Cross Wavelet Analysis to Study Periodic Behaviour of Animals in Relation to Environmental Cues

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Introduction

Individual based studies of animal movement have recently gained momentum due to extensive accessibility to telemetry data from tagged animals. A key challenge in understanding animal behaviour from movement data has been explaining the role of environmental cues. This is because animals moving through complex environments are influenced by multifarious factors, and it becomes challenging to extract the influence of each environmental control at the right scale. To understand the decision making process during animal movement triggered by organism–environment information fluxes, there is a need to link environmental data with statistics of animal movement.

In order to confront these challenges we propose a statistically robust method that extracts distinct patterns in moving animals as repetitive cyclic behaviour. In case of animals, repetitive or periodic behaviour can be expected to be a result of periodic cues from nature such as temporal oscillations in temperature, precipitation, light, wind, forage etc. as well as the animal's circadian rhythm. The periodic movement pattern associated with environmental cue is likely to have a degree of temporal correlation and also operate at multiple scales [1]. Since the period (the regular time intervals in a periodic motion) that is affected by different cues is an unknown parameter, one needs a signal processing method that automatically detects periodicity in the data. Among the different period detection techniques that can be applied to signal processing, wavelet transform can be directly applied to movement data [2] and results in exploratory analysis of the auto-correlative properties of the movement data. In this study we show the use of a novel method in animal movement studies by applying a bivariate extension of the wavelet transform, namely cross wavelet analysis, to extract periodic patterns in moving animals in relation to environmental cues. First, significant locations that can be designated as reference spots (such as nesting sites) were identified from which the periodicities can be viewed. Cross wavelet analysis between a movement parameter and an environmental parameter was then used to study repetitive movement behaviour in animals. We use empirical data of GPS tagged Lesser Black-backed gulls (Larus fuscus) to assess our method.

Material and Method

Cross wavelet analysis was applied in two phases:

1. Step length during the breeding season of a single gull (ID 41781) was tested against three environmental variables, namely temperature, precipitation and wind speed.
2. Step length of 12 gulls during the breeding season was tested against temperature to illustrate individual variations and group behaviour.

Tracking data

The tracking data of the Lesser Black-backed Gull (here after gull) used for this study was provided by the Avian Research Institute, Wilhelmshaven, Germany and SOVON Dutch Centre For Field Ornithology, Nijmegen. Each bird was equipped with an Argos-GPS solar-powered Platform Terminal Transmitter (PTT; Microwave Telemetry Inc., Columbia, MD, USA). The Argos-GPS PTTs have an accuracy of ±18 m. For this study the gull with the PTT id 41781(sampling interval 1 hour) was used to test the effect of animal movement with different environmental variables at different temporal scales. Data from twelve gulls (PTT id's 41742, 41749, 41752, 41757, 41758, 41762, 41763, 41764, 41767, 41771, 41775, and 41781) were used to demonstrate the use of cross wavelet analysis in analyzing individual variations and group pattern of gulls with temperature as the environmental variable. We selected the month of May, during the breeding season to test our methods. Animals with periodic behaviour commonly have a central location that they visit repeatedly. These are termed as "reference spots"[3]. In the present study we use the breeding site as the main reference spot to further analyze the effect of environmental variables on behaviour of the gulls.

Environmental Data

To test the application of cross wavelet analysis for mining periodic behavior of the gulls in relation to environmental co-variates, we use the movement parameter, step length during the breeding season, as well as three environmental variables: temperature, precipitation and wind speed. Environmental data was downloaded from the Royal Netherlands Meteorological Institute, Station Vlieland. Mean hourly data for temperature, precipitation and wind speed were used for the study.

