Singing of *Neoconocephalus robustus* as an example of deterministic chaos in insects

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We use nonlinear time series analysis methods to analyse the dynamics of the sound-producing apparatus of the katydid *Neoconocephalus robustus*. We capture the dynamics by analysing a recording of the singing activity. First, we reconstruct the phase space from the sound recording and test it against determinism and stationarity. After confirming determinism and stationarity, we show that the maximal Lyapunov exponent of the series is positive, which is a strong indicator for the chaotic behaviour of the system. We discuss that methods of nonlinear time series analysis can yield instructive insights and foster the understanding of acoustic communication among insects.

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1. Introduction

Nonlinear time series analysis (Abarbanel 1996; Kantz and Schreiber 1997; Sprott 2003) offers tools that bridge the gap between experimentally observed irregular behaviour and the theory of deterministic dynamical systems (Kaplan and Glass 1995; Ott 1993; Schuster 1989; Strogatz 1994). It is thus a powerful theory that enables the determination of characteristic quantities, e.g. the number of active degrees of freedom or invariants, such as Lyapunov exponents, of a particular system solely by analysing the time course of one of its variables. Although this basic concept is enchanting, care should be exercised when applying methods of Nonlinear time series analysis to real-life data. In particular, the notions of determinism and stationarity should always be tested for, since they cannot be taken for granted as in dynamical systems theory. An observed irregular behaviour can be easily advertised as being chaos. However, since deterministic chaos is neither the only nor the most probable origin of irregularity in real-life systems, other potential sources, such as noise or varying parameters during data acquisition, have to be eliminated. These are very important issues that have to be addressed before attempting further analyses, especially on real-life recordings, as we will emphasize throughout this work.

In this study, we analyse the sound recording of the katydid *N. robustus* (Scudder 1862), belonging to the genus *Neoconocephalus*, family Tettigoniidae, order Orthoptera, which lives preferably at the periphery of tall rank vegetation and is widespread in the northeastern and midwestern United States, extending also southward into Florida and westward into New Mexico. For a comprehensive review on various aspects of *N. robustus* we refer the reader to the works of Walker *et al* (1973, 1999); here we constrain ourselves to the most important facts. Adults normally grow from 53 to 74 mm and their wings extend beyond the abdomen. They are univoltine throughout their ranges and overwinter as eggs. Of direct importance for the present study is the fact that katydids produce their sounds via a file on the left wing and a scraper on the right. Upon stridulatory wing movements, they produce loud stridulatory sounds that are additionally amplified by the so-called stridulatory area. In *N. robustus* the latter measures more than 4.9 mm in width and heats up during singing. Interestingly, the thorax of *N. robustus*

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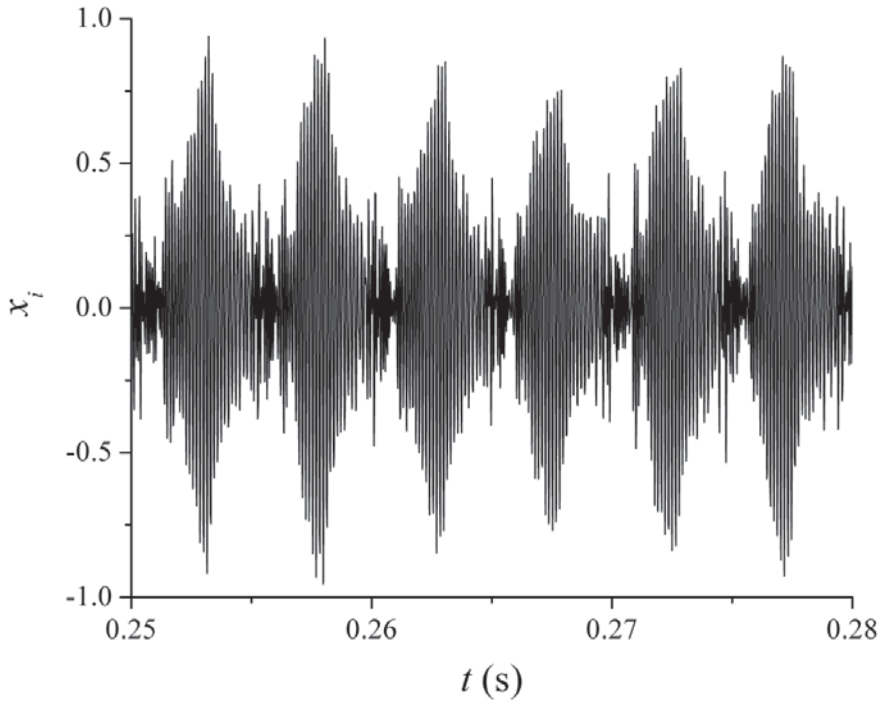

