

# Identifying Predator–Prey Processes from Time-Series

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**The functional response is a key element in predator–prey models as well as in food chains and food webs. Classical models consider it as a function of prey abundance only. However, many mechanisms can lead to predator dependence, and there is increasing evidence for the importance of this dependence. Identification of the mathematical form of the functional response from real data is therefore a challenging task. In this paper we apply model-fitting to test if typical ecological predator–prey time series data, which contain both observation error and process error, can give some information about the form of the functional response. Working with artificial data (for which the functional response is known) we will show that with moderate noise levels, identification of the model that generated the data is possible. However, the noise levels prevailing in real ecological time-series can give rise to wrong identifications. We will also discuss the quality of parameter estimation by fitting differential equations to such time-series.** © 2000 Academic Press

**Key Words:** predator–prey model; functional response; model selection; time series; observation error; process error.

## INTRODUCTION

Finding the functional relationship between observed variables is one of the major tasks in ecology. Often, several mathematical forms based on different assumptions about the dominant mechanisms at work are available. Fitting these functions to the data and applying goodness of fit as a criterion to select the best model are then used to detect the dominant mechanism for the particular system from which the data were obtained. One particular application of this concept is to test alternative dynamic predator–prey models against predator–prey time series data and thus to identify the processes that drive these dynamics. While these processes can sometimes be identified by direct experimentation, such experiments often involve very artificial conditions (e.g., using starved predators to estimate consumption) or are not performed on the appropriate time scale (on the behavioral scale instead of the demographic scale), or the dynamic

changes during the experiment are difficult to consider (e.g., prey depletion during the consumption experiment). The dynamic approach to fitting the dynamic model to time-series data avoids these problems and has the additional advantage that it can be applied to data from historical experiments where only the time-series were reported. Furthermore, not only conformance between the processes and the data is tested, but also how these processes are connected to build the full model (e.g., conservation of mass). However, the dynamic approach suffers from other constraints due to the fact that process is inferred indirectly from the dynamics. We thus regard the dynamic approach as complementary to other, more direct studies.

How these dynamic models are fitted to a time series depends on the source of stochastic noise in this time series: if the dynamics are deterministic and there is only observation error (measurement error), then the whole trajectory (solution of the dynamic model) is fitted to the

data (termed “observation error fit” by Pascual and Kareiva, 1996). If there is only dynamic noise (environmental or demographic stochasticity) and the data are measured exactly, then each observation is taken as an initial condition and the fitting is based on predicting a short time period ahead (termed “process error fit” by Pascual and Kareiva, 1996).

Harrison (1995), for example, reanalysed Luckinbill’s (1973) classical protozoan data and fitted them to 11 different (continuous) predator–prey models. He assumed that the data contained only noise due to observation error. Unfortunately, his statistical comparison tests did not take into account the different numbers of parameters among the different models. It is therefore not surprising that a rather complicated model with 11 parameters fitted the data best. Carpenter *et al.* (1994) fitted (discrete) predator–prey models to phyto- and zooplankton time series from North American freshwater lakes to test whether the predation process depended significantly on predator density. Their analysis was designed to treat data that contained noise due to both observation error and process error, fitting in such a way that the prediction one time step ahead was minimized. To avoid any assumptions about the presence or absence of higher predation on the predators they fitted only the prey equation, using the predator data as an input. While their tests took the number of parameters into account, they did not justify the use of discrete models (with the time step being the time between measurements) to describe a system showing the characteristics of a continuous system.

Does a better fit of one model compared to another one always imply that its functional form represents the actual processes at work more accurately? There exist, for example, simple algebraic differential equations that can fit perfectly to any finite time series (Rubel, 1981). It can also happen that very different models fit equally well to the same data (Feller, 1939). A slightly better fit of one of these models could be an artifact of the time series being one particular realisation of an ecological process with all its random influences. Another realisation (replicate) might give a different result. Therefore, the reliability of goodness of fit to determine the functional form of a process from time series data should be examined, e.g., with artificial data for which the functional form is known.

Carpenter *et al.* (1994) were aware of this problem and they tested their method with artificial data that they created with parameter values typical of their limnological system. In this article, we will perform a similar analysis for a larger range of ecological systems. We will test whether predator–prey time series that represent the

(continuous) dynamics of a stable focus contain sufficient information to detect if predator density influences the predation process strongly enough to influence the dynamics of the system. Such time series typically contain noise due to both observation error and process error. The fitting techniques will include observation error fit (as used by Harrison, 1995) and a modified process error fit (as used by Carpenter *et al.*, 1994). Unlike Carpenter *et al.*, we will predict  $s$  steps ahead instead of only one step ahead. The idea is to predict over a time range during which nonlinear effects become detectable. The determination of  $s$  will be based on the arguments developed and justified by Ellner and Turchin (1995).

We will work with very simple predator–prey models whose purpose is not to describe the dynamics of a specific system perfectly but rather to describe it in a qualitatively correct manner. Simplicity in the description of the key processes (growth, death) is essential in models of more complex food chains or whole food webs, where the number of parameters becomes a limiting factor for analysis and parameterization. Although such complex models are not the subject of this article, it is with this purpose in mind that we deliberately consider simple predator–prey models.

Based on the principles of mass conservation (Ginzburg, 1998) and decomposition of the dynamics of a population into birth and death processes, the canonical form of such a predator–prey model is

$$\begin{aligned} \frac{dN}{dt} &= f(N)N - g(N, P)P =: F_N(N, P) \\ \frac{dP}{dt} &= eg(N, P)P - \mu P =: F_P(N, P), \end{aligned} \quad (1)$$

where  $N$  and  $P$  are the abundances of prey and predator respectively,  $e$  is the conversion efficiency, and  $\mu$  is the death rate of the predator in the absence of prey. The key processes are the prey growth function  $f$  and the link between prey and predator, the functional response  $g$  (prey eaten per predator per unit of time, Solomon, 1949). The latter represents the predation process. We will test if model fitting can reveal whether  $g$  is approximately a function of prey abundance only ( $g = g(N)$ , as it is the case in standard functional response models, e.g., Lotka (1924) or Holling (1959)) or  $g$  also depends significantly on predator abundance. Such predator dependence influences the stability of predator–prey systems (DeAngelis *et al.*, 1975; Murdoch and Oaten, 1975) and the response of the prey equilibrium to an enrichment of the system (Arditi and Ginzburg, 1989).

Its detection in natural predator–prey time series is therefore a challenging task.

