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Periodicity analysis of movement recursions

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HIGHLIGHTS

- ▶ Understanding recursion patterns is key to understand animal movements.
- ▶ We present an approach to study the periodicity of recursions.
- ▶ The approach is based on Fourier and wavelet analyses.
- ▶ Several periodic patterns are revealed in an example with real-world data.

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ABSTRACT

Many animals adaptively use their environments by adjusting how long and how often they use specific areas of their home range. Whereas questions about residence times have been addressed for a long time, the study of movement recursions has only recently received due interest. A key question concerns the potential periodicity of such recursions, as many potential drivers of movement behaviour such as light, climate or plant–herbivore interactions can be periodic. We propose here to build upon well-established Fourier and wavelet analyses to extract periodic patterns from time-series of presence/absence, arrival or departure from areas of interest, and introduce reliable null models for assessing the statistical significance of the periods detected. We provide an illustrative example which shows how an impala (*Aepyceros melampus*) expressed periodic use of the main open area of its home range. The significant periods found (12 h using arrival times; 24 h, 7 days, and 30 days using presence/absence records) were consistent with a use of this area linked to predation and disturbance, as the area was used more at night, closer to dark moon, and during week-days. Our approach is a further step towards building up a wider analytical framework for the study of movement ecology.

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1. Introduction

Most animals exhibit uneven use of their environment to adapt to its heterogeneity by spending more time in more favourable areas (Benhamou and Bovet, 1989). Moreover, in numerous species animals perform home range behaviour, i.e., restrict their movements to self-limited portions of space far smaller than expected from their sole locomotion capacities (Börger et al., 2008). Because of their adaptive use of the environment within a limited region, home range owners are likely to repeatedly visit some areas more than others (Van Moorter et al., 2009), and thus perform frequent movement recursions (Bar-David et al., 2009). So far, few studies have specifically focused on this fundamental aspect of animal movement. How often a given area within a home range is revisited, and to what extent revisits are regularly spaced in time,

are indeed important questions linking small (daily movements) and large (home ranges) scales.

The occurrence of periodic visits to particular areas is likely to reflect the adaptation of movement behaviour to periodic drivers. For example, the diel cycle is a well-known driver of animal activities. At a larger temporal scale, seasonal changes in resource availability may lead to periodic movements. Less obvious patterns may exist as well. Food availability and quality may be cyclic, as in the case of herbivores, for which periodically revisiting a previously grazed area may be adaptive if the vegetation is in a regrowing stage (Rowcliffe et al., 1995). Detecting significant periodicities in movement recursions acting at possibly different time scales will therefore help to identify some of the important drivers of an animal's space use. This should improve our understanding of the processes leading to recursion patterns and the emergence of a home range, which remains a key ecological question (Van Moorter et al., 2009).

Two recent studies (Bar-David et al., 2009; Li et al., 2012) developed Fourier-based methodologies to detect movement recursions and associated periodicities. The Fourier method decomposes

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the variance of a time series over frequencies by fitting a combination of sine waves so as to construct the power spectrum, where peaks indicate the frequencies that best explain the variance of the data. Thus, this method is a reliable tool able to simultaneously detect multiple periodicities in noisy time series without prior specification of the periodicities of interest. Bar-David et al. (2009) did pioneering work in detecting recursions and in providing a qualitative indication of the time scale at which they occur, and used Fast Fourier transform to identify if the movement leading to the recursion was circular. Li et al. (2012) went further by proposing to directly apply the Fast Fourier transform to a binary time series of presence/absence events in a given area to detect periodicity in recursions.

This later study opens very promising perspectives, as using a binary time series makes it possible to filter out the spatial noise that would complicate the period detection procedure. A major drawback in Li et al. (2012) study, however, is that their significance test for presence/absence data lacks a reliable null model. They just proposed to compare the actual Fourier power spectrum values with a flat (i.e., frequency-independent) significance threshold based on unconstrained random permutations of all the presence/absence events, so fully ignoring the Markovian structure of this type of time series. Indeed, the probability of presence of the animal within a given area at a given time step is largely conditioned by its presence at the previous time step. Significance thresholds respecting this constraint should be frequency-dependent because the Markovian constraint should prevent frequencies to be evenly distributed. Ironically, the test proposed by Li et al. (2012) is (almost) appropriate for binary time series defined in terms of arrival or departure events, which can be assumed to be independent of each other as a null hypothesis, but these authors did not pay any attention to such time series despite the fact that they may provide valuable complementary information (see illustrative example below).

