

Bootstrap estimated uncertainty of the dominant Lyapunov exponent for Holarctic microtine rodents

WILHELM FALCK, OTTAR N. BJØRNSTAD
AND NILS CHR. STENSETH*

Division of Zoology, Department of Biology, University of Oslo, P.O. Box 1050 Blindern, N-0316 Oslo, Norway

SUMMARY

The dominant Lyapunov exponent, as estimated from time series using the Jacobian-based method, is often used for indicating whether the underlying dynamic system is chaotic or not. The Jacobian-based method together with Response Surface Methodology has been suggested as a method for detecting chaotic dynamics in ecological time series. Besides pointing out that this may not be an appropriate method, we report on estimates of the uncertainty in the estimates of the dominant Lyapunov exponent. For this purpose, we have used time series data on Holarctic microtines. On the basis of our analyses, we are unable to find general evidence for chaotic dynamics in northern microtine populations (north of 60° N) as recently suggested in the ecological literature. It seems, however, that the dynamic properties of the northern and southern populations are different. These patterns are supported by testing for nonlinearity.

1. INTRODUCTION

The periodic fluctuations commonly seen in northern microtines (see, for example, Hansson & Henttonen 1985; Hanski *et al.* 1991; Stenseth & Ims 1993) have recently been claimed to be chaotic (Hanski *et al.* 1993; Turchin 1993) as a result of nonlinear ecological interactions (Hanski *et al.* 1993). To demonstrate the existence of chaotic behaviour, Turchin (1993) used Response Surface Methodology (RSM) (Box & Draper 1987) in combination with the Jacobian-based method (Ellner *et al.* 1991; Nychka *et al.* 1992) – as implemented in the program EcoDyn/RSM (Turchin & Millstein 1993) – to estimate the dominant Lyapunov exponent of 34 time series, representing seven Holarctic microtine species from a total of 12 locations. The studied time series were from populations located along a latitudinal gradient between 39° N and 71° N (in our analyses we use the same data files as used by Turchin (1993)). Both Hanski *et al.* (1993) and Turchin (1993) concluded that populations south of 60° N are characterized by stable one-dimensional processes, whereas populations further north may be characterized by chaotic dynamics resulting from nonlinear processes.

Deterministic chaos is characterized by sensitivity to initial conditions (Eckmann & Ruelle 1985). The dominant Lyapunov exponent, Λ , measures the rate of divergence between two nearby trajectories resulting from the same dynamical process. A positive Λ indicates chaos whereas a negative Λ indicates non-chaotic dynamics.

Ecological time series, such as those analysed by

Turchin (1993), can hardly be considered the result of any deterministic process. They are inflated both by observational noise and environmental and demographic stochasticity (Nisbet & Gurney 1982). In ecology, therefore, care must be exercised when adopting deterministic based definitions of chaos (Tong 1994; Yao & Tong 1994a).

Assuming that ecological time series is generated by a deterministic process coupled with (exogenous) noise, the dominant Lyapunov exponent reveals whether the underlying deterministic model amplifies ($\Lambda > 0$) or dampens ($\Lambda < 0$) exogenous perturbations (see, for example, Hastings *et al.* 1993; Ellner & Turchin 1995). Hence, Λ , may be taken as an indication of whether the underlying deterministic process is chaotic or not. It is crucial, however, to realize that Λ in such a stochastic system measures the average rate of trajectory divergence caused by the deterministic component, using two trajectories that start near each other and being affected by an identical sequence of random shocks (see, for example, Hastings *et al.* 1993).

A shortcoming of ecological studies (Hanski *et al.* 1993; Turchin 1993; Hastings *et al.* 1993) using the dominant Lyapunov exponent for drawing inferences about chaos, is that no measure of uncertainty is provided for the point estimate of Λ . This is, however, a drawback common to all algorithms proposed thus far for estimating Lyapunov exponents from time series (Gershenfeld & Weigend 1994; Parlitz 1992). Without a solid theory for the derivation of such uncertainty measures, any interpretation of its meaning should be done with great care (Ellner *et al.* 1995).

In this paper we utilize bootstrapping theory to provide confidence intervals for the Lyapunov exponents as found by EcoDyn/RSM (see §2).

* To whom correspondence should be addressed.

Specifically we calculate Bias Corrected Confidence (BCC) intervals (Efron 1982; Dixon 1993) for the 34 Λ s reported by Turchin (1993). We compare these confidence intervals with the point estimates provided by Turchin (1993) and discuss to what extent our refined analyses support his published conclusions. It should be noted that Turchin (1993) did not use the EcoDyn/RSM package as described by Turchin & Millstein (1993). The methodology applied by Turchin (1993) is, however, essentially identical to the one implemented in EcoDyn/RSM (P. Turchin, personal communication).

It should be kept in mind that there are several alternatives to the RSM approach (for example, Ellner & Turchin 1995). We have chosen to focus on the RSM as implemented by the EcoDyn/RSM-software, because this is gaining popularity within microtine biology for the purpose of estimating the Lyapunov exponent (see, for example, Turchin 1993; Ellner & Turchin 1995). We urge, however, the investigation of the usefulness of alternative approaches.

