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PERIODIC SOLUTIONS IN A MATHEMATICAL MODEL OF THE TEMPERATURE SEX DETERMINATION WITH PERIODIC FLOODS

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ABSTRACT

The sex of some species, including crocodiles, is determined by the incubation temperature of the egg during gestation. In this article a mathematical model describing the evolution of crocodile population is presented. The considered model is a modification of the one presented in the book by J.D. Murray and it includes periodic changes of the number of available nesting sites. The model consists of four non-autonomous ordinary differential equations. The existence and global asymptotic stability of the periodic solution is proven. In addition, results are illustrated by numerical simulations conducted in Matlab©.

MODEL DESCRIPTION

Unlike among mammals, the sex of crocodiles is determined by the conditions, mainly the temperature, in which the egg incubates. Roughly speaking, the higher the incubation temperature is, more males hatch. It is called temperature sex determination (TSD). For different species in the order Crocodilia the ranges of temperatures in which females or males are hatched differ but it is not relevant for us since the aim of the model is the qualitative, not the quantitative description of this phenomenon. An important fact for the model construction is that the nests' temperature increases with the distance from the river, so the ratio of males to females hatched increases with an increasing distance from the river.

In this paper we consider a modification of the model presented in [3, Chapter 4]. We briefly remind the construction of the model. It is assumed that the nesting region can be divided into three subregions such that in the region I located near the river (we call it wet marsh), where the incubation temperature is low, only females are hatched. In the region II that lies further (we call it dry marsh), the incubation temperature is higher and the same numbers of males and females are hatched. Finally, in the region III (dry levees), where the incubation temperature is high, only males are hatched.

Biological observation indicates that females choose a nesting site with thermical conditions optimal for a three-month incubation period. Moreover, they prefer to lay eggs in the environment as similar to the environment they were hatched as possible [4], so they prefer to choose regions I and II. This justifies the assumption that the capacity of the region I is limited; otherwise it would be possible to get an all-female population. Moreover, we assume that there are enough males to fertilize all the females. As in Murray's book [4], functions $f_1(t)$ and $f_2(t)$ denote the number of females incubated in regions I and II respectively, while $m_2(t)$ and $m_3(t)$ — the number of males incubated in regions II and III, respectively. The effective birth rate b and the death rate p are assumed to be positive constants such that $b > p$ which prevents the population from vanishing.

By k_1, k_2 and k_3 we denote the capacities of regions I, II and III, respectively. In [3] the model with constant $k_i, = 1, 2, 3$ was considered. In this paper we consider the modification of that model that takes into account periodic floodings influencing the capacity of the region I, as in [5]. We assume that k_1 is a continuos periodic function that fluctuates around some mean value k, while k_2 and k_3 are positive constants. The modified model is a system of four ordinary differential equation (for detailed derivation see [3])

$$\frac{\mathrm{d}f_1}{\mathrm{d}t} = b\left(\frac{k_1(t)}{k_1(t) + f_1}\right) f_1 - pf_1, \tag{1a}$$

$$\frac{\mathrm{d}f_2}{\mathrm{d}t} = \frac{b}{2}\left(\frac{{f_1}^2}{k_1(t) + f_1} + f_2\right)\left(\frac{k_2}{k_2 + f_1 + f_2}\right) - pf_2, \tag{1b}$$

$$\frac{\mathrm{d}m_2}{\mathrm{d}t} = \frac{b}{2}\left(\frac{{f_1}^2}{k_1(t) + f_1} + f_2\right)\left(\frac{k_2}{k_2 + f_1 + f_2}\right) - pm_2, \tag{1c}$$

$$\frac{\mathrm{d}m_3}{\mathrm{d}t} = b\left(\frac{k_3}{k_3 + f_1 + f_2}\right)\left(\frac{{f_1}^2}{k_1(t) + f_1} + f_2\right)\left(\frac{f_1 + f_2}{k_2 + f_1 + f_2}\right) - pm_3. \tag{1d}$$

