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沈聖娥 教授指導
碩士學位 請求論文

Mathematical Models of Temperature-Dependent Sex Determination (TSD)

온도에 따른 성별 결정의 수학적 모델

2008

誠信女子大學校 教育大學院
教育學科 數學教育專攻
盧 延 敬

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2008 年 2 月

誠信女子大學校 教育大學院
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盧 延 敬

認 准 書

盧 延 敬의 碩士學位 論文을 認准함

審査委員 ______________ 印

審査委員 ______________ 印

審査委員 ______________ 印

誠信女子大學校 敎育大學院

논 문 개 요

이 논문은 해석학에 기초한 미분방정식론에서 다루는 지식과 분석 기법들을 이용하여 실제 현장조사에서 얻어진 생물학적 자료로부터 수학적 모델을 구성한다. 그리고 이를 통하여 실제 현상에 내재한 자연의 원리를 규명하고자 한다.

악어류의 부화 온도에 따른 성별변화를 설명하는 수학적 모델을 적용하고자 한다. 이 구체적인 모델을 통하여 수학적인 분석의 결과를 실제에 적용하여 여러 현상을 해석하고, 의도에 부합하는 방법을 수학적으로 제시하고자 한다.

악어류가 신생대 이후 현재까지의 오랜기간 동안 존속할 수 있었던 원인이 되는 생물학적인 특성으로, 악어류의 부화온도에 따른 성별변화를 들 수 있다. 낮은 온도(30°C)에서 거의 암컷이 부화되고, 높은 온도(34°C)에서 거의 수컷이 부화되며, 중간온도(32°C)에서 암컷과 수컷이 부화된다. 온도에 따른 세 지역을 구분하여 암컷과 수컷의 개체밀도를 함수로 두고 이 함수들에 대한 미분방정식 모델을 세운다.

목 차

논문개요

I Introduction

It is a fascinating subject why some species extinct and others do not. The three families of crocodilia (alligators, crocodiles and gavials) have not become extinct during the past 100 million or so years. They have survived essentially unchanged for around 63 million years after the dinosaurs became extinct and clearly have great survival powers. In spite of the massive extinctions, the families that have survived are rightly viewed as living fossils. Meyer [1] give a general overview of them while Pooley and Gans [1] focuses on the Nile crocodile and describes, among other things, its unique biology and social behavior which have contributed so much to its long survival.

A crucial difference between the crocodilia and most other species is that their 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 thesis we discuss models to investigate this hypothesis. We first search some biological background and clarify the terms used in their study. We shall frequently use the word crocodile or alligator to represent the crocodilia in general and the exact name, such as Alligator mississippiensis or A. mississippiensis when we mean the specific reptile. An excellent and comprehensive review of the reproductive biology of the crocodilians is given by Ferguson [1].

In genetic sex determination (GSD), such as for mammals and birds, sex is fixed at conception. Environmental sex determinant (ESD) is when sex is determined by environmental factor and occurs in other vertebrates and some invertebrates (see, for example, Charnov and Bull [6], Deeming and Ferguson [7], [8], [9]). Temperature-dependent sex determination (TSD) is often observed in reptiles. Other than crocodiles, alligators and the rest of the crocodilia, several reptiles, such as some lizards and certain turtles, the temperature of egg incubation is the major factor determining sex. Gutzke and Crews [10], for example , specifically studied the leopard gecko (Eublepharis macularius) which has a similar pattern to the crocodilia but with a lower temperature range from 26 to 32°C. With turtle it is the high temperatures that give only females, except for the snapping turtle which is like the crocodile.

The temperatures that produce all male and or all female hatchlings vary little between the different species of crocodilia. 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 mississppiensis* artificial incubation of eggs at low temperature , 30°C and below, produces females; 33°C produces all males; while high temperature, 35°C, give 90% female hatchlings (but these are usually not viable). Ferguson and Joanen [4] incubated 500 alligator eggs and found that all the young are male if the eggs incubated in the 32.5-33°C. Temperatures in between, that is, 32°C and from 33.5-34.5°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 mississipiensis* 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 [5].