2. THE ECODYN/RSM APPROACH

The approach used in EcoDyn/RSM (Turchin & Millstein 1993) is to represent a time series by a model for the growth rate, r_t , as a function of previous densities: that is,

$$r_t \equiv \log N_t / N_{t-1} = f(N_{t-1}, \dots, N_{t-d}) + \epsilon_t, \quad (1)$$

where N_t is the density at time t , $f(\cdot)$ is a function of densities, and ϵ_t is an exogenous noise term. The function $f(\cdot)$ is called 'the skeleton'.

Here, we define the data set $X = [x_1, x_2, \dots, x_m]$, where x_t is the observed density at time t corresponding to the variable N_t in model (1). The length of the time series is denoted by m .

In EcoDyn/RSM the skeleton is a polynomial function of at most order two and dimension (i.e. number of lags) three with Box-Cox transformed densities (Turchin & Millstein 1993). The appropriate skeleton is selected through cross validation done by omitting one point in the data set X , fitting the polynomial using Ordinary Least Squares methods (OLS) and then predicting the omitted point. Such cross validation is done for all data points in turn. Comparing the predicted and observed values, a measure for the accuracy of prediction is calculated. The skeleton model providing the best prediction is chosen. Using the chosen model, the dominant Lyapunov exponent, is estimated using a Jacobian-based method (Ellner *et al.* 1991; Nychka *et al.* 1992; Ellner & Turchin 1995). For further details, see Turchin & Millstein (1993).

Fitting the skeleton model to data by OLS, implicitly assumes the noise-term to be time-invariant, state-independent and additive (cf. Chan & Tong 1994). This is a critical assumption if statistical inference is to be attempted. This property of the noise-term is used in the bootstrapping approach adopted in this study.

3. BOOTSTRAPPING

The basic idea is to use the f -function given by equation (1) for the purpose of generating bootstrap

replicates of the original time series and use EcoDyn/RSM to estimate Λ for each bootstrapped time series. For this purpose we use the discrete time simulation model defined by

$$N_t = N_{t-1} \exp(f(N_{t-1}, \dots, N_{t-d}) + \epsilon_t). \quad (2)$$

The first d observations from the original time series X are used as initial values when generating the simulated data series. A single bootstrap replicate (pseudoreplicate) i from the original time series X is denoted \tilde{X}_i .

The generation of pseudoreplicated time series proceeds as follows (cf. Hjort 1994).

1. EcoDyn/RSM is treated as a 'black box' to, for each original time series X , produce an 'optimal' skeleton model, $f(\cdot)$, and a dominant Lyapunov exponent, Λ .

2. We generate pseudoreplicated time series \tilde{X}_i , by simulating equation (2) using the 'optimal' skeleton function, $f(\cdot)$. The noise is approximated by random sampling with replacement from the empirical distribution of OLS residuals, $\{\epsilon_t\}$.

3. We proceed until we have a time series with as many simulated data points as the original series.

Step two and three are repeated until we have n pseudoreplicated time series; i.e. \tilde{X}_i , where $i = 1, \dots, n$.

For each time series, we created n ($= 500$; but see below) bootstrap series and used EcoDyn/RSM to estimate the dominant Lyapunov exponent, Λ_i , for each \tilde{X}_i ($i = 1, \dots, n$). It is important to note that we treat the EcoDyn/RSM package as a black-box estimator. This means that the EcoDyn/RSM package may select different skeleton models $f_i(\cdot)$ for the various time series replicates \tilde{X}_i . The distribution of the Lyapunov exponents thus obtained is for each original time series used to calculate Bias Corrected Confidence intervals (BCC) (Efron 1982). The bias correction is done by calculating the fraction of bootstrap replicated Lyapunov exponents that are smaller than the point estimate, and using this fraction to adjust the upper and lower percentile of the confidence interval for the given data set.

One problem with the polynomial skeleton models underlying the EcoDyn/RSM approach is that its resulting dynamics may be unstable (i.e. diverge to infinity, cf. Cox 1977; Turchin & Taylor 1992; Perry *et al.* 1993; Chan & Tong 1994) if the trajectories jumps outside the range of observed values. In such divergent time series (determined by an excessive growth rate somewhat arbitrarily defined as $r_t > 10$) floating point errors quickly occurred in the simulations. These pseudoreplicates were therefore discarded and new time series produced. This causes an unavoidable bias in our results.

If the pseudoreplicated time series had an $r_t < -10$ at any given point we set $r_t = -10$. This could be considered as local extinction. Stochastic processes (i.e. the noise term) may then be seen as preventing the time series from converging to zero.

With these constraints we produced, for all the 34 time series, 500 non-divergent bootstrap time series. A summary of the data used in this paper is provided in table 1.

