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# Cycles, chaos, and noise in predator–prey dynamics

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## Abstract

In contrast to the single species models that were extensively studied in the 1970s and 1980s, predator–prey models give rise to long-period oscillations, and even systems with stable equilibria can display oscillatory transients with a regular frequency. Many fluctuating populations appear to be governed by such interactions. However, predator–prey models have been poorly studied with respect to the interaction of nonlinear dynamics, noise, and system identification. I use simulated data from a simple host–parasitoid model to investigate these issues. The addition of even a modest amount of noise to a stable equilibrium produces enough structured variation to allow reasonably accurate parameter estimation. Despite the fact that more-or-less regular cycles are generated by adding noise to any of the classes of deterministic attractor (stable equilibrium, periodic and quasiperiodic orbits, and chaos), the underlying dynamics can usually be distinguished, especially with the aid of the mechanistic model. However, many of the time series can also be fit quite well by a wrong model, and the fitted wrong model usually misidentifies the underlying attractor. Only the chaotic time series convincingly rejected the wrong model in favor of the true one. Thus chaotic population dynamics offer the best chance for successfully identifying underlying regulatory mechanisms and attractors. © 2000 Elsevier Science Ltd. All rights reserved.

## 1. Introduction

Ecological population dynamics are inevitably 'noisy'. Even in systems dominated by a few strong feedbacks, there are exogenous perturbations from weather-driven environmental variability and from the network of species that interact weakly with the population. Thus, despite the fact that many simple ecological models easily generate chaos [1], it has proven difficult to unequivocally distinguish chaos from noise or noisy periodicity in real ecological data. Analyses that explicitly take into account dynamical noise in the time series suggest that most ecological populations are not chaotic [2], but there have only been limited tests of these techniques with ecological models [2,3].

As a result of these difficulties, ecologists have largely abandoned the search for chaos. Instead, new efforts focus on identifying the biological processes underlying the dynamics by fitting simple mechanistic models to the time series data [4–8]. An interesting philosophical and practical question becomes, does strongly nonlinear dynamics in general, and chaos in particular, improve our chances of correctly identifying the underlying mechanism? This certainly seems to be true in one-dimensional systems [9]. However, many oscillating populations display long-period cycles characteristic of predator–prey dynamics [10]. Models of predator–prey systems are quite different from one-dimensional maps. The equilibrium is a focus rather than a node, and so displays oscillatory transients even when stable. The equilibrium is destabilized by a Hopf bifurcation and the system follows the torus route to chaos. Thus, all forms of attractors (stable equilibrium, periodic and quasiperiodic orbits, and chaos) may display oscillations with similar characteristic frequencies. In the presence of noise it may be particularly difficult to distinguish these attractors.

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The interaction of nonlinear dynamics and noise, and the resulting effects on our ability to identify both the dynamics and the underlying mechanisms, has never been systematically examined in consumer–resource systems. In the paper I use a simple host–parasitoid model to address three questions:
1. Do the oscillatory transients allow us to identify the model at a noisy equilibrium?
2. Do the oscillatory transients confound efforts to distinguish different forms of dynamics?
3. Does chaos provide any 'benefit' from the standpoint of system identification?

## 2. The model and simulated data

To generate simulated data, I used a host–parasitoid model initially introduced by Beddington, Free, and Lawton [11], henceforth denoted BFL. A parasitoid is a special form of insect predator that lays an egg inside a living host organism. Once the egg hatches, the developing parasitoid larva consumes the host from the inside, and emerges once the host is consumed. If multiple eggs are laid in the same host, there is usually contest competition among the developing larvae, such that at most one parasitoid emerges from each parasitized host. If parasitoids choose hosts at random for oviposition, then the fraction of hosts escaping parasitism should be the zero term in a Poisson distribution; all other hosts produce parasitoids instead. Such models are unstable in the absence of host density-dependence or other regulating factors [12]. The BFL model includes host density dependence:

$$H_{t+1} = H_t e^{r(1-H_t)-aP_t}$$

$$P_{t+1} = H_t(1 - e^{-aP_t}),$$

where $H_t$ and $P_t$ are the host and parasitoid densities (the host density is scaled so that the carrying capacity is one), $r$ is the intrinsic growth rate of the host, and $a$ is the attack rate of the parasitoid.

The 'coexistence equilibrium' (in which both host and parasitoid have densities greater than zero) in this and similar models is a focus over a majority of the parameter space in which it is stable. This equilibrium can lose stability through a number of different bifurcations [13], but the only one that maintains persistence of both species is a Hopf bifurcation, leading to long-period cycles (4–20 generations). A number of forest insect pests display such long-period cycles (Fig. 1), and parasitoids have been proposed as a general mechanism for producing those patterns [14].

Using the bifurcation diagram in Fig. 1 of [11] as a guide, I selected parameters associated with four different attractors: a stable focus, a quasiperiodic orbit, a phase-locked period-five orbit, and chaos (Table 1). I added dynamic noise to the simulation by multiplying both state variables by independent log-normally distributed random numbers at each generation: $z_t = \exp(\sigma x_t)$, where $x_t$ is normally distributed with variance one. Independent random numbers were applied to the host and parasitoid. I used four noise levels: $\sigma = 0, 0.01, 0.1$, and $0.3$. At the highest noise level, typical perturbations range from 0.5 to 1.8; larger variances resulted in rapid extinction of one or both species.

I generated time series of 50 generations for each set of parameters (Fig. 2). Notice that in the presence of noise, the 'stable focus' displays fairly regular oscillations as the trajectory spirals back from large perturbations. Also, at the largest noise level it would be difficult to visually distinguish among the putative attractors – they all look like 'noisy periodicity', with the chaotic simulation being somewhat more erratic. These noisy simulations look qualitatively similar to some of the insect data portrayed in Fig. 1, and may be a real challenge to distinguish from one another.