TSD has evolved. It has been postulated that TSD is the ancestral form and GSD evolved from it. Deeming and Ferguson ([7], [8]a, [9]b) have proposed an explanation of the mechanism of temperature-dependent sex determination in crocodilians. Their hypothesis is that the temperatures producing males are those that are best for the expression of the gene for the male-determining factor. In a warm nest eggs develop faster (see, for example, the graph in chapter II. Preliminaries below and Murray et al. [11] than in a colder one and this means the young hatch more quickly. The adults are also bigger when developed in a higher temperature; this turns out to be crucial in determining the stripe pattern in alligators. One possible explanation in the case of the crocodile is that it is better for the male to be big to fight off competitors whereas for the turtle it is better for the female to be big so that she can lay more eggs. The latter, however, could just as well apply to the crocodile. In this thesis we investigate a different possible explanation, which could be a significant factor in their long survival.

Observations of TSD in the natural habitat of *A. mississipiensis* in Louisiana, U.S.A., 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% males while in the wet marsh, nests are cool(30°C) and hatch approximately 100% 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 [3], [4]). Since so few viable reproductive female alligators are hatched at temperatures higher than 34°C we do not include this cohort in our modeling. Those that are incubated at these temperatures have very low relative fitness.

II Preliminaries

In this thesis we use a basic three-region model for the populations of males and females which depends only on time. Based on the observations of Ferguson and Joanen ([4],[13]) we incorporate some crucial spatial elements in the model. We assume that there are three distinct nesting regions as explained in the following :

- **I** wet marsh, producing all female hatchlings because of low incubation temperature in these nest sites,
- **II** dry marsh, producing 50% male and 50% female hatchlings,
- **III** dry levees, producing all male hatchlings because of higher incubation temperatures.

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

We further assume that there is a limited number of nest sites near the water which prevents a totally female population: typical figure for percentages of the total nest sites in each of these regions are given by Joanen([12]) as 79.7% for region I, 13.6% for region II and 6.7% for region III.

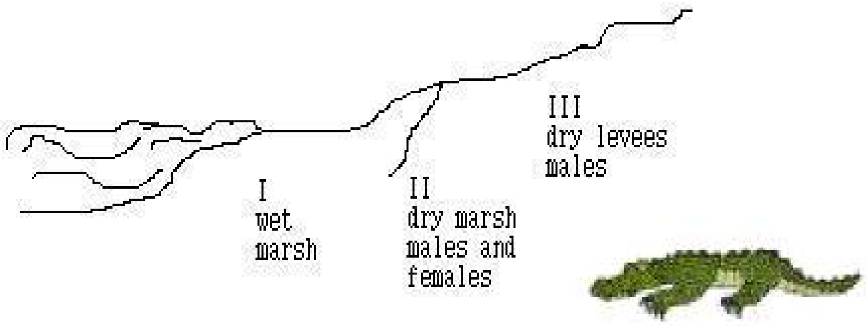

Figure 1: Three basic nesting regions, representing the environmental influence.

The population at time, t, is divided into four classes, $f_1(t)$ and $f_2(t)$ denoting females themselves incubated in regions I and II respectively and $m_2(t)$ and $m_3(t)$ denoting males incubated in II and III. In region I which is the wet marsh, the hatchlings are all female with the population $f_1(t)$. In region II, the dry marsh, 50% of hatchlings become female and the other 50% become male, and their populations are denoted by $f_2(t)$ and $m_2(t)$, respectively. Finally region III, the dry levees, has all male hatchlings with the population $m_3(t)$. Hence the total female population $f(t)$ and the total male population $m(t)$ are obtained as the following.

$$f(t) = f_1(t) + f_2(t),$$

$$m(t) = m_2(t) + m_3(t).$$

An idealized spatial distribution of the sex ratio of males to the total population in the three-region scenario in Figure 1 is shown in Figure 2(a). The continuous curve represents the actual distribution. Figure 2(b) illustrates schematic curves for relative fitness (survival times fertility) as compared with others of the same sex. We note that it is highest foe both males and females in the middle range of temperatures, around 32°C.

