The hunt on canards in population dynamics: a predator-prey system

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Abstract

Equations with periodic coefficients for singularly perturbed growth can be analysed by using fast and slow timescales which involves slow manifolds, canards and the dynamical exchanges between several slow manifolds. We extend the time-periodic P.F. Verhulst-model to predator-prey interaction where two slow manifolds are present. The fast-slow formulation enables us to obtain a detailed analysis of non-autonomous systems. In the case of sign-positive growth rate, we have the possibility of periodic solutions associated with one of the slow manifolds, also the possibility of extinction of the predator. Under certain conditions, sign-changing growth rates allow for canard periodic solutions that arise from dynamic interaction between slow manifolds.

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1 Introduction

This note is a continuation of [**?**] which considers simple time-periodic systems with slow-fast motion in a singularly perturbed setting; the slow motion involves exponential closeness of solutions to slow manifolds. The theory of slow manifolds was developed by N. Fenichel, for an introduction and references see [**?**]. In the case that the solution moves along a stable slow invariant manifold and at some point the slow manifold becomes unstable, we have the possibility of "exponential sticking" or canard (French duck) behaviour. In this case, the solution continues for an $O(1)$ time along the slow invariant manifold that has become unstable and jumps after that away, for instance to the neighbourhood of another invariant set. Following Pontrjagin, see Neishtadt [**?**], one also calls this "delay of stability loss".

This delay- or sticking process is closely connected to the so-called *canard* phenomenon for differential equations that can be described as follows: *Canard solutions are bounded solutions of a singularly perturbed system that, starting near a normally hyperbolic attracting slow manifold, cross a singularity of the system of differential equations and follow for an* $O(1)$ *time a repelling slow manifold.*

The canard behaviour will depend on the dimension of the problem and the nature of the

singularity. An example of canard behaviour was found by the Strassbourg group working in non-standard analysis for a Van der Pol-equation with additional perturbation parameter; see for details and references [**?**]. In this example, the singularity crossed is a fold point. The analysis of this problem is quite technical.
Canards arising at transcritical bifurcations have been described in [**?**], [**?**] and [**?**]. The purpose of the present note is to study such phenomena in examples that can be handled both analytically and numerically; this may increase our understanding. In section **??** we summarize some of the results of [**?**] for the P.F. Verhulst-model extended to growth phenomena with daily or seasonal fluctuations. They are a natural modification of the logistic model introduced in [**?**].
After section **??**, we study an extension of the periodic P.F. Verhulst-model by coupling the equation to a predator population. It is of interest to see what remains of the phenomena found in the one-dimensional model equation in the cases of sign-definite and sign-changing growth rates.
The numerics which we used for illustrations is based on CONTENT [**?**] using RADAU5. The results may serve as examples of periodic solutions contained in slow manifolds and canard periodic solutions arising from dynamic interaction between different slow manifolds.

2 The periodic P.F.Verhulst model

In [**?**] we considered an extension of the classical logistic equation of [**?**], in particular the presence of periodically varying growth rate $r(t)$ and carrying capacity $K(t)$, both with period T. Here and in the sequel we will often express the $T-$periodic growth rate in the form:

$$r(t) = a + f(t),\ F(t) = \int_0^t f(s)ds,\ F(T) = 0.$$

The constant a is the T-periodic average of $r(t)$. We summarise some of the results of [**?**].
In standard notation for the population size $N(t)$ with positive growth rate $r(t)$, the equation is

$$\varepsilon \dot{N} = r(t)N\left(1 - \frac{N}{K(t)}\right),\ N(0) > 0. \tag{1}$$

We have $K(t) > m > 0$ with m a positive constant independent of ε. Without the fast growth perspective, the equation was studied in [**?**], [**?**] and [**?**]. The solution can be written as:

$$N(t) = \frac{e^{\frac{1}{\varepsilon}\Phi(t)}}{\frac{1}{N_0} + \frac{1}{\varepsilon}\int_0^t \frac{r(s)}{K(s)} e^{\frac{1}{\varepsilon}\Phi(s)} ds},\ \Phi(t) = \int_0^t r(s)ds = at + F(t) \tag{2}$$

If for limited intervals of time, the growth rate $r(t)$ can take negative values, we modify the logistic equation to:

$$\varepsilon \dot{N} = r(t)N - \frac{N^2}{R(t)},\ N(0) > 0. \tag{3}$$

with $R(t) > 0$ and T-periodic. Without this modification, a negative growth rate would be accompanied by a positive nonlinear term; there is no rationale for this. The solution of eq. (**??**) is:

$$N(t) = \frac{e^{\frac{1}{\varepsilon}\Phi(t)}}{\frac{1}{N(0)} + \frac{1}{\varepsilon}\int_0^t \frac{1}{R(s)} e^{\frac{1}{\varepsilon}\Phi(s)} ds},\ \Phi(t) = \int_0^t r(s)ds = at + F(t). \tag{4}$$