Introducing explicit predator dependence,  $g = g(N, P)$ , as was done by DeAngelis *et al.* (1975), normally increases the complexity of the function  $g$ , making it difficult to compare with the simpler prey-dependent form  $g = g(N)$ . A special case of a simple predator-dependent function was suggested by Arditi and Ginzburg (1989), assuming that  $g = g(N/P)$ . Models of this type are equally simple as prey-dependent models and can therefore be directly compared with them. However, ratio dependence represents only one special case of predator dependence, and the only reason to favour it against other predator-dependent functions is its simplicity. This ratio-dependent functional response, like other predator-dependent functional responses, but in contrast to prey-dependent functional responses, leads to the observed correlated equilibria of prey and predators along a gradient of richness (Arditi and Ginzburg, 1989; Mazumder, 1994; McCarthy *et al.*, 1995). The issue of ratio-dependence is currently subject to some debate (Abrams, 1994; Sarnelle, 1994; Akçakya *et al.*, 1995; Abrams, 1997; Bohannan and Lenski, 1997; Hansson *et al.*, 1998).

In this article, we do not address the question of the ecological significance of one model or the other. Instead, we attempt to answer whether it is possible to assess the importance of predator dependence from typical time series. In particular, we analyse the dynamics of predator–prey systems with low initial conditions and trajectories reaching a stable, non-trivial equilibrium after one or two large amplitude oscillations. Such dynamics are considered typical of seasonal dynamics of phyto- and zooplankton in freshwater lakes of the temperate zone (Sommer *et al.*, 1986) or of chemostat and batch culture experiments with protozoa (another source of published time series data, e.g., Gause *et al.*, 1936, Luckinbill, 1973). Typically, such time series are short (about 20 data points per season in lakes, 10–50 data points with protozoa), and can have considerable observation and process error. Differential equations seem an adequate tool to describe these systems since there are overlapping generations and large numbers of individuals. Using a simulation approach, we will generate artificial time series (“pseudo-data”) with a prey-dependent and a ratio-dependent functional response of the same simplicity, to which we will add process and observation error. Regression techniques will then be applied and we will test whether the best-fitting model is indeed the one that created the data. A by-product of this kind of identification is the computation of the actual model parameters. We will analyze the quality of these estimates (value, standard deviation) to

test the power of the regression method for parameter estimation.

## THE ALTERNATIVE MODELS

Building on the canonical form (1) we use a standard logistic growth for the reproduction function  $f$ ,

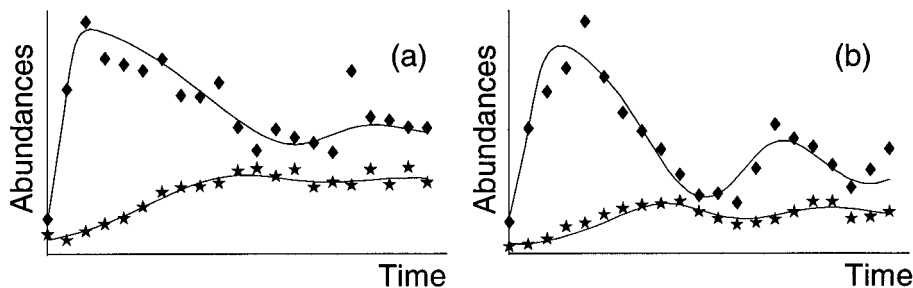
$$f(N) = r \left( 1 - \frac{N}{K} \right),$$

with maximum growth rate  $r$  and carrying capacity  $K$ . Two models (that both have the same number of parameters) are chosen for the functional response, a prey-dependent one and a predator-dependent one. We chose the classical Holling type II model on the one hand, and a ratio-dependent model (Arditi and Michalski, 1995) on the other,

$$\frac{aN}{1 + ahN} \leftarrow g(N, P) \rightarrow \frac{\alpha N/P}{1 + \alpha hN/P},$$

where  $a$  is the searching efficiency,  $h$  the handling time, and  $\alpha$  some kind of total predator searching efficiency. We selected the Holling type II form rather than equally plausible alternatives such as the Ivlev functional response (Ivlev, 1961) simply because it is more widely used in ecology as well as in microbiology (Monod, 1942). The particular form of the predator-dependent functional response closely resembles the Holling type II function, thus making direct comparison between the two models possible. This form also tends to be regarded as the standard form of a ratio-dependent functional response in mathematical studies (Freedman and Mathsen, 1993; Cosner, 1996; Kuang and Beretta, 1998) and it is known in the microbiological literature as Contois’ model (Contois, 1959).

Despite their structural difference, the two models can produce very similar temporal dynamics. This is illustrated in Fig. 1: time series were created with both models (with parameters corresponding to a stable focus), process error and observation error were added, and then both models were fitted crosswise to these time series (see the next section for the details of these methods). It can be seen that each model fits very well to the data created by the other model. A good fit alone is therefore a poor indicator whether the used model correctly describes the processes that generated the data.



**FIG. 1.** Examples illustrating that each model (the prey-dependent and the ratio-dependent one) can approximate satisfactorily time series data that were created by the other model. (a) Ratio-dependent model fitted to prey-dependent data. (b) Prey-dependent model fitted to ratio-dependent data. Diamonds represent the prey time series and stars the predator time series. See the text for further details.

## MATERIALS AND METHODS

### Artificial Time Series

For this analysis to be valid for many different predator–prey systems, the pseudo-data must be generated with widely differing parameter values. Possible parameter values must adhere to ecological and dynamical constraints. Such a constraint applies to the conversion efficiency  $e$ , which should be within the interval  $(0, 1)$  if abundances of both prey and predator are measured in biomass (the usual case in freshwater studies). Parameters  $K$  and  $h$  can be chosen arbitrarily since they depend entirely on the time and weight scales that are used. Given these three parameters, we can find intervals for the remaining parameters by the requirement defined above: existence of a non-trivial stable equilibrium reached through oscillations. Within these intervals, the parameters are chosen randomly. Initial values of prey and predator abundances are then chosen 2 to 10 times below their equilibrium abundances. Such a randomly created parameter set (with initial values) is retained only if the following properties are respected: (1) prey and predator equilibria do not differ by more than a factor of 100 and (2) the deterministic trajectories of prey and predator show at least two distinct oscillations before reaching the equilibrium. The simulation time  $T$  is set in order to have these two oscillations. These final criteria assure an at least twofold variation in predator abundance (which is essential for model identification) and keep prey and predator abundances on comparable scales (see Fig. 1 for two examples).

