Nonlinearities in mating sounds of American crocodiles

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We use nonlinear time series analysis methods to analyze the dynamics of the sound-producing apparatus of the American crocodile (Crocodylus acutus). We capture its dynamics by analyzing a recording of the singing activity during mating time. First, we reconstruct the phase space from the sound recording and thereby reveal that the attractor needs no less than five degrees of freedom to fully evolve in the embedding space, which suggests that a rather complex nonlinear dynamics underlies its existence. Prior to investigating the dynamics more precisely, we test whether the reconstructed attractor satisfies the notions of determinism and stationarity, as a lack of either of these properties would preclude a meaningful further analysis. After positively establishing determinism and stationarity, we proceed by showing that the maximal Lyapunov exponent of the recording is positive, which is a strong indicator for the chaotic behavior of the system, confirming that dynamical nonlinearities are an integral part of the examined sound-producing apparatus. At the end, we discuss that methods of nonlinear time series analysis could yield instructive insights and foster the understanding of vocal communication among certain reptile species.

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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 behavior and the theory of deterministic dynamical systems (Schuster, 1989; Ott, 1993; Strogatz, 1994; Kaplan and Glass, 1995). 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 analyzing the time course of one of its variables. Thereby, intimate links between the chaos theory and experimental observations can be weaved. Since famous chaotic attractors, like for example the Lorenz butterfly attractor (Lorenz, 1963) or the Rössler attractor (Rössler, 1976) have inspired generations of scientists, and continue to inspire even today, this basic concept is truly enchanting. Importantly, however, 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 behavior can be easily advertised as 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 important issues that have to be addressed before attempting further analyses, especially on real-life recordings, as we will emphasize throughout this work.

Presently, we analyze the sound recording of the mating sound of the American crocodile (Crocodylus acutus), belonging to the genus Crocodylus, family Crocodylidae, order Crocodylia, living at the Atlantic and Pacific coasts extending from southern Mexico to Central America, as well as in South America as far as Peru and Venezuela. It also breeds on Cuba and Jamaica, and there is a remnant population in Florida. American crocodiles predominantly inhabit freshwater or brackish water coastal regions, and mangrove swamps. For a comprehensive review on various aspects of C. acutus as well as other crocodile species we refer the reader to the relevant “Status survey and conservation action plan” (Ross, 1998), while here we constrain ourselves to the most important facts. The American crocodile is one of the largest crocodile species, with males reaching lengths of up to 6 m. Despite its impressive size and strength, and history of existence reaching back 65 million years, the species could barely withstand exploitations from humans, and although some quite ambitious attempts have been made to increase the numbers of wild specimens, the U.S. Fish and Wildlife Service still classifies the American crocodile as a threatened species, thus protecting the reptile from illegal harassing, poaching or killing under the federal Endangered Species Act. Currently, no more than 2000 American crocodiles exist in Mexico, Central and South America.

Of a more direct importance for the present work is the fact that Crocodilia are considered the most vocal of all reptiles. Although
using physical displays, chemical and vocal signals to communicate, the sound plays a key role during mating time, as it is used by both female and males to signal either readiness or attempts of courtship. Since American crocodiles have no vocal cords, they produce sounds by forcing air out of their lungs through the back of the throat or nostrils situated on the top of their heads. Importantly though, they do possess a pair of membranous folds within the glottis that serve as vocal cords, which indeed may be responsible for a qualitatively identical dynamics as reported previously for vocal cord vibrations in mammals (Wilden et al., 1998). It is the dynamics of this sound-producing apparatus that we are currently investigating with methods of nonlinear time series analysis.

