

Detecting chaotic dynamics of insect populations from long-term survey data

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Abstract 1. Estimates of the Lyapunov exponent, a statistic that measures the sensitive dependence of the dynamic behaviour of a system on its initial conditions, are used to characterize several sets of insect time series.

2. A new method is described to overcome the difficulty of defining the dynamics of an observed, noisy, short ecological time series. This method provides two test statistics for the estimated Lyapunov exponent.

3. This method is applied to forty-six time series comprising six aphid species from five sites and four moth species from six sites. There are few positive Lyapunov exponents and none is sufficiently large to characterize its time series as chaotic.

4. Two methods to estimate the Lyapunov exponent are compared; that based on logarithmically transformed counts yields less variable estimates for highly variable insect data than that based on untransformed counts.

Key words. Chaos, aphids, moths, population dynamics, time series, Lyapunov exponent.

Introduction

Complex dynamics can arise from simple, theoretical and ecological models involving difference equations (May, 1974, 1976). Advances in computing power have rekindled this interest in recent years and chaotic dynamics in ecology have been the subject of several reviews (May, 1987; Logan & Allen, 1992; Hastings *et al.*, 1993). Until recently, the perception of the prevalence of chaos in ecology was largely determined by a very influential study of life-table data of twenty-eight insect populations with discrete generations (Hassell *et al.*, 1976). The authors concluded that most of these populations were stable and that examples of complex dynamics were rare in nature. This conclusion was criticized by Turchin & Taylor (1992) on the basis that Hassell *et al.*'s (1976) single-species model was overly simple and lacked delayed density-dependence. Complex dynamics are more likely to arise in systems with a larger number of dimensions. Delayed density-dependence occurred frequently in the multispecies communities typically found in many insect populations (Turchin, 1990). Perry (1994) suggested that the incidence of complex dynamics found by Hassell *et al.* (1976) was possibly

underestimated because the degree of density-dependence was underestimated. Turchin & Taylor (1992) proposed a response-surface model that they claimed had many advantages over other methods to characterize the non-linear dynamic behaviour of insect populations from real ecological data. Perry *et al.* (1993) used this technique to study the endogenous dynamics underlying two ecological time series for the aphid *Phyllaphis fagi* (Linn.); the method was sensitive to a number of factors, including further data from the same population and extra data from different but comparable populations.

Observed ecological time series are the consequences of density-dependent processes and density-independent random processes and their interactions in multispecies communities (Turchin & Taylor, 1992). Clearly, a mixture of density-dependent and delayed density-dependent processes is common in many insect populations (Sinclair, 1989; Turchin, 1990; Woiwod & Hanski, 1992; Hanski *et al.*, 1993b; Holyoak, 1993; Perry, 1994). However, it remains a challenge in ecology to separate the density-dependent, endogenous dynamics from the exogenous density-independent noise. Turchin & Taylor (1992) suggested that the fitted response-surface model be used to reconstruct directly the endogenous dynamics of a time series, but their approach was superseded by that of Ellner & Turchin (1995) who regard the exogenous noise as an integral part of the dynamics of the series, and as a possible modulator of the qualitative dynamics to be estimated. For example, whereas the endogenous dynamics might indicate limit cycles,

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consideration of the exogenous dynamics could alter the overall estimated dynamics qualitatively, to stability (less complex) or chaos (more complex). They recommended definition of the qualitative dynamics through estimation of the Lyapunov exponent, by the Jacobian method of Nychka *et al.* (1992). Perry *et al.* (1993) and Renshaw (1994) stressed the difficulties caused by the need to investigate complex, multiparameter response-surface models, for data that are strictly limited by the length of the time series available.

The Lyapunov exponent, λ , is a quantitative measure of the sensitive dependence of the subsequent dynamics on initial conditions: it quantifies the rate of growth (if $\lambda > 0$), or decay (if $\lambda < 0$) over time, of the effects of a small perturbation on a system's dynamics (Ellner & Turchin, 1995). It is used increasingly to characterize the dynamic behaviour of both ecological models (Bascompte & Sole, 1994; Rohani *et al.*, 1994; Sole & Bascompte, 1994; Rohani & Miramontes, 1995) and observed ecological time series (Turchin & Taylor, 1992; Hanski *et al.*, 1993a; Turchin, 1993). A system with $\lambda > 0$ is a 'noise amplifier': after a small perturbation occurs, the effects of the perturbation are magnified over time by the system's intrinsic dynamics. This property causes unpredictability in the system's dynamics, one of the most important signatures of chaos. On the other hand, a system with $\lambda < 0$ is a 'noise muffler': the effects of the perturbation decay to zero over time, the system's intrinsic dynamics are predictable and any unpredictability is due solely to the direct effects of external noise.

The data analysed here comprise some of the longest series of field data available, yet the number of points remains minimal for the analyses attempted. Often, for a single series, the dynamics found are dependent on the type of model fitted. Too complex a model will overfit the data by treating the noise as part of the signal; too simple a model cannot represent the complexity of the endogenous process. Therefore, caution should prevent firm conclusions concerning the dynamic behaviour of the time series analysed here. To ameliorate some of these problems, two test statistics were developed, to attempt to strengthen the conclusions available from the estimate of the Lyapunov exponent. This paper introduces this new methodology to characterize chaotic dynamics using observed time series of various aphid and moth species.

Materials and Methods

Data

The data are annual total counts from the Rothamsted Insect Survey, which samples winged aphids throughout Great Britain using 12.2-m suction traps and moths using standard Rothamsted light traps (Woiwod & Harrington, 1994).

Five suction trap sites were selected with 23 years or more of data, at Wye, Rothamsted, Broom's Barn, Newcastle and Dundee, to span the geographical range of latitudes in Great Britain (Fig. 1). Six aphid species were selected: *Brachycaudus helichrysi* (Kltb), *Elatobium abietinum* (Walker), *Hyperomyzus lactucae* (Linn.), *Myzus ascalonicus* Doncaster, *M. persicae*

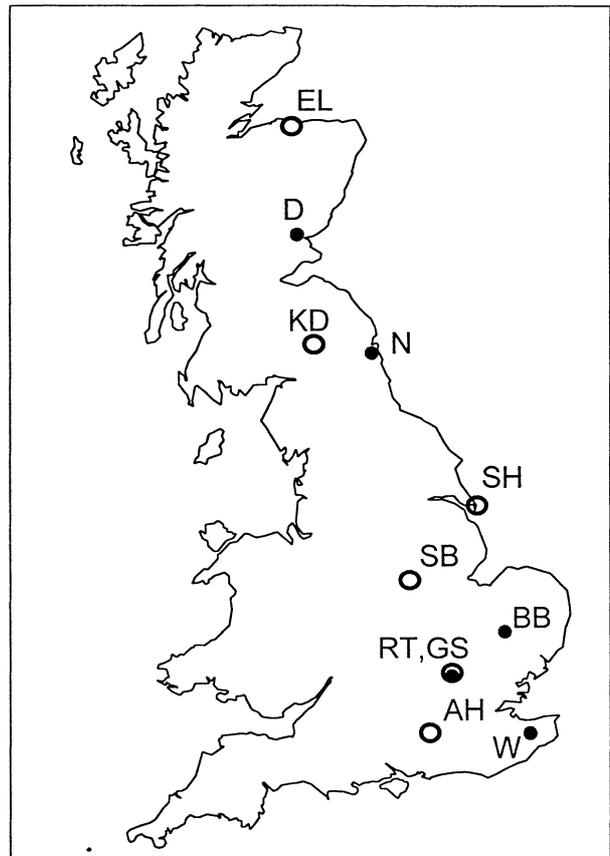


Fig. 1. Locations of aphid suction traps (●: RT, Rothamsted; W, Wye; BB, Broom's Barn; N, Newcastle; D, Dundee) and moth light traps (○: AH, Alice Holt; GS, Geescroft; SB, Sutton Bonnington; SH, Spurn Head; KD, Kielder; EL, Elgin).

