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COMPLEX DYNAMICS IN ECOLOGICAL TIME SERIES¹

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Abstract. Although the possibility of complex dynamical behaviors—limit cycles, quasiperiodic oscillations, and aperiodic chaos—has been recognized theoretically, most ecologists are skeptical of their importance in nature. In this paper we develop a methodology for reconstructing endogenous (or deterministic) dynamics from ecological time series. Our method consists of fitting a response surface to the yearly population change as a function of lagged population densities. Using the version of the model that includes two lags, we fitted time-series data for 14 insect and 22 vertebrate populations. The 14 insect populations were classified as: unregulated (1 case), exponentially stable (three cases), damped oscillations (six cases), limit cycles (one case), quasiperiodic oscillations (two cases), and chaos (one case). The vertebrate examples exhibited a similar spectrum of dynamics, although there were no cases of chaos. We tested the results of the response-surface methodology by calculating autocorrelation functions for each time series. Autocorrelation patterns were in agreement with our findings of periodic behaviors (damped oscillations, limit cycles, and quasiperiodicity). On the basis of these results, we conclude that the complete spectrum of dynamical behaviors, ranging from exponential stability to chaos, is likely to be found among natural populations.

Key words: *autocorrelation function; chaos; complex deterministic dynamics; delayed density dependence; dynamical behaviors of populations; insect population dynamics; limit cycles; long-term population records; nonlinear time-series modelling; quasiperiodicity; time-series analysis.*

INTRODUCTION

The relative importance of density-dependent vs. density-independent factors in determining population abundances and dynamics is a central issue in ecology. Much of the debate over this question has focused on two opposing viewpoints (e.g., Nicholson 1954, Andrewartha and Birch 1954). According to the first viewpoint populations are regulated around a stable point equilibrium by density-dependent mechanisms, while the second one maintains that population change is largely driven by density-independent factors. There is, however, a third possibility. In addition to stable point equilibria, density-dependent processes can produce complex population dynamics—limit cycles, quasiperiodic oscillations, and aperiodic chaos. While the possibility of such dynamics has been recognized theoretically since the 1970s (May 1974, 1976), most ecologists have remained skeptical of their importance in nature.

One well-known attempt to determine the frequency of various kinds of dynamic behaviors in insect populations was made by Hassell et al. (1976). They concluded that most natural populations show monotonic damping (the most stable kind of equilibrium behavior), with only 1 case (out of 24) of damped oscillations, 1 case of a limit cycle, and no cases of chaos. Despite a number of caveats listed by Hassell et al. (1976), this

result was very influential in convincing ecologists that complex dynamics are rarely found in nature (e.g., Berryman and Millstein 1989, Nisbet et al. 1989). In this paper we argue that the results obtained by Hassell et al. (1976) largely resulted from their overly simple method of analysis. Most importantly, they used a single-species model that lacked delayed density dependence. Delayed density dependence, however, is expected to arise as a result of biotic interactions in multispecies communities and as a result of population structure (Royama 1981, Murdoch and Reeve 1987; L. R. Ginzburg and D. E. Taneyhill, *unpublished manuscript*), and in fact is found in many insect populations (Turchin 1990). Using a single-species model without delayed density dependence biases the results in favor of stability, since complex dynamics are more likely in higher-dimensional systems, and mistakenly analyzing such systems in fewer dimensions will tend to hide this complexity (Guckenheimer et al. 1977, Schaffer and Kot 1985).

One approach to higher-dimensional analysis of ecological time series has been advocated by Schaffer and co-workers (Schaffer 1985, Schaffer and Kot 1985, 1986, Kot et al. 1988), who used the method of “phase-space reconstruction” in which unknown densities of interacting populations are represented with lagged densities of the studied population. Schaffer and Kot (1986) examined time series of several natural populations and concluded that reconstructed dynamics of these populations resembled chaos. The major weakness of such analysis, however, is its reliance on visual (and

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therefore inherently subjective) examination of reconstructed attractors (Berryman and Millstein 1989, Ellner 1989).

In this paper we build on ideas of both Hassell et al. (1976) and Schaffer and Kot (1986). Our goal is to develop an objective methodology for extracting deterministic dynamics from short and noisy ecological time series. Unlike Hassell et al. (1976) who specified a particular equation with which to model data, we used a general and flexible methodology described by Box and Draper (1987), the response-surface methodology (RSM). We followed Schaffer and Kot (1985) by using lags to represent the multidimensional dynamics of the system (e.g., unknown densities of interacting species or age structure). We used our methodology to reconstruct deterministic dynamics from long-term records of population fluctuations of 14 insects (with some further comparisons to 22 mammal and bird species).

Since the methodology proposed here is new, we do not know how well it succeeds at reconstructing complex dynamics from data. This is especially true for detecting chaos. However, methodologies for detecting periodic behaviors (e.g., limit cycles) are well understood. Accordingly, we begin by using one of these methodologies, which is based on estimating the autocorrelation function (ACF) for each data set. We use ACF patterns to characterize presence or absence of periodic behaviors in natural populations, and then compare ACF results to conclusions reached with the response-surface methodology. Our logic is that if RSM is not capable of extracting limit cycles from data, then there is little hope that we can use it to detect chaos. If, on the other hand, we can accurately reconstruct one kind of nonequilibrium behavior, limit cycles, then confidence in our ability to reconstruct another kind, chaos, is correspondingly enhanced:

METHODS

The data set

We collected and analyzed every terrestrial animal population time series we could obtain, subject to the following criteria: (1) Data were annual and continuous; if a time series had missing data, only the longest uninterrupted period was used. (2) Time series had to contain at least 18 yr of continuous census data, so that no less than half the total degrees of freedom would always be available for the error term in our response surface model (see *Reconstructing endogenous dynamics* . . . , below). (3) The data were for a single locality (spatial scale having been determined by the original author). Where several time series were available for the same species, we selected the longest one, to avoid overrepresentation of much-studied species.

We exercised no selectivity beyond applying these criteria. Nonetheless, our data set cannot be regarded as representative of natural populations, since the orig-

inal investigators' selection of populations for study is inherently biased. In particular, forest pests exhibiting outbreaks clearly are over-represented.

Considerations of space prevent us from fully discussing our results for all 36 time series (Table 1 and Table 2). As a compromise, we show the complete spectrum of results for all series in one group—insects. We selected insects for detailed discussion partly because we are most familiar with this group. More importantly, insect data sets tend to be more reliable, since the majority of insect data were collected with the specific goal of quantifying insect population fluctuations, unlike the data extracted from fur returns or bag records. Nevertheless, as will be seen later, many of the patterns found in mammal and bird data sets are very similar to insect patterns.

Investigating time series with autocorrelation functions

As the first step in our analysis of the population time series, we used the qualitative diagnostic techniques based on estimating the autocorrelation function (ACF; Box and Jenkins 1974; for discussions of ACF in ecological context see Finerty [1980], Nisbet and Gurney [1982]). Prior to the analysis the values of population density at each year, N_t , were log-transformed, $L_t \equiv \log N_t$. The autocorrelation function is estimated by calculating the correlation coefficient between pairs of values $L_{t-\tau}$ and L_t separated by lag τ ($\tau = 1, 2, \dots$). These correlation coefficients are then plotted as a function of lag τ .

The shape of the estimated ACF provides insights regarding two aspects of population dynamics: stationarity and periodicity. A process is stationary if its dynamical properties do not change during the period of the study. Stationary processes fluctuate around constant mean levels, with constant variances. As will be seen later, our ability to reconstruct the endogenous dynamics of a system depends considerably on whether they are stationary, or not. ACFs of stationary processes are characterized by an exponential decay to zero, either monotonic or oscillatory (Box and Jenkins 1974).

Other ACF patterns indicate various forms of nonstationarity. A possible cause of nonstationary dynamics is density independence, perhaps arising because density regulation only occurs at extreme levels—"floors" and "ceilings"—that were not encountered by the population during the study. Such a population undergoes a "random walk," in which the population gradually wanders away from its initial density. There is, then, no true mean around which fluctuations occur. Alternatively, environmental changes occurring on a time scale comparable to the length of the observed time series could produce a gradual trend in the mean. In either of these situations, the ACF will decay slower than exponentially, and will become increasingly negative at long lags (Fig. 1A).

TABLE 1. Summary of insect time series.

Species	Time period	Reference
<i>Phyllopertha horticola</i> (garden chafer)	1947–1975	Milne 1984
<i>Choristoneura fumiferana</i> (spruce budworm)	1945–1972	Royama 1981
<i>Dendrolimus pini</i> (pine spinner moth)	1881–1940	Schwerdtfeger 1941
<i>Hyloicus pinastri</i> (pine hawkmoth)	1881–1930	Schwerdtfeger 1941
<i>Dendroctonus frontalis</i> (southern pine beetle)	1958–1987	Turchin et al. 1991
<i>Panolis flammea</i> (pine beauty moth)	1881–1940	Schwerdtfeger 1941
<i>Lymantria monacha</i> (nun moth)	1900–1941	Bejer 1988
<i>Bupalus piniarius</i> (pine looper)	1881–1940	Schwerdtfeger 1941
<i>Hyphantria cunea</i> (fall webworm)	1937–1958	Morris 1964
<i>Vespula</i> spp. (wasps)	1921–1946	Southwood 1967
<i>Drepanosiphum platanooides</i> (sycamore aphid)	1969–1987	Dixon 1990
<i>Lymantria dispar</i> (gypsy moth)	1954–1979	Montgomery and Wallner 1987
<i>Zeiraphera diniana</i> (larch budmoth)	1949–1986	Baltensweiler and Fischlin 1987
<i>Phyllaphis fagi</i> (beech aphid)	1969–1987	Dixon 1990

Nonstationarity can also be caused by externally driven periodic changes in the mean. The resulting dynamics have been called “phase-remembering quasi-cycles” (Nisbet and Gurney 1982), since the exogenous forcing factor maintains the regularity of the oscillation despite random perturbations in abundances. The ACF of such a system might look like the one in Fig. 1C: it does not decay to zero, but rather oscillates around zero with constant amplitude. The period of oscillation of the ACF is determined by the periodicity of the external forcing factor. In ecology the most important such periodic factor is seasonality. By using only data sets that reported population densities on a yearly basis, however, we have avoided the complications of seasonality.