Table 1. *The Holarctic microtine rodent data set*

(Characteristics of the time series data used in the analysis: all series are provided by Peter Turchin and are the same as those listed in Turchin (1993: table 1); original sources to the data are given in Turchin (1993). The series are numbered for convenience of reference; no. 1–23 are those north of 60° N (called the ‘northern microtine populations’), whereas the remaining are those south of 60° N (called the ‘southern microtine populations’). Latitude is given as °N. Asterisk denotes time series of which we have not been able to reproduce the results reported by (Turchin 1993); see the main text. Season refers to the time of the year from which the samples are taken and is given as: S, spring or early summer; F, autumn or late summer; W, winter; A, single annual sample, or annual averages of several samples (see Turchin 1993). Failures is the number of (divergent) discarded simulations. Qualitatively evaluated goodness of fit indicates how well the pseudoreplicated time series compares with the original time series, + indicate good fit, – denotes poor fit and ± denotes intermediate fit (see figure 3). The reported scores are the median scores of the three authors. Test for nonlinearity indicates whether the null hypothesis of linearity was rejected + or not – (based on O. N. Bjørnstad *et al.*, unpublished data).)

| no. | species | location | latitude | years of observation | season | failures | qualitatively evaluated goodness of fit | test for nonlinearity |
|-----|--------------------------------|--------------|----------|----------------------|--------|----------|---|-----------------------|
| 1 | <i>Lemmus trimucronatus</i> | Point Barrow | 71 | 1946–66 | A | 164 | + | + |
| 2 | <i>Lemmus trimucronatus</i> | Point Barrow | 71 | 1955–72 | S | 7118 | + | + |
| 3 | <i>Lemmus trimucronatus</i> | Point Barrow | 71 | 1955–72 | F | 15 | ± | + |
| 4 | all species | Kilpisjärvi | 69 | 1964–86 | S | 0 | + | + |
| 5 | all species | Kilpisjärvi | 69 | 1964–86 | F | 6 | + | + |
| 6 | <i>Clethrionomys glareolus</i> | Pallasjärvi | 68 | 1970–85 | S | 0 | + | + |
| 7 | <i>Clethrionomys glareolus</i> | Pallasjärvi | 68 | 1970–85 | F | 0 | + | – |
| 8 | <i>Clethrionomys rutilus</i> | Pallasjärvi | 68 | 1970–85 | S | 0 | + | + |
| 9 | <i>Clethrionomys rutilus</i> | Pallasjärvi | 68 | 1970–85 | F | 105 | + | – |
| 10* | <i>Clethrionomys rufocanus</i> | Pallasjärvi | 68 | 1970–85 | S | 2649 | ± | – |
| 11 | <i>Clethrionomys rufocanus</i> | Pallasjärvi | 68 | 1970–85 | F | 125 | ± | – |
| 12* | <i>Microtus agrestis</i> | Pallasjärvi | 68 | 1970–85 | S | 0 | – | + |
| 13 | <i>Microtus agrestis</i> | Pallasjärvi | 68 | 1970–85 | F | 299 | ± | – |
| 14 | <i>Microtus oeconomus</i> | Pallasjärvi | 68 | 1970–85 | S | 20665 | – | – |
| 15 | <i>Microtus oeconomus</i> | Pallasjärvi | 68 | 1970–85 | F | 11446 | ± | – |
| 16 | <i>Clethrionomys rufocanus</i> | Kola | 67 | 1946–64 | F | 66 | + | + |
| 17 | <i>Clethrionomys glareolus</i> | Kola | 67 | 1946–64 | F | 338 | – | + |
| 18 | <i>Clethrionomys glareolus</i> | Umeå | 64 | 1971–88 | S | 56 | + | – |
| 19 | <i>Clethrionomys glareolus</i> | Umeå | 64 | 1971–88 | F | 554 | ± | + |
| 20* | <i>Clethrionomys rufocanus</i> | Umeå | 64 | 1971–88 | S | 307 | ± | + |
| 21 | <i>Clethrionomys rufocanus</i> | Umeå | 64 | 1971–88 | F | 320 | – | + |
| 22 | <i>Microtus agrestis</i> | Umeå | 64 | 1971–88 | S | 9119 | ± | + |
| 23 | <i>Microtus agrestis</i> | Umeå | 64 | 1971–88 | F | 578 | ± | + |
| 24 | <i>Clethrionomys glareolus</i> | Tataria | 56 | 1936–58 | A | 0 | ± | – |
| 25 | <i>Clethrionomys glareolus</i> | Serpukhov | 55 | 1936–58 | A | 351 | + | – |
| 26 | <i>Clethrionomys glareolus</i> | Tula | 54 | 1936–58 | A | 4 | + | – |
| 27 | <i>Clethrionomys glareolus</i> | Wytham Wood | 51 | 1948–70 | S | 0 | + | – |
| 28 | <i>Clethrionomys glareolus</i> | Wytham Wood | 51 | 1948–70 | W | 0 | + | – |
| 29 | <i>Clethrionomys rufocanus</i> | Hokkaido | 45 | 1961–85 | S | 0 | + | – |
| 30 | <i>Clethrionomys rufocanus</i> | Hokkaido | 45 | 1961–85 | S | 1533 | + | – |
| 31 | <i>Clethrionomys rufocanus</i> | Hokkaido | 45 | 1961–85 | F | 0 | ± | – |
| 32 | <i>Microtus montanus</i> | Wyoming | 43 | 1969–87 | F | 0 | – | + |
| 33 | <i>Microtus californicus</i> | California | 39 | 1959–77 | A | 0 | – | – |
| 34 | <i>Microtus californicus</i> | California | 39 | 1959–77 | A | 0 | – | – |