(Sulzer) and *Metopolophium dirhodum* (Walker), based on those for which relationships between temperature and phenology are known and which represent a range of life cycle types (Table 1). The six selected light trap sites, at Alice Holt, Geescroft, Sutton Bonnington, Spurn Head, Kielder and Elgin, covered a similar geographical range as the suction trap sites (Fig. 1). The four moth species, *Apamea monoglypha* (Hufn.), *Cerapteryx graminis* (Linn.), *Perizoma alchemillata* (Linn.) and *Xanthorhoe montanata* (D & S) are univoltine.

The annual total counts from the aphid series come from daily samples of winged aphids accumulated during the year, in which most aphid species have three migratory periods (here *B. helichrysi*, *H. lactucae*, *M. persicae* and *M. dirhodum*). The first period occurs in spring. For aphid species with a majority of clones that are anholocyclic in the U.K., reproducing parthenogenetically throughout the year (here *E. abietinum*, *M. ascalonicus* and *M. persicae*), winged aphids develop from overwintering aphid populations and migrate to more nutritious host plants, including crops. For species with a majority of clones that are holocyclic in the U.K., producing male and female sexual morphs in autumn and overwintering as eggs but reproducing parthenogenetically throughout the rest of the year (here *B. helichrysi*, *H. lactucae* and *M. dirhodum*), winged

Table 1. A summary of the time series of annual total catches for the six aphid species at five sites: Rothamsted (RT), Wye (W), Broom's Barn (BB), Newcastle (NC) and Dundee (DD) with series lengths of 27, 25, 27, 25 and 25 years, respectively, except for *Brachycaudus helichrysi*, for which 24 years of data were available at all sites. M is the sample mean; SD is the standard deviation. Non-integer counts arise from estimated missing values.

Site	Min.	Max.	M	SD	Min.	Max.	M	SD	Min.	Max.	M	SD
	<i>Brachycaudus helichrysi</i>				<i>Elatobium abietinum</i>				<i>Myzus ascalonicus</i>			
RT	45.0	2837.0	1089.0	815.5	2.0	380.9	66.9	85.7	7.0	364.6	111.1	91.3
W	99.9	2722.0	831.6	638.3	5.0	441.6	133.1	126.1	3.0	107.9	42.4	31.0
BB	47.4	3655.0	802.4	765.3	2.0	209.9	38.7	48.2	3.0	190.9	56.2	47.5
NC	23.0	597.4	151.8	127.9	3.0	1573.0	308.4	455.8	0.0	82.0	26.1	23.2
DD	34.0	475.4	203.4	123.3	4.1	1034.0	137.3	243.1	0.0	31.4	9.1	8.6
	<i>Myzus persicae</i>				<i>Hyperomyzus lactucae</i>				<i>Metopolophium dirhodum</i>			
RT	42.0	911.0	211.8	202.5	14.0	171.6	58.1	40.8	19.0	18449.0	1564.0	3671.0
W	75.0	1113.0	300.6	256.6	29.0	366.3	79.5	68.9	54.1	34434.0	2006.0	6786.0
BB	72.0	1737.0	419.9	397.1	10.0	362.1	73.8	72.9	73.0	187931.0	9704.0	35951.0
NC	4.6	313.1	59.5	75.2	0.0	36.7	12.1	8.9	16.3	3572.0	644.2	878.2
DD	4.0	670.4	165.6	171.2	5.0	93.4	23.4	19.8	22.0	44667.0	3473.0	8813.0

aphids develop from aphids originating from overwintering eggs on primary (usually woody) hosts where they are laid in the previous autumn. These migrate to specific herbaceous host plants where they reproduce parthenogenetically. The second migratory period occurs in summer. For both anholocyclic and holocyclic species, winged aphids develop and disperse in response to crowding and decline in host plant nutrients. The third migratory period occurs in autumn. Winged aphids of anholocyclic clones move to overwintering host plants, usually herbaceous weeds and grasses. In holocyclic clones, winged males and gynoparae (parents of the wingless, sexual females, the oviparae) develop in response to short photoperiod and migrate to the primary hosts where overwintering eggs are laid. *Elatobium abietinum* feeding on spruce (*Picea*) and *M. ascalonicus* feeding on Compositae, Cruciferae and Rosaceae have only one migratory period in May and June, when winged aphids develop and disperse in response to a decline in plant nutrients (Zhou *et al.*, 1996).

The annual total counts from the moth series come from nightly catches of adult moths in light traps. *Apamea monoglypha* overwinters as larvae that feed on Gramineae and the adults fly between June and August. *Cerapteryx graminis* overwinters as eggs, feeds on Gramineae and the adults fly between July and September. *Perizoma alchemillata* overwinters as pupae, feeds on *Galeopsis* spp. and the adults fly between June and July. *Xanthorhoe montanata* overwinters as larvae, feeds on herbaceous plants such as *Galium* and *Primula* spp. and the adults fly between May and July (Emmet & Heath, 1991).

Each time series of annual total catch (N_t) analysed for these sites and species met two additional criteria: it had no more than a single zero catch and was stationary, in the sense that its autocorrelation function (ACF) decayed to zero (Box & Jenkins, 1976). The mean (M), minimum (Min), maximum (Max) and standard deviation (SD) of these time series are presented in Tables 1 and 2. Decimal points in the aphid data

are due to a very few missing values in daily catches that were estimated (Zhou *et al.*, 1996). The criteria for some moth time series were not met at all sites, so these were not analysed (Table 2). All data were transformed from N_t to $(N_t + 1)$, to avoid problems caused by the logarithm of zero.