Finally, it is worth noting that Fourier analysis can detect periodicities that are expressed only during a restricted amount of time relative to the time span of the entire time series analyzed. This is both its strength, as it can detect a signal that is periodic only for a limited fraction of the whole time series, but also its weakness, as it cannot indicate whether there are some regime shifts nor when they occur. Such shifts can easily be detected using wavelet analysis, which nicely complements Fourier analysis by providing an estimation of spectral components of the data as a function of time Torrence and Compo (1998).

In the present paper, we propose a simple four-step method to extend (Li et al., 2012) work and provide a consistent framework to investigate the periodic characteristics of movement recursions, and use impala (*Aepyceros melampus*) movements as an illustrative example. We suggest how the areas of interest can be selected, then show why it is important to consider both presence/absence and arrival or departure series and how adequate statistical tests can be built up for testing the significance of periodicity peaks, and finally how wavelet analysis complements Fourier analysis when studying the periodicity of movement recursions.

2. Methodological principles

The method we propose is made of 4 steps. The first step consists in defining areas the studied animal is likely to recurrently visit, and for which we will look for periodicities in the return dynamics. It is preferable, to help reaching biologically relevant interpretations, to focus on areas that have been defined on an ecological basis, rather than to simply consider every quadrat of a virtual grid overlaid on the home range (Bar-David et al., 2009). In

this way, one can answer the question of how often and how regularly a given area that is remarkable because of such and such ecological characteristics is visited. In the illustrative example below, we focused on an open area lying at the heart of an impala's home range, because this area was assumed to play a key role in antipredator strategies. When such biological insights are lacking, areas of interest can be defined statistically as the home range areas that are the most highly used (Li et al., 2012), or preferably in a context of recursion analysis, as the home range areas that involve most frequent recursions (at the risk of ignoring areas that are periodically but infrequently visited). Such areas can be easily found using a new method (Benhamou and Riotte-Lambert, 2012) that mixes movement-based kernel density estimation (Benhamou and Cornélis, 2010; Benhamou, 2011) with residence time estimation (Barraquand and Benhamou, 2008). Disjoint areas with common characteristics (e.g., water holes) can also be considered together, so as to determine the potential periodicity in a type of behaviour (e.g., drinking) rather than in the returns to a given area.

The second step consists in building up three binary time series describing movement recursions in the specified area: one time series coding for presence/absence (as initially proposed in Li et al. (2012)), as well as two time series coding for arrival or departure events. The questions of determining whether the animal is periodically present in a given area and whether it periodically enters (leaves) this area are not equivalent, because the time spent within the area can be extremely variable. As a consequence, arrival times to, departure times from, and presence within a given area may present different periodicities (see Illustrative example below). For presence/absence time series, a given time step is attributed the value 0 when the individual was out of the area and 1 when it was inside. For arrival and departure time series, a time step is attributed the value 1 when the animal enters or leaves, respectively, the area considered, and 0 otherwise (irrespectively of its presence or absence in the area). Note that, in any case, 0 and 1 values can be used interchangeably. Original tracking data have to be temporally rediscrretized, so as to obtain locations that are regularly spaced in time prior to be submitted to the periodicity analyses. The length of the rediscrretization time step has no impact on the results by itself. It should however be short enough to avoid missing any arrival to, presence in, and departure from the area considered when this area was crossed with a relatively high speed. Shorter time steps are unnecessary as they just entail longer computation times.

