately showed 21 significant regimes (13.9 % of the duration of the movement), i.e. with negative and positive coefficient values higher than the 99 % CL (not shown). This estimation would be slightly different in another null-hypothesis test and with another minimum regime width (here equal to 100 successive time steps). The S time-spectrum showed approximately 43 significant regimes (94.9 %). This high value is due to a quite low 99 % CL for the S parameter. S regimes were not strongly marked (colored) on average until time step l = 8000: this observation is probably related to the energy available to the animal at the beginning of the trip or to more regular environmental conditions encountered (or both). S regimes were longer in time (1.37 hours) than TA regimes (24.8 minutes) on average. In addition, the S regimes often responded uniformly at all scales, while the TA regimes responded strongly at fine and/or at intermediate scales, but not systematically at broad scales.
It is possible that the TA dynamic of this predator depended more on local factors, and that birds have a greater ability to adjust their turning angle than their speed.

Finally, approximately 18 significant intensive modes were detected with the intensive search index curve (dashed segments, Fig. 3d). They lasted about 24.2 minutes (12.3 % of the movement duration) on average. All modes detected by this mean correspond to visible (i.e. obvious) intensive searches along the movement. Ten of them correspond to first passage time ARS (big black circles, Fig. 3a), while eight of them had not been detected by the first passage time method. Only five modes detected by wavelets corresponded to prey captures (green circles, Fig. 3a). Indeed, the five remaining observed captures corresponded to the albatross resting on the sea, which is a situation excluded by the construction of the intensive search index.