Figure 1. An insert of the studied sound recording of *N. robustus*.

can be up to 12°C warmer than the ambient temperature (Heath and Josephson 1970). The typical bursts of acoustic activity shown in figure 1, which give the singing a whiny or buzzy modulation, are made during wing closures. It is the dynamics of this sound-producing mechanism that we currently investigate with methods of Nonlinear time series analysis.

In the past, animal sound recordings have often been analysed by methods of Nonlinear time series analysis. Wilden *et al* (1998), for example, introduced the concept of Nonlinear dynamics to mammal bioacoustics in order to quantify the complexity of animal vocalizations. Mammalian sounds were also investigated by Fitch *et al* (2002), and Riede *et al* (2000, 2001, 2005). Other examples where Nonlinear dynamics was found to play an important role for sound generation include bird songs (Fee *et al* 1998; Fletcher 2000) as well as human speech signals (Behrman 1999; Herzel *et al* 1994; Kumar and Mullick 1996; Mende *et al* 1990; Narayanan and Alwan 1995; Titze *et al* 1993). However, despite the rather extensive literature available on this topic, we found no applications of Nonlinear time series analysis methods on insect sounds. The present study thus aims to fill this gap.

We start the analysis by applying the embedding theorem (Takens 1981; Sauer *et al* 1991), which enables the reconstruction of the phase space from a single observed variable, thereby laying the foundation for further analyses. To determine proper embedding parameters for the phase space reconstruction, we use the mutual information (Fraser and Swinney 1986) and false nearest neighbour method (Kennel *et al* 1992). Next, we apply the determinism (Kaplan and Glass 1992) and stationarity (Schreiber 1997) tests to verify if the studied sound recording originates from a deterministic stationary system. By applying the determinism test we determine whether the analysed irregular behaviour is indeed a consequence of deterministic Nonlinear dynamics, whereas the stationarity test enables us to verify if system parameters were constant during the recording of the song. After establishing that the recording originates from a deterministic stationary sound-producing apparatus, we calculate the maximal Lyapunov exponent (Wolf *et al* 1985). We find that the latter is positive, from which we conclude that the sound of *N. robustus*, and thus also its sound-producing apparatus, possess properties typical of deterministic chaotic systems. At the end, we summarize the results and outline possible biological implications of our findings.

2. Nonlinear time series analysis

2.1 *Studied sound recording*

We analyse the sound recording of *N. robustus*, which was recorded in Washington County, Ohio, United States (Walker

1999). The audio file was sampled at 44 kHz, thus occupying $2.2 \cdot 10^5$ points at a length of 5 s. An insert of the time series x_i resulting from the audio file is shown in figure 1, whereby *i* is an integer indexing consecutive points in time *t*. A visual inspection of the time series presented in figure 1 reveals that the signal is characterized by at least two predominant frequencies, namely, the one between consecutive bursts of activity equalling 0.18 kHz, and the one between consecutive spikes in each bursting phase equalling 6.6 kHz. The fact that the studied recording comprises at least two different frequencies, accompanied by its overall irregular appearance, suggests that the sound might originate from a Nonlinear or even chaotic deterministic system. We apply powerful methods of Nonlinear time series analysis to confirm this conjecture in a more rigorous manner.

