The Impact of Temperature-Dependent Sex Determination on the Population Dynamics of Green Sea Turtles (*Chelonia mydas*)

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Abstract

The sex of the turtles is determined by the incubation temperature of the eggs during the mid-trimester of development. In Green sea turtles (*Chelonia mydas*), recent studies show that sex ratios are changing, producing a female-biased sex ratio within the population. We developed a novel continuous model to analyze the dynamics of the green sea turtle population long-term. We determine the safe operating space for the proportion of eggs that become male at which the population of Green sea turtle can exist without going to extinction. When the proportion of male eggs leaves this range the overall population of turtles collapses. Additionally, we examined how temperature changes affect the sex ratios of the Green sea turtle population.

Keywords: Green sea turtle, Sex ratio, Temperature-dependent sex determination, Population dynamics

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1. Introduction

In this paper, we examine the sex ratio of sea turtles in relation to population collapse. We are particularly concerned with the population of Green sea turtles (*Chelonia mydas*), in which temperature-dependent sex determination has been observed. Temperature-dependent sex determination (TSD) is a process where the temperature of an embryo's environment results in the production of sex hormones that dictate the embryo's sex development. This is an environmental sex determination system (ESD), meaning that the sex is determined depending on factors derived form physical and biotic environment like temperature. [1, 2]. Every reptile species that exhibits TSD has a thermosensitive period during which the embryo sex is developed. For turtles, this period has been observed to take place during the mid-trimester of the embryo incubation period [3].

Within the realm of TSD, there are three different possible patterns that a species uses for sex determination: FM-pattern, MF-pattern, and FMF-pattern. In the FM-pattern, female eggs are developed in low hatching temperatures while male eggs occur in high hatching temperatures; the MF-pattern is the inverse of the FM-pattern. The FMF-pattern dictates that female eggs develop in high and low temperatures while a medium range of temperature results in male eggs. Turtle embryos follow the MF-pattern, so at lower temperatures, the result is a mostly male hatchling population and at higher temperatures, a mostly female hatchling population exists [4]. The temperature at which the sex differentiates is around 29.4°C [2, 5]. When the mean temperature of the nest during the thermosensitive period is at 29.4 °C, known as pivotal temperature, then we see an even distribution of male and female hatchlings occur. Whereas, when the mean temperature is above the pivotal temperature, then hatchling sex population will be mostly female, and below it, will result in a mostly male population [5, 6, 2]. In recent years a disproportionate ratio of female to male turtle eggs has been observed in a number of different studies and has also been predicted to possibly lead to the extinction of sea turtles in the future [7, 5, 8].

Since female sea turtles lay their eggs in chambers that they dig into the sand of their nesting beaches, it is reasonable to look into the factors that could be directly affecting these sand temperatures to understand why there is an imbalance in the ratio of female to male turtles. To determine these factors, researchers have proposed multiple hypotheses. One such hypothesis credits climate change with potentially leading to rising sand temperatures. This comes from the fact that global air temperatures are projected to increase and there is a strong relationship between air temperatures and sand temperatures [9, 10, 11]. Another possible explanation for potential increases in temperature is an accumulation of microplastic on and within the beach sediment [12].

This problem naturally lends itself to investigation via a sex-structured population model. An overview of the history of sex-structured models was described by Iannelli et al. [13]. The discussion of sex-structured models first arose after it was realized that the one-sex stable population theory was insufficient in answering questions in relation to existence and interrelations of the sexes. It was found that trying to apply a one-sex model to both sexes at the same time resulted in contradictory results. This inconsistency was first noted by Kuczynski [14]. These inconsistencies between male and female reproduction rates were further noted and explored by Karmel [15], making him the first to note many of the ideas of two-sex population modeling. Whilst Karmel [15] introduced many of the two-sex population ideas, the first significant dynamic model was brought by Kendall [16]. The work done by Kendall [16] on two-sex populations more accurately accounted for the dynamics of observed systems leading to further research based off his work [13]. Although Kendall's work has inspired a number of further studies into sex-structured models, the majority of published population models are unstructured with respect to sex [17]. Some of the papers that use sex-structured models are Lee et al. [18] and Mignatti et al. [19]. In both papers, the sex-structure modeling framework was utilized because it was noticed that the sexual dimorphism was critical in understanding the dynamics of the population as a whole.

In this paper we developed a system of ordinary differential equations (ODE's) model for general Green sea turtles focusing on the impacts of the TSD on the overall population dynamics in order to determine a male to female sex ratio that leads to extinction.

2. Methods

2.1. Model Development

The life cycle of green sea turtles starts on land when they emerge from their nests as hatchlings and immediately travel to the sea. Upon entering the ocean the hatchlings are relatively unseen until they reappear as juveniles in the open sea [20]. This period of time between the hatchling and juvenile stage is composed of several years, and is the life-stage that remains relatively unknown [20]. Thus, scientists have coined the term ‘lost years’ to describe this stage of life [21, 20]. Since these two first stages of the life cycle of the turtles do not carry relevant information for the development of the model, a simplified life cycle can be seen in Figure (1), which shows the ‘egg’ stage as each individual that has not yet reached sexual maturity and the adult stage as only the sexually mature adults.

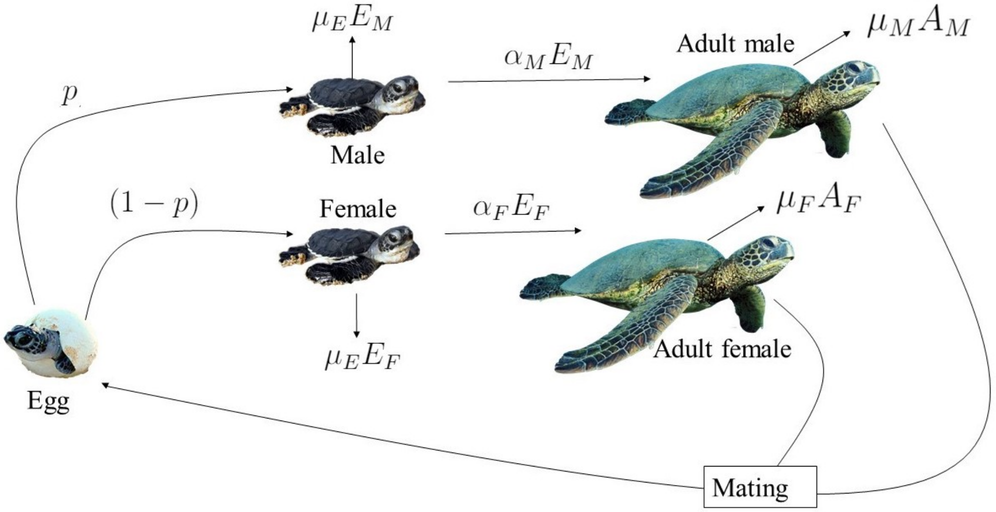


Figure 1: Schematic diagram of the mathematical model.