The model

The model of Perry *et al.* (1993) was used in this study to provide a more stable alternative to that suggested by Turchin & Taylor (1992). Denoting the population density in year t as N_t ; and the transformed population growth rate, $\log_{10}(N_t/N_{t-1})$, in year t as γ_t ; the model with three time lags is:

$$\gamma_t = F(X, Y, Z) = a_0 + a_1X + a_{11}X^2 + a_2Y + a_{22}Y^2 + a_3Z + a_{33}Z^2 + a_{12}XY + a_{13}XZ + a_{23}YZ + \epsilon_t \quad (1)$$

where

$$X = \log_{10}(N_{t-1}), Y = \log_{10}(N_{t-2}), Z = \log_{10}(N_{t-3}).$$

For models with one and two lags, terms with Y and Z , and Z in eqn 1 are deleted, respectively. As a preliminary screen of the dynamics and to assess stationarity, diagnostic plots of the ACF and the partial autocorrelation function (PACF) (Turchin, 1990; Berryman, 1992) and power spectra (Kadanoff, 1983) were produced for each time series. The parameters in eqn 1 were estimated using the statistical package, GENSTAT 5 (GENSTAT 5 Committee, 1993). Models were fitted with one, two and three lags to each of the time series and the percentage variance accounted for (PVA) by the different lags was compared (Perry *et al.*, 1993). The GENSTAT 5 definition of 'percentage variance accounted for' is an adjusted R^2 statistic, a measure of the goodness of fit of the model, calculated as: $100[1 - (\text{residual mean square}) / (\text{total mean square})]$. The model with three lags improved the fit of about half of the time series, compared to the models with one or two lags (Fig. 2). The

Table 2. A summary of the time series of annual total catches for the four moth species at six sites: Alice Holt (AH), Geescroft (GS), Sutton Bonnington (SB), Spurn Head (SH), Kielder (KD) and Elgin (EL) with series lengths of 28, 28, 24, 24, 25 and 27 years, respectively. M is the sample mean; SD is the standard deviation. —, values are not presented where time series failed to meet minimum criteria (see text).

Site	Species															
	<i>Apamea monoglypha</i>				<i>Cerapteryx graminis</i>				<i>Perizoma alchemillata</i>				<i>Xanthorhoe montanata</i>			
	Min.	Max.	M	SD	Min.	Max.	M	SD	Min.	Max.	M	SD	Min.	Max.	M	SD
AH	—	—	—	—	1	20	6.8	4.5	1	133	34.3	35.2	2	59	19.3	14.2
GS	3	112	32.4	29.6	—	—	—	—	1	209	70.1	66.2	—	—	—	—
SB	4	90	24.1	19.5	—	—	—	—	—	—	—	—	3	120	48.5	32.6
SH	6	137	38.8	34.5	—	—	—	—	—	—	—	—	4	45	16.8	11.5
KD	4	151	40.8	33.9	5	143	38.1	34.0	5	239	58.7	66.2	—	—	—	—
EL	4	149	37.7	37.2	4	73	24.9	16.0	4	115	28.9	25.6	5	77	41.9	18.2

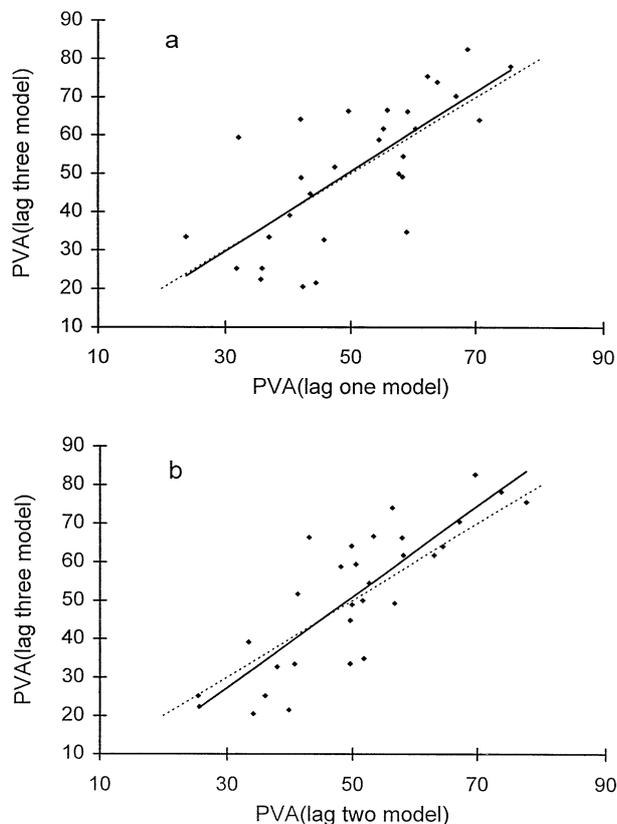


Fig. 2. Relationships between percentage of variance accounted for (PVA), after fitting models with one, two and three lags to the data for the full time series. The solid line is the fitted regression line and the dotted line is the equality line. (a) lag-three model (Y) against lag-one model (X): $Y = -1.691 + 1.045X$, $F_{1,28} = 32.0$; (b) lag-three model (Y) against lag-two model (X): $Y = -8.20 + 1.182X$, $F_{1,28} = 64.4$.

most appropriate lag for each species was selected using cross-validation, as described by Turchin & Millstein (1993). This involved the generation of $2n-1$ new series from each original series, by the removal of first one, and then two successive

data points, starting in each case with the first data point and ending with the last. The PVA values from the resulting $2n-1$ series were averaged over the sites for each species, and the model with the largest average PVA selected (Table 3).

Characterizing dynamics with Lyapunov exponents

The Lyapunov exponent, λ , was adopted as a quantitative measure of the sensitive dependence of the subsequent dynamics on initial conditions (Turchin & Millstein, 1993; Ellner & Turchin, 1995). For $\lambda < 0$ the dynamics are classified as stable, with a fixed point equilibrium or cyclic equilibrium. For $\lambda = 0$ the dynamics are classified as quasiperiodic. For $\lambda > 0$ the dynamics are classified as chaotic, when the effects of small perturbations are compounded and therefore cannot be ignored in predicting the future dynamics of the system. Wolf *et al.* (1985) gave two methods to estimate the Lyapunov exponent: the trajectory and the Jacobian (Turchin & Millstein, 1993). The trajectory method calculates the rate at which two nearby trajectories diverge in time. It requires a large number of data values, especially in high-dimensional systems (Wolf *et al.*, 1985; Turchin, 1991a). This method, if used for stochastic systems, is likely to yield more biased and highly variable estimates than the Jacobian method (Turchin, 1991a; Turchin & Millstein, 1993). Here, Ellner *et al.*'s (1991) modified Jacobian method was used, that calculates the rate of divergence using the Jacobian matrix comprising partial derivatives of the system map, and which Ellner & Turchin (1995) note is less sensitive to the dynamic noise that most biological systems contain. The estimated value of λ is calculated from:

$$\hat{\lambda} = \frac{1}{n} \log \|J_n J_{n-1} \dots J_1 v\| \quad (2)$$

where J_t is the Jacobian matrix of partial derivatives of eqn 1 evaluated at N_t ; $\|\cdot\|$ is a matrix norm; v is a vector of length one $(1, 0, 0, \dots, 0)^T$; and n is the length of the time series.

The following is a brief explanation. For the three-lag model denote x_t as N_t , x_{t-1} as N_{t-1} , y_{t-1} as N_{t-2} , and z_{t-1} as N_{t-3} . The system map of eqn 1 may be rewritten in terms of functions: $d()$, $g()$ and $p()$ as:

Table 3. Average ‘percentage variance accounted for’ (PVA) from cross-validations of models for each time series over five sites for each aphid and moth species, and the model selected for each species.