2.2 *Phase space reconstruction*

We reconstruct the phase space from the sound recording by applying the embedding theorem (Takens 1981; Sauer *et al* 1991), which states that for a large enough embedding dimension *m* the delay vectors

$$\mathbf{p}(i) = (x_i, x_{i+\tau}, x_{i+2\tau}, \ldots, x_{i+(m-1)\tau}), \tag{1}$$

yield a phase space that has exactly the same properties as the one formed by the original variables of the system. In eq. (1) variables $x_i, x_{i+\tau}, x_{i+2\tau}, \ldots, x_{i+(m-1)\tau}$ denote values of the sound recording at times $t = i\mathrm{d}t$, $t = (i + \tau)\mathrm{d}t$, $t = (i + 2\tau)\mathrm{d}t$,..., $t = (i + (m-1)\tau)\mathrm{d}t$, respectively, whereby τ is the so-called embedding delay and d*t* is the sampling time of data points currently equalling $2.27 \cdot 10^{-5}$ s.

Although the implementation of eq. (1) is straightforward, we first have to determine proper values for embedding parameters τ and *m*. For this purpose, the mutual information (Fraser and Swinney 1986) and false nearest neighbour methods (Kennel *et al* 1992) can be used, respectively. Since the mutual information between x_i and $x_{i+\tau}$ quantifies the amount of information we have about the state $x_{i+\tau}$ presuming we know x_i (Shaw 1981), Fraser and Swinney (1986) proposed to use the first minimum of the mutual information as the optimal embedding delay. The algorithm for calculating the mutual information can be summarized as follows. Given a time series of the form $\{x_0, x_1, x_2, \ldots x_i, \ldots, x_n\}$, one first has to find the minimum (x_{min}) and the maximum (x_{max}) of the sequence. The absolute value of their difference $|x_{max} - x_{min}|$ then has to be partitioned into *j* equally sized intervals, where *j* is a large enough integer number. Finally, one calculates the expression

$$I(\tau) = -\sum_{h=1}^{j}\sum_{k=1}^{j} P_{h,k}(\tau) \ln \frac{P_{h,k}(\tau)}{P_h P_k}, \tag{2}$$

where P_h and P_k denote the probabilities that the variable assumes a value inside the *h*–th and *k*–th bin, respectively, and $P_{h,k}(\tau)$ is the joint probability that x_i is in bin *h* and $x_{i+\tau}$ is in bin *k*. For the studied sound recording presented in figure 1, the first minimum of $I(\tau)$ is obtained already at $\tau = 2$. We use this τ in all future calculations.

We now turn to establishing a proper embedding dimension *m* for the examined sound recording by applying the false nearest neighbour method introduced by Kennel *et al* (1992). The method relies on the assumption that the phase space of a deterministic system folds and unfolds smoothly with no sudden irregularities appearing in its structure. By exploiting this assumption we must come to the conclusion that points that are close in the reconstructed embedding space have to stay sufficiently close also during forward iteration. If a phase space point has a close neighbour that does not fulfil this criterion it is marked as having a false nearest neighbour. As soon as the *m* chosen is sufficiently large, the fraction of points that have a false nearest neighbour Φ converges to zero. In order to calculate Φ the following algorithm is used. Given a point $\mathbf{p}(i)$ in the *m* – dimensional embedding space, one first has to find a neighbour $\mathbf{p}(j)$, so that $\| \mathbf{p}(i) - \mathbf{p}(j) \| < \varepsilon$, where $\|\ldots\|$ is the square norm and ε is a small constant usually not larger than 1/10 of the standard data deviation. We then calculate the normalized distance R_i between the $m+1^{\text{st.}}$ embedding coordinate of points $\mathbf{p}(i)$ and $\mathbf{p}(j)$ according to the equation:

$$R_i = \frac{\left| x_{i+m\tau} - x_{j+m\tau} \right|}{\left\| \mathbf{p}(i) - \mathbf{p}(j) \right\|}. \tag{3}$$