## 3. Lyapunov exponents

Recent efforts to characterize the dynamics of short noisy time series have focussed mainly on the Lyapunov exponent, in contrast to studies in the 1980s that also attempted to estimate the correlation dimension. The most successful of these techniques use some variant of the following algorithm:
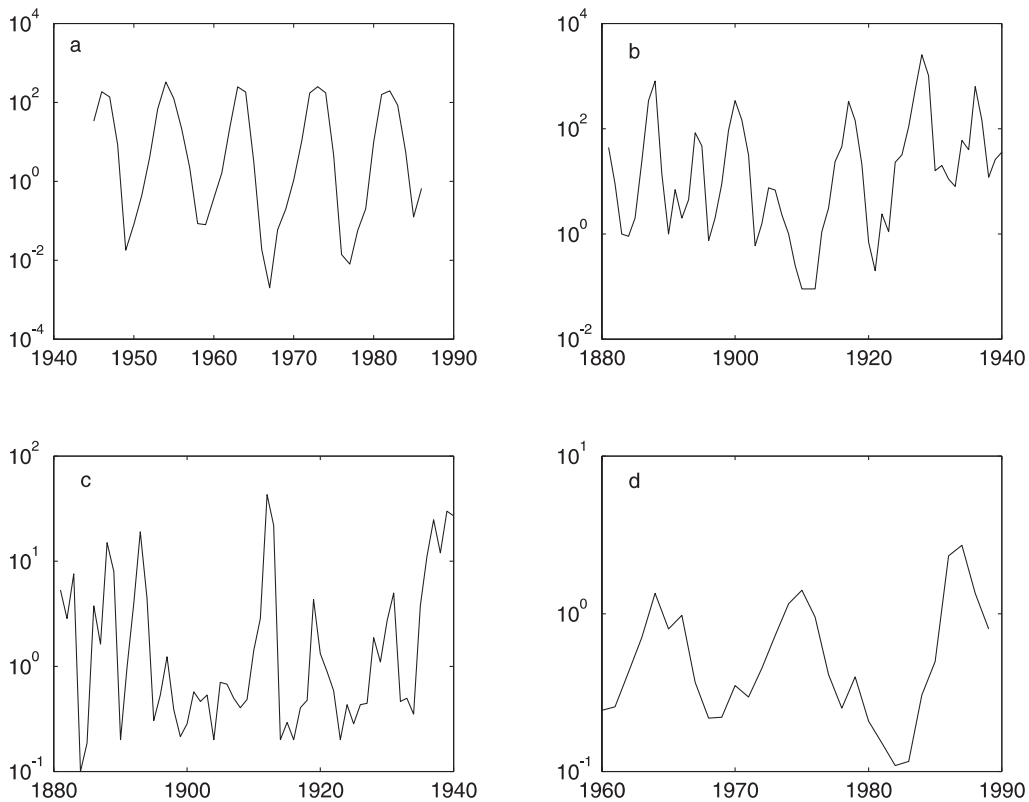
Fig. 1. Long-period oscillations in the density of several forest insect species, all with one-year generation times: (a) Larch budmoth (*Zeiraphera diniana*) [28]; (b) pine looper moth (*Bupalus piniaria*) [29]; (c) pine beauty moth (*Panolis flammea*) [29]; (d) winter moth (*Operophthera brumata*) [30].

Table 1
Parameter values used for generating simulated data from the BFL model and their associated attractors

| Attractor | $r$ | $a$ |
|---|---|---|
| Stable focus | 2.0 | 3.0 |
| Quasiperiodic | 1.8 | 4.0 |
| Periodic (phase locked) | 2.2 | 4.5 |
| Chaotic | 2.7 | 5.0 |

1. Embed the time series using lagged values of the observations: $X_t = (x_t, x_{t-1}, x_{t-2}, \ldots)$.
2. Use nonlinear regression to fit a parametric or nonparametric model, of the form $x_{t+1} = f(X_t)$, to the data. These models include generalized polynomials [15], neural networks [16], and thin plate splines [17].
3. Evaluate the Jacobian of $f$ at each data point $X_t$, and use the eigenvectors and eigenvalues to calculate the average Lyapunov exponent along the trajectory.

The subtleties are in the choice of embedding and the procedures for nonlinear regression.