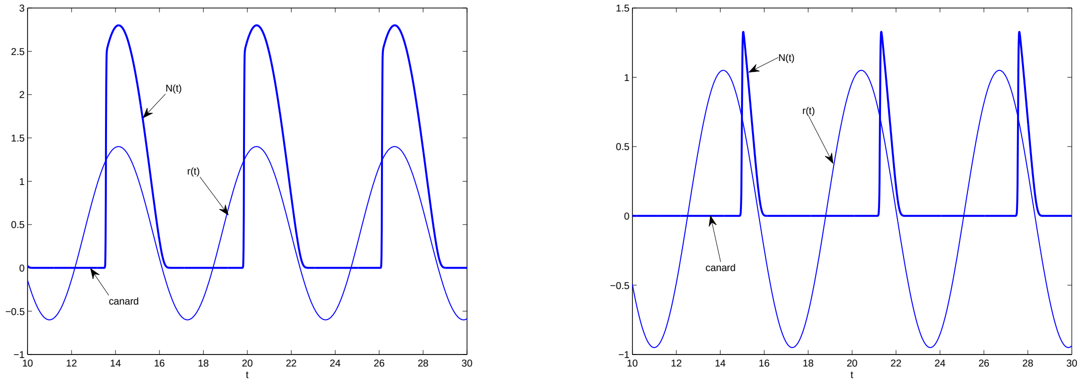

Figure 1: Two solutions of eq. (**??**) with sign changing growth rate. We have $R(t) = 2 + \cos t, \varepsilon = 0.01$; left $r(t) = 0.4 + \sin t$, right $r(t) = 0.05 + \sin t$. In both cases, the population periodically faces extinction, but in the case of smaller growth $a = 0.05$, these canard intervals of time become more extended.

The following results are straightforward.

Lemma 2.1 1. If in eq. (**??**) $0 < K(t) \leq K_0$ with K_0 a positive constant, then, after some time, the solution of eq. (**??**) will satisfy $N(t) \leq K_0 + O(exp.(-at/\varepsilon))$.
If in eq. (**??**) $r(t) \leq r_0$, $0 < R(t) \leq R_0$ with r_0, R_0 positive constants, then $N(t) \leq r_0 R_0$ plus exponentially small terms.

2. If $r(t) \geq \delta > 0$, $0 \leq t \leq T$ with δ a positive constant independent of ε, a unique T-periodic solution $N(t)$ exists with

$$N(t) = K(t) + O(\varepsilon).$$

3. If $r(t)$ changes sign and its average $a \leq 0$, no periodic solution exists. The solutions decrease monotonically (see for the general theory [**?**]) and they show permanent canard behaviour in the terminology of [**?**].

4. If $r(t)$ changes sign and its average $a > 0$, a unique T-periodic solution exists with

canard behaviour. The periodicity condition is:

$$N(0) = \frac{e^{\frac{aT}{\varepsilon}} - 1}{\frac{1}{\varepsilon}\int_0^T \frac{1}{R(s)} e^{\frac{1}{\varepsilon}\Phi(s)} ds}. \tag{5}$$

As during each period an exchange takes place between the neighbourhoods of the slow manifold $N(t) = r(t)R(t)$ (when $r(t) > 0$) and the slow manifold $N(t) = 0$, the population faces near-extinction during each period; see fig. **??**.

3 A predator-prey problem

The near-extinction stage in the periodic logistic equation with slow manifolds could be sensitive to stochastic perturbations and to coupling to a predator population $P(t)$. Will such a coupling mean extinction of the population $N(t)$? We distinguish between the case of positive definite growth rate and the sign-changing case.

3.1 Positive definite growth rate

Consider for $r(t) = a + f(t) \geq \delta > 0$ and continuous, T-periodic $r(t)$ and $K(t)$ the system:

$$\begin{cases} \varepsilon \dot{N} & = r(t)N\left(1 - \frac{N}{K(t)}\right) - cNP,\ N(0) \geq 0, \\ \dot{P} & = \bar{c}NP - dP,\ P(0) \geq 0, \end{cases} \tag{6}$$

with positive parameters $c, \bar{c}, d$. The parameter $\bar{c}$ tends to zero as c tends to zero as the case $c = 0, \bar{c} > 0$ would mean predation without a reduction of the prey population $N(t)$. By rescaling N and P, we could put $c = \bar{c} = 1$, but we will not do this as this makes the interaction between prey and predator less transparent.
We identify the exact slow (critical) manifold $N = 0$ and a critical manifold of dimension two in solution space:

$$SM_1 : N = 0 \text{ and } \mathrm{SM_2} : \mathrm{N} = \mathrm{K(t)}\left(1 - \frac{\mathrm{c}}{\mathrm{r(t)}}\mathrm{P}\right). \tag{7}$$

SM_2 exists if $cP(t) \leq r(t)$. Linearization near the critical manifolds produces for $SM_1 (N = 0)$ the 'eigenvalue' $(r(t) - cP(t))/\varepsilon$; the second critical manifold, SM_2, has 'eigenvalue' $(-r(t) + cP(t))/\varepsilon$. We have existence and stability of the second slow manifold, $O(\varepsilon)$ close to SM_2, if the growth rate is big enough, $r(t) > cP(t)$ (or $P(t)$ is small enough); the trivial solution $N = 0$ is unstable in this case. If $r(t) < cP(t)$, SM_2 is not present, SM_1 is stable.
From system (**??**) we derive by integration

$$P(t) = P(0)e^{\int_0^t (\bar{c}N(s) - d)ds}. \tag{8}$$

Independent of the size of the positive parameter ε, we have the following statements:

Lemma 3.1 1. If $N(t) \to 0$, then $P(t) \to 0$.

