# Hybrid Species and Closed-Form Solutions of the Lotka-Volterra Equations 

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#### Abstract

The classical Lotka-Volterra system of two coupled non-linear ordinary differential equations is expressed in terms of a single positive coupling parameter $\lambda$, ratio of the respective natural growth and decay rates of the prey and predator populations. "Hybrid-species" are introduced resulting in a novel $\lambda$ - invariant Hamiltonian of two coupled first-order ODE albeit with one being linear; a new exact, closed-form, single quadrature solution valid for any value of $\lambda$ and the system's energy is derived. In the particular case $\lambda=1$ the ODE system partially uncouples and new, exact, closed-form time-dependent solutions are derived for each individual species. In the case $\lambda \neq 1$ an accurate practical approximation uncoupling the non-linear system is proposed; solutions are provided in terms of explicit quadratures together with analytical high energy asymptotic solutions. A novel, exact, closed-form expression of the system's oscillation period valid for any value of $\lambda$ and orbital energy is derived; two fundamental properties of the period are established; for $\lambda=1$ the period is expressed in terms of a universal energy function and shown to be the shortest.


Keywords: Single coupling parameter; Quadrature solutions; Asymptotic solutions; Period

## Introduction

This paper is a revised version of two articles which were first published on arXiv and subsequently merged [1,2].

The historic Predator-Prey problem, also known as the Lot-ka-Volterra ("LV") system of two coupled first-order nonlinear differential equations has first beeninvestigated in ecological and chemical systems [3,4]. This idealized model describes the competition of two isolated coexisting species: a 'prey population' evolves while feeding from an infinitely large resource supply, whereas 'predators' interact by exclusively feeding on preys, either through direct predation or as parasites. This two-species model has further been generalized to interactions between multiple coexisting species in biological mathematics [5], ecology [6], virus propagation [7], and also in molecular vibration-vibration energy transfers [8]. As a result oftheir competition, the respective populations exhibit undamped oscillations as a function of time with a period which depends on the species interaction rates together with the system's energy.

## Normalized Equations and Single Coupling Parameter

The classical LV model is based on four time-independent, pos itive, and constant rates with two representing species self-inter
action, i.e. natural exponential growth rate $\alpha$ and decay rate $\delta$ per individual of the respective prey and predator populations, and two others characterizing inter-species interaction.

Without any loss of generality, the LV system of two coupled first order ordinary differential equations (ODE) can be simplified by simultaneously scaling the predator and prey populations together with time through a dimensionless time $t$ based on the factor $1 / \sqrt{\alpha \delta}$. The system is shown to only depend on a single positive coupling parameter $\lambda$, ratio of the respective growth and decay rates of each species taken separately, defined as

$$
\begin{equation*}
\lambda=\sqrt{\frac{\alpha}{\delta}} \tag{1}
\end{equation*}
$$

Let $u(t) \geq 0$ and $v(t) \geq 0$ be the respective instantaneous populations of preys and predators assumed to be continuous functionsoftimet: uponinserting $\lambda$ asdefined in(1)intothestandard LV two-equation system, a normalized form is obtained as a set of two coupled first-order autonomous nonlinear ODEs solely depending on this single coupling ratio $\lambda,[1]$.

[^0]The "dot" in $u$ and $v$ indicates a derivative with respect to the time $t$ : in the sudden absence of coupling between species, the prey population would grow at an exponential rate $\lambda$ while predators would similarly decay at an inverse rate $-1 / \lambda$ from their respective positive initialvalues.

Remarkably, the normalized ODE system (2) is invariant in the transformation $u \rightarrow v$ together with $\lambda \rightarrow-1 / \lambda$ : this fundamental property, subsequently referred to as " $\lambda$ - invariant", is extensively used throughout to considerably simplify the LV problem analysis.

Numerous solutions of the non-linear system (2) using a variety of techniques have been proposed including trigonometric series [9], mathematical transformations [10], Taylor series expansions [11], perturbation techniques [12,13], numeric-analytic techniques [14] and Lambert W-functions [15,16]. Also, an exact solution has previously been derived in the special case when the prey growth rate and predator decay rate are identical in magnitude, but with opposite signs, i.e. $\alpha=-\delta$, a condition which precludes population oscillation. The basic system (2) is non-trivial and analytical closed form solutions are unknown.

Since the original publications [3,4], the system (2) has been known to possess a dynamical invariant or "constant of motion K" expressed here in $\lambda$-invariant form

$$
\begin{equation*}
\frac{1}{\lambda} u+\lambda v-\ln \left(u^{\frac{1}{\lambda}} v^{\lambda}\right)=K \tag{3}
\end{equation*}
$$

In the following sections, through a functional Hamiltonian transformation combined with a suitable linear change of variables, a novel $\lambda$-invariant Hamiltonian based on new "hybrid-species" reduces the system (2) to a new set of two coupled first-order ODEs with one being linear. As a result, a new, exact analytical solution is derived for one hybrid-species in terms of a simple quadrature: we then proceed with an original method to uncouple the system and derive complete, closed-form quadrature solutions of the LV problem. In the case $\lambda=1$, an exact analytical solution of the LV system for each individual prey and predator species $u(t)$ and $v(t)$ is derived as a function of time. The population oscillation period is further expressed in terms of a unique energy function and two fundamental properties of the period are established.

## Solutions with Hybrid Predator-Prey Species

The logarithmic functional transformation originally introduced by Kerner [17] reduces the normalized LV system (2) to a Hamiltonian form: the coupling between the respective species is modified through a change of variables $y$ and $x \in \mathbb{R}$ according to

$$
\begin{equation*}
y=\ln (u) \text { and } x=\ln (v) \tag{4}
\end{equation*}
$$

The LV system (2) for the respective "logarithmic" prey-like and predator-like species $y(t)$ and $x(t)$ becomes

$$
\begin{aligned}
& \dot{y}=\lambda\left(1-e^{x}\right) \\
& \dot{x}=\frac{1}{\lambda}\left(e^{y}-1\right)
\end{aligned}
$$

Similarly to Eq. (3) this $\lambda$-invariant system (5) admits a primary conservation integral H expressed as the linear combination of two positive convex functions

$$
\begin{equation*}
H(x, y)=\lambda\left(e^{x}-x-1\right)+\frac{1}{\lambda}\left(e^{y}-y-1\right) \tag{6}
\end{equation*}
$$

As already established $[18,19], H(x, y)$ is the Hamiltonian of the conservative LVsystem since Eqs. (5) satisfy Hamilton's equations with x as thecoordinate conjugate to the canonicalmomentumy. Equation (6) expresses the conservative coupling between species $x(t)$ and $y(t)$ : it is further rendered $\lambda$-invariant by introducing a scaled Hamiltonian $h(x, y)$ with total constant positive energysimply labeled $h$, according to

$$
H(x, y)=\left(\lambda+\frac{1}{\lambda}\right) h(x, y)
$$

We introduce a $\lambda$-invariant linear first-order ODE between the species $x(t)$ and $y(t)$ by further combining the system (5) with (6) and (7)

$$
\begin{equation*}
\stackrel{\rightharpoonup}{x-y-}\left(\lambda x+\frac{y}{\lambda}\right)=\left(\lambda+\frac{1}{\lambda}\right) h \tag{8}
\end{equation*}
$$