A positive (because we consider the population) initial condition $[f_1(0), f_2(0), m_2(0), m_3(0)]$ will close the system. It can be easily seen that the right hand side of system (1) is Lipchitz continuous with respect to (f_1, f_2, m_2, m_3), thus solutions of the system (1) exist and are unique. Note also that Eq. (1a) can be written in an exponential form, which implies $f_1(t) > 0$ for all $t \geq 0$. Moreover Eq. (1a) does not depend on f_2, m_2 and m_3, and the derivative of f_1 is negative for f_1 sufficiently large. This proves that the solution of Eq. (1a) can be prolonged on the whole $\mathbb{R}$. Similarly, we can prove that f_2, m_2 and m_3 are positive for all $t \geq 0$ and can be prolonged on the whole $\mathbb{R}$.

In the next Section we prove that there exists a periodic solution of (1a) and later we prove that this solution is locally asymptotically stable. Finally, we present results of some numerical simulations.

EXISTENCE AND STABILITY OF PERIODIC SOLUTIONS

First, we formulate precise assumptions on the function k_1.

(A1) $k_1 \colon \mathbb{R} \to (0, +\infty)$ is continuous;

(A2) k_1 is T-periodic, that is for all $t \in \mathbb{R}$ we have $k_1(t) = k_1(t + T)$, $T > 0$.

Denote also

$$\bar{k}_1 = \max_{t \in (0,T]} k_1(t), \quad \underline{k}_1 = \max_{t \in (0,T]} k_1(t).$$

Theorem 1. *Let assumptions* (A1)–(A2) *be fulfilled, and* $b > p > 0$. *Then there exists a periodic solution of Eq.* (1a).

First we prove two lemmas.

Lemma 2. *Let assumptions of Theorem 1 be fulfilled and let* f_1 *be a solution of* (1a) *with*

$$f_1(0) > \frac{2b - p}{p}\bar{k}_1\,\mathrm{e}^{pT}\,. \tag{2}$$

Then $f_1(T) < f_1(0)$.

Proof. From Eq. (2) and definition of $\bar{k}_1$ it follows that

$$\forall t \in (0, T] \quad f_1(0) \geq \frac{2b - p}{p} k_1(t)\,\mathrm{e}^{pt}\,. \tag{3}$$

Because k_1 is strictly positive due to Assumption (A1), we have $\frac{k_1(t)}{k_1(t)+f_1(t)} > 0$ for all $t \in (0,T]$. Hence, $f_1'(t) > -pf_1(t)$. Because $f_1(t) > 0$, the Gronwall inequality yields

$$\forall t \in (0,T] \quad f_1(t) > f_1(0)\,\mathrm{e}^{-pt}.$$

From Eq. (3) and above comments one concludes that

$$\forall t \in (0,T] \quad f_1(t) > \frac{2b-p}{p}k_1(t) = \frac{1-\frac{p}{2b}}{\frac{p}{2b}}k_1(t).$$

Simple algebraic manipulations give

$$\forall t \in (0,T] \quad \frac{k_1(t)}{k_1(t)+f_1(t)} - \frac{p}{b} < -\frac{p}{2b} \implies f_1'(t) < -\frac{p}{2}f_1(t) < 0$$

Therefore, f_1 is decreasing, so $f_1(T) < f_1(0)$, which completes the proof. □

Lemma 3. *Take $\varepsilon \in (0,1)$ such that*

$$\frac{p}{b} < (1-\varepsilon). \tag{4}$$

Let assumptions of Theorem 1 be fulfilled and let f_1 be a solution of (1a) *with*

$$f_1(0) < \frac{(1-\varepsilon)b-p}{p}\underline{k}_1\,\mathrm{e}^{(p-b)T}. \tag{5}$$

Then $f_1(T) > f_1(0)$.