For green sea turtles the mean age of sexual maturity is estimated to be within the range of 40-60 years [22, 23, 24]. When sea turtles reach sexual maturity, females and males return to their natal beaches to mate and nest. Male sea turtles usually breed every year or every two years, whereas female sea turtles generally breed every 2 to 5 years [25, 26]. During mating season sea turtles have multiple mates and lay several clutches of eggs at approximately 2 week intervals [27]. This scheme of the life cycle focuses mainly on the relationship between adults during the mating period. This interaction eventually will result in the production of eggs that can later develop into either female or male mature sea turtles. Also, it shows how the death of the adults and the movement out of the reproductive stage decreases the population of adult sea turtles, while the death of eggs and juveniles reduces the population of the ‘eggs’ class. On the other hand, successful mating of adults will increase the number of eggs deposited every season. Each clutch can be divided into female and male eggs depending on the incubation temperatures [7]. If eggs reach maturity, this will increase the number of adults in the population.

In order to describe the long-term behavior of the green sea turtle population, we study the dynamics of the population with a continuous model. The main objective is to figure out the sex ratio that would ultimately lead the overall population of green sea turtles to extinction. We chose the continuous model to be able to witness the change within the turtle's entire life cycle (60-70 years) [24] and for the whole population over time. Modeling the distinctive aspects of the reproductive biology and nesting behavior of green sea turtles poses a great challenge. The mating process is a complex interaction between male and female sea turtles that involves a variety of factors that could strongly affect the birth rate of the population. To clearly understand the principles involved in this interaction we consider the mating process as a functional response, similar to continuous-time predator-prey models [28].

Such as in predator-prey models, we can conveniently classify most of our variables involved in the mating process: (1) density of female population, (2) density of male population, (3) behavioral response of females during mating process, (4) characteristics of the males, e.g., searching efficiency [29]. To represent the successful number of mating interactions between males and females per unit time, that will eventually result in the production of eggs, we used the Holling type II functional response [29, 30]. In predator-prey models, researchers suggest that ratio-dependence is suitable when the predator must seek its prey and consequently compete for food [31]. In modeling the process of mating interactions between green sea turtles, we have to consider that male sea turtles have to search for females, and that male turtles will compete with one another to mate with a female [32]. Moreover, we have to consider some aspects, such as coupling time, associated with each female being found by a male and the fact that not every male will interact with every female, thus, it made more sense to use a ratio-dependent system to produce more accurate results [31].

In our model, we focus on the proportion of eggs allocated to males and females in the population, which is influenced by the temperature they are exposed to during the incubation period. Since the juvenile stage does not provide relevant information to the main objective of this investigation, the population is divided into two groups: eggs and adults, where 'eggs' refers to the pre-reproductive life stages of the turtles. We denote the egg population and adult population for males and females as $A_M(t)$, $A_F(t)$, $E_M(t)$, and $E_F(t)$ at time t.

2.2. Model Description

The first two differential equations (1a) and (1b) in our system show the total number of eggs that will reach adulthood after passing the hatchling and juvenile stage, which is denoted by $\alpha_M E_M$ for males and $\alpha_M E_F$ for females. They also show the total number of adults that leave the sexual reproductive stage, which includes those who are dying and those who are reaching the post-reproductive stage, denoted by $\mu_M A_M$ for males and $\mu_F A_F$ for females. The last two differential equations (1c) and (1d) show the flow of turtles leaving the 'egg' stage and entering to the sexual maturity stage. The total number of male eggs in (1c) and female eggs in (1d) produced per successful interaction per unit of time is represented as the product of the successful number of interactions between males and females per unit of time $\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M}+a}\right) A_M$, the maximum average number of eggs found in a clutch (r), the proportion of male (p) or female ($1-p$) eggs and the saturation constraint $\left(1-\frac{A_M+A_F}{K}\right)$. The expression, $\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M}+a}\right) A_M$, is derived from the product of a ratio-dependence Holling type II functional response and the adult male population. The saturation constraint shows that when the adult population approaches the carrying capacity K, then the egg per-capita approaches zero.

The parameters α_M and α_F are maturity rates that ultimately show us the number of male and female hatchlings that survive onto the reproductive stage, while μ_M and μ_F tell us the leaving rates for reproductive males and females. These leaving rates for adult female and male turtles in our model symbolize either one of two things, the death rate of the sexually mature turtles, or the rate at which they move onto the post-reproductive stage. The parameter μ_E defines the death rate of the pre-reproductive sea turtles (hatchlings and juveniles). The combined duration of courtship and copulation is considered to be handling time (t_h), and the rate at which a male finds a female is considered the searching efficiency (c). We denote the copulation rate as $b = \frac{1}{t_h}$ and the half saturation constant as $a = \frac{1}{ct_h}$. The carrying capacity, K, tells us the maximum population size of green sea turtles that the environment can sustain indefinitely. The description and units for our parameters are described in Table (1)

$$\frac{dA_M}{dt} = \underbrace{\alpha_M E_M}_{\text{Maturity}} - \underbrace{\mu_M A_M}_{\substack{\text{Leaving}\\ \text{population}}}, \tag{1a}$$

$$\frac{dA_F}{dt} = \alpha_F E_F - \mu_F A_F, \tag{1b}$$

$$\frac{dE_M}{dt} = -\alpha_M E_M + \overbrace{p}^{\substack{\text{Male}\\ \text{proportion}}} \overbrace{r\left(1-\frac{A_M+A_F}{K}\right)}^{\text{Number of eggs}} \overbrace{\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M}+a}\right)}^{\text{Copulation rate}} A_M - \mu_E E_M, \tag{1c}$$

$$\frac{dE_F}{dt} = -\alpha_F E_F + \overbrace{(1-p)}^{\substack{\text{Female}\\ \text{proportion}}} \underbrace{r}_{\substack{\text{Avg.}\\ \text{eggs}}} \underbrace{\left(1-\frac{A_M+A_F}{K}\right)}_{\text{Saturation constraint}} \underbrace{\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M}+a}\right) A_M}_{\text{Interactions}} - \underbrace{\mu_E E_F}_{\mathit{Mortality.}} \tag{1d}$$

The initial values, A_M^0, A_F^0, E_M^0 and E_F^0 are all $\in [0, K]$, and all the parameters are $\in \mathbb{R}^+$.