Species	Model selected	PVA		
		Lag one	Lag two	Lag three
<i>Brachycaudus helichrysi</i>	Lag three	51.186	49.694	51.780
<i>Elatobium abietinum</i>	Lag one	58.566	53.618	57.278
<i>Hyperomyzus lactucae</i>	Lag three	55.114	56.020	62.390
<i>Myzus ascalonicus</i>	Lag one	38.756	33.224	29.314
<i>Metopolophium dirhodum</i>	Lag one	59.464	57.220	57.642
<i>Myzus persicae</i>	Lag two	45.804	49.648	44.910
<i>Apamea monoglypha</i>	Lag one	36.796	36.100	35.614
<i>Cerapteryx graminis</i>	Lag one	17.880	17.002	15.396
<i>Perizoma alchemillata</i>	Lag three	35.485	45.075	49.810
<i>Xanthorhoe montanata</i>	Lag one	29.852	23.262	22.842

$$\begin{aligned}
 x_t &= d(x_{t-1}, y_{t-1}, z_{t-1}), \\
 y_t &= g(x_{t-1}, y_{t-1}, z_{t-1}) \text{ and} \\
 z_t &= p(x_{t-1}, y_{t-1}, z_{t-1}),
 \end{aligned}$$

where $g(x_{t-1}, y_{t-1}, z_{t-1}) \equiv x_{t-1}$ and $p(x_{t-1}, y_{t-1}, z_{t-1}) \equiv y_{t-1}$. Then, for stability analysis, this may be linearized using a Taylor series expansion as:

$$\begin{pmatrix} \nabla x_t \\ \nabla y_t \\ \nabla z_t \end{pmatrix} = J_t \begin{pmatrix} \nabla x_{t-1} \\ \nabla y_{t-1} \\ \nabla z_{t-1} \end{pmatrix} \tag{3}$$

where ∇ represents a small difference between two nearby trajectories on the map at a particular time and J_t is the Jacobian matrix evaluated at time t , whose components are:

$$J_t = \begin{pmatrix} \partial d/\partial x & \partial d/\partial y & \partial d/\partial z \\ \partial g/\partial x & \partial g/\partial y & \partial g/\partial z \\ \partial p/\partial x & \partial p/\partial y & \partial p/\partial z \end{pmatrix} \tag{4}$$

and $\partial/\partial x$ represents the partial derivative with respect to x . The divergence or convergence of ∇ from time $t-1$ to time t depends on the nature of the Jacobian at time $t-1$, specifically whether it is of the stretching or shrinking kind. The value of ∇ is amplified for the former, for which the dominant eigenvalue of the Jacobian is greater than unity, and reduced for the latter, for which the dominant eigenvalue is less than unity. However, the divergence rate of ∇ may vary, because the Jacobians may change over time. It is therefore necessary to measure the average divergence rate, over an infinite time period:

$$\lambda = \lim_{t \rightarrow \infty} [\| J_{t-1} J_{t-2} \dots J_0 \| / t] \tag{5}$$

Two methods were used to obtain the Jacobian matrix of the system map. The first was used by Turchin & Millstein (1993) (here termed the indirect method), who transformed the system map to logarithms by considering, instead of N_t , $L_t = \log_{10} N_t$ to obtain the Jacobian, J_t :

$$J_t = \begin{pmatrix} U_{11}^t & U_{12}^t & U_{13}^t \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix} \tag{6}$$

where U_{11}^t , U_{12}^t and U_{13}^t are partial derivatives of the logarithmically transformed function of $x_t = d(x_{t-1}, y_{t-1}, z_{t-1})$

with respect to Lx_{t-1} , Ly_{t-1} and Lz_{t-1} , respectively, i.e. where $Lx_{t-1} = \log_{10}(x_{t-1})$, $Ly_{t-1} = \log_{10}(y_{t-1})$, $Lz_{t-1} = \log_{10}(z_{t-1})$, $U_{11}^t = 1 + \partial F/\partial Lx_{t-1}$, $U_{12}^t = 1 + \partial F/\partial Ly_{t-1}$ and $U_{13}^t = 1 + \partial F/\partial Lz_{t-1}$.

The second method used the partial derivatives of the original system map, with respect to x_{t-1} , y_{t-1} and z_{t-1} (here termed the direct method). Defining $\log_{10} \eta_t = v_t$, the components of the alternative Jacobian matrix, J_t , are:

$$\begin{aligned}
 \partial d/\partial x_{t-1} &= \eta_t [1 + x_{t-1} (\partial F/\partial Lx_{t-1})(\partial Lx_{t-1}/\partial x_{t-1})] = \eta_t U_{11}^t, \\
 \partial d/\partial y_{t-1} &= \eta_t [x_{t-1} (\partial F/\partial Ly_{t-1})(\partial Ly_{t-1}/\partial y_{t-1})] = \\
 &\quad \eta_t (x_{t-1}/y_{t-1}) U_{12}^t, \\
 \partial d/\partial z_{t-1} &= \eta_t [x_{t-1} (\partial F/\partial Lz_{t-1})(\partial Lz_{t-1}/\partial z_{t-1})] = \\
 &\quad \eta_t (x_{t-1}/z_{t-1}) U_{13}^t,
 \end{aligned}$$

and the rest of the components are the same as those in eqn 6.

Randomization tests

A method is required to assess the importance of deviations of estimated Lyapunov exponents from zero. Dynamics with a positive estimated Lyapunov exponent cannot be ascribed as definitely chaotic with any confidence, because noise in the data may give rise to positive estimates for stable systems, or negative estimates where the underlying dynamics are chaotic. The method developed here is in the spirit of Pollard *et al.* (1987), who constructed a randomization distribution for a density-dependence statistic, by random permutation of a time series. Firstly, consider a null hypothesis of complete compensation, where the series returns to its overall mean value each year and ‘forgets’ any deviation experienced in the previous year. This corresponds to an extreme form of density-dependence in which the series exhibits strong stability; all fluctuations from the mean are merely temporary shocks. The model here is $N_t = \mu + \epsilon_t$ or $\log_{10} N_t = \mu + \epsilon_t$. Series corresponding to this null hypothesis (hypothesis I) may be generated by randomly permuting the observed counts in the series. Secondly, consider a null hypothesis of complete density-independence, when the growth rate for one year is unrelated to the population in the previous year (Pollard *et al.*, 1987) and is assumed to be a constant, k , apart from some stochastic