The problem of unstable dynamics could have been avoided by using surrogate methods (Theiler *et al.* 1992). The close link with the underlying model would, then, have been lost. Obviously much methodological work remains to be done at this point. We have no reason, however, to believe that the main conclusion reached in this paper rests on the problem of unstable time series. Indeed we feel confident that the pseudoreplicated time series used in our analysis reflect those of the original time series. This is so because we compared the power spectra of the bootstrapped and the original time series (cf. Tsay 1992) (see below). A remaining problem with our analysis is, nevertheless, the shortness of the original time series. This is a

problem we share with Turchin and others estimating dominant Lyapunov exponents, etc., on the basis of rodent time series.

4. BIAS-CORRECTED CONFIDENCE INTERVALS FOR HOLARCTIC MICROTINES

Figure 1 depicts the *bocs* and point estimates for all 34 time series. The width of the confidence intervals for the 34 series are rather variable. The bias of the estimates also vary substantially between the series. Figure 2 depicts typical bootstrap distributions of the estimated dominant Lyapunov exponents for four time

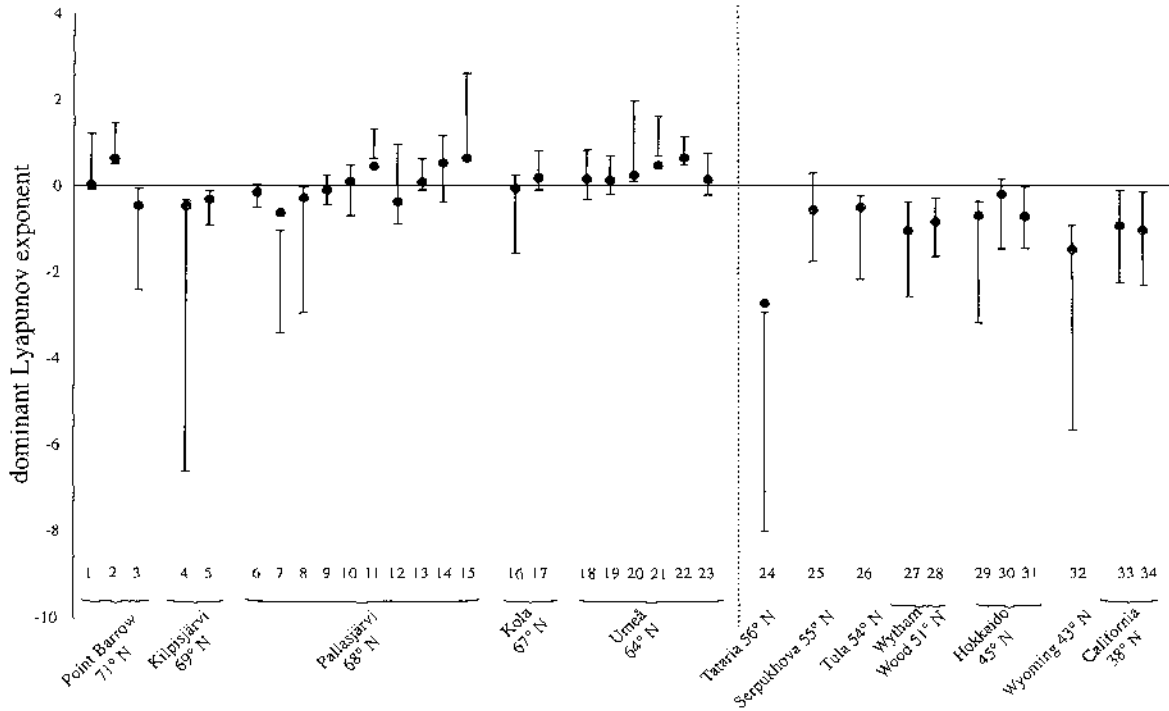


Figure 1. The 80% bootstrap intervals for the estimated dominant Lyapunov exponent for 34 time series located along a latitudinal gradient between 39° N and 71° N (see table 1). Filled circles represent the point estimates provided by the EcoDyn/RSM package.