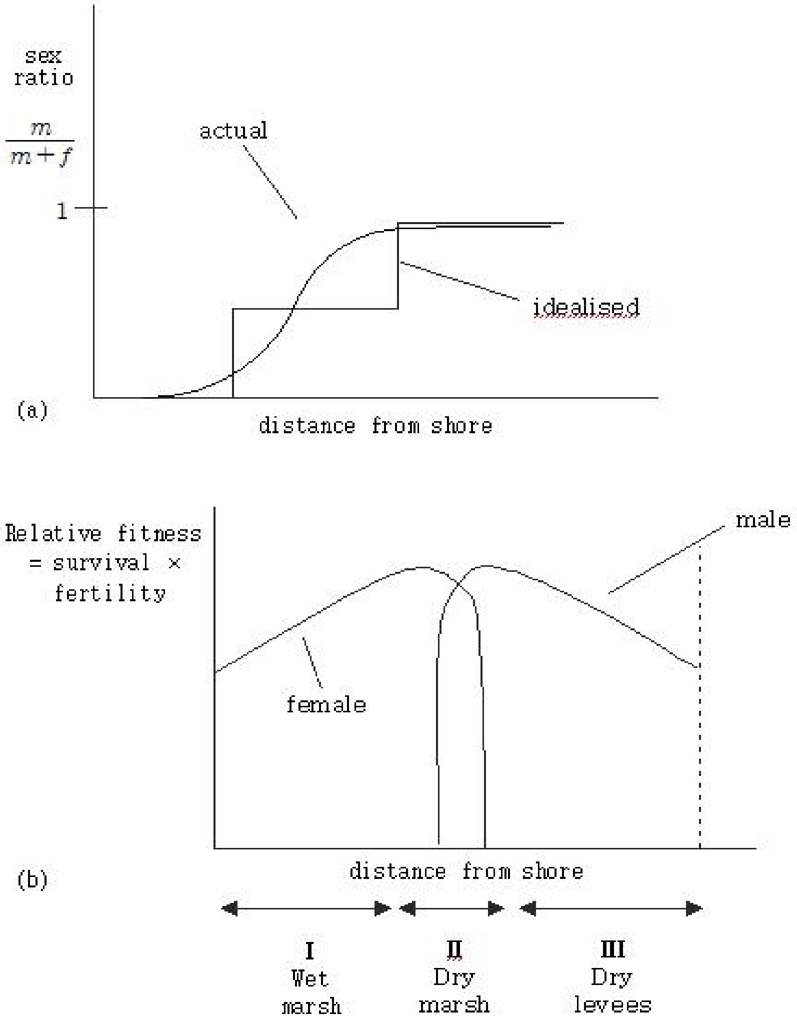

Figure 2: (a) Idealized sex ratio $\frac{m}{m+f}$ in a three region situation. (b) Schematic curves for relative fitness.

III Main Results

Based on the basic nesting assumptions in Preliminaries we introduce necessary variables and constants, and make observations to establish a mathematical model for Temperature-Dependent Sex Determination (TSD). Firstly, only a fraction of females can incubate their eggs in the wet marsh region (I). Let k_1 denote the carrying capacity of region I. This fraction, say F , must be a function of k_1 and the female population f_1 and it must satisfy certain criteria. If there are only a few females f_1, $F \approx 1$ since essentially all of them can nest in region I while for a very large number of females f_1, $F \approx 0$ since in this situation most of them have to move away from the wet marsh region I. As an approximation to this function, the fraction