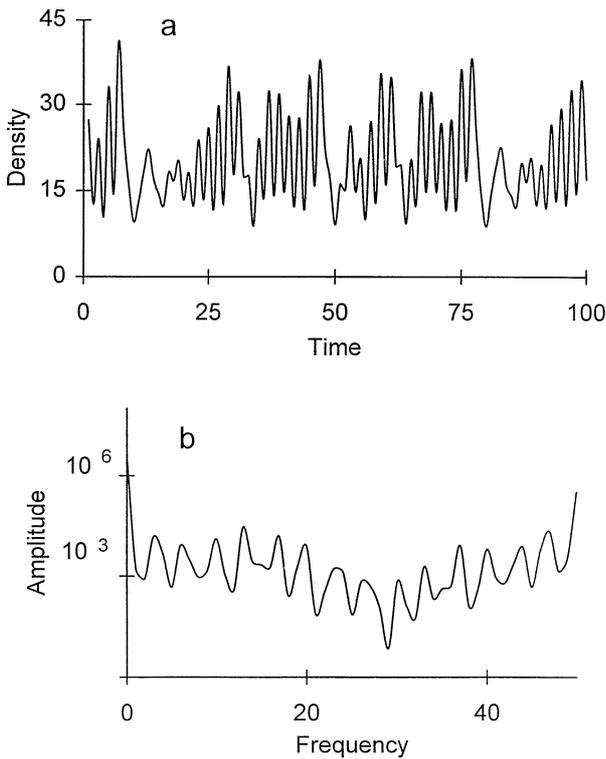


Fig. 3. (a) 100 points from a known chaotic time series with a Lyapunov exponent of 0.624 reconstructed from the Turchin–Taylor model with an additional temperature variate (T) (here $T = 4.81$): $\gamma_t = 4.49 + 0.212T - 35.8N_{t-1}^{0.364} + 57.4N_{t-2}^{4.59} + 1.05 \times 10^7 N_{t-3}^{1.39} + 5.01 \times 10^{11} N_{t-1}^{0.728} - 289.0N_{t-2}^{9.18} + 7727N_{t-3}^{2.78} - 3.80 \times 10^7 N_{t-1}^{0.364} N_{t-2}^{4.59} + 665.8N_{t-1}^{0.364} N_{t-3}^{1.39} - 2.28 \times 10^8 N_{t-2}^{4.59} N_{t-3}^{1.39}$, and (b) its power spectrum.

fluctuation. The model here is: $\log_{10}N_t = \log_{10}N_{t-1} + k + \epsilon_t$, or similar. A stationary series corresponding to this null hypothesis (hypothesis II) may be generated by calculating each of the $(n-1)$ observed growth rates, γ_t , of the series, permuting them, and constructing a new series with those permuted growth rates plus a starting value, N^1 , randomly selected from one of the observed values of N_t from the actual series. Both hypotheses cover extreme situations, so are not ideal, but the multiplicity of different models that can generate chaotic dynamics makes it difficult to select an obvious alternative. The rationale of the randomization test used here is whether the estimate of λ_{obs} from the observed time series should be judged as unusual compared with those obtained from all the possible random permutations of the time series (Pollard *et al.*, 1987). Firstly, the model parameters were estimated and used to calculate the Lyapunov exponent λ_{obs} for the observed time series. Then the bootstrapping techniques (Efron & Tibshirani, 1986) outlined above were used, with the random number generator of Wichmann & Hill (1982), to obtain 1000 new series for each hypothesis. The model parameters were estimated and the exponent λ_{rdm} calculated for each of these series, and a probability distribution was formed from these values. This distribution was used to test the null hypothesis that the value, λ_{obs} , of the observed time

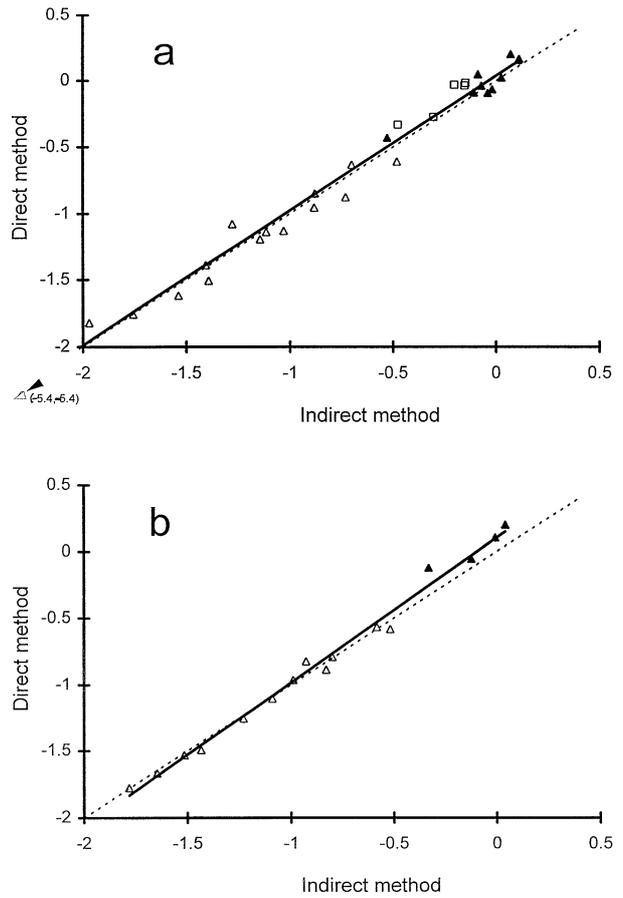


Fig. 4. Relationships between estimated Lyapunov exponents obtained using the direct (Y) and indirect (X) method. The solid line is the fitted regression line and the dotted line is the equality line. (a) aphid time series, $Y = 0.036 + 1.013X$, $F_{1,28} = 3648$; (b) moth time series, $Y = 0.104 + 1.088X$, $F_{1,14} = 1414$. Δ are data from one-lag models, \square data from two-lag models, \blacktriangle data from three-lag models.

series was no larger than that expected from (I) a completely compensating series or (II) a density-independent series, composed of those identical counts. The null hypothesis was rejected at a 5% (or 95%) level of significance if more than 95% of the λ_{rdm} values were less (or more) than the value λ_{obs} . The consistent occurrence of positive values of λ_{obs} that were judged significant by this test over the sites studied was taken as evidence of possible chaotic dynamics for a particular species.

Effects of time series length and number of permuted time series

Two time series known to be chaotic were used to obtain some idea of the power of the above methods to detect complex non-linear dynamics, and of the effect of the length of the time series on the test results. The first time series used was a Turchin–Taylor, three-lag, response-surface model with an additional temperature variate (Fig. 3). The data points used

Table 4. Effects of noise level and series length on estimates of Lyapunov exponents from the Ricker model using both direct (Dir.) and indirect (Ind.) methods. The percentages in the noise level column headings express the average noise as a percentage of the mean of the time series.

Series length	No noise		Small noise (6.3%)		Moderate noise (25%)		Large noise (50.9%)	
	Dir.	Ind.	Dir.	Ind.	Dir.	Ind.	Dir.	Ind.
30	0.302	0.480	0.115	0.503	-0.610	0.410	-0.860	1.053
50	0.438	0.509	0.201	0.475	-0.468	0.415	-0.855	0.940
100	0.524	0.546	0.226	0.447	-0.379	0.438	-0.869	0.875
1000	0.546	0.548	0.226	0.447	-0.436	0.443	-0.884	0.903

were the next 30, 50 and 100 points after discarding the initial 5000 time steps from the reconstructed dynamics of the model (Fig. 3). The time series had a Lyapunov exponent of 0.624 and its power spectrum confirmed that it was chaotic. Each of these artificially constructed series was permuted 1000, 3000, 5000 and 10 000 times. The parameters and Lyapunov exponents were estimated for each of these series as described above.