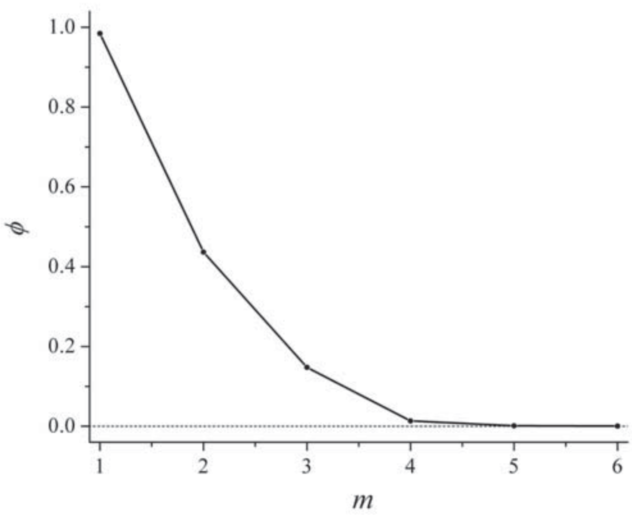

Figure 2. Determination of the minimal required embedding dimension. The fraction of false nearest neighbours Φ drops convincingly to zero at $m = 5$.

If R_i is larger than a given threshold R_{tr}, then $\mathbf{p}(i)$ is marked as having a false nearest neighbour. Equation (3) has to be applied for the whole time series and for various $m = 1,2,\ldots$ until the fraction of points Φ for which $R_i > R_{tr}$ is negligible. According to Kennel *et al* (1992), R_{tr}=10 has proven to be a good choice for most datasets. The results obtained with the false nearest neighbour method are presented in figure 2. It can be observed that Φ drops convincingly to zero (<1%) for $m = 5$. Hence, the underlying system that produced the studied sound recording has five active degrees of freedom. In other words, it would be justified to mathematically model the *N. robustus* sound-producing apparatus with no more than five first-order ordinary differential equations.

By now we have determined all the parameters that are necessary to successfully reconstruct the phase space of the system from a single observed variable. However, prior to investigating crucial dynamical properties of the attractor, we first have to verify if the studied signal originates from a deterministic stationary system. As already emphasized in the Introduction, determinism and stationarity are crucial properties that guarantee a relevant analysis and are the best protection against spurious results and false claims. Thus, in order to justify further analyses, we have to verify if the studied sound recording possesses properties typical of deterministic stationary signals.

2.3 *Determinism test*

We apply a simple yet effective determinism test, originally proposed by Kaplan and Glass (1992), which measures average directional vectors in a coarse-grained embedding space. The idea is that neighbouring trajectories in a small portion of the embedding space should all point in the same direction, thus assuring uniqueness of solutions in the phase space, which is the hallmark of determinism. To perform the test, the embedding space has to be coarse-grained into equally sized boxes. The average directional vector pertaining to a particular box is obtained as follows. Each pass p of the trajectory through the k–th box generates a unit vector $\mathbf{e}_p$, whose direction is determined by the phase space point where the trajectory first enters the box and the phase space point where the trajectory leaves the box. In fact, this is the average direction of the trajectory through the box during a particular pass. The average directional vector $\mathbf{V}_k$ of the k–th box is then simply

$$\mathbf{V}_k = \frac{1}{n}\sum_{p=1}^{n}\mathbf{e}_p\,, \tag{4}$$

where n is the number of all passes through the k–th box. Completing this task for all occupied boxes gives us a directional approximation for the vector field of the system. If the time series originates from a deterministic system, and the coarse-grained partitioning is fine enough, the obtained directional vector field should consist solely of vectors that have unit length (remember that each $\mathbf{e}_p$ is also a unit vector). Hence, if the system is deterministic, the average length of all directional vectors κ will be 1, while for a completely random system $\kappa \approx 0$. The determinism factor pertaining to the five-dimensional embedding space presented in figure 3 that was coarse-grained into a $12\times12\times\ldots\times12$ grid is $\kappa = 0.97$, which clearly confirms the deterministic nature of the studied sound recording.