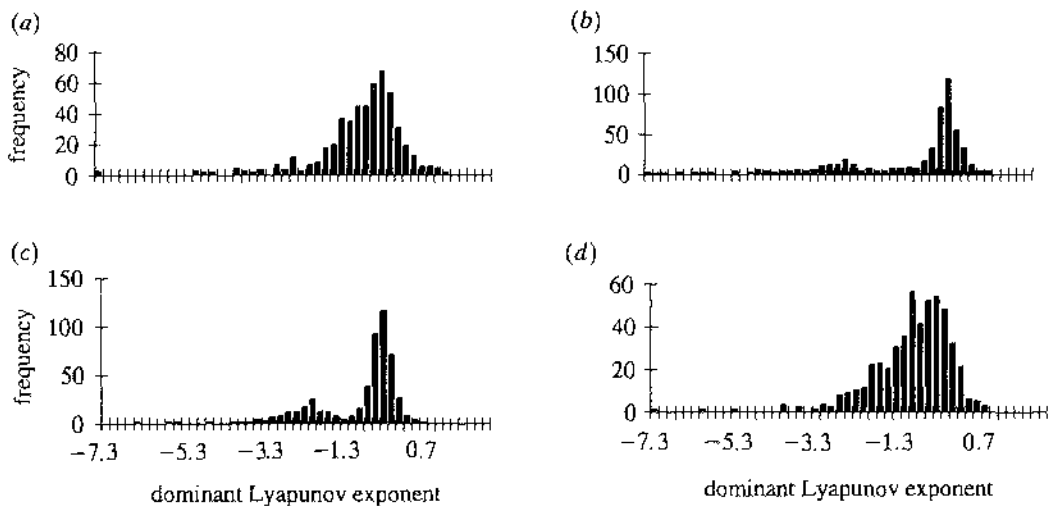


Figure 2. Four representative bootstrap distributions of Lyapunov exponents. These are time series (a) no. 12, point estimate -0.35 , (b) no. 19, point estimate 0.17 , (c) no. 28, point estimate -0.79 , (d) no. 34, point estimate -0.99 , chosen to demonstrate the various shapes of distributions which we obtain.

series with 500 replicates. As can be seen, these distributions have long negative tails. With such skewed distributions and only 500 pseudoreplicates, 80% confidence intervals are used to reduce the impact of negative extreme values.

For some of the series we had to discard a high number of time series before obtaining 500 non-divergent series (cf. table 1). Two of the series of root vole (*Microtus oeconomus*) from Pallasjärvi (Finland) are the most extreme ones with 20 665 and 11 446 discarded time series.

For three time series (marked with an asterisk in table 1) we have not been able to reproduce the same

point estimate for the Lyapunov exponent as reported by Turchin (1993). This is due to the fact that Turchin (1993) did not use the EcoDyn/RSM package to estimate the reported Lyapunov exponent for these time series (P. Turchin, personal communication). Following Peter Turchin's (personal communication) suggestion, we have used the EcoDyn/RSM estimate for these time series as well. It is worth noting though that the 'evidence' for chaotic dynamics in northern microtine populations is based on the mean Lyapunov exponent of the 23 northern populations being $0.2 (\pm 0.09)$ (Turchin 1993). Using the EcoDyn/RSM estimates of the Lyapunov exponents for all time series (also for the

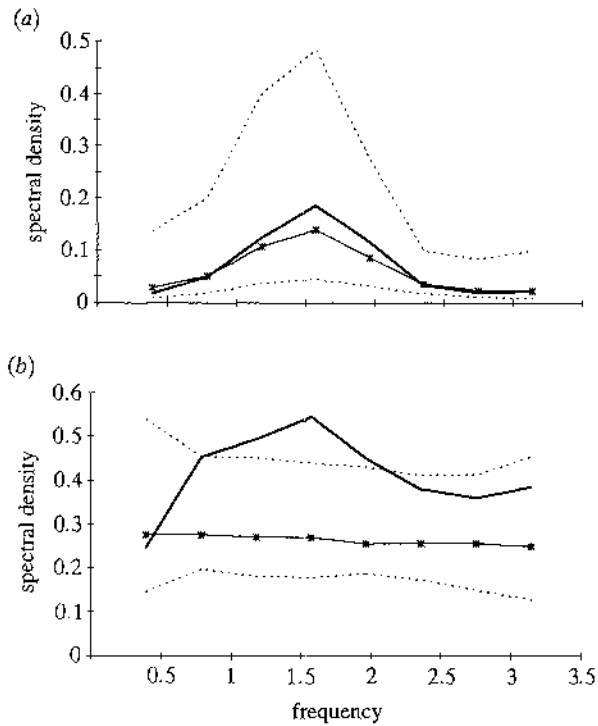


Figure 3. 'Goodness of fit' of the pseudoreplicated time series: solid line = observed spectral density; solid line plus star = median; dashed line = 90% probability interval. (a) A good fit (in table 1 denoted as +) for a time series. (b) A poor fit (in table 1 denoted as -) for a time series. A good fit is defined as one for which EcoDyn/RSM provides a skeleton model from which we can generate pseudoreplicates corresponding well to the original time series. For a specific time series this is evaluated by calculating the spectral density (using the Parzen window with a truncation point $M = 3$) for 1000 simulations of the skeleton model provided by EcoDyn/RSM. At each fixed frequency the 5% and 95% quantiles are selected to form a 90% probability interval. The median is the 50% quantile. If the estimated spectral density calculated for the original time series falls largely in the 90% probability interval we conclude that there is a good fit.

three time series which Turchin did not use the EcoDyn/RSM estimate), this average is reduced to 0.1 (± 0.09). The estimated mean and standard error remained unchanged for the southern populations (-0.93 ± 0.20). These numbers should be interpreted with great care, which certainly is done by Turchin. It should also be noted that many of the populations cannot be considered as independent. Several populations are either different species in the same rodent community, or spring and fall samples of the same population.