Equation (8) suggests introducing a $\lambda$-invariant linear transformation of the set $\{x(t), y(t)\}$ to a new set $\{\xi(t), \eta(t)\}$ representing the symbiotic coupling between "hybrid predator-prey species"

$$
\begin{array}{r}
\xi=\frac{\lambda x+\frac{1}{\lambda} y}{\lambda+\frac{1}{\lambda}} \\
\eta=\frac{x-y}{\lambda+\frac{1}{\lambda}} \tag{9b}
\end{array}
$$

The original Hamiltonian (6) together with (7) and the linear transformation (9) then becomes

$$
\begin{equation*}
h(\eta, \xi)=\frac{\lambda e^{\frac{\eta}{\lambda}}+\frac{1}{\lambda} e^{-\lambda \eta}}{\lambda+\frac{1}{\lambda}} e^{\xi}-\xi-1 \tag{10}
\end{equation*}
$$

Here $h(\eta, \xi)$ is a new Hamiltonian for the coordinate $\eta$ and its conjugate momentum $\xi$. Notice that for small amplitudes, $h(\eta, \xi)$ identically reduces to the Hamiltonian of a harmonic oscillator. Upon further introducing the following $\lambda$-invariant G - function
$G \lambda(n)=\frac{\lambda e^{\frac{\eta}{\lambda}}+\frac{1}{\lambda} e^{-\lambda \eta}}{\lambda+\frac{1}{\lambda}}$ with $G_{\lambda}(\eta)=G_{1 / \lambda}(-\eta) \lambda$-invariant $(11)$
the conservation relationship (10) between the conjugate functions $\eta(\mathrm{t} n(t)$ and $\xi(t)$ is recast into a compact form which provides a natural separation of variables

$$
\begin{equation*}
G_{\lambda}(\eta)=(h+1+\xi) e^{-\xi}(1 \tag{12}
\end{equation*}
$$

In the followingwedefinea usefulcompactauxiliary function $U(\xi) \geq 1$ appearing throughout as

$$
\begin{equation*}
U(\xi)=(h+1+\xi) e^{-\xi} \tag{13}
\end{equation*}
$$

Even though still nonlinear, the fundamental conservation relationship (12) partially uncouples the $\xi(t)$-function from the $n(t)$ -function, resulting in three essential $G$-function properties:
I. The system's energy $h \geq 0$ is explicitly associated with the function $U(\xi)$ only;
II. The positive function $G_{\lambda}(\eta)$ is a generalized hyperbolic cosine function that reaches its minimum $G_{\lambda}=1$ at $\eta=0$ for any value of $\lambda$ : hence its inverse function $G_{\lambda}^{-1}$ exists, and, for any
value of $\lambda$, Eq. (12) admits two respective positive and negative roots $\eta^{ \pm}(\xi, \lambda)$ functions of $\xi$ only satisfying

$$
\begin{equation*}
\eta^{ \pm}(\xi, \lambda)=G_{\lambda}^{-1}(U(\xi)) \tag{14}
\end{equation*}
$$

III. Since the $\eta$-function is associated with the coupling ratio $\lambda$ only, $\lambda$-invariance of the G-function (11) implies that, for a given $\lambda$, any positive solution $\eta^{+}(\xi, \lambda)$ is directly derived from the negativesolutionassociated with the ratio $1 / \lambda$, and reciprocally

$$
\begin{equation*}
\eta^{ \pm}(\xi, \lambda)=-\eta^{\mp}(\xi, 1 / \lambda) \tag{15}
\end{equation*}
$$

From Eq. (13) the hybrid-species population $\xi(t)$ thus oscillates between the $\lambda$ - independent respective negative and positive roots $\xi^{-}(h)$ and $\xi^{+}(h)$, solutions of the equation $U(\xi)=1$, solely dependent on the system's energy $h$ as displayed in Table 1 for several increasing values of $h$

Table 1: Roots of $e^{\xi}-\xi-1=h$ as a function of the energy $h$ from Eq. (16).

| $\mathbf{h}$ | $\mathbf{0 . 3}$ | $\mathbf{0 . 5}$ | $\mathbf{1}$ | $\mathbf{2}$ | $\mathbf{3}$ | $\mathbf{5}$ | $\mathbf{7}$ | $\mathbf{1 0}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $\xi^{-}(h)$ | -0.889 | -1.198 | -1.841 | -2.948 | -3.981 | -5.998 | -8 | -11 |
| $\xi^{+}(h)$ | 0.686 | 0.858 | 1.146 | 1.505 | 1.749 | 2.091 | 2.336 | 2.611 |

$$
\begin{equation*}
e^{\xi}-\xi-1=h \text { with } h \geq 0 \tag{16}
\end{equation*}
$$

For any value of the energy $h$, in the $\xi-\eta$ plane Eq. (12) represents a closed- orbit loop consisting of two branches $\eta^{+}(\xi, \lambda)$ and $\eta^{-}(\xi, \lambda)$ around the fixed point $(0,0)$. This mapping is bounded by the roots $\xi^{-}(h)$ and $\xi^{+}(h)$ on the horizontal axis; since $U(\xi)$ admits a maximum $e^{h}$ located at $\xi=-h$, it is also bounded vertically by the two respective positive and negative roots solutions of the equation $\eta^{ \pm}(-h, \lambda)=G_{\lambda}^{-1}\left(e^{h}\right)$. An orbit is displayed on Figure 1 for an energy $h=2$ and two inverse coupling parameters $\lambda=2$ and $\lambda=1 / 2$. Per Eq. (15), the respective branches associated with the $\lambda$ and $1 / \lambda$-mappings are readily observed to besymmetric with respect to the $\eta=0$ axis.

Except when $\lambda=1$, algebraic solutions of Eq. (14) may generally not be obtained directly. However, for any value
$\xi \in\left[\xi^{-}(h), \xi^{+}(h)\right]$ the two roots $\eta^{ \pm}(\xi, \lambda)$ of Eq. (14) may be obtained numerically through a standard "Newton-Raphson" algorithm. Appendix 1 establishes that each root admits lower and upper bounds for any value of $U(\xi)$, thereby ensuring algorithm convergence.

Lastly, upon inserting the linear transformation (9) into the modified LV system (5), or equivalently using the standard Hamilton equations with Eq. (10), a new semi-linear system of coupled $1^{\text {st }}$ order ODEs is obtained

$$
\begin{gather*}
\dot{\eta}=\xi+h \\
\dot{\xi}=-G_{\lambda}^{\prime}(\eta) e^{\xi} \tag{17a}
\end{gather*}
$$



Figure 1: $\xi-\eta$ Mapping for $\lambda=2$ and $\lambda=1 / 2$, and energy $h=2$.