3. Analysis

3.1. Equilibrium

By continuously extending the vector field of system (1) to the origin, then the point $(0, 0, 0, 0)$ is a biologically meaningful equilibrium, which contributes to explain the dynamics of the model. Since the vector field is not differentiable at the origin, one cannot determine its stability with a linearization approach. However we used a different approach to show

Parameter	Description	Estimates	Citations
α_M	Maturity rate of eggs that become adult males	0.022 $\pm$0.004 yr^{-1}	[33] [22]
α_F	Maturity rate of eggs that become adult females	0.029 $\pm$0.05 yr^{-1}	[33][34]
μ_M	Leaving rate for adult males	0.05 $\pm$0.09 yr^{-1}	[24]
μ_F	Leaving rate for adult females	0.04 $\pm$0.07 yr^{-1}	[24]
μ_E	Death rate for eggs	0.36 $\pm$0.33 yr^{-1}	[35][33][36]
p	Proportion of eggs that become male	N/A	
r	Average number of eggs per successful interaction	117 $\pm$38	[37][38]
b	Interaction rate	180 $\pm$20 yr^{-1}	[39]
a	Half saturation constant	N/A	
K	Carrying capacity of adults	N/A	

Table 1: Parameters description and values.

that $(0,0,0,0)$ is globally attractive when $rb < \mu = \min\{\mu_M, \mu_F, \mu_E\}$ (see subsection 3.3).

The system (1) also has a unique positive equilibrium,

$$I^* = \left(A_M^*, \frac{H}{G} A_M^*, \frac{\mu_M}{\alpha_M} A_M^*, \frac{H \mu_F}{G \alpha_F} A_M^* \right),$$

with

$$A_M^* = \frac{(K - Q)\, G}{H + G}.$$

For simplification we let $H = \frac{(1-p)(\mu_E + \alpha_M)\mu_M}{\alpha_M p}$, $G = \frac{(\alpha_F + \mu_E)\mu_F}{\alpha_F}$, and $Q = \frac{(\mu_E + \alpha_M)\mu_M (H + a) K}{\alpha_M p b H r}$.

Specific existence conditions and proof of existence conditions for both equilibrium points will be discussed in the next subsection.

3.2. Existence

The positive equilibrium I^* biologically exists if $K > Q$ which is equivalent to the demographic basic reproductive number (R_0^d) is greater than one.

$$R_0^d = \frac{rbp \left(\frac{\alpha_M}{\alpha_M + \mu_E} \right) (\frac{1}{\mu_M})(1-p) \left(\frac{\alpha_F}{\alpha_F + \mu_E} \right) \left(\frac{1}{\mu_F} \right)}{ap \left(\frac{\alpha_M}{\alpha_M + \mu_E} \right) \left(\frac{1}{\mu_M} \right) + (1-p) \left(\frac{\alpha_F}{\alpha_F + \mu_E} \right) (\frac{1}{\mu_F})} > 1$$

The same condition can be analyzed in terms of p, given as a result,

$$p^2 + (D - J - 1)\, p + J < 0,$$

where $J = \frac{(\mu_E+\alpha_M)\mu_M}{\alpha_M br}$ and $D = \frac{a\mu_F(\alpha_F+\mu_E)}{\alpha_F br}$. Taking the inverse of J and D we can actually analyze the biological meaning of those expressions.

$$
\begin{aligned}
J^{-1} &= \underbrace{b}_{\text{Copulation}} \underbrace{r}_{\substack{\text{max avg} \\ \text{eggs}}} \underbrace{\left(\frac{1}{\mu_M}\right)}_{\substack{\text{Lifespan} \\ \text{of males}}} \underbrace{\left(\frac{\alpha_M}{\alpha_M+\mu_E}\right)}_{\substack{\text{Prop. of male eggs} \\ \text{that reach adulthood}}} && (2) \\
D^{-1} &= \underbrace{\frac{b}{a}}_{\substack{\text{Searching} \\ \text{efficiency}}} \underbrace{r}_{\substack{\text{max avg} \\ \text{eggs}}} \underbrace{\left(\frac{1}{\mu_F}\right)}_{\substack{\text{Lifespan} \\ \text{of males}}} \underbrace{\left(\frac{\alpha_F}{\alpha_F+\mu_E}\right)}_{\substack{\text{Prop. of female eggs} \\ \text{that reach adulthood}}} && (3)
\end{aligned}
$$

In (2), the parameter r is the average number of eggs, while the product of our interaction rate (b) and the average reproductive lifespan of males gives us the maximum number of copulations in a males lifetime. When we multiply this by the proportion of male eggs that survive until adulthood, we get J^{-1}, which gives the ratio of male death rate to maximum theoretical egg production. In (3), we have the the product of the maximum number of eggs, searching efficiency, the average reproductive life-span of female turtles, and the number of female eggs that reach adulthood. Thus, D^{-1} is the ratio of female death rate to maximum theoretical egg production.
Solving quadratic expression $p^2 + (D - J - 1)p + J = 0$, we get

$$p_1 = \frac{J - D + 1 - \sqrt{\Delta}}{2}, \qquad p_2 = \frac{J - D + 1 + \sqrt{\Delta}}{2}.$$

with $\Delta = (D - J - 1)^2 - 4J$. The existence condition for the positive equilibrium point I^* is

$$\Delta > 0, \quad \text{and} \quad p_1 < p < p_2. \tag{4}$$

When this condition is met, all dependent variables are positive and the equilibrium point exists. However, when that existence condition is not met, all dependent variables must be less than or equal to zero. We have already established that all of the dependent variables are non-negative, suggesting that they must be zero. Therefore, the existence condition for the point $(0, 0, 0, 0)$ can be derived by negating the existence condition for the positive equilibrium point I^*. When the condition for $(0, 0, 0, 0)$ is met, the population decays to zero toward extinction.