The third step consists in detecting periodicities in the time series using a Fast Fourier Transform algorithm, and to determine whether these periodicities are expressed all along the time series or only at particular epochs using wavelet analysis. An important aspect of wavelet analysis is the choice, to be made by the analyst, of the mother wavelet function. A good choice in the present context is the Morlet wavelet, which is conceptually related to the Fourier analysis and is extensively used due to its good estimation of the frequency of periodic patterns. For practical details and examples, the reader is referred to other studies for Fourier (Vlachos et al., 2005; Cowperton and Metcalfe, 2009) and wavelet (Torrence and Compo, 1998; Cazelles et al., 2008) analyses applied to ecological time series (see also (Wittemyer et al., 2008; Polansky et al., 2010; Gaucherel, 2011) for the specific application of wavelet analysis to some movement parameters such as speed and turning angle). It is worth noting that the values of low frequencies (long periods) are often hard to determine accurately on the Fourier power spectrum. When such frequencies are detected, a simple additional autocorrelation procedure (Vlachos et al., 2005) makes it possible to specify their value accurately.

The fourth and last step consists in determining which periodicities can be considered as statistically significant. The null hypothesis H_0 is "there is no periodic structure in the time

series". This hypothesis can be reliably tested using a bootstrapping procedure which generates random permutations of the 0 and the 1 in the observed time series so as to obtain a set of randomized (H0-compatible) time series against which the observed time series can be compared. A very simple random permutation procedure can be used when considering time series of arrival or departure events. Indeed, as arrivals and departures are instantaneous events, the main constraint – that the randomized time series must have the same numbers of 0 and of 1 (and thereby the same global length and the same relative proportions of 0 and 1) as the observed time series (the total power of Fourier and wavelet spectra is sensitive to these characteristics) – is automatically fulfilled by the simplest random permutation procedure. A basic additional constraint has however to be added: there cannot be two successive arrivals (or departures) in any randomized time series, in agreement with what occurs in observed time series. In contrast, when considering time series of presence/absence, which correspond to persistent events, a strong additional constraint has to be taken into account in the bootstrap procedure because the randomized time series has also to keep the same number of transitions ($0 \rightarrow 1$ and $1 \rightarrow 0$) as the observed time series. In a nutshell, a randomized presence/absence series is built up by randomly drawing the times of occurrence of one type of transition, say $0 \rightarrow 1$, with the additional constraint that two successive ones are spaced by at least two time steps. Then, the remaining 1s are queued iteratively in the inter-transition intervals, which are chosen at random with probabilities proportional to their relative sizes (which are updated after each iteration). Once all 1s have been attributed, the remaining empty time steps are filled with 0s. In this way, although the randomized time series will show no periodicity (except by chance), they will respect the internal structure of the observed time series in terms of global length, number of visits, proportion of time spent in the area, and serial correlation. In practice, the significance level p for each frequency in an observed Fourier power spectrum is determined as the $100(1-p)$ upper percentile of the power spectra of a large number of randomized time series generated from the observed one, optionally submitted to a smoothing procedure to reduce the large variability that is intrinsic to randomized time series. Similarly, for wavelet spectra, significant regions are delimited by comparing the observed spectrum with the distribution of spectra of the randomized time series (see (Torrence and Compo, 1998; Cazelles et al., 2008) for details on the estimation of significance levels in wavelet analysis). R (version 2.12.1 (R Development Core Team, 2010)) scripts are provided in Supplementary Data.

3. An illustrative example

Here we provide a case study to demonstrate how the method can reveal key patterns in the periodicity of animal space use. We investigated how an impala used an open area (about 800×300 m; Fig. 1) within its home range, located in "The Hide" tourist concession in Hwange National Park, Zimbabwe. We chose this area because it was the main open area used by this animal. It was clearly distinct from the surrounding more bushy landscape, and contrasts in woody cover are often critical in predator–prey interactions. We predicted that the use of this area could be linked to the periodic daylight and moonlight patterns which are strong determinants of predators' activity.