In addition to externally driven nonstationary periodicity, stationary periodicity may arise from the endogenous dynamics of the system. Population fluctuations with an endogenous periodic component (“phase-forgetting quasi-cycles,” Nisbet and Gurney 1982) will be produced when the deterministic dynamics are damped oscillations (around a stable point equilibrium), a limit cycle, or “weak” chaos (Poole 1977). The ACF of these systems is characterized by an oscillatory decay to zero (Fig. 1D). In contrast, a nonperiodic stationary system, resulting from exponential stability (of a point equilibrium), will have a monotonically decaying ACF (Fig. 1B).

As a diagnostic tool the estimated ACF is much more useful than “eyeballing” the observed time series. By averaging over, and thus smoothing, the noisy time series, ACF reveals the periodic pattern in the data if it is present. The average period of oscillations is readily determined by observing at which lags ACF achieves its maxima. The speed with which ACF maxima approach zero reveals the strength of the periodic component, that is, how long the process “remembers” its history. Finally, a quick, although crude, test of the hypothesis that there is a periodic component in population fluctuations can be performed by determining whether ACF at the lag equal to one period is greater than the 95% confidence limit.

Using lags to represent multidimensional dynamics of the system

Numerical changes of a population typically affect and are in turn affected by the population abundances of resources, natural enemies, and competitors. Thus, in order to understand and predict how a population changes with time, we need information about the abundances of interacting species. However, usually data are available only for a single population, and we never know abundances of all populations in the community. This difficulty can be overcome by considering the population change from the previous year $t - 1$ to the current year t as a function of not only previous year's density, N_{t-1} , but also of densities N_{t-2} , N_{t-3} , The mathematical justification for this methodology is provided by a theorem proved by Takens (1981), and the method has been successfully used in many physical and chemical applications (e.g., Argoul et al. 1987), where it is called “attractor reconstruction

TABLE 2. Summary of vertebrate time series.

Species	Time period	Reference
Lynx	1821–1934	Moran 1953
Foxes (two species)	1879–1930	Elton 1942
Colored fox	1834–1925	Elton 1942
Marten	1834–1925	Elton 1942
Arctic fox	1834–1925	Elton 1942
Mink	1914–1957	Keith 1963
Muskrat	1914–1957	Keith 1963
Coyote	1914–1957	Keith 1963
Snowshoe hare	1847–1903	Leigh 1968
Varying hare	1884–1908	Naumov 1972
Squirrel	1933–1955	Naumov 1972
Belyak hare	1932–1954	Labutin 1960
Lynx	1932–1954	Labutin 1960
Fox	1932–1954	Labutin 1960
Wolf	1932–1954	Labutin 1960
Parchment beaver	1752–1849	Jones 1914
Wolverine	1752–1911	Jones 1914
Rabbit	1862–1932	Middleton 1934
Ruffed Grouse	1915–1972	Keith 1963
Black-capped Chickadee	1958–1983	Loery and Nichols 1985
Heron	1934–1952	Lack 1954
Great Tit	1912–1941	Lack 1954

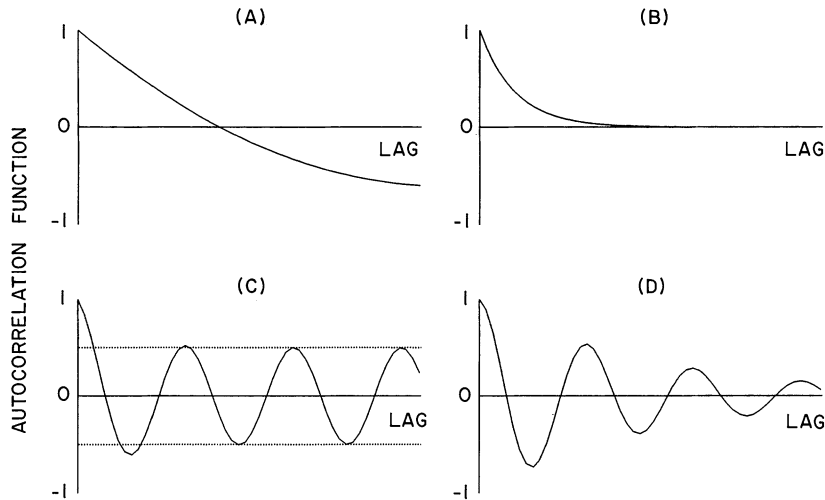


FIG. 1. Theoretical shapes of autocorrelation functions for (A) a process with nonstationary mean and no periodicity; (B) a stationary process with exponential return to equilibrium; (C) a process driven by an exogenous periodic force, or phase-remembering quasi-cycle; (D) a stationary process with endogenously generated periodicity, or phase-forgetting quasi-cycle.

in time delay coordinates" (Schaffer 1985, Ellner 1989). Representing the unknown densities of interacting species with delayed density dependence is also a venerable tradition in population ecology (Hutchinson 1948, Moran 1953, Berryman 1978, Royama 1981). Essentially, one replaces the "true" multivariate system describing deterministic population change

$$\begin{aligned} N_t^1 &= G^1(N_{t-1}^1, N_{t-1}^2, \dots, N_{t-1}^k) \\ N_t^2 &= G^2(N_{t-1}^1, N_{t-1}^2, \dots, N_{t-1}^k) \\ &\vdots \\ N_t^k &= G^k(N_{t-1}^1, N_{t-1}^2, \dots, N_{t-1}^k) \end{aligned}$$

(where N_t^i is the density of species i at time t , and G^i is a function describing the change in the density of species i with respect to the densities of interacting species) with a single equation for one species that involves lags

$$N_t^i = F^i(N_{t-1}^1, N_{t-2}^1, \dots, N_{t-p}^1). \quad (1)$$

It is important to note that N^i can refer not only to populations of interacting species, but also to abundances of different cohorts of the same species, if the population has age, physiological, or spatial structure.

The above argument leads us to the following general model:

$$N_t = F(N_{t-1}, N_{t-2}, \dots, N_{t-p}, \epsilon_t), \quad (2)$$

where we have added the exogenous component ϵ_t to the equation for population change. ("Endogenous" refers to dynamical feedbacks affecting the system, including those that involve a time lag, e.g., natural enemies. "Exogenous" refers to density-independent factors that are not a part of the feedback loop.) We will model the exogenous component as a random, normally distributed variable with mean zero, and variance σ^2 . The quantity p is the *order* of the process, that

is, the maximum lag time beyond which a past value of population density has no direct effect on the current population change (autocorrelations can persist much longer than p , since past values of N affect intermediate values, which in turn affect present).

Reconstructing endogenous dynamics with response-surface methodology

Our major goal in this paper is to develop a methodology that would objectively determine the type of the dynamic behavior that characterizes the endogenous component of population change. Several approaches have been suggested, all based on the method of reconstructing the attractor in time-delayed coordinates described in the preceding section. One is to estimate the dimensionality of the reconstructed attractor (for the explanation of this approach see Ellner [1989]). This approach appears to work for perfectly accurate data even with relatively short time-series (50 points), although dealing with noisy data sets remains problematic (Ellner 1989). Another approach relies on the direct estimation of Lyapunov exponents from experimental time series (Eckmann and Ruelle 1985, Wolf et al. 1985; for an explanation of Lyapunov exponents see Abraham and Shaw [1983]). This method requires enormous amounts of data: a minimum of several thousand data points is needed to characterize a low-dimensional attractor (Vastano and Kostelich 1986). The method of Sugihara and May (1990), which uses nonlinear forecasting to detect chaos in noisy time series, also requires substantial amounts of data (500–1000 points in their applications).

Making as few assumptions as possible about the nature of the process that has produced the observed time series is a powerful feature of the above methods, but it is also their weakness. Such nonparametric, mod-

el-independent approaches typically require plentiful data points. In ecology, where the length of time series rarely exceeds 20–30 yr, one is forced to use a parametric approach, which is much more frugal with data points.

The approach that we followed in this paper consists of approximating the function F in Eq. 2. This function describes the behavior of trajectories on the reconstructed attractor, and thus knowing its properties gives us a complete description of the system dynamics. For example, the dynamic behavior of F could be formally characterized by calculating its dominant eigenvalue and dominant Lyapunov exponent. Alternatively, one may determine the type of dynamics simply by iterating Eq. 2 on the computer, and observing the resulting dynamics. We have followed the latter course in this paper.

A potential problem associated with using a parametric approach, however, is that one may happen to choose an inappropriate model with which to approximate F . This possibility can be minimized by using the general method of response-surface fitting described by Box and Draper (1987). Briefly, this method is similar to regular regression in that it employs polynomials for approximating the shape of F . However, both the response (dependent) variable and the predictor (independent) variables are transformed using the Box-Cox power transformation (Box and Cox 1964), with the transformation parameter (the exponent) being also estimated from the data. In the following paragraphs we describe the logic and details of the approach with which we have extracted endogenous dynamics from ecological time series.

