

Testing Conversion Efficiency for Some Cyclic Predator-prey Populations

Sévérien Nkurunziza

Department of Mathematics and Statistics

University of Windsor

401 Sunset Avenue, Windsor

Ontario, N9B 3P4

E-mail: severien@uwindsor.ca

S. Ejaz Ahmed

Department of Mathematics and Statistics

University of Windsor

401 Sunset Avenue, Windsor

Ontario, N9B 3P4

E-mail: seahmed@uwindsor.ca

[Received March 10, 2009; Revised March 31, 2009; Accepted April 20, 2009]

Abstract

We consider the testing problem for the conversion efficiency of the Lotka-Volterra ordinary differential equations system (ODEs). In this article, we assume that the perturbations follow correlated Ornstein-Uhlenbeck processes. We derive the uniformly most powerful unbiased test for the parameter of interest. The large-sample properties of the test are investigated.

Keywords and Phrases: Conversion Efficiency, Lotka-Volterra ODEs, Gaussian Process, Ornstein-Uhlenbeck Process, The Uniformly Most Powerful Unbiased Test, Wiener Process.

AMS Classification: Primary 62M10; Secondary 62F03.

1 Introduction

Consider the predator-prey system commonly known as the Lotka-Volterra system of differential equations:

$$\frac{dx(t)}{dt} = (\eta - \beta y(t))x(t), \quad \frac{dy(t)}{dt} = (\gamma x(t) - \delta)y(t), \quad (x(0), y(0)) = (x_0, y_0) \text{ fixed}, \quad (1.1)$$

where $\eta, \beta, \gamma, \delta$ are all positive quantities and the components of initial value (x_0, y_0) are the positive. Further, we assume that (x_0, y_0) is different from an equilibrium point. The trajectory $(x(t), y(t))$ is a periodic function, whose period is denoted by $\varrho(\gamma, \beta, \delta, \eta, x_0, y_0)$ and, is a function of $(\gamma, \beta, \delta, \eta, x_0, y_0)$. In model (1.1), $x(t)$ and $y(t)$ are the population sizes (at time t) of the prey and the predator, respectively. The parameter, η is the birth rate of the prey when the predator is absent, δ is the death rate of the predator when the prey is absent. In ecological modelling, the parameters δ and η , are usually considered as intrinsic to the species prey and predator. The parameters β and γ are the interaction parameters. The ratio γ/β is called “conversion efficiency” and represents a percentage of consumed prey that is converted into biomass predator. The parameter of interest is

$$\theta = \frac{\gamma}{\beta}.$$

A plug-in estimator of θ will be $\hat{\theta}$

$$\hat{\theta} = \frac{\hat{\gamma}}{\hat{\beta}},$$

where $\hat{\gamma}$ and $\hat{\beta}$ are the strongly consistent estimators of γ and β , respectively (Froda and Nkurunziza, 2007).

In practice, we have N pairs of observations $(X_i, Y_i)_{i=1,2,\dots,N}$ collected at discrete times t_i , where $0 < t_i < t_{i+1}$; X_i and Y_i , represent respectively the sizes of the prey and the predator observed at time t_i , $i = 1, 2, \dots, N$. We assume that each component of error process follows Ornstein-Uhlenbeck process that is the continuous version of a first-order autoregressive model AR(1) in discrete times.

The point estimation problem of the parameters $\eta, \beta, \gamma, \delta$ is considered by Froda and Colavita (2005), and Froda and Nkurunziza (2007). Further, Nkurunziza (2008) proposed the likelihood ratio test for the interaction parameters β, γ . In this article, the parameter of interest is the ratio of the two interaction parameters, i.e., θ . We consider the following testing problem

$$H_0 : \theta \leq \theta_0 \quad \text{against} \quad H_A : \theta > \theta_0. \quad (1.2)$$

For $\theta_0 = 1$, the above test allows us to test the homogeneity of the two interaction parameters γ and β .

The parameters δ and η are considered as constants with respect to the interaction parameters γ and β . This is not unrealistic because η and δ are considered as intrinsic to predator-prey species. Hence, η and δ can be considered as nuisance parameters. We give a sufficient condition for the period “ $\varrho(\gamma, \beta, \delta, \eta, x_0, y_0)$ ” to be constant with respect to the interaction parameters γ and β . This sufficient condition is in agreement with the fact that, when the initial value is close to the equilibrium point $(\delta/\gamma, \eta/\beta)$, the period $\varrho(\gamma, \beta, \delta, \eta, x_0, y_0) \approx 2\pi/\sqrt{\delta\eta}$ and this last term does not depend on the interaction parameters. For further discussion, see Nkurunziza (2008) and reference therein.

From the methodological point of view, we adopt the statistical model presented in Froda and Nkurunziza (2007). In this model, the error process is considered as mainly measurement (observation) error which does not interfere with the deterministic function. In practice, this assumption is related to the fact that, had this interference been present, the oscillatory behaviour might have been lost, as is the case in the corresponding Lotka-Volterra Stochastic Differential Equations (SDE) models (see, e.g. Gard and Kannan, 1976, Gard, 1988 or Chen and Kulperger, 2005). In order to take care of a possible correlation between the predator population sizes and the prey population sizes, we also defined the dependance structure between the errors. The more details about the statistical model used, we refer to Froda and Nkurunziza (2007).

In Section 2, we showcase the statistical model and give some preliminary results. Section 3 presents the uniformly most powerful unbiased test, when the nuisance parameters are assumed to be known. In Section 4, we deal with the testing problem when these nuisance parameters are unknown. The technical results and details are given in the Appendix.