In the past, animal sound recordings have often been analyzed with methods of nonlinear time series analysis. Wilden et al. (1998), for example, introduced the concept of nonlinear dynamics to mammalian bioacoustics in order to quantify the complexity of mammalian vocalization. Mammalian sounds were investigated also in Riede et al. (2000, 2001, 2005) and Fitch et al. (2002). 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 (Mende et al., 1990; Titze et al., 1993; Kantz, 1994). However, despite the rather extensive literature existing on this topic, we found no applications of nonlinear time series analysis methods on reptile 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 foundations for further analyses. To determine proper embedding parameters for the phase space reconstruction, we use the mutual information method (Fraser and Swinney, 1986) and the false nearest neighbor method (Kennel et al., 1992). Next, we apply a determinism test (Kaplan and Glass, 1992) and draw a recurrence plot analysis to confirm this conjecture in a more rigorous manner. Prior to that, however, we apply a standard high-frequency Wiener filter with a cut-off at 1.0 kHz to eliminate background noise and other sounds of nature not inherent to that of the crocodile. The result of this procedure is shown in the insert above the main panel of Fig. 1. Clearly, the overall outlay and markers of nonlinearity of the series are preserved, while at the same time high-frequency pollution (marked with gray) is eliminated. It is also worth noting that such noise filtering serves mostly a faster and more accurate convergence of the subsequently applied methods for nonlinear time series analysis, but other than that has no appreciable impact on the final results.

Before starting with the nonlinear time series analysis, we show the spectrogram (Kantz and Schreiber, 1997) of the full series, resulting from the whole 70 s long sound recording, in Fig. 2. The spectrogram is a classical tool of sound/speech processing, used predominantly to determine spectral properties of examined recordings. Results presented in Fig. 2 were obtained by calculating power spectra for 545 segments comprising 4096 points each, whereby the overlap between segments was 2048 points. It can be observed that, as already noted, the sound recording of the American crocodile is characterized by a predominant oscillation frequency within the interval $f = 100$ Hz and $f = 300$ Hz (note that in Fig. 2 this horizontal stripe is the whitest, indicating that the largest portions of overall signal power are contributed within this frequency span). Moreover, it can be observed nicely that the singing activity varies in time. In particular, there exist bursts of intense singing activity (vertical white stripes in Fig. 2), which are intermit-tently disrupted by phases of quiescence. This fact directly implies that the complete (whole 70 s) sound recording is non-stationary, and thus that care must be exercised when applying methods of nonlinear time series analysis in order to examine it. Note that properties like non-stationarity or lack of determinism may manifest as markers of nonlinearity or even chaos, yet they have nothing in common with deterministic chaos observed in some nonlinear deterministic dynamical systems (Lorenz, 1963; Rössler, 1976).
Given a time series, Swinney (1986) proposed to use the first minimum of the mutual information between the delay vectors 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 \( t = (i + \tau) \Delta t, \ldots, t = (i + (m - 1)\tau) \Delta t \), respectively, whereby \( \tau \) is the embedding delay and \( \Delta t \) is the sampling time of data points, currently equaling 6.25 \times 10^{-5} \text{s}.

Although the implementation of Eq. (1) is straightforward, we first have to determine proper values for the embedding parameters \( \tau \) and \( m \). For this purpose, the mutual information (Fraser and Swinney, 1986) and false nearest neighbor method (Kennel et al., 1992) can be used, respectively. Since the mutual information between \( x_i \) and \( x_{i+\tau} \) quantitates 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 \( x_i \), one first has to find the minimum \( x_{\text{min}} \) and the maximum \( x_{\text{max}} \) of the sequence. The absolute value of their difference \( |x_{\text{max}} - x_{\text{min}}| \) then has to be partitioned into \( j \) equally sized intervals, where \( j \) is a large enough integer number. Finally, one calculates the expression

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

where \( P_{h,k} \) and \( P_h \) 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 Fig. 1, the first minimum of \( I(\tau) \) is obtained at \( \tau = 17 \), as can be inferred from Fig. 3. We will use this \( \tau \) in all future calculations. Noteworthy, the steadily decaying mutual information implies that the system looses memory of its initial state as \( \tau \) increases, thus suggesting that nonlinear or even chaotic dynamics might underlie the recorded mating sound.