For each functional response, 20 such parameter sets were created. In analogy with the replicates of a typical ecological experiment, we created 5 replicate time series with each parameter set by numerical integration of a stochastic version of the differential equations (1),

$$\begin{aligned} N_{t+\Delta t} &= N_t + F_N(N_t, P_t) \Delta t + \sigma_p N_t \varepsilon_{N,t} \Delta t \\ P_{t+\Delta t} &= P_t + F_P(N_t, P_t) \Delta t + \sigma_p P_t \varepsilon_{P,t} \Delta t, \end{aligned} \quad (2)$$

with  $\varepsilon_{N,t}$  and  $\varepsilon_{P,t}$  being random normal variates with mean zero and variance one,  $\Delta t := T/500$ , and  $\sigma_p$  the process error level. This stochastic process was sampled at 20 equal time steps and a lognormally distributed observation error (with coefficient of variation CV) was incorporated by multiplication by the exponential of a normal variate with mean zero and variance  $\log(1 + CV^2)$ . With this formulation, both process error and observation error are of a multiplicative type, as suggested to be typical for natural populations (Hilborn and Mangel, 1997; Carpenter *et al.*, 1994). Time series with two noise levels were created, with CV and  $\sigma_p$  both set to 0.05 or both set to 0.1. The first case is comparable to protozoan laboratory data and the latter to data from freshwater plankton experiments (Carpenter *et al.*, 1994). This makes a total of 400 data sets (2 models  $\times$  20 parameter sets  $\times$  5 replicates  $\times$  2 noise levels).

### Error Functions

The key part in fitting a model to data is the formulation of the function to be minimized. Depending on the stochastic elements in the data (process and/or observation error), the error function must be chosen accordingly. Ecological data have usually both types of error. However, statistical methods that take both into account are rare and little is known in the case of nonlinear regression. The usual practical solution is therefore to neglect one of the errors and to develop the error function for the other (Pascual and Kareiva, 1996). We will follow this approach but also test two error functions that claim to be able to take both errors into account.

For ease of notation, consider a simple autonomous differential equation  $\dot{y} = f(y)$  with time series data

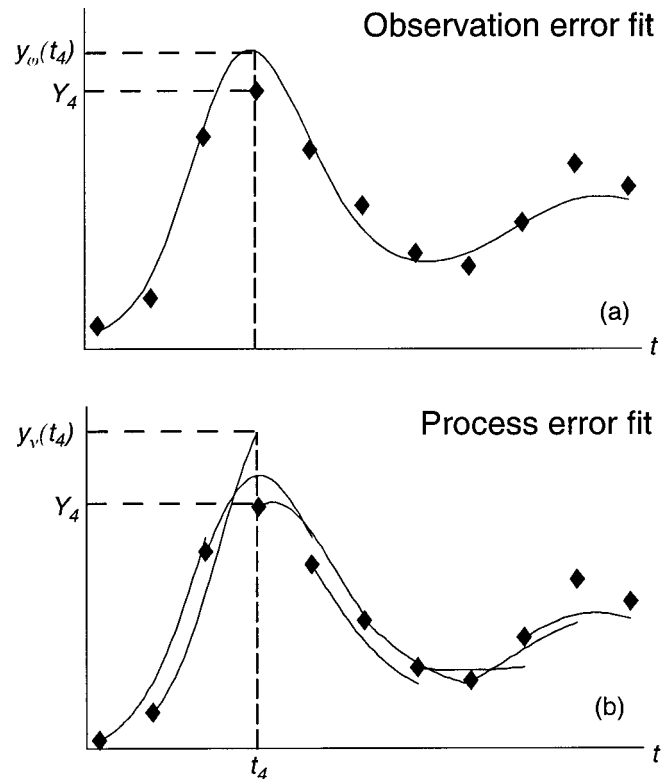
$(t_i, Y_i)_{1 \leq i \leq m}$ , where  $t_i$  is the time at which the population  $y$  is observed to have density  $Y_i$ , and  $m$  is the number of data points. [For predator-prey models  $y$  has to be replaced by the pair  $(N, P)$  and adaptations for this case that are not obvious in the development below will be noted in brackets.] Let  $y(t_i)$  be the deterministic solution of the differential equation at time  $t_i$  and  $\hat{y}_i$  the (unknown) real population density at time  $t_i$ . If the data have only observation error, then there is only one initial condition,  $y(t_0) = \hat{y}_0$ , that is treated as a free parameter. In this case we will denote the deterministic prediction as  $y_\omega(t_i)$ . If there is only process error, then the initial conditions are different for each consecutive data point and are defined as the data value  $s$  steps previously,  $y(t_{i-s}) = Y_{i-s}$ , with deterministic prediction  $y_v(t_i)$  (see Fig. 2).  $s$  is chosen as the smallest value for which the autocorrelation in the time series is below 0.5. Ellner and Turchin (1995) had developed this method to choose  $s$  on empirical rounds and argued that nonlinear patterns can be detected more reliably with this  $s$ -step-ahead prediction than by the standard one-step-ahead prediction. In our artificial data,  $s$  always took the value 2. With these notations, the process can be written as

Observation error only	Process error only
$\hat{y}_i = y_\omega(t_i, \theta)$	$\hat{y}_i = y_v(t_i, \theta) v(\Delta t_i, f, \theta)$
$Y_i = \hat{y}_i \omega$	$Y_i = \hat{y}_i$
$y(t_0) = \hat{y}_0$	$y(t_{i-s}) = Y_{i-s}$

where  $\theta$  is the vector of model parameters. We will suppose that the observation error  $\omega$  in the densities is of a multiplicative type (lognormal), as used in Carpenter *et al.* (1994) and Hilborn and Mangel (1997), with a constant coefficient of variation  $CV_\omega$ . The (accumulated) process error  $v_i$  depends in general on the time interval  $\Delta t_i = t_i - t_{i-s}$  and on the dynamics  $f$  over this interval. However, for many ecological time series the interval  $\Delta t_i$  is constant and we further simplify by ignoring the effect of the dynamics of  $f$ . Thus, process error  $v \equiv v_i$  will be considered to be a lognormal variate with constant  $CV_v$  (Carpenter *et al.* 1994). These two lognormal errors are considered to be exponentials of two normal variates with expectation 0 and variance  $\sigma_k^2 = \log(CV_k^2 + 1)$ ,  $k = \omega, v$ .

The log-transformed data  $Y_i$  are therefore Gaussian with expectation  $\log(\hat{y}_i)$  and standard deviation  $\sigma_k$ . We define the residuals

$$d_{i,k} = \log(Y_i) - \log(y_k(t_i)), \quad k = \omega, v. \quad (3)$$



**FIG. 2.** The fitting procedure changes with different types of error in the data. (a) Observation error only. The whole trajectory is fitted to the data, treating initial conditions as parameters. (b) Process error only. The best approximation is to fit from one point  $s$  points ahead (two-step-ahead prediction in this case).