2 Preliminaries and Statistical Model

Let μ_x and μ_y be the population means during a period, then

$$\begin{aligned}\mu_x &= \frac{1}{\varrho(\gamma, \beta, \delta, \eta, x_0, y_0)} \int_s^{s+\varrho(\gamma, \beta, \delta, \eta, x_0, y_0)} x(t) dt, \\ \mu_y &= \frac{1}{\varrho(\gamma, \beta, \delta, \eta, x_0, y_0)} \int_s^{s+\varrho(\gamma, \beta, \delta, \eta, x_0, y_0)} y(t) dt.\end{aligned}\quad (2.1)$$

From (2.1), we get $(\mu_x, \mu_y) = (\delta/\gamma, \eta/\beta)$ and therefore, $\mu_y/\mu_x = \theta \eta/\delta$. Hence, when η, δ are fixed and known, the testing problem in (1.2) is equivalent to:

$$H_0 : \frac{\mu_y}{\mu_x} = \mu^\diamond \leq \frac{\eta}{\delta} \theta_0 = \mu_0^\diamond \text{ against } H_A : \mu^\diamond > \mu_0^\diamond. \quad (2.2)$$

In methodological point of view, we adopt a statistical model in continuous time whose corresponding model in discrete times is commonly used in ecological setting for the cyclic populations. In fact, in ecology, there is a long tradition to model

population sizes of interacting species by the deterministic trajectory of ODEs (see e.g. Renshaw, 1991). Such models serve mainly to assess qualitative behaviour, but they are rarely used in quantitative studies. In order to make quantitative assessments, some models based on stochastic differential equations system (SDEs) have been proposed (see, e.g. Gard, 1988, Chapter 6). However, the SDEs models rarely predict oscillatory behaviour (see, e.g. Gard, 1988, Chapter 6). In particular, for the ODEs (1.1), the corresponding SDEs model (see, e.g. Gard and Kannan 1976, Gard, 1988 or Chen and Kulperger, 2005) gives rise to trajectories which are highly likely to become extinct during the first cycle and thus, this model is not appropriate to predict oscillatory behaviour.

In practice, the trajectory of many animal population sizes has oscillatory behaviour (see e.g. Kendall et al., 1999, Ginzburg and Taneyhill, 1994 or Royama, 1992, chapters 5-6). However, the trajectory of the observed predator-prey population sizes are not as smooth and regular as the solution of the ODEs (1.1). Further, the model (1.1) is too simple to capture all complexity present in nature, since it neglects many other factors that can affect the predator-prey interaction. Thus, even though the prey is the main source of food for the predator, the theoretical model (1.1) ignores, for example, the possible competition for food inside each species and assumes exponential growth for the prey population in the absence of the predator. Also, in mathematical modelling, when the number of the parameters increases, the goodness-of-fit increases but the model becomes too complex and inconvenient for the user.

In this paper, we consider a measurement type model where the observed population sizes are viewed as the solutions to the ODE system (1.1) plus a pair of random process whose each component follows an Ornstein-Uhlenbeck process. The choice of such error process with continuous paths is agreement with the continuity in time of the solution of the ODEs (1.1). Also, the choice of Ornstein-Uhlenbeck process is justified by the fact, if $\{(e_t^X, t \geq 0)\}$ is an Ornstein-Uhlenbeck process, then $\{(e_{t_i}^X, 0 < t_1 < t_2 < \dots < t_N, \text{ with } t_{i+1} - t_i \text{ constant for all } i)\}$ a first-order autoregressive model AR(1). Further, the statistical model which is commonly used by ecologists with population cycles is the linear autoregressive (AR) model (see Kendall et al., 1999, Berryman, 1995 or Royama, 1992), with an order less than or equal to 2. In our case, the periodicity is captured by the solution of the ODEs (1.1) and then, to simplify some computations, we can reduce the order by considering an AR(1) model.

Namely, let $(x(t), y(t))$ be the solution of ODEs (1.1) and let us assume that the N pairs of observations $(X_i, Y_i)_{i=1,2,\dots,N}$ are collected at discrete times $0 < t_1 < t_2 < \dots < t_N$, where $X_i \equiv X(t_i)$, $Y_i \equiv Y(t_i)$. Further, these observations are generated by a process with continuous paths $\{(X(t), Y(t)), 0 \leq t \leq T\}$ satisfying

$$\log X_t = \log x(t) + e_t^X, \quad \log Y_t = \log y(t) + e_t^Y, \quad (2.3)$$

here we assume that each noise component $\{(e_t^X, e_t^Y), 0 \leq t \leq T\}$ is Ornstein-Uhlenbeck process (Kutoyants, 2004, p. 51), with a particular dependance structure given in As-

sumption (C_1). More precisely, we assume that

$$de_t^X = -ce_t^X dt + \tau dW_t^X, \quad de_t^Y = -ce_t^Y dt + \tau dW_t^Y, \quad c, \tau > 0, \quad (2.4)$$

where $\{W_t^X, t \geq 0\}$ and $\{W_t^Y, t \geq 0\}$ are Wiener processes which satisfy the following assumption.

Assumption (C_1) The Wiener processes $\{W_t^X, t \geq 0\}$ and $\{W_t^Y, t \geq 0\}$ are jointly Gaussian such that, for all $i, j = 1, 2, 3, \dots$,

$$\text{Cov}(W_{t_i}^X, W_{t_j}^Y) = \rho \min(t_i, t_j) \text{ where } |\rho| < 1.$$

Proposition A.1 in the Appendix allows us to guarantee the existence of Wiener processes which satisfy the Assumption (C_1).

Assumption (C_2) The initial random variables e_0^X and e_0^Y are independent and normally distributed with mean 0 and variance $\sigma^2 = \tau^2/2c$. Furthermore, (e_0^X, e_0^Y) is independent of $\{(W_t^X, W_t^Y), t \geq 0\}$.

The assumption (C_2) guarantees that each noise component is stationary. Indeed, each equation of the diffusion processes system (2.4) satisfies the ergodicity conditions given in Kutoyants (2004, p. 1, Properties (02) and (03)). Further, from a result given in Kutoyants (2004, p. 2), it follows that the invariant distribution of $\{e_t^X, t \geq 0\}$ and $\{e_t^Y, t \geq 0\}$ is Gaussian with mean 0 and variance $\tau^2/2c$.

The independence between the initial random values, e_0^X and e_0^Y is assumed for simplifying some computations.

The model (2.3) is flexible and has some familiar properties for the practitioners. In fact, the error processes $\{e_t^X, t \geq 0\}$, $\{e_t^Y, t \geq 0\}$ are ergodic Markov processes and, under the Assumption (C_2) given above, they are stationary Gaussian. Further, this model has an advantage to account for stochastic modeling, while preserving the oscillatory behaviour inherent with model of Lotka-Volterra (Nkurunziza, 2008 and reference therein).

Also, the model (2.3) places emphasis on analyzing predator-prey couples, rather than one species at a time. For other references on the study of cyclic behaviour in the ecological literature, we refer the reader to Berryman (1995), Kendall *et al.* (1999) or Haydon *et al.* (2001). Further, for a mathematical perspective, we refer to Brillinger (1981), and for a recent review from an applied ecological perspective, we refer to Boyce (2000).