The impala was equipped with a GPS collar acquiring one location every hour from the 16th of August 2009 to the 14th of November 2009 (Julian days 228–318). Data were temporally rediscritized at 15 min intervals so as to record presence events within the area of interest even when crossed in less than 1 h. We set a 50 m wide buffer zone along the boundary of the area of interest (25 m inside, 25 m outside) so as to avoid, through hysteresis-based rules, getting artefactual high frequencies of arrival or departure events when the tracked individual moved near the boundary. Practically, an arrival or departure event was recorded only if the buffer zone had been fully crossed through, from the outer bushy area to the inner open area, or from the inner open area to the outer bushy area, respectively. A presence status in the area of interest was given to each time step occurring between arrival and departure events.

The Fourier spectrum of the presence/absence time series (Fig. 2, bottom) revealed three periods that were significant at $p=0.01$ –24 h, 7 days and 30 days—for which we have biological interpretations. The 24 h period arose because the impala mainly used the area of interest at night (Fig. 3, 1st row), on most nights. The 7-day period was apparently linked to weekdays with a lower use of the area just before and during week-ends (Fig. 3, 2nd row). Finally, the 30-day period appeared to be caused by a differential use of the area with moon phase, as the proportion of night time spent in this area decreased sharply when closer to full moon (Fig. 3, 3rd row). Other peaks were statistically significant at $p=0.05$ but we had no biological interpretations for them.

A $p=0.01$ significant ca. 12 h period was also detected by a Fourier analysis of the arrival time series (Fig. 2, top). This apparent discrepancy between 12 h (arrival events) and 24 h (presence/absence) periods can be explained conjointly by the distribution of the hours of day at which the tracked impala entered the open area, which was clearly bimodal, with a peak in

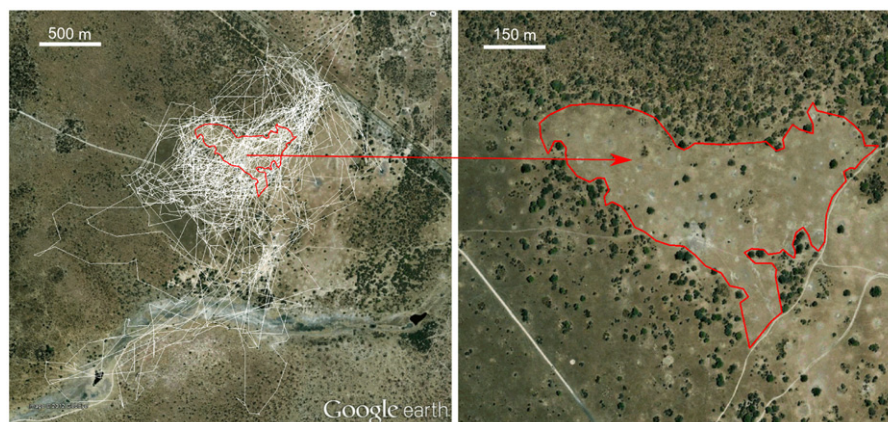


Fig. 1. Movement of the studied impala between the 16th of August and the 14th of November 2009 (white line, left panel). The area of interest on which we focused is the open area delimited by a solid red line (right panel). Background: Google Earth® (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