### 3.1. Model-based estimates

To obtain a baseline of 'truth', I performed Jacobian-based Lyapunov exponent calculations using the BFL model and the true parameter values, following the classic algorithm of Wolf et al. [18]. I applied the Gram–Schmidt reorthonormalization at every time step, and evaluated the average Lyapunov exponent after 5000 model iterations, at which point the estimate had converged to three or more decimal places. I used a slightly modified version of the implementation in Dynamical Software [19,20].
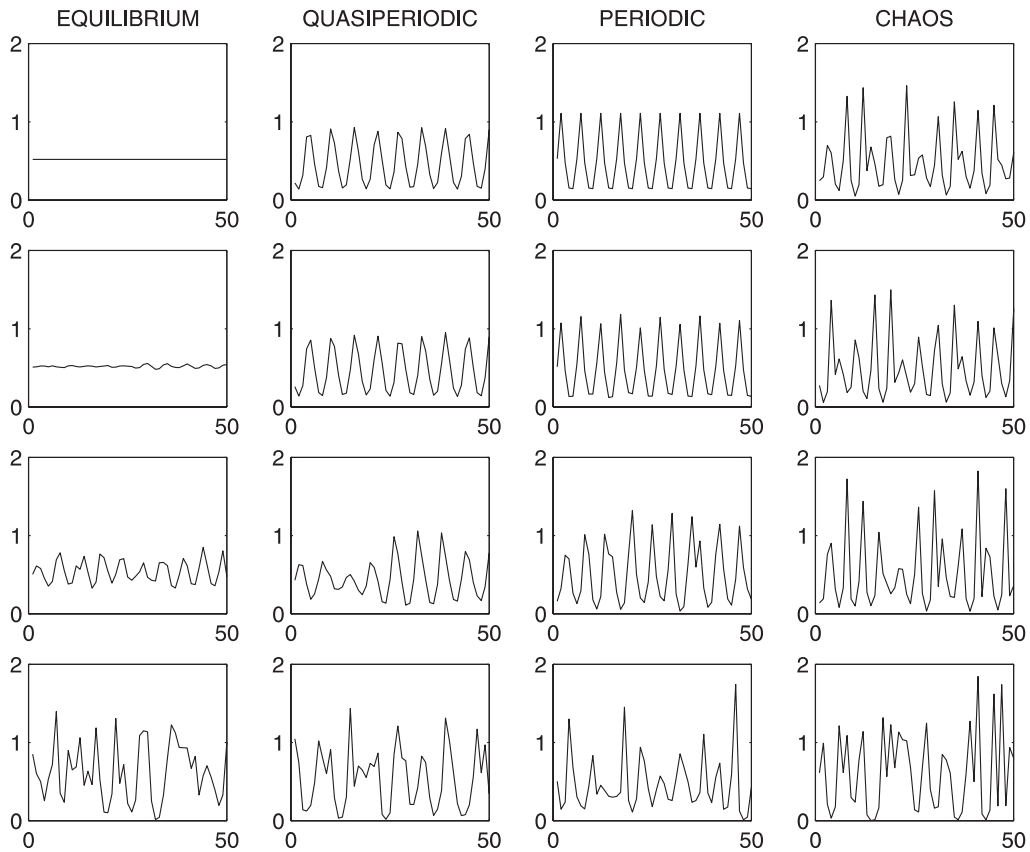
Fig. 2. Simulated time series from the BFL model. Each column represents a single deterministic attractor, with parameters *a* and *r* from Table 1. Each row is a different noise variance: in order from the top, $\sigma = 0$, 0.01, 0.1, and 0.3.

Table 2
Model-based Lyapunov exponent estimates from the BFL model using the parameters in Table 1

| Noise | Focus | Quasiperiodic | Periodic | Chaos |
|---|---|---|---|---|
| 0 | −0.045 | −0.0001 | −0.032 | 0.20 |
| 0.01 | −0.047 | −0.001 | −0.072 | 0.21 |
| 0.10 | −0.14 | −0.040 | 0.039 | 0.20 |
| 0.30 | −0.10 | 0.052 | 0.11 | 0.24 |

In the absence of noise, the Lyapunov exponents are as expected (Table 2): negative for the focus and periodic orbit, zero for the quasiperiodic orbit, and positive for chaos. With increasing noise, these estimates start to vary. This is to be expected: the trajectory is exploring new regions of the phase space, where the Jacobian may have characteristics quite different from the region of the attractor. A notable feature of these results is that whereas the focus and chaotic orbit have consistently negative and positive exponents, respectively, the exponents of the quasiperiodic and periodic orbits become more negative at small noise levels and then become positive at larger noise levels, suggesting that there is qualitatively more heterogeneity in the Jacobian in this region of the parameter space.

### 3.2. Estimates from time series

I analyzed the time series in Fig. 2 with a neural network algorithm [2,21] that has recently been ported to S-PLUS [22,23]. There are two fitting parameters that need to be chosen: the embedding dimension (*d*) and the number of independent units in the neural net (*k*). Larger values of both quantities increase the

Table 3
Parameters of the neural network models with the best GCV(2) scores as fitted to each simulated time series

| $\sigma$ | Focus | | Quasiperiodic | | Periodic | | Chaos | |
|------|-----|-----|-----|-----|-----|-----|-----|-----|
| | $d$ | $k$ | $d$ | $k$ | $d$ | $k$ | $d$ | $k$ |
| 0.00 | | | 2 | 5 | 2 | 2 | 2 | 5 |
| 0.01 | 2 | 1 | 4 | 2 | 2 | 3 | 2 | 4 |
| 0.10 | 3 | 1 | 3 | 1 | 2 | 2 | 3 | 3 |
| 0.30 | 2 | 1 | 3 | 1 | 2 | 1 | 3 | 1 |

Table 4
Lyapunov exponents estimated by the neural network model for the simulated time series[a]

| $\sigma$ | Focus | Quasiperiodic | Periodic | Chaos |
|------|-----|-----|-----|-----|
| 0 | | 0.006 | −0.011 | 0.154 |
| | | (0.006, 0.007) | (−0.206, 0.028) | (0.154, 0.155) |
| 0.01 | −0.030 | −0.022 | 0.038 | 0.130 |
| | (−0.098, 0.047) | (−0.065, 0.101) | (0.024, 0.049) | (0.119, 0.156) |
| 0.10 | −0.048 | 0.023 | 0.194 | 0.254 |
| | (−0.203, 0.004) | (−0.013, 0.052) | (−0.344, 0.242) | (0.026, 0.380) |
| 0.30 | −1.559 | −0.459 | −0.352 | −0.219 |
| | (−1.845, −1.468) | (−0.634, −0.310) | (−0.408, −0.271) | (−0.301, −0.204) |

[a] 95% confidence intervals (based on 500 re-fits) in parentheses.

degrees of freedom of the model, and so will increase the goodness of fit. However, over-fitting will produce a function that is too 'wiggly' and has spurious variation in the Jacobian. Following [2], I used generalized cross validation with an overweighting factor of 2 (GCV(2)) to find the simplest model that adequately describes each time series; these are reported in Table 3. Notice that different models were selected for the different time series.