Note that the conversion efficiency parameter is an argument of an implicit function, which is the mean of the model (2.3). Now, we suggest the following theorem on a re-parametrization of the solution of ODE (1.1).

Theorem 1 Let κ_1 and κ_2 be two positive real numbers, let (x_0, y_0) be fixed initial value and let $(x(t; \gamma, \beta, \delta, \eta, x_0, y_0), y(t; \gamma, \beta, \delta, \eta, x_0, y_0))$ be a solution to the Lotka-

Volterra ODE system (1.1). Then,

$$\begin{aligned} x(t; \gamma, \beta, \delta, \eta, x_0, y_0) &= \kappa_1 x \left(t; \kappa_1 \gamma, \kappa_2 \beta, \delta, \eta, \frac{x_0}{\kappa_1}, \frac{y_0}{\kappa_2} \right) \\ y(t; \gamma, \beta, \delta, \eta, x_0, y_0) &= \kappa_2 y \left(t; \kappa_1 \gamma, \kappa_2 \beta, \delta, \eta, \frac{x_0}{\kappa_1}, \frac{y_0}{\kappa_2} \right), \end{aligned} \quad (2.5)$$

for $t \geq 0, \eta, \beta, \gamma, \delta > 0$. \square

Proof Refer to Nkurunziza (2008, Theorem 1.1). \square

From Theorem 1, we establish Corollary 1, which guarantees that, under some assumptions, the period of the populations is an intrinsic characteristic of the interacting species.

Corollary 1 Assume that there exists $(u_0, v_0) \in \mathbb{R}_+^2$, fixed, and that (x_0, y_0) is chosen such that, for all $\gamma > 0$, $\beta > 0$, $x_0 = u_0/\gamma$ and $y_0 = v_0/\beta$. Then, for $\eta, \beta, \gamma, \delta > 0$,

$$\varrho(\gamma, \beta, \delta, \eta, x_0, y_0) = \varrho(1, 1, \delta, \eta, u_0, v_0). \quad \square$$

Thus, according to Corollary 1, we give a sufficient condition for which the period of the ODEs (1.1) $\varrho(\gamma, \beta, \delta, \eta, x_0, y_0)$ is constant with respect to the interaction parameters, and the conversion efficiency. This sufficient condition is given explicitly in the following assumption.

Assumption (C₃) There exists $(u_0, v_0) \in \mathbb{R}_+^2$, fixed, and that (x_0, y_0) is chosen such that, for all $\gamma > 0$, $\beta > 0$, $x_0 = u_0/\gamma$ and $y_0 = v_0/\beta$.

In section 3, we suppose that (u_0, v_0) is known while, in Section 4, we assume that (u_0, v_0) is either known or replaced by its strongly consistent estimator (\hat{u}_0, \hat{v}_0) .

Further, let

$$\Gamma = (\gamma, \beta, \delta, \eta), \quad (x(t; \Gamma; x_0, y_0), y(t; \Gamma; x_0, y_0)) = (x(t), y(t)) \quad ,$$

$$\xi(t) = x(t; 1, 1, \delta, \eta; u_0, v_0) \text{ and } v(t) = y(t; 1, 1, \delta, \eta; u_0, v_0), \quad (2.6)$$

where (u_0, v_0) is the same as given in Corollary 1. Following Theorem 1,

$$(x(t), y(t)) = \left(\frac{1}{\gamma} \xi(t), \frac{1}{\beta} v(t) \right), \quad \forall t \geq 0.$$

In passing, we would like to remark that the most original contribution of this paper is the application of Theorem 1. Using Theorem 1, we are able to transform the hypothesis testing problem in hand into usual testing problems.

3 The uniformly most powerful unbiased test

In this section, we develop the UMPU test for the conversion efficiency parameter, θ . The composite null and alternative hypotheses are given as follows:

$$H_0 : \theta \leq \theta_0 \text{ against } H_A : \theta > \theta_0, \quad (3.1)$$

where θ_0 is positive and known.

In order to solve the testing problem (3.1), let us consider the differences

$$\Delta_x(j) = \log(X_j) - \log(\xi(j)), \quad \Delta_y(j) = \log(Y_j) - \log(v(j)),$$

where, for all $j = 1, 2, \dots, N$, the pair (X_j, Y_j) are generated by the stochastic model (2.3) and $(\xi(j), v(j))$ is given by (2.6). Also, let the vectors

$$\mathbf{\Delta}_x = (\Delta_x(1), \Delta_x(2), \dots, \Delta_x(N))', \quad \mathbf{\Delta}_y = (\Delta_y(1), \Delta_y(2), \dots, \Delta_y(N))'.$$

Let

$$\phi = \exp(-c) \quad \text{and the } N \times N \text{ matrix } \Upsilon = \sigma^2 \left(\phi^{|i-j|} \right)_{i,j=1,2,\dots,N}. \quad (3.2)$$

Further, let the real quantities

$$\begin{aligned} \|\mathbf{e}_N\|_{\Upsilon}^2 &= \mathbf{e}_N' \Upsilon^{-1} \mathbf{e}_N, \\ \overline{\mathbf{\Delta}}_x &= \left(\mathbf{e}_N' \Upsilon^{-1} \mathbf{e}_N \right)^{-1} \mathbf{e}_N' \Upsilon^{-1} \mathbf{\Delta}_x, \quad \overline{\mathbf{\Delta}}_y = \left(\mathbf{e}_N' \Upsilon^{-1} \mathbf{e}_N \right)^{-1} \mathbf{e}_N' \Upsilon^{-1} \mathbf{\Delta}_y, \end{aligned} \quad (3.3)$$

where \mathbf{e}_m is the column vector of dimension m with all entries equal to 1. It can be verified (see Nkurunziza, 2008 and reference therein), that

$$\begin{aligned} \sigma^2 \|\mathbf{e}_N\|_{\Upsilon}^2 &= [2 + (1 - \phi)(N - 2)] (1 + \phi)^{-1}, \\ \overline{\mathbf{\Delta}}_x &= T_1 \sigma^{-2} \|\mathbf{e}_N\|_{\Upsilon}^{-2}, \quad \overline{\mathbf{\Delta}}_y = T_2 \sigma^{-2} \|\mathbf{e}_N\|_{\Upsilon}^{-2}, \end{aligned}$$

where

$$T_1 = \Delta_x(1) + \frac{1}{1 + \phi} \sum_{j=2}^N (\Delta_x(j) - \phi \Delta_x(j - 1)), \quad (3.4)$$

and

$$T_2 = \Delta_y(1) + \frac{1}{1 + \phi} \sum_{j=2}^N (\Delta_y(j) - \phi \Delta_y(j - 1)). \quad (3.5)$$

From the well known properties of exponential families, the statistic (T_1, T_2) is complete and sufficient for the interaction parameters (γ, β) . The UMPU test for conversion efficiency is given the following proposition.