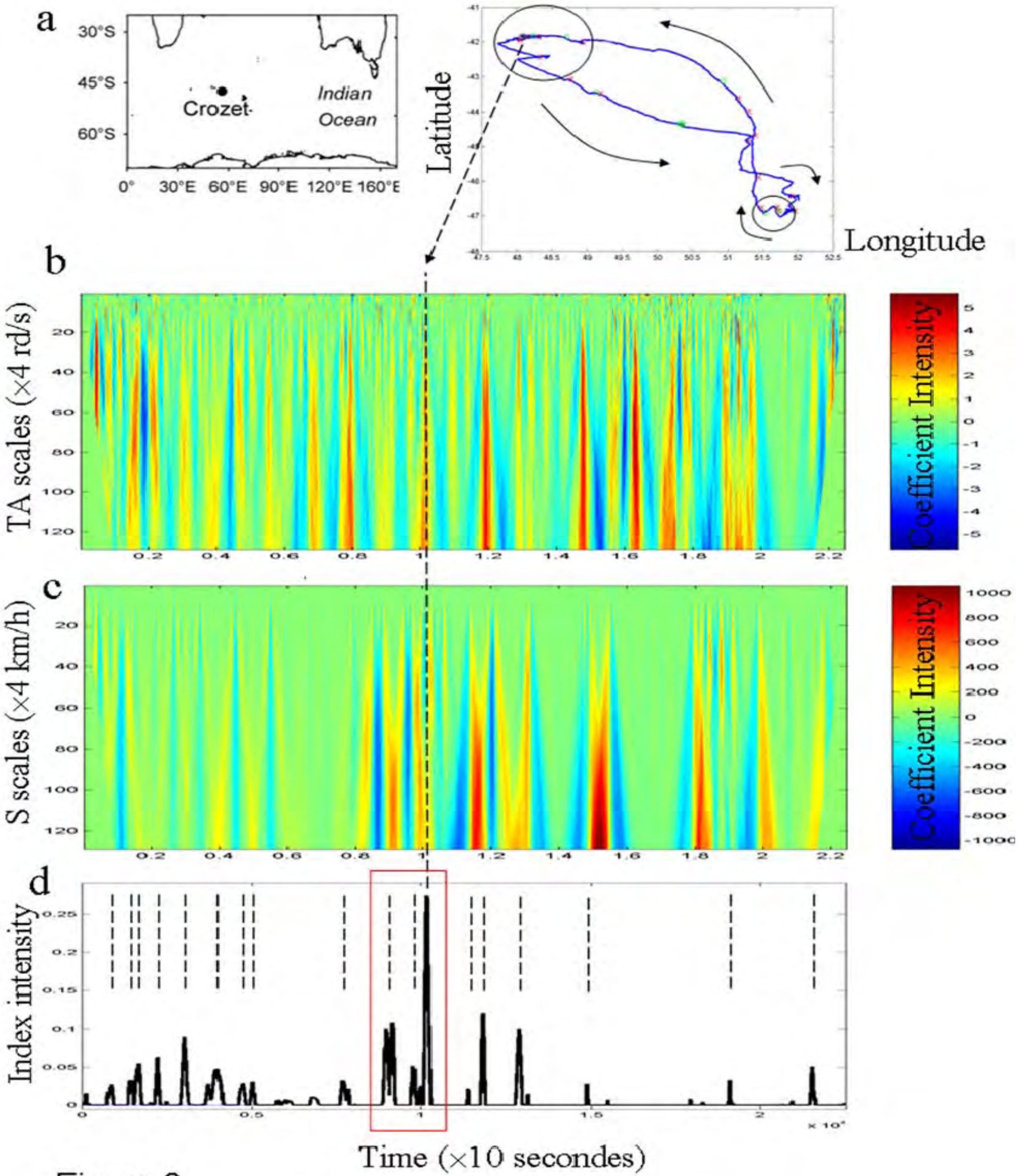

Figure 3

Fig. 3 Movement of the wandering albatross as seen by the wavelet analysis method. The albatross was tracked by GPS and fitted with a stomach sensor. The movement started from the Crozet Islands southern Indian Ocean (a, left). Prey capture events (green circles) and intensive searches detected by wavelets (red crosses) are superimposed to the movement. Black open circles indicate zones of area-restricted search (ARS) detected by the first passage time method and are proportional to the scale (30 and 80 km) of ARS zones. The turning angle (b) and speed (c) wavelet coefficient maps, and their respective colour scales were computed to locate and quantify successive "regimes" of movement. The intensive search index (d) was then computed from the respective (signed) time-spectra in order to enhance synchronous regimes between these two parameters. The significant regimes enhanced by this index thus define behavioural modes (e.g. dashed arrow and dashed lines). The red rectangle corresponds to the zoom of the Fig. 4.

3.3 Zoomed movement

A fine inspection of the zoom of the turning angle (Fig. 4a, top in black) and the speed (Fig. 4a, bottom in black) time series of the 5.55 hour movement of the albatross helped analysing in depth the transition dynamic. The modified TA (Fig. 4a, top in red) and S (Fig. 4a, bottom in red) time spectra of the same part of the movement (first) quantified features visually identified. These signed time spectra were computed by keeping the signs of the wavelet coefficient: each crossing of the x-axis outlined a new regime and helped constrain the final intensive search index (Fig. 4b, dotted line). Resting regimes (Fig. 4c, A and C zones) were easily observed on the S time series (40 % of the 5.55 hour zoom). When the animal was resting at sea surface, it continued to turn at a rate depending on both wind and wave regimes. Without speed data, it would be difficult to identify whether this period was a resting or a flying behaviour. Similarly, it would be difficult to discriminate flight types on the sole basis of their speed values (Fig. 4c, B and D). These regimes were not synchronized between the two parameters, highlighting the fact that the animal may change turning angle without changing the speed (e.g. after an intensive search) or may change the speed without changing turning angle (e.g. after a landing).

TA and S wavelet coefficient maps showed four dominant regimes (noted A, B, C and D, Fig. 4d and c). The TA map detected two regimes of higher value (l = [200 – 700] and l = [1200 – 1800]), yet with different profiles. The first regime (B) appeared to be quite powerful (i.e. with higher magnitudes) at large scales. The power of the second regime (D) was high at the beginning at low scales (Fig. 4c, dashed ellipse) and at the end at all scales (Fig. 4c, red area). Higher TA wavelet coefficient values highlight the fact that the animal was turning with a significant (either positive or negative) trend, i.e. with relatively constant TA, rather than the possibility of the animal to be turning more or more rapidly. Regular ballistic flights between l = 700 - 900 were also easily detected (Fig. 4d, blue zone).