The first step is to decide on the number of lags p to include in the model, that is, the “embedding dimension” (Schaffer 1985). Ideally, since the correct p is unknown, one should start with a low-dimensional model and then increase the dimension until the result does not depend on further increase in dimensionality. In practice, due to data limitations (primarily the length of a time series) only a few lags can be examined. In their attempt to extract deterministic dynamics from data, Hassell et al. (1976) used a model with only one lag (only direct density dependence):

$$N_t = \lambda N_{t-1}(1 + aN_{t-1})^{-\beta}. \quad (3)$$

We took the next step and used a model with two lags (in other words, we added delayed density dependence). Thus, the general model (Eq. 2) becomes

$$N_t = F(N_{t-1}, N_{t-2}, \epsilon_t). \quad (4)$$

Biological considerations indicate that F can be represented as a product of N_{t-1} and the per-capita replacement rate $f(N_{t-1}, N_{t-2}, \epsilon_t)$. In general, f will have a simpler form, and can be approximated with a polynomial of one order lower than F . For example, if f is a monotonically decreasing function of N_{t-1} and N_{t-2} , it can be approximated with a first-order polynomial

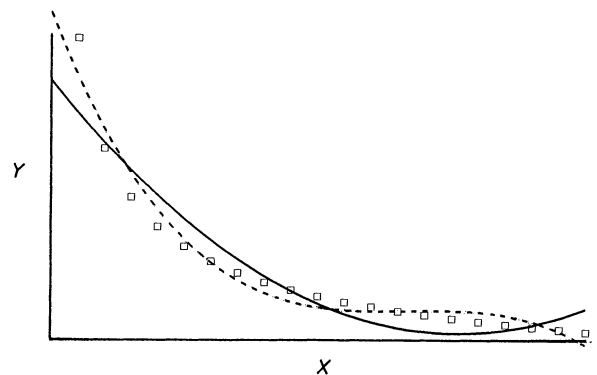


FIG. 2. Results of fitting a function $Y = aX^{-1/2}$ (\square) with polynomials of second (—) and third order (---).

(together with appropriate transformations of the predictor variables), while the function F will have a maximum and will need to be approximated with a quadratic polynomial. These considerations lead us to the following model:

$$N_t = N_{t-1}f(N_{t-1}, N_{t-2}, \epsilon_t). \quad (5)$$

We are now in position to estimate f by fitting a response surface to the observed replacement rate N_t/N_{t-1} as a function of N_{t-1} and N_{t-2} . Highly nonlinear dependence of the replacement rate on lagged population densities in several data sets and in some theoretical models (P. Turchin and A. D. Taylor, *personal observation*), necessitated using polynomials of at least second order (see Box and Draper 1987). However, polynomials by themselves are notoriously bad at approximating both the function and its derivative, especially for log-like functions that are characterized by rapidly changing derivatives. Consider, for example, data plotted in Fig. 2. Fitting a quadratic polynomial to the nonlinear function represented by points, we find that at high values of the predictor variable, the fitted function has a positive slope, while the actual function has a negative slope. Correct estimation of the slope of f is crucial to the success of accurately reconstructing endogenous dynamics, since whether an equilibrium is stable or not, and whether the attractor is periodic or chaotic will depend on the derivatives of f . Using higher-degree polynomials does not help, even though they provide a progressively better approximation to f , since higher-degree polynomials “oscillate” around the true function (e.g., the cubic polynomial in Fig. 2). In addition, such an approach is very wasteful of degrees of freedom. A better approach, proposed by Box and Cox (1964), is to power-transform either predictor, or response variables, or both. The logarithm is naturally embedded in the power transformation family, since letting $\theta \rightarrow 0$ is equivalent to a log transformation (Box and Cox 1964; see also Sokal and Rohlf 1981: 423–426).

While transforming predictor variables affects only

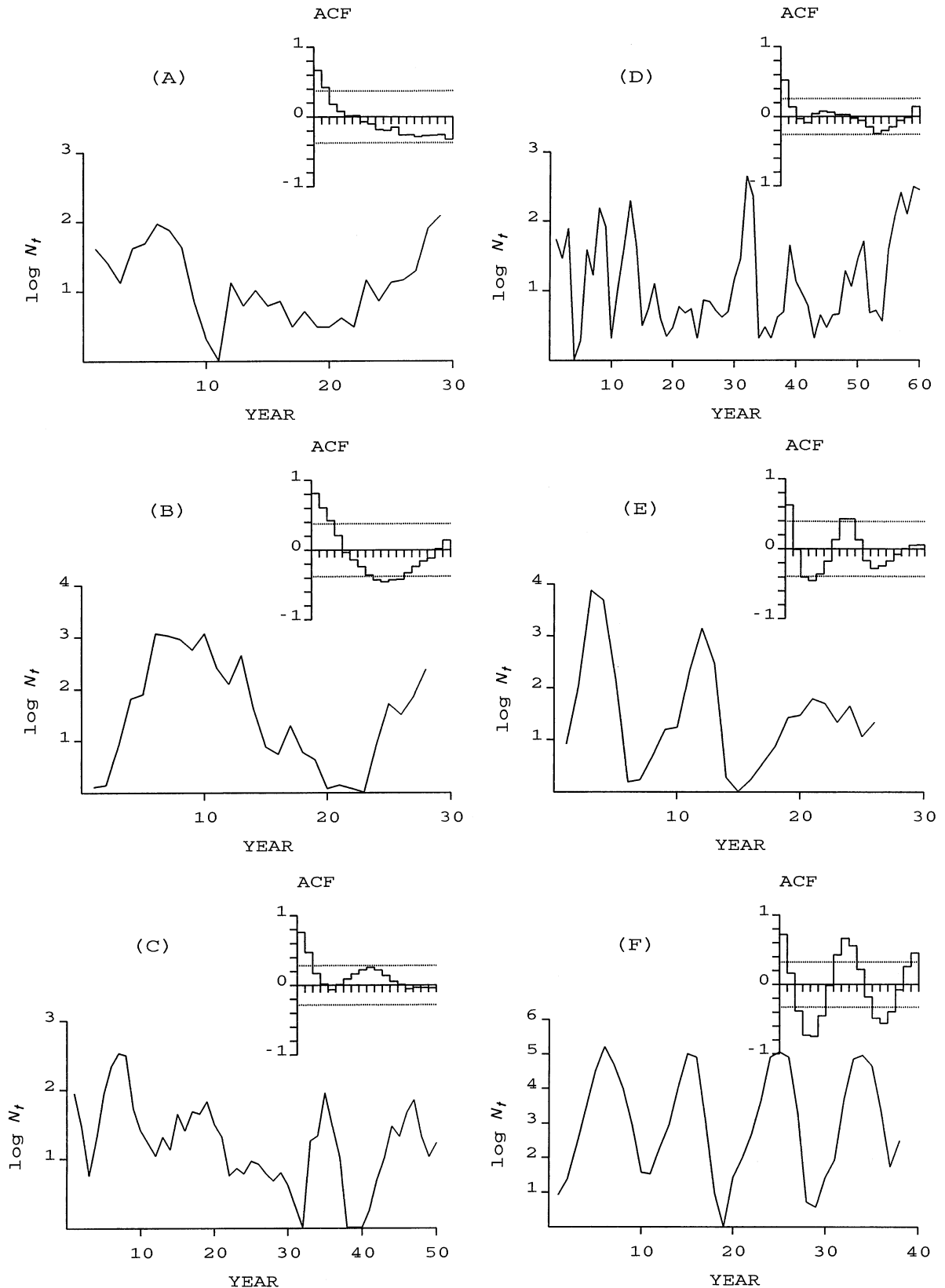
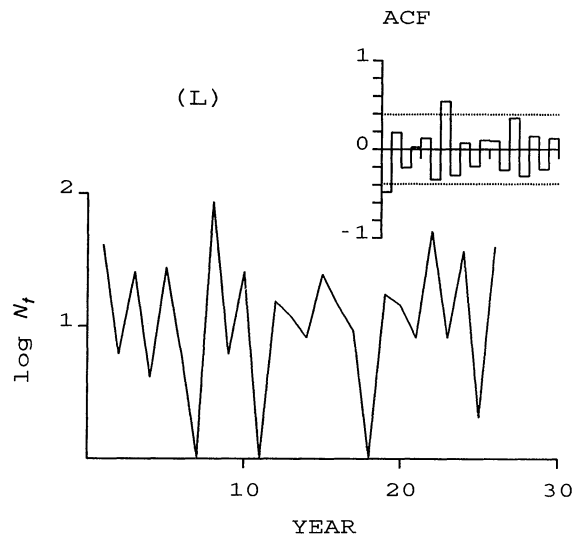
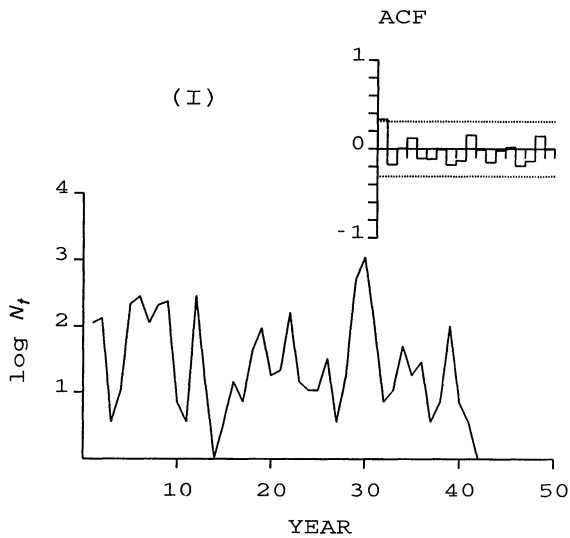
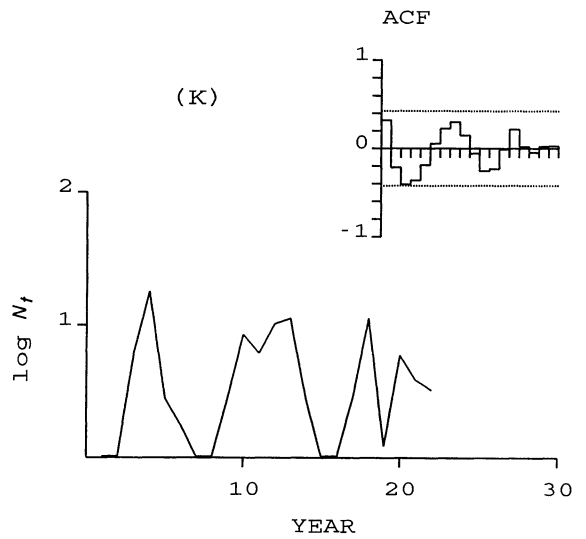
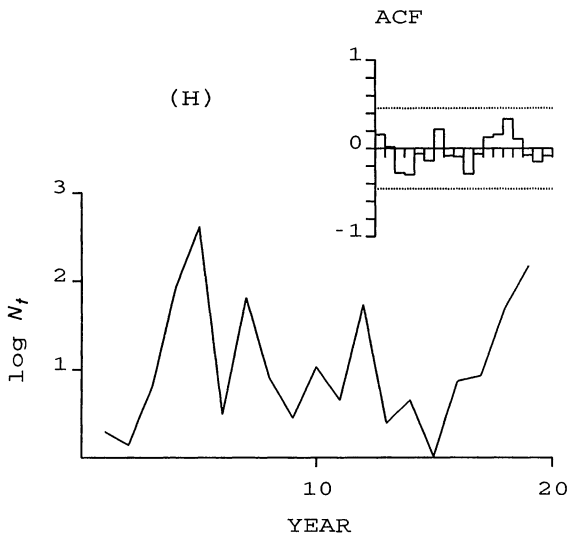
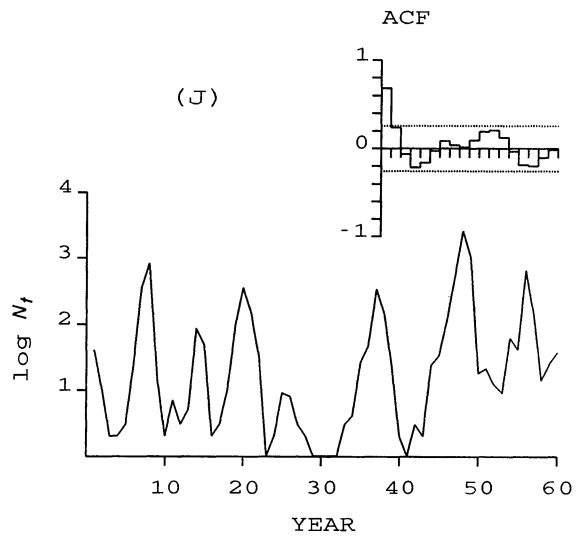
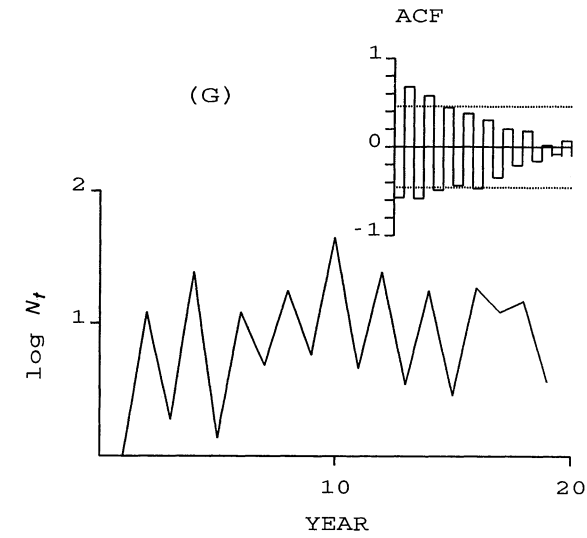