Assuming now only one type of error, the error function to be minimized becomes

$$X_k^2 = \sum_{i=1}^m \frac{d_{i,k}^2}{\sigma_k^2}, \quad k = \omega, v. \quad (4)$$

Figure 2 shows the difference between the error functions assuming observation error  $\omega$  or process error  $v$  only. It is visible in this figure that in the case of process error, the first summand ( $i=1$ ) is 0. Note that in  $s$ -step-ahead prediction the error is only computed after the  $s$  steps, not taking into account deviation from intermediate data points where we have made no assumptions about accumulated process error. For vector-valued  $y_k(t_i)$  the residual  $d_{i,k}$  is a vector and Eq. (4) becomes  $X_k^2 = \sum d_{i,k}^T V^{-2} d_{i,k}$  ( $^T$  stands for transposed) with the covariance matrix  $V$  (which is in our case a diagonal matrix with the respective standard deviations as elements). Minimizing Eq. (4) is equivalent to a maximum likelihood approach (Press *et al.*, 1992) and since  $\sigma_k$  is a constant, it is also equivalent to the usual least-squares regression.

Notice that the expectations of  $v$  and  $\omega$  are not 1 but  $\exp(\sigma_k^2/2) = \sqrt{\text{CV}_k^2 + 1}$ ,  $k = \omega, v$ . This may seem strange on first view, but in fact allows the simple formulation of the residuals as the difference of the logs. If we had  $E(v) = E(\omega) = 1$ , then we would have to add  $\sigma_k^2/2$  to the residual (3) for it to have expectation 0 (Hilborn and Mangel 1997, personal communication with R. Hilborn). The problem is purely technical: one may prefer the log-normal variate to have expectation 1 or its log-transform to have expectation 0. With real data, one does not know which assumption is more reasonable. Furthermore, since the  $\sigma_k$ 's are often not known very precisely, there is a risk of doing more harm than good by adding the term  $\sigma_k^2/2$  to the residuals  $d_{i,k}$ . Therefore, one usually finds in the statistical literature the difference of the logs only (Ratkowsky, 1983; Hilborn and Mangel, 1997), and we will follow this safer approach.

If both types of error are present simultaneously,  $y(t_i)$  also depends on the observation error in the data point  $s$  steps previously,  $Y_{i-s}$ . The statistical literature proposes several solutions to this problem of "errors-in-variables." Clutton-Brock (1967) suggested using weighted loss functions with the weights taking account of the uncertainty in  $Y_{i-s}$ ,

$$\text{CB}_1 = \sum_{i=1+s}^m \frac{(y(t_i) - Y_i)^2}{w_i},$$

with

$$w_i = \eta_{\omega, i}^2 + \eta_{\omega, i-s}^2 \left( \frac{dy(t_i)}{dY_{i-s}} \right)^2. \quad (5)$$

The standard deviation of the observation error,  $\eta_{\omega, i}$ , must be known in advance (by multiple samples) and independent of the process error. Here, we assume that the observation error has a constant  $\text{CV}_\omega$  known from replicate measurements. The standard deviation can thus be approximated by  $\eta_{\omega, i} = \text{CV}_\omega Y_i$ . The last term in Eq. (5),  $dy(t_i)/dY_{i-s}$ , is the derivative of the predicted abundance  $y(t_i)$  with respect to the initial condition  $y(t_{i-s}) = Y_{i-s}$ . [Note that for  $y(t_i) = (N_i, P_i)$ , the weight for state variable  $y^j(t_i)$  ( $j = 1, 2$ ) is calculated by

$$w_i^j = \eta_{\omega, j, i}^2 + (\partial_{N_{i-s}} y^j(t_i), \partial_{P_{i-s}} y^j(t_i)) \times \begin{bmatrix} \eta_{\omega, 1, i-s}^2 & 0 \\ 0 & \eta_{\omega, 2, i-s}^2 \end{bmatrix} \begin{bmatrix} \partial_{N_{i-s}} y^j(t_i) \\ \partial_{P_{i-s}} y^j(t_i) \end{bmatrix}$$

and adapted similarly for higher dimensional state variables].

Another loss function, similar to the negative log-likelihood, was also introduced by Clutton-Brock (1967),

$$\text{CB}_2 = \sum_{i=i+s}^m 0.5 \left( \frac{(y(t_i) - Y_i)^2}{w_i} + \log(2\pi w_i) \right),$$

with  $w_i$  defined as in Eq. (5).

Note that in error functions  $\text{CB}_1$  and  $\text{CB}_2$  the residual is no longer the difference of the logs as suggested with the lognormal error type. However, the property of the lognormal error, that the standard deviation is proportional to population size, is preserved. We have also tested the lognormal versions of these equations, as proposed by Clutton-Brock (1967) and by Carpenter *et al.* (1994), but these functions converged very often to strange solutions, maximizing the dependence on the initial condition ( $dy(t_i)/dY_{i-s}$ ) rather than minimizing the residuals. They also converged much more slowly. Using functions  $\text{CB}_1$  and  $\text{CB}_2$  thus simplifies the regression task without losing much generality with respect to the error type.

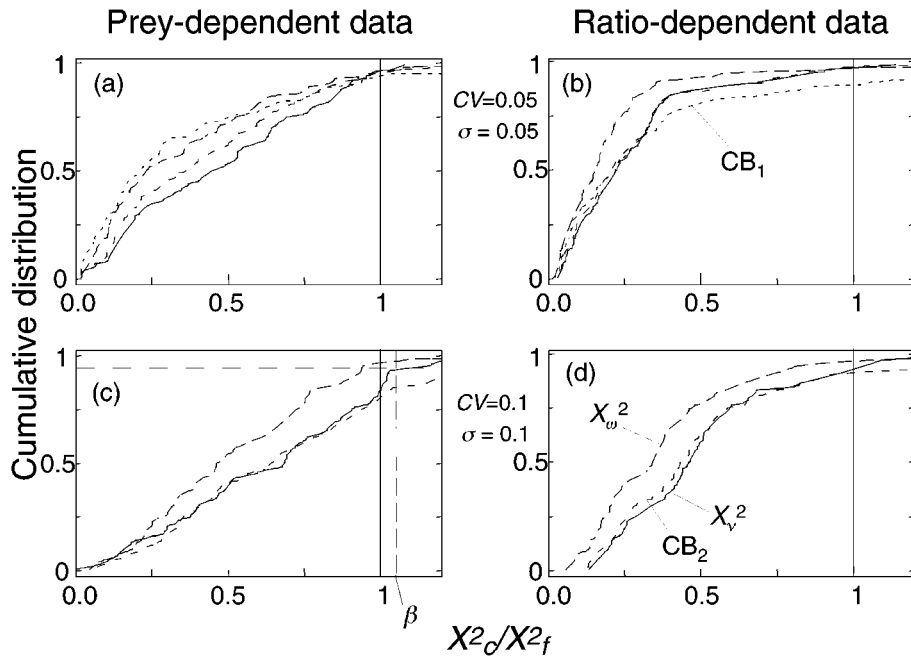
In sum, if the source of error in the data is assumed to be observation error only, the function  $X_\omega^2$  must be used as a regression criterion. If it is thought that process error only is present, the criterion  $X_v^2$  must be used. And if both errors are present simultaneously,  $\text{CB}_1$  or  $\text{CB}_2$  can be used. In our study of identifiability with artificial data, we will consider all situations and we will assess empirically the discriminative performance of all four error functions.