Cross wavelet analysis

The wavelet transform of a time series decomposes the data using a wavelet function resulting in a time-scale representation of a temporal pattern [4]. Scale in a wavelet analysis is generated by contraction and dilation of the wavelet function. Contraction or dilation changes the time window over which the wavelet function is applied on the time series. Increasing the size of the window increases the scale at which the wavelet coefficients are calculated. The parameter scale in the wavelet analysis can be paralleled to scales used in maps. Corresponding to high scales in maps, in wavelet analysis higher scales (or periods) represent global view of the signal that usually spans the entire signal and low scales (or periods) correspond to a detailed view that relatively lasts a short time. Thus wavelet coefficients are obtained for a series of scales and at each time stamp. We use the Morlet wavelet for this study defined as

$$\psi(\eta) = \pi^{-1/4} \exp(-i\omega_0\eta) \exp(-{\eta^2}/{2}) \qquad \text{Equation 1}$$

The continuous wavelet transform of the discrete time series $X_n$at scale a and time t_i is defined by

$$W\,[a, t_j] = \frac{1}{\sqrt{a}} \sum_{l=1}^{N} X_j \ \ \psi * [\frac{(l-j)\Delta t}{a}] \qquad \text{Equation 2}$$

where ψ* denotes the complex conjugate of the analyzing wavelet function ψ.

A local power spectrum of a wavelet transform is the square of the wavelet coefficient $|W_n^X\,(s)|^2$for each scale and at each time stamp. Cross wavelet transform (XWT) of two time series x_n (movement parameter) and y_n(environmental parameter) can be defined as

$$W^{XY} = W^X\, W^{Y*} \qquad \text{Equation 3}$$

where * indicates the complex conjugate. As the cross wavelet transform gives complex values, it can be decomposed into amplitude and phase angles. The phase angles describe the delay between the two signals at a time t on a scale s.

Thus cross wavelet transform exposes regions with high common power and correlation between the two time series and further reveals information about the phase relationship. The circular mean of the phase angles can be used to quantify the phase relationship with in phase shown by arrows pointing right, anti-phase pointing left, x leading y by 90 degree pointing down and y leading x by 90 degree pointing up.

Regions of significant scalogram values were defined by the "area wise test" [5] which is a bootstrapping test. Regions of modulus values greater than or equal to the 0.95 sample quantile of 1000 bootstrapped coefficient values against a red noise null model fit to the data were considered significant and marked in black contour lines [1, 5-8]. Cross wavelet software was provided by Aslak Grinsted (2002-2004) and used in the Matlab environment.

Results

In Figure 1 cross wavelet analysis of step length and temperature, precipitation and wind speed reveals strong diurnal cycles with specific periods of high common power. For example step length and temperature show consistent high powers at a scale or period of 24 hours, 6 and 24 hour cycles with precipitation and 24 hour cycles with wind speed. For two time series to be related, areas with consistent or slowly varying phase angles should be considered in the regions of high common power. The phase angles give an indication of the lag between the two time series. Step length when analyzed with temperature in the 24 hour period, both time series are in-phase over the entire breeding season. This suggests that a daily activity of one cycle per day is a result of daily oscillation in temperature. The 5% significant areas of high power are phase-locked suggesting a strong link between the two time series. For shorter cycles (periods), the phase angles are not consistent and show that that hourly movement is probably not significantly dependent on the temperature and is affected by other factor. The average phase angle for the 24 hour period is 24 $\pm$ 15° and proves that step length of movement essentially mirrors temperature and does not have a significant lag between them.
Cross wavelet analysis of step length with precipitation in Figure 1(b) showes an average angle of 169 $\pm$15°demonstrating that movement and precipitation are predominantly in anti-phase. This indicates that movement and precipitation are inversely related to each other. Cross wavelet analysis between step length and wind speed showed that movement was mainly in-phase at a period of 24 hours. However at higher powers (64 hours or 3 days) the phase angles gradually varies from in phase to anti phase.

Figure 2(a) shows individual variations using cross wavelet analysis of step length with temperature. Consistent high powers from the cross wavelet analysis indicates diurnal cycles in all individuals but also shows heterogeneity in time periods of movement bouts and resting phases. The power spectral values from cross wavelet analysis of all individuals were stacked into a 3D matrix and averaged for each time stamp and at all scales in Figure 2(b). The result shows that correlation between distance moved and temperature was not continuous across time for the temporal scale 24, thereby showing a distinct pattern in the sample under study that can be further linked to other ecological and social factors.