2. Assume that $N(t)$ and $P(t)$ are T-periodic solutions, then we have:

$$\frac{1}{T}\int_0^T N(t)dt = \frac{d}{\bar{c}}. \tag{9}$$

3. Denoting the solution of eq. (**??**) with initial value $N(0)$ by $N_v(t)$, we have for the solution $N(t)$ of system (**??**):

$$N(t) \leq N_v(t). \tag{10}$$

Consider the equation

$$\dot{P} = \bar{c}N_v(t)P - dP, \; P(0) \geq 0.$$

with solution $P_v(t)$. We have for $P(t)$ of system (**??**) the estimate:

$$P(t) \leq P_v(t). \tag{11}$$

Proof
1. This follows directly from eq. (**??**).
2. Consider the integral

$$I = \int_0^T (\bar{c}N(s) - d)ds.$$

As $P(0) = P(T)$, we have $I = 0$ which yields the result.
3. Observe that if $P(0) > 0$, $P(t) > 0$ for $t \geq 0$. As $N_v(t)$ is bounded (lemma **??**), $N(t)$ of system (**??**) is bounded. $N(t)$ is majorized by the solutions of an equation where a negative term has been deleted, and $P(t)$ is majorized by the solution of an equation where a positive terms has been replaced by a larger positive term.
This completes the proof.

Note that if $P(t)$ vanishes, $N(t)$ is T-periodic. If $I < 0$, $P(t) \to 0$, the predator becomes extinct. The case $I > 0$ will be discussed below. See fig. **??**. It also follows that the propositions of section **??** where the population $N(t)$ becomes extinct, remain valid in the predator-prey model.

The slow manifold close to SM_2 is approximated with error $O(\varepsilon)$ by the expression in (**??**). Substituting this into the equation for P of system (**??**) yields:

$$\dot{P} = (\bar{c}K(t) - d)P - \bar{c}c\frac{K(t)}{r(t)}P^2. \tag{12}$$

$P(0) > 0$ is given; as long as $r(t) > cP(t)$, the seasonal or other periodic changes yield the predator population given by eq. (**??**). Using variation of constants, we find for $P(t)$ the $O(\varepsilon)$ approximation in SM_2:

$$P(t) = \frac{e^{\Psi(t)}}{\frac{1}{P(0)} + \bar{c}c\int_0^t \frac{K(s)}{r(s)}e^{\Psi(s)}ds}, \; \Psi(t) = \int_0^t (\bar{c}K(s) - d)ds. \tag{13}$$

We consider two cases:

1. Assume
$$\Psi(T) = \int_0^T (\bar{c}K(s) - d)ds > 0. \tag{14}$$
For a positive T-periodic solution of $P(t)$ to exist, there has to be a $P(0) > 0$ such that $P(0) = P(T)$. This requirement produces with eq. (**??**):
$$P(0) = \frac{e^{\Psi(T)} - 1}{\bar{c}c} \int_0^T \frac{K(s)}{r(s)} e^{\Psi(s)} ds. \tag{15}$$
As $\exp(\Psi(T) > 1$, we have a positive solution for $P(0)$, see figs. **??**-**??**. From eq. (**??**) we conclude that the periodic solution $P(t)$ is bounded from below by a constant independent of ε. The approximate periodic solution $N(t), P(t)$ is located in the attracting manifold SM_2. There are no canards in this case.

2. Assume
$$\Psi(T) = \int_0^T (\bar{c}K(s) - d)ds < 0.$$
There is no periodic solution for $P(t)$. In the Fourier expansion of $\Psi(t)$, a negative constant will be the first term, the predator population will tend to zero with time. The population $N(t)$ will tend to a T-periodic solution approximated by $K(t)$, see fig. **??**.

We conclude with a result on the existence and approximation of periodic solutions:

Proposition 3.1 Consider system (**??**) with positive definite growth rate $r(t)$, $r(t)$ and $K(t)$ are continuous and T-periodic; moreover

1. Condition (**??**) holds:$\Psi(T) > 0$;
2. For the solution $N(t), P(t)$ given by eq. (**??**) and eq. (**??**) with initial condition (**??**) we have $cP(t) < r(t)$ for $0 \leq t \leq T$ ($cP(t)$ can be calculated using eq. (**??**) or estimated using inequality (**??**);

then $N(t), P(t)$ given by eq. (**??**) and eq. (**??**) are $O(\varepsilon)$ approximations of periodic solutions that exist in the slow manifold $O(\varepsilon)$-close to SM_2.

Proof
The stable, normally hyperbolic slow manifold, $O(\varepsilon)$ approximated by SM_2, exists for all time. Consider the time-T map of the N, P-plane into itself and in particular a compact, convex $O(\varepsilon)$ neighbourhood Ω_ε of $N(0), P(0)$ determined by eq. (**??**) and eq. (**??**). Ω_ε is continuously mapped into itself by the flow of system (**??**) and contracts with rate $\exp((-r(t) + cP(t))/\varepsilon)$. According to Brouwer's fixed point theorem there exists at least one fixed point of this map corresponding with a T-periodic solution.

Note that in the case of proposition 3.1, the critical manifold is attracting for all time and it might be possible to use a contraction argument to obtain a unique periodic solution for this problem. However, such an approach would not be possible in the problem of sign-changing growth rate; also in the case of higher-dimensional problems, one cannot expect uniqueness.