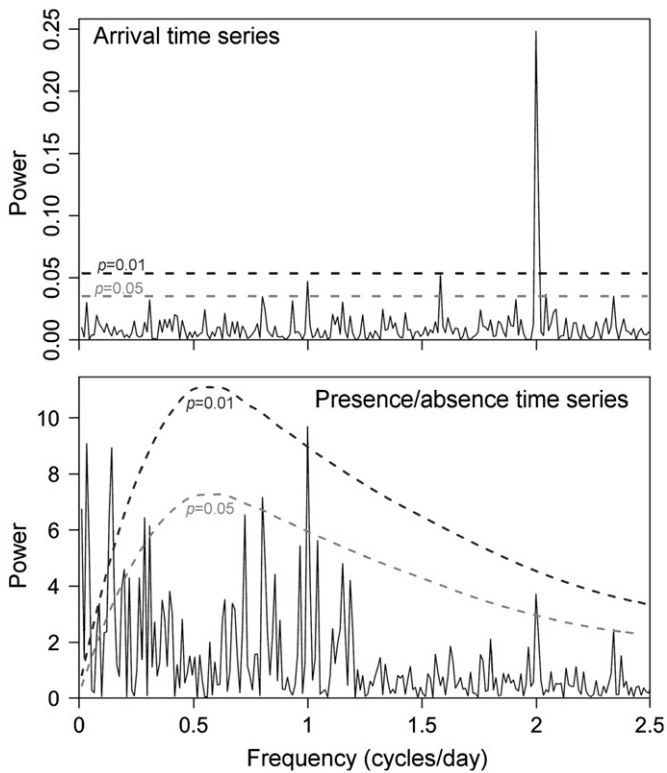


Fig. 2. Fourier power spectrum for the arrival (top) and presence/absence (bottom) time series. Spectrum is drawn as a solid line. The 1% and 5% significant thresholds are shown as black and gray (respectively) dashed lines. These thresholds were obtained by generating 1000 randomized time series from each observed one. As the threshold for the arrival time series does not depend on the frequency, the threshold value shown was obtained by averaging the values obtained for the various frequencies. For the presence/absence time series, the threshold depends on the frequency, and the threshold curve shown was obtained using a local smoothing procedure (see the Supplement for the R code used).

early morning and another one in the afternoon, and the distribution of the corresponding stay durations, which shows that the impala alternated between short stays in the early morning and long stays starting in the late afternoon (Fig. 3, 4th row). In contrast, Fourier analysis of departure time series (not shown) revealed significant 12 h- and 24 h-periods at $p=0.01$.

Wavelet analysis of presence/absence (Fig. 4, bottom) showed that the 24 h period was not expressed continuously across the time series, and that the 7-day period was expressed only from ca. 9 October (Julian day 282) till the end of the time series, showing here a regime shift. The length of the time series was too short however to reveal possible regime shifts for the 30-day period. Wavelet analysis of arrivals (Fig. 4, top) also revealed that a 12 h periodicity occurred roughly simultaneously with a 24 h-periodicity in the presence/absence time series. Finally, wavelet analysis of departures (not shown) did not find any time interval during which a 12 h- periodicity was significant at $p=0.01$, and found only a short time interval during which a 24 h- periodicity was significant at $p=0.01$, which roughly corresponded to a time interval during which a 24 h-period was significant in the presence/absence time series.

The observed periodicities are likely to be linked to predation/disturbance avoidance. Indeed, in Hwange National Park, the main predators of impala are leopards and lions (Fritz et al., 2011), which hunt at night by ambushing prey in the relatively dense vegetation. Open areas are thus safer than the rest of the landscape, and expected to be used when detecting predators is the hardest, i.e., especially at night during dark moon. The weekly cycle is likely to be linked to human activity in the week-end, which could affect the impala itself or its potential predators.