3.3. Global stability condition for extinction

Assume $N = A_M + A_F + E_M + E_F$. Based on our assumptions, we know that the total amount of adult females and males turtles is less than the environmental capacity of turtles, that is $A_M + A_F < K$. Letting $\mu = \min\{\mu_M, \mu_F, \mu_E\}$, then we obtain

$$\begin{aligned}
\frac{dN}{dt} &= r\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right)A_M - \mu_M A_M - \mu_F A_F - \mu_E E_M - \mu_E E_F \\
&\leq rbA_M - \mu_M A_M - \mu_F A_F - \mu_E E_M - \mu_E E_F \\
&\leq rbA_M - \mu\left(A_M + A_F + E_M + E_F\right) \\
&= rbA_M - \mu N \\
&\leq rbN - \mu N \\
&= \left(rb - \mu\right)N
\end{aligned} \tag{5}$$

Solving this differential inequality, we arrive at

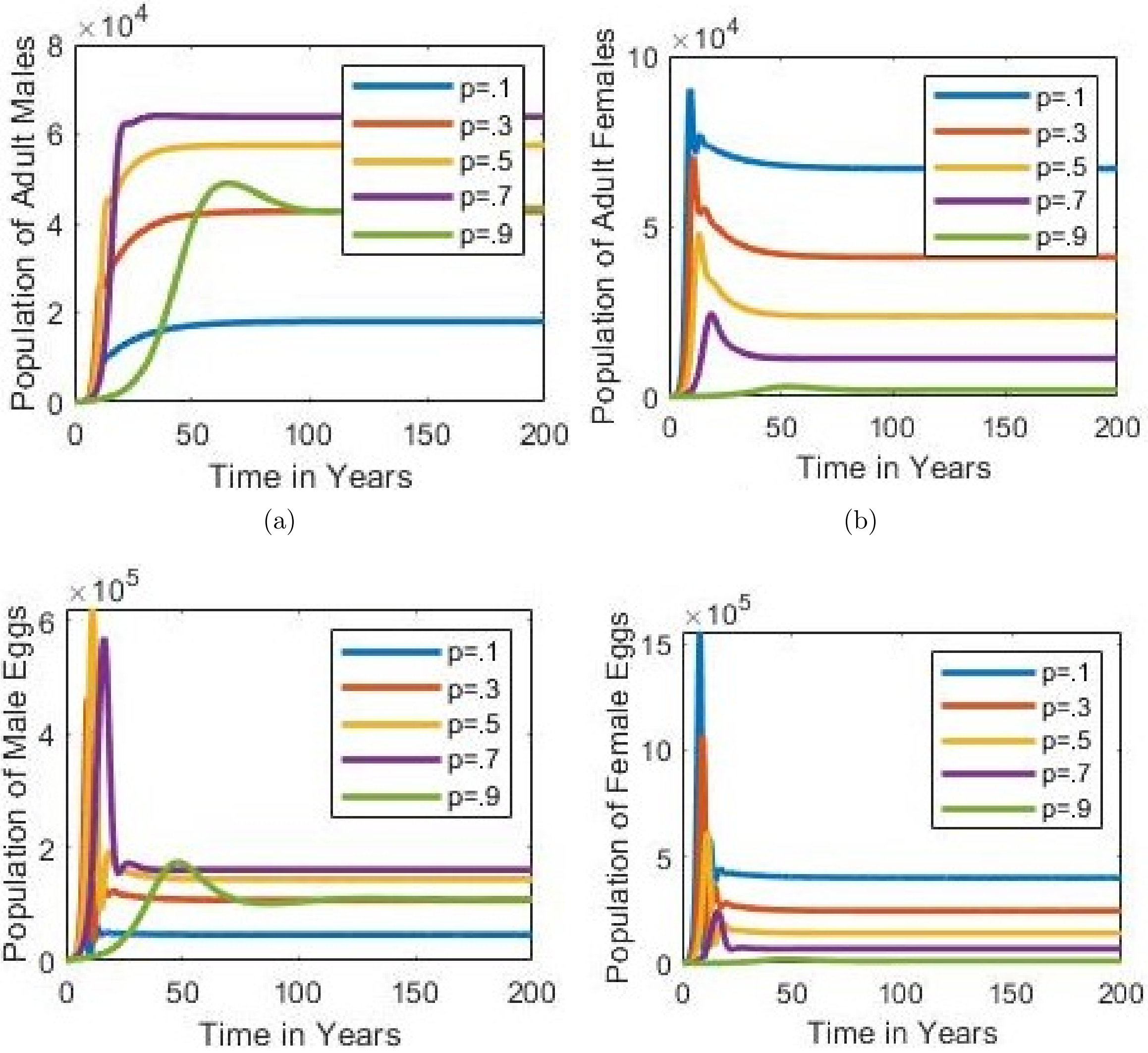
$$N(t) \leq N_0 e^{(rb-\mu)t}. \tag{6}$$

If $rb-\mu < 0$, then $N(t)$ approaches 0 as t approaches ∞. This shows that when the condition $rb-\mu < 0$ is met, the zero equilibrium point is globally asymptotically attractive. Therefore, the turtle population goes to extinction.

In the global stability condition of $(0, 0, 0, 0)$, r is the average number of eggs per successful interaction, b is the interaction rate, and μ is the minimum mortality between egg mortality μ_E, adult male mortality μ_M, and adult female mortality μ_F. Therefore, rb is the birth rate of eggs. So $rb - \mu < 0$ means the birth rate is less then the minimum mortality, which leads to extinction of the turtle population.

4. Results

The following simulations were developed by using parameter estimations as seen in Table (1). All parameter values in Table (1) are kept constant except for values of p.