We now turn to establishing a proper embedding dimension \( m \) for the examined sound recording by applying the false nearest neighbor method introduced by Kennel et al. (1992). The method relies on the assumption that the phase space of a deterministic system unfolds smoothly with no sudden irregularities appearing in its structure. By extrapolating this assumption one comes 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 neighbor that does not fulfill this criterion it is marked as having a false nearest neighbor. As soon as \( m \) is chosen sufficiently large, the fraction of points that have a false nearest neighbor \( \phi \) should converge to zero. In order to calculate \( \phi \) the following algorithm is used. Given a point \( p(i) \) in the \( m \)-dimensional embedding space, one first has to find a neighbor \( p(j) \), so that ||\( p(i) - p(j) \)|| < \( \epsilon \), where ||\( . \)|| is the square norm and \( \epsilon \) 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 \( m + 1 \)st embedding coordinate of points \( p(i) \) and \( p(j) \) according to the equation:

\[
R_i = \frac{|x_{i+m} - x_{j+m}|}{||p(i) - p(j)||}.
\]

If \( R_i \) is larger than a given threshold \( R_0 \), then \( p(i) \) is marked as having a false nearest neighbor. Eq. (3) has to be applied for the whole time series and for various \( m = 1, 2, \ldots \) until the fraction of points \( \phi \) for which \( R_i > R_0 \) is negligible. According to Kennel et al. (1992), \( R_0 = 10 \) has proven to be a good choice for most data sets. The results obtained with the false nearest neighbor method are presented in Fig. 4. It can be observed that \( \phi \) drops to zero (\( <1\% \)) convincingly 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 American crocodile’s 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 dynamics, we first have to verify if the studied signal originated from a deterministic stationary system. As already emphasized in Section 1, 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), that measures average directional vectors in a coarse-grained embedding space. The idea is that neighboring trajectories in a small portion of the embedding space should all point in the same direction, thus ensuring 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 \( V_k \) of the \( k \)th box is then

\[
V_k = \frac{1}{n} \sum_{p=1}^{n} \mathbf{e}_p.
\]

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 (note that each \( \mathbf{e}_p \) is also a unit vector). Hence, if the system is deterministic, the average length of all directional vectors \( \kappa \) will be 1, while for a completely random system \( \kappa = 0 \). The determinism factor pertaining to the whole five-dimensional embedding space (using \( \tau = 17 \) and \( m = 5 \)) that was coarse grained into a \( 16 \times 16 \times \cdots \times 16 \) grid is \( \kappa = 0.98 \), 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 system. For this purpose, we apply the method of recurrence plots (Eckmann et al., 1987). The recurrence plot is a powerful graphical tool enabling the assessment of stationarity in the system, as well as execution of other tasks, like for example the estimation of the noise level in a signal, or the evaluation of the correctness of chosen embedding parameters for the phase space reconstruction (Marwan, 2003; Marwan et al., 2007).

Recurrent behavior is an inherent property of oscillatory systems. For regular oscillators time-distinct states in the phase space can be arbitrarily close, i.e. \( \|\mathbf{p}(i) - \mathbf{p}(j)\| = 0 \) if times \( i \) and \( j \) differ exactly by some integer of the oscillation period, whereas for chaotic systems this distance is always finite (larger than zero). The recurrence plot is a 2D square-grid graph with time units on both axes, whereby, in the most common case, points \((i,j)\) that satisfy \( \|\mathbf{p}(i) - \mathbf{p}(j)\| < \varepsilon \) are marked with black dots while all others are marked white. The most important feature of each recurrence plot is its large- and small-scale structure, being termed typology and texture (Eckmann et al., 1987), respectively. By visually inspecting the typology and texture of a recurrence plot, stationarity as well as determinism can be assessed. In particular, a homogenous typology indicates that the studied data set originated from a stationary process. Contrary, a non-homogenous or disrupting typology indicates non-stationarity in the system. Texture, on the other, provides information regarding the deterministic vs. stochastic origin of the signal, as well as gives insights on the complexity of oscillations. Lack of texture, i.e. solely isolated recurrence points, often indicate stochastic origin of the examined time series, while diagonal lines indicate deterministic oscillations, which depending on the complexity of small-scale patterns can be classified further into simple, complex, or chaotic oscillations. The recurrence plot of the studied time series obtained for \( \tau = 17, m = 5 \) and \( \varepsilon = 0.1 \) (note that the span of the series has been rescaled to the unit interval; see Fig. 1 and the pertaining caption) is presented in Fig. 5. Since the typology is clearly homogenous, and also because the small-scale structure is characterized by diagonal lines of variable length, we can clearly refute non-stationarity in the studied sound recording. Notably, this implies that during the recording time the environmental influences on the crocodile did not change, and thus its humming was stationary both from the listeners as well as from the dynamical point of view. This is of course not surprising since not much can happen in a few seconds time (note that we consider only a short excerpt from the whole 70 s long recording). However, it is important to bear in mind that longer recordings of real-life activities almost always yield non-stationary data sets since subjects under study often cannot be isolated from environmental effects, or even more likely, it is explicitly not of interest to do so.