The second time series used was a simple, single-lag, Ricker equation: $N_{t-1} = N_t \exp[\tau(1-N_t)]$, with $\tau = 3.50$, for which the model is known to be chaotic (Ricker, 1954; May, 1976; Kadanoff, 1983; Stone, 1993). One thousand points were taken after the initial 5000 points were discarded. Noise was added at three levels to each value of this series by adding a uniform random number on $(0, \alpha)$, where α was selected as, respectively, 0.125, 0.5 and 1.0, for small, moderate and large noise levels. The Lyapunov exponents were estimated from the first 30, 50, 100 and 1000 points from this extracted series, using the Jacobian matrix derived from the Ricker equation.

Results

The results of the cross-validations revealed that models with one, two or three lags had similar values for the PVA for most species except *M. ascalonicus*, *P. alchemillata* and *X. montanata* (Table 3).

The Lyapunov exponents estimated from the direct method were significantly and positively correlated with those from the indirect method in both aphid and moth time series (Fig. 4). However, for the simulated data from the Ricker model, a decrease in the series length seriously affected the Lyapunov estimates for the direct method. Whilst use of the indirect method obtained accurate exponents at all but the largest level of noise, the direct method performed less well, especially when the time series contained a moderate or large level of noise (Table 4). Therefore only the indirect method is considered further in this paper.

The Lyapunov exponents from the randomly permuted series under hypothesis I were normally distributed, but the distribution of exponents under hypothesis II was skewed to the right. The means of these exponents were smaller under hypothesis I than II at all five sites and the majority of exponents under hypothesis II were between -0.6 and zero (Table 5). For the actual data, positive exponents were obtained only from lag-three models for both aphid and moth series,

but none was significantly large under either hypothesis (Tables 6 and 7). For *B. helichrysi*, exponents were positive at two sites and significantly negative at Broom's Barn under both hypotheses. All exponents obtained for *H. lactucaae* were close to zero. Those for *E. abietinum*, *M. ascalonicus* and *M. persicae* were all negative, and significantly so ($P < 0.05$) under hypothesis II for *E. abietinum* at three sites and *M. ascalonicus* at two sites (Table 6). For *M. dirhodum* estimates of λ were significantly negative under hypothesis II at four sites, but not at Wye. For the moths (Table 7), estimates for all species were negative except for *A. monoglypha* at three sites, for *P. alchemillata* at Kielder and for *X. montanata* at Spurn Head ($P < 0.05$). For both aphid and moth species, hypothesis II yielded more significant negative estimates, especially for the one-lag model (Tables 6 and 7).

For the simulated data from the Turchin-Taylor model, an increase in series length decreased the values of the estimated Lyapunov exponents. As the length increased to 100, the values approached zero, but remained positive (Table 8), a similar result to that found by Turchin & Taylor (1992). As expected, the number of permutations had no effect. All time series with fifty points or greater yielded significant results with the randomization tests.

Discussion

Turchin & Millstein (1993) demonstrated that the Jacobian method was better than the trajectory method for quantifying the dynamic behaviour of short, noisy, time series. The present study shows that there are apparent differences between estimated Lyapunov exponents using the direct and indirect Jacobian methods, especially from the three-lag models, although the values from both methods were highly correlated. However, the crucial evidence informing a choice between the methods is the unreliability of the direct method for the Ricker model when noise is present. Thus the present authors support Turchin & Millstein's (1993) and Ellner & Turchin's (1995) use of the indirect method to estimate Lyapunov exponents, for ecological data in the form of counts.

Results from non-linear time series analysis are subject to errors due both to exogenous noise within the time series and in the functional form of the model assumed. Positive estimates of Lyapunov exponents arising from reconstructions of the endogenous dynamics of time series data are now seen to be insufficient to characterize the series as chaotic, so previous

Table 5. Samples of distributions of values of estimated Lyapunov exponents, $\hat{\lambda}$, of 1000 permuted series for the aphid *Myzus ascalonicus* at five sites under hypotheses I and II.

Range of $\hat{\lambda}$ value	Sites									
	Rothamsted		Wye		Broom's Barn		Newcastle		Dundee	
	I	II	I	II	I	II	I	II	I	II
<-3.8	5	0	6	0	7	0	9	0	5	0
-3.8~-3.6	5	0	4	0	3	0	5	0	2	0
-3.6~-3.4	4	0	3	0	8	0	5	0	3	1
-3.4~-3.2	11	0	10	0	8	0	7	0	6	0
-3.2~-3.0	15	0	15	1	19	0	15	0	6	0
-3.0~-2.8	22	0	16	0	28	1	13	0	20	0
-2.8~-2.6	25	0	25	1	29	0	8	1	18	0
-2.6~-2.4	33	0	31	0	57	2	33	0	21	0
-2.4~-2.2	50	0	61	1	58	1	34	0	34	0
-2.2~-2.0	60	1	83	1	101	2	58	1	54	0
-2.0~-1.8	82	3	97	2	117	1	82	1	65	1
-1.8~-1.6	113	3	130	5	122	3	76	3	86	2
-1.6~-1.4	126	2	146	12	147	10	84	6	82	8
-1.4~-1.2	104	10	130	16	114	30	101	8	87	9
-1.2~-1.0	129	23	111	32	90	26	113	23	122	17
-1.0~-0.8	91	47	66	61	60	58	133	46	105	43
-0.8~-0.6	74	85	51	87	29	93	65	82	99	90
-0.6~-0.4	35	199	13	199	3	187	85	179	74	191
-0.4~-0.2	15	382	2	356	0	384	44	359	67	352
-0.2~-0.0	0	245	0	226	0	202	21	291	29	285
0.0~0.2	1	0	0	0	0	0	7	0	12	1
>0.2	0	0	0	0	0	0	2	0	3	0
Mean $\hat{\lambda}$	-1.565	-0.398	-1.655	-0.443	-1.779	-0.453	-1.375	-0.383	-1.291	-0.383

work (Turchin & Taylor, 1992; Hanski *et al.*, 1993a; Perry *et al.*, 1993) requires re-evaluation. Confidence limits have been developed for Lyapunov exponent estimates by using replicated laboratory populations (Turchin, 1991b), populations from different geographical locations (Turchin, 1993) or bootstrap techniques (Falck *et al.*, 1995) to try to overcome the uncertainties involved in the analysis of relatively short series. However, this study shows that estimates of Lyapunov exponents may be very different at different localities, especially for species with a three-lag model (Tables 6 and 7). The second randomization test developed here employs a null hypothesis (II) which may be questionable, because most species display density-dependent dynamics, but it provides some confidence to aid the interpretation of small positive or negative exponents. Data from several sites have been used to strengthen the conclusions from this test and as an examination of the consistency and robustness of the estimated Lyapunov exponents. Longer time series with more than fifty points may be needed to obtain much greater confidence. The time series analyses yielded only few positive Lyapunov exponents, mainly in aphid series with lengths between twenty-four and twenty-eight values. None of these was large enough to provide evidence of chaotic dynamics. These results indicate that evidence of chaotic dynamics in aphid and moth populations may be difficult to obtain at the spatial and temporal scales studied.