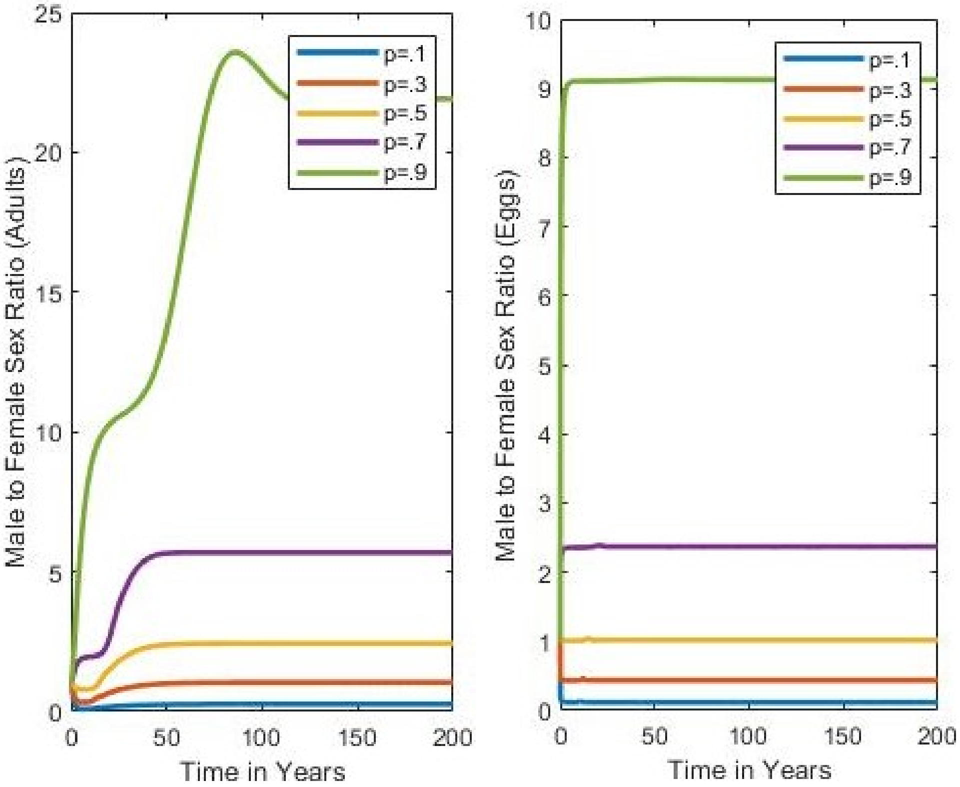
(a)

(b)

(c)

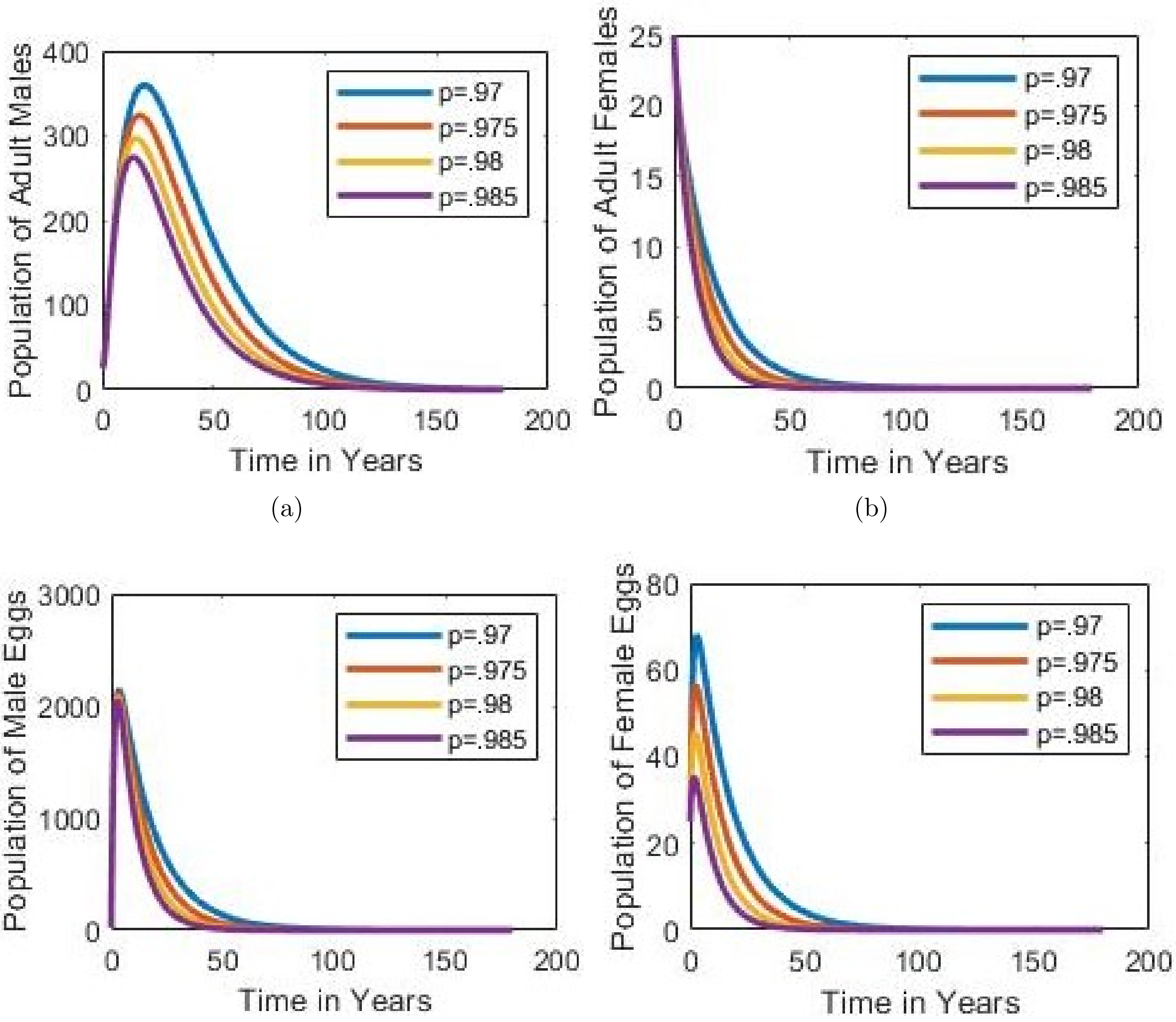
(d)

Figure 2: These plots show the population of individuals in the adult and egg stages over time. Variations in population are due to changes in the proportion of male eggs (p). When the equilibrium point (I^*) is locally asymptotically stable, for any deviation of p, the population numbers change until they reach a steady state. Because we are examining values of p that are within our existence condition for the proportion of males, our population remains viable.



