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On the Asymptotic Stability of Discrete Crocodilians Model

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Abstract

The sex ratio of crocodiles is strongly biased towards females, often as high as 10 females to 1 male. In crocodilians, the temperature of egg incubation is the environmental factor determining sex. If the temperature is low, around 30°C, the hatchlings are all females. Higher temperature, around 34°C, hatch all males. This study was made to consider the asymptotic stability of a positive equilibrium point in a nonlinear discrete model of the basic nesting population model, which is described in three-region depending on the temperature of egg incubation. This model is based on key life-historical data and Murray's research. To study above, we have applied the classical linearization method and P. Cull's method and moreover, we employ non-standard discretization methods for later our Equations (6)-(8) and (15).

Keywords

Asymptotic Stability, Crocodilians Population Model, Positive Equilibrium Point

1. Introduction and Motivation

Recently, Murray [1] has studied crocodilians population model with time-dependent. However, he and other investigators only treat differential equations model. It is well known that differential equations are advantageous for ecological models when the number of individuals is large, but the difference equations are more realistic for biological populations where the population is not so large (in the case of crocodiles, its population is about 10 million less than human population). So, in this paper, we consider the difference equation models.

By the way, in the following all sentence, we modified the introduction to [2].

Some species are extinct and some are not, making it a fascinating theme, and

for example, we know the three families of crocodilian (crocodiles, alligators and gavials) not become extinct during the past 100 million or so years. They have survived essentially unchanged for around over 63 million years after the dinosaurs became extinct and clearly have great survival powers [3].

In 1988, Carroll [4] suggested that the decline of the genera was probably due to climatic deterioration from around the beginning of the Caenozoic (over 63 million years ago) era. A crucial difference between the crocodilian and most other species is that their hard sex is determined by the incubation temperature of the egg during gestation, basically females at low temperatures and males at high temperatures. It is interesting to speculate whether this could be a possible explanation, or at least a significant contributory factor, for their incredible survivorship, and if so, how.

In this paper, we discuss mathematical models to investigate this hypothesis. In genetic sex determination (GSD) such as for mammals and birds, sex is fixed at conception. Environmental sex determination (ESD), is when sex is determined by environmental factors and occurs in other vertebrates and some invertebrates (see, for example, Charnov and Bull [5] and Deeming and Ferguson [6] [7] [8]). Temperature-dependent sex determination (TSD) is often observed in reptiles. Other than crocodiles, alligators and the rest of the crocodilian, several reptiles, such as some lizards and certain turtles, the temperature of egg incubation is the major factor determining sex. The temperatures that produce all male or all female hatchlings vary little between the different species of crocodilian. Females are produced at one or both extremes of the range of viable incubation temperatures, and the intermediate temperatures produce males. For example, in Alligator Mississippians is artificial incubation of eggs at low temperatures, 30°C and below, produces females; 33°C produces all males; while high temperatures, 35°C, give 90 percent female hatchlings. Ferguson and Joanen [9] incubated 500 alligator eggs and found that all the young are male if the eggs are incubated in the range 32.5°C - 33°C. Temperatures in between, that is, 32°C and from 33.5°C - 34.5°C produce both sexes.

Reproductive fitness of males and females are strongly influenced in different ways by environment. Sex starts to be determined quite early in gestation, by about the twelfth day into gestation, but is not irrevocably fixed until as late as 32 to 35 days. For Alligator Mississippians, the gestation is around 65 days for males and up to 75 days for females. Exact data can be found in the review by Ferguson [10].

A very important question is that TDS has evolved to crocodilian. To answer this, we see that observation of TDS in the natural habitat of Mississippians in Louisiana, USA, indicate there are basically three different types of nest site: wet marsh, dry marsh and levee (elevated firm ground). Broadly, levee nests are hot (34°C) and hatch approximately 100 percent males while in the wet marsh, nests are cool (30°C) and hatch approximately 100 percent females. There are also temperature variations within the nest but we do not include this aspect in our models, although they could be incorporated in a more sophisticated version.

Dry marsh nests have an intermediate temperature profile, the hot (34˚C) top center hatching males, and the cold (30˚C) peripheries and base, hatching females (Ferguson and Joanen [9] [11]). Since so few viable reproductive female alligators are hatched at temperatures higher than 34˚C we do not include this cohort in our modelling.

The female alligator (and crocodile) does not choose the sex of her offspring perse. In particular, a limited number of marsh nest sites will prevent a totally female population from occurring although female alligators and crocodiles tend to seek a temperature environment that is as close as possible to that of their own incubation (see Pooley [12]) and so the preferred habitat of females is marsh. Joanen [13] gives some field data for the relative size of these different nest site areas; we give these at the appropriate place in the modelling below when we estimate parameter values. In the models, we develop here we focus on the principal feature of TSD, namely, the effect of temperature on sex determination.

However, one of the selective advantages of TSD is the association of maximum potential for adult growth with sex. Male alligators and crocodiles control harems of females; large males control bigger harems, mate more often and for a longer season (see Deeming and Ferguson [8]). Selective advantages for TSD in alligators and crocodiles is possibly explained in terms of survival of the species rather than the fitness of the individual which is a fundamentally different approach to that of the selfish gene.