The solution of the system (17), in which $G_{\lambda}(\eta)$ is the derivative $G_{\lambda}^{\prime}(\eta)=d G_{\lambda} / d \eta$, represents the time-evolution of the hybrid-species $n(t)$ and $\xi(t)$, albeit due to the linear transformation (9), the first coupled equation (17a) becomes linear as expected. Remarkably, as a result of this hybrid-species transformation, the linearity considerably simplifies the solution of the system (17). The exact solution of the LV problem is derived by integration of (17a) as a simple closed-form quadrature for $t(\xi)$ : upon using the initial conditions $\eta_{0}=0$ and $\xi_{0}=\xi^{ \pm}(h)$ when $t=0$, the exact LV solution corresponding to the respective negative and positive branches $\eta^{-}(\xi, \lambda)$ and $\eta^{+}(\xi, \lambda)$ becomes

$$
\begin{equation*}
t(\xi)=\int_{\xi^{ \pm}}^{\xi} \frac{d \eta^{ \pm}(x, \lambda)}{h+x} \tag{18}
\end{equation*}
$$

This quadrature is not divergent at $x=-h$, since the differential $d \eta$ in Eq. (14) contains the factor $U^{\prime}(\xi)=-(h+\xi) e^{-\xi}$ in the numerator. Upon using the same initial conditions, the solution (18) is expressed in terms of the function $\eta^{ \pm}(\xi, \lambda)$ itself through a standard integration by parts in which the singularity at $\xi=-h$ is further eliminated by adding and subtracting the expression $\frac{n^{ \pm}(-h, \lambda)}{h+\xi}$ in the integral. The final, exact, closed-form, regular solution of the entire LV problem for any value of the coupling ratio $\lambda$ and/or of the orbital energy $h$ isexplicitly expressed as a quadrature over each of the two branches $\eta^{ \pm}(\xi, \lambda)$ solutions of (14)
$t(\xi)=\frac{\eta^{ \pm}(\xi, \lambda)-\eta^{ \pm}(-h, \lambda)}{h+\xi}+\frac{\eta^{ \pm}(-h, \lambda)}{h+\xi^{ \pm}}+\int_{\xi^{ \pm}}^{\xi} \frac{\eta^{ \pm}(x, \lambda)-\eta^{ \pm}(-h, \lambda)}{(h+x)^{2}} d x$
This exact solution is further analyzed in the following section. Numerical solutions for $\xi(t)$ and $\eta(t)$ are also obtained by integrating Eqs. (17) using a standard fourth-order Runge-Kutta (RK4) method as presented in Figure 2 for values of $h$ and $\lambda$ exactly identical to those of Figure 1, together with the above initial conditions $\eta_{0}$ and $\xi_{0}$. The function $\xi(t)$ is observed to principally depend on two time constants: a quasi-exponential increase atarate of order $\lambda$ followed byan exponential decrease at a rate $-1 / \lambda$ : from $\lambda$-invariance (15) the two functions $\xi(t)$ respectively corresponding to $\lambda=2$ and its inverse $\lambda=1 / 2$ are mirrors of each other; so are the functions $\eta(t)$, but with the change $\eta \rightarrow-\eta$.

For the general case $\lambda \neq 1$, upon explicitly relating $G_{\lambda}(\eta)$ to its derivative $G_{\lambda}^{\prime}(\eta)$ and expressing the latter as an analytical function of $\xi$ only through (12), an ap- proximate yet accurate ODE for $\xi(t)$ is proposed below.

Case $\lambda=1$. The LV problem is solved exactly in the particular case $\lambda=1$, [2]. TheG-function (11) (omitting the index for simplicity) reduces to the hyperbolic cosine function and the energy conservation equation (12) becomes

$$
\begin{equation*}
G(\eta)=\cosh (\eta)=(h+1+\xi) e^{-\xi} \tag{20}
\end{equation*}
$$



Figure 2: Solutions for $\xi(t)$ and $\eta(t)$ as a function of time $t$ with $\lambda=2$ and energy $h=2$ : numerical integration of Eq. (17) by RK4.

The resulting $\xi-\eta$ closed-orbit mapping is symmetric with two branches $\eta^{ \pm}(\xi)$ explicitly expressed in terms of the inverse hyperbolic cosine function

$$
\begin{equation*}
\eta^{ \pm}(\xi)= \pm \cosh ^{-1}(h+1+\xi) e^{-\xi} \tag{21}
\end{equation*}
$$

Equation (21) again establishes the symbiotic coupling between the hybrid species $\eta$ and $\xi$. Evidently, in this $\lambda=1$ case, the explicit relationship between $G(\eta)$ and its derivative $G^{\prime}(\eta)$ is

$$
\begin{equation*}
G^{\prime}(\eta)= \pm\left(G^{2}-1\right)^{1 / 2} \tag{22}
\end{equation*}
$$

Upon inserting (22) together with (20) into (17b) the nonlinear LV system (17) completely uncouples: it consists in the $1^{\text {st }}$ order linear ODE (17a) together with a $1^{\text {st }}$ order nonlinear autonomous ODE for the species $\xi$ population

$$
\eta=\xi+h(23 \mathrm{a})
$$

$$
\begin{equation*}
\left.\left.\dot{\xi}= \pm e^{\xi}(U(\xi))^{2}-1\right)^{1 / 2}= \pm(h+1+\xi)^{2}-e^{2 \xi}\right)^{1 / 2} \tag{23b}
\end{equation*}
$$

The linear equation (23a) is directly solved by inserting $\eta(\xi)$
from (21) into the solution (19). Together with $U(\xi)$ defined in (13), the exact, closed-form analytic solution on the interval $\xi^{-} \leq \xi \leq \xi^{+}$is thus expressed as a simple quadrature in terms of elementary functions

$$
\begin{align*}
& t(\xi)=\frac{\cosh ^{-1}\left(e^{h}\right)-\cosh ^{-1}(U(\xi))}{h+\xi}-\frac{\cosh ^{-1}\left(e^{h}\right)}{h+\xi^{-}}+ \\
& \int_{\xi^{-}}^{\xi} \frac{\cosh ^{-1}\left(e^{h}\right)-\cosh ^{-1}(U(x))}{(h+x)^{2}} d x \tag{24}
\end{align*}
$$

By applying l'Hôpital's rule, it is readily verified that the integrand in (24) is regular at $\xi=-h$. Figure 3 presents the $\xi(t)-$ solution obtained by numerical RK4 integration of (24) for an energy $h=2$ with initial condition $\xi(0)=\xi^{-}(h)$. The growth and decay phases of the function $\xi(t)$ are observed to be symmetric relative to the half-period $t^{*}$ when $\xi\left(t^{*}\right)=\xi^{+}(h)$. The IV solution is finalized for the two branches $\eta^{ \pm}(t)$ by inserting $\xi(t)$ derived above into Eq. (21).

Alternatively, over the respective intervals $\xi^{-} \leq \xi(t) \leq \xi^{+}$and $\xi+\geq \xi(t) \geq \xi^{-}$corresponding to the growth and decay phases of $\xi(t)$, an expression for $t(\xi)$ is readily obtained by performing the integration with the respective positive root (growth phase) and negative root (decay phase) of the autonomous Eq.(23b), yielding the following quadrature solution which only depends on the energy h

$$
\begin{gather*}
t(\xi)=\int_{\xi}^{\xi}-\frac{d x}{\sqrt{(h+1+x)^{2}-e^{2 x}}}  \tag{25a}\\
t(\xi)=t^{*}+\int_{\xi}^{\xi}-\frac{d x}{\sqrt{(h+1+x)^{2}-e^{2 x}}} \tag{25b}
\end{gather*}
$$

Even though the $\xi(t)$ hybrid species population is not explicitly
expressed as a function of time $t$, the function $t(\xi)$ being monotonic and continuous on each respective integration interval, its inverse function $t^{-1}: \mathbb{R} \rightarrow \mathbb{R}$ defined by $\xi(t)=t^{-1}(\xi)$, exists and is unique, monotonic, and continuous on each interval. At the respective limits $\xi^{-}(h)$ and $\xi^{+}(h)$ the integrand of (25) has a weak singularity of the square root type but is strictly continuous over the interval and the integral is convergent. It is readily verified that integrating (24) by partsidentically results in solution (25).


Figure 3: Solutions for $\xi(t)$ and $\eta(t)$ as a function of time $t$ obtained by numerical integration of the quadrature solution Eq. (23b) with $\lambda=1$ and energy $h=2$

Together with (21), the exact solution (25) for $\xi(t)$ over the respective intervals $\xi^{-} \leq \xi \leq \xi^{+}$and $\xi^{+} \geq \xi \geq \xi^{-}$constitutes the final solution of the LV problem for the "hybrid species" in the special $\lambda=1$ case considered here.