Conclusion

The cross wavelet analysis is used for exploratory data analysis as a first step towards modeling moving animals. The traditional methods of visually analyzing trajectories of animals tagged with telemetry devices are replaced with mathematical models and statistics. Advanced data mining techniques can process large amounts of telemetry data in a conceptually standardized way. The method proposed serves as the first step towards understanding the organism-environment interaction, and is the basis for choosing the right environmental variables at the right scale for detailed modeling.While the study uses only a few environmental variables, it illustrates that it can easily be replicated to test for a large range of variables and in doing so we can identify parameters that are capable of explaining cyclic behaviors. This is essential for segregating complex variables into categories such as limiting factors, or into factors that affect the cognitive senses of the animal.

Most studies that examine animal behavior with environmental variables are not able to account for the fact that different components of the environment are important to animals at different scales (temporal scales). Identifying when or for how long a particular environmental cue triggers a specific behavior is the first step towards explaining why and when animals move to certain parts of their range. However this important step is often skipped due to lack of sufficient data at the right scale or tools to identify the scales according to the species under study. Incorrect definition of scales, relative to the perception of space and time by an animal may result in the failure to measure response to variables and variation relevant to the process of interest.

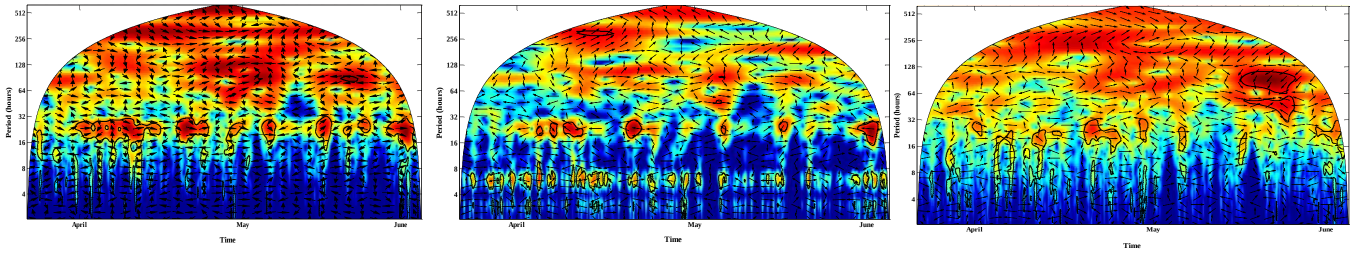
Ethical statement and acknowledment

In order to catch and fix transmitters a license of the "Flora en Fauna Wet", number FF75A/2007/056 and approval from the Dutch Ethical Committee under protocol number CL 0703 was obtained for the gulls. This project was performed thanks to the bird migration data collected through FlySafe (http://iap.esa.int/flysafe), a project of the European Space Agency Integrated Applications Promotion (IAP) programme (http://iap.esa.int/). This work was supported by the European Union Erasmus Mundus Programme (2008-3620/001-001-MUN ECW) PhD award to Maitreyi Sur.