FIG. 3. Log-transformed (base 10) time series and autocorrelation functions (ACF) for insect populations: (A) *Phyllopertha horticola*, (B) *Choristoneura fumiferana*, (C) *Hyloicus pinastri*, (D) *Panolis flammea*, (E) *Lymantria dispar*, (F) *Zeiraphera*



diniana, (G) *Drepanosiphum platanoides*, (H) *Phyllaphis fagi*, (I) *Lymantria monacha*, (J) *Bupalus piniarius*, (K) *Hyphantria cunea*, (L) *Vespula* spp.

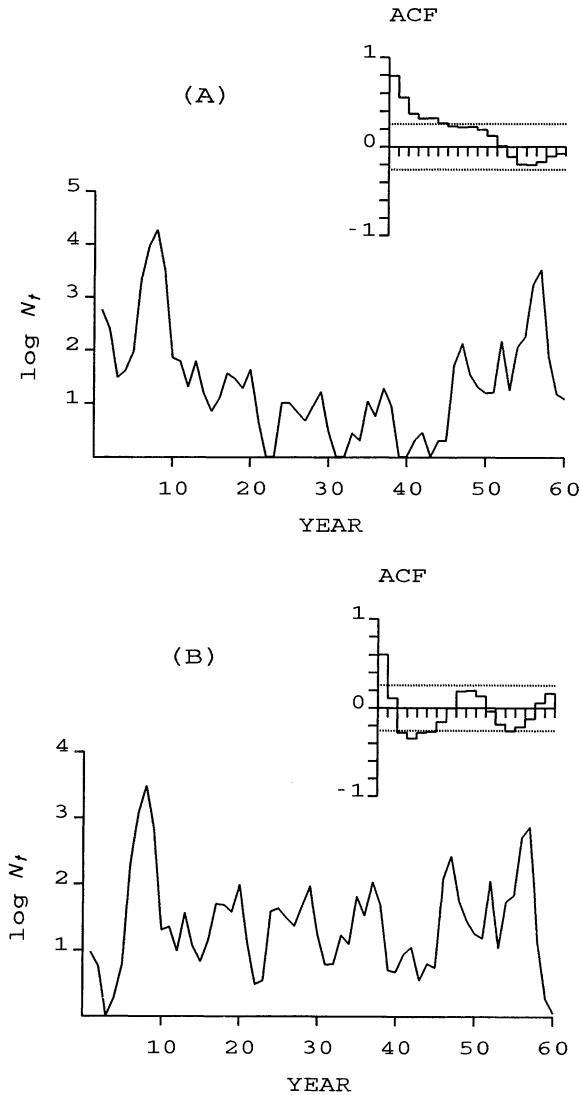


FIG. 4. The time series of *Dendrolimus pini* and its autocorrelation function (ACF). (A) actual data; (B) quadratically detrended data.

the functional shape of f , transformation of the response variable also affects the error structure. Population data are non-negative, often right-skewed, and more variable when the mean is large. Taking log-transforms of the response variable, a standard procedure in population ecology (Moran 1953, Finerty 1980, Royama 1981, Pollard et al. 1987), tends to alleviate all these problems at the same time (Ruppert 1989). Accordingly, we log-transformed the replacement rate N_t/N_{t-1} , obtaining the rate of population change, $r_t \equiv \log(N_t/N_{t-1})$. Defining $X \equiv N_{t-1}^0$ and $Y \equiv N_{t-2}^0$, the above argument leads to the following model for extracting deterministic dynamics from data:

$$r_t = a_0 + a_1X + a_2Y + a_{11}X^2 + a_{22}Y^2 + a_{12}XY + \epsilon_t. \tag{6}$$

This model has a total of eight parameters (six parameters defining the quadratic surface and two transformation exponents). The best transformations (θ -values) of the predictor variables for any specific system are unknown, and need to be estimated from the data. The transformations were estimated by fitting the model (Eq. 6) by least squares for all combinations of θ_1 and θ_2 equal to $\{-1, -0.5, 0, \dots, 2.5, 3\}$ (using log-transform when $\theta_i = 0$) and selecting the θ -values that resulted in the smallest residual sum of squares (Box and Draper 1987). The farther the estimated θ_i is from 1, the more nonlinear is the transformation.

The type of RSM-extracted dynamics was determined by iteration of the model (Eq. 6) on the computer. The initial values N_1 and N_2 were set equal to the mean population density of the observed series. This procedure decreased the likelihood of being misled by multiple attractors, if any were present. The simulated trajectory was plotted as an N_t vs. N_{t-1} phase plot. If the trajectory approached a single point, the system was classified as stable. If the trajectory settled onto several points, the dynamics were classified as a limit cycle. In many cases the trajectory would not settle onto a finite number of points, but instead all the points in the phase space would be lying on an ellipse (after discarding transients). Such dynamical behavior, called "quasiperiodic" in mathematical literature, results when the period of the oscillation is irrational, so that the solution never repeats itself exactly (Schaffer and Kot 1985). This kind of behavior is commonly found in discrete models of order > 1 , such as the model (Eq. 6). From the ecologist's point of view, the distinction between limit cycles and quasiperiodic dynamics is not very important, so we will treat them together as a single category. Finally, a "strange" at-

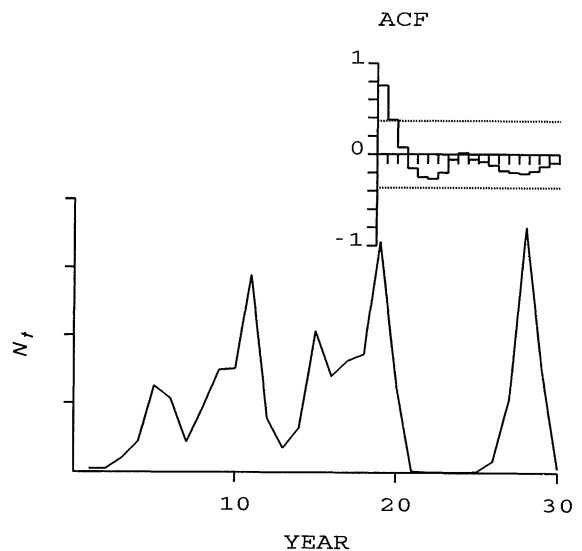


FIG. 5. Population fluctuations in *Dendroctonus frontalis* and its autocorrelation function (ACF). Data are plotted on the arithmetic (not log-transformed) scale.