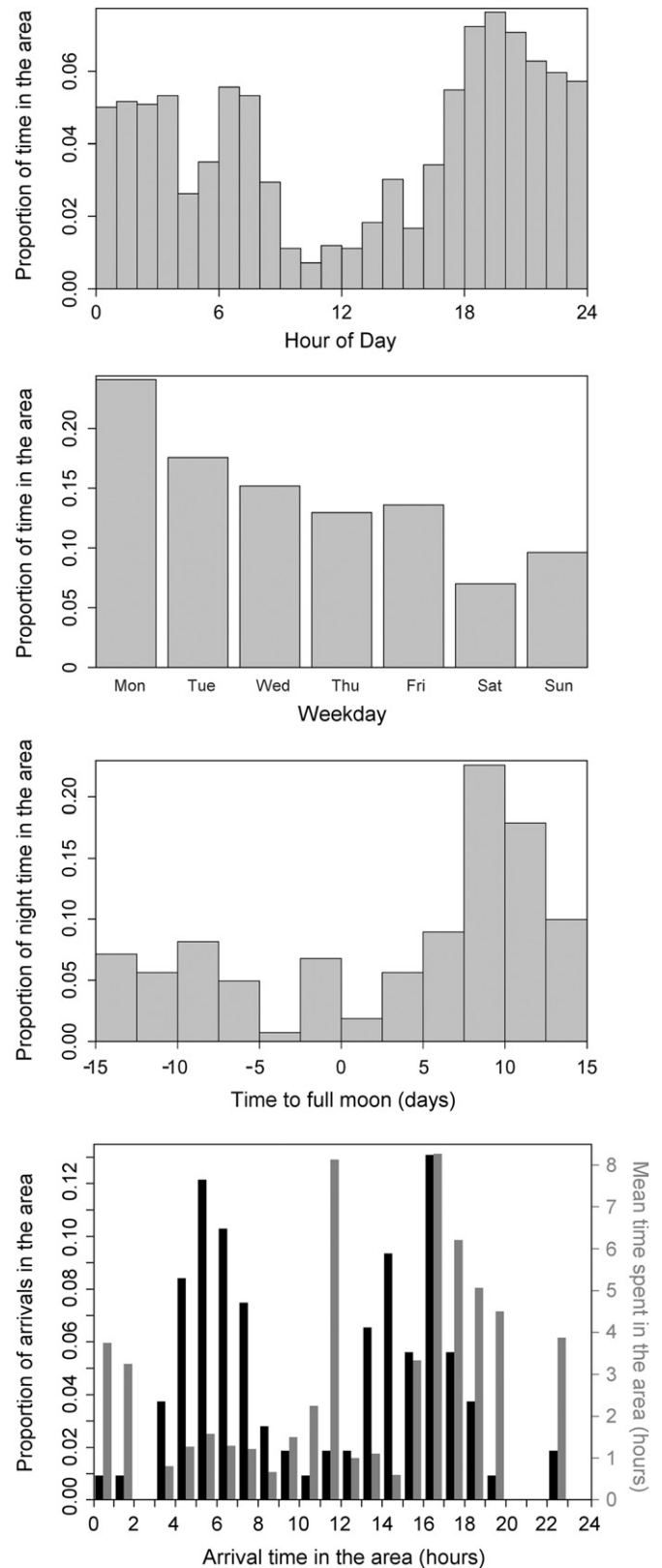


Fig. 3. Proportion of time spent in the open area as a function of the hour of day (1st row), weekday (2nd row), time to full moon (3rd row). Note that the time considered is the total time in 1st and 2nd row panels, and the night time in 3rd row panel. Fourth-row panel shows the proportion of arrival events (in black) and the time spent in the area (in gray) as a function of time of arrival.

Interestingly, the wavelet analysis revealed that the various periods found to be significant by the Fourier analysis existed