### Fitting and Model Selection

The models are fitted to the data in a three-step procedure that uses a genetic algorithm, a Levenberg-Marquardt method, and a simplex algorithm combined with simulated annealing (see Appendix A for all details).

The quality of adjustment of models to data is assessed with the familiar sum of squares  $X^2$ . This selection criterion is identical to the regression criterion when regression is done using  $X_\omega^2$  or  $X_v^2$  (Eq. (4)). The error functions  $\text{CB}_1$  and  $\text{CB}_2$  cannot be used directly for model selection because the estimators use weightings that differ among models (Carpenter *et al.*, 1994). Since both models have the same number of parameters, no adjustment for this number is needed in the comparison. Therefore, we based model selection for all error functions on the sum of squared residuals of log-transformed values (4).

To quantify the identifiability of the models, we calculate the ratio  $X_c^2/X_f^2$  for each time series with  $X_c^2$  being the sum of squares after the correct model is fitted and  $X_f^2$  the sum of squares after the false model is fitted (i.e., a ratio



**FIG. 3.** Quantile plots of fitting the models to the artificial data.  $X_c^2$  is the error after fitting the correct model,  $X_f^2$  is the error after fitting the wrong model, and the curves are the cumulative distributions of the ratios  $X_c^2/X_f^2$  for the different error functions:—: error function  $X_w^2$ ;—: error function  $X_v^2$ ;---: error function  $CB_1$ ;---: error function  $CB_2$ . CV is the coefficient of variation of the observation error and  $\sigma$  is the standard deviation of the process error with which the data have been created. The dashed straight lines in (c) show for error function  $X_v^2$  the estimation process of  $\beta$  that is used to have 95% confidence of not having misidentified the model (see the text for more details).

smaller than one indicates that the correct model has been identified). The cumulative distribution curves of these ratios ( $X_c^2/X_f^2$  on the  $x$ -axis, the quantile on the  $y$ -axis) give a visual representation of the selection performance of the different types of error functions (see Fig. 3): the height at which the curve hits the vertical line through  $x = 1$  gives the probability of selecting the wrong model (misidentification). Therefore, an error function whose curve crosses this line at a higher  $y$ -value is better than an error function whose curve crosses this line lower. It should be noted that this method of computing the probability of misidentification requires that the correct model be known and is used here to evaluate the candidate error functions for eventual use on real data, but the method cannot be used directly with real data.

### Parameter Estimation

Before we try to fit our six-parameter models it should be verified that the problem is well defined, in the sense that parameters are uniquely identifiable if the state variables are known with arbitrary precision and arbitrary resolution in time (Walter, 1987). Under this assumption, the derivatives of any order ( $\dot{y}$ ,  $\ddot{y}$ , etc.) are known and differentiating Eq. (1) (with logistic prey growth and our two functional response functions) two more times

results in six equations with six unknown parameters. It can be shown (Jost, 1998) that, in both models, this algebraic system has a unique solution and thus our six parameters are identifiable.

Since system stability is of much interest in ecosystems (return time after perturbations, persistence in stochastic environments) we will assess how well we can estimate the local stability of the nontrivial equilibrium with the parameters obtained from the fitting. Stability is measured by  $-\text{Re}(\lambda)$ , with  $\lambda$  being the dominant eigenvalue of the community matrix (the Jacobian at the equilibrium point). This eigenvalue has been calculated analytically (to reduce numerical roundoff errors) before plugging in the estimated or correct parameter values. We will plot the cumulative distribution of the ratios,  $|\text{Re}(\lambda_e)/\text{Re}(\lambda_c)|$ , with  $\lambda_e$  the dominant eigenvalue for the estimated parameters and  $\lambda_c$  the dominant eigenvalue for the correct parameters. The steepness of this curve indicates the variation in the estimation of stability and, if the curve passes through the point (1.0, 0.5), then there is no deviation from the expected median.

The quality of the individual parameter estimates will be assessed by computing their coefficients of variation from fitting the correct model to the five replicated time series (with each error function and for each parameter set). These CVs are computed either with the empirical

mean or with the true parameter value taken as the mean. Averaging the CVs over all parameter sets will give a general idea of the quality to be expected with this type of fitting and data.

## ANALYSIS AND RESULTS

A first comment concerns the numerical efficiency of the algorithms. The Levenberg-Marquardt search worked fast and efficiently close to the optimum (compared to the simplex algorithm), but it often failed when the starting values obtained with the genetic algorithm were far from the optimum. In these cases, the simplex algorithm usually found the basin of attraction much faster. The combination of both algorithms almost always ensured convergence to the optimum (visual control of the fit).