To improve the model-fitting, I log-transformed the time series before analyzing them. This normalizes the log-normal process noise and should eliminate most biases in the model estimation. At first glance it seems that this should produce inappropriate estimates the Lyapunov exponents, but the Lyapunov exponent is called a 'dynamical invariant' precisely because it is insensitive to smooth transformations of the state space.

I estimated the Lyapunov exponents for each of the time series using the model parameters in Table 3 (Table 4). Within the minimization routine, I used $200k$ 'rough fits' and $20k$ 'polished fits': the dependence on $k$ was to force the minimization routine to work harder at fitting the more complex models. I also estimated confidence intervals for the Lyapunov exponents (Table 4). These are calculated by finding fits of the neural network model that are nearly as good (based on normal approximation theory) as the best fit, and estimating the Lyapunov exponents with those fits [24]. The confidence intervals are based on 500 fits.

The quality of these estimates is mixed. The confidence interval covers the 'true' value (from Table 2) only for six cases: equilibrium at low and intermediate noise; quasiperiodicity at low noise; periodicity at no and intermediate noise; and chaos at intermediate noise. The estimates have the wrong sign in six of the fifteen cases, and the confidence intervals span zero in another six cases. The estimates fail spectacularly at the highest noise levels, always being extremely negative.

## 4. Model fitting

I next fitted the BFL model to the simulated time series, to discover whether the model parameters can be recovered empirically. If I were to use time series of both state variables, then this would be a simple regression exercise. However, I wished to use only the time series of hosts, as being representative of the problem faced when analyzing real ecological data. The problem becomes much harder, because there is no analytical formulation for the mapping between the embedded state space and the true state space.

One approach to this problem adapts the technique of nonlinear forecasting (NLF) [25,26,4,27,8]. In essence, the model is run with a trial set of parameters to generate an 'atlas' of points with which to forecast the data. The actual forecasts are based on local kernel regression:

$$\hat{y}_{t+1} = \sum_{i=1}^{n_a} x_{i+1} w(X_i, Y_i),$$

where $y$ is the time series to be fit, $x$ the model-generated atlas, $Y$ and $X$ their embeddings, $n_a$ the number of atlas points, and $w$ is a weighting function based on the distance between $X$ and $Y$.

The accuracy of the prediction is assessed with the 'prediction $r^2$' [27]:

$$r^2 = 1 - \frac{\sum(y_t - \hat{y}_t)^2}{\sum(y_t - \bar{y})^2}.$$

This has an unfortunate name, for the $r^2$ can be negative; a negative $r^2$ simply means that the predictions are *worse* than would be obtained by simply predicting the mean of the time series at each time step.

A nonlinear fitting algorithm is then applied to find the parameter values that maximize the prediction $r^2$.

For these analyses I used a weighting function that declined as a Gaussian function of the Euclidean distance [27], and used atlases 2000 points long. I used a two-dimensional embedding, and log-transformed the data and atlas before doing the forecasting.

## 4.1. Fitting results

In most cases the fits are fairly accurate, although the errors in the parameters increase (Fig. 3) and the $r^2$ decreases with increasing amounts of noise (Table 5). For the nonchaotic datasets, the fitting routine chooses noise levels similar to the true values: although this noise degrades the prediction accuracy at any given point in state space, it is required for the atlas to fully explore the state space. For the chaotic fits, the estimates of $\sigma$ are lower, as the chaotic trajectory traverses much of the state space anyway. The fits of $r$ to the equilibrium time series are worst at all noise levels, and the fits to the periodic time series are relatively poor at the higher noise levels. The chaotic time series receive the best estimates of $r$ at the higher noise levels, and along with the quasiperiodic time series receives the best estimates of $a$.

## 4.2. Dynamics of fitted models

To characterize the dynamics of the fitted model, I performed model-based Lyapunov exponent estimates using the fitted parameters. I analyzed both 'noisy' trajectories (using $\hat{\sigma}$) and deterministic trajectories ($\sigma$ set to zero). The former characterized the dynamics of the trajectories, comparable to Table 2, while the latter characterized the underlying attractor.

In all cases, the deterministic attractor was correctly identified, although the magnitude of the Lyapunov exponents was sometimes too large, especially at large noise amplitudes (Table 6). The noisy Lyapunov exponents were substantially in error only at the largest noise amplitude; noisy periodicity and quasiperiodicity predicted the wrong sign.

## 5. Fitting the wrong model

In the real world, we do not know the 'true' model, and indeed we may want to make inferences about mechanism based on which model best fits the data [8]. Under what circumstances can we be sure that the 'true' model will fit better than a wrong one? Furthermore, we may want to use our fitted model to make inferences about the underlying dynamics [4]; could accepting a 'wrong', but well-fitting, model lead to false dynamical conclusions?