Example 3.1 Assume that the conditions of the theorem have been satisfied and in particular that:

$$K(t) = k_0 + k_1(t),\ \int_0^T k_1(t)dt = 0,\ \frac{K(t)}{r(t)} = e^{-\bar{c}\int_0^t k_1(s)ds}.$$

From eqs. (**??**, **??**) we find:

$$N(t) = \frac{d}{\bar{c}} + k_1(t),\ cP(t) = (k_0 - \frac{d}{\bar{c}})e^{\bar{c}\int_0^t k_1(s)ds},$$

with condition $d/\bar{c} > k_1(t)$, $0 \leq t \leq T$.

3.2 Sign-changing growth rate $r(t)$

Using our modeling from section **??** we formulate:

$$\begin{cases} \varepsilon\dot{N} & = r(t)N - \frac{N^2}{R(t)} - cNP,\ N(0) > 0, \\ \dot{P} & = \bar{c}NP - dP,\ P(0) \geq 0, \end{cases} \tag{16}$$

with positive parameters $c, \bar{c}, d$. The growth rate $r(t)$ and the function $R(t)$ are continuous and T-periodic, $R(t) > 0, 0 \leq t \leq T$.

Lemma 3.2 *The statements of lemma* **??** *carry over to the case of sign changing $r(t)$ if we replace in the fourth item eq. (**??**) by eq. (**??**).*

If $r(t)$ is sign-changing and $a < 0$, it will turn out we have a permanent canard. Two slow manifolds of dimension two in solution space may exist:

$$SM_1:\ N = 0 \text{ and } \mathrm{SM_3:\ N = (r(t) - cP(t))\, R(t).} \tag{17}$$

The second critical manifold SM_3 exists and is stable on intervals of time where $r(t) > cP(t)$, SM_1 is unstable in this case. Stability changes of SM_1 are forced when $r(t) - cP(t)$ changes sign; as $r(t) < 0$ at certain intervals of time, this can not be avoided.

Near the exact slow manifold SM_1, the first order approximation of $P(t)$ is found immediately:

$$P(t) = P(0)e^{-dt} + O(\varepsilon).$$

This simple result shows that during the same interval of time, $N(t)$ will approach the extinction phase $N = 0$ much closer than $P(t)$ approaches the extinction phase $P = 0$.

Applying variation of constants to the equation for $N(t)$ in system (**??**) we find:

$$N(t) = \frac{e^{\frac{1}{\varepsilon}\int_0^t (r(s) - cP(s))ds}}{\frac{1}{N(0)} + \frac{1}{\varepsilon}\int_0^t \frac{1}{R(s)} e^{\frac{1}{\varepsilon}\int_0^s (r(u) - cP(u))du} ds}. \tag{18}$$

From eq. (**??**) and the periodicity condition $N(0) = N(T)$ we derive:

$$N(0) = \frac{e^{\frac{1}{\varepsilon}\int_0^T (r(s) - cP(s))ds} - 1}{\frac{1}{\varepsilon}\int_0^T \frac{1}{R(s)} e^{\frac{1}{\varepsilon}\int_0^s (r(u) - cP(u))du} ds}. \tag{19}$$

From periodicity condition (**??**) we have that a periodic solution $N(t)$ exists if $P(t)$ is T-periodic and

$$\int_0^T (r(t) - cP(t))dt > 0 \text{ or } \mathrm{a} > \frac{\mathrm{c}}{\mathrm{T}} \int_0^{\mathrm{T}} \mathrm{P(t)dt}. \tag{20}$$

Note that periodicity condition (**??**) does not imply uniqueness. A necessary requirement to have positive, periodic solutions $N(t), P(t)$ is $a > 0$; this is not surprising as for the problem without predator in section **??**, we have the same requirement for the existence of a periodic solution. From lemma **??** we have that $P(t) \leq P_v(t)$, so a sufficient condition for the existence of a periodic solution $N(t)$ is that $P(t)$ is T-periodic and

$$a > \frac{c}{T} \int_0^T P_v(t)dt. \tag{21}$$

Surprisingly enough, we will show that $a > 0$ is a necessary and sufficient condition for periodic solutions $N(t)$ to exist for system (**??**) .
If $a < 0$ in the case of sign-changing $r(t)$, we have a permanent canard. This follows from the estimates in section **??** in combination with eq. (**??**) or directly from eq. (**??**).
Consider for the case $a > 0$ as an introduction the following scenario. The stable manifold SM_3 exists initially and is stable, $r(t) - cP(t) > 0$ and initially $\int_0^T (\bar{c}N(s) - d)ds > 0$. $P(t)$ will increase so that, after some time, $r(t) - cP(t) < 0$, which will destroy the slow manifold SM_3. The slow manifold $N(t) = 0$ will become stable, $N(t)$ will decrease and so will $P(t)$. $P(t)$ decreases exponentially and if $P(t)$ is small enough, $N(t) = 0$ will become unstable again and the process can start over again. Numerical experiments are shown in figs. **??**-**??**. As expected for this type of system, $N(t)$ and $P(t)$ are out-of-phase, but it may look surprising that the exponential smallness of $N(t)$ which is experienced periodically because of the attraction of the slow manifold $N = 0$, is not always reflected by a corresponding smallness of $P(t)$. However, from eq. (**??**) we deduce that the exponential rate for $P(t)$ is $O(1)$. Consider in figs. **??**-**??** solutions of system (**??**) with various parameter values. In these cases $P(t)$ approaches $P = 0$ periodically, the periodic solutions show canard behavior.

Proposition 3.2 Consider system (**??**) with sign-changing growth rate $r(t)$; the functions $r(t)$ and $R(t)$ are continuous and T-periodic; moreover $a > 0$ (in the notation of section **??**). Then, for ε small enough, a T-periodic solution $N(t)$ exists.