TABLE 3. Summary of reconstructed dynamics.

Species	Autocorrelation function	Response-surface model result
<i>Phyllopertha horticola</i>	Non-stationary Non-periodic	No regulation
<i>Choristoneura fumiferana</i>	Non-stationary or a very long cycle	Exponentially stable
<i>Dendrolimus pini</i>	Non-stationary Non-periodic*	Exponentially stable†
<i>Hyloicus pinastri</i>	Non-stationary Non-periodic*	Damped oscillations
<i>Dendroctonus frontalis</i>	Non-stationary Non-periodic	Damped oscillations‡
<i>Panolis flammea</i>	Stationary Non-periodic	Exponentially stable
<i>Lymantria monacha</i>	Stationary Non-periodic	Damped oscillations
<i>Bupalus piniarius</i>	Stationary Suggestive of periodicity	Damped oscillations
<i>Hyphantria cunea</i>	Stationary Suggestive of periodicity	Damped oscillations
<i>Vespula</i> spp.	Stationary Suggestive of periodicity	Damped oscillations
<i>Drepanosiphum platanoides</i>	Stationary Periodic (2 yr)	Limit cycle (2 yr)
<i>Lymantria dispar</i>	Stationary Periodic (8.5 yr)	Quasiperiodicity (≈ 7 yr)
<i>Zeiraphera diniana</i>	Stationary Periodic (9 yr)	Quasiperiodicity (≈ 8 yr)
<i>Phyllaphis fagi</i>	Stationary Suggestive of periodicity	Chaos

* Autocorrelation function of the detrended series suggests periodicity.

† Damped oscillations extracted from the detrended series.

‡ Diverging oscillations and chaos extracted from the first and second half of the series, respectively.

tractor, indicating chaotic dynamics, can look much like an ellipse that has been stretched and then folded. Another possibility is for a strange attractor to be separated into several discontinuous pieces (see Schaffer [1987] for the explanation of many routes to chaos, and examples of phase graphs for various kinds of attractors).

When iterating the model (Eq. 6) using an estimated response surface with noise, or a chaotic response surface without noise, the trajectory occasionally jumps

outside the range of observed N_t values. This causes a difficulty, because the shape of the response surface where it is not constrained by data points may be quite strange, e.g., the surface could blow up to infinity. In order to prevent such occurrences, the values of the function $f(N_{t-1}, N_{t-2})$, at the boundary of the box in the $N_{t-1} - N_{t-2}$ phase space defined by the maximum and the minimum of the observed series, were extrapolated for areas outside the box. In other words, when the simulated trajectory left the minimum-maximum box,

TABLE 4. Estimated response-surface parameters, as defined by Eq. 6.

Species	θ_1	θ_2	a_0	a_1	a_2	a_{11}	a_{22}	a_{12}
<i>Phyllopertha horticola</i>	-1.0	0.5	-2.637	0.399	6.280	-0.003	-2.887	-0.661
<i>Choristoneura fumiferana</i>	0.0	-1.0	0.028	-0.282	-0.007	-0.081	0.000	-0.002
<i>Dendrolimus pini</i>	3.0	1.0	0.163	0.034	-0.665	0.000	0.089	-0.024
<i>Hyloicus pinastri</i>	1.5	2.0	0.339	-0.217	-0.326	0.029	0.005	-0.009
<i>Dendroctonus frontalis</i>	0.0	1.5	0.291	-1.157	0.193	-0.211	-0.125	0.386
<i>Panolis flammea</i>	0.5	3.0	1.306	-2.660	-0.010	0.700	-0.000	0.013
<i>Lymantria monacha</i>	0.0	-1.0	-1.370	-0.262	0.062	0.054	-0.002	-0.037
<i>Bupalus piniarius</i>	3.0	1.0	0.655	0.003	-1.522	0.000	0.185	-0.005
<i>Hyphantria cunea</i>	3.0	-1.0	0.408	-0.061	-0.632	0.001	0.176	-0.046
<i>Vespula</i> spp.	0.5	0.0	5.241	-10.251	-0.646	3.986	0.303	1.385
<i>Drepanosiphum platanoides</i>	1.0	-1.0	2.722	-3.665	0.292	0.646	-0.027	-0.108
<i>Lymantria dispar</i>	-0.5	0.5	2.894	-0.208	-8.170	0.005	1.753	0.297
<i>Zeiraphera diniana</i>	0.5	0.0	-4.174	4.349	-1.790	-1.280	-0.124	0.437
<i>Phyllaphis fagi</i>	2.5	3.0	1.130	-2.532	-0.452	0.564	0.001	-20.363

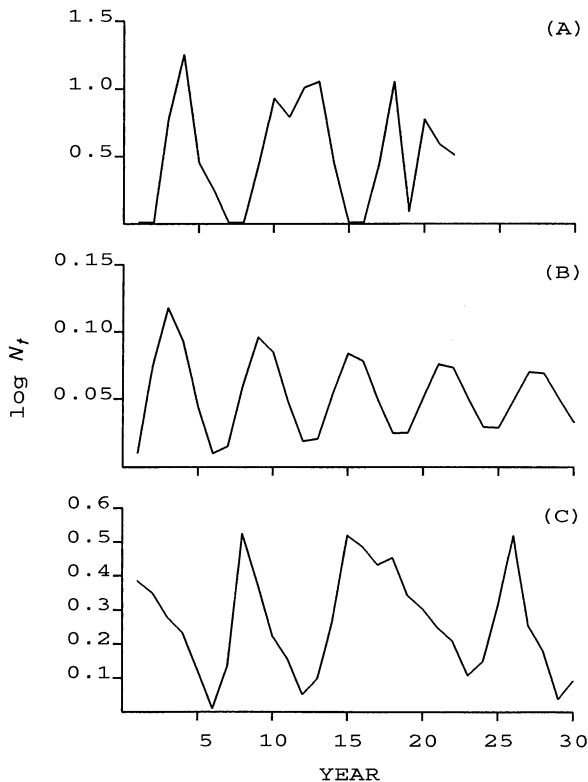


FIG. 6. *Hyphantria cunea*: observed time series (A), and trajectories predicted by response-surface model (RSM) without noise (B), and with noise (C) (ϵ_t is normally distributed with mean zero and standard deviation $\sigma = 0.2$).

the computer program evaluated the function $f(N_{t-1}, N_{t-2})$ at the point on the box boundary nearest to the point (N_{t-1}, N_{t-2}) .

RESULTS

Autocorrelation function (ACF) patterns

Several insect data sets exhibit ACFs suggestive of nonstationarity. The ACF of *Phyllopertha horticola*, the garden chafer, does not decay to zero, but instead becomes progressively more negative as the lag increases (Fig. 3A). Two other populations appear to oscillate around a nonstationary mean (Figs. 4 and 3C). The level around which the *Dendrolimus pini* population is fluctuating appears to have first decreased, and then increased, while the population of *Hyloicus pinastri* exhibited a downward trend. We estimated the long-term trend for *Dendrolimus* by fitting a quadratic polynomial to N_t as a function of time. Subtracting the estimated trend from the time series ("detrending"), we obtain a series that appears to fluctuate around a constant level, and whose ACF is of the periodic phase-forgetting kind (although not quite significantly periodic at 95% level) (Fig. 4). This example shows that the ability of the ACF to detect periodic behaviors is sensitive to whether the underlying process is stationary or not (see also Box and Jenkins 1974).

The *Dendroctonus frontalis* population exhibited a different kind of nonstationarity, in which the mean stayed more or less constant, but the amplitude of the oscillation increased with time, with both the peaks becoming higher and the troughs lower (Fig. 5). One possible explanation of this pattern is increased instability of the *Dendroctonus* population as a result of a several-fold enrichment of this beetle's food base over the last 30 yr (Turchin et al. 1991).

Several insect populations appeared to have periodic dynamics: significant periodicity was found in the ACF's of three populations (Fig. 3E, F, and G), and the ACF was suggestive of an oscillation in an additional four cases (Fig. 3H, J, K, and L). In each of the three periodic cases the ACF was of the phase-forgetting kind, that is, the peaks in ACF decayed at higher lags. This suggests that oscillations in these populations are driven not by an exogenous periodic force, but by endogenous dynamics.

Reconstructed endogenous dynamics

Applying response-surface methodology (RSM) to the insect time series indicated the following spectrum of endogenous dynamics: no regulation (one case); sta-

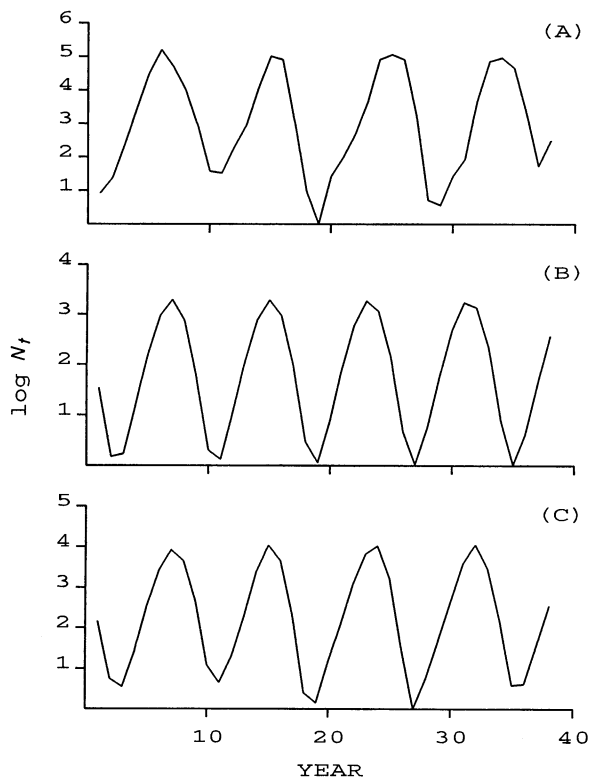


FIG. 7. *Zeiraphera diniana*: observed time series (A), and trajectories predicted by response-surface model (RSM) without noise (B), and with noise (C) (ϵ_t is normally distributed with mean zero and standard deviation $\sigma = 0.2$). Note that the deterministic trajectory in (B) does not exactly repeat itself every oscillation. This is an example of quasiperiodic behavior, in which the period of oscillation is an irrational number.