Here we mainly focus on the link between temperature-dependent sex determination, sex ratio and survivorship in crocodile populations. We first describe a simple density-dependent model involving only time to highlight the ideas and motivate the more complex density-dependent model for the population dynamics of crocodilians based on the fact that sex is determined by temperature of egg incubation.

We follow the model of Woodward and Murray [1], and our modelling reflects the stability of crocodilian populations in the wild, and this stability suggests selective advantages for environmental sex determination over genetic sex determination that cannot be explained in terms of traditional sex ratio theory.

Some reptiles, such as the crocodilian, are not genetic sex determination (GSD) as in mammals but temperature-dependent sex determination (TSD). In crocodiles, females are produced at one or both extremes of the range of viable incubation temperatures, and the intermediate temperatures produce males. Female crocodiles account for a significant proportion of the population which is the heavily biased sex ratio, as high as 10:1 in favor of females in crocodilians. This is difficult to explain in terms of traditional sex ratio theory.

Therefore, Murray's paper [1] has shown the asymptotic stability of a positive equilibrium point in a nonlinear differential equation of crocodilians population model which is based on life history date from studies of crocodile and alligator populations in the wild. Furthermore, in order for crocodiles to preserve their species by themselves, he proved that temperature-dependent sex determination

(TSD) is superior to genetic sex determination (GSD).

Murray [1] [2] has shown only the simplified two-region model of crocodilian population, but he does not prove clearly the stability analysis of the model taking into account three nesting region. Moreover, the number of crocodilian populations is decreasing to such an extent they are endangered (e.g., the wild population of Alligator Mississippians is about 1 million).

The purpose of this paper is to demonstrate that the asymptotic stability of a positive equilibrium points in the difference equation of crocodilians population model by using non-standard discretization method for some biological models by H. Alkahby, F. Dannan and S. Elaydi [14]. Especially, we are not only considering two-region but also prove the stability property in three-region model of crocodile population, because Murray does not detailed proof that. And also, Hamaya and Saito [15] consider the asymptotic behavior of crocodilians model with diffusion for the region II and III of their inhabits. However, we should take notice that our mathematical model is ultimately mathematical analysis to research the population of crocodilian in the future.

2. The Crocodilian Population Model

We describe a basic three-region model for the populations of males and females which depends only on time. We incorporate some crucial spatial elements in the model based on the observations of Ferguson and Joanen [9] [11]. We assume that there are 3 distinct nesting regions:

I. Wet marsh, producing all female hatchlings because of low incubation temperatures in these sites,

II. Dry marsh, producing 50 percent male and 50 percent female hatchlings,

III. Dry levees, producing all male hatchlings because of higher incubation temperatures.

Table 1 schematically illustrates what we have in mind for these three regions.

We comply with the Murray's model and assume that there are 3 distinct nesting regions as following Table 1 which is indicated from the source of [2] [16]. Male and female populations depend on density. We assume that there is a limited number of nest sites near the water which prevents a totally female population. According to Joanen (1969 [13], cf. [1] [2]), typical figures for percentages of the total nest sites in each of these regions are region I: 79.7%, region II: 13.6%, region III: 6.7%. Also, total number females are $f(n) = f_1 + f_2$ and total number of males are $m(n) = m_2 + m_3$.

Table 1. Environment of three distinct nesting regions.

	Region I	Region II	Region III
Nesting area	wet marsh	dry marsh	dry levees
Temperature	30°C	32°C	34°C
Population	$f_1(n)$	$f_2(n), m_2(n)$	$m_3(n)$
Incubated sex	only females	males and females (50/50)	only males

Now, for each subscript i, k_i denotes the carrying capacity of each region, f_i denotes the number of females of region, m_i denotes the number of males. Furthermore, all females can nest in region I when f_1 is smaller, but if f_1 is larger, most females have to go away region I for making a nest. Here, let F be the population of female that can make a nest in region I;

$$F = \frac{k_1}{k_1 + f_1}. \tag{1}$$

Equation (1) satisfies the following,

$$F = \frac{k_1}{k_1 + f_1} \to 0 \left(f_1 \to \infty \right) \text{ and } F = \frac{k_1}{k_1 + f_1} \to 1 \left(f_1 \to 0 \right). \tag{2}$$

In Murray's differential population model, the equation of the population model in region I as follows;

$$\frac{df_1}{dt} = b_0 \left(\frac{k_1}{k_1 + f_1} \right) f_1 - df_1. \tag{3}$$

For Equation (3), b denotes the birth rate. Let C be the number of eggs per time, S be the survival rate, we can denote the effective birth rate by $CSb = b_0$. d denotes proportional parameter, the death rate are proportional to the population with d a parameter. Still, all parameter are the positive constants.