The solution (25) is similar in form to one derived by Evans and Findley (Eq. (17) in [10]); however, the above integral expression lends itself to simpler analytical or numerical integration. An exact expression for (25) is further proposed in Appendix 1 in terms of exponential integral functions.

Exact Solutions for the Prey and Predator Species Popu-
lations. In this $\lambda=1$ case, exact solutions for the time evolution of the prey and predator populations are derived by inserting the respectivehybrid-speciespopulations $\xi(t)$ and $\eta(t)$ obtainedfrom Eqs. (25) and (21) into the original definitions (4) and (9). This results in two uncoupled solutions for the individual populations $u(t)$ and $v(t)$ of the prey and predator species.

Over the growth and decay phases of the symmetric $\xi(t)$ function, these exact un- coupled analytical solutions for the respective prey and predator populations are expressed as follows

Interval $0 \leq t \leq t * \mapsto$ interval $\xi^{-} \leq \xi(t) \leq \xi^{+}$, i.e. $\xi(t)$ growth phase $u(t)=h+1+\xi(t)+\sqrt{(h+1+\xi(t))^{2}-e^{2 \xi(t)}}$ (26a) for preys $\mathrm{v}(\mathrm{t})=\mathrm{h}+1+\xi(\mathrm{t})-\sqrt{(\mathrm{h}+1+\xi(\mathrm{t}))^{2}-\mathrm{e}^{2 \xi(\mathrm{t})}}$ (26b) for predators with $\xi(t)=t^{-1}(\xi)$ derived from (25a) together with $\xi(0)=\xi^{-}(h)$. $\underline{\text { Interval } t * \leq t \leq 2 t *} \mapsto$ interval $\xi^{+} \geq \xi(t) \geq \xi^{-}$, i.e. $\xi(t)$ decay phase $\mathrm{u}(\mathrm{t})=\mathrm{h}+1+\xi(\mathrm{t})-\sqrt{(\mathrm{h}+1+\xi(\mathrm{t}))^{2}-\mathrm{e}^{2 \xi(\mathrm{t})}}$ (27a) for preys $\mathrm{v}(\mathrm{t})=\mathrm{h}+1+\xi(\mathrm{t})+\sqrt{(\mathrm{h}+1+\xi(\mathrm{t}))^{2}-\mathrm{e}^{2 \xi(\mathrm{t})}}(27 \mathrm{~b})$ for predators with $\xi(t)=t^{-1}(\xi)$ derived from (25b) together with $\xi\left(t^{*}\right)=\xi^{+}(h)$.

Figure 4 displays the exact uncoupled analytical solutions for the time evolution of the preys $u(t)$ and the predators $v(t)$ when their respective growth and decay rates are equal in magnitude, and when the system's energy is $h=2$.


Figure 4: Exact analytical solutions for $u(t)$ and $v(t)$ as a function of time tobtained from Eqs. (26) and (27) with energy $h=2$.

It is observed that the prey population $u(t)$ exhibits an initial growth at rate significantly slower than its own fast decay rate with the opposite for predators;also the peak population of the preys occurs when the population is mature, i.e. when the predator population is small ( $v=1$ ), and vice-versa.

Case $\lambda \neq 1$. In the general case when $\lambda \neq 1$ the relationship between $G_{\lambda}(\eta)$ and its derivative $G_{\lambda}^{\prime} \eta$ is obtained by observing that
$G_{\lambda}^{\prime}(\eta)=\frac{e^{\frac{\eta}{\lambda}}-e^{-\lambda \eta}}{\lambda+\frac{1}{\lambda}} \quad$ with $G_{\lambda}^{\prime}(\eta)=-G^{\prime}{ }_{1 / \lambda}^{(-\eta)} \quad(\lambda-$ invariance $)(28)$
Upon eliminating $\eta$ between Eqs. (11) and (28), an implicit non-linear $1^{\text {st }}$ order ODE relating $G$ to its derivative $G^{j}$ is derived (for clarity the index $\lambda$ is omitted in the remainder of this section)

$$
\left(G+\frac{1}{\lambda} G^{\prime}\right)^{\lambda}\left(G-\lambda G^{\prime}\right)^{1 / \lambda}=1 \text { (29) }
$$

Equation (29) is completely invariant in the change $\lambda \rightarrow-1 / \lambda$, or equivalently changing $\lambda \rightarrow 1 / \lambda$ together with $G^{\prime} \rightarrow-G^{\prime}$. As a result, similarly to Eq. (22), in the $G-G^{\prime}$ phase space, Eq. (29) represents the positive and negative branches of a "skewed" hyperbola with orthogonal asymptotes, respectively $G^{\prime}=G / \lambda$ and $G^{\prime}=-\lambda G$, and a vertex $G^{\prime}=0$ located at $G^{\prime}=1$. For any value of the coupling parameter $\lambda$, the function $G^{\prime}(\eta)$ reaches its extremes at the two roots of $G(\eta)=e^{h}$. Also, as expected, in the case $\lambda=1$ Eq. (29) identically reduces to (22).

Being implicit, (29) can generally not be solved for $G^{\prime}$ as a function of $G$ by standard algebraic techniques. A practical yet accurate approximation for the function $G^{\prime}(G)$ predicated on Eq. (22), which uncouples the system, is proposed below.

For the positive branch $G^{\prime} \geq 0$, for large $G$ the function $G^{\prime}$ is asymptotic to $G^{\prime}=G / \lambda$ : Eq. (29) is recast as

$$
\begin{equation*}
\lambda \frac{G^{\prime}}{G}=1-\frac{1}{G^{\lambda^{2}+1}\left(1+\frac{1}{\lambda} \frac{G^{\prime}}{G}\right)^{\lambda^{2}}} \tag{30}
\end{equation*}
$$

Furthermore, the factor in parenthesis in the denominator always satisfies the following inequality

$$
\begin{equation*}
\left(1+\frac{1}{\lambda} \frac{G^{\prime}}{G}\right)^{\lambda^{2}}<e^{\frac{G^{\prime}}{G}} \tag{31}
\end{equation*}
$$

Upon approximating this factor by its exponential limit, Eq. (30) becomes

$$
\begin{equation*}
e^{\lambda \frac{G^{\prime}}{G}}\left(1-\lambda \frac{G^{\prime}}{G}\right) \cong \frac{1}{G^{\lambda^{2+1}}} \tag{32}
\end{equation*}
$$

Since the G-function is bounded by $\mathrm{e}^{\mathrm{h}}$, a Taylor expansion of the exponential factor to first order yields an explicit approximation for the two branches of $G^{\prime}(G)$. Notice that the negative branch $G^{\prime} \leq 0$ is directly obtained by $\lambda$-invariance applied to the equation representing the positive branch $G^{\prime} \geq 0$.

$$
\begin{align*}
& G^{\prime}(G) \cong \frac{G}{\lambda}\left(1-\frac{1}{G^{\lambda^{2}+1}}\right)^{1 / 2} \quad\left(\text { positive branch } G^{\prime} \geq 0\right) \quad \text { (33a) } \\
& G^{\prime}(G) \cong-\lambda G\left(1-\frac{1}{G^{1 / \lambda^{2}+1}}\right)^{1 / 2} \quad\left(\text { negative branch } G^{\prime} \leq 0\right) \tag{33b}
\end{align*}
$$

Remarkably, the above approximate function $G^{\prime}(G)$ satisfies the following three basic properties identical to those of an exact numerical solution of Eq. (29):

1. At its vertex, when $G=1$, the function $G^{\prime}(G)$ reaches $G^{\prime}=0$,
2. For $G \gg 1$, as expected, the positive branch of the function $G^{\prime}(G)$ is asymptotic to $G^{\prime}=G / \lambda$ whereas the negative branch is asymptotic to $G^{\prime}=-\lambda G$,
3. For $\lambda=1, G^{\prime}(G)$ reduces to the exact predicate expression (22).