Proposition 1 Consider the testing problem in (3.1), at level $0 < \alpha < 1$. Under (C_1) , (C_2) and (C_3) with $\rho = 0$, the UMPU test, at the level α , is given by

$$\Psi = \begin{cases} 1, & \text{if } \frac{1}{\sqrt{2}} \|e_N\|_{\Upsilon} [\overline{\Delta}_x - \overline{\Delta}_y + \log(\theta_0)] < z_{1-\alpha}, \\ 0, & \text{if } \frac{1}{\sqrt{2}} \|e_N\|_{\Upsilon} [\overline{\Delta}_x - \overline{\Delta}_y + \log(\theta_0)] > z_{1-\alpha}, \end{cases} \quad (3.6)$$

where $\Phi(z_\alpha) = 1 - \alpha$, with

$$\Phi(x) = \int_{-\infty}^x \frac{1}{\sqrt{2\pi}} \exp(-t^2/2) dt.$$

The statistic $(\overline{\Delta}_x, \overline{\Delta}_y)$ is given by (3.4). \square

Proof From Proposition B.2 in the Appendix, Section B, the likelihood functions of the observations $(X_i, Y_i)_{i=1,2,\dots,N}$ is an exponential family. Further, its representation in the natural parametric space can be written as

$$dP_{\theta^*, \vartheta^*}(\underline{x}, \underline{y}) = \tilde{\psi}(\theta^*, \vartheta^*) \times \exp\{\theta^* U(\underline{x}, \underline{y}) + \vartheta^* S(\underline{x}, \underline{y})\} d\mu^*(\underline{x}, \underline{y}),$$

where μ^* is a dominant measure, and

$$\begin{aligned} \theta^* &= \log(\theta), \quad \vartheta^* = \log(\beta) \\ U(\underline{x}, \underline{y}) &= -\|e_N\|_{\Upsilon}^2 \overline{\Delta}_x, \quad S(\underline{x}, \underline{y}) = -\|e_N\|_{\Upsilon}^2 (\overline{\Delta}_x + \overline{\Delta}_y), \\ \tilde{\psi}(\theta^*, \vartheta^*) &= \psi(\exp(\theta^* \vartheta^*), \exp(\vartheta^*)). \end{aligned}$$

Let h be a real-valued function on \mathbb{R}^2 such that $h(u, s) = 2u - s$, for u and s real numbers. Further, let $V = h(U, S)$ and let us denote by $\theta_0^* = \log(\theta_0)$. Moreover, from Proposition B.3 given in the Appendix, $V = -\|e_N\|_{\Upsilon}^2 (\overline{\Delta}_x - \overline{\Delta}_y)$. Also, if $\theta^* = \theta_0^*$ the distribution of V does not depend on ϑ^* whereas the statistic S is complete and sufficient for the interaction parameter β . Therefore, by Basu Theorem (Lehmann, 1997, p. 191), V is independent of S when $\theta^* = \theta_0^*$.

Moreover, the function h is increasing in u for each fixed s . Therefore, from the Theorem 1 in Lehmann (1997, Chap. 5, p. 190), for the testing problem (3.1) there exists the UMPU test. By routine manipulation the UMPU test is given by (3.6), which completes the proof. \square

In passing, we would like to notice here that the maximum likelihood estimator of θ is $\hat{\theta}$, such that

$$\log(\hat{\theta}) = -\overline{\Delta}_x + \overline{\Delta}_y = \frac{1 + \phi}{2 + (1 - \phi)(N - 2)} (T_1 - T_2). \quad (3.7)$$

Moreover, $-\overline{\Delta}_x$ and $-\overline{\Delta}_y$ are the maximum likelihood estimator of $\log(\gamma)$ and $\log(\beta)$ respectively.

4 Large-sample test and practical aspects

Note that the test Ψ is useful if the parameters $\delta, \eta, \phi, \sigma$ are known. However, in practice, these parameters are usually unknown. Accordingly, we modify the test Ψ by replacing the parameters $\delta, \eta, \phi, \sigma$ with their strongly consistent estimators, $\hat{\delta}, \hat{\eta}, \hat{\phi}, \hat{\sigma}$. The estimators and their properties are given in Froda and Nkurunziza (2007).

Let's denote by $\Pi_{\Psi}(\kappa_1, \kappa_2)$ the power of the test Ψ evaluated at the point (κ_1, κ_2) . Moreover, we let

$$\zeta(\phi) = \frac{1-\phi}{1+\phi}, \quad \zeta_N(\phi) = \frac{2+(1-\phi)(N-2)}{1+\phi} \quad \text{and} \quad \zeta_N(\hat{\phi}) = \frac{2+(1-\hat{\phi})(N-2)}{1+\hat{\phi}}. \quad (4.1)$$

Also, to avoid the asymptotic degeneracy, we confine ourselves to a sequence of local alternatives, defined as

$$H_{A;N} : \log(\theta) = \log(\theta_0) + \frac{\lambda}{\sqrt{N}}, \quad \lambda \neq 0.$$

As a preliminary step, in the following proposition we prove that Ψ is consistent test.