All regimes of S time-spectrum were quite smooth as they often showed similar coefficient values at various scales (A to D, Fig. 4d). Such boundaries between regimes may be accurately located in time by the use of wavelet phases (illustrated by two plain lines in Fig. 4c), thus acting as a segmentation method. The typical “antenna shape” of various modes reminded us that fine scales are more sensitive to fine temporal structures, such as transitions between regimes, while large scale features responded to long trends. A decrease of speed to around l = 1500 identified a short landing, while a change in the speed regime around l = 1700 emphasized different profile movements between the beginning and the end of the flight (l = [1200 - 1800], Fig. 4a). The l = [1600 – 1700] flight is clearly a short intensive search (with slightly lower speed and higher turning angles than neighbouring flights) and is correctly detected by the index. Finally, the intensive search index is based on TA and S time-spectra only (Fig. 4c, dotted line). It highlighted significant behavioural modes (B and D) corresponding to high S and high TA periods. The beginning of the D regime was weak due to relatively weak TA at all scales except the fine ones.

4 Discussion

4.1 Continuous transitions between behavioural modes

The results on the simulated movements showed that wavelet coefficient maps, time-spectra and intensive search index were able to characterize continuous transitions between distinct behavioural modes (Fig. 2e). Results on wandering the albatross’ data showed that approximately 12 % of the 62 hour movement were identified as intensive search modes, with a wide variety of transitions between them. This was the first hypothesis of this study. For this mode detection, I built a very simple index combining speed and turning