Thus, in the ${ }_{G-G}{ }^{\prime}$ phase space, the explicit expressions (33) represent approximate positive and negative branches of the "skewed" hyperbola defined by Eq. (29) with the same orthogonal asymptotes. Upon comparing graphic representations of the explicit expressions (33) to the exact numerical solution of (29) for the implicit function $G^{\prime}(G)$ it is found that the agreement is quite reasonable particularly for the positive $G^{\prime}(G)$-branch when $\lambda \geq 1$, and conversely for the negative branch when $\lambda \leq 1$. This is understandable in light of the above first two properties of (33). As $\lambda \rightarrow 1$ the approximation (33) approaches the exact solution (22); for $\lambda \gg 1$ the graph of (33) exhibits two branches tightly bounded by their respective orthogonal asymptotes with the accuracy of this approximation increasing with increasing $\lambda$.

As intended, approximation (33) effectively uncouples the system (17) by explicitly removing the dependence on $\eta$ in the original ODE (17b): upon inserting the con- servation Eq. (12) into (33), Eq. (17b) is replaced by a pair of two $\lambda$-invariant $1^{\text {st }}$ order nonlinear ODEs for the hybrid species population $\xi(t)$

$$
\begin{gathered}
\dot{\xi}=-\frac{h+1+\xi}{\lambda}\left(1-\frac{e^{\xi\left(\lambda^{2}+1\right)}}{(h+1+\xi)\left(\lambda^{2+1}\right)}\right)^{1 / 2} \quad \text { (positive } \eta \text {-branch: } \eta \geq 0 \text { ) (34a) } \\
\left.\dot{\xi}=\lambda(h+1+\xi)\left(1-\frac{e^{\xi\left(1 / \lambda^{2}+1\right)}}{(h+1+\xi)}\right)^{1 / 2} \text { (negative } \eta \text {-branch: } \eta \leq 0\right)(34 \mathrm{~b})
\end{gathered}
$$

Evidently, for $\lambda=1$ the two branches of (23b) are recovered. Even though $\xi(t)$ is not explicitly expressed as a function of time t , the arbitrary $\lambda \neq 1$ problem has thus been reduced to a pair of simple quadratures for the function $\xi(t)$. As already stated, the function $\xi(t)$ oscillates between the $\lambda$-independent respective
roots $\xi^{-}(h)$ and $\xi^{+}(h)$ solutions of Eq. (16). The process for solving Eq. (34) is identical to that of Eq. (23b): upon again choosing the time origin $\mathrm{t}=0$ when $\xi_{0}=\xi^{-}(h)$, a complete period is obtained by integration over the corresponding negative $\eta$-branch in (34b) until $\xi(t)$ reaches $\xi^{+}(h)$, followed by an integration over the positive $\eta$-branch (34a) until $\xi^{-}(h)$ is reached
$t(\xi)=\int_{\xi^{-}}^{\xi} \frac{1}{\lambda(h+1+\chi)}\left(1-\frac{e^{x\left(1 / \lambda^{2}+1\right)}}{(h+1+x)\left(1 / \lambda^{2}+1\right)}\right)^{-1 / 2} d x$ (negative $\eta$-branch)
$t(\xi)=-\int_{\xi^{+}}^{\xi} \frac{\lambda}{h+1+x}\left(1-\frac{e^{x\left(\lambda^{2}+1\right)}}{(h+1+x)\left(\lambda^{2}+1\right)}\right)^{-1 / 2} d x$ (positive $\eta$-branch $)$
The function $t(\xi)$ being monotonic and continuous on the respective integration intervals $\xi^{-} \leq \xi \leq \xi^{+}$and $\xi^{+} \geq \xi \geq \xi^{-}$its inverse function $\xi(t)$ exists and is unique, monotonic, and continuous on each interval. The LV problem is then completed for the function $\eta(t)$ by directly integrating the linear Eq. (17a) through standard numerical techniques.

To assess the accuracy of the uncoupled approximate solutions (34), a comparison is made with the exact numerical solutions of the original coupled LV system (17). Upon using the respective values $\lambda=2$ and $h=2$ identical to those of Figure 2 for the coupling ratio and system energy, Figure 5 presents the comparison between the functions $\xi(t)$ and $\eta(t)$ respectively obtained by numerically integrating (34) and (17) simultaneously through a standard $4^{\text {th }}$ order RK4 method. From the figure it is observed that the ODEs (34) provide a reasonably accurate solution for both functions $\xi(t)$ and $\eta(t)$ over an entire period, yet, when $\lambda>1$, with an underestimation of the time taken to reach $\xi^{+}(h)$ compensated by an overestimation of the time to reach $\xi^{-}(h)$. As expected, the accuracy of the solutions obtained with approximations (34) increases with increasing $\lambda$.

From Figure 5, regardless of the value of $\lambda$, the hybrid species population $\xi(t)$ oscillates with exponential-like growth and decay phases with an amplitude determined by its energy-dependent interval $\xi^{+}(h)-\xi^{-}(h)$.

Remarkably, in the high energy limit $h \gg 1$, upon keeping the leading asymptotic term in (34), the asymptotic behavior of the LV system becomes modeled as a system of two coupled linear $1^{\text {st }}$ order ODEs for each hybrid species. In this asymptotic limit, together with the linear ODE (17a) for $\eta(t)$, the system admits trivial exponential solutions remarkably representative of the exact solutions of (17). For example, the asymptotic solutions $h \gg 1$ for the growth phase $\left(\xi^{-} \leq \xi \leq \xi^{+}\right)$simply are

$$
\begin{aligned}
& \xi(t)=e^{\xi^{-}+\lambda t}-(h+1) \\
& \eta(t)=\frac{1}{\lambda}\left(\xi(t)-\xi^{-}(h)\right)-t(36 \mathrm{~b})
\end{aligned}
$$



Figure 5: Solutions for $\xi(\mathrm{t})$ and $\eta(\mathrm{t})$ as a function of time t with $\lambda=2$ and energy $h=2$; comparison between RK4 numerical integration of Eq. (17) and Eq. (34).

The asymptotic decay phase solutions for $\xi(t)$ and $\eta(t)$ are obtained by $\lambda$-invariance, namely $\lambda \rightarrow-1 / \lambda$ together with $\xi^{-}(h) \rightarrow \xi^{+}(h)$.