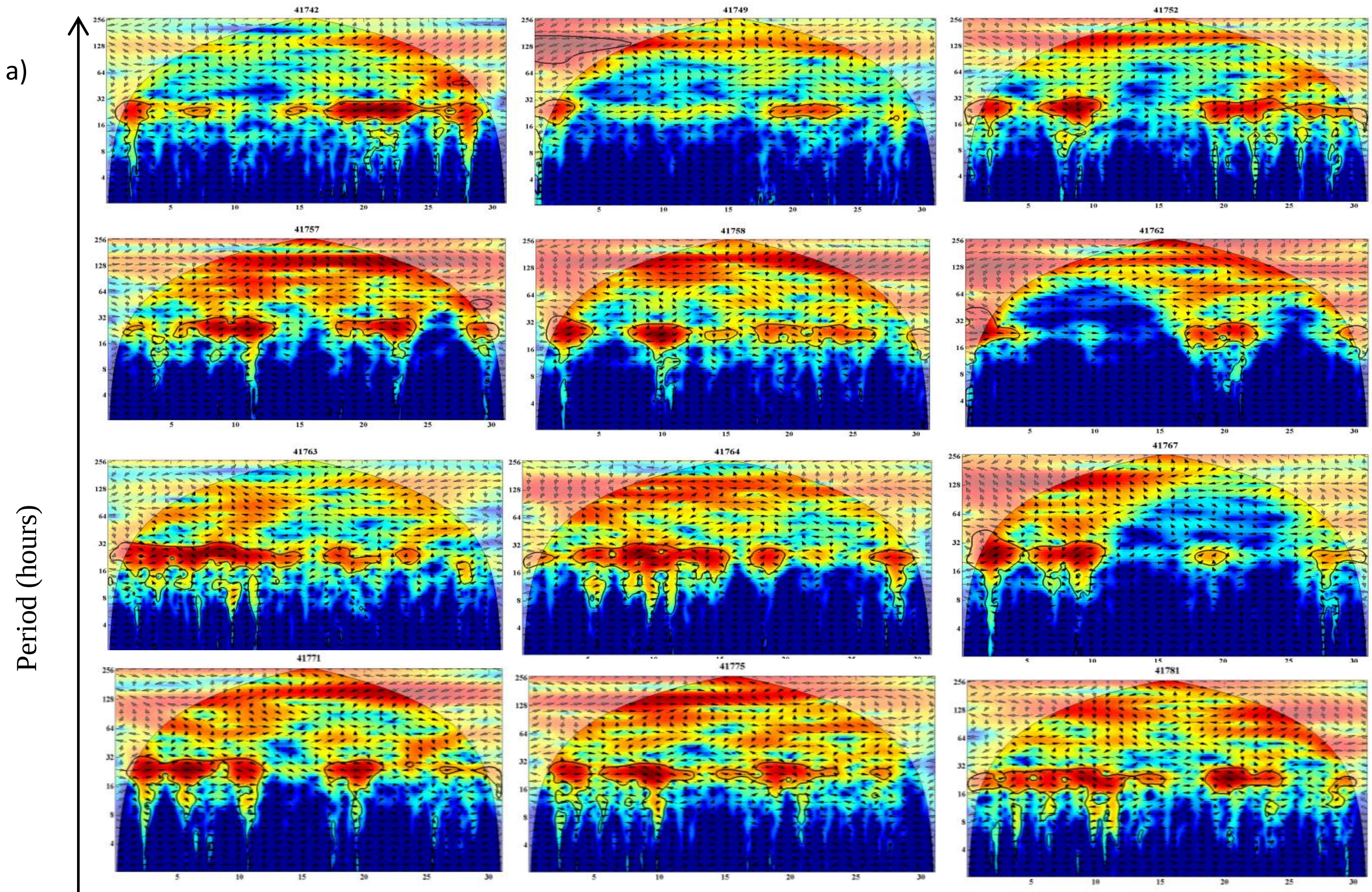
Cross wavelet analysis of step length and temperature

a) Cross wavelet analysis of step length and temperature

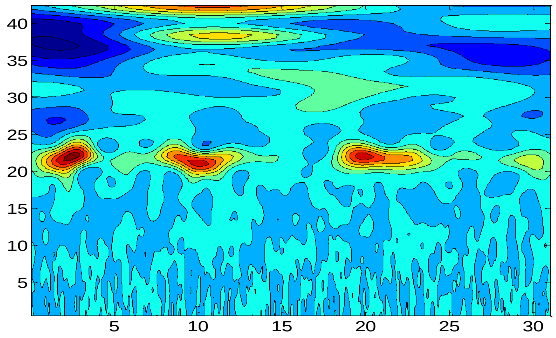
c) Cross wavelet analysis of step length and wind speed



Figures 1. Cross wavelet transform of time series of movement parameter step length and environmental variables. The 5% significant level against red noise is shown as a thick contour. Larger squared modulus values correspond to warmer colours (red, yellow) and smaller values correspond to cooler colours (blues).The relative phase relationship is shown as arrows.



b)



Time (days)

Figure 2. a) Cross wavelet analysis of step length and temperature of twelve gulls during the breeding season (May2008). b) Average power spectral values from cross wavelet analysis of step length and temperature of all the individuals.

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