![Fig. 4. Determination of the minimal required embedding dimension. The fraction of false nearest neighbors \( \phi \) drops convincingly to zero (<1%) at \( m = 5 \).](image)

![Fig. 5. Recurrence plot of the examined time series obtained with \( \tau = 17, m = 5 \) and \( \varepsilon = 0.1 \).](image)
2.5. Maximal Lyapunov exponent

Finally, it is of interest to determine the maximal Lyapunov exponent pertaining to the studied sound recording. In order to calculate the maximal Lyapunov exponent of the system, we use the algorithm developed independently by Kantz (1994) and Rosenstein et al. (1993). The algorithm tests the exponential divergence of nearby trajectories directly, thus allowing a robust estimation of the maximal Lyapunov exponent. To estimate the exponent, we first have to find all neighbors $p(k)$ that are closer to a particular reference point $p(i)$ than $\varepsilon$. Thereby, we obtain a set of starting points for nearby trajectories. Further, we have to calculate the average distance of all trajectories to the reference trajectory ($D_i$) as a function of the relative time $\Delta n$ (counted from $i$ and $k$ onwards). Finally, the average of the logarithm of $D_i$ obtained for several different reference points $p(i)$, is the effective expansion rate $S(\Delta n)$ of which the linear slope in dependence on $\Delta n$ is a robust estimate for the maximal Lyapunov exponent. To obtain an accurate result, the whole algorithm has to be repeated for a few hundred different $p(i)$ and various $\varepsilon$. In particular, $\varepsilon$ should be chosen as small as possible, but still large enough so that on average each reference point $p(i)$ has at least a few neighbors. For further details we refer the reader to the original articles (Rosenstein et al., 1993; Kantz, 1994). The results obtained for $\varepsilon = 0.07, 0.1, 0.14$ (note that the span of the series has been rescaled to the unit interval; see Fig. 1 and the pertaining caption) and $m = 4, 5, 6$ are presented in Fig. 6. The function $S(\Delta n)$ shows a robust linear increase from $\Delta n = 20$ to 120 for all $\varepsilon$ and $m$. Thus, the slope of $S(\Delta n)$, indicated by the two linear lines, is a good estimate for the maximal Lyapunov exponent of the system. We find that the latter equals $\approx 0.013$ in dimensionless units (note that in units of $s^{-1}$ this is much larger given the 16 kHz sampling of the sound), from which we conclude that the studied short stationary data segment of the American crocodile mating sound possesses properties typical of time series that are produced by deterministic nonlinear chaotic systems.

3. Discussion

We systematically analyze the sound recording of an American crocodile with methods of nonlinear time series analysis. In particular, we outline a careful approach, encompassing a determinism and stationarity test, 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. Thus, we conclude that the sound-producing mechanism of the American crocodile possesses properties that are characteristic for deterministic chaotic systems.

In this respect presented results are similar to what was reported earlier for mammalian vocal communication (see e.g. Fitch et al., 2002), both in terms of the chaotic nature of the sound as well as quantities that characterize it. The reason for this similarity lies in the fact that, although Crocodylia – crocodiles, alligators, caimans or gavials, for example – do not have vocal cords as mammals, they do possess a pair of membranous folds within the glottis that serve as vocal cords, which are responsible for a qualitatively identical dynamics as reported previously for vocal cord vibrations in mammals. By snorting air through the back of the throat or nostrils, the membranous folds vibrate in much the same fashion as mammalian vocal cords. Despite the fact that the vocal repertoire of crocodiles cannot match that of the mammals (their vocal cords are more sophisticated and governed by typically higher intelligence), the overall similarity of the sound-producing apparatus nevertheless leads to the sound of the American crocodile having very similar characteristics in terms of its chaotic dynamics as reported previously for mammalian vocal communication.