Proof. From Eq. (1a) and Assumption (A3) it follows that

$$\forall t \in (0,T] \quad f'_1(t) < (b-p)f_1(t).$$

Because $f_1(t) > 0$, $b > p$, the Gronwall inequality yields

$$\forall t \in (0,T] \quad f_1(t) < f_1(0)\,\mathrm{e}^{(b-p)t} \le f_1(0)\,\mathrm{e}^{(b-p)T}. \tag{6}$$

Applying Eq. (5) to (6) one concludes that

$$\forall t \in (0,T] \quad f_1(t) < \frac{(1-\varepsilon)b-p}{p}k_1(t).$$

Simple algebraic manipulations and the inequality $b < 1 < \frac{1}{1-\varepsilon}$ give for all $t \in (0,T]$

$$\frac{bk_1(t)}{k_1(t)+f_1(t)} - p > \frac{p}{(1-\varepsilon)b}\left[1-(1-\varepsilon)b\right] \implies f'_1(t) > \frac{p}{(1-\varepsilon)b}\left[1-(1-\varepsilon)b\right]f_1(t) > 0.$$

Therefore, f_1 is increasing, so $f_1(T) > f_1(0)$, which completes the proof. □

Proof of Th. 1. From lemmas 2 and 3 and the continuity of the solution of Eq. (1a) with respect to the initial condition it follows that there exists an initial condition $f_1(0)$ such that $f_1(T) = f_1(0)$. It means that Eq. (1a) has a periodic solution. □

Theorem 4. *The periodic solution $\bar{f}_1(t)$ of Eq.* (1a) *is unique. If f_1 is a solution of Eq.* (1a) *for a positive initial condition, then* $\lim_{t\to+\infty} |\bar{f}_1(t) - f_1(t)| = 0$.

Proof. We adapt here the method used in [1] for equations with delay. First, we prove, that every solution of Eq. (1a) with positive initial condition converges to some periodic solution. Writing Eq. (1a) in an exponential form we have for any $\xi, t \in \mathbb{R}$

$$f_1(t+\xi) = f_1(t)\exp\left(\int_t^{t+\xi}\left(\frac{bk_1(s)}{k_1(s)+f_1(s)} - p\right)\mathrm{d}s\right). \tag{7}$$

Due to Theorem 1 there exists a periodic solution $\bar{f}_1$, so for them we have $f_1(t) = f_1(t+T)$, and therefore, due to (7)

$$\int_t^{t+T}\left(\frac{bk_1(s)}{k_1(s)+\bar{f}_1(s)} - p\right)\mathrm{d}s = 0. \tag{8}$$

Consider now a solution of Eq. (1a) different from $\bar{f}_1$. Because of the uniqueness of solutions of Eq. (1a) we have for all $t \in \mathbb{R}$ either $f_1(t) > \bar{f}_1(t)$ or $f_1(t) < \bar{f}_1(t)$. Assume that the first inequality holds. Thus, due to (7) and (8) we have

$$\begin{aligned} f_1(t+T) =& f_1(t)\exp\left(\int_t^{t+T}\left(\frac{bk_1(s)}{k_1(s)+f_1(s)} - p\right)\mathrm{d}s\right) \\ <& f_1(t)\exp\left(\int_t^{t+T}\left(\frac{bk_1(s)}{k_1(s)+\bar{f}_1(s)} - p\right)\mathrm{d}s\right) = f_1(t). \end{aligned}$$

Thus, the sequence $f_1(nT)$ is a strictly decreasing bounded sequence so it has a limit. Denote this limit by $\zeta \geq \bar{f}_1(0)$. Moreover, if $\tilde{f}_1$ is a solution of Eq. (1a) with an initial condition $\tilde{f}_1(0) = \zeta$, then $\tilde{f}_1(T) = \zeta$. However, if $\zeta > \bar{f}_1(0)$ would hold then again using (7) and (8) we would obtain $\tilde{f}_1(T) < \tilde{f}_1(0)$ which is a contradiction. This completes the proof. □

Corollary 5. *Let assumptions of Theorem 1 be fulfilled. Then there exits a unique periodic solution* $(\bar{f}_1, \bar{f}_2, \bar{m}_2, \bar{m}_3)$ *of the system* (1) *that is globally stable in* $(0, +\infty)^4$.