Within the set of northern populations, we have searched for trends in the estimated Lyapunov exponents using linear regression (both with and without various types of weightings): no significant trends has thus been detected. If anything, a tendency towards larger positive Lyapunov exponents for the southernmost populations within the northern set are found, not the opposite.

Using the bootstrap procedure as described above, we calculated bootstrap distributions of the spectral density for each of the 34 time series. To indicate how

well properties of the original time series are preserved in the pseudoreplicated time series we compared the spectral density of each of the original time series with the median and the 90% probability interval from the empirical bootstrap distribution (cf. Tsay 1992). All three authors of this report have independently scored the series as good, intermediate or poor. Figure 3 exemplifies a 'good' and a 'poor fit'. The result of the subjective evaluations for all 34 time series are summarized in table 1. Any conclusion based on the Jacobian method is critically dependent on the skeleton model capturing the essence of the dynamical features of the time series. Conclusions based on pseudoreplicated time series with poor fit should be treated with caution. From the studied time series, 7 out of 34 series provided poor fit, whereas 16 out of 34 series provided good fit; 11 of 34 provided intermediate fit.

We have been unable to find any relation between the failures due to instability of the bootstrapped time series and the quality of fit between the pseudoreplicated and the original time series.

5. DISCUSSION

The Lyapunov exponent as a measure of sensitivity to initial conditions (i.e. chaos) originates from deterministic dynamical system theory (see, for example, Schuster 1988). Recently Tong and co-workers (Chan & Tong 1994; Tong 1995) have demonstrated that the Lyapunov exponent as a measure of sensitivity to initial conditions has severe limitations in any stochastic system. Indeed, they question whether the estimation of the Lyapunov exponent (as done by packages such as EcoDyn/RSM) has any clear interpretation in stochastic systems. The Jacobian method works well in the deterministic case. However, if this method is to be applied to stochastic systems, restrictive assumptions have to be made (Tong 1995): in estimating the divergence of two nearby trajectories one has to assume that they are exposed to exactly the same sequence of noise (the 'identical noise assumption'). Without this assumption, the estimated value provided by packages such as EcoDyn/RSM has no clear interpretation as a Lyapunov exponent similar to the one used in deterministic systems. The reason for making the 'identical noise assumption' is due to the fact that two nearby trajectories of a stochastic dynamic system will always diverge if they are influenced by different sequences of random perturbations. Ellner & Turchin (1995, pp. 348–350) provide a very relevant and important discussion. Yao and Tong (Tong 1995; Yao & Tong 1994a, b) are currently developing a different way of handling chaos in a stochastic environment. Their approach is based on stochastic process theory and may therefore avoid assumptions such as the 'identical noise assumption'.

Consistent with Turchin (1993) and Hastings *et al.* (1993) we have, however, in this paper assumed that the estimated Lyapunov exponent indicates the underlying dynamic sensitivity to initial conditions. On this basis, figure 1 may be taken to indicate that the southern and northern populations of microtines have

qualitatively different dynamics, a conclusion which compares favourably with earlier conclusions (see, for example, Hansson & Henttonen 1985; Stenseth *et al.* 1985; Hanski *et al.* 1991, 1993; Turchin 1993; for a review, see Stenseth & Ims 1993). When interpreting figure 1, it is important to keep in mind that the southern and northern time series are in general taken from widely different geographic regions (the northern populations are mainly from the Fennoscandian peninsula, whereas the southern populations are from North America and Japan). Eight out of 11 southern time series have confidence intervals which do not include positive values. The remaining four have confidence intervals containing zero. For the northern populations, most of the confidence intervals are either strictly or partly positive. However, because only six of 23 have a confidence interval which is strictly positive, we caution against concluding that the northern populations in general exhibit chaotic behaviour.

From some studies of chaos in noisy time series, it is indicated by numerical experiments that estimating the sign of the dominant Lyapunov exponent from time series, using assumption free-methods, requires 200–500 or more data points (depending on the method used; see Nychka *et al.* 1992; Wilson & Rand 1993). Somewhat less data may be required if we know the models describing the ecological processes to the extent that only one or two free parameters in the dynamic equations remains to be estimated from the time series (T. Schreiber, personal communication). Having as few as 16 to 28 data points per time series, as Turchin (1993), is far below what would, in general, be required. It should be noted though that EcoDyn/rsm does attempt to reduce the model uncertainty through specifying, and thereby restricting the possible models. Nevertheless, the EcoDyn/rms-model with maximal model complexity, still contain ten free parameters with an addition of three parameters due to the Box-Cox transformation. We are convinced that approaches like the one taken by EcoDyn/rsm would have been much better if we, somehow, could restrict the number of unknown parameters more than is currently done. We have difficulties, though, in seeing how this could be done with any degree of certainty for microtine rodents dynamics.