Proposition 2 *Let λ be fixed and positive real number. Suppose that the assumptions (C_1) , (C_2) and (C_3) hold with $\rho = 0$. Then, uniformly in λ belonging to a fixed compact of \mathbb{R}^+ ,*

$$\lim_{N \rightarrow \infty} \Pi_{\Psi} \left(\log(\theta_0) + \frac{\lambda}{\sqrt{N}} \right) = \Phi \left(z_{1-\alpha} + \frac{\sqrt{\zeta(\phi)\lambda}}{\sigma} \right).$$

Further

$$\lim_{N \rightarrow \infty} \Pi_{\Psi}(\log(\theta)) = 1.$$

□

As a consequence of Proposition 2, the asymptotic power of Ψ , under the local alternatives is

$$\Phi \left(z_{1-\alpha} + \frac{\sqrt{\zeta(\phi)\lambda}}{\sigma} \right).$$

For practical reasons, we modify the test Ψ by replacing the parameters $\delta, \eta, \phi, \sigma$ with their strongly consistent estimators, $\hat{\delta}, \hat{\eta}, \hat{\phi}, \hat{\sigma}$. Hence, the new test is

$$\Psi_a = \begin{cases} 1, & \text{if } \sqrt{\frac{\zeta_N(\hat{\phi})}{2\hat{\sigma}^2}} \left[\frac{T_{a1} - T_{a2}}{\zeta_N(\hat{\phi})} + \log(\theta_0) \right] < z_{1-\alpha}, \\ 0, & \text{if } \sqrt{\frac{\zeta_N(\hat{\phi})}{2\hat{\sigma}^2}} \left[\frac{T_{a1} - T_{a2}}{\zeta_N(\hat{\phi})} + \log(\theta_0) \right] > z_{1-\alpha}, \end{cases} \quad (4.2)$$

where $\zeta_N(\hat{\phi})$ is given by (4.1). Further (T_{a_1}, T_{a_2}) are obtained from (3.2) and (3.4) respectively, by replacing $\delta, \eta, \phi, \sigma$ with $\hat{\delta}, \hat{\eta}, \hat{\phi}, \hat{\sigma}$. In a similar way, a plug-in estimator of θ is derived from (3.7), by replacing $\delta, \eta, \phi, \sigma$ with $\hat{\delta}, \hat{\eta}, \hat{\phi}, \hat{\sigma}$. Again, to simplify some computations, we assume that (u_0, v_0) is known. Nevertheless, by replacing (u_0, v_0) by its strongly consistent estimator (\hat{u}_0, \hat{v}_0) , we preserve the asymptotic properties of the test. This follows from the Theorem on continuous dependence of trajectories on the initials conditions, for the ODE system (Perko, 1996, p. 92).

Noting that, the proposed new test-statistic Ψ_a , is not the UMPU test-statistic. However, in the following proposition, we demonstrate that Ψ_a is indeed asymptotically as powerful as the uniformly most powerful unbiased test.

Proposition 3 *Let λ be any fixed and positive real number. If the assumptions $(C_1) - (C_3)$ hold and $\rho = 0$, then,*

$$\lim_{N \rightarrow \infty} \Pi_{\Psi_a} \left(\log(\theta_0) + \frac{\lambda}{\sqrt{N}} \right) = \Phi \left(z_{1-\alpha} + \frac{\sqrt{\zeta(\phi)}\lambda}{\sigma} \right). \quad \square$$

5 Concluding Remarks

This paper deals with the testing problem for the variation of the conversion efficiency parameter. Methodologically, we used measurement type model. This model has the advantage of incorporating a stochastic differential equations modeling, while preserving the oscillatory behaviour of the ODE system. This is in accordance with the fact that many animal populations exhibit periodic behavior (see e.g. Kendall et al., 1999, Ginzburg and Taneyhill, 1994 or Royama, 1992, chapters 5-6).

For other type of models provided in the mathematical biology literature, we refer to the monograph by Renshaw (1991), and the review paper by Brillinger (1981).

In testing problems, we derived the one-sided UMPU test for testing the conversion efficiency parameter when the nuisance parameters $(\delta, \eta, \sigma, \phi)$ are to be known. In particular, the test presented allows the ecologists to compare the interaction parameters γ and β . Furthermore, the suggested test is also useful for testing the one-sided hypothesis regarding the ratio, mean of the predator by the mean of the prey during a period of the ODEs (1.1). Further, we extended this test to a more realistic situation. That is the case when the interaction parameters $(\delta, \eta, \sigma, \phi)$ are unknown. In this case, by replacing these parameters by their strongly consistent estimators $(\hat{\delta}, \hat{\eta}, \hat{\sigma}, \hat{\phi})$, we derive a test which is asymptotically as powerful as the UMPU test for the known nuisance parameters case. The new contribution of this paper consists in the use of Theorem 1 to transform the hypothesis testing problem into some familiar problems. Basically, after this re-parametrization, we applied classical techniques in testing hypotheses, in particular, for the Gaussian case. For some simulation result we refer to Nkurunziza and Ahmed (2009).

6 Acknowledgements

The authors are grateful to Dr. S. Froda for encouragement and many useful comments and suggestions. this research is supported by grants from Natural Sciences and Engineering Research Council of Canada.

Appendix

A Theoretical result concerning the Lotka-Volterra ODEs

Proof of Corollary 1

Here the proof is presented for the convenience of the reader, it is similar to that given in Nkurunziza (2008). From the Theorem 1, by taking $\kappa_1 = 1/\gamma$ and $\kappa_2 = 1/\beta$, we get

$$\begin{aligned} x(t; \gamma, \beta, \delta, \eta, x_0, y_0) &= \frac{1}{\gamma} x(t; 1, 1, \delta, \eta, u_0, v_0), \\ y(t; \gamma, \beta, \delta, \eta, x_0, y_0) &= \frac{1}{\beta} y(t; 1, 1, \delta, \eta, u_0, v_0). \end{aligned}$$

Therefore, for $\gamma, \beta > 0$, the function

$$(x(t; 1, 1, \delta, \eta, u_0, v_0), y(t; 1, 1, \delta, \eta, u_0, v_0))$$

has the same period as the function

$$(x(t; 1, 1, \delta, \eta, u_0, v_0)/\gamma, y(t; 1, 1, \delta, \eta, u_0, v_0)/\beta).$$

This completes the proof. \square

B Some properties of the error process

We outline the proof of the propositions stated in Section 2 and Section 3. The full proofs are given in Nkurunziza (2008) to which we refer the reader. We begin by giving Proposition B.1 which allows us to guarantee the existence of a process $\{(W_t^X, W_t^Y), t \geq 0\}$ satisfying the assumption (C_1) .