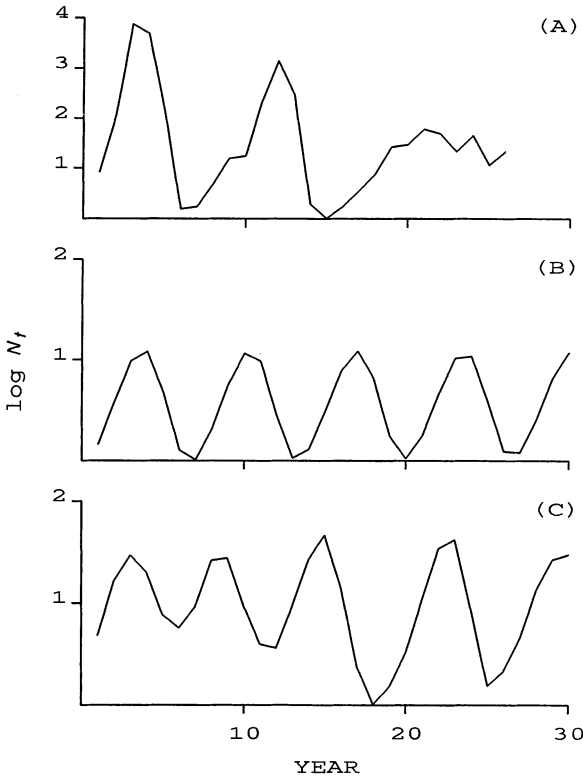


FIG. 8. *Lymantria dispar*: observed time series (A), and trajectories predicted by the response-surface model (RSM) without noise (B), and with noise (C) (ϵ_t is normally distributed with mean zero and standard deviation $\sigma = 0.2$).

ble, exponential damping (three cases); stable, oscillatory damping (six cases); limit cycle (one case); quasi-periodicity (two cases); and chaos (one case) (Table 3). The parameters defining estimated response surfaces are listed in Table 4 for each insect species. In the following subsections we will consider each of these categories in turn, paying particular attention to whether the RSM results are consistent with those from the ACFs, and to the effects of nonstationarity.

No regulation.—Iteration of the model estimated by RSM for the garden chafer, *Phyllopertha horticola*, exhibited unstable behavior: at first the population grew at a very slow rate, and then it suddenly crashed (population density decreasing by about five orders of magnitude). Regressions of r_t on lagged population densities N_{t-1} and N_{t-2} (Turchin 1990) did not indicate any density regulation in this population, suggesting that the garden chafer population may undergo a density-independent “random walk.” This conclusion is supported by the nonstationary shape of the ACF (Fig. 3A), and is in agreement with the previous analysis of Milne (1984). With a very large number of data points that were generated by a density-independent population process, RSM would fit a level plane to the scatterplot of r_t as a function of N_{t-1} and N_{t-2} . Since we had to deal with a limited amount of data, it appears

that RSM fitted the vagaries of the data rather than the actual relationship, producing a meaningless result.

Equilibrium dynamics: exponential stability.—Of the three cases classified by RSM as exponentially stable, one (*Dendrolimus pini*) had an ACF that exhibited evidence of nonstationarity. When the *Dendrolimus* data were made stationary with quadratic detrending, RSM suggested that this population may be in the oscillatory damping regime, which agrees with the periodicity exhibited by the ACF of the detrended series (Fig. 4). This result demonstrates the sensitivity of RSM results to nonstationarity.

The case of *Choristoneura fumiferana* presents a puzzle. Although it was suggested that this population undergoes periodic outbreaks (Royama 1984), regressing r_t on lagged population densities did not detect any signs of density-dependent regulation. The shape of the ACF is consistent with either of the two hypotheses: that the budworm population cycles with a very long period, or that it is nonstationary (for example, the population could be tracking a long-term oscillatory trend in its food base). It is clear that data on more than a single outbreak will be needed before we are able to reach any conclusions about this insect’s dynamics.

The final case for which RSM indicates exponential stability is *Panolis flammea*. This finding is consistent

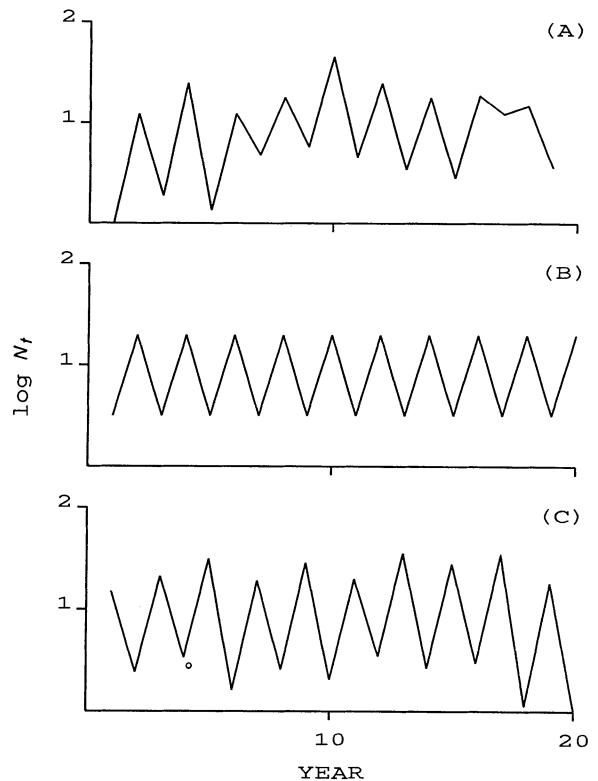


FIG. 9. *Drepanosiphum platanoides*: observed time series (A), and trajectories predicted by the response-surface model (RSM) without noise (B), and with noise (C) (ϵ_t is normally distributed with mean zero and standard deviation $\sigma = 0.2$).

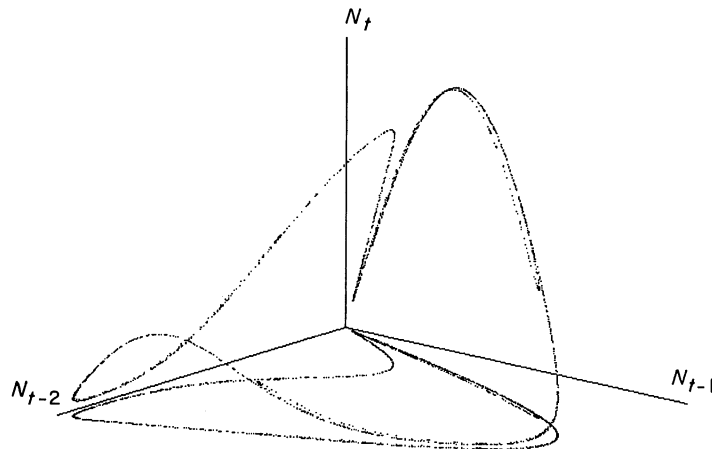


FIG. 10. The strange attractor extracted from the *Phyllaphis* time series. This graph was produced by iterating Eq. 6 2200 times on the computer. The first 200 points were discarded, and the last 2000 points were plotted in the N_t vs. N_{t-1} vs. N_{t-2} phase space. To aid in visualizing the attractor, a projection of the attractor onto the N_{t-1} vs. N_{t-2} plane is also shown.

with the shape of the ACF, which rapidly decays to zero and does not show any signs of periodicity thereafter. Thus, our result suggests that density fluctuations of almost three orders of magnitude observed in this population were produced by density-independent factors. Nevertheless, the population is regulated around

an equilibrium, as indicated by the RSM result of exponential stability and significant regressions of r_t on both N_{t-1} ($F_{1,55} = 7.31$, $P < .01$) and N_{t-2} ($F_{1,55} = 7.00$, $P < .05$).

Equilibrium dynamics: damped oscillations.—Two of the six cases classified as damped oscillations were nonstationary. One, the southern pine beetle (*Dendroctonus frontalis*), may have been misclassified, since we do not know how to detrend a series with the kind of nonstationarity exhibited by the southern pine beetle (constant mean but increasing amplitude of oscillations). The second nonstationary case, *Hyloicus pinastri* showed a trend in the mean. Removing the trend did not alter the RSM result, but did produce stronger evidence for periodicity in the ACF (ACF was significantly negative at the half-period, but not significantly positive at the full period).

The damped-oscillation dynamics reconstructed by RSM for the stationary cases ran the complete spectrum from rapid to slow convergence to the equilibrium. The slowest convergence to equilibrium was found in the fall webworm population (Fig. 6B), which is one of the populations with ACF suggestively, but not significantly periodic. It is known that populations characterized by oscillations slowly converging to an equilibrium will behave like noisy limit cycles in a stochastic environment (e.g., Poole 1977). Thus, adding a modest amount of stochastic variation to the deterministic dynamics extracted by RSM produces sustained pseudoperiodic oscillations (Fig. 6C).