Lastly, as done with the exact solutions (26) and (27) when $\lambda=1$, upon inserting the hybrid-species populations $\xi(t)$ and $\eta(t)$ derived from Eqs. (34) together with thetransformation (9) into the prey and predator species definition (4), the respective standard solutions for the original populations $u(t)$ and $v(t)$ are fully recovered when $\lambda \neq 1$

$$
\begin{gather*}
u(t)=e^{\xi(t)-\lambda \eta(t)} \text { for preys } \\
v(t)=e^{\xi(t)+\eta(t) / \lambda} \text { for predators } \tag{37b}
\end{gather*}
$$

## Oscillation Period of the LV System

The unique $\lambda$-invariance property of $\eta^{ \pm}(\xi, \lambda)$ in (15) directly enables to establish two fundamental properties of the LV system period [1]. Consider the double mapping of Figure 1 and follow in a counter clockwise direction the two branches $A B^{-}$ and $B A^{+}$corresponding to the respective branches $\eta^{-}(\xi, \lambda)$ and $\eta^{+}(\xi, \lambda)$ : the negative branch $A B^{-}$starts at $\xi^{-}(h)$ and ends at $\xi^{+}(h)$ and conversely for the positive $B A^{+}$branch. Upon integrating (18) over the $\xi$-variable and recalling the earlier dimensionless time definition, the oscillation period $T_{\lambda}(h)$ associated with the $\lambda$ -mapping is directly obtained as a quadrature over these two branches in (38a) in which the negative sign for the second integral reflects integration from $\xi^{+}$to $\xi^{-}$. Similarly, for the $1 / \lambda$-mapping the oscillation period is expressed as (38b)

$$
\begin{align*}
& T_{\lambda}(h)=\frac{1}{\sqrt{\alpha \delta}}\left(\int_{A B^{-}} \frac{d \eta^{-}(\xi, \lambda)}{h+\xi}-\int_{B A^{+}} \frac{d \eta^{+}(\xi, \lambda)}{h+\xi}\right)  \tag{38a}\\
& T_{1 / \lambda}(h)=\frac{1}{\sqrt{\alpha \delta}}\left(\int_{A B^{-}} \frac{d \eta^{-}(\xi, 1 / \lambda)}{h+\xi}-\int_{B A^{+}} \frac{d \eta^{+}(\xi, 1 / \lambda)}{h+\xi}\right) \tag{38b}
\end{align*}
$$

Upon recalling the $\lambda$-invariance property of Eq. (15), substitution into (38b) establishes that:

$$
T_{\lambda}(h)=T_{1 / \lambda}(h)
$$

Theorem 1. For anyvalue of the positive orbital energyh, the $L V$ system oscillation periods respectivelycorresponding to the coupling ratio $\lambda$ anditsinverse $1 / \lambda$ are equal.

Consequently, an exact, closed-form, regular expression for the nonlinear LV system oscillation period, valid for any value of the coupling ratio $\lambda$ and any value of the orbital energy $h$, is directly derived from (38a) as a single integral over the two branches $\eta^{ \pm}(\xi, \lambda)$

$$
\begin{align*}
& T_{\lambda}(h)=\frac{1}{\sqrt{\alpha \delta}} \frac{\left(\eta^{-}(-h, \lambda)-\eta^{+}(-h, \lambda)\right)\left(\xi^{+}-\xi^{-}\right)}{\left(h+\xi^{+}\right)\left(h+\xi^{-}\right)}+  \tag{40}\\
& \frac{1}{\sqrt{\alpha \delta}} \int_{\xi^{-}}^{\xi^{+}} \frac{\eta^{-}(x, \lambda)-\eta^{-}(-h, \lambda)+\eta^{+}(-h, \lambda)-\eta^{+}(x, \lambda)}{(h+x)^{2}} d x
\end{align*}
$$

In Appendix 1, for any $\xi \in\left[\xi^{-}(h), \xi^{+}(h)\right]$, the interval $\eta^{+}(\xi, \lambda)-\eta^{-}(\xi, \lambda)$ is shown to be a positive increasing function
of $\lambda$ when $\lambda \geq 1$ (and decreasing when $0<\lambda \leq 1$ ) admitting respective lower and upper bounds, both of which are minimal when $\lambda=1$ . Together with Eq. (40) this establishes:

Theorem 2. For any value of the positive orbital energy $h$, the $L V$ system oscillation period $T_{\lambda}(h)$ is an increasing function of $\lambda$ for $\lambda \geq 1$ (decreasing for $0<\lambda \leq 1$ ) and the period is shortest for $\lambda=1$.

In the particular case when $\lambda=1$, the exact LV system period $T_{1}(h)$ is uniquely expressed in terms of a universal energy function $\Theta_{1}(h)$ as

$$
T_{1}(h)=\frac{2 \pi}{\sqrt{\alpha \delta}} \Theta_{1}(h)
$$

The LV energy function $\Theta_{1}(h)$ introduced in is defined by integrating (25a) over the entire $\xi$-interval

$$
\Theta_{1}(h)=\frac{1}{\pi} \int_{\xi^{-}}^{\xi^{+}} \frac{d x}{\sqrt{(h+1+x)^{2}-e^{2 x}}} \text { (42) }
$$

At small orbital energy $(h \ll 1)$ where $\xi^{ \pm}(h)= \pm \sqrt{2 h}$, the function $\Theta_{1}(h)$ is directly expressed in terms of the complete elliptic integral of the first kind $K(k)$ with its modulus $k$

$$
\begin{equation*}
\Theta_{1}(h)=\frac{1}{\sqrt{1+\sqrt{2 h}}} \frac{2}{\pi} K(k) \text { with } k=\sqrt{\frac{2 \sqrt{2 h}}{1+\sqrt{2 h}}} \tag{43}
\end{equation*}
$$

A standard series expansion for $K(k)$ yields

$$
\begin{equation*}
\Theta_{1}(h)=1+\frac{1}{3} h+\frac{1}{42} h^{2}+o\left(h^{3}\right) \tag{44}
\end{equation*}
$$

For small oscillation amplitudes, the integral (42) becomes independent of the energy h and is exactly equal to $\pi$, hence $\Theta_{1}(h)=1$; the LV system becomes that of two coupled harmonic oscillators for which the period $T(h)$ solely depends on the pulsation $\sqrt{\alpha \delta}$, as already established [3,20].

At high orbital energy ( $h \gg 1$ ), the contribution from the exponential term in (42) becomes negligible since $\xi<0$ over most of the integration intervalexcept when $\xi$ approaches $\xi^{+}(h)$ : since by definition $\xi(t) \geq \xi^{-}(h)$, approximating the exponential term by its lowest value $e^{2 \xi-(h)}$ and performing the integration yields a useful asymptotic expression for $\Theta(h)$

$$
\begin{equation*}
\Theta_{\text {asymp }}(h) \cong \frac{1}{\pi}\left(\xi^{+}(h)-\xi^{-}(h)+\ln (2)\right) \text { with } h \gg 1 \tag{45}
\end{equation*}
$$

When $\lambda \neq 1$ the exact LV oscillation period $T_{\lambda}(h)$ is obtained by numerically solving the ODE system (17) as done for Figure 2. Similarly to Eq. (41), for each value of the coupling ratio $\lambda$, the period $T_{\lambda}(h)$ is then uniquely expressed in terms of a universal LV energy functions $\Theta_{\lambda}(h)$

$$
T_{\lambda}(h)=\frac{2 \pi}{\sqrt{\alpha \delta}} \Theta_{\lambda}(h)
$$

As shown on Figure 6 and consistent with Theorem 2, for any value of the coupling parameter $\lambda$, each function $\Theta_{\lambda}(h)$, and by extension $T_{\lambda}(h)$, is a monotonically increasing function of the en-ergy-dependent amplitude $\xi^{+}(h)-\xi^{-}(h)$ of the $\xi(t)$ function only [20]. Also displayed is the asymptotic approximation (45) which is practically indistinguishable from the exact function $\Theta_{1}(h)$ for $h \geq 4$.


Figure 6: Energy function $\Theta_{\lambda}(h)$ for $\lambda=1,2,3,4,5$ and asymptotic approximation for $\lambda=1$.