In region II, the total number of females is the sum of population who moved from region I and want to make nest in region II, but can nest population in region 2 is limited. Furthermore, because of male and female is fifty-fifty ratio in region II, equation of the population model in region II are

$$\begin{aligned}
\frac{df_2}{dt} &= \frac{b_0}{2} \left(\frac{f_1^2}{k_1 + f_1} + f_2 \right) \left(\frac{k_2}{k_2 + f_1 + f_2} \right) - df_2, \\
\frac{dm_2}{dt} &= \frac{b_0}{2} \left(\frac{f_1^2}{k_1 + f_1} + f_2 \right) \left(\frac{k_2}{k_2 + f_1 + f_2} \right) - dm_2.
\end{aligned} \tag{4}$$

For Equation (4), $\left(f_1^2 / (k_1 + f_1) + f_2 \right)$ denotes the total number of females who want to nest in region II, $\left(k_2 / (k_2 + f_1 + f_2) \right)$ denotes the total number of females nesting region II.

The female who could not nest in region II, move to region III to make nest. Since only male is born in region III, equation of the population model in region III is

$$\frac{dm_3}{dt} = b_0 \left(\frac{k_3}{k_3 + f_1 + f_2} \right) \left(\frac{f_1^2}{k_1 + f_1} + f_2 \right) \left(\frac{f_1 + f_2}{k_2 + f_1 + f_2} \right) - dm_3. \tag{5}$$

For Equation (5), $\left(f_1^2 / (k_1 + f_1) + f_2 \right) \left((f_1 + f_2) / (k_2 + f_1 + f_2) \right)$ denotes the total number of females of who want to nest in region III and $\left(k_3 / (k_3 + f_1 + f_2) \right)$ denotes the total number of females nesting region III.

3. Difference Equations Model

Now, we rewrite Equations (3), (4), (5) with the following difference equations

in order to verify the Murray's model. After this we consider these equations.

From Equation (3) of region I, we have

$$f_1(n+1) - f_1(n) = \varphi_1(h)b_0\left(\frac{k_1}{k_1 + f_1(n)}\right)f_1(n+1) - \varphi_1(h)df_1(n),$$

where $\varphi_1(h) = \dfrac{1 - e^{-dh}}{d}$, $\varphi_1(h) = h + o(h)$ and $o(\cdot)$ is Landau's small order, and then, we have

$$f_1(n+1) = \frac{\left(1 - \varphi_1(h)d\right)\left(k_1 + f_1(n)\right)}{\left(1 - \varphi_1(h)b_0\right)k_1 + f_1(n)} f_1(n). \tag{6}$$

Similarly, from Equation (4) of region II we obtain

$$f_2(n+1) = \frac{\varphi_2(h)b_0}{2}\left(\frac{f_1^2(n)}{k_1 + f_1(n)} + f_2(n+1)\right)\left(\frac{k_2}{k_2 + f_1(n) + f_2(n)}\right)$$
$$+ \left(1 - \varphi_2(h)d\right)f_2(n),$$
$$m_2(n+1) = \frac{\varphi_2(h)b_0}{2}\left(\frac{f_1^2(n)}{k_1 + f_1(n)} + f_2(n)\right)\left(\frac{k_2}{k_2 + f_1(n) + f_2(n)}\right)$$
$$+ \left(1 - \varphi_2(h)d\right)m_2(n). \tag{7}$$

From Equation (5) of region III

$$m_3(n+1) = \varphi_3(h)b_0\left(\frac{f_1^2(n)}{k_1 + f_1(n)} + f_2(n)\right)\left(\frac{k_3}{k_3 + f_1(n) + f_2(n)}\right)$$
$$\times\left(\frac{f_1(n) + f_2(n)}{k_2 + f_1(n) + f_2(n)}\right) + \left(1 - \varphi_3(h)d\right)m_3(n). \tag{8}$$

4. Stability of the Population: Considering Two-Region

First, we assume $f_2 = 0$ and consider the simplified model which making region I and region III because the number of nesting females in region II is significantly lower than in region I. Incidentally, this assumption is biologically realistic.

As we do not consider region II, we set $f_2 = k_2 = 0$. From Equations (6) and (8)

$$f_1(n+1) - f_1(n) = \varphi_1(h)b_0\left(\frac{k_1}{k_1 + f_1(n)}\right)f_1(n+1) - \varphi_1(h)df_1(n),$$
$$m_3(n+1) - m_3(n) = \varphi_3(h)b_0\left(\frac{k_3}{k_3 + f_1(n)}\right)\left(\frac{f_1^2(n)}{k_1 + f_1(n)}\right) - \varphi_3(h)dm_3(n), \quad n \geq 0. \tag{9}$$

We set initial condition of (9) is given by

$$f_1(0) = f_0 > 0, \quad m_3(0) = m_0 > 0. \tag{10}$$

Existence of unique positive solution (f_1, m_3) of (9) is guaranteed when the initial conditions (10) hold. In (9), let $E^+ = \left(f_1^*, m_3^*\right)$ be a positive equilibrium point (steady state).

