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The hunt for 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.

1. Introduction

This note is a continuation of [12] 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 [11]. 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 [6], 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 [2]. 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 [3,8,5]. 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 2 we summarize some of the results of [12] for the P.F. Verhulst-model extended to growth phenomena with daily or seasonal fluctuations. They are the natural modification of the logistic model introduced in [13].

After Section 2, 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 [4] 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 [12] we considered an extension of the classical logistic equation of [13], 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

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

The constant a is the T-periodic average of $r(t)$. We summarize some of the results of [12].

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In standard notation for the population size $N(t)$ with positive growth rate $r(t)$, the equation is

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

We have $K(t)>m>0$ with m a positive constant independent of ε. Without the fast growth perspective, the equation was studied in [10,1,9]. The solution can be written as

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

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

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

with $R(t)>0$ and T-periodic. Without this modification, a negative growth rate would be accompanied by a positive non-linear term; there is no rationale for this. The solution of Eq. (3) is

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

The following results are straightforward.

Lemma 2.1.

1. *If in Eq.* (1) $0<K(t)\le K_0$ *with* K_0 *being a positive constant, then, after some time, the solution of Eq.* (1) *will satisfy* $N(t)\le K_0+O(\exp.(-at/\varepsilon))$.
   If in Eq. (3) $r(t)\le r_0$, $0<R(t)\le R_0$ *with* r_0, R_0 *being positive constants, then* $N(t)\le r_0R_0$ *plus exponentially small terms.*
2. *If* $r(t)\ge\delta>0$, $0\le t\le T$ *with* δ *being 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* $a\le 0$, *no periodic solution exists. The solutions decrease monotonically (see for the general theory* [7]) *and they show permanent canard behaviour in the terminology of* [12].
4. *If* $r(t)$ *changes sign and its average* $a>0$, *a unique T-periodic solution exists with canard behaviour. The periodicity condition is*

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

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. 1.

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

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

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:

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

SM_2 exists if $cP(t)\le r(t)$. 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.

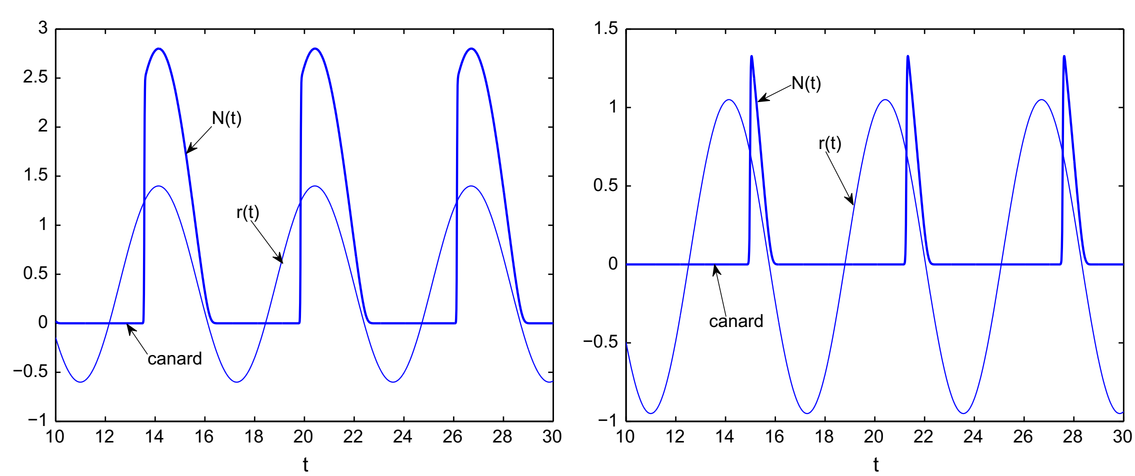

Fig. 1. Two solutions of Eq. (3) with sign changing growth rate. We have $R(t)=2+\cos t, \varepsilon=0.01$; left $r(t)=0.4+\sin t$, right $r(t)=0.05+\sin t$. In both cases, the population periodically faces extinction, but in the case of smaller growth $a=0.05$, these canard intervals of time become more extended.