(a) (b)

Figure 3: These plots show the sex ratios of individuals in adult (3(a)) and egg (3(b)) stages over time for when the interior equilibrium exists. Variation in sex ratios are due to changes in the proportion of male eggs (p).



(a) (b)

(c) (d)

Figure 4: In this case, we plot the population of individuals over time for variations of p outside of the existence condition for p. When the existence condition is not satisfied, the interior equilibrium (I^*) does not exist and system (1) only has an equilibrium point at (0,0,0,0). For values outside of the existence condition, the adult and egg populations approach zero towards extinction.

For system (1), the parameter p was defined as the proportion of eggs that become male as determined by incubation temperature (T). To examine p as a function of incubation temperature $p(T)$, we use the following function derived in a previously published paper by Girondot [40]:

$$p(T) = \frac{1}{1 + e^{-\frac{1}{S}(\beta - T)}} \tag{7}$$

In this particular equation the pivotal temperature is represented by β and is in the range of 29.34 ± 0.17. The shape of transition from masculinizing to feminizing is given by S and is in the range of 1.01 ± 0.24. The estimates and their standard deviations were found in the same paper from which the expression was taken [40].

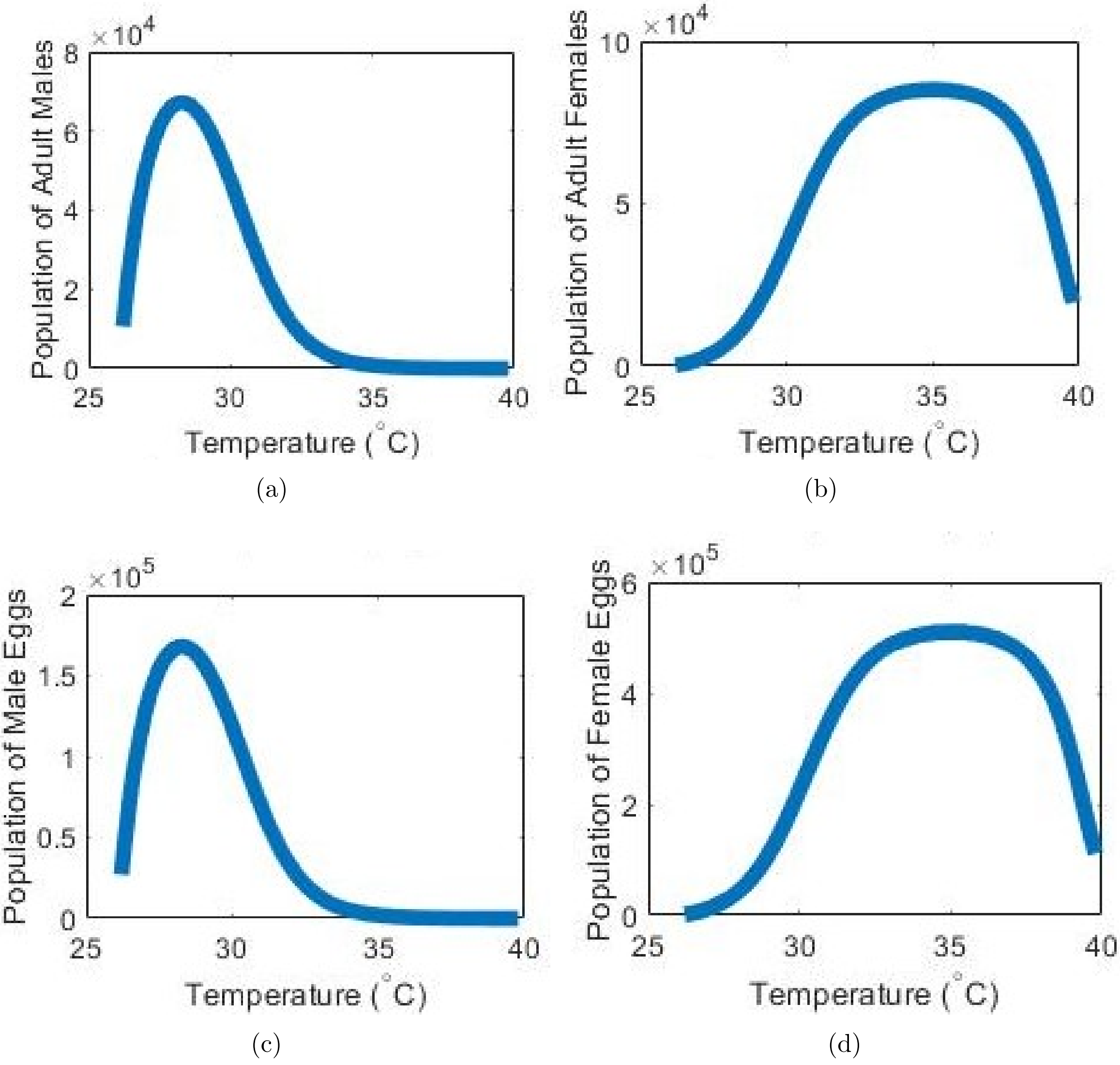


Figure 5: These plots show the population of adults and eggs as daily mean temperature increases. The changes in the population are due to variations in the proportion on male eggs caused by temperature $p(T)$.

We only analyzed our system for values of p that satisfy the equilibrium existence condition. In other words, since p is a function of T, we analyzed our system for temperatures that allowed $p(T)$ to still be within the equilibrium condition (8). Since our system is now analyzed with the new $p(T)$ function, the graphs in Figure (5) reflect how temperature changes lead to different proportions of males and how those proportions lead to different population numbers for the different stages.

$$ln\left(\frac{1}{p_2}-1\right)S+\beta<T<ln\left(\frac{1}{p_1}-1\right)S+\beta \tag{8}$$