Proposition B.1 *Let $\{Z_t^X, t \geq 0\}$ and $\{Z_t^Y, t \geq 0\}$ be two independent Wiener processes and let*

$$W_t^X = \frac{1}{\sqrt{2}} \left(\sqrt{1+\rho} Z_t^X - \sqrt{1-\rho} Z_t^Y \right), \quad W_t^Y = \frac{1}{\sqrt{2}} \left(\sqrt{1+\rho} Z_t^X + \sqrt{1-\rho} Z_t^Y \right) \quad (\text{B.1})$$

Then, Assumption (C_1) holds. \square

Nkurunziza (2008) proved the converse of the proposition. That is, if (C_1) holds, then there exist two independent Wiener processes $\{Z_t^X, t \geq 0\}$ and $\{Z_t^Y, t \geq 0\}$ such that (B.1) holds. We wish to establish the likelihood function of the model (2.3). Let

$$A(s, t) = \begin{pmatrix} e^{-ct} & 0 \\ 0 & e^{-cs} \end{pmatrix} \quad \text{and} \quad B_\rho(u, s) = \begin{pmatrix} 1 & 0 \\ 0 & I_{\{u \leq s\}} \end{pmatrix} \begin{pmatrix} \sqrt{1+\rho} & -\sqrt{1-\rho} \\ \sqrt{1+\rho} & \sqrt{1-\rho} \end{pmatrix}.$$

Further, using the converse of the Proposition B.1 as well as the standard stochastic calculus techniques, Nkurunziza (2005, Proposition 1.3) established the following result.

Corollary B.1 Suppose that the assumption (C_1) holds. Then, for all $t \geq s \geq 0$,

$$(e_t^X, e_s^Y)' = A(s, t) \left\{ (e_0^X, e_0^Y)' + \frac{\tau}{\sqrt{2}} \int_0^t e^{cu} B_\rho(u, s) d\mathbf{Z}_u \right\}$$

where $\{\mathbf{Z}_u, u \geq 0\}$ is a bivariate Wiener process, whose components are Z_t^X, Z_t^Y given in (B.1). \square

Let $\mathbf{e}_t = (e_t^X, e_t^Y)$, and let

$$k(s, t) = e^{-c(t \vee s)} \sinh(c(t \wedge s)), \quad \Sigma^{XY}(s, t) = \sigma^2 \begin{pmatrix} 1 & 2\rho k(s, t) \\ 2\rho k(s, t) & 1 \end{pmatrix}.$$

Corollary B.2 (Nkurunziza (2005, Proposition 1.3)) Suppose that the assumptions $(C_1) - (C_2)$ hold. Then, $\{(e_t^X, e_s^Y)', s \geq 0, t \geq 0\}$ is Gaussian with

$$(e_t^X, e_s^Y)' \sim \mathcal{N}_2(\mathbf{0}, \Sigma^{XY}(s, t)), \quad s \geq 0, t \geq 0. \quad \square$$

By applying Corollary B.2, we establish Corollary B.3 for the likelihood function of $(e_{t_i}^X, e_{t_i}^Y)_{i=1,2,\dots,N}$ where $\{(e_t^X, e_t^Y)', t \geq 0\}$ satisfies the relation (2.4). Before stating Corollary B.2, let us introduce some notations used in this corollary. Let $\mathbf{e}_t = (e_t^X, e_t^Y)'$ and denoted by

$$\begin{aligned} \Sigma_{11}(s) &= \sigma^2 \begin{pmatrix} 1 & \rho(1 - \phi^{2s}) \\ \rho(1 - \phi^{2s}) & 1 \end{pmatrix} = \Sigma^{XY}(s, s) \quad \text{and} \\ \tilde{\Sigma}_n &= \left(\Sigma_{11}(t_{i \wedge j}) \phi^{|t_j - t_i|} \right)_{i,j=1,2,\dots,N}. \end{aligned} \quad (\text{B.2})$$

Corollary B.3 (Nkurunziza, 2005, Corollary 1.7) Let $\{e_t^X, t \geq 0\}$ and $\{e_t^Y, t \geq 0\}$ be two Ornstein-Uhlenbeck processes given by (2.4). Suppose that the assumptions (C_1) and (C_2) hold. Then, for all $0 < s < t$,

(i)

$$\begin{pmatrix} \mathbf{e}_s \\ \mathbf{e}_t \end{pmatrix} \sim \mathcal{N}_4 \left(\mathbf{0}, \begin{pmatrix} \Sigma_{11}(s) & \phi^{t-s} \Sigma_{11}(s) \\ \phi^{t-s} \Sigma_{11}(s) & \Sigma_{11}(t) \end{pmatrix} \right).$$

(ii) Generally, for all $0 < t_1 < t_2 < \dots < t_n$,

$$(\mathbf{e}'_{t_1}, \mathbf{e}'_{t_2}, \dots, \mathbf{e}'_{t_n})' \sim \mathcal{N}_{2n}(\mathbf{0}, \tilde{\Sigma}_n). \quad \square$$

In the following proposition, we combine the Corollary B.3 and Theorem 1 in establishing the likelihood function of the model (2.3). As notation, given any vector \mathbf{a} , we denote by $\|\mathbf{a}\|_{\Upsilon}^2 = \mathbf{a}'\Upsilon^{-1}\mathbf{a}$. Also, let

$$\varsigma(\sigma, \phi, \rho) = \frac{\rho^2 \phi^2 (2 - \phi^2)}{\sigma^2 (1 - \rho^2) [1 - \rho^2 (1 - \phi^2)^2]},$$

$$\begin{aligned} G(\underline{X}, \underline{Y}, \sigma, \phi, \rho, \delta, \eta) &= (\det(\Upsilon))^{-1} \exp \left\{ -\frac{1}{2} \|\Delta_x - \overline{\Delta}_x \mathbf{e}_N\|_{\Upsilon}^2 - \frac{1}{2} \|\Delta_y - \overline{\Delta}_y \mathbf{e}_N\|_{\Upsilon}^2 \right\} \\ &\quad \times \exp \left\{ \varsigma(\sigma, \phi, \rho) [\Delta_x(1)^2 + \Delta_y(1)^2 - 2\rho \Delta_x(1) \Delta_y(1)] \right\} \\ &\quad \times \exp \left\{ -\frac{1}{2} [(\overline{\Delta}_x)^2 + (\overline{\Delta}_y)^2] \|\mathbf{e}_N\|_{\Upsilon}^2 \right\} \end{aligned}$$

and

$$\begin{aligned} \psi(\gamma, \beta, \sigma, \phi, \rho) &= \exp \left\{ -\frac{1}{2} \left[(\log(\gamma))^2 + (\log(\beta))^2 \right] \right\} \mathbf{e}_N' \Upsilon^{-1} \mathbf{e}_N \\ &\quad \times \exp \left\{ \varsigma(\sigma, \phi, \rho) [\log(\gamma)^2 + \log(\beta)^2 - 2\rho \log(\gamma) \log(\beta)] \right\} \\ &\quad \times (2\pi)^{-N} \left[1 - \rho^2 (1 - \phi^2)^2 \right]^{-1}, \end{aligned}$$

where $\overline{\Delta}_x$ et $\overline{\Delta}_y$ are given in (3.2). Furthermore, let $Q(\gamma, \beta)$ be the likelihood function of $(X_i, Y_i)_{i=1,2,\dots,N}$.