Proof
Note that if $P(t)$ vanishes, the existence of a T-periodic solution follows directly from eqs. (**??**-**??**). Assume now that $P(t)$ does not tend to zero.
The stable critical manifold SM_3 exists on intervals where $r(t) - cP(t) > 0$, for instance for $t_0 < t < t*$; negative values of this quantity may arise. Such a $t*$ always exists as $r(t)$ changes sign. Suppose that $r(t*) - cP(t*) = 0$. For $t_0 < t < t*$, the solution moves along SM_3 approaching SM_1 ($N = 0$). At $t = t_1 < t*$ we have $N(t_1) = O(\delta(\varepsilon))$ with $\varepsilon = o(\delta(\varepsilon))$ and $\delta(\varepsilon) = o(1)$. Consider a $\delta(\varepsilon)$-neighbourhood D_δ of the slow manifold $N = 0$. Rescale $N = \delta(\varepsilon)\bar{N}$. This rescaling produces for system (**??**) with initial values $\bar{N}(t_1), P(t_1)$:

$$\begin{cases} \varepsilon\dot{\bar{N}} &= r(t)\bar{N} - c\bar{N}P - \delta(\varepsilon)\frac{\bar{N}^2}{R(t)},\ \bar{N}(t_1) > 0, \\ \dot{P} &= -dP + \delta(\varepsilon)\bar{c}\bar{N}P,\ P(t_1) > 0, \end{cases} \tag{22}$$

Putting $0 < \bar{c}\bar{N} \leq C$, we find from the equation for $P(t)$ in D_δ the inequality:

$$P(t) \leq P(t_1)e^{-dt+\delta(\varepsilon)Ct},$$

with constant C independent of ε. For $\bar{N}(t)$ we formulate a differential inequality in D_δ:

$$\varepsilon\frac{d\bar{N}}{dt} \geq r(t)\bar{N} - c\bar{N}P(t_1)e^{-dt+\delta(\varepsilon)Ct} + O(\delta(\varepsilon)).$$

Putting $d_0 = d - \delta(\varepsilon)C$ and solving this differential inequality we find:

$$\bar{N}(t) \geq \bar{N}(t_1)e^{\frac{1}{\varepsilon}[(a+O(\delta(\varepsilon)))(t-t_1)+F(t)-F(t_1)+\frac{c}{d_0}P(t_1)(e^{-d_0t}-e^{-d_0t_1})]}.$$

It is clear from this estimate that in D_δ, $N(t)$ will always increase after some time. We conclude that the solutions $N(t)$ of system (**??**) have a positive lower bound; the solutions have a positive upper bound $N_v(t)$ (lemma **??**) where $N_v(t)$ starts at $N_v(t*) = N(t*)$. Consider for $t > t*$ the interval of N-values bounded by a positive lower bound of $N(t)$ and upper bound of $N_v(t)$; the period-T map of this interval into itself under the flow of system (**??**) will have a fixed point according to the Brouwer theorem. This concludes the proof.

Example 3.2 Consider the system:

$$\begin{aligned}
\varepsilon\dot{N} &= (a+\sin t)N - \frac{N^2}{3+\sin t} - NP, \\
\dot{P} &= 4NP - 4P.
\end{aligned}$$

If $a = 0.9$ we have a periodic solution $N(t), P(t)$ for which the predator $P(t)$ is periodically near to extinction, see fig. **??**. Decreasing a, both $N(t)$ and $P(t)$ become periodically very small, see fig. **??** where $a = 0.3$.

3.3 Extreme values and synchonisation

The maxima and minima values of prey N and predator P will depend on the parameters. It follows from systems (**??**) and (**??**) that $N_s = d/\bar{c}$ corresponds with stationary values of $P(t)$. It follows from lemma **??** that in the case of the existence of a periodic solution $P(t)$ this value of N corresponds with the average of $N(t)$, so N_s will not be a maximum or minimum of $N(t)$. We conclude that maxima and minima of $N(t)$ and $P(t)$ are not alternating in the sense that a maximum of $P(t)$ corresponds with a minimum of $N(t)$.
A more explicit result can be obtained in the case of positive growth rate. Assume $r(t) > 0$ for all time. The slow manifold SM_2 persists for $0 \leq t \leq T$ if $cP(t) < r(t)$ (subsection **??**). In this case we have from eq. (**??**) and the periodicity condition:

$$cP(t) = \frac{e^{\Psi(t)}}{\frac{\bar{c}\int_0^T \frac{K(s)}{r(s)}e^{\Psi(s)}ds}{e^{\Psi(T)}-1} + \bar{c}\int_0^t \frac{K(s)}{r(s)}e^{\Psi(s)}ds}, \tag{23}$$

with $\Psi(t) = \int_0^t(\bar{c}K(s) - d)ds$ and the requirement $\Psi(T) > 0$.

In the critical manifold SM_2 we have from eq. (**??**) that in the case of positive growth rate and if $cP(t) < r(t)$ that $P(t)$ is inverse proportional to c and depends in a more complicated way on $\bar{c}$. We can consider the explicit example **??** for illustration of the behaviour. Note that for the choice of $K(t)$ and $r(t)$ in example **??**, we have assumed synchronisation of the carrying capacity and the growth rate.
It is of interest to look into the part played by synchronisation as we expect different behaviour if varying capacity and growth rate are out of phase.