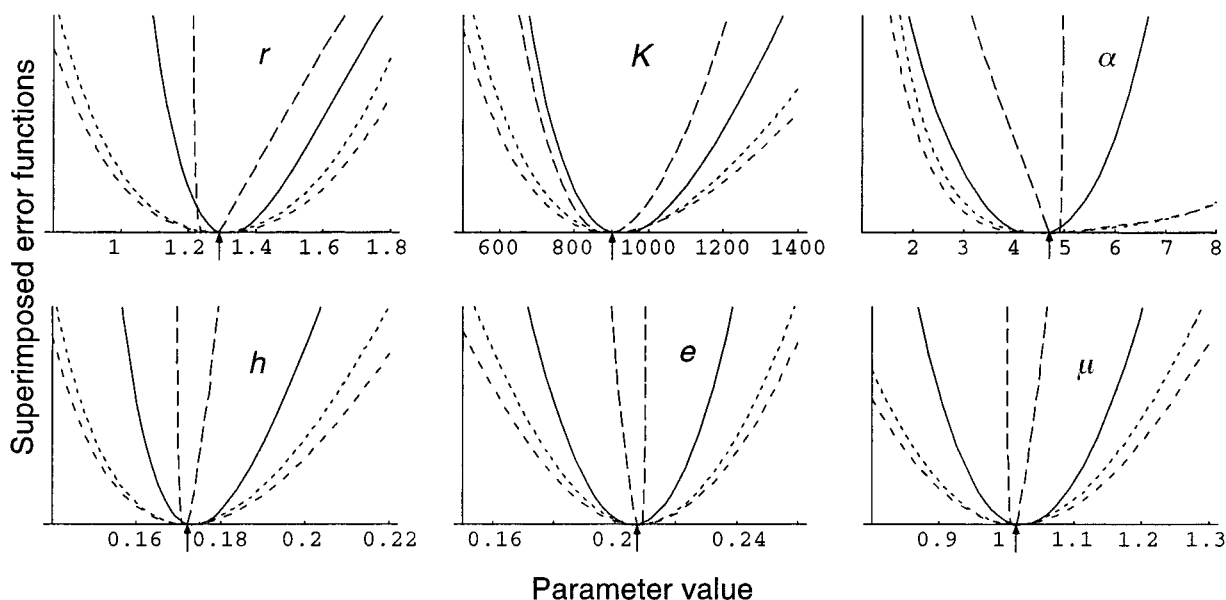
### Model Identification

Figure 3 shows the cumulative distributions of the ratios  $X_c^2/X_r^2$  for all error functions and noise levels. At low noise levels ( $CV = 0.05$ ,  $\sigma_p = 0.05$ ) we see that the error functions  $X_\omega^2$ ,  $X_v^2$ , and  $CB_2$  led to less than 5% misidentifications, while  $CB_1$  had about 15% erroneous identifications. Therefore, we did not use the error function  $CB_1$  at the higher noise levels ( $CV = 0.1$ ,  $\sigma_p = 0.1$ ). At this higher noise, the error function  $X_\omega^2$  still had less

than 5% wrong identifications, while the error function  $X_v^2$  had up to 10% and the function  $CB_2$  performed even worse. Therefore, we concluded that the error functions  $CB_1$  and  $CB_2$  are not useful for model selection, probably because the function that is minimized and the model selection criterion are not the same. If we want 95% confidence in the identification with error function  $X_v^2$ , then there can be at most 5% wrong identifications. From Fig. 3 we can estimate a  $\beta$  such that the probability  $P[X_c^2/X_r^2 > \beta] = 5\%$ . This is done by drawing a horizontal line at the 95% level and projecting the intersection point with the distribution curve onto the  $x$ -axis (illustrated in Fig. 3c). Applied to real data with similar characteristics (dynamics, length, errors) this means that we get 95% confidence of not having misidentified the model by requiring that the ratio of better fit to worse fit is smaller than  $1/\beta$  (since  $P[X_r^2/X_c^2 < 1/\beta] = P[X_c^2/X_r^2 > \beta]$ ), at the cost of not selecting a model when this ratio is too close to 1. In this study  $1/\beta = 0.95$ .

### Parameter Estimation

Figure 4 shows the sensitivity of all four error functions to variations of one parameter at a time (fixing the others at the values with which the time series was created) for the example of a ratio-dependent data set with high noise ( $CV = 0.1$ ,  $\sigma = 0.1$ ). We see that they are all quite unbiased with mostly symmetric error functions.



**FIG. 4.** Four error functions vs parameter values for the example of a ratio-dependent time series with large noise. The curves were shifted vertically to put their minima all at the same height. For this reason we put no label on the  $y$ -axis, but the scale between the curves was preserved to permit comparison. Patterns are the same as in Fig. 3. Actual parameters are  $r = 1.29$ ,  $K = 900$ ,  $\alpha = 4.7$ ,  $h = 0.172$ ,  $e = 0.207$ ,  $\mu = 1.01$ . They are indicated by an arrow.



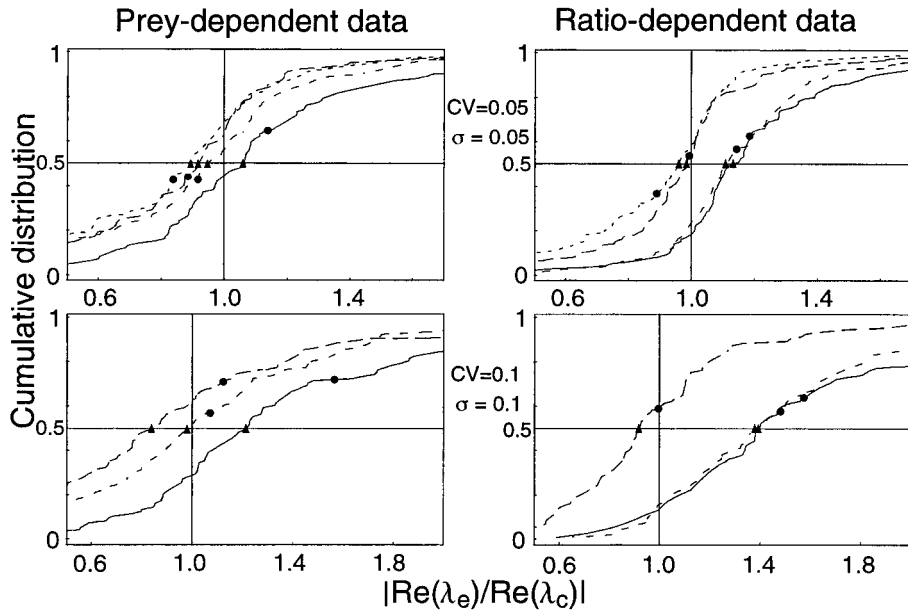


FIG. 5. Quality of the estimated local stability: cumulative distributions of the ratios of the real part of the estimated dominant eigenvalue  $\text{Re}(\lambda_e)$  by the real part of the correct dominant eigenvalue  $\text{Re}(\lambda_c)$ . Thus, curves passing on the right of the point (1, 0.5) show overestimation of stability. Line patterns are the same as in Fig. 3. The dots indicate for each error function the mean of the ratios, while the triangles indicate the medians.

The observation error  $X_\omega^2$  always gave the narrowest function, often asymmetric and with error increasing very fast with distance from the true parameter value [the steepest increase occurs if a too efficient predator (high  $\alpha$  and  $e$  or low  $h$ ,  $\mu$ , and  $r$ ) drives the system to extinction]. This illustrates why we needed a genetic algorithm to find initial parameter estimates within the basin of attraction of the optimal parameter values. But once this basin is found, convergence with the simplex algorithm or the Levenberg-Marquardt method is very

fast.  $\text{CB}_1$  and  $\text{CB}_2$  show the flattest error functions, indicating slower convergence rates of the optimization process. This same picture emerged with other data sets and models.