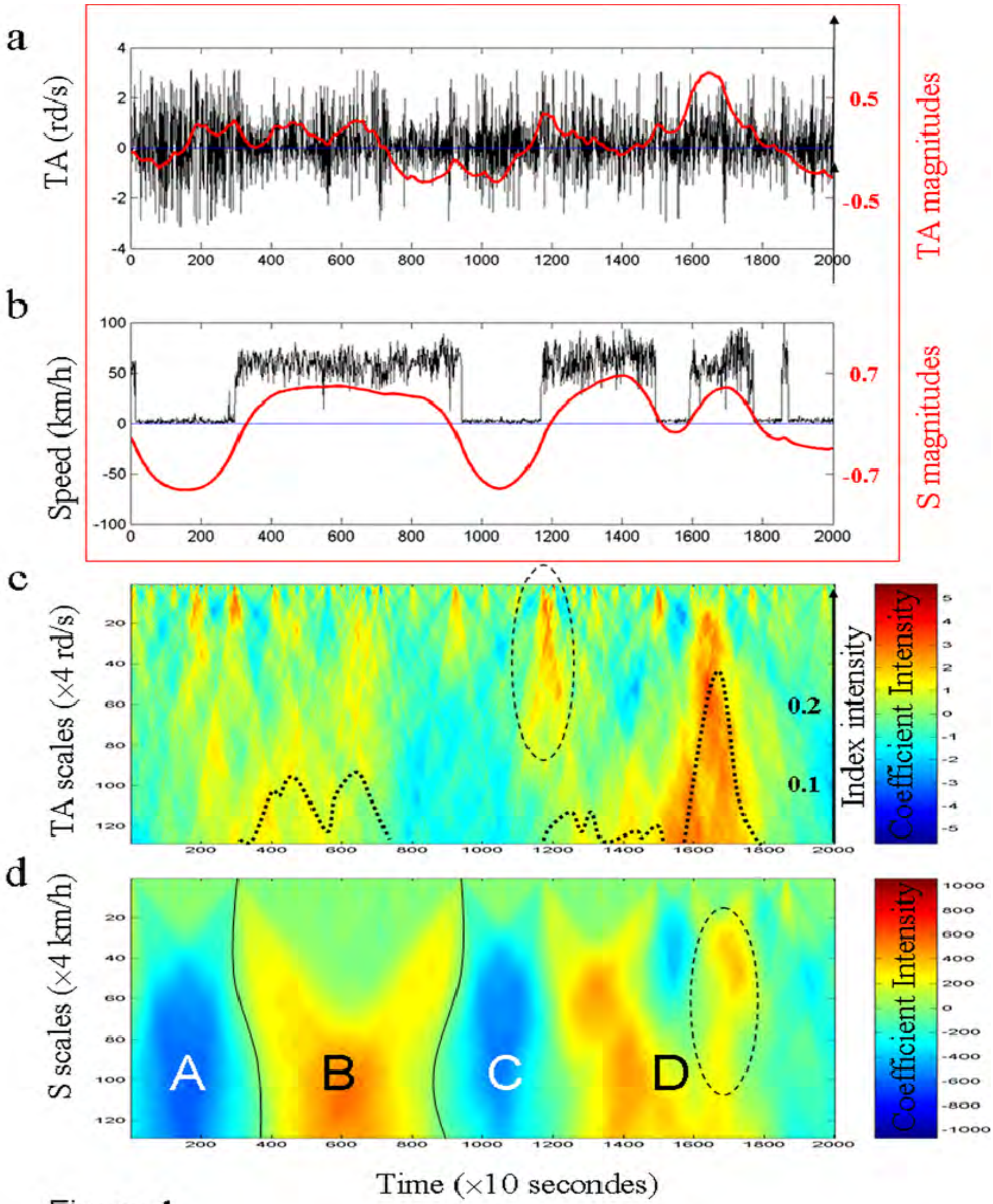

Figure 4

Fig. 4 Zoom of the observed wandering albatross movement (red rectangle on Fig. 3d). The turning angle (a) and speed (b) parameter values over these 2000 time steps are plotted simultaneously with the turning angle (a, red curve) and speed (b, red curve) time-spectra, with their respective y-axis (a, right). The turning angle (c) and speed (d) wavelet coefficient maps, and their respective colour scales were zoomed over at the same period. The intensive search index (c, doted curve) was then computed from the (signed) turning angle and speed time-spectra in order to define behavioural modes (d, A to D). Boundaries between these modes may be computed by using the wavelet phases (d, plain lines). Other scale specific features are identified and quantified on wavelet coefficient maps (c and d, dashed ellipses).

angle information from the corresponding wavelet time-spectra. The underlying hypothesis for this was that during intensive search the bird has higher speeds than during resting modes and higher turning angles than during flying modes. This hypothesis is a conservative adaptation of the usual hypothesis that during intensive search, animals exhibit higher than average turning angles and lower than average speeds (Barraquand and Benhamou, 2008; Fauchald and Tveraa, 2003). Obviously, the central result is not the choice of the definition of this index, as computing other indices with smooth time-spectra or with specific wavelet scales would enhance signal-to-noise ratios and would probably help for detection of behavioural modes.

The 18 detected intensive search modes of the wandering albatross movement lasted on average about 24 minutes (dashed segments, Fig. 3d), yet with highly variable signatures. This average time appeared to be much lower than that of the intensive searches detected by the first passage time method (Fauchald and Tveraa, 2003; Weimerskirch et al., 2007). Approximately half of these modes only corresponded to modes detected by the first passage time method (Fig. 3a). The other modes detected here were visually confirmed. It is worth noting that the latter method did not allow for a good segmentation of the movements (Barraquand and Benhamou, 2008), thus explaining why we trust more prey captures identified by stomach records. All the registered prey captures during flights were detected by the wavelet method, i.e. five out of ten, the others having been registered during resting modes thus excluded by construction (Weimerskirch et al., 2007).

Finally, objective confidence levels were estimated on the basis of the described simulated movements. Such simulated movements should be adapted to every case study; in particular they should be taken into account for the properties of animal’s movements and the spatial distribution of prey. We are confident here in the general ability of the chosen simulations to detect intensive search modes when lacking information about the environmental factors or animal biology. More generally, and this is the central result of this study, wavelet analysis of an observed movement was able to accurately recover the record of prey capture without additional information (about the environment). We guess that this assertion has to be reevaluated for nonpredator movements. As perspectives, it could be recommended to combine movement data with environmental and/or physiological data in order to systematically interpret movement patterns in terms of ecological processes.