In this general $\lambda \neq 1$ case, an asymptotic formula for the LV system oscillation period $T_{\lambda}(h)$ valid at high energy $(h \gg 1)$ is obtained from the asymptotic solutions (36). The contribution $T_{\lambda}^{+}(h)$ of the exponential growth phase of $\xi(t)$ to the period is readily obtained from (36b) since $\eta(t)=0$ when $\xi(t)$ reaches its maximum $\xi^{+}(h)$; the contribution $T_{\lambda}^{-}(h)$ of the decay phase is obtained by $\lambda$-invariance. As a result the high energy ( $h \gg 1$ ) asymptotic expression for the LV system period $T_{k}(h)$ simply becomes proportional to the sum of the $\xi(t)$ - functiongrowth and decay rates, $\lambda$ and $1 / \lambda$, respectively

$$
\begin{equation*}
T_{\lambda}(h) \cong \frac{\pi}{\sqrt{\alpha \delta}}\left(\lambda+\frac{1}{\lambda}\right)\left(\xi^{+}(h)-\xi^{-}(h)\right) \tag{47}
\end{equation*}
$$

This asymptotic formula which separately factorizes the LV system coupling from the $\lambda$-independent energy contribution satisfies both Theorem 1 and Theorem 2 since it is minimal when $\lambda=1$.

Upon comparing the methods of Volterra [3], Hsu [21], Waldvogel [20], and Rothe [22], Shih demonstrated that all of these integral representations of the period of the two-species LV system are equivalent to his own solution in terms of a sum of convolution integrals [15]. Subsequent approximations of the LV system period in terms of power series [23] or perturbation expansions [24] have also been published. In Appendix 3, following the derivation of Rothe [22], we show that the Hamiltonian (10) based on hybrid-species populations defined in (9) provides a "state sum" identical to that of Rothe thereby establishing direct equivalence between our LV oscillator period and Rothe's convolution integral.

## Conclusion

The coupled $1^{\text {st }}$ order non-linear ODE system for the LV problem of two interacting prey and predator species has been analyzed in terms of a single positive coupling parameter $\lambda$, ratio of the relative growth/decay rates of each species taken independently. Based on a standard functional transformation in-troducing"hybrid-species populations", a novel $\lambda$-invariant set of two $1^{\text {st }}$ order ODEs is obtained with one being linear. As a result, an exact, closed-form quadrature solution of the LV problem is derived for any value of the coupling ratio $\lambda$ and any value of the system's energy (19).

In the $\lambda=1$ case, the LV problem partially uncouples and an exact explicit closed form solution is derived in terms of the system's orbital energy $h$ as a simple quadrature for the time evolution of the hybrid-species population $\xi(t)$; the other hybrid species' solution $\eta(t)$ is explicitly expressed in terms of the former (Eqs. (25) and (21)).Asaresult, exact uncoupled analytical solutions for each of the original prey and predator populations $u(t)$ and $v(t)$ are derived as a function of time.

In the $\lambda \neq 1$ case, a $\lambda$-invariant accurate practical approximation is derived that explicitly uncouples the LV system and provides a closed-form solution in terms of a single quadrature for one of the hybrid-species populations. Remarkably, at high orbital energies ( $h \gg 1$ ), the original coupled non-linear LV ODE system totally uncouples and becomes entirely linear admitting
trivial asymptotic exponential solutions.
Further, as a consequence of $\lambda$-invariance, for any value of the orbital energy $h$, the LV system oscillation period $T_{\lambda}(h)$ is shown to be identical when the coupling parameter $\lambda$ is inverted to $1 / \lambda$ and is smallest when $\lambda=1$. In this particular case, an exact, closed-form expression for the non-linear LV system oscillation period $T_{1}(h)$ is derived in terms of a universal LV energy function. In the $\lambda \neq 1$ case, a simple asymptotic expression for the LVsystem oscillation period is derived for high energies ( $h \gg 1$ ).

## Appendix 1

This Appendix presents a proof of Theorem 2 introduced after Eq. (40). For the positive root $\eta^{+}(\xi, \lambda)$, Eq. (12) is written

$$
\begin{equation*}
\lambda^{2} e^{\frac{n}{\lambda}}+e^{-\eta \lambda}=\left(\lambda^{2}+1\right) U(\xi) \tag{A1.1}
\end{equation*}
$$

For any given value of $\xi \in\left\{\xi^{-}(h), \xi^{+}(h)\right\}$, since we seek a positive root and since by definition $0 \leq e^{-\eta \lambda} \leq 1$, this root admits a lower and an upperbound

$$
\lambda \ln \left(\left(1+\frac{1}{\lambda^{2}}\right) U(\xi)-\frac{1}{\lambda^{2}}\right) \leq \eta^{+}(\xi, \lambda) \leq \lambda \ln \left(\left(1+\frac{1}{\lambda^{2}}\right) U(\xi)\right)(\mathrm{A} 1.2 \mathrm{a})
$$

Similarly, by $\lambda$-invariance, the negative root satisfies

$$
-\frac{1}{\lambda} \ln \left(\left(1+\lambda^{2}\right) U(\xi)\right) \leq \eta^{-}(\xi, \lambda) \leq-\frac{1}{\lambda} \ln \left(\left(1+\lambda^{2}\right) U(\xi)-\lambda^{2}\right)(\mathrm{A} 1.2 \mathrm{~b})
$$

From Eqs. (A1.2) the lower and upper bounding of the roots $\eta^{ \pm}(\xi, \lambda)$ of Eq. (14) enables to prove Theorem 2. From Eq. (40), the period depends on the magnitude of the positive interval $\eta^{+}(\xi, \lambda)-\eta^{-}(\xi, \lambda)$. Upon introducing the "outer limit" $\Delta_{\text {out }}(\xi, \lambda)$ as

$$
\Delta_{\text {out }}(\xi, \lambda)=\lambda \ln \left(\left(1+\frac{1}{\lambda^{2}}\right) U(\xi)\right)+\frac{1}{\lambda} \ln \left(\left(1+\lambda^{2}\right) U(\xi)\right) \text { (A1.3a) }
$$

It is readily seen that $\Delta_{\text {out }}(\xi, \lambda)$ is a positive, increasing function of $\lambda$ when $\lambda \geq 1$ (and decreasing when $\lambda \leq 1$ ) whose partial derivative $\partial \Delta_{\text {out }}(\xi, \lambda) / \partial \lambda$ vanishes when $\lambda=1$. Similarly, upon introducing the "inner limit" $\Delta_{\text {in }}(\xi, \lambda)$ as

$$
\begin{equation*}
\Delta_{i n}(\xi, \lambda)=\lambda \ln \left(\left(1+\frac{1}{\lambda^{2}}\right) U(\xi)-\frac{1}{\lambda^{2}}\right)+\frac{1}{\lambda} \ln \left(\left(1+\lambda^{2}\right) U(\xi)-\lambda^{2}\right)( \tag{A1.3.b}
\end{equation*}
$$

It is also seen that $\Delta_{i n}(\xi, \lambda)$ is a positive, increasing function of $\lambda$ when $\lambda \geq 1$ (and decreasing when $\lambda \leq 1$ ) whose partial derivative $\partial \Delta_{\text {in }}(\xi, \lambda) / \partial \lambda$ also vanishes when $\lambda=1$. Since the positive interval $\eta^{+}(\xi, \lambda)-\eta^{-}(\xi, \lambda)$ obviously satisfies

$$
\Delta_{\text {in }}(\xi, \lambda) \leq \eta^{+}(\xi, \lambda)-\eta^{-}(\xi, \lambda) \leq \Delta_{\text {out }}(\xi, \lambda)
$$

This proves Theorem 2.