From direct comparison of the dominant eigenvalues of the nontrivial equilibrium with the estimated and the correct parameters, strong differences between the error functions emerge. Figure 5 shows the cumulative distribution functions of the ratios of the dominant eigenvalues for all estimated parameter sets, error functions,

TABLE 1

The Medians of the Coefficients of Variation for the Fitted Parameters over the 20 Different Parameter Sets for Each Model, Computed Either with the Empirical Mean or with the True Parameter Values Taken as the Mean (in Parentheses), and the Medians of the Standard Deviations of the Estimated Dominant Eigenvalues,  $\sigma_\lambda$  (the Medians of the True Dominant Eigenvalues Are  $-0.053$  and  $-0.14$  for the Prey-, Respectively Ratio-Dependent Parameter Sets)

	$\text{CV}_r$	$\text{CV}_K$	$\text{CV}_\alpha$	$\text{CV}_h$	$\text{CV}_e$	$\text{CV}_\mu$	$\sigma_\lambda$
Prey-dep.							
$X_\omega^2$	0.17 (0.22)	0.094 (0.12)	0.42 (0.80)	0.60 (0.60)	0.56 (0.73)	0.53 (0.82)	0.029
$X_v^2$	0.20 (0.20)	0.083 (0.098)	0.47 (0.61)	0.96 (0.73)	0.52 (0.52)	0.41 (0.52)	0.027
$\text{CB}_2$	0.24 (0.25)	0.081 (0.097)	0.53 (0.71)	0.63 (0.65)	0.49 (0.52)	0.42 (0.46)	0.025
Ratio-dep.							
$X_\omega^2$	0.12 (0.12)	0.10 (0.10)	0.40 (0.57)	0.30 (0.28)	0.58 (0.82)	0.47 (0.76)	0.033
$X_v^2$	0.20 (0.23)	0.17 (0.18)	0.46 (0.57)	0.54 (0.48)	0.78 (0.81)	0.64 (0.70)	0.039
$\text{CB}_2$	0.18 (0.18)	0.16 (0.18)	0.47 (0.51)	0.41 (0.39)	0.65 (0.70)	0.52 (0.56)	0.031

Note. All values are calculated from the results of fitting the correct model to the data with high observation and process error ( $\text{CV} = 0.1$ ,  $\sigma_p = 0.1$ ). The first column indicates the error function that was minimized.

and models. The steepness of each curve is approximately the same, meaning that each error function shows the same variation in the estimation of local stability, although there seems to be a slightly smaller variation with ratio-dependent data. With respect to deviation from the expected median, we see that error function  $X_{\omega}^2$  (fitting the whole trajectory) performed overall best, followed by  $CB_2$ . Error function  $X_v^2$  always overestimated stability.

Table 1 reports for each parameter the median of the coefficients of variation  $CV_{\theta}$  (computed over the different sets of true parameter values for each combination of correct model and error function, using the fits to data with high noise only). We computed the medians rather than the means because there were a few datasets where the estimated parameters  $K$  and  $a$  differed from the correct ones by one to three orders of magnitude. These outliers completely distorted the mean values. The important point to note in Table 1 is that these values are generally high (10–90%), indicating that even with five replicates, there remains much uncertainty in the estimated parameters. The estimation of  $K$  and  $r$  were the most reliable, and all other parameters had median CVs above 40%.

## DISCUSSION

We addressed the problem of model selection in this article by fitting dynamic models to predator–prey time series that contained both observation and process errors. Fitting assuming observation error only (error function  $X_{\omega}^2$ ) allowed for the more reliable model identification with both noise levels. Figure 3 suggests that identification should remain possible even with noise levels slightly higher than  $CV = 0.1$  and  $\sigma_p = 0.1$  or with some outliers in the data.

Fitting assuming process error (function  $X_v^2$ ) leads to less reliable identification. Identification worked well with the low noise level. But for the higher noise level, the ratio of the lower error by the larger error should be below 0.95 to have 95% confidence in not having misidentified the model. Higher noise levels or outliers in the data will further aggravate the reliability of model selection. The error functions  $CB_1$  and  $CB_2$  that were supposed to take both observation and process error into account gave unreliable identification results, probably because the function that is minimized is not identical to the selection criterion, as this is the case with error functions  $X_k^2$ . Preference must be given to functions  $X_k^2$  (or more general maximum likelihood approaches and information criteria when comparing models of different complexity) that use for regression and selection the same function.

Comparing our results with the work of Carpenter *et al.* (1994), we can notice that model selection is more reliable for the continuous models studied here than for the discrete models studied by these authors. However, Carpenter *et al.* fitted the prey equation only (using predator data as input into this prey equation). Therefore, they only selected for agreement with the prey dynamics, while we selected for agreement with both prey and predator dynamics. These authors also stated that manipulation of the biological system is necessary to identify models. Our analyses confirm that it is necessary to have initial conditions far from the equilibrium state, in order to generate strong dynamics of the system on its way back to the equilibrium. This can be accomplished in natural lakes by stocking or in laboratory cultures (batch or chemostat) by using low initial populations.

There is an interesting difference between the two models: the ratio-dependent time series were always more reliably identified, in the sense that the difference between the sum of squares  $X^2$  after fitting both models was on average larger with ratio-dependent data than with prey-dependent data (pushing the cumulative distribution functions to the left in Fig. 3). It seems that the ratio-dependent model is more flexible, adjusting itself more easily and with smaller residuals to given data. Carpenter *et al.* (1994) had found the same difference (their Fig. 3B and 3E). This raises the problem that real prey-dependent time series are more often wrongly identified as being ratio-dependent than the other way round.

A most interesting observation is that the error functions  $X_{\omega}^2$  and  $X_v^2$  made simultaneous wrong selections in only 2 of the 400 time series. Therefore, for the type of dynamics and the length of time series that we analysed, we can conclude that the most reliable model identification is obtained by fitting both error functions and by accepting a selected model only if both functions give the same result. Unfortunately, for longer time series that describe sustained or slowly decreasing oscillations, accumulated process error diverts the system from the deterministic description and fitting the whole trajectory can become unreasonable. Harrison (1995) encountered this problem because the time between peaks in Luckinbill's data is irregular (see his Fig. 6c), probably because of process error.

Regarding the performance of the error functions with respect to individual parameter identification, all error functions give parameter estimates close to the actual values (Fig. 4). However, Table I (calculated CVs from the replicated time series) shows that only parameters  $r$  and  $K$  are estimated with high precision, all others having large CVs. Assessing the quality of the system stability estimate with the method of the dominant eigenvalue (Fig. 5) shows

that, at the low noise level, this estimation is quite reliable for all error functions but with the higher noise level, there is a large variation with a considerable deviation from the expected median (Fig. 5). The error functions  $X_v^2$  and  $CB_1$  overestimate local stability (the estimated dominant eigenvalue  $\lambda$  is too negative).