4.2 Movement wavelet analysis

Recent work has highlighted the ability of wavelet analysis to help detect non-stationary statistical properties of animal movement (Wittemyer et al., 2008), but this method offers many other advantages. Wavelet analysis is quite parsimonious in parameters, as its main constraint relies on the mother-wavelet. Depending on its response to the signal the mother wavelet can be adapted to highlight various features of the movement. In this sense, wavelets are close to a non-parametric analysis, needing no hypothesis about the animal movement (the number of behavioural modes, the movement auto-correlation in space or time, etc.). This method benefit from strong mathematical foundations, which is the main lack of previous studies (Wilson et al., 2007; Fauchald and Tveraa, 2003). By working with wavelet phases it is even possible to recover discrete behavioural modes (briefly illustrated at Fig. 4d), thus bridging the gap with other existing segmentation methods (Barraquand and Benhamou, 2008; Jonsen et al., 2005; Morales et al., 2004). Finally, another powerful property of wavelets is their ability to reconstruct a new signal on the basis of the properties of the analyzed signal (i.e. the wavelet moments) (Cazelles et al., 2008; Mallat, 1989b). This makes wavelets able to model animal movements in a complementary way to already used Lévy-walks, Brownian random walks or state-space models (Benhamou, 2007; Edwards et al., 2007). Recent improvements on wavelet transform found in neighbouring disciplines may even help movement analyses (Ravelli et al., 2008).

4.3 Multiscale movement properties

Results showed that animal behaviours should be intrinsically multiscale. This was the second hypothesis. Several works have already illustrated the scaling (or scale invariant) properties of animal movements (Fritz et al., 2003; Sims et al., 2008; Tremblay et al., 2007; Wilson et al., 2007). Most of them are based on the computation of self-similar (fractal) dimension, i.e. linear loglog behaviour of a specific movement property, to which are subject to the usual limits of fractals (Benhamou, 2004, Halley et al., 2004, Turchin, 1996). First, fractals are very poor in information, as similar fractal dimensions often characterise very different patterns (and likely different processes). Secondly, the self-similar property is quite difficult to rigorously establish as we need to compute its corresponding dimension over several magnitude orders, with unbiased interpolation methods (Halley et al., 2004). Fractals often hide mixed-fractals (combination of different dimensions at successive scales) or even multifractals (curves instead of linear loglog plots). Finally, and certainly the most critical limit, we are usually not able to relate the self-similar dimension value to a clearly identified ecological process (or processes) at the origin of the scaling behaviour (Sims et al., 2008). Some relations exist between animal movements and either heterogeneous environment or self-similar distribution of prey fields, but we have not yet identified a specific foraging behaviour with its associated scaling pattern (in particular for albatrosses).

Wavelets are one of the best ways to improve the knowledge that we already have on scaling properties using self-similar relationships. Wavelets applied to animal movement provide a quantified information at all scales analyzed and at all time steps registered. Hence, it allows not only to identify the dominant organization levels of a pattern or a process (if it exists, such as intensive search) by studying a signal at all scales, but also informs about the specific properties of this process by quantifying its inner-dynamics. In this context, the most relevant way to describe the environment of the animal is as a series of patches, to be considered as circular and/or regularly dispersed in space (Barraquand and Benhamou, 2008). Every regular part of space may be considered as a patch, and intra-patch and inter-patch movement bouts are “blurred” into a multiscale continuum. This makes wavelet a relevant method to study transitions as well as regime properties. In the real world, landscape patches are likely to be highly irregular in shape, in size and in arrangement (i.e. in topology) (Gaucherel, 2009, Kotliar and Wiens, 1990). Time-frequency analyses such as wavelets are convenient tools to avoid making assumptions about the structure. Animal movement will influence the wavelet coefficient maps in case of an explicit response from the animal to the landscape. Finally, to suppose that a process has a dominant organization level (e.g. animal foraging or resting) is a useful preliminary task, but we may bypass such a mono-scale typology to more precisely characterize the processes.

Different foraging behaviours of the same individual are likely to have different characteristics, yet are similarly classified by segmentation methods. Observed movements are the ultimate consequence of individual behaviour, physiological constraints and environmental influences. Identifying the corresponding intensive search is an interesting preliminary stage, but analyzing intra-foraging patterns at finer scales is crucial to link such patterns to their behavioural mechanisms. Finally, this multiscale behaviour hypothesis is probably a heuristic way to discover and characterize new or different behaviours.

Acknowledgments

I deeply thank F. Barraquand, S. Benhamou and M. Rolland for carefully reading earlier versions of the manuscript and H. Weimerskirch for having generously provided the wandering albatross data. This work was developed in the course of several projects funded by the Agence Nationale de la Recherche (projects “INC”, ANR-biodiversité 2007, project “STAMP”, ANR-blanc 2007).

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