2.4 *Stationarity test*

It remains of interest to verify if the studied sound recording originated from a stationary process. For this purpose, we apply the stationarity test proposed by Schreiber (1997). In general, stationarity violations manifest so that various non-overlapping segments of the time series have different dynamical properties. Since linear statistics, such as the mean or standard data deviation (Kantz and Schreiber 1997), usually do not posses enough discrimination power when analysing irregular signals, Nonlinear statistics have to be applied. One of the most effective is the cross-prediction error statistic. The idea is to split the time series into several short non-overlapping segments, and then use a particular data segment to make predictions in another data segment. By calculating the average prediction error (δ_{gk}) when considering points in segment g to make predictions in segment k, we obtain a very sensitive statistic capable of detecting minute changes in dynamics, and thus a very powerful probe for stationarity. If for any combination of g and k δ_{gk} is significantly above average, this is a clear indicator that the examined dataset originated from a non-stationary process. An accurate description of the whole algorithm can be found in Kantz and Schreiber (1997; p. 42 onwards), while here we concentrate on the results that are presented in figure 4 and were obtained by dividing 100,000 data points into 50 non-overlapping segments of 2000 points, thus yielding 50^2 combinations to evaluate δ_{gk}. The average value of all δ_{gk} is 0.11, while the minimum and maximum values are 0.093 and 0.12, respectively. Since all cross-prediction errors differ maximally by a factor of 1/3, we can clearly refute non-stationarity in the studied sound recording. This implies that during the recording time the environmental influences on the katydid did not change and thus its singing was stationary both from the listeners' as well as from the dynamical point of view. This is not surprising since not much can happen in a few seconds' time. However, it is important to bear in mind that longer recordings of real-life activities almost always yield non-stationary datasets since subjects under study often cannot be isolated from environmental effects or, even more likely, it is explicitly not of interest to do so.

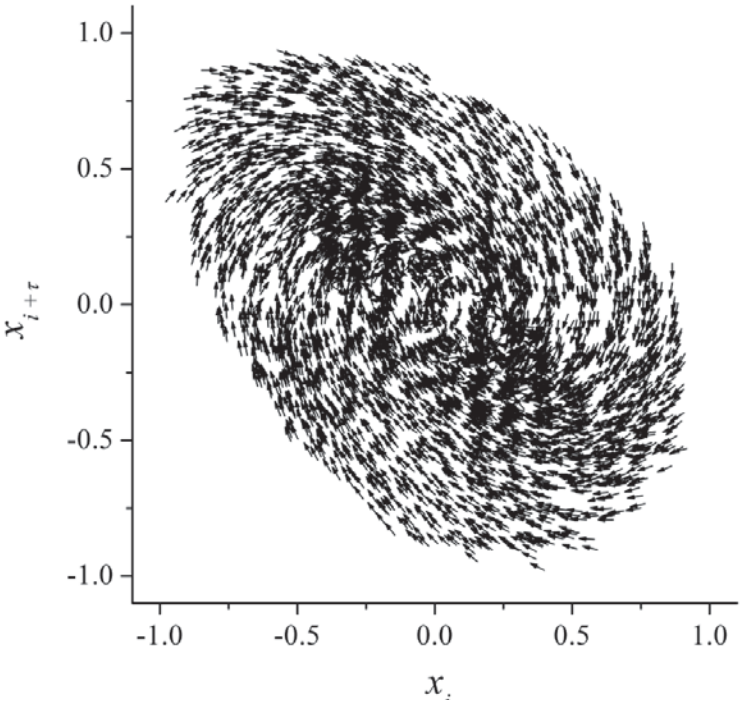

Figure 3. Determinism test. The approximated directional vector field for the embedding space reconstructed with $\tau = 2$ and $m = 5$. The pertaining determinism factor is $\kappa = 0.97$.