Complex dynamics: limit cycles and quasiperiodicity.—The three insect time series that were classified by RSM as limit cycles or quasiperiodic dynamics were also the ones for which the ACF had a significantly periodic component (Fig. 3E, F, and G and Table 3). Moreover, the period of extracted oscillations was very close to the observed period: 8 vs. 9 yr for larch budmoth (Fig. 7), 7 vs. 8.5 yr for gypsy moth (Fig. 8), and

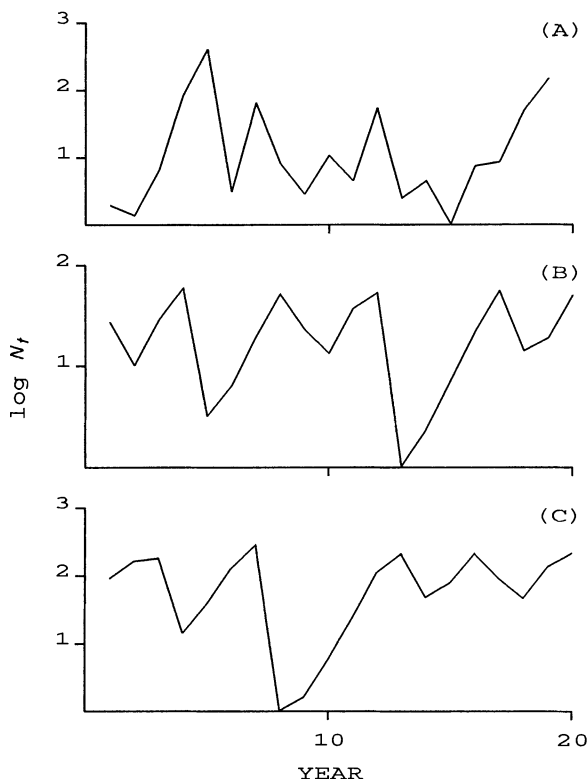


FIG. 11. *Phyllaphis fagi*: observed time series (A), and trajectories predicted by the response-surface model (RSM) without noise (B), and with noise (C) (ϵ_t is normally distributed with mean zero and standard deviation $\sigma = 0.2$).

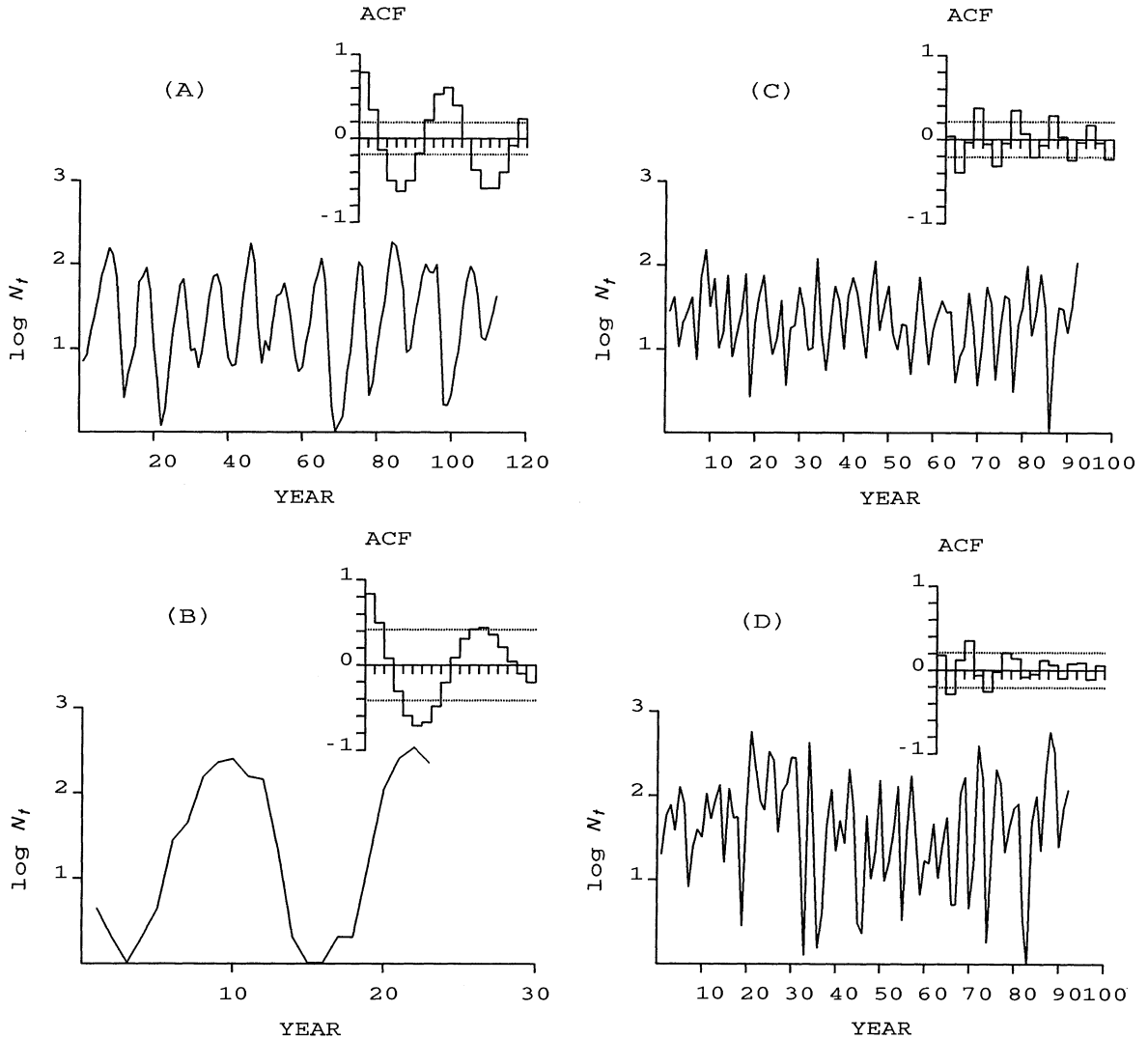


FIG. 12. Four mammal time series for which the autocorrelation function (ACF) was significantly periodic. (A) lynx, (B) belyak hare, (C) colored fox, (D) arctic fox.

2 vs. 2 yr for sycamore aphid (Fig. 9). The relative amplitude of the oscillation in the larch budmoth and the sycamore aphid was also matched by the RSM trajectories (Figs. 7 and 9), although RSM underestimated the amplitude of gypsy moth oscillations. Such a close correspondence between patterns observed in actual time series and the time series generated by response surfaces is a strong indication that RSM is at the very least capable of correctly reconstructing periodic complex dynamics.

Complex dynamics: chaos.—Finally, in one case, *Phyllaphis fagi*, RSM-extracted dynamics were of the chaotic kind. The “strange” nature of the attractor extracted from this time series is apparent when it is plotted in the $N_t - N_{t-1} - N_{t-2}$ phase space (Fig. 10). It is not clear, however, how robust this result is. Does the prediction of chaos depend on a delicate balance

of RSM-estimated parameters? We addressed this question by performing a sensitivity analysis on the data set. We excluded each data point in turn, estimated the response surface for the reduced data set, and determined its qualitative behavior. Our results indicate that the prediction of chaos in this case was not due to a freak combination of “just right” data values, since chaos was extracted in 9 out of 17 reduced data sets, with the rest divided between limit cycles (2 cases, with periods of 8 and 5), stability (3 cases), and diverging oscillations leading to extinction (3 cases).

RSM-predicted dynamics (Fig. 11B and C) were characterized by periods of exponential growth for 3–4 yr (lines of constant slope on the log scale) followed by crashes, as well as by periods of rapid oscillations. Some features of the observed trajectory were similar to RSM dynamics. Observed time series had two pe-

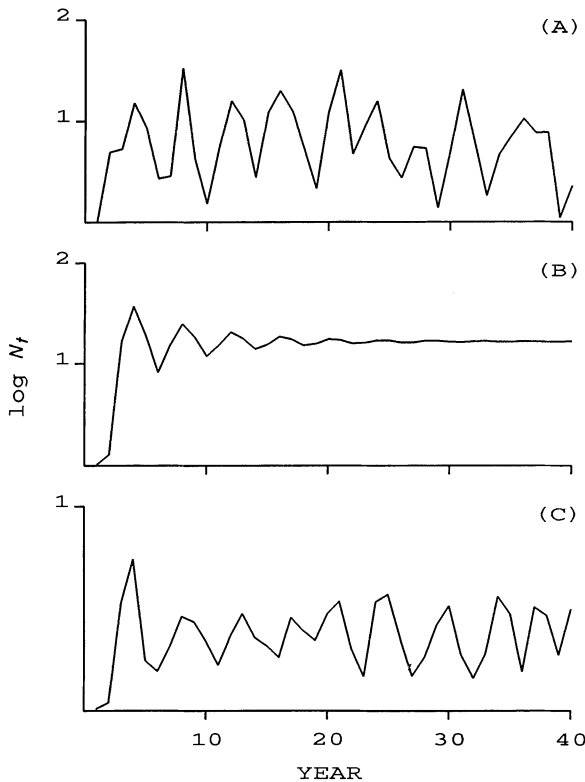


FIG. 13. Colored fox: observed time series (A) (only the middle 40 yr are shown), and trajectories predicted by the response-surface model (RSM) without noise (B), and with noise (C) (ϵ_t is normally distributed with mean zero and standard deviation $\sigma = 0.2$).

riods of almost exponential growth (3 and 4 yr), with the first period followed by a crash (what happened after the second period is unknown), and there was a period of rapid oscillations during the middle portion of the time series (Fig. 11A). On the other hand, the actual trajectory did not exhibit a rigid regulatory “ceiling” that was a characteristic feature of simulations. Another point of similarity between the observed and extracted dynamics was that ACFs of both exhibited weak periodicities, with a period of 7 yr in the data and 5 yr in the RSM model.