In fact, there is no general statistical solution to the problem of fitting nonlinear models to data that have both observation and process error. As stated by Pascual and Kareiva (1996), the practical solution is often to fit as if there were only one type of error in the data. If neither of the error types should be neglected we suggest using both types of fitting and basing model selection on the joint result. This conclusion will probably remain valid for systems that do not fit into the framework of this study (e.g., systems that have only one state variable, unstable dynamics, or more available data points), but in these cases identifiability should again be verified by a simulation analysis similar to the one presented in this paper. It should be noted here that the error function  $X_v^2$  could probably be improved by taking into account not only the error  $s$  steps ahead but also the errors at intermediate time steps. The distribution of the accumulated process error at each step can be computed numerically and can be used in a likelihood criterion that would serve for regression and selection. Similarly, the errors-in-variables method (with the initial conditions as the independent variables) could help to construct a likelihood function that takes both process error and observation error into account. It remains to be tested whether the additional numerical costs can be justified by higher reliability of model selection and parameter estimation.

There exist alternatives to the way we addressed the problem of model selection in this article. In particular, one could take a versatile model that is either prey-dependent or ratio-dependent, depending on a specific parameter value (e.g., using the models of Hassell and Varley (1969) or DeAngelis *et al.* (1975)), and then directly estimate this parameter. However, estimating it by fitting the whole model (as done in this paper) will also result in a large uncertainty of the estimate, thus reducing the selective power of this approach. Using Bayesian approaches to estimate posterior distribution functions of this parameter is another possibility (Stow *et al.*, 1995), but they require sophisticated multidimensional integration techniques. The direct comparison performed in this paper is more parsimonious and has the additional advantage of choosing between models that can be incorporated into complex food webs (Arditi and Michalski, 1995; Michalski and Arditi, 1995).

Generally, goodness of fit as a criterion for model selection has its limitations, as indicated by the existence

of the already mentioned universal differential equations (Rubel, 1981) or by the classical demonstration of Smale (1976) that simple models of several competing populations can produce any type of qualitative dynamics. While our analysis shows that gross differences such as prey dependence versus ratio dependence can be identified, a preliminary study with three different general predator-dependent functional responses (that have all three instead of the two parameters in this study) resulted in up to 50% wrong identifications from data of similar quality and quantity as the ones used in this study.

Our general conclusion is that, to address the question of identification of dynamic predator-prey models, the scientist should first try to reduce observation and/or process error as much as possible. If both errors remain important, then model selection is most reliable if both observation error fit and process error fit select the same model. To perform this identification with models that are different from the ones analysed in this paper another simulation analysis should be done to validate the inference process. Parameter estimates obtained by these methods are characterized by large coefficients of variation. The data should also exhibit dynamics of much higher amplitude than the errors in the data. This can be obtained either by low initial conditions in laboratory experiments or by perturbation of natural systems.

## APPENDIX A

### Algorithmic Details

There does not exist much customizable software that allows fitting differential equations to data. Fitting and visualization are usually separate steps in most software, which further slows down the fitting process. Therefore we programmed the whole procedure directly in C++ to create an application that allows immediate visual control of the fitted model. This proved to be an indispensable tool to analyze large numbers of data sets. (The software can be obtained from the first author upon request; it requires a Power Macintosh.)

In a first step, the time series data were used to determine upper and lower bounds of the parameters. These bounds were found by first computing a rough estimate of each parameter. For  $r$ ,  $a(\alpha)$ ,  $\mu$ , and  $h$ , this was done by an analogy with exponential growth:

$$\dot{y} = ry \Leftrightarrow r = \frac{\log(y(t_{i+1})) - \log(y(t_i))}{t_{i+1} - t_i}.$$

For example, a rough estimate of the maximal prey growth rate  $r$  was obtained by calculating

$$\max_{1 \leq i \leq m-1} \left\{ \frac{\log(N_{i+1}) - \log(N_i)}{t_{i+1} - t_i} \right\}.$$

The parameter  $K$  was roughly estimated as the maximal prey abundance. These estimates were then multiplied by some constants to get upper and lower bounds. The constants were calibrated with the artificial data sets in such way that the intervals contained the real parameters that had generated all these data sets.  $e$  was restricted to the ecologically reasonable interval  $(0, 1)$ .

In a second step, a genetic algorithm (GAlib 1.4.2 from <http://lancet.mit.edu/ga/>) was used to search within these bounds, with population size 50, mutation rate 0.01, crossover rate 0.1 and 400–600 generations. In this step and the following step, the solutions of the ordinary differential equations needed to calculate  $X_k^2$  were simulated with the adaptive stepsize fifth-order Runge–Kutta method `odeint` from Press *et al.* (1992).

In a third and final step, starting from the parameter values found by the genetic algorithm, the fitting was completed by using repeatedly a Levenberg–Marquardt method and the downhill simplex method of Nelder and Mead combined with simulated annealing (routines `mrqmin` and `amotsa` from Press *et al.*, 1992) until the fit could not be improved any further. The computation of the gradient in the Levenberg–Marquardt method, i.e., the derivation of the solution of an ordinary differential equation with respect to the parameters, requires the simulation of a system of 20 (or more) coupled ordinary differential equations (Pavé, 1994, p. 509). The trick is that the order of differentiation can be inverted,

$$\frac{d}{da} \frac{dy(t)}{dt} \left( = \frac{d}{da} f(y(t)) \right) = \frac{d}{dt} \frac{dy(t)}{da} =: \frac{d}{dt} \xi(t),$$

and  $\xi(t)$  can be computed as the solution of a larger system. The parameters were forced to remain within the calculated intervals during the optimization (by blocking the parameter in the Levenberg–Marquardt method or by penalizing the error function in the simplex algorithm, with a penalty that grows exponentially with increasing distance from the bound).

The stopping criterion for both algorithms was determined dynamically from the data set: let  $E_n$  be the error at step  $n$  (expression  $X_k^2$ ,  $CB_1$ , or  $CB_2$ ),  $\theta_n^j$  the estimate

of parameter  $j$  at step  $n$  ( $1 \leq j \leq p$ ), and  $c = \max_{1 \leq i \leq m} \{ Y_i \} \cdot CV \cdot m \cdot C$  ( $C$  being a constant, set to  $10^{-8}$ ). Then the algorithm was stopped if either

$$0 \leq \frac{E_n - E_{n+1}}{E_n} \leq c$$

or

$$0 \leq \max_{1 \leq i \leq p} \left| \frac{\theta_n^j - \theta_{n+1}^j}{\theta_n^j} \right| \leq c$$

(Seber and Wild, 1989). With simulated annealing, the error  $E_n$  might actually increase at the beginning of the optimization process. Therefore, this algorithm was not stopped if the first expression became negative.

In sum, both models were fitted with each of the four error functions to each of the 400 time series by the following procedure: (1) Calculate upper and lower bounds for the parameters, (2) run a genetic algorithm, (3) use alternately and repeatedly the Levenberg–Marquardt method and the simulated annealing simplex algorithm with the stopping criteria above until the error does not diminish any further.

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