To address these questions I used the nonlinear forecasting techniques described in the preceding section to fit a different host-parasitoid model to the simulations generated by the BFL model:
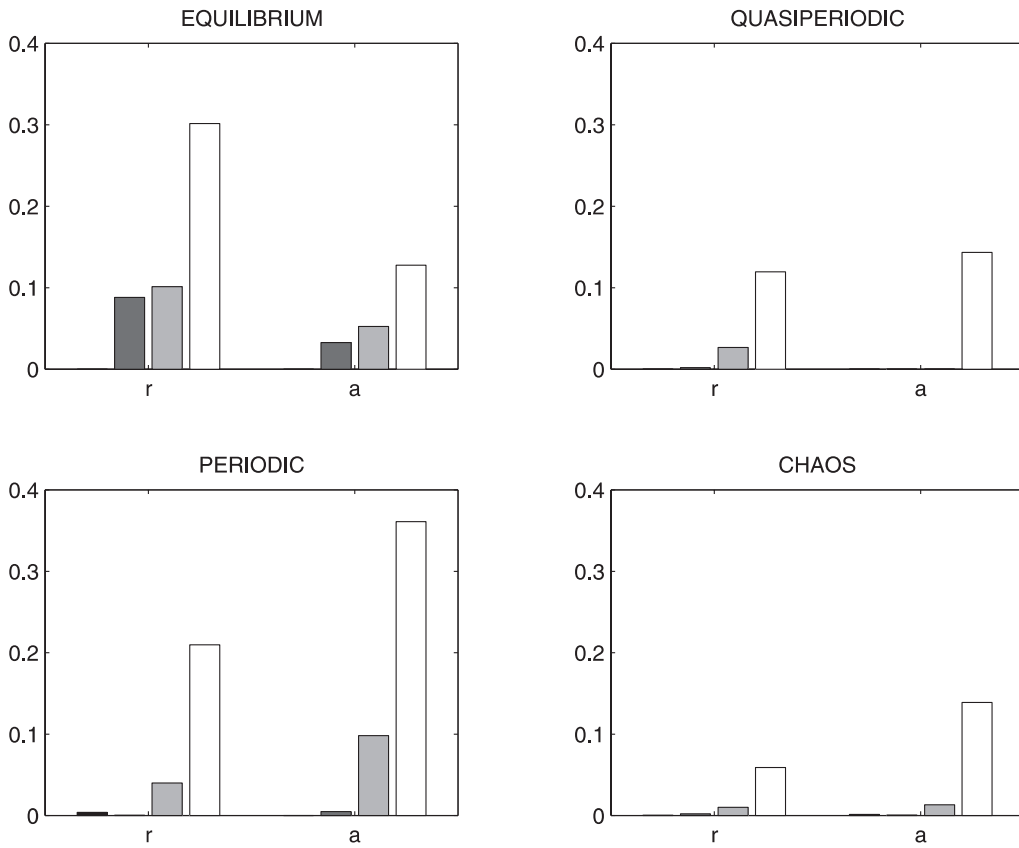
Fig. 3. Relative errors of the estimated values of $r$ and $a$ in the BFL model. Within each cluster, $\sigma$ increases from left to right.

Table 5
Prediction $r^2$ of the best fit BFL models applied to each of the BFL simulations

| $\sigma$ | Focus | Quasiperiodic | Periodic | Chaos |
|---|---|---|---|---|
| 0.00 | | 1.000 | 1.000 | 0.999 |
| 0.01 | 0.814 | 0.999 | 0.999 | 0.999 |
| 0.10 | 0.812 | 0.952 | 0.932 | 0.937 |
| 0.30 | 0.684 | 0.743 | 0.760 | 0.835 |

Table 6
Model-based Lyapunov exponent estimates from the BFL model using the estimated parameters from the nonlinear fitting[a]

| $\sigma$ | Focus | | Quasiperiodic | | Periodic | | Chaos | |
|---|---|---|---|---|---|---|---|---|
| | N | D | N | D | N | D | N | D |
| 0 | | | −0.000 | −0.000 | −0.074 | −0.031 | 0.204 | 0.210 |
| 0.01 | −0.072 | −0.065 | −0.000 | −0.000 | −0.100 | −0.022 | 0.208 | 0.212 |
| 0.10 | −0.179 | −0.081 | −0.046 | 0.000 | 0.080 | −0.020 | 0.207 | 0.213 |
| 0.30 | −0.073 | −0.113 | −0.003 | −0.001 | −0.090 | −0.068 | 0.314 | 0.293 |

[a] N (noisy) denotes estimates that used the estimated noise variance, while D (deterministic) denotes estimates that used a deterministic trajectory with the estimated values of $r$ and $a$.

$$H_{t+1} = H_t \exp\left( r\left(1 - \frac{H_t}{K}\right) - aP_t \right),$$

$$P_{t+1} = H_t \exp\left( r\left(1 - \frac{H_t}{K}\right) \right)(1 - e^{-aP_t}).$$

This model (which I denote HP2) differs from the BFL model only in the leading term of the parasitoid equation, and in the addition of the host scaling parameter $K$. Biologically this represents differences in the timing of parasitoid attack and host density dependence, which may be difficult to distinguish in field data. The scaling parameter is required because the relationship between the mean of the time series and the host carrying capacity differs between the two models.

## 5.1. Fitting results

The prediction $r^2$ for the HP2 model fitted to the periodic and quasiperiodic time series were only marginally worse than the $r^2$ from the BFL model (Table 7). For the equilibrium and chaotic series the HP2 model fit substantially worse than the BFL model.

## 5.2. Dynamics of fitted models

The fitted HP2 models find the correct underlying attractor for the equilibrium and quasiperiodic simulations, and get the correct sign of the noisy exponents in all but one case (Table 8). However, they fail spectacularly with the periodic and chaotic time series, misidentifying both the attractor and the noisy exponent at almost all noise levels. The periodic attractor is variously classified as quasiperiodic and chaotic, and the chaotic attractor is classified as stable, quasiperiodic, and chaotic.

It is important to ask whether this model, which appears biologically very similar to the BFL model, is in fact capable of reproducing the same range of dynamics. Certainly, it generates the full range of qualitative dynamics, as illustrated by the Lyapunov exponents in Table 8. However, it is conceivable that a chaotic time series from the HP2 model might look nothing like one from the BFL model. In Fig. 4 I plot simulated time series from the HP2 model, using the parameters from the best fit to each BFL time series. The shapes of the time series are very similar to those in Fig. 2, suggesting that the two models are capable of very similar dynamics, at least in the host population.