4 The predator-prey problem with weak interaction

The interaction coefficient c in system (**??**) is $O(1)$ which implies that the predator $P(t)$ profits strongly from the large growth rate of the prey $N(t)$. Suppose now that this interaction is $O(1)$, we replace c by εc. In the model $\bar{c}$ still has to tend to zero if c tends to zero, but we have to take $O(1)$ values for $\bar{c}$. Paradoxally, this poses another modeling problem in the case of positive growth rate. The critical manifold SM_2 of the preceding section has as a condition of existence the inequality $r(t) > cP(t)$, this limits the growth of $P(t)$. In the case of weak interaction, the slow manifold is of the form $N(t) = K(t) + O(\varepsilon)$ and for the equation

$$\dot{P} = \bar{c}N - d,$$

$P(t)$ will grow without bounds if

$$\int_0^T (\bar{c}K(t) - d)dt > 0.$$

So we have to add a logistic term to limit the growth of the solutions $P(t)$.

4.1 Positive definite growth rate

Consider for continuous, T-periodic coefficient $r(t) = a + f(t) \geq \delta > 0$ and continuous, positive T-periodic $K(t), C(t)$ the system:

$$\begin{cases} \varepsilon\dot{N} & = r(t)N\left(1 - \frac{N}{K(t)}\right) - \varepsilon cNP, \ N(0) \geq 0, \\ \dot{P} & = \bar{c}NP - dP - \frac{P^2}{C(t)}, \ P(0) \geq 0, \end{cases} \tag{24}$$

with positive parameters $c, \bar{c}, d$. We have the exact slow manifold $N = 0$ and an $O(\varepsilon)$ approximate slow manifold of dimension two in solution space:

$$SM_1 : \ N = 0 \text{ and } \mathrm{SM}_4 : \ \mathrm{N} = \mathrm{K(t)}. \tag{25}$$

The dynamics is relatively easy to describe as the critical manifold SM_4 is stable. The equation describing the slow drift is:

$$\dot{P} = \bar{c}K(t)P - dP - \frac{P^2}{C(t)}.$$

Using again $\Psi(t)$ from eq. (**??**) we find with variation of constants:

$$P(t) = \frac{e^{\Psi(t)}}{\frac{1}{P(0)} + \int_0^t \frac{1}{C(s)} e^{\Psi(s)} ds}, \; \Psi(t) = \int_0^t (\bar{c}K(s) - d) ds. \tag{26}$$

If $\Psi(T) < 0$, we will have $P(t) \to 0$ as $t \to \infty$. Assuming that $P(t)$ is T-periodic, we find from the periodicity condition $P(0) = P(T)$:

$$P(0) = \frac{e^{\Psi(T)} - 1}{\int_0^T \frac{1}{C(s)} e^{\Psi(s)} ds}.$$

The condition for existence of a unique periodic solution $P(t)$ is:

$$\Psi(T) > 0.$$

4.2 Sign changing growth rate

For positive $R(t), C(t)$ the system becomes:

$$\begin{cases} \varepsilon \dot{N} &= r(t)N - \frac{N^2}{R(t)} - \varepsilon c NP, \; N(0) \geq 0, \\ \dot{P} &= \bar{c}NP - dP - \frac{P^2}{C(t)}, \; P(0) \geq 0, \end{cases} \tag{27}$$

with positive parameters $c, \bar{c}, d$. From the $O(1)$ boundedness of $N(t), P(t)$ (lemma **??**) and the (exact) solution (**??**), replacing c by εc, we have:

$$N(t) = \frac{e^{\frac{1}{\varepsilon}\int_0^t r(s)ds}}{\frac{1}{N(0)} + \frac{1}{\varepsilon}\int_0^t \frac{1}{R(s)} e^{\frac{1}{\varepsilon}\int_0^s r(u)du} ds} + O(\varepsilon). \tag{28}$$

From periodicity condition (**??**) applied to this case we conclude that a T-periodic solution $N(t)$ exists if $P(t)$ is T-periodic and $a > 0$.
If $P(t)$ is not periodic, $P(t)$ will tend to zero; if $a > 0$, $N(t)$ will tend to a periodic solution.

5 Conclusions

In general the analysis of two-dimensional, nonlinear ODEs with time-periodic coefficients is difficult. It is remarkable that one can obtain many explicit results in a slow-fast setting using slow manifold theory.
Two major open problems should be considered. In contrast to the results for the time-periodic P.F. Verhulst equations in [**?**], the periodic solutions obtained for the predator-prey systems in this article are not necessarily unique. Numerical experiments show that in particular the case of sign-changing growth rates looks interesting in this respect. These questions should be studied using bifurcation theory.
Secondly, it would be interesting to consider the time-periodic P.F. Verhulst equations and the time-periodic predator-prey problems in the context of spatial diffusion. This will pose interesting stability problems.