Until approaches like EcoDyn/rsm have been refined so as to incorporate statistical properties, a better approach for short time series could be to ask a more fundamental question: can we reject the hypothesis of linearity? Nonlinearity is after all necessary, but of course not sufficient, for producing chaotic dynamics (Schuster 1988). If we do not find support for nonlinearity in a time series, it does not make sense to search for chaos.

Recently statistical methods with known properties have been developed to test for nonlinearity (Chan & Tong 1990; Tong 1990; Brock & Potter 1992; Theiler *et al.* 1992; Hjellvik & Tjøstheim 1995; Teräsvirta 1994; Tjøstheim 1994). Using a nonlinearity test developed by Chan & Tong (1990) confirm what has been found in the above reported analysis (O. N. Bjørnstad *et al.* unpublished data). As summarized in table 1, O. N. Bjørnstad *et al.* (unpublished

results) found that for 14 out of 23 northern time series, the null-hypotheses of linearity was rejected. For the southern time series the null hypothesis of linearity was rejected for one out of eleven. In short, this suggests that the northern time series may be more nonlinear than the southern time series. It is, however, important to realize that evidence for nonlinearity in the northern time series is not sufficient for concluding that the dynamics is chaotic (see, for example, Subba Rao 1992). The existence of nonlinearity only implies that currently we are unable to rule out the possibility that the underlying dynamics of these time series may be chaotic. Therefore, concluding that the northern microtine time series are chaotic seems (at present) unwarranted. It is, for example, worrying that the three most northern time series with strictly positive confidence intervals are all concluded to be linear. However, as nonlinearity is a necessary condition for chaotic dynamics, we may infer that the southern time series are non-chaotic.

6. CONCLUSION

On the basis of our analysis, we conclude the following.

1. Our analyses based on the EcoDyn/rsm package show no convincing and general evidence for chaos in northern microtine populations. There are, however, some indications of chaos in some populations, and some support for presence of nonlinearity. We have, however, found some indications that the more southern populations (south of 60° N) exhibit stable non-chaotic dynamics.
2. Packages such as EcoDyn/rsm may be useful, but would need to include statistical properties if viable conclusions about ecological dynamics are to be derived.
3. If we are to explore complex behaviour in ecological time series as short as the one discussed in this paper, it may be more rewarding to test for nonlinearities than to provide point estimates for Lyapunov exponents, the meaning of which is very unclear indeed.

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REFERENCES

- Box, G. E. P. & Draper, N. R. 1987 *Empirical model-building and response surfaces*. New York: John Wiley & Sons.
- Brock, W. A. & Potter, S. M. 1992 Diagnostic testing for nonlinearity, chaos and general dependence in time series data. In *Nonlinear modeling and forecasting* (ed. M. Casdagli & S. Eubank), pp. 137–161. Reading, Massachusetts: Addison-Wesley.
- Chan, K. S. & Tong, H. 1990 On likelihood ratio tests for threshold autoregression. *Jl R. statist. Soc.* **52**, 469–476.
- Chan, K. S. & Tong, H. 1994 A note on noisy chaos. *Jl R. statist. Soc.* **56**, 301–311.
- Cox, D. R. 1977 Discussion on the papers by Campbell and Walker, Ton and Morris. *Jl R. statist. Soc.* **140**, 453–454.