At this time we know little about the ability of RSM to extract deterministic chaos from data. In addition, the data are sparse. Therefore we cannot make any definite statements about whether endogenous dynamics of the *Phyllaphis* population are chaotic or not. However, the fact that RSM did extract chaotic dynamics in at least one case indicates that the region within the parameter space where the model (Eq. 6) is chaotic overlaps with the region enclosing parameter estimates for actual insect populations. In other words, one does not need to postulate biologically unrealistic values of parameters to obtain chaotic dynamics within the framework of the model (Eq. 6).

Vertebrate data sets

The time series of vertebrate populations exhibited a similar spectrum of ACF patterns. In particular, examination of ACFs suggested that there were four cyclic mammal populations (Fig. 12). Vertebrate populations also exhibited many of the same dynamic behaviors that we found among insects: 3 cases exhibited unstable oscillations leading to extinction, 6 cases were classified as exponential damping, 11 cases as damped oscillations, and 2 as quasiperiodic dynamics. There were no cases of chaos. Of the four mammal populations that had significantly periodic ACF, two were found to have quasiperiodic RSM dynamics (lynx and belyak hare). RSM-reconstructed dynamics for the colored fox and the arctic fox were damped oscillations. The damped oscillations regime is more plausible than a four-point cycle for these populations because the ACF peaks were of rather small magnitude: ACF at the first peak, 4 yr (ACF[4]) was <0.4 (compare this with the lynx ACF[10] = 0.6, or the larch budmoth ACF[9] = 0.7). Such a sharp drop-off in ACF reflects a much noisier-looking time series of the two foxes, compared to either lynx or belyak hare, and therefore is more consistent with RSM-indicated oscillatory damping, than with limit cycles. The period of damped oscillations predicted by RSM was 4 yr (Fig. 13), the same as the pattern in the ACF. This result once again demonstrates the ability of RSM to accurately mimic the patterns observed in actual time series.

DISCUSSION

Our results are very different from those of Hassell et al. (1976), who concluded that all but 2 of their 24 insect populations had exponentially stable point equilibria. By contrast, our response-surface methodology (RSM) found exponential stability in only 3 of our 14 insect populations. The remaining populations were classified as unregulated (one case), damped oscillations (six cases), limit cycles (one case), quasiperiodic oscillations (two cases), and chaos (one case). The vertebrate examples exhibited a similar spectrum of dynamics, although there were no cases of chaos. We do not wish to claim that all of these classifications (especially the two most extreme ones, *Phyllaphis* and *Phyllopertha*) are correct. This fairly small number of examples does, however, include convincing cases of periodic dynamics (damped oscillations, limit cycles, and quasiperiodicity) and one case with parameter values at least approaching those producing chaos. We conclude, then, that the complete spectrum of dynamical behaviors, ranging from exponential stability to chaos, is likely to be found among natural populations.

The contrast between our findings and those of Hassell et al. (1976) resulted from three important differences in methodology: (1) fitting actual time-series data instead of the two-step method of Hassell et al., (2) using a model with a much more flexible functional

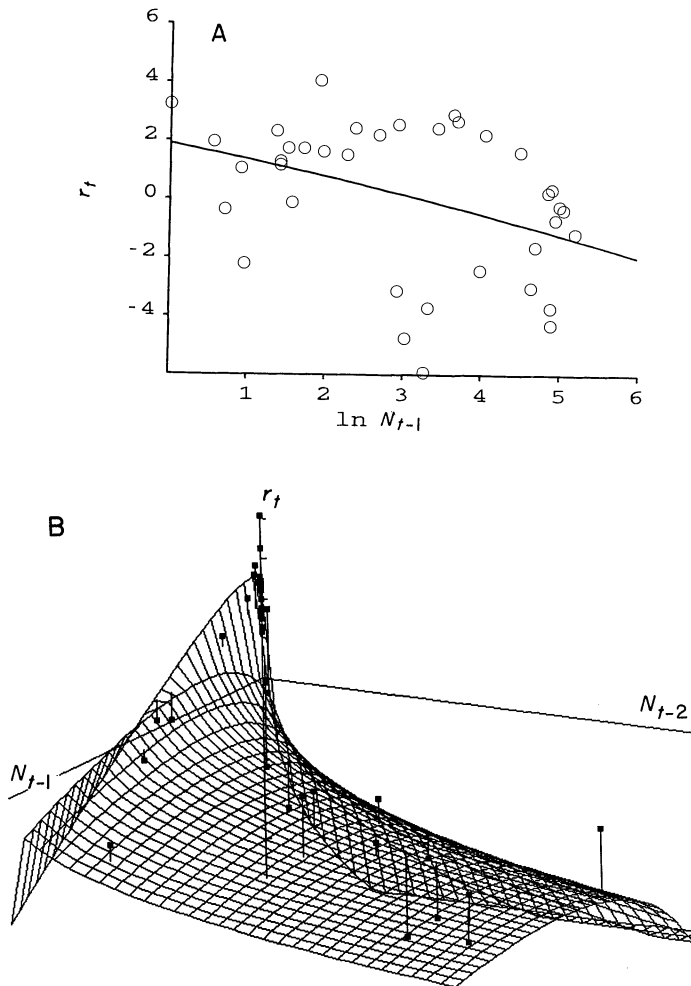


FIG. 14. Response function estimated for larch budmoth: (A) r_t is a function of N_{t-1} only, and (B) r_t is a function of both N_{t-1} and N_{t-2} .

form, and (3) accounting, albeit indirectly, for the multidimensional nature of population dynamics that could be due to interactions with other populations within the community, or to population structure. We believe that the last of these differences is the most critical. Indeed, fitting data with a first-order model (only terms involving N_{t-1} [the previous year's density]), which in all other respects was identical to model (Eq. 6), produced results very similar to those of Hassell et al.: 11 cases of exponential stability, 2 cases of damped oscillations, and one limit cycle (the sycamore aphid). It is revealing that this truncated model, as well as the analysis of Hassell et al. (1976), classified the larch budmoth population in the Engadine Valley in Switzerland (see Baltensweiler and Fischlin 1987) as exponentially stable, although this population is arguably the most convincing example of a quasiperiodic attractor in our data set. This misclassification happened because in this population there is little effect of N_{t-1} on r_t (the rate of population change), and a large effect of N_{t-2} (compare Fig. 14A to 14B). When we reduce

the dimensionality of the model by ignoring N_{t-2} , we turn a clean, strongly nonlinear response surface in three dimensions into a cloud of largely uninformative points in two dimensions. Fitting the model to these points then yields a gentle slope (Fig. 14A), indicating mild direct density dependence and thus stability.

The flexibility of our RSM model, provided by inclusion of both the Box-Cox transformation and quadratic terms, also was essential for correct classification. For example, the quadratic term (although not the second lag) was necessary for an accurate reconstruction of the sycamore aphid dynamics. Fitting a model with either one or two lags but no quadratic terms leads to a classification of damped oscillations, in contrast to the conclusion of a two-point limit cycle obtained by a quadratic RSM (with either one or both lags). Simulations of the RSM model with no quadratic terms produced an ACF that decayed to zero much faster than the ACF of either the data or the full RSM model. In addition, the full model came much closer to reproducing the perfect alternation of increases and

decreases seen in the observed series. Thus, the quadratic term was essential for reaching the correct conclusion in this case.

The preceding examples suggest that leaving out important factors, such as delayed density dependence or strong nonlinearities, may lead to incorrectly classifying a population as more stable than it actually is. In other words, use of overly simple models for reconstructing endogenous dynamics from data may be biased in favor of finding stability. This may well apply to our own analysis, since regressions of r_t on lagged population densities indicate that lags of order higher than two are not infrequent (P. Turchin and A. D. Taylor, *unpublished analysis*). Analysis of cases with higher dimensional response surfaces might well result in additional findings of complex dynamics, though the feasibility of such expanded analysis will be limited by the relatively short length of a typical ecological time series.

The methodology used in this paper is by no means perfect. For instance, it cannot effectively handle systems with multiple equilibria. By applying a standard model to each case, we also risk misclassifying some instances by using an inappropriate model. As we noted above, inclusion of additional lags may be appropriate in a number of cases (subject to data constraints). However, our model may be more complex than needed for some systems; whether such overfitting in any way biases the results is unknown but under investigation.

Another limitation is that our approach currently lacks any means for determining "confidence intervals" around our dynamical predictions. Confidence limits can be obtained for each parameter estimate of the model (Eq. 6), but they tell us nothing about how variation in parameter estimates will affect our conclusion about the type of extracted dynamics. Another potential problem is the estimation bias that arises when models such as Eq. 6 are fitted to data with substantial observation errors (Walters and Ludwig 1987).

In closing we note that much controversy surrounding the issue of population regulation stems from the one-dimensional viewpoint, held by many, that attempts to place all populations within the spectrum ranging from tight control around a stable point equilibrium (regulation) to little or no dynamical feedback in population density (no regulation). Bias against complex endogenous dynamics is so strong that most discussions or criticisms of population regulation do not mention (e.g., Wolda 1989)—or even dismiss outright—the possibility that populations may undergo cyclic or chaotic fluctuations. The following quotations show that this view is shared both by experimentalists: "the rarity with which populations fluctuate cyclically in nature . . ." (Hairston 1989:6), and theoreticians: "deterministic stability is the rule rather than the exception, at least with insect populations" (Nisbet and

Gurney 1982:55). Our results suggest otherwise. We argue, therefore, that natural populations cannot be ranked within a one-dimensional spectrum going from no regulation to tight regulation around a point equilibrium. Instead, a two-dimensional scheme needs to be employed, with one axis indicating the relative strength of the exogenous (density-independent) component, and the other axis indicating the type of endogenous dynamics.

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