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

satisfies the following,

$$F = \frac{k_1}{k_1 + f_1} \ \rightarrow \ 0 \ \ as \ \ f_1 \ \rightarrow \ \infty, \ \ F = \frac{k_1}{k_1 + f_1} \ \rightarrow \ 1 \ \ as \ \ f_1 \ \rightarrow \ 0$$

as required. It is, of course, just an approximation to the actual fraction

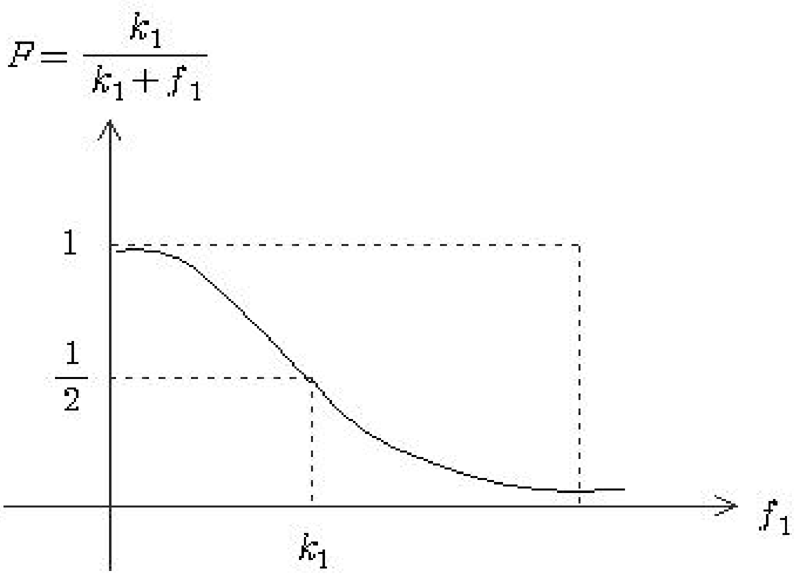

Figure 3: The graph of F as a function of f_1.

function. Strictly $F(f_1, k_1)$ is one until f_1 reaches the carrying capacity k_1 of region I after which the extra females have to move away from the wet marsh region. The fraction (1) is clearly not the best approximation we could choose (for example, if the total $f_1 = k_1$, the carrying capacity, $F = 0.5$ whereas it should still be one). We use this form, (1), for algebraic simplicity; it broadly has the required qualitative behavior. We use the same fraction approximation in the other regions and also in the age-dependent analysis below.

It b is the effective birth rate, that is, it includes clutch size, C, and the high mortality of hatchlings and egg predation, in other words survival, S, then, in a simple population model we have a dynamic equation for the population in region I (all female)

$$\frac{df_1}{dt} = b\left[\frac{k_1}{k_1 + f_1}\right] f_1 - d\, f_1 \tag{2}$$

Here we have taken the death rate as proportional to the population with d a parameter. If f_1 is large the maximum reproduction is then proportional to k_1 which accounts for its role as a measure of habitat capacity. The birth rate, b, is a function of the total male population, m, and is reasonably taken as

$$b = b(m) = \frac{b_0 m}{(c+m)} \quad \rightarrow \quad b_0, \quad \text{for small c}, \tag{3}$$

where c is a constant which, from field data, is indeed very small. With c small, equation (2) is uncoupled from the other equations in the model system below.

If we now consider region II where both females and males are produced, the fraction of females which have to move from the wet marsh region I to the dry marsh region II is simply

$$1 - \frac{k_1}{k_1 + f_1} = \frac{f_1}{k_1 + f_1}$$

So, the total number of females who want to nest in region II is the number who like this temperature plus those that had to move from region I:

$$\frac{f_1^2}{k_1 + f_1} + f_2$$

There is also a limited number of nest sites in region II and only a fraction of females can incubate in II, which is (cf. (1)) :

$$\frac{k_2}{k_2 + \frac{f_1^2}{k_1 + f_1} + f_2}$$

where, in the same way as we saw for (1), k_2 relates to the maximum number of hatchlings possible in the dry marsh region II. For algebraic simplicity we approximate this fraction by

$$\frac{k_2}{k_2 + f_1 + f_2}$$

which has roughly the same qualitative behavior. Compared with other assumptions and approximations this approximation is minor. It can, of course, easily be included in a numerical simulation of the equation: this was done and the resulting solutions were in general qualitative agreement. Thus the equations for the females and males in region II are:

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

The factor 1/2 is because half the hatchlings are male and half are female.