Furthermore, we would like to note that the above-performed analysis is a viable approach for obtaining insights into mechanisms of reptile sound generation. In particular, it can be seen as the necessary prelude to mathematical modeling 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 estimates for the Lyapunov exponents. In this sense, nonlinear time series analysis provides the basic theoretical framework for such studies, indicating the dimensionality as well as the complexity of a potentially appropriate mathematical model. Furthermore, as already noted by Wilden et al. (1998) for mammalian vocal communication, such analyses can lay foundations for a more broad classification of acoustic communication also among reptiles, which surpasses the rather limited dichotomous separation of signals on harmonic and atonal sounds (Hauser, 1993) that is often employed by biologists.

However, it should be emphasized that reptiles, in general, are not particularly vocal animals, and that indeed Crocodylia are rather special in this respect. Although lacking vocal cords, they can hiss, grunt, cough, growl, and bellow to convey quite an impressive array of up to 20 different messages, including threats, distress signals, hatching calls, contact calls, and courtship readiness. Moreover, the sounds of crocodiles may vary by species, age, size, sex and context, and individualized differences in tones, intensity and calling patterns can also occur, just as individual humans have distinct voices and speech mannerisms. Notably, a recent study of the Nile crocodile ($Crocodylus niloticus$) hatchlings (Britton, 2001) showed that a baby actually begins calling while still in the egg and continues immediately after coming out. The calls do not seem to identify the hatching as an individual, but they do influence the behavior of other nearby juveniles and elicit maternal care from the mother. During the first several days after hatching, the baby Nile crocodiles gradually change the sounds of their calls. It has been suggested that the new sounds give the mother information about the age and size of each hatching so that she can customize her care for each individual. The theory of nonlinear dynamics employed in the present work offers tools for evaluating and quantifying the specific characteristics of the dynamical system that produces chaotic outputs. Here we focused on the analysis of the mating sound of the American crocodile, and it will be interesting to examine further potential applications of this approach in the light of above-mentioned facts.
Other notable exceptions of reptiles that may qualify for such an analysis include the Tokay Gecko (Gekko gecko) (Moore et al., 1991), which is unique in having vocal cords able to produce a multipart advertisement call that begins with a rattling sound that is followed by a series of two-syllable chirps (Brillet and Paillette, 1991), as well as some species of Testudinidae (Testudo hermanni, T. graeca, and T. marginata) (Sacchi et al., 2004), which are also known to use vocalization as part of their communication. The approach outlined in this work may be useful in further extending the understanding of vocalization in these particular examples, whereas in general reptiles seem to be more mysterious in their vocal skills than mammals or birds.

An interesting avenue to study further is also the interrelation between the biomechanical sound-producing apparatus and the neural network (Enquist and Ghirlanda, 2005) that controls it; in particular, given that the output is chaotic, what can we say about the neural network? Given that Crocodilia do possess an organ that is similar to vocal cords in mammals, and that they are the most vocal of all reptiles, able to communicate quite an impressive array of different messages via sound, it seems safe to claim that the nervous system responsible for the control of such a complex apparatus, which in some ways is similar to our own, needs to be highly developed, and that certainly both, the sound-producing apparatus and the neural network that controls it, contribute to the complexity of the mating sound in a synergetic fashion. In particular, it seems reasonable to argue that the neural network generates the blueprint and the apparatus needs to be sophisticated enough to produce the desired sound.

At the end, 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., 2005a; Perc, 2005a, 2005b) for each implemented method in this paper, so that interested readers can easily apply the theory on their own recordings. An even more comprehensive set of programs is available through the TISEAN project (Hegger and Kantz, 1999; Hegger et al., 2007). We recommend greatly exploiting the benefits offered by these sources.

References

Perc, M., 2005b. All results presented in this paper can be reproduced with the set of programs that can be downloaded from: http://www.matja sper.com/epj/time.html.