Inspection of Fig. 4 and Table 8 reveals some incongruities. For example, the fit to the chaotic time series with $\sigma = 0.1$ has a negative Lyapunov exponent, yet the time series fluctuates quite irregularly. This is not driven by noise, as the noise parameter in this fit is very small ($\sigma = 0.00006$). Instead, what is happening is that with these parameter values, the HP2 model has a very long chaotic transient (with a Lyapunov exponent of about 0.13) that eventually relaxes to a periodic orbit. The fitting, which was based on 2000 model iterations, was matching the chaotic transient to the data, whereas the Lyapunov exponent calcu-

Table 7
Prediction $r^2$ of the best fit HP2 models applied to each of the BFL simulations[a]

| $\sigma$ | Focus | Quasiperiodic | Periodic | Chaos |
|---|---|---|---|---|
| 0.00 | | 0.978 | 0.993 | 0.636 |
| 0.01 | −0.565 | 0.974 | 0.933 | 0.631 |
| 0.10 | 0.620 | 0.903 | 0.784 | 0.545 |
| 0.30 | 0.582 | 0.780 | 0.580 | 0.605 |

[a] Compare with Table 5.

Table 8
Model-based Lyapunov exponent estimates from the HP2 model using the estimated parameters from the nonlinear fitting[a]

| $\sigma$ | Focus | | Quasiperiodic | | Periodic | | Chaos | |
|---|---|---|---|---|---|---|---|---|
| | N | D | N | D | N | D | N | D |
| 0 | | | −0.001 | −0.001 | 0.163 | 0.171 | 0.054 | −0.001 |
| 0.01 | −0.093 | −0.099 | −0.002 | −0.001 | 0.017 | 0.016 | −0.019 | 0.000 |
| 0.10 | −0.071 | −0.055 | −0.036 | −0.000 | −0.036 | 0.000 | −0.120 | −0.188 |
| 0.30 | −0.102 | −0.021 | −0.005 | −0.001 | −0.015 | 0.000 | 0.115 | 0.066 |

[a] N (noisy) denotes estimates that used the estimated noise variance, while D (deterministic) denotes estimates that used a deterministic trajectory with the estimated values of $r$, $a$, and $K$.
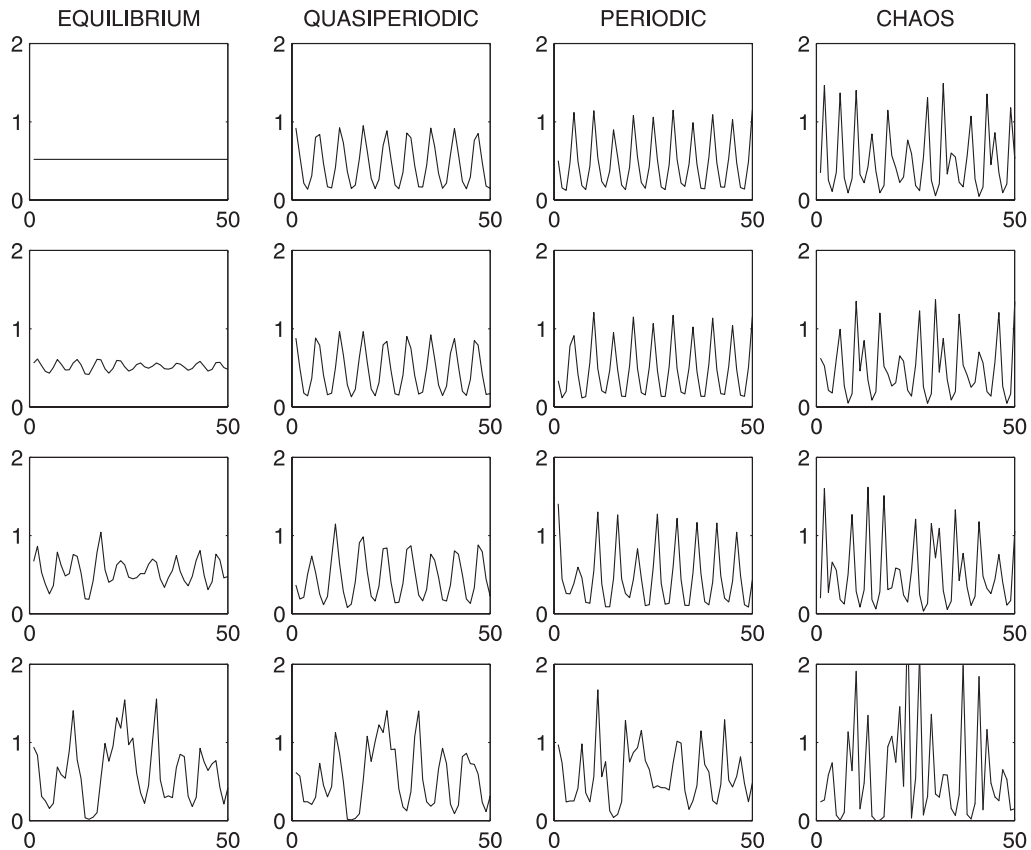
Fig. 4. Simulated time series from the HP2 model. Each panel shows a realization of the model with the parameter values from fitting the HP2 model to the corresponding time series in Fig. 2. The values displayed were preceded by 100 convergence iterations.

lation, which was based on 5000 iterations, was dominated by the periodic attractor. However, this effect of transient dynamics does not appear to affect the other fitted models, which have sufficiently high noise levels to keep the trajectory on a chaotic transient if one exists.

## 6. Discussion

The results of this analysis are somewhat promising. It is possible to estimate the model parameters of a noisy equilibrium with reasonable accuracy in the host–parasitoid model. The oscillatory transients of the stable focus provide sufficient structure to allow not only parameter estimation but a distinctively better fit by the 'true' model than by a wrong one (Tables 5 and 7). This is in stark contrast to one-dimensional models, in which a noisy equilibrium displays a 'largely uninformative cloud of points' [9].