If $f_1^* \neq 0$,

$$0 = b_0 \frac{k_1}{k_1 + f_1^*} - d,$$

then

$$f_1^* = k_1 \left(\frac{b_0}{d} - 1 \right). \tag{11}$$

Similarly, we have

$$m_3^* = \frac{b_0}{d} \left(\frac{k_3}{k_3 + f_1^*} \right) \left(\frac{f_1^{*2}}{k_1 + f_1^*} \right). \tag{12}$$

Theorem 1. *If* $b_0 (= CSb) > d$ *, then the positive equilibrium point:* $E^+ = \left(f_1^*, m_3^* \right)$ *of* (9) *with two-nesting regions is locally asymptotically stable, and more over* $E^+ = \left(f_1^*, m_3^* \right)$ *of* (9) *is globally asymptotically stable.*

Proof. We put $f_1 = x$, $m_3 = y$. From (9), we define

$$f(x,y) = \frac{(1-\varphi(h)d)(k_1+x)}{(1-\varphi(h)b_0)k_1+x} x,$$

$$m(x,y) = \psi(h) \left(b_0 \frac{k_3}{k_3+x} \cdot \frac{x^2}{k_1+x} \right) + (1-d\psi(h))y, \tag{13}$$

where $\varphi(h) = \varphi_1(h), \psi(h) = \varphi_3(h)$. Then we have

$$f_x = \frac{\partial f(x,y)}{\partial x} = \frac{e^{-dh} \left(x^2 + 2k_1(1-\varphi(h)b_0)x + (1-\varphi(h)b_0)k_1^2 \right)}{\left((1-\varphi(h)b_0)k_1+x \right)^2},$$

$$f_y = \frac{\partial f(x,y)}{\partial y} = 0,$$

$$m_x = \frac{\partial m(x,y)}{\partial x} = \psi(h)b_0 \left(\frac{-k_3}{(K_3+x)^2} \cdot \frac{x^2}{k_1+x} + \frac{k_3}{k_3+x} \cdot \frac{2x(k_1+x)-x^2}{(k_1+x)^2} \right),$$

$$m_y = \frac{\partial m(x,y)}{\partial y} = 1 - d\psi(h).$$

In the case of a positive equilibrium point $E^+ = \left(f_1^*, m_3^* \right)$ of (9), Jacobian matrix is given by

$$J(E^+) = \begin{pmatrix} \dfrac{e^{-dh} \left(C^2 + 2k_1\Phi(h)C + \Phi(h)k_1^2 \right)}{\left(\Phi(h)k_1 + C \right)^2} & 0 \\ \psi(h)b_0 \left(\dfrac{\left(k_1k_3+k_3^2 \right)C^2 + 2k_1k_3^2C}{\left(k_3+C \right)^2 \left(k_1+C \right)^2} \right) & e^{-dh} \end{pmatrix}, \tag{14}$$

where, $\Phi(h) = 1 - \varphi(h)b_0$ and $C = k_1 \left(\dfrac{b_0}{d} - 1 \right)$. The eigenvalue of (14) is its diagonal elements and less than 1 (cf. [17]);

$$\lambda_1 = \frac{e^{-dh}\left(C^2 + 2k_1\Phi(h)C + \Phi(h)k_1^2\right)}{\left(\Phi(h)k_1 + C\right)^2} < 1 \text{ and } \lambda_2 = e^{-dh} < 1 \text{ for } d > 0, h > 0.$$

Because, it is clear from $d < b_0 \left(= CSb\right)$ that $\Phi(h) = 1 - \varphi(h)b_0 < 1$, and moreover, we set

$$\tilde{f}(h) = \frac{e^{-dh}\left(C + k_1\right)^2}{\left(\Phi(h)k_1 + C\right)^2} > 0.$$

Since, $\tilde{f}(0) = 1, \tilde{f}'(h) < 0$ and $\lim_{h\to\infty} \tilde{f}(h) = 0$, we obtain that $\tilde{f}(h) < 1$. Thus, we have

$$\lambda_1 < \frac{e^{-dh}\left(C^2 + 2k_1 \cdot 1 \cdot C + 1 \cdot k_1\right)^2}{\left(\Phi(h)k_1 + C\right)^2} = \frac{e^{-dh}\left(C^2 + k_1\right)^2}{\left(\Phi(h)k_1 + C\right)^2} = \tilde{f}(h) < 1.$$

That is, $d < b_0$ is necessary condition with a positive equilibrium point f_1^*. Moreover, from (13) we obtain

$$f_x + 1 = \frac{e^{-dh}\left(x^2 + 2k_1\Phi(h)x + \Phi(h)k_1^2\right)}{\left(\Phi(h)k_1 + x\right)^2} + 1 \neq 0, \quad (x \geq 0).$$

Equation $x_{n+1} = f(x_n)$ for $x \geq 0$ has no two-cycle since $f_x + 1 \neq 0$. Therefore, f_1^* is globally asymptotically stable of $x_{n+1} = f(x_n)$ (cf. Theorem 2.6 and Theorem 2.7 in [18]).

Similarly,

$$m_y + 1 = 2 - d\psi(h) \neq 0, \quad (y \geq 0).$$

Equation $y_{n+1} = m(y_n)$ for $y \geq 0$ has no two-cycle since $m_y + 1 \neq 0$. Therefore, m_3^* is globally asymptotically stable of $y_{n+1} = m(y_n)$.