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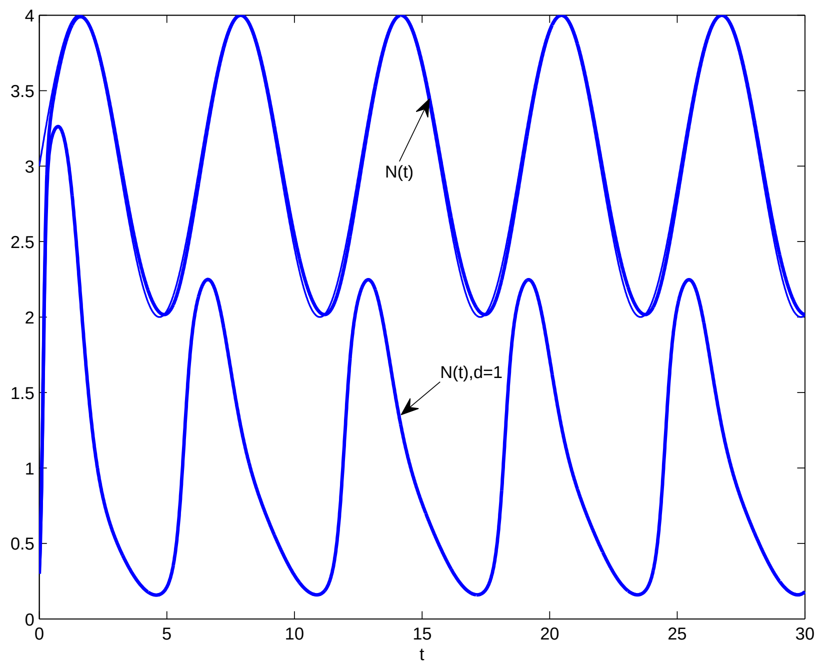

Figure 2: The solution $N(t)$ of system (**??**) with positive growth rate $r(t) = 1.5 + \sin t$ in two cases with $K(t) = 3 + \sin t, \varepsilon = 0.01, \bar{c} = 1, c = 0.1$. For the top solution we have $d = 5$, so $\Psi(T) = -2$ and $P(t) \to 0, N(t) \to K(t)$ (the thin line approximating $N(t)$ closely). For the solution below we have $d = 1$ so that $N(t), P(t)$ approach a periodic solution with positive varying $P(t)$.

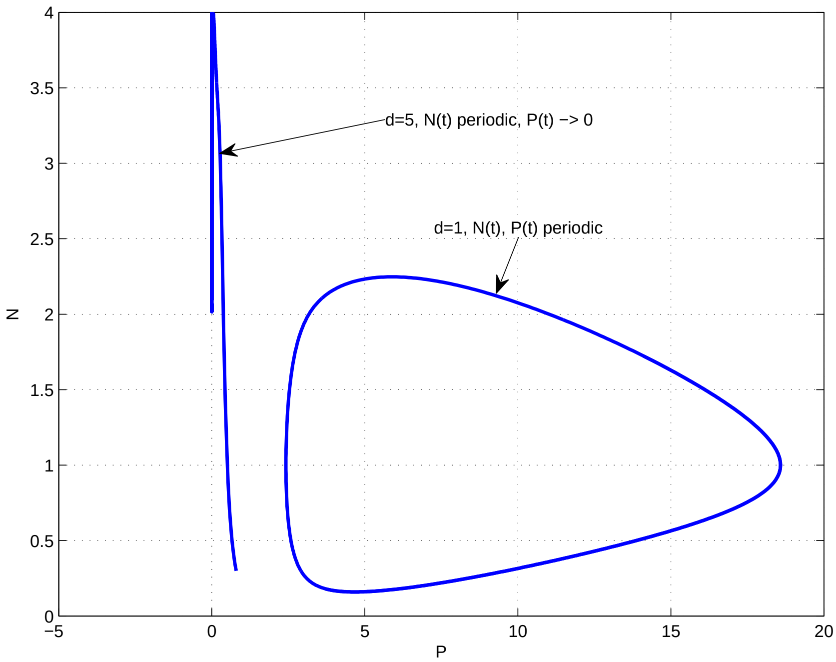

Figure 3: N, P-diagram of system (**??**) corresponding with fig. **??**. The closed curve corresponds with periodic $N(t), P(t)$ for $d = 1$. In the case $d = 5$, the predator $P(t)$ becomes extinct, $N(t)$ is periodic.

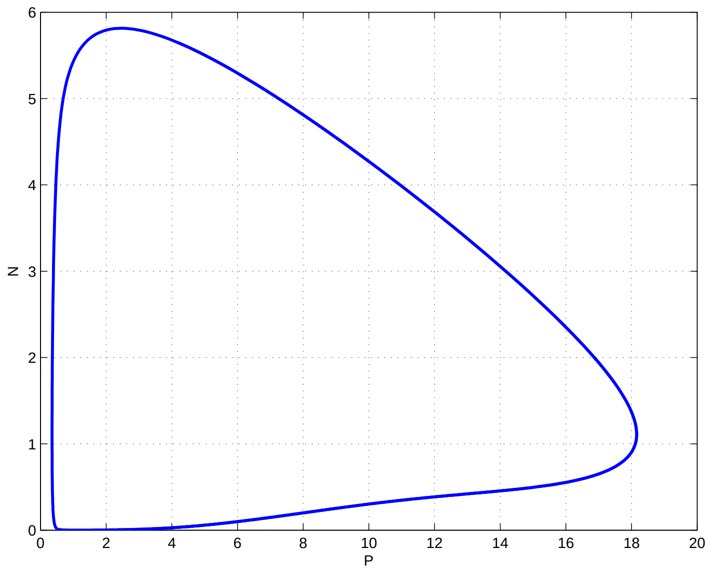

Figure 4: Growth rate with sign changes: $r(t) = 0.9 + \sin t, R(t) = 3 + \sin t, \varepsilon = 0.1$ with $\bar{c} = 0.9, c = 0.1, d = 1$ in system (**??**). The periodic $N(t), P(t)$ solution left shows the decay of slow manifold SM_3, followed by motion near $SM_1(N = 0)$. The fast motion between the two slow manifolds is displayed in fig. **??**.