## Appendix 2

Upon recalling the definition (13) of $U(\xi)$, the solution (25a) is expressed as

$$
\begin{equation*}
\mathrm{t}(\xi)=\cosh ^{-1}(U(\xi))+e^{\xi} \sqrt{U(\xi)^{2}-1}+\int_{\xi}^{\xi} \frac{e^{2 x}}{(h+1+x) \sqrt{1-U(x)^{-2}}} d x \tag{A2.1}
\end{equation*}
$$

Since $1 \leq U(\xi) \leq e^{h}$, a binomial expansion of the integrand with binomial coefficients expressed in terms of the Gamma function $\Gamma(p)$ yields an exact solution in terms of a converging series

$$
\begin{align*}
& \mathrm{t}(\xi)=\cosh ^{-1}(U(\xi))+e^{\xi} \sqrt{U(\xi)^{2}-1}+ \\
& \sum_{p=0}^{\infty} \frac{\Gamma\left(\frac{1}{2}\right)}{\Gamma\left(\frac{1}{2}-p\right) \Gamma(p+1) \xi^{-}} \frac{\xi}{h+1+x} \frac{e^{2 x} U(x)^{-2} p}{h} \tag{A2.2}
\end{align*}
$$

The first integral ( $p=0$ ) is directly expressed in terms of the exponential integral function $\operatorname{Ei}(x)$, with the argument $x>0$

$$
\begin{equation*}
\int_{\xi^{-}}^{\xi} \frac{e^{2 x}}{h+1+x} d x=e^{-2(h+1)}\left(\operatorname{Ei}(2(h+1+\xi))-\operatorname{Ei}\left(2 e^{2 \xi^{-}}\right)\right) \tag{A2.3}
\end{equation*}
$$

When inserted into (A2.2) this expression provides a zeroth order $(p=0)$ solution for $t(\xi)$, hence for $\xi(t)=t^{-1}(\xi)$ as discussed earlier.

When the integer p is $1,2,3, \ldots$, each integral $I_{2 p}(\xi)$ in (A2.2) is of the form

$$
I_{2 p}(\xi)=\int_{\xi^{-}}^{\xi} \frac{e^{2 p x} d x}{(h+1+x)^{2 p+1}}(\mathrm{~A} 2.4)
$$

Successive integration by parts and substitution into (A2.2) result in a convergent series of exponential integral functions with positive argument of the form $e^{-2 p(h+1)} E i(2 p(h+1+\xi))$.

## Appendix 3

Based on thermodynamics, Rothe [22] established that the Laplace transform of the period function $T(h)$, in which h is the system's energy, is the canonical state sum $Z(\beta)$ of the Hamiltonian (6), with $\beta \in(0, \infty)$ as the inverse of the absolute temperature, namely

$$
\begin{equation*}
Z(\beta)=\int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} e^{-\beta H(x, y)} d x d y=\int_{0}^{\infty} e^{-\beta h} T(h) d h \tag{A3.1}
\end{equation*}
$$

From Eqs. (10) and (7) together with the definition (11) of the G-function, the LV system's Hamiltonian is

$$
\begin{equation*}
H(\eta, \xi)=\left(\lambda+\frac{1}{\lambda}\right)\left(G_{\lambda}(\eta) e^{\xi}-\xi-1\right) \tag{A3.2}
\end{equation*}
$$

For notation purposes, we introduce the reduced $g$-function $g_{\lambda}(\eta)$ defined as

$$
\begin{equation*}
g_{\lambda}(\eta)=\lambda e^{\frac{\eta}{\lambda}}+\frac{1}{\lambda} e^{-\eta \lambda} \tag{A3.3}
\end{equation*}
$$

Consequently, upon inserting the Jacobian $|J|=\left(\lambda+\frac{1}{\lambda}\right)$ of the linear transformation (9)

$$
Z(\beta)=\left(\lambda+\frac{1}{\lambda}\right) \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} e^{-\beta g_{\lambda}(\eta) e^{\xi}+\left(\lambda+\frac{1}{\lambda}\right) \beta(\xi+1)} d \xi d \eta \text { (А3.4) }
$$

Upon substituting $s=e^{\xi}$ with $s \in(0, \infty)$, (A3.4) becomes

$$
Z(\beta)=\left(\lambda+\frac{1}{\lambda}\right) e^{\beta\left(\lambda+\frac{1}{\lambda}\right)} \int_{-\infty}^{+\infty} \int_{0}^{\infty} s^{\beta\left(\lambda+\frac{1}{\lambda}\right)-1} e^{-\beta s g_{\lambda}(\eta)} d s d \eta \text { (A3.5) }
$$

The integration over $S$ is expressed in terms of the Gamma function $\Gamma(s)$ :

$$
\begin{equation*}
Z(\beta)=\left(\lambda+\frac{1}{\lambda}\right)\left(\frac{e}{\beta}\right)^{\beta\left(\lambda+\frac{1}{\lambda}\right)} \Gamma\left(\beta\left(\lambda+\frac{1}{\lambda}\right)\right) \int_{-\infty}^{+\infty}\left(g_{\lambda}(\eta)\right)^{-\beta\left(\lambda+\frac{1}{\lambda}\right)} d \eta \tag{A3.6}
\end{equation*}
$$

Together with the above definition of $g_{\lambda}(\eta)$ this definite integral has been evaluated (see 3.314 in [25]); the $\lambda$-invariant state sum $Z(\beta)$ thus becomes

$$
\begin{equation*}
Z(\beta)=\left(\frac{e}{\beta \lambda}\right)^{\beta \lambda} \Gamma(\beta \lambda)\left(\frac{e \lambda}{\beta}\right)^{\left(\frac{\beta}{\lambda}\right)} \Gamma\left(\frac{\beta}{\lambda}\right) \tag{A3.7}
\end{equation*}
$$

Although the Hamiltonian (A3.2) is defined in the $\xi-\eta$ space, the result (A3.7) for the state sum $Z(\beta)$ is identical to that of Rothe (Eqs. (9) and (10) in [22]) who used the "planar" Hamiltonian (6) in the $x-y$ space. The derivation of the period then directly follows Rothe who defines a function $\tau(h)$ (Eqs. (15), (16), and (17) in [22]) whose Laplace transform is

$$
\begin{equation*}
\int_{0}^{\infty} e^{-\beta h} \tau(h) d h=\left(\frac{e}{\beta}\right)^{\beta} \Gamma(\beta) \tag{A3.8}
\end{equation*}
$$

Since our state sum (A3.7) is expressed as the product of two Laplace transforms similar to (A3.8), use of the Hamiltonian (A3.2) establishes that the period $T_{\lambda}(h)$ of the LV system (17) is directly equivalent to that of Rothe. Upon recalling the earlier definition of the dimensionless time, the period is expressed as a $\lambda$-invariant convolution integral satisfying Theorem 1 with $\tau(h)$ defined above

$$
\begin{equation*}
\mathrm{T}_{\lambda}(h)=\frac{1}{\sqrt{\alpha \delta}} \int_{0}^{h} \tau\left(\frac{s}{\lambda}\right) \tau(\lambda(h-s)) d s \tag{A3.9}
\end{equation*}
$$

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    $u=\lambda u(1-v) \quad$ for preys (2a)
    $\stackrel{\rightharpoonup}{v}=\frac{1}{\lambda} v(u-1) \quad$ for predators (2b)