Proposition B.2 Suppose that the assumptions $(C_1) - (C_3)$ are satisfied. Then,

$$\begin{aligned} Q(\gamma, \beta) &= G(\underline{x}, \underline{y}, \sigma, \phi, \rho, \delta, \eta) \psi(\gamma, \beta, \phi, \rho) \\ &\quad \times \exp \left\{ \left[\varsigma(\sigma, \phi, \rho) [\Delta_x(1) - \rho \Delta_y(1)] - \frac{\|\mathbf{e}_N\|_{\Upsilon}^2}{1 - \rho^2} [\overline{\Delta}_x - \rho \overline{\Delta}_y] \right] \log(\gamma) \right\} \\ &\quad \times \exp \left\{ \left[\varsigma(\sigma, \phi, \rho) [\Delta_y(1) - \rho \Delta_x(1)] - \frac{\|\mathbf{e}_N\|_{\Upsilon}^2}{1 - \rho^2} [\overline{\Delta}_y - \rho \overline{\Delta}_x] \right] \log(\beta) \right\}. \end{aligned} \quad (\text{B.3})$$

In particular, if $\rho = 0$ then

$$\begin{aligned} Q(\gamma, \beta) &= G(\underline{x}, \underline{y}, \sigma, \phi, 0, \delta, \eta) \psi(\gamma, \beta, \phi, 0) \\ &\quad \times \exp \left\{ -\|\mathbf{e}_N\|_{\Upsilon}^2 [\overline{\Delta}_x \log(\gamma) + \overline{\Delta}_y \log(\beta)] \right\}. \end{aligned} \quad (\text{B.4})$$

□

Proof We outline the proof for a particular case where $\rho = 0$. Following the Theorem 1,

$$\left(\frac{1}{\gamma}\xi(t), \frac{1}{\beta}v(t)\right) = (x(t), y(t)) \quad \text{then,}$$

$$\Delta_x + e_N \log(\gamma) = (e_1^X, e_2^X, \dots, e_N^X)' \quad \text{and} \quad \Delta_y + e_N \log(\beta) = (e_1^Y, e_2^Y, \dots, e_N^Y)',$$

where $\{(e_t^X, e_t^Y), 0 \leq t \leq T\}$ is a process which verifies the system (2.4) as well as the assumptions (C_1) and (C_2) . Therefore, if $\rho = 0$, by using Corollary B.3, we get

$$(\Delta'_x, \Delta'_y)' \sim \mathcal{N}_{2N} ((-\log(\gamma), -\log(\beta))' \otimes e_N, I_2 \otimes \Upsilon). \quad (\text{B.5})$$

By some computations, we get the desired result.

From the following proposition, we consider a particular case where $\rho = 0$. Thus, we use the likelihood function given in (B.4). The general case where $\rho \neq 0$ and known can be studied in the similar way by using the more general likelihood function given by (B.3).

Proposition B.3 Suppose that the assumptions $(C_1) - (C_3)$ hold. If $\rho = 0$, then,

(i)

$$(\overline{\Delta}_x + \log(\gamma), \overline{\Delta}_y + \log(\beta))' \sim \mathcal{N}_2 \left(\mathbf{0}, I_2 \|e_N\|_{\Upsilon}^{-2} \right);$$

(ii) if $\gamma/\beta = \theta = \theta_0$,

$$\begin{aligned} \overline{\Delta}_x - \overline{\Delta}_y &\sim \mathcal{N} \left(-\log(\theta_0), 2 \|e_N\|_{\Upsilon}^{-2} \right) \quad \text{and} \\ \overline{\Delta}_x + \overline{\Delta}_y &\sim \mathcal{N} \left(-\log(\theta_0) - 2 \log(\beta), 2 \|e_N\|_{\Upsilon}^{-2} \right). \end{aligned}$$

□

Proof of Proposition 2 By Proposition B.3, $(\overline{\Delta}_x - \overline{\Delta}_y)$ is Gaussian. Indeed, from the definition of test power,

$$\lim_{N \rightarrow \infty} \Pi_{\Psi} \left(\log(\theta_0) + \frac{\lambda}{\sqrt{N}} \right) = \lim_{N \rightarrow \infty} \Phi(z_{1-\alpha} + \|e_N\|_{\Upsilon} (\log(\theta) - \log(\theta_0))) \quad \text{where,}$$

$$\|e_N\|_{\Upsilon} (\log(\theta) - \log(\theta_0)) = \|e_N\|_{\Upsilon} \frac{\lambda}{\sqrt{N}} \xrightarrow{N \rightarrow \infty} \sqrt{\frac{1-\phi}{\sigma^2(1+\phi)}} \lambda = \frac{\sqrt{\zeta(\phi)}}{\sigma} \lambda,$$

and $\zeta(\phi) = (1-\phi)/(1+\phi)$. Therefore,

$$\lim_{N \rightarrow \infty} \Pi_{\Psi} \left(\log(\gamma_0) + \frac{\lambda}{\sqrt{N}}, \log(\beta_0) + \frac{\lambda_2}{\sqrt{N}} \right) = \Phi \left(z_{1-\alpha} + \frac{\sqrt{\zeta(\phi)}}{\sigma} \lambda \right).$$

By the Dini Theorem (see Corollary 1 of Toma, 1997) or by compactness and continuity arguments (see Theorem 4.1 of Beer and Diconcilio, 1991), we conclude that this convergence is uniformly in every compact of \mathbb{R}^2 . Also, one can verify that $\lim_{N \rightarrow \infty} \Pi_{\Psi}(\gamma, \beta) = 1$, that completes the proof. \square