Proof. Note that in the proofs of Theorems (1) and (4) we have used only the facts that the function $k_1/(k_1 + f_1)$ is decreasing in f_1, derivative of f_1 is negative for large f_1 and positive for sufficiently small f_1. After solving the equation for f_1, we can reduce Eq. (1b) to one that fulfills such assumptions. We can do the same with Eqs. (1c) and (1d). □

NUMERICAL SIMULATIONS

We have shown that there exists a periodic solution of system (1) which attracts all positive solutions of the system. In order to illustrate the behaviour of the system (1) numerical simulations were conducted. To do that we had to choose a particular form of the function k_1. To avoid the influence of other factors as well as dependence of results on the initial conditions, we decided to solve the system with a constant k_1 for $t < 50$ and later introduce the effect of the floods. The function $k_1(t)$ is continuous for all t. In [2] ratios between available nests sites in all three regions are given. Thus, we rescaled all variables of the system (1) by a number of total available nesting sites. As a result, k_i can be interpreted as a fraction of the nesting sites available in the region I, II and III. Thus, as in [2, 5], the following values of parameters are chosen:

$$b = 0.826, \quad p = 0.0928, \quad k_{1,\mathrm{av}} = 0.797, \quad k_2 = 0.136, \quad k_3 = 0.067, \tag{9}$$

and

$$k_1(t) = \begin{cases} k_{1,\mathrm{av}}, & \text{for } t \leq 50 \\ k_{1,\mathrm{av}} + 0.79\sin\left(\frac{t-50}{10}\right), & \text{for } t > 50. \end{cases}$$

System (1) was solved with the following initial conditions (they were taken arbitrarily since this choice does not influence the population dynamics after some time):

$$f_1(0) = 0.1, \quad f_2(0) = 10, \quad m_2(0) = 10, \quad m_3(0) = 10. \tag{10}$$

The floodings are introduced after the time $t = 50$. The function k_1 oscillates for $t > 50$ with the period $20\pi \approx 63$ and the amplitude 0.79, which was chosen in a way that makes $k_1(t)$ positive for all t as the region capacity cannot be negative. During the flooding's peak, $k_1(t)$ reaches its minimal value 0.007 which is close to 0. When the region I is under water, females must migrate to next regions, increasing the competition for nesting sites. We want to emphasize that the units are arbitrary since the aim of the simulation was to show general trends, not focus on specific biological data.

The results confirmed the conjecture that all the solutions of the system converge to the periodic one. Furthermore, this solution does not depend on the chosen initial conditions which also was checked using the same program. In Figs. 1, 2 and the left panel of Fig. 3 the dynamics of the populations in all regions were shown. The left panel of Fig. 3 illustrates populations of males

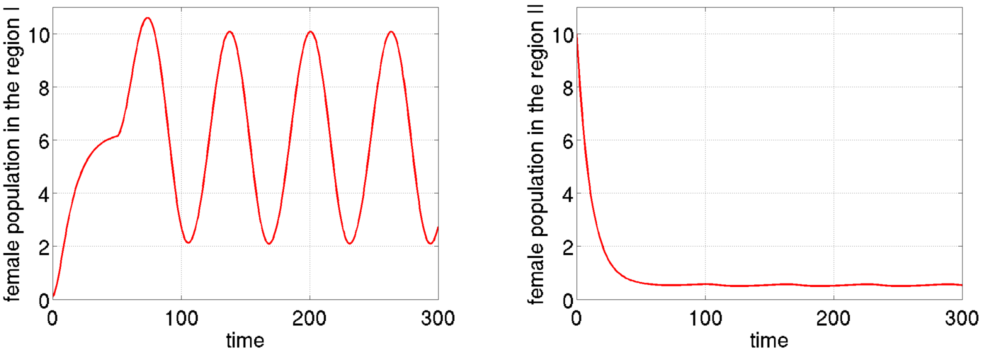

Figure 1. Left panel: dynamics of the female population in the region I. Right panel: dynamics of the female population in the region II.