Finally in region III, the dry levees, the number of females forced to move from region II to III to nest is

$$\left[\frac{f_1^2}{k_1+f_1}+f_2\right]\left[\frac{\frac{f_1^2}{k_1+f_1}+f_2}{k_2+\frac{f_1^2}{k_1+f_1}+f_2}\right]$$

and the fraction able to incubate eggs in region III is

$$\frac{k_3}{k_3+\frac{f_1^2}{k_1+f_1}+f_2},$$

where k_3 is a direct measure of the carrying capacity of III. For the same algebraic reasons as above we approximate these expressions for the two fractions respectively by

$$\left[\frac{f_1^2}{k_1+f_1}+f_2\right]\left[\frac{f_1+f_2}{k_2+f_1+f_2}\right] \quad \text{and} \quad \frac{k_3}{k_3+f_1+f_2}.$$

The remaining females cannot nest in any suitable site. So, with these expressions the equation for males in region III (in our model there are only males here) is

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

The system of equations (2), (4) and (5) constitute the model for the populations in the various regions and from which we can obtain the sex ratio of the total population.

Theorem 1. *The steady state populations the system of equation* (2), (4) *and* (5) *are as follows.*

$$\begin{aligned} f_1^* &= (\frac{b_0}{d} - 1)k_1, & (6) \\ f_2^* &= m_2^* = \frac{1}{2}[-A + (A^2 + C)^{\frac{1}{2}}] & (7) \\ m_3^* &= \frac{2k_3 f_2^*(f_1^* + f_2^*)}{k_2(k_3 + f_1 * + f_2^*)} & (8) \\ A &= f_1^* - k_2(\frac{b_0}{2d} - 1), & (9) \\ C &= \frac{2k_2 f_1^{*2}}{k_1} & (10) \end{aligned}$$

Proof. The steady state populations are given by setting the right-hand sides of (2), (4) and (5) equal to zero and solving the algebraic equations.

From (2) with $\frac{df_1}{dt} = 0$ we have that $b[\frac{k_1}{k_1+f_1}] - df_1 = 0$, and thus

$$f_1 = \frac{bk_1}{d} - k_1 = (\frac{b}{d} - 1)k_1.$$

Since $b = b_0$, and we obtain $f_1^* = (\frac{b_0}{d} - 1)k_1$ as in equation (6).

In order to prove equation (7) we set $\frac{df_2}{dt} = \frac{dm_2}{dt} = 0$ in (4). Let us denote that $A = f_1^* - k_2(\frac{b}{2d} - 1)$, and $C = \frac{2k_2f_1^{*2}}{k_1}$ as in (9) and (10). Then we have

$$0 = \frac{b_0}{2}[\frac{f_1^2}{k_1+f_1} + f_2][\frac{k_2}{k_2+f_1+f_2}] - df_2$$

$$= \frac{b_0(f_1^2+k_1f_2+f_1f_2)k_2-2df_2(k_1k_2+k_1f_1+k_1f_2+k_2f_1+f_1^2+f_1f_2)}{2(k_1+f_1)(k_2+f_1+f_2)}$$

$$= -2d(k_1+f_1)f_2^2 + b_0k_1k_2 + b_0f_1k_2 - 2d(k_1k_2 + k_1f_1 + k_2f_1 + f_1^2)f_2 + b_0k_2f_1^2$$

$$= -2d(k_1+f_1)f_2^2 + (k_1+f_1)(b_0k_2 - 2d(k_2+f_1))f_2 + b_0k_2f_1^2$$

$$= (k_1+f_1)[-2df_2^2 + (b_0k_2 - 2d(k_2+f_1))f_2 + \frac{bdk_2f_1^2}{k_1+f_1}].$$

Now let us compute D, the determinant of the quadratic equation above for the variable f_2.