- Dixon, P. M. 1993 The bootstrap and the jackknife: Describing the precision of ecological indices. In *Design and analysis of ecological experiments* (ed. S. M. Scheiner & J. Gurevitch). London: Chapman & Hall.
- Eckman, J. P. & Ruelle, D. 1985 Ergodic theory of chaos and strange attractors. In *Reviews of modern physics*, **57**, 617–656.
- Efron, B. 1982 *The jackknife, the bootstrap, and other resampling plans*. Philadelphia, U.S.A.: Society for Industrial and Applied Mathematics.
- Ellner, S. & Turchin, P. 1995 Chaos in a noisy world: new methods and evidence from time-series analysis. *Am. Nat.* **154**, 343–375.
- Ellner, S., Gallant, A. R., McCaffrey, D. & Nychka, D. 1991 Convergence rate and data requirements for jacobian-based estimates of lyapunov exponents from data. *Physics Lett. A* **153**, 357–363.
- Ellner, S., Gallant, A. R. & Theiler, J. 1995 Detecting nonlinearity and chaos in epidemic data. In *Proceedings of NATO ARV on epidemic models* (ed. D. Mollison). Cambridge University Press.
- Gershensfeld, N. A. & Weigend, A. S. 1994 The future of time series: learning and understanding. In *Time series prediction-forecasting in future and understanding the past* (ed. A. S. Weigend & N. A. Gershensfeld), pp. 1–70. Reading, Massachusetts: Addison-Wesley.
- Hanski, I., Hansson, L. & Henttonen, H. 1991 Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* **60**, 353–367.
- Hanski, I., Turchin, P., Korpimäki, E. & Henttonen, H. 1993 Population oscillations of boreal rodents: Regulation by mustelid predators leads to chaos. *Nature, Lond.* **364**, 232–235.
- Hansson, L. & Henttonen, H. 1985 Gradients in density variations of small rodents: the importance of latitude snow cover. *Oecologia* **67**, 394–402.
- Hastings, A., Hom, C. L., Ellner, S., Turchin, P. & Godfray, H. C. J. 1993 Chaos in ecology: is nature a strange attractor? *A. Rev. Ecol. Syst.* **24**, 1–33.
- Hjellevik, V. & Tjøstheim, D. 1995 Nonparametric tests of linearity for time series. *Biometrika*. (In the press.)
- Hjort, S. S. V. 1994 *Computer intensive statistical methods*. New York: Chapman & Hall.
- Nisbet, R. M. & Gurney, W. S. C. 1982 *Modelling fluctuating populations*. New York: John Wiley & Sons.
- Nychka, D., Ellner, S., McCaffrey, D. & Gallant, A. 1992 Finding chaos in noisy systems. *Jl R. statist. Soc.* **54**, 399–426.
- Parlitz, U. 1992 Identification of true and spurious Lyapunov exponents from time series. *Int. J. Bifurc. Chaos* **2**, 155–165.
- Perry, J. N., Wiwod, I. P. & Hanski, I. 1993 Using response surface methodology to detect chaos in ecological time series. *Oikos* **68**, 329–339.
- Schuster, H. G. 1988 *Deterministic chaos: an introduction*, edn 2. Weinheim: Physik.
- Stenseth, N. C. & Ims, R. A. 1993 *The biology of lemmings*. London: Academic Press.
- Stenseth, N. S., Gustafsson, T. O., Hansson, L. & Ugland, K. I. 1985 On the evolution of reproductive rates in microtine rodents. *Ecology* **66**, 1795–1808.
- Subba Rao, T. 1992 Analysis of nonlinear time series (and chaos) by bispectral methods. In *Nonlinear modeling and forecasting* (ed. M. Casdagli & S. Eubank), pp. 199–226. Reading, Massachusetts: Addison-Wesley.
- Teräsvirta, T. 1994 Testing linearity and modeling nonlinear time series. *Kybernetika* **30**, 319–330.
- Theiler, J., Eubank, A., Longtin, A., Galdrikian, B. & Farmer, J. D. 1992 Testing for nonlinearity in time series: the method of surrogate data. *Physica* **58**, 77–94.
- Tjøstheim, D. 1994 Non-linear time series: A selective review. *Scan. J. Stat.* **21**, 97–130.
- Tong, H. 1990 *Non-linear time series analysis*. Oxford Science Publications.
- Tong, H. 1995 A personal overview of nonlinear time series analysis from a chaos perspective. *Scan. J. Stat.* (In the press.)
- Tsay, R. S. 1992 Model checking via parametric bootstraps in time series analysis. *Appl. Statist.* **41**, 1–15.
- Turchin, P. 1993 Chaos and stability in rodent population dynamics: evidence from non-linear time-series analysis. *Oikos* **68**, 167–172.
- Turchin, P. & Taylor, A. 1992 Complex dynamics in ecological time series. *Ecology* **73**, 289–305.
- Turchin, P. & Millstein, P. J. A. 1993 *EcoDyn/RSM Response surface modeling of nonlinear ecological dynamics*. Setauket, New York: Applied Biomathematics.
- Wilson, H. & Rand, D. A. 1993 Detecting chaos in a noisy time series. *Proc. R. Soc. Lond. B* **253**, 239–244.
- Yao, Q. & Tong, H. 1994a On prediction and chaos in stochastic systems. *Phil. Trans. R. Soc. Lond. A* **348**, 357–369.
- Yao, Q. & Tong, H. 1994b Quantifying the influence of initial values on nonlinear prediction. *Jl R. Statist. Soc.* **348**, 357–369.

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Experimental evidence for habitat dependent selection in a *Bombina* hybrid zone

By C. J. MACCALLUM, B. NÜRNBERGER AND N. H. BARTON

During field work in Croatia earlier this summer, we became aware of the close similarity between *Bombina bombina* eggs and those of *Hyla arborea*: they are indistinguishable except for a difference in average egg size (with overlapping distributions) and in the compactness of the egg cluster. Although fresh eggs had been taken from the immediate vicinity of *B. bombina* choruses, contamination of our samples with *H. arborea* appeared likely. Close re-examination of our frozen tadpole samples has confirmed this concern. We therefore wish to retract this paper.

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Bootstrap estimated uncertainty of the dominant Lyapunov exponent for Holarctic microtine rodents

By W. FALCK, O. N. BJØRNSTAD AND N. C. STENSETH

In Falck *et al.* (1995, table 1), the years of observation should have been listed as 1951–1975 for Serpukhov, 1949–1976 for Tula, and 1948–1969 for Wytham Wood.