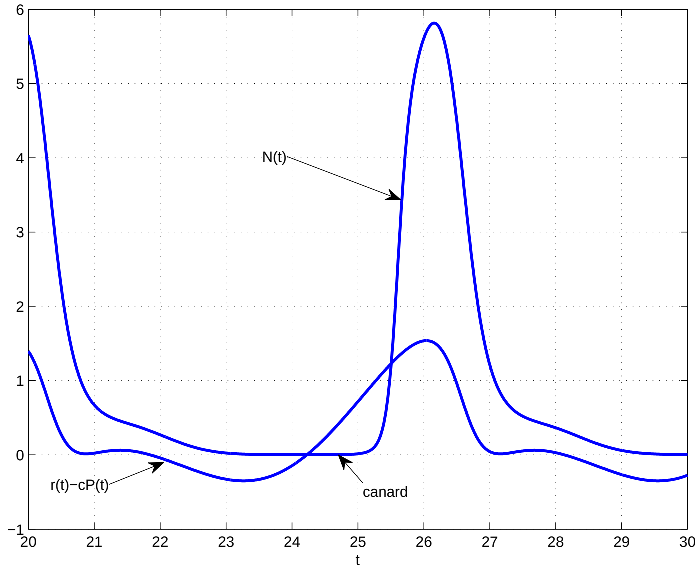

Figure 5: Growth rate with sign changes: $r(t) = 0.9 + \sin t, R(t) = 3 + \sin t, \varepsilon = 0.1$ with $\bar{c} = 0.9, c = 0.1, d = 1$ in system (**??**). The projected periodic $N(t), P(t)$ solution is shown in fig. **??**. The fast motion with time between the two slow manifolds is displayed for $N(t)$. A canard arises when the quantity $r(t) - cP(t)$ changes from negative to positive.

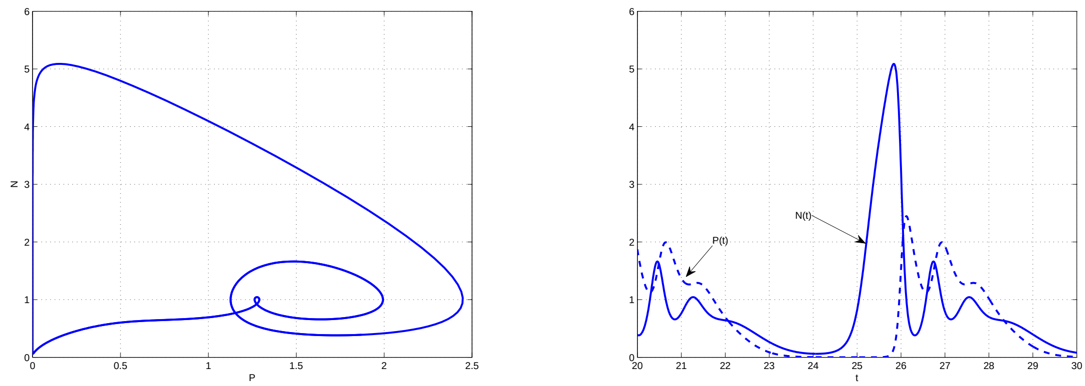

Figure 6: Growth rate with sign changes: $r(t) = 0.9 + \sin t, R(t) = 3 + \sin t, \varepsilon = 0.1$ with $\bar{c} = 4, c = 1, d = 4$ in system (**??**). Left the N, P-diagram; $P(t)$ is out-of-phase with $N(t)$ and is periodically near to extinction (right figure).

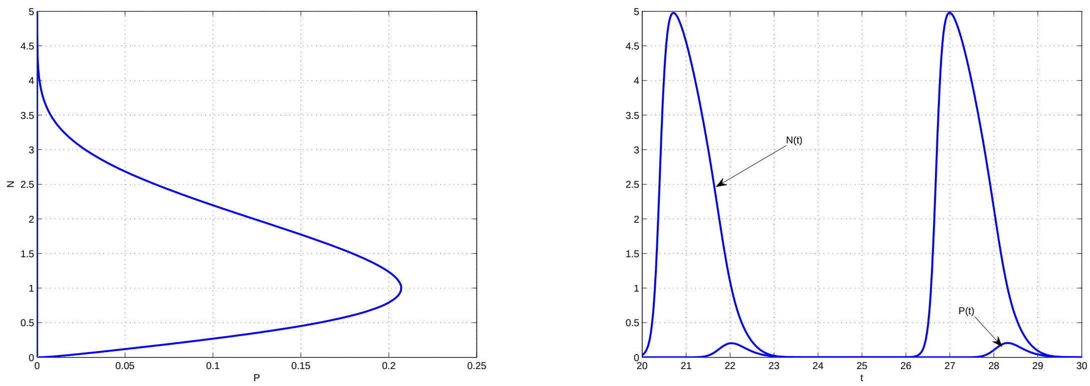

Figure 7: Growth rate with sign changes: $r(t) = 0.3 + \sin t, R(t) = 3 + \sin t, \varepsilon = 0.1$ with $\bar{c} = 4, c = 1, d = 4$ in system (**??**). Left the N, P-diagram; if a is decreased, $P(t)$ becomes smaller and is periodically near to extinction (right figure).