For the data studied here, complex models with two or three lags were appropriate only for holocyclic aphid species or anholocyclic species with three migratory periods per year, while one-lag models were appropriate only for anholocyclic species with a single migratory period per year. This may suggest that species with more complex life-history strategies and migratory patterns may undergo more complex population regulation. Although high levels of the incidence of density-dependence and delayed density-dependence were found from 5715 time series of both aphid and moth species by Woiwod & Hanski (1992), it remains unclear whether the differences between life history strategies in aphids and moths are related to their strength of density-dependence (Hanski & Woiwod, 1993). Further studies are necessary to verify this theory, as the selection of the appropriate complexity of a model to best describe the underlying dynamics of a time series is crucial in defining its dynamic type. The use of more complex models than necessary is likely to yield estimates of exponents biased towards positive values (Table 6, and P. Turchin, personal communication).

Aphids usually have complex life histories. In addition to the many complications arising from the switch between sexual and asexual reproduction, often involving a change of host plant, and the production of winged and wingless forms, aphids have a telescoping of generations whereby live offspring are produced that already have the next generation developing

Table 6. Estimated Lyapunov exponents, λ , and results of randomization tests on the time series of the six aphid species (indirect method). The percentages, p_1 and p_2 , show how many simulated series under hypothesis I and II, respectively, had estimated Lyapunov exponents that were less than λ for the observed series.

Species		Site				
		Rothamsted	Wye	Broom's Barn	Newcastle	Dundee
<i>Brachycaudus helichrysi</i> (lag three model)	λ	0.113	0.109	-0.528	-0.087	-0.018
	p_1	67.5	77.2	0.0	33.0	47.7
	p_2	68.0	72.8	0.0	20.8	37.1
<i>Elatobium abietinum</i> (lag one model)	λ	-0.878	-1.392	-5.376	-1.537	-1.030
	p_1	89.2	58.2	0.0	65.9	80.6
	p_2	10.1	1.8	0.0	1.3	6.9
<i>Hyperomyzus lactucae</i> (lag three model)	λ	-0.039	-0.107	-0.070	0.027	0.072
	p_1	63.5	27.4	58.3	53.6	75.8
	p_2	43.0	18.9	37.8	56.5	62.8
<i>Myzus ascalonicus</i> (lag one model)	λ	-0.882	-1.145	-1.755	-0.481	-0.731
	p_1	84.5	79.6	47.2	89.1	75.3
	p_2	6.7	4.5	0.8	25.3	10.8
<i>Metopolophium dirhodum</i> (lag one model)	λ	-1.115	-0.701	-1.405	-1.970	-1.278
	p_1	91.1	99.0	68.7	26.7	80.3
	p_2	4.5	22.3	1.5	0.2	1.4
<i>Myzus persicae</i> (lag two model)	λ	-0.476	-0.148	-0.152	-0.202	-0.302
	p_1	45.4	85.9	94.2	74.3	68.8
	p_2	12.1	67.2	75.3	57.8	36.2

Table 7. Estimated Lyapunov exponents, λ , and results of randomization tests on the time series of the four moth species (indirect method). The percentages, p_1 and p_2 , show how many simulated series under hypothesis I and II respectively, had estimated Lyapunov exponents that were less than λ for the observed series, — indicates values not calculated as time series failed to meet minimum criteria (see text).

Species		Site					
		Alice Holt	Geescroft	Sutton Bonnington	Spurn Head	Kielder	Elgin
<i>Apamea monoglypha</i> (lag one model)	λ	—	-0.926	-1.091	-1.646	-1.515	-1.781
	p_1	—	96.5	84.9	48.3	59.6	44.5
	p_2	—	5.4	7.2	1.2	1.9	1.3
<i>Cerapteryx graminis</i> (lag one model)	λ	-0.584	—	—	—	-0.829	-0.518
	p_1	96.5	—	—	—	91.3	100.0
	p_2	24.6	—	—	—	11.6	19.4
<i>Perizoma alchemillata</i> (lag three model)	λ	-0.123	0.042	—	—	-0.330	-0.007
	p_1	69.5	68.3	—	—	3.9	73.9
	p_2	24.5	21.1	—	—	1.4	60.7
<i>Xanthorhoe montanata</i> (lag one model)	λ	-1.434	—	-0.989	-1.231	—	-0.800
	p_1	63.5	—	79.2	62.8	—	91.9
	p_2	10.0	—	7.4	3.2	—	12.5

inside them. Under these circumstances it is practically impossible to separate generations as might be required for the assumptions of certain restrictive population-dynamic models, although these assumptions may usually be rewritten to give a fully valid analysis. Survey suction traps such as those used here monitor the migrating aerial phase of the aphid life cycle

and are known to give a very good representation of general field population levels over a considerable area (Tatchell, 1991). Hence, the use of annual suction trap catches as a measure of overall annual population size for analyses relating several successive years is not unreasonable for most purposes and was used in this way in previous dynamic studies with

Table 8. Effects of series length and the number of randomizations on estimated Lyapunov exponents, $\hat{\lambda}$, from a known chaotic time series under hypotheses I and II. The percentages show how many simulated series had estimated Lyapunov exponents less than the value of $\hat{\lambda}$.

Series length	$\hat{\lambda}$	Hypothesis	Number of permutations (%)		
			1000	3000	10 000
25	0.165	I	89.1	88.0	87.8
		II	83.8	84.3	83.4
30	0.163	I	96.7	96.1	96.9
		II	93.0	92.8	92.8
50	0.066	I	99.8	99.8	99.7
		II	96.4	95.6	95.7
100	0.035	I	100	100	100
		II	99.9	99.9	99.9

these data (Woiwod & Hanski, 1992; Hanski & Woiwod, 1993). The univoltine moth species chosen as examples in this analysis conform much more closely to the assumptions made in commonly used population-dynamic models. However, even here the samples do not measure density directly, but provide a correlate that combines density and activity. The resulting figure seems to give a reasonably accurate measure of population levels in the immediate vicinity of the trap, although an exact definition of the area from which the sample is drawn or its calibration with absolute population size is not possible currently.

Non-linearity is necessary, although not sufficient, for producing chaotic dynamics (Schuster, 1988). Statistical methods have been developed to test for the non-linearity of a time series (Chan & Tong, 1990; Tong, 1990; Thieler *et al.*, 1992; Terasvirta, 1994). For instance, Falck *et al.* (1995) used the method of Chan & Tong (1990) on thirty-four Holarctic microtine rodent time series and found that nineteen were linear. The methods to estimate Lyapunov exponents described here may be used independently of these.

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References

- Bascompte, J. & Sole, R.V. (1994) Spatially induced bifurcations in single-species population dynamics. *Journal of Animal Ecology*, **63**, 256–264.
- Berryman, A. (1992) On choosing models for describing and analyzing ecological time series. *Ecology*, **73**, 694–698.