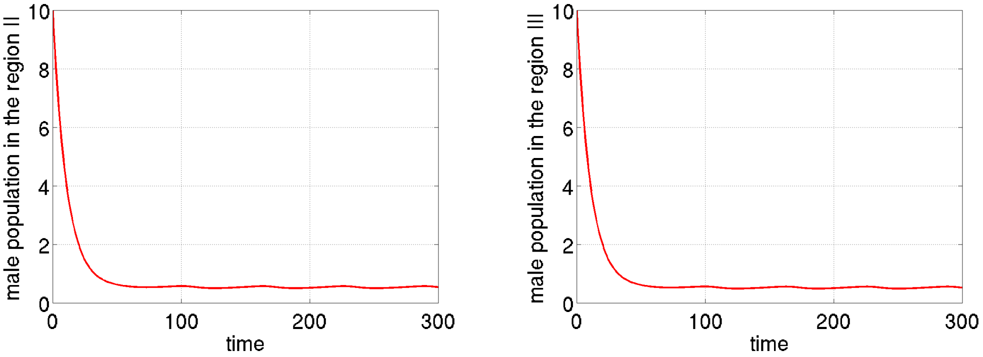

Figure 2. Left panel: dynamics of the male population in the region II. Right panel: dynamics of the male population in the region III.

in regions II (red line) and III (blue dashed line), beginning from the time $t = 50$ in order to draw attention to periodic oscillations and differences between these two regions. In this picture one can see that male populations in regions II and III oscillate with an agreement in phase. After closer investigation the oscillations of the population of females in the region II also have the same phase. However, there is a clear phase difference between oscillations of the number of females in the region I and other populations

It can be noticed that although the initial number of females in the region I was smaller than numbers of crocodiles in other regions, they quickly became the largest population. Moreover, the number of females in the first region oscillates with much greater amplitude than other populations. One of the reasons for such a behaviour is that only this region is affected directly by floods. In the right panel of Fig. 3 the dynamics of the sex ratio in the whole population presented. In addition, Fig. 3 shows that the sex ratio oscillates between around 0.1 and 0.3 which confirms biological observations mentioned in [3]. It means that in average one male gets a chance to fertilize 7–8 females. It might have been one of the reasons why crocodiles have survived for millions of years, unlike species whose sex is determined genetically (GSD — Genetic Sex Determination). This could be due to the fact that in case of a catastrophe surviving males fertilize many females which leads to a big number of hatchlings.

CONCLUSIONS

Periodic floodings of the region I result in periodic solutions of the system of equations. The

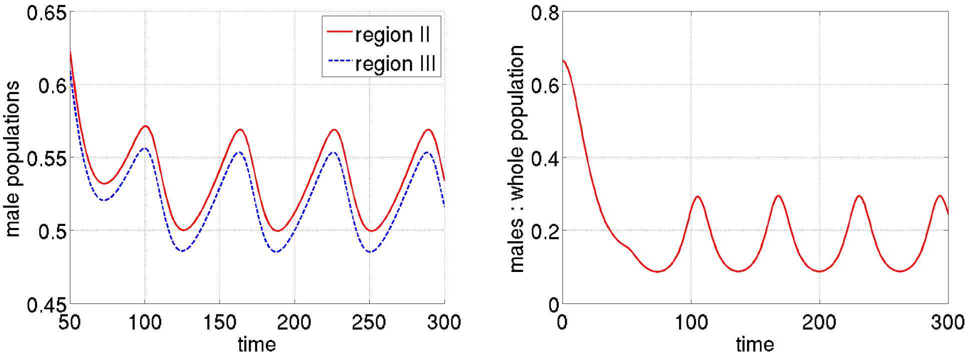

Figure 3. Left panel: dynamics of the male populations in regions II and III. Right panel: the changes in the sex ratio.

sex ratio of crocodile population also oscillates periodically with maxima during the flood and minima during the time without flooding. Moreover, it was proven that periodic solutions are locally asymptotically stable which was confirmed by numerical simulations.

The proposed model could be further developed in a number of ways. Firstly, one might introduce the age structure which would lead to equations with delays. Also, another factors influencing the population could be researched into, such as human activity including hunting or destroying crocodiles' natural habitat. Additionally, another model for floodings may be proposed, namely one introducing the noise in the system of equations; this is due to the random character of this phenomenon. The stochastic model of floods' influence on the population would be useful for biologists and ecologists.

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