5. Stability of the Population: Considering Three-Region

Next, we consider the stability of the population in three-region model which included region II. From (6), (7), (8), we have

$$f_1(n+1) = \frac{\left(1 - \varphi_1(h)d\right)\left(k_1 + f_1(n)\right)}{\left(1 - \varphi_1(h)b_0\right)k_1 + f_1(n)}f_1(n),$$

$$f_2(n+1) = \frac{\varphi_2(h)b_0k_2f_1^2(n) + 2\left(k_1 + f_1(n)\right)\left(k_2 + f_1(n) + f_2(n)\right)\left(1 - \varphi_2(h)d\right)f_2(n)}{\left\{2\left(k_2 + f_1(n) + f_2(n)\right) - \varphi_2(h)b_0k_2\right\}\left(k_1 + f_1(n)\right)},$$

$$m_2(n+1) = \frac{\varphi_2(h)b_0}{2}\left(\frac{f_1^2(n)}{k_1 + f_1(n)} + f_2(n)\right)\left(\frac{k_2}{k_2 + f_1(n) + f_2(n)}\right) + \left(1 - \varphi_2(h)d\right)m_2(n), \quad (15)$$

$$m_3(n+1) = \varphi_3(h)b_0\left(\frac{f_1^2(n)}{k_1 + f_1(n)} + f_2(n)\right)\left(\frac{k_3}{k_3 + f_1(n) + f_2(n)}\right)$$

$$\times \left(\frac{f_1(n) + f_2(n)}{k_2 + f_1(n) + f_2(n)}\right) + \left(1 - \varphi_3(h)d\right)m_3(n), \quad n \geq 0,$$

whenever $k_2 + f_1(n) + f_2(n) > \varphi_2(h)b_0k_2$ for an equation of $f_2(n+1)$ in (15).

However, this condition: $k_2 + f_1(n) + f_2(n) > \varphi_2(h)b_0k_2$ automatically yields. We set the initial condition of (15) is given by

$$f_1(0) = f_0 > 0, \quad f_2(0)(= m_2(0)) > 0, \quad m_3(0) = m_0 > 0. \qquad (16)$$

We also hold for unique positive solution of (15) with the initial condition (16). Moreover, as in the case of three-region, we can get the following equilibrium points which are given by setting the left-hand sides of each equation of (15) equal to $f_i^*, m_j^* \ (i = 1, 2, 3; j = 2, 3)$,

$$f_1^* = k_1\left(\frac{b_0}{d} - 1\right), \quad f_2^*(= m_2^*) = \frac{-\alpha + \sqrt{\alpha^2 + \beta}}{2},$$

$$m_3^* = \frac{2k_3 f_2^*\left(f_1^* + f_2^*\right)}{k_2\left(k_3 + f_1^* + f_2^*\right)}, \qquad (17)$$

$$\text{where } \alpha = f_1^* - k_2\left(\frac{b_0}{2d} - 1\right), \quad \beta = \frac{2k_2 f_1^{*2}}{k_1}.$$

Theorem 2. If $d < b_0 < 2d$, then a positive equilibrium $\left(f_1^*, f_2^*(= m_2^*), m_3^*\right)$ of (15) with three-nesting regions is locally asymptotically stable.

Proof. We put $f_1(n) = x, f_2(n) = y, m_2(n) = z$ and $m_3(n) = w$. From (15), we have

$$f_1(x, y, z, w) = \frac{(1 - \varphi_1(h)d)(k_1 + x)}{(1 - \varphi_1(h)b_0)k_1 + x} x$$

$$f_2(x, y, z, w) = \frac{\varphi_2(h)b_0k_2 x^2 + 2(k_1 + x)(k_2 + x + y)(1 - \varphi_2(h)d)y}{\{2(k_2 + x + y) - \varphi_2(h)b_0k_2\}(k_1 + x)},$$

$$m_2(x, y, z, w) = \frac{\varphi_2(h)b_0}{2}\left(\frac{x^2}{k_1 + x} + y\right)\left(\frac{k_2}{k_2 + x + y}\right) + (1 - \varphi_2(h)d)z, \qquad (18)$$

$$m_3(x, y, z, w) = \varphi_3(h)b_0 \cdot \frac{k_3}{k_3 + x + y}\left(\frac{x^2}{k_1 + x} + y\right)\left(\frac{x + y}{k_2 + x + y}\right) + (1 - \varphi_3(h)d)w.$$

In the case of a positive equilibrium point $E^+ = \left(f_1^*, f_2^*, m_2^*, m_3^*\right)$ of (15), Jacobian matrix is given by

$$J = J\left(E^+\right) = \begin{pmatrix} f_{1x}^* & 0 & 0 & 0 \\ f_{2x}^* & f_{2y}^* & 0 & 0 \\ m_{2x}^* & m_{2y}^* & 1 - \varphi_2(h)d & 0 \\ m_{3x}^* & m_{3y}^* & 0 & 1 - \varphi_3(h)d \end{pmatrix}, \qquad (19)$$

and then

$$|J - \mu E| = \begin{vmatrix} f_{1x}^* - \mu & 0 & 0 & 0 \\ f_{2x}^* & f_{2y}^* - \mu & 0 & 0 \\ m_{2x}^* & m_{2y}^* & (1 - \varphi_2(h)d) - \mu & 0 \\ m_{3x}^* & m_{3y}^* & 0 & (1 - \varphi_3(h)d) - \mu \end{vmatrix} = 0, \qquad (20)$$

where

$$m_{ix}^* = \left.\frac{\partial m_i(x,y,z,w)}{\partial x}\right|_{\left(x=f_1^*,\,y=f_2^*,\,z=m_2^*,\,w=m_3^*\right)},$$

$$m_{iy}^* = \left.\frac{\partial m_i(x,y,z,w)}{\partial y}\right|_{\left(x=f_1^*,\,y=f_2^*,\,z=m_2^*,\,w=m_3^*\right)} \quad (i=2,3).$$