- Box, G.E.P. & Jenkins, G.M. (1976) *Time Series Analysis: Forecasting and Control*. Holden Day, Oakland, California.
- Chan, K.S. & Tong, H. (1990) On likelihood ratio tests for threshold autoregression. *Journal of the Royal Statistical Society Series B*, **52**, 469–476.
- Efron, B. & Tibshirani, R. (1986) Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Statistical Science*, **1**, 54–77.
- Ellner, S. & Turchin, P. (1995) Chaos in a 'noisy' world: new methods and evidence from time series analysis. *American Naturalist*, **145**, 343–375.
- Ellner, S., Gallant, A.R., McCaffrey, D. & Nychka, D. (1991) Convergence-rates and data requirements for jacobian-based estimates of Lyapunov exponents from data. *Physics Letters A*, **153**, 357–363.
- Emmett, A. M. & Heath, J. (1991) *The Moths and Butterflies of Great Britain and Ireland*. Vol. 7, Part 2. Harley Books, Essex.
- Falck, W. M., Bjornstad, O. N. & Stenseth, N.C. (1995) Bootstrap estimated uncertainty of the dominant Lyapunov exponent for Holarctic microtine rodents. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **261**, 159–165.
- Genstat 5 Committee (1993) *Genstat 5 Reference Manual*. Oxford University Press, Oxford.
- Hanski, I. & Woiwod, I.P. (1993) Mean-related stochasticity and population variability. *Oikos*, **67**, 29–39.
- Hanski, I., Turchin, P., Korplmaki, E. & Henttonen, H. (1993a) Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature*, **364**, 232–235.
- Hanski, I., Woiwod, I.P. & Perry, J.N. (1993b) Density dependence, population persistence, and largely futile arguments. *Oecologia*, **95**, 595–598.
- Hassell, M.P., Lawton, J.H. & May, R.M. (1976) Patterns of dynamical behaviour in single-species populations. *Journal of Animal Ecology*, **45**, 471–486.
- Hastings, A., Hom, C.L., Ellner, S., Turchin, P. & Godfray, H.C.J. (1993) Chaos in ecology: is mother nature a strange attractor? *Annual Review of Ecology and Systematics*, **24**, 1–33.
- Holyoak, M. (1993) The frequency of detection of density dependence in insect orders. *Ecological Entomology*, **18**, 339–347.
- Kadanoff, L.P. (1983) Simple mathematical systems exhibit complex patterns of behaviour that can serve as models for chaotic behavior, including perhaps turbulent flow in real hydrodynamic systems. *Physics Today*, **36** (12), 46–53.
- Logan, J.A. & Allen, J.C. (1992) Nonlinear dynamics and chaos in insect populations. *Annual Review of Entomology*, **37**, 455–477.

- May, R.M. (1974) Biological populations with non-overlapping populations: stable points, stable cycles, and chaos. *Science*, **186**, 645–647.
- May, R.M. (1976) Simple mathematical models with very complicated dynamics. *Nature*, **261**, 459–467.
- May, R.M. (1987) Chaos and the dynamics of biological populations. *Proceedings of the Royal Society of London Series A-Mathematical and Physical Sciences*, **413**, 27–44.
- Nychka, D., Ellner, S., Gallant, A.R. & McCaffrey, D. (1992) Finding chaos in noisy systems. *Journal of the Royal Statistical Society Series B-Methodological*, **54**, 399–426.
- Perry, J.N. (1994) Chaotic dynamics can generate Taylor's power law. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **257**, 221–226.
- Perry, J.N., Woiwod, I.P. & Hanski, I. (1993) Using response-surface methodology to detect chaos in ecological time series. *Oikos*, **68**, 329–339.
- Pollard, E., Lakhani, K.L. & Rothery, P. (1987) The detection of density dependence from a series of annual censuses. *Ecology*, **68**, 2046–2055.
- Renshaw, E. (1994) Chaos in biometry. *IMA Journal of Mathematics Applied in Medicine and Biology*, **11**, 17–44.
- Ricker, W.E. (1954) Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, **11**, 559–623.
- Rohani, P. & Miramontes, O. (1995) Host-parasitoid metapopulations: the consequences of parasitoid aggregation on spatial dynamics and searching efficiency. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **260**, 335–342.
- Rohani, P., Miramontes, O. & Hassell, M.P. (1994) Quasiperiodicity and chaos in population models. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **258**, 17–22.
- Schuster, H.G. (1988) *Deterministic Chaos, an Introduction*. VCH, Weinheim, Germany.
- Sinclair, A.R.E. (1989) Population regulation in animals. *Ecological Concepts* (ed. by J. M. Cherratt), pp. 197–241. Blackwell Scientific Publications, Oxford.
- Sole, R.V. & Bascompte, J. (1994) Ecological chaos. *Nature*, **367**, 418.
- Stone, L. (1993) Period-doubling reversals and chaos in simple ecological models. *Nature*, **365**, 617–620.
- Tatchell, G.M. (1991) Monitoring and forecasting aphid problems. *Aphid-Plant Interactions: Populations to Molecules* (ed. by D.C. Peters and J.A. Webster), pp. 215–230. Oklahoma Agricultural Experiment Station, Miscellaneous Publication 132, Oklahoma.
- Terasvirta, T. (1994) Testing linearity and modeling nonlinear time series. *Kybernetika*, **30**, 319–330.
- Theiler, J., Eubank, S., Longtin, A., Galdrikian, B. & Farmer, J.D. (1992) Testing for nonlinearity in time-series – the method of surrogate data. *Physica D*, **58**, 77–94.
- Tong, H. (1990) *Non-linear Time Series Analysis*. Oxford Science Publication, Oxford.
- Turchin, P. (1990) Rarity of density dependence or population regulation with lags? *Nature*, **344**, 660–663.
- Turchin, P. (1991a) Nonlinear modeling of time series data: limit cycles and chaos in forest insects, voles, and epidemics. *Chaos and Insect Ecology* (ed. by J.A. Logan and F.P. Hain), pp. 39–62. Virginia Experiment Station, information series 91–3 edn. Blacksburg, Virginia.
- Turchin, P. (1991b) Reconstructing endogenous dynamics of a laboratory *Drosophila* population. *Journal of Animal Ecology*, **60**, 1091–1098.
- Turchin, P. (1993) Chaos and stability in rodent population-dynamics – evidence from nonlinear time-series analysis. *Oikos*, **68**, 167–172.
- Turchin, P. & Millstein, J.A. (1993) *EcoDyn/RSM Response Surface Modeling of Nonlinear Ecological Dynamics I. Theoretical Background*. Applied Biomathematics, Setauket, New York.
- Turchin, P. & Taylor, A.D. (1992) Complex dynamics in ecological time-series. *Ecology*, **73**, 289–305.
- Wichmann, B.A. & Hill, I.D. (1982) An efficient and portable pseudo-random number generator. *Applied Statistics*, **31**, 188–190.
- Woiwod, I.P. & Hanski, I. (1992) Patterns of density dependence in moths and aphids. *Journal of Animal Ecology*, **61**, 619–629.
- Woiwod, I.P. & Harrington, R. (1994) Flying in the face of change: the Rothamsted Insect Survey. *Long-term Experiments in Agricultural and Ecological Sciences* (ed. by R. A. Leigh and A. E. Johnston), pp. 321–342. CAB International, Wallingford.
- Wolf, A., Swift, J.B., Swinney, H.L. & Vastano, J.A. (1985) Determining Lyapunov exponents from a time series. *Physica*, **16D**, 285–317.
- Zhou, X., Harrington, R., Woiwod, I.P., Perry, J.N., Bale, J.S. & Clark, S.J. (1996) Effects of temperature on aphid phenology. *Global Change Biology*, **1**, 303–313.

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