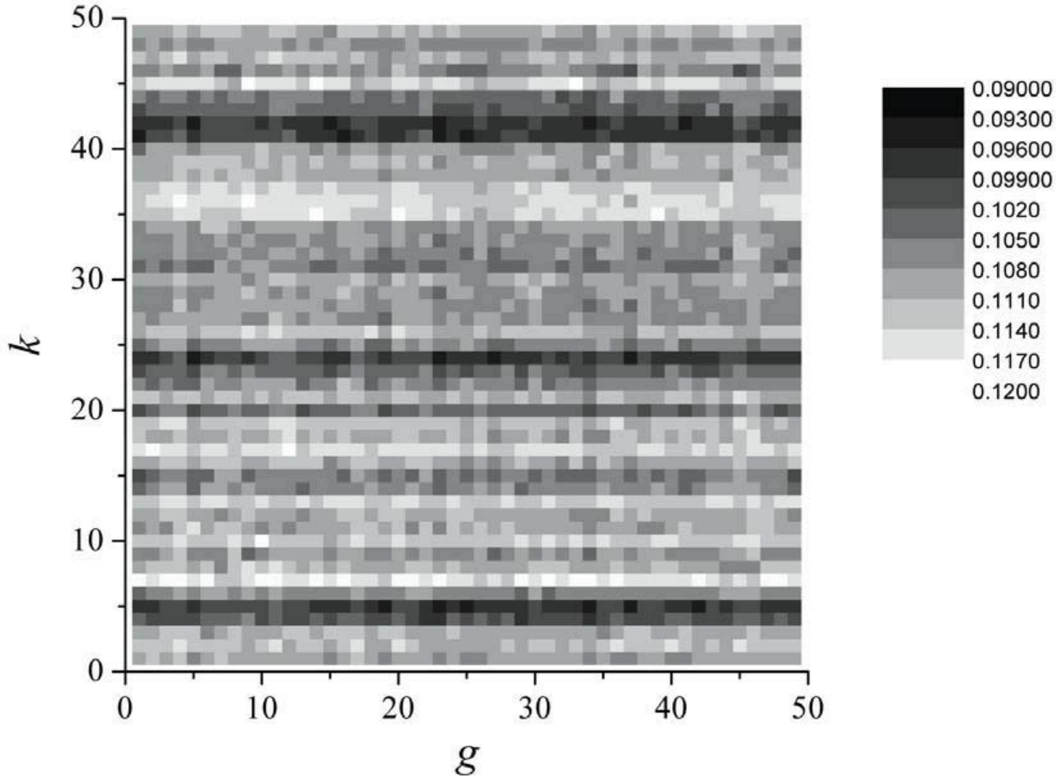

Figure 4. Stationarity test. The time series was partitioned into 50 non-overlapping segments each occupying 2000 data points. The colour map displays average cross-prediction errors δ_{gk} in dependence on different segment combinations (*see* main text for details).

2.5 *Maximal Lyapunov exponent*

Finally, it is of interest to determine the maximal Lyapunov exponent pertaining to the studied sound recording. Importantly, since we have already positively established determinism and stationarity in the time series, the following can be considered a truly relevant analysis based on which robust conclusions regarding the nature of the katydid's sound-production apparatus can be drawn. In general, Lyapunov exponents determine the rate of divergence or convergence of initially nearby trajectories in phase space (Strogatz 1994). An *m*–dimensional system has *m* different Lyapunov exponents Λ_i, where i=1,2,…,m. Most importantly, already a single positive Lyapunov exponent suffices to positively establish chaos in the studied system. Usually, this Lyapunov exponent is referred to as the largest or maximal and is thus appropriately denoted as Λ_{max}. Λ_{max} uniquely determines whether the time series under study originated from a chaotic system or not. If $\Lambda_{max} > 0$, two initially nearby trajectories of the attractor diverge exponentially fast as time progresses (on average), constituting the extreme sensitivity to changes in initial conditions which is the hallmark of chaos. Presently, we use the algorithm developed by Wolf *et al* (1985), which implements the theory in a very simple and direct fashion, while virtually identical results as reported below can be obtained also with other methods (Rosenstein *et al* 1993; Kantz 1994) for determining Λ_{max} from recorded datasets. The first step of the algorithm consists of finding a near neighbour of the initial point $\mathbf{p}(0)$. Let L_0 denote the Euclidian distance between them. Next, we have to iterate both points forward for a fixed evolution time t_{evolv}, which should be of the same order of magnitude as the embedding delay τ (in our case t_{evolv} =5), and denote the final distance between the evolved points as L_{evolv}. After each t_{evolv} a replacement step is attempted in which we look for a new point in the embedding space whose distance to the evolved initial point is as small as possible, under the constraint that the angular separation between the evolved and replacement element is small. This procedure is repeated until the initial point $\mathbf{p}(0)$ reaches the end of the trajectory in the phase space. Finally, Λ_{max} is calculated according to the equation

$$\Lambda_{\mathrm{max}} = \frac{1}{Rt_{\mathrm{evolv}}} \sum_{i=1}^{R} \ln \frac{L^{(i)}_{\mathrm{evolv}}}{L^{(i)}_{0}}, \tag{5}$$

where *R* is the total number of replacement steps. By using Eq. (5), we calculate Λ_{max} for the attractor presented in figure 3. As seen in figure 5, the maximal Lyapunov exponent converges extremely well to Λ_{max}=0.041±0.002. This is firm evidence that the studied sound recording from *N. robustus* originated from a deterministic chaotic system.