Thus, $\mu = f_{1x}^*, f_{2y}^*, 1-\varphi_2(h)d$ and $1-\varphi_3(h)d$. Here, the eigenvalue μ of (20) is its diagonal elements and $\left|f_{1x}^*\right|<1$, $\left|1-\varphi_i(h)d\right|<1\,(i=2,3)$ are clear. We next can see $\left|f_{2y}^*\right|<1$. From (18), we have

$$f_{2y} = \frac{-2\varphi_2(h)b_0k_2x^2}{(k_1+x)\left(2(k_2+x+y)-\varphi_2(h)b_0k_2\right)^2}$$

$$+\frac{2\left(1-\varphi_2(h)d\right)(k_2+x+2y)\left(2(k_2+x+y)-\varphi_2(h)b_0k_2\right)-4\left(1-\varphi_2(h)d\right)\left(k_2y+xy+y^2\right)}{\left(2(k_2+x+y)-\varphi_2(h)b_0k_2\right)^2}$$

and

$$f_{2y}^* = \left.\frac{\partial f_2(x,y,z,w)}{\partial y}\right|_{\left(x=f_1^*,\,y=f_2^*,\,z=m_2^*,\,w=m_3^*\right)}$$

$$= \frac{-2\varphi_2(h)b_0k_2 f_1^{*2}}{\left(k_1+f_1^*\right)\left(2\left(k_2+f_1^*+f_2^*\right)-\varphi_2(h)b_0k_2\right)^2}$$

$$+\frac{2\left(1-\varphi_2(h)d\right)\left\{\left(k_2+f_1^*+2f_2^*\right)\left(2\left(k_2+f_1^*+f_2^*\right)-\varphi_2(h)b_0k_2\right)-2\left(k_2f_2^*+f_1^*f_2^*+f_2^{*2}\right)\right\}}{\left(2\left(k_2+f_1^*+f_2^*\right)-\varphi_2(h)b_0k_2\right)^2} \quad (21)$$

$$= \frac{-2\varphi_2(h)b_0k_2 f_1^{*2}}{\left(k_1+f_1^*\right)\left(2\left(k_2+f_1^*+f_2^*\right)-\varphi_2(h)b_0k_2\right)^2}$$

$$+\frac{2\left(1-\varphi_2(h)d\right)\left(k_2+f_1^*+2f_2^*\right)}{2\left(k_2+f_1^*+f_2^*\right)-\varphi_2(h)b_0k_2} - \frac{4\left(1-\varphi_2(h)d\right)f_2^*\left(k_2+f_1^*+f_2^*\right)}{\left(2\left(k_2+f_1^*+f_2^*\right)-\varphi_2(h)b_0k_2\right)^2}.$$

Now, from (17), we obtain

$$f_2^*\left(k_2+f_1^*+f_2^*\right) = \frac{k_2b_0}{2d}\left(\frac{f_1^{*2}}{k_1+f_1^*}+f_2^*\right), \quad (22)$$

and here, we note that

$$\alpha = f_1^* - k_2\left(\frac{b_0}{2d}-1\right)>0, \quad \text{and} \quad 2\left(k_2+f_1^*+f_2^*\right)>\varphi_2(h)b_0k_2,$$

by (15), (17) and the assumption $b_0<2d$. Then, by inserting (22) into the third term of (21), we have

$$f_{2y}^* = \frac{-2\varphi_2(h)b_0k_2 f_2^*/\left(k_1+f_1^*\right)-2b_0k_2\left\{f_1^{*2}/\left(k_1+f_1^*\right)+f_2^*\right\}\left(1-\varphi_2(h)d\right)/d}{L^2}$$

$$+\frac{2\left(1-\varphi_2(h)d\right)\left(k_2+f_1^*+2f_2^*\right)}{L}$$

$$
\begin{aligned}
&= \frac{-2\varphi_2(h)b_0 k_2 f_1^* / d - 2b_0 k_2 (1/d - \varphi(h))(k_1 + f_1^*)f_2^*}{L^2} \\
&\quad + \frac{2(1 - \varphi_2(h)d)(k_2 + f_1^* + 2f_2^*)}{L} \\
&= \frac{-\dfrac{2\varphi_2(h)b_0 k_2 f_2^*}{k_1 + f_1^*} - \dfrac{2b_0 k_2 f_1^{*2}}{k_1 + f_1^*}(1/d - \varphi_2(h)) - 2b_0 k_2 f_2^*(1/d - \varphi_2(h))}{L^2} \\
&\quad + \frac{2(1 - \varphi_2(h)d)(k_2 + f_1^* + 2f_2^*)}{L},
\end{aligned}
\tag{23}
$$