Proof of Proposition 3 From Proposition B.3, if λ is a fixed real and positive number, we get,

$$\begin{aligned} \|e_N\|_{\Upsilon} (\overline{\Delta}_x - \overline{\Delta}_y + \log(\theta_0)) &= \|e_N\|_{\Upsilon} \left(\frac{T_1 - T_2}{\sigma^2 \|e_N\|_{\Upsilon}^2} + \log(\theta_0) \right) \\ &\xrightarrow[N \rightarrow \infty]{\mathcal{L}} \mathcal{N} \left(-\frac{\sqrt{\zeta(\phi)}\lambda}{\sigma}, 1 \right). \end{aligned} \quad (\text{B.6})$$

Let's denote by $a_N \asymp b_N$ when ratio a_N/b_N tends to 1, *a.s.* as $N \rightarrow \infty$. From (4.1), we deduce that,

$$\|e_N\|_{\Upsilon} = \sqrt{\frac{\zeta_N(\phi)}{\sigma^2}} \asymp \sqrt{\frac{\zeta_N(\hat{\phi})}{\hat{\sigma}^2}} \quad \text{and then,} \quad \|e_N\|_{\Upsilon} \left(\sqrt{\frac{\zeta_N(\hat{\phi})}{\hat{\sigma}^2}} \right)^{-1} \xrightarrow[N \rightarrow \infty]{a.s.} 1. \quad (\text{B.7})$$

Moreover, under H_A ,

$$\frac{\left(\frac{T_1 - T_2}{\sigma^2 \|e_N\|_{\Upsilon}^2} + \log(\theta_0) \right)}{\left(\frac{T_{a_1} - T_{a_2}}{\zeta_N(\hat{\phi})} + \log(\theta_0) \right)} \asymp \frac{-\log(\theta) + \log(\theta_0)}{-\log(\theta) + \log(\theta_0)} \xrightarrow[N \rightarrow \infty]{a.s.} 1. \quad (\text{B.8})$$

$$\frac{\sqrt{\zeta_N(\hat{\phi})}}{\sqrt{\hat{\sigma}^2}} \left(\frac{T_{a_1} - T_{a_2}}{\zeta_N(\hat{\phi})} + \log(\theta_0) \right) \xrightarrow[N \rightarrow \infty]{\mathcal{L}} \mathcal{N} \left(-\frac{\sqrt{\zeta(\phi)}\lambda}{\sigma}, 1 \right), \quad \text{for } \lambda > 0.$$

Therefore,

$$\lim_{N \rightarrow \infty} \Pi_{\Psi_a} \left(\log(\theta_0) + \frac{\lambda}{\sqrt{N}} \right) = \Phi \left(z_{1-\alpha} + \frac{\sqrt{\zeta(\phi)}\lambda}{\sigma} \right). \quad \square$$

References

- [1] Beer, G., and Diconcilio, A. (1991). Uniform continuity on bounded sets and the attouch-wets topology. *Proceedings of the American mathematical society*, **112**: 1, 235–243.

- [2] Berryman A. A. (1995). Population cycles : a critique of the maternal and allometric hypotheses. *Journal of Animal Ecology*. **64**: 290–293.
- [3] Bickel, J. P., and Doksum, K. A. (2001). *Mathematical Statistics : Basic Ideas and selected topics*. 2nd ed. vol. 1. Upper Saddle River, N.J.: Prentice-Hall.
- [4] Boyce. M. S. (2000). Modeling predator-prey dynamics, in *Research Techniques in Animal Ecology: Controversies and Consequences*, Eds. L Boitani and TK Fuller. Columbia University Press, New York: 253-287.
- [5] Brillinger, D. R. (1981). Some aspects of modern population mathematics. *Canad. J. Statist.* **9**: 173–194.
- [6] Bulmer, M.G. (1974). A statistical analysis of the 10-year cycle in Canada. *J. Animal Ecol.* **43**: 701-718.
- [7] Chen, Z., and Kulperger, R. (2005). A stochastic competing-species model and ergodicity. *J. Appl. Probab.* **42**: 3, 738–753.
- [8] Froda, S., and Nkurunziza, S. (2007). Prediction of predator-prey populations modeled by perturbed ODEs. *Journal of Mathematical Biology*, **54**: 407–451.
- [9] Froda, S., and Colavita, G. (2005). Estimating predator-prey systems via ordinary differential equations with closed orbits. *Aust. N.Z. J. Stat.*, **2**: 235–254.
- [10] Gard, C. T., and Kannan, D. (1976). On a stochastic differential equation modeling of prey-predator evolution. *J. Appl. Prob.* **13**: 429–443.
- [11] Gard, T. (1988). *Introduction to stochastic differential equations*. Marcel Dekker.
- [12] Ginzburg, L. R. and Taneyhill, D. E. (1994). Populations cycles of forest Lepidoptera : a maternal effect hypothesis. *Journal of Animal Ecology* **63**: 79–92.
- [13] Haydon, D. T., Stenseth N. C., Boyce M. S. and Greenwood, P. E. (2001). *Phase coupling and synchrony in the spatiotemporal dynamics of muskrat and mink populations accross Canada*. Edited by Simon A. Levin, Princeton University, Princeton.
- [14] Kendall, B. E., Briggs. C. J. Murdoch, W. W., Turchin, P., ellner, S. P., McCauley E., Nisbet. R. and Wood, S. N. (1999). Why do populations cycle? A synthesis of statistical and mechanistic modelling approaches. *Ecology*, **80**: 6, 1789-1805.
- [15] Kutoyants, A. Y. (2004). *Statistical Inference for Ergodic Diffusion Processes*. New York: Springer.
- [16] Lehmann, E. L. (1986). *Statistical Hypotheses*. 2nd ed. New York: John Wiley.

- [17] Nkurunziza, S. (2008). The likelihood ratio test for a special predator-prey system. *Statistics*, **42**: 2, 149–166.
- [18] Nkurunziza, S. (2005). *Inférence statistique dans certains systèmes écologiques : système proie-prédateur*. Ph.D Thesis. UQAM.
- [19] Perko, L. (1996). *Differential equations and dynamical systems*, 2nd ed. New York: Springer-Verlag.
- [20] Renshaw, E. (1991). *Modelling Biological Populations in Space and Time*. Cambridge University Press.
- [21] Royama, E. (1992). *Analytical population dynamics*. Chapman & Hall, London.
- [22] Toma, V. (1997). Strong convergence and Dini theorems for non-uniform spaces. *Annales mathématiques Blaise Pascal*, **4**: 2, 97-102.