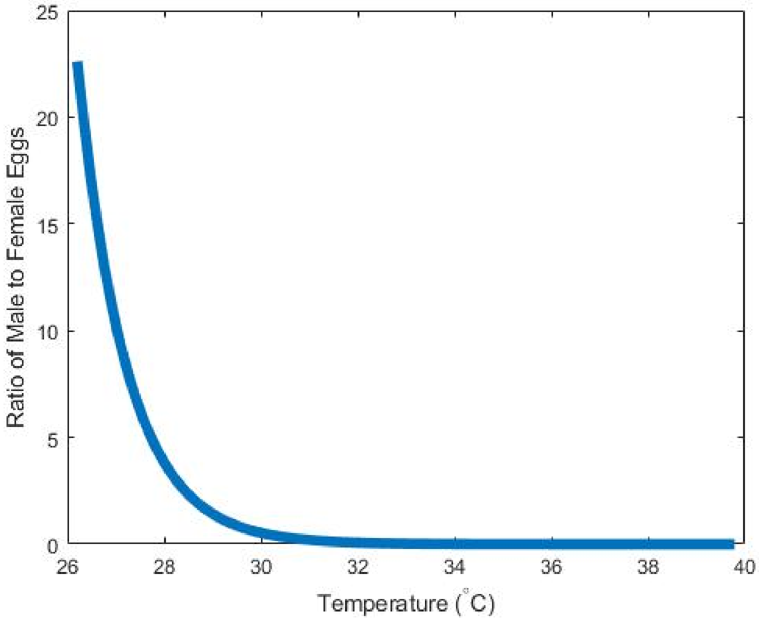


Figure 6: We take the ratio of (5(c)) and (5(d)) to obtain the changes in the male to female sex ratio of eggs as daily mean temperature increases. The graph reflects that as temperatures increase, the sex ratio decreases because the proportion of male eggs becomes smaller than the proportion of female eggs.

5. Discussion

According to the International Union for Conservation of Nature (UICN) Red List Threatened Species [41], Green sea turtle is considered as an endangered species and its population is continuously decreasing. This population decline is due to many factors like illegal trade of eggs, turtle-shell trade, plastic and other marine debris, ocean pollution, and global warming [42, 43, 44, 45]. Most studies focus on how these factors harm the adult population and have determined that we should maintain current efforts to reduce mortality of long juvenile and adult stages to keep a sustainable population [46]. Our concern, in contrast, focuses in some aspects at the earliest stages of the life cycle that can harm the adult population long-term. Due to this, we studied how the temperature at the mid-trimester of the incubation period impacts the sex ratios of the population. Fluctuations in the incubation temperature can cause a female or male biased sex ratios in the population. With this model we analyzed how the sex ratio is decisive for the population growth and how this is affected by the temperature. We determined a safe operating space at which temperature can alter the sex ratios without taking the population to collapse. It has been shown that different populations of sea turtles have female-biased offspring production due to temperature increases during the incubation period [47, 48]. Regardless of that, our results show that the proportion of female eggs can go to extreme values without having a severe impact on the turtle population. However, our numerical results depend completely on the values that our parameters take, since many of these are not found in the literature most of them had to be estimated affecting the accuracy of the results. In order to avoid this, more field work is necessary to strengthen the parameter estimations.

A system of ordinary differential equations was used to represent the life cycle of the turtle population. The emphasis of our study is the mechanics of sex structure on population stability. A closed form analytic condition for temperature to ensure species persistence was found. The previous literature relating to this subject has been relatively sparse, but our results seem to be in general accordance with prior publications [49]. At the moment, the paucity of studies on the subject has left us without any current contrary findings.

Since we simplified our model to denote all pre-reproductive stages as the egg stage and the reproductive stage as the adult stage, we think that this might propose limitations on the details of each sub-stage in the life cycle, as well as including the post reproductive stage. A dearth of information has been reported with regards to the searching efficiency and coupling time of Green sea turtles. We believe that having inaccurate parameter estimations and a simplified model probably caused our condition on p and our condition on T to be so large, thus giving us a large range where highly skewed proportions are viable. We also based our model in a very general sense, rather than focusing on a specific area such as a beach or ocean. Male sea turtles often never come back to land after they are born and females only come to lay their eggs, so much is unknown about Green sea turtles, thus proposing further limitations for us to study population dynamics, this proposes uncertainties in our mathematical model. The well mixed, homogeneous assumption has far more severe limitations based on our understanding of sea turtle biology than in other cases. Green sea turtles both male and female return, mate, and lay there eggs at their natal beaches. A discrete time model of a single beach or a discrete time model that takes into spatial dynamics would be far more appropriate. The limitations of our continuous time approach cannot be stated until these other methods are explored.

Our model can be used as a basis for a more complex model involving details about each stage in the life cycle of males and females and determine which stage is the most critical for the survival of the population. It can also be used in future research to include the thermodynamics of microplastic in the sediment and see how it is directly affecting the sea turtle population sex-ratio. We believe that one can incorporate climate change into the model, to show that many species and ecosystems are being affected by it. We also think it'd be nice to create a proportion of male eggs as a time-dependent function of temperature $p(T(t))$ to replace $p(T)$. First the random variation from mean daily temperatures in June and July would be the most appropriate complication added to the model. Secondly, it would be essential to include a general trend of climate change into the stochastic yearly variation as this is a clear observable trend. If we could find better information about the impact of microplastic proliferation on beaches on soil thermodynamics, then we could begin to include some sort of heuristic to capture this effect. Lastly, a much more complicated model might be interested in studying how cyclical climate variations like El Niño on the long term stability of turtle populations. It will be essential in the future to have broad trans-disciplinary collaborations to properly account for the edaphoclimatic factors that impact the turtles TSD. Lastly, it will be essential in further models to include egg death induced by extreme temperatures[49].

We found that there is a limited safe operating space of temperature for Green sea turtle sustainability as seen from Equation (8). If this condition is not met, then the total population approaches extinction. However, it is important to note that this threshold is very large, so the probability that the temperature would be outside of this range is unlikely. Based on our simulations in Figure (5), we found that the proportion of eggs that become male can decrease dramatically without severe impact on turtle populations. When the proportion of males p approaches zero, the population of females can still survive in high numbers. Highly skewed sex ratios do not necessarily mean that the population is no longer viable because males will breed with many females, suggesting that just few males are sufficient to father multiple clutches [50]. Moreover, male sea turtles breed twice as frequently as female sea turtles, meaning females can continue to find mates even when males are low in numbers [49]. However, when the male proportion actually reaches zero, then the whole population of Green sea turtles will go extinct. Our research indicates that it is necessary to urge policy makers and environmental managers about the importance of monitoring beach temperatures in order to ensure the continued existence of Green sea turtles. If temperatures get too high and exceed our threshold, then the population will go extinct, thus hurting the two ecosystems that they are a part of.