The efforts to distinguish the attractors using time series analysis was also reasonably successful. Except at the highest noise level, the neural network model correctly identified the sign of the Lyapunov exponent for the equilibrium and the periodic (mostly) and chaotic orbits, although the confidence interval often crossed zero (Table 4). Even the magnitude of the exponent was often not too far off. The poor identification of the quasiperiodic trajectory is curious and somewhat worrisome, as quasiperiodic attractors are far more common than periodic attractors in these models.

Previously published tests that demonstrate that the neural network model can identify noisy chaos use lognormal noise with $\sigma = 0.1$ [2], corroborating my results at $\sigma = 0.1$ but suggesting that the failure is rapid with increasing noise. The neural network model produced very negative exponent estimates in nearly half of the population time series analyzed by [2]; this may be an artifact of high noise levels in those data.

Closer inspection reveals that the problem is not with the neural network model itself, but instead with the strategy for selecting the model complexity. For example, when I applied the neural network model to the chaotic time series with $\sigma = 0.3$ using $d = 2$ and $k = 5$, I got a point estimate of the Lyapunov exponent that matched the true value to two significant digits! However, the GCV(2) criterion selected a much simpler model. Standard GCV *would* select this model; however, it also selects complex models for all of the time series. For the series with lower noise levels this would almost certainly be overfitting, and indeed frequently results in positive Lyapunov exponent estimates for time series such as the stable equilibrium with low noise. It is notable that simple neural network models were selected for almost all of the time series analyzed by [2], in which GCV(2) was the selection criterion.

An alternate model selection scheme that is intermediate between GCV and GCV(2) is the Bayesian Information Criterion (BIC). Models selected with this criterion led to Lyapunov exponents that are accurate for the chaotic and periodic time series, but consistently return large positive values for the equilibrium and quasiperiodic series. Thus none of the standard model selection algorithms works consistently across all types of dynamics and all levels of noise. Since we do not know either of these a priori with real data, finding a solution for this model selection problem is an important avenue for future work.

The wide confidence intervals for the neural net Lyapunov exponent estimates are also a matter of concern. In many cases, the confidence interval extends across the origin, which can be interpreted as meaning that any type of dynamics is plausible. This is not a very useful result, especially when the confidence interval often does not even cover the true value. The rationale behind the confidence interval estimators was based on large-sample theory, and was tested on time series of length 400 [24]. It is likely that the asymptotic theory does not apply to the short time series that I have analyzed. It is possible, however, that estimates are going to be inherently uncertain with short time series, in which case the large confidence intervals are correct. An alterative approach is to use bootstrap techniques to estimate the confidence intervals; this should be computationally feasible with short time series. This is an issue that can be addressed with simulation studies, and is a valuable future direction for research. As a first step, I analyzed a set of time series of length 100. There was no consistent improvement: some confidence intervals became smaller, and others larger. The number of confidence intervals crossing the origin remained the same. The quality of the confidence intervals will also be affected by the model selection issue discussed above.

As with any analysis of stochastic processes, there is a risk that any particular realization of the model will be 'atypical'. In this paper I chose to apply a breadth of analyses, and since each is computationally intensive I could not perform replication for them all. I did, however, create 10 replicates of the chaotic time series with $\sigma = 0.1$, and subject them to the nonparametric estimate of the Lyapunov exponent. The results were fairly consistent: the same neural network model was selected each time, the Lyapunov exponent estimates ranged from 0.12 to 0.29, and the confidence interval crossed zero in only one of the ten replicates. Thus I have high confidence in at least the qualitative results of my study.

When fitting the true mechanistic model to the time series, the best parameter estimates, for a given noise level, are generally found in the chaotic and quasiperiodic trajectories. Thus complex dynamics do seem to promote our ability to parameterize mechanistic models. However, the differences in estimation error among the different dynamics are not that great (Fig. 3). In contrast to one-dimensional models [9], predator–prey models have sufficient structure even around a stable equilibrium to allow reasonable characterization of the system.

With all of the time series, the true model fit better than the wrong one. However, with many of the periodic and quasiperiodic time series, the difference in prediction $r^2$ was small (Tables 5 and 7). In the real world, in which even the 'true' model does not capture all of the precesses exactly, the two models are likely to be indistinguishable. In contrast, the wrong model fit the chaotic time series rather poorly, suggesting that chaos provides enough structure to distinguish the models. This occurs even when the Lyapunov exponent of the fitted model is positive, so it is not simply an artifact of a chaotic transient leading to a periodic attractor. There was also a substantial difference in the $r^2$ for the periodic attractor with $\sigma = 0.3$; this trajectory has a strongly positive exponent (Table 2).

The fitted BFL model always produced the correct deterministic attractor, although the Lyapunov exponents associated with the noisy time series were not always accurate. The latter is not surprising, as the estimated $\sigma$ is trying to be as small as possible (to reduce prediction error) while still being large enough to

allow the trajectory to explore the state space occupied by the data. In contrast, the fitted HP2 model was able to reliably identify the quasiperiodic attractor and stable equilibrium; the chaotic and periodic attractors were almost always misidentified. Even the estimates along the noisy trajectories were usually wrong. Thus the risks associated with drawing dynamical conclusions from fitted models are high, so such conclusions should only be drawn when there is very high confidence that the model is correct.

In general, it appears that use of the 'correct' model is superior to nonparametric techniques that simply use information from the time series; but that the nonparametric techniques are superior to using the 'wrong' model. Thus in the absence of confidence in the 'truth' of the model, nonparametric time series techniques would be the preferred approach. An important open question is where an 'incomplete' model (with components that are all true, but missing a key process) falls in this hierarchy. Likewise, it is unclear what would occur with a model that captured all of the dynamical processes, but had an incorrect noise specification.