where $L = 2(k_2 + f_1^* + f_2^*) - \varphi_2(h)b_0 k_2$. It is sufficient from (23) to prove $f_{2y}^* < 1$ that

$$
\begin{aligned}
&2\varphi_2(h)b_0 k_2\left(\frac{f_1^{*2}}{k_1 + f_1^*} + f_2^*\right) + 2(k_2 + f_1^* + 2f_2^*)L \\
&< L^2 + \frac{2b_0 k_2}{d}\left(\frac{f_1^{*2}}{k_1 + f_1^*} + f_2^*\right) + 2\varphi_2(h)d(k_2 + f_1^* + 2f_2^*)L + \frac{2b_0 k_2 f_2^*}{k_1 + f_1^*},
\end{aligned}
$$

that is, we show that

$$
\begin{aligned}
2(k_2 + f_1^* + 2f_2^*)L &< L^2 + \frac{4b_0 k_2}{2d}\left(\frac{f_1^{*2}}{k_1 + f_1^*} + f_2^*\right)(1 - \varphi_2(h)d) \\
&\quad + 2\varphi_2(h)d(k_2 + f_1^* + 2f_2^*)L + \frac{2b_0 k_2 f_2^*}{k_1 + f_1^*}.
\end{aligned}
$$

We now have

$$
\begin{aligned}
&2(\varphi_2(h)d - 1)(k_2 + f_1^* + 2f_2^*)L + (L \times L) \\
&\quad + 4f_2^*(k_2 + f_1^* + f_2^*)(1 - \varphi_2(h)d) + \frac{2b_0 k_2 f_2^*}{k_1 + f_1^*} \\
&= 2(\varphi_2(h)d - 1)(k_2 + f_1^* + f_2^* + f_2^*)L + 2(k_2 + f_1^* + f_2^*)L \\
&\quad - \varphi_2(h)b_0 k_2 L + 4(k_2 + f_1^* + f_2^*)f_2^*(1 - \varphi_2(h)d) + \frac{2b_0 k_2 f_2^*}{k_1 + f_1^*} \\
&= 2\varphi_2(h)dk_2 L + 2\varphi_2(h)d(f_1^* + f_2^* + f_2^*)L - 2(k_2 + f_1^* + f_2^*)L \\
&\quad - 2f_2^* L + 2(k_2 + f_1^* + f_2^*)L - \varphi_2(h)b_0 k_2 L \\
&\quad + 4f_2^*(k_2 + f_1^* + f_2^*)(1 - \varphi_2(h)d) + \frac{2b_0 k_2 f_2^*}{k_1 + f_1^*} \\
&= \varphi_2(h)k_2 L(2d - b_0) + 2\varphi_2(h)d(f_1^* + f_2^* + f_2^*)L - 2f_2^* L \\
&\quad + 4f_2^*(k_2 + f_1^* + f_2^*)(1 - \varphi_2(h)d) + \frac{2b_0 k_2 f_2^*}{k_1 + f_1^*} \\
&= \varphi_2(h)k_2 L(2d - b_0) + 2\varphi_2(h)d(f_1^* + f_2^* + f_2^*)\left(2(k_2 + f_1^* + f_2^*)\right) \\
&\quad - \varphi_2(h)b_0 k_2) - 2f_2^*\left(2(k_2 + f_1^* + f_2^*) - \varphi_2(h)b_0 k_2\right) \\
&\quad + 4f_2^*(k_2 + f_1^* + f_2^*) - 4\varphi_2(h)d(k_2 + f_1^* + f_2^*)f_2^* + \frac{2b_0 k_2 f_2^*}{k_1 + f_1^*}
\end{aligned}
$$

$$
\begin{aligned}
&= \varphi_2(h) k_2 L (2d - b_0) + 4\varphi_2(h) d (k_2 + f_1^* + f_2^*)(f_1^* + f_2^*) \\
&\quad - 2\varphi_2(h)^2 db_0 k_2 (f_1^* + f_2^*) - 2\varphi_2(h)^2 db_0 k_2 f_2^* + 2\varphi_2(h) b_0 k_2 f_2^* + \frac{2b_0 k_2 f_2^*}{k_1 + f_1^*} \\
&= \varphi_2(h) k_2 L (2d - b_0) + 2\varphi_2(h)(f_1^* + f_2^*)(2d(k_2 + f_1^* + f_2^*) - db_0 k_2 \varphi_2(h)) \\
&\quad + 2\varphi_2(h) b_0 k_2 (f_2^* - \varphi_2(h)d) + \frac{2b_0 k_2 f_2^*}{k_1 + f_1^*} \\
&> 0,
\end{aligned}
$$

because, $f_2^* - \varphi_2(h)d > 0$ and
$2d(k_2 + f_1^* + f_2^*) - db_0 k_2 \varphi_2(h) = 2d(f_1^* + f_2^*) + (2k_2 d - k_2 db_0) > 0$ by $b_0 < 2d$,
$b_0 < 1$ and $d\varphi_2(h) < 1$. Therefore, we have $f_{2y}^* < 1$.