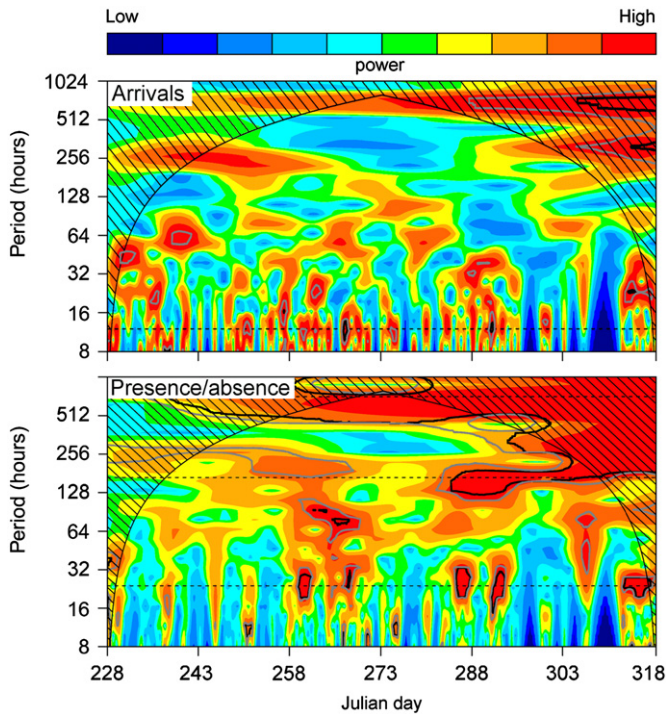


Fig. 4. Wavelet power spectra for the arrival (top) and the presence/absence (bottom) time series. The areas of statistical significance at the 1% and 5% levels are delineated by solid black and gray lines, respectively. The “cone of influence” (stripped area) indicates where spectrum values are unreliable due to edge effects. Horizontal dashed black lines represent periods which were significant at the 1% level in the Fourier spectra: 12 h for the arrival time series, and 24 h, 7 days (169 h), and 30 days (720 h) for the presence/absence time series.

only temporarily within the time series. This calls for further investigations of the environmental changes that could trigger a switch in the spatial behaviour. For instance, impala are more likely to select grasslands when lions are actually present in an area (Valeix et al., 2009).

4. Discussion

In this paper, we propose an approach based on Fourier and wavelet analyses that can simultaneously reveal several important patterns of periodicity in space use and movement recursions. Two recent studies (Wittemyer et al., 2008; Polansky et al., 2010) proposed to use both Fourier and wavelet analyses to detect periodicities and regime shifts in movement speed time series. Although Fourier analysis has become a standard tool in numerous fields, its practical application is not always straightforward. When investigating potential periodicities in movement recursions, it is preferable to consider binary time series such as presence/absence (Li et al., 2012), whereas for other parameters such as movement speed, its simple and direct application on numerical values provide reliable results (Wittemyer et al., 2008; Polansky et al., 2010). Furthermore, applying Fourier analysis to movement recursions pre-requires to determine areas of interest, and post-requires to reliably test whether the dominant periodicities are statistically significant or not, two key points that were not yet properly considered. Wavelet analysis is also currently becoming a standard tool in movement ecology. For instance, this kind of analysis has recently been performed on speeds and turning angles to characterize multiscale properties of movement behaviour and to detect regime shifts (Gaucherel, 2011). Surprisingly, wavelet analysis had never been applied before in a recursion study context, even though it shows considerable potential. In particular, wavelet

analysis makes it possible to determine both the periodicities and the duration during which they are expressed. It may be theoretically possible to bypass Fourier analysis. We nevertheless advise to first perform Fourier analysis, as it is a very fast and convenient way to determine the frequencies that are potentially relevant, and so help interpreting the wavelet power spectrum.

As seen in our illustrative example, randomization procedures performed in the framework of Fourier analysis, which focuses only on periodic time, are likely to be more sensitive in periodic peak detection than those performed in the framework of wavelet analysis, but only wavelet analysis, which simultaneously considers time both as a periodic and as a linear variable (respectively on the Y-axis and on the X-axis of the spectrum), makes it possible to specify whether the periodic events detected by Fourier analysis occur along the whole time series or only at some particular epochs. Another way of approaching the study of periodicity in animal movement is to build up mechanistic models of animal space use and compare observed and expected periodic patterns. For instance, one can build up predator–prey shell games integrating within-patch habitat space use (which is currently lacking, see (Mitchell, 2009)) to investigate under which conditions predictable, periodic, habitat use may emerge, as temporal unpredictability should often be favoured for both predator and prey (Roth and Lima, 2007; Valeix et al., 2011) (but see (Ferrari and Chivers, 2009)). Grazing optimization in models of herbivore foraging may also lead to periodic patch use of herbivores (e.g., Rowcliffe et al., 1995). Our approach provides a way to test the predictions of these models using the more and more common individual-based tracking data.

Recursion patterns are a fundamental aspect of home range behaviour. In conjunction with residence time, they result from how an animal adjusts to resource heterogeneity in space and time and to interactions with conspecifics, guild members, and predators. It is therefore likely that the study of recursion patterns will bring new insights regarding the importance of these factors, but ecologists still lack adequate tools for data exploration and hypothesis testing in this area. Our approach, specific to the study of periodicity in recursions, is a step forward building up a wider analytical framework.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.jtbi.2012.10.026>.

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