$$D = -\frac{1}{4a}\left[-b_0 + k_2 + 2d(k_2+f_1) \pm \sqrt{(b_0k_2 - 2d(k_2+f_1))^2 + \frac{8dbk_2f_1^2}{k_1+f_1}}\right]$$

$$= \frac{1}{2}[-(f_1 + k_2 - \frac{bk_2}{2d})] \mp \frac{1}{4d}\sqrt{(2Ad)^2 + \frac{8dbk_2f_1^2}{k_1+f_1}}$$

$$= \frac{1}{2}\left[-A \mp \frac{1}{d}\sqrt{d^2A^2 + \frac{2d^2k_2f_1^2}{k_1}}\right]$$

$= \frac{1}{2}[-A \mp \sqrt{A^2 + C}]$

Hence we have obtained $m_2^* > 0$ as in equation (7),

$$m_2^* = f_2^* = \frac{1}{2}[-A + (A^2 + C)^{\frac{1}{2}}].$$

In equation (5) let $\frac{dm_3}{dt} = 0$, and use the equation

$$(\tfrac{f_1^2}{k_1+f_1} + f_2)(\tfrac{1}{k_2+f_1+f_2}) = \tfrac{2dm_2}{b_0k_2}$$

to derive that

$0 = b_0[\frac{k_3}{k_3+f_1+f_2}][\frac{f_1^2}{k_1+f_1} + f_2][\frac{f_1+f_2}{k_2+f_1+f_2} - dm_3] \ = \ b_0[\frac{k_3}{k_3+f_1+f_2}]\frac{2dm_2}{b_0k_2}[f_1 + f_2] - dm_3,$

$0 = \frac{k_3}{k_3+f_1+f_2}\frac{2f_2}{k_2}[f_1 + f_2] - m_3$

Hence we obtain that $m_3^* = \frac{2k_3f_2^*(f_1^*+f_2*)}{k_2(k_3+f_1^*+f_2^*)}$ as in (8). $\square$

It is easy to see from linearizing the model equations that the steady states in Theorem 1 is always unstable. Since, from field studies, b_0/d, the effective births over the lifetime of an alligator or other crocodilia, is of the order of 100 to 300, we can approximate these steady states as in the following theorem.

Theorem 2. *The steady states in* Theorem 1 *is approximated as*

$$f_1^* \approx \frac{b_0k_1}{d}, \quad f_2^* = m_2^* \approx \frac{b_0}{d}F_2(k_1,k_2), \quad m_3^* \approx \frac{b_0}{d}F_3(k_1,k_2,k_3), \tag{11}$$

where $F_2(k_1,k_2) = \frac{k_2}{2}$ *and* $F_3(k_1,k_2,k_3) = \frac{b_0k_3(2k_1+k_2)}{2dk_3+2b_0k_1+b_0k_2}$.

Proof. Since we deal with the cases in which $\frac{b_0}{d} > 100$, from equation (6) in Theorem 1 we can approximate f_1, A, and C as the following.

$$\begin{aligned} f_1^* &= (\frac{b_0}{d}-1)k_1 \approx \frac{b_0k_1}{d}, \\ A &= f_1^* - k_2(\frac{b_0}{2d}-1) \approx \frac{b_0}{2d}(2k_1-k_2), \\ C &= \frac{2k_2f_1^{*2}}{k_1} \approx \frac{2b_0^2}{d^2}k_1k_2. \end{aligned}$$

Now we find approximations for $f_2^* = m_2^*$.

$$\begin{aligned} f_2^* = m_2^* &= \frac{1}{2}[-A+(A^2+C)^{\frac{1}{2}}] \\ &\approx \frac{1}{2}\left[-\frac{b_0}{2d}(2k_1-k_2)+\frac{b_0}{2d}\sqrt{(2k_1-k_2)^2+8k_1k_2}\right] \\ &= \frac{b_0}{4d}[-2k_1+k_2+2k_1+k_2] \\ &= \frac{b_0}{2d}k_2 \end{aligned}$$

Hence $F_2(k_1, k_2) = \frac{k_2}{2}$. Finally m_3^* is approximated as follows.