6. Advantage of Sex Determination with Temperature Dependent

In the sex determination of Crocodilian, we show whether temperature-dependent sex determination (TSD) or genetic sex determination (GSD) is superior. From (11) and (12), as with Murray [2], we verify with a simple model considering two-region and the sex ration, male to female offspring, is given by

$$
\frac{m_3^*}{f_1^*} = \frac{k_3(CSb - d)}{k_3 d + k_1(CSb - d)}.
$$

where, b is the birth rate and d is the death rate, which are constant parameters. C is the clutch size and S is the hatchling and egg survival rate. On the other hand, we suppose that the crocodile sex is genetically determined. Now, $k_1 + k_3$ is the available carrying capacity. We assume that the corresponding equations for females $f_1(n)$ and males $m_3(n)$ have same sex ratio.

Then, we consider the following equation.

$$
\begin{aligned}
f_1(n+1) - f_1(n) &= \frac{\varphi(h)CSb}{2}\left(\frac{k_1 + k_3}{k_1 + k_3 + f_1(n)}\right) f_1(n+1) - \varphi(h) d f_1(n), \\
m_3(n+1) - m_3(n) &= \frac{\psi(h)CSb}{2}\left(\frac{k_1 + k_3}{k_1 + k_3 + m_3(n)}\right) m_3(n+1) - \psi(h) d m_3(n).
\end{aligned}
\tag{24}
$$

We set initial condition $f_1(0) = f_0 > 0$, $m_3(0) = m_0 > 0$. There is symmetry between males and females in this case, with half the births being female and the other half male. From (24), the steady state population are given by

$$
f_1^* = m_3^* = (k_1 + k_3)\left(\frac{CSb}{2d} - 1\right),
\tag{25}
$$

which are nonnegative only if $b_0 > 2d$. The sex ratio of males to females is always 1:1.

Even with the equilibrium points of (24) and (25) we can see the advantages of TSD over GSD for the crocodilian. From (24), that is, with TSD, a positive equilibrium points exists if $b_0 > d$ whereas for GSD it requires $b_0 > 2d$.

Now, we yield the following theorem which omits the proof.

Theorem 3. If $\left(b_0 = (CSb)\right)/d > 1$, then a positive equilibrium point: $\left(f_1^*, m_3^*\right)$ of (24) with TSD exists, while for GSD of (25) it requires $\left(b_0 = (CSb)\right)/d > 2$.

7. Conclusions

The analysis of our stability results shows that there are no periodic solutions and the positive equilibrium point is always stable. We also investigate the effect of some catastrophe which greatly reduced the populations and obtain estimates for the recovery time to their equilibrium points. This has to be done numerically except for small perturbations about the equilibrium points by applying linear theory. If the equations are to be studied in depth numerically then more appropriate fractional functions could be used but the general results would not be qualitatively different.

The critical value where GSD has equilibrium point is twice of the value of TSD. In short, we can see the advantage of TSD over GSD for crocodilian.

In Murray [1] [2], he did not deal with three-region model. In Section 4, we consider this model and also, in Theorem 2 we have shown the sufficient new-condition for asymptotic stability of a positive equilibrium point. This new ecological condition: $d < b_0 < 2d$ is natural one. Because, it is necessary for the survival strategy of crocodilians that the effective birth rate b_0 is larger than the death rate d, and also b_0 is not too large that means $b_0 < 2d$. If $b_0 > 2d$, by Theorem 3, then GSD yields. However, this is contradiction. Furthermore, the crocodilian population discrete model with three-nesting region, we have a conjecture that a positive equilibrium point: $E^+ = \left(f_1^*, f_2^*, m_2^*, m_3^*\right)$ of (15) is globally asymptotically stable.

It is intuitively clear how the crocodilian, because of TSD, can recover from a catastrophic reduction in their population. Following a major reduction, all the female crocodiles will be able to build their nests in region I and hence produce only females and this then allows the remaining males to have larger harems. The skewed sex ratio in the crocodilian thus maintains a large breeding population which provides the mechanism for rapid repopulation after a disaster. What is certainly not in doubt is that TSD has been a very effective reproductive mechanism in view of the remarkable survivorship of the crocodilian. Catastrophes, natural or otherwise, raise the question of extinction. If we consider extinction this would certainly happen if we have, from (9), $b < d$. With $b = b_0 m/(c + m)$ this implies that $m < cd/(b_0 - d) = O(1/b_0)$ for c small and b_0 large, which implies that essentially all the males have to be eliminated. The natural habitat of males is in the water where it is virtually impossible to kill them all which, in turn, implies the almost impossibility of extinction except through the elimination of all the nest sites, that is, by completely destroying their habitat. With the increasing encroachment of their habitat by human population pressures it is certainly possible that alligators could disappear at least from the southern USA and others.

In addition to the advantage of producing more females than males, the cro-

codilian have evolved life-history tactics, and temperature-dependent sex determination may also be important in enabling populations to survive environmental changes, and more, not only is a rapid expansion of the population associated with the production of large numbers of females, but also different incubation temperatures produce a population adapted to a range of environments after they hatch, independent of sex (see Deeming and Ferguson [8]).

In this area, as the research is still being promoted, there are many new articles on population dynamics of crocodilians, for example see [19] [20] [21] [22], especially, [21] is interesting, and has treated delay-differential mode of population of crocodilians.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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