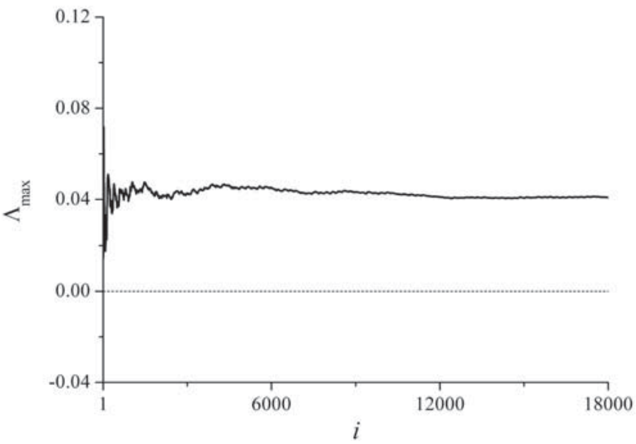

Figure 5. Determination of the maximal Lyapunov exponent. The value converges extremely well to Λ_{max}= 0.041 ± 0.002 in dimensionless units, thus, combined with the results obtained from the determinism and stationarity tests, indicating deterministic chaos in the studied sound recording of *N. robustus*.

3. Discussion

We systematically analyse the sound recording of *N. robustus* (Scudder 1862) with methods of Nonlinear time series analysis. In particular, we outline a careful approach, encompassing a determinism (Kaplan and Glass 1992; Wayland *et al* 1993; Salvino and Cawley 1994) and stationarity test (Schreiber 1997), which largely eliminates the occurrence of spurious results, and thus guarantees a relevant analysis of the observed system. We find that the studied sound recording originates from a deterministic stationary system and is characterized by a positive maximal Lyapunov exponent (Wolf *et al* 1985; Rosenstein *et al* 1993; Kantz 1994). Thus, we conclude that the sound-producing mechanism of the katydid species studied possesses properties that are characteristic of deterministic chaotic systems.

We argue that the above-performed analysis is a viable approach for obtaining insights into mechanisms of insect sound generation. In particular, it can been seen as the necessary prelude to mathematical modelling, since it provides important information regarding the dynamical properties of the underlying system, such as, for example, the number of active degrees of freedom given by the dimensionality of the phase space or Lyapunov exponents. In this sense, the Nonlinear time series analysis provides the basic framework for such studies, indicating the dimensionality as well as complexity of the appropriate mathematical model. Furthermore, as already advocated by Wilden *et al* (1998), for mammalian communication, such analyses can lay the foundations for a broader classification of acoustic and vibrational communication also among insects, which surpasses the rather limited dichotomous separation of signals on harmonic and atonal sounds (Hauser 1993) that is often employed by biologists.

Moreover, we argue that if used carefully, methods of Nonlinear time series analysis can also serve as means to distinguish different insect species either from each other or under various environmental influences, whereby the fact that one can intimately and rather accurately characterize a particular sound only by a single Lyapunov exponent opens the possibility of automating the process. Finally, we note that if the precise physiological significance of chaos in the present case remains unclear, the presented analysis can still prove very useful as a discriminating tool since it provides an additional approach to characterize sound generation in insects.

Finally, we would like to note that since this work is intended to inspire physicists, mathematicians and biologists alike, we also developed a set of user-friendly programs (Kodba *et al* 2005; Perc 2005a,b) for each implemented method in this paper, so that interested readers can easily apply the theory to their own recordings. An even more comprehensive set of programs is available through the TISEAN project (Hegger and Kantz 1999; Hegger *et al* 1999). We recommend that the benefits offered by these sources be exploited.

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