$$\begin{aligned} m_3^* &= \frac{2k_3 f_2^*(f_1^* + f_2^*)}{k_2(k_3 + f_1^* + f_2^*)} \\ &\approx \frac{2k_3(\frac{b_0}{2d}k_2)(\frac{b_0 k_1}{d} + \frac{b_0 k_2}{2d})}{k_2(k_3 + \frac{b_0 k_1}{d} + \frac{b_0 k_2}{2d})} \\ &= \frac{b_0^2 k_3(2k_1 + k_2)}{d(2dk_3 + 2b_0 k_1 + b_0 k_2)}. \end{aligned}$$

Therefore $F_3(k_1, k_2, k_3) = \frac{b_0 k_3(2k_1+k_2)}{2dk_3+2b_0k_1+b_0k_2}$. $\square$

we are particularly interested in the sex ratio, R. This is given by (11) for large b_0/d as

$$\begin{aligned} R &= \frac{m_2^*+m_3^*}{f_1^*+f_2^*+m_2^*+m_3^*} \\ &\approx \frac{F_2(k_1,k_2)+F_3(k_1,k_2,k_3)}{k_1+2F_2(k_1+k_2)+F_3(k_1,k_2,k_3)} = \phi(k_1, k_2, k_3). \end{aligned} \tag{12}$$

In this asymptotic case the sex ratio is independent of b_0/d, and so the parameters, k_i with $i = 1, 2$ and 3, that is, those parameters proportional to the carrying capacities in the various regions I-III, are the key parameters. The environment is clearly seen to have a crucial influence on the sex ratio. With the estimates for the percentage carrying capacity in the three regions given by Joanen ([12]), namely, 79.7 : 13.9 : 6.7, the sex ratio of males to the total population is given by equation (12) above as approximately 0.13 which means there are roughly 7 to 8 females to 1 male.

IV Applications

Although we do not do it here, it is possible to carry out a stability analysis of these steady state with the methods we described earlier in the book but it is algebraically complex. Interestingly, such an analysis shows that there can be no periodic solutions:the positive steady state is always stable. Using the equations we can also investigate the effect of some catastrophe which greatly reduced the populations and obtain estimates for the recovery time to their steady states: this has to be done numerically except for small perturbations about the steady state where linear theory could apply. 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.

It is intuitively clear how the crocodilia, 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; this allows the remaining males to have larger harems. The skewed sex ratio in the crocodilia 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 crocodilia.

Catastrophes, natural or otherwise, raise the question of extinction. If we consider extinction this would certainly happen if we have, from (2), $b < d$. With $b = b_0 m/(c + m)$ this implies that $m < cd/(b_0 - d) = 0(1/b_0)$ for c small and b_o 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 ism by completely destroying their habitat. With the increasing encroachment of their habitat by human population pressures it is certainly possible that alligators could could disappear at least from the southern U.S. Figure 4.3(b) shows the approximate area in U.S. where they are currently found.

The survival of alligators in the U.S. could depend in alligator farms which are already on the increase in these states. These, however, must be commercially viable and so the sale of alligator skin for shoes, belts, or whatever products appeal to consumers, is perhaps to be encouraged. Conservation takes on a different hue in these circumstances. Bustard [14] discusses one such conservation strategy for the captive breeding of the gharial *Gavialis gangeticus* in India. After an extensive survey of the situation in India he made a strong case for captive breeding programmes. He also discussed the crocodile situation in Australia. It is clear we have to redefine what we mean by 'conservation' and survival of a species if it means only managed survival. It is a subject which already gives rise to heated discussion—and not only between conservationists and evolutionary biologists.

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ABSTRACT

This dissertation use knowledge and analysis technique from a differential equation theory which was based on analytic. This constitute mathematical model from gained biological data on the spot survey. Through the medium of this investigate a intrinsic law of nature at real phenomenon.

The mathematical models explain sex distinction change on the crocodilian hatching temperature. Through specific model it have application to mathematic analysis results on the fact and analyze various condition.

Because crocodilian have the mechanism of temperature-dependent sex determination. At low temperature , 30℃ and below, they produces females; at high temperature 34℃ produces all males; Temperatures in between, that is, 32℃ produce both sexes.

It is divided temperature variations within the nest. The function is female and male individual density function. A differential equation model uses these functions.