As the debate about whether there is chaos in population ecology waned, I began to believe that the distinction between 'noisy chaos' and 'noisy periodicity' in oscillatory populations was largely academic, with neither biological significance or practical consequence. The issue of biological significance remains open, but the results in this paper suggest that chaos does indeed have great practical benefit from the standpoint of identifying the mechanisms that underlie the population dynamics. As scientists, we should hope that nature is chaotic!

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## References

[1] May RM. Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos. Science 1974;186:645–7.
[2] Ellner S, Turchin P. Chaos in a noisy world: new methods and evidence from time-series analysis. Am Naturalist 1995;145:343–75.
[3] Nychka D, Ellner S, McCaffrey D, Gallant AR. Finding chaos in noisy systems. J Roy Statist Soc B 1992;54:399–426.
[4] Tidd CW, Olsen LF, Schaffer WM. The case for chaos in childhood epidemics. II. Predicting historical epidemics from mathematical models. Proc Roy Soc Lond B 1993;254:257–73.
[5] Harrison GW. Comparing predator–prey models to Luckinbill's experiment with *Didinium* and *Paramecium*. Ecology 1995;76:357–74.
[6] Morris WF. Problems in detecting chaotic behavior in natural populations by fitting simple discrete models. Ecology 1990;71:1849–62.
[7] Ellner SP, Kendall BE, Wood SN, McCauley E, Briggs CJ. Inferring mechanism from time-series data: delay-differential equations. Physica D 1997;110:182–94.
[8] Kendall BE, Briggs CJ, Murdoch WW, Turchin P, Ellner SP, McCauley E, Nisbet RM, Wood SN. Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. Ecology 1999;80:1789–805.
[9] Schaffer WM, Ellner S, Kot M. Effects of noise on some dynamical models in ecology. J Math Biol 1986;24:479–523.
[10] Krukonis G, Schaffer WM. Population cycles in mammals and birds: does periodicity scale with body size? J Theoret Biol 1991;148:469–93.
[11] Beddington JR, Free CA, Lawton JH. Dynamical complexity in predator–prey model framed in simple difference equations. Nature 1976;225:58–60.
[12] Nicholson AJ, Bailey VA. The balance of animal populations – Part I. P Zoo Soc Lond 1935;3:551–98.
[13] Neubert MG, Kot M. The subcritical collapse of predator populations in discrete-time predator–prey models. Math Biosci 1992;110:45–66.
[14] Berryman AA. What causes population cycles of forest Lepidoptera? Trends Ecol Evolution 1996;11:28–32.
[15] Turchin P, Taylor AD. Complex dynamics in ecological time series. Ecology 1992;73:289–305.
[16] McCaffrey D, Ellner S, Nychka DW, Gallant AR. Estimating the Lyapunov exponent of a chaotic system with nonlinear regression. J Am Statist Assoc 1992;87:682–95.
[17] Schluter D, Nychka DW. Exploring fitness surfaces. Am Naturalist 1994;143:597–616.

[18] Wolf A, Swift JB, Swinney HL, Vastano JA. Determining Lyapunov exponents from a time series. Physica D 1985;16:285–317.
[19] Schaffer WM. Dynamical Software: I. User's Manual and Introduction to Chaotic Systems. Tucson, AZ: Dynamical Systems Inc; 1986.
[20] Schaffer WM, Truty GL, Fulmer SL. Dynamical Software: II. User's Manual and Introduction to Chaotic Systems. Tucson, AZ: Dynamical Systems Inc; 1987.
[21] Ellner S, Nychka DW, Gallant AR. LENNS, a program to estimate the dominant Lyapunov exponent of noisy nonlinear systems from time series data. Institute of Statistics Mimeo Series # 2235 (BMA Series # 39), Statistics Department, North Carolina State University, Raleigh, NC 27695-8203, 1992.
[22] Statistical Sciences S-PLUS Guide to Statistical and Mathematical Analysis, Version 3.2. StatSci, a division of MathSoft, Inc., Seattle, Washington, USA, 1993.
[23] Nychka D, Haaland PD, O'Connell M, Ellner S. FUNFITS, data analysis and statistical tools for estimating functions. In: Nychka D, Piegorsch WW, Cox LH. editors. Case studies in environmental statisitics. New York: Springer; 1998. p. 159–79.
[24] Bailey BA, Ellner S, Nychka DW. Chaos with confidence: asymptotics and applications of local Lyapunov exponents. In: Cutler DC, Kaplan DT, editors. Nonlinear dynamics and time series: building a bridge between the natural and statistical sciences. Providence, Rhode Island, USA: American Mathematical Society; 1997. p. 115–33.
[25] Farmer JD, Sidorowich JJ. Predicting chaotic time series. Phys Rev Lett 1987;59:845–8.
[26] Casdagli M. Nonlinear prediction of chaotic time series. Physica D 1989;35:335–56.
[27] Ellner SP, Bailey BA, Bobashev GV, Gallant AR, Grenfell BT, Nychka DW. Noise and nonlinearity in measles epidemics: combining mechanistic and statistical approaches to population modeling. Am Naturalist 1998;151:425–40.
[28] Baltensweiler W, Fischlin A. The larch budmoth in the Alps. In: Berryman AA, editor. Dynamics of forest insect populations: patterns, causes, implications. New York: Plenum Press; 1988. p. 331–51.
[29] Schwerdtfeger F. Über die Ursachen des Massenwechsels der Insekten. Zeitschrift für angewandte Entomologie 1942;28:254–303.
[30] Altenkirch W. Zyklische Fluktuation beim kleinen Frostspanner. Allgemeine Forst und Jagdzeitung 1991;162:2–7.