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7. Appendix

7.1. Computation of the equilibrium point

In order to calculate the equilibrium point of the system (1), all of the equations must first be set equal to zero, and then solved.

$$\alpha_M E_M - \mu_M A_M = 0, \tag{9a}$$

$$\alpha_F E_F - \mu_F A_F = 0, \tag{9b}$$

$$-\alpha_M E_M + pr\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M - \mu_E E_M = 0, \tag{9c}$$

$$-\alpha_F E_F + (1-p)\, r\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M - \mu_E E_F = 0. \tag{9d}$$

7.1.1. Non-zero equilibrium point

First we add the four equations together to get

$$r\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M = \mu_M A_M + \mu_F A_F + \mu_E E_M + \mu_E E_F. \tag{10}$$

From (9a) and (9b), we know

$$E_M = \frac{\mu_M}{\alpha_M} A_M, \quad E_F = \frac{\mu_F}{\alpha_F} A_F. \tag{11}$$

Substituting (11) into (10), we obtain

$$r\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M = \frac{\alpha_M \mu_M + \mu_M \mu_E}{\alpha_M} A_M + \frac{\alpha_F \mu_F + \mu_F \mu_E}{\alpha_F} A_F. \tag{12}$$

Equation (9c) can be rewritten as

$$r\left(1 - \frac{A_M + A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M} + a}\right) A_M = \frac{(\alpha_M + \mu_E)}{p} E_M, \tag{13}$$

and substituting (11) into (13) we get

$$r\left(1-\frac{A_M+A_F}{K}\right)\left(\frac{b\frac{A_F}{A_M}}{\frac{A_F}{A_M}+a}\right)A_M=\frac{(\mu_E+\alpha_M)\,\mu_M}{\alpha_M p}A_M. \tag{14}$$

Using equations (10) and (14) we obtain

$$\frac{\alpha_M\mu_M+\mu_M\mu_E}{\alpha_M}A_M+\frac{\alpha_F\mu_F+\mu_F\mu_E}{\alpha_F}A_F=\frac{(\mu_E+\alpha_M)\,\mu_M}{\alpha_M p}A_M. \tag{15}$$

Rewriting (15), we obtain the relationship between A_M and A_F.

$$HA_M=GA_F$$

That is $\frac{A_F}{A_M}=\frac{H}{G}$ and $A_M+A_F=(1+\frac{H}{G})A_M$, where $H=\frac{(p-1)(\mu_E+\alpha_M)\mu_M}{\alpha_M p}$ and $G=-\frac{\alpha_F\mu_F+\mu_F\mu_E}{\alpha_F}$. substituting into (15), we obtain

$$\frac{r}{K}\left(K-\left(1+\frac{H}{G}\right)A_M\right)\left(\frac{bH}{H+aG}\right)A_M=\frac{(\mu_E+\alpha_M)\,\mu_M}{\alpha_M p}A_M$$

$$A_M^*=\frac{(K-Q)\,G}{H+G}$$

Solving non-zero solution of above equation gives us, Where $Q=\frac{(\mu_E+\alpha_M)\mu_M(H+aG)K}{\alpha_M pbHr}$. From the relationship between A_M, A_F, E_M and E_F the non-zero equilibrium point is

$$I^*=\left(A_M^*,\frac{H}{G}A_M^*,\frac{\mu_M}{\alpha_M}A_M^*,\frac{H\mu_F}{G\alpha_F}A_M^*\right).$$

7.2. Existence condition

The existence condition for I^* existence condition is

$$A_M^*=\frac{(K-Q)\,G}{H+G}>0 \tag{16}$$

where $H=\frac{(1-p)(\mu_E+\alpha_M)\mu_M}{\alpha_M p}$, $G=-\frac{\alpha_F\mu_F+\mu_F\mu_E}{\alpha_F}$, $Q=\frac{(\mu_E+\alpha_M)\mu_M(H+aG)K}{\alpha_M pbHr}$ and H, G, $Q>0$. Then $A_M^*>0$ if and only if $K>Q$, which is equivalent to

$$p>\frac{(\mu_E+\alpha_M)\,\mu_M\,(H+aG)}{\alpha_M bHr} \tag{17}$$

By inserting this simplification into our expression , we can rewrite (17) and define new expressions.

Refine, $J^* = \frac{(\mu_E+\alpha_M)\mu_M}{\alpha_M br}$ and $S^* = \frac{a\mu_F(\alpha_F+\mu_E)}{\alpha_F br}$,then (17)is rewritten as

$$p > J^* + S^* \frac{p}{1-p}. \tag{18}$$

The inequality is solved in terms of p producing the next quadratic expression

$$p^2 + (S^* - J^* - 1)\,p + J^* < 0, \tag{19}$$

where p_1 and p_2 are the solutions of $p^2 + (S^* - J^* - 1)p + J^* = 0$,namely

$$p_1 = \frac{J^* - S^* + 1 - \sqrt{\Delta}}{2}, \quad p_2 = \frac{J^* - S^* + 1 + \sqrt{\Delta}}{2}.$$

Finally, the existence condition is

$$\Delta = (S^* - J^* - 1)^2 - 4J^* > 0 \quad \text{and} \quad p_1 < p < p_2. \tag{20}$$

To check the existence condition we found the condition when solving the equilibrium in terms of E_M. To do this we analyzed the E_M found for the equilibrium. Since E_M is an actual population it cannot be less than 0. So, we can set $E_M > 0$. Since r and b always come together, we write $r' = rb$.

$$K \frac{1}{\frac{\alpha_M}{\mu_M} + \frac{\alpha_F}{\mu_F}L} \left(1 - \frac{\mu_E + \alpha_M}{p} \left(\frac{1}{\frac{\alpha_M}{\mu_M}} + \frac{a}{\frac{\alpha_F}{\mu_F}L}\right) \frac{1}{r'}\right) > 0 \tag{21}$$

If we divide both sides by the first product then the result is

$$\left(1 - \frac{\mu_E + \alpha_M}{p} \left(\frac{1}{\frac{\alpha_M}{\mu_M}} + \frac{a}{\frac{\alpha_F}{\mu_F}L}\right) \frac{1}{r'}\right) > 0 \tag{22}$$

From here we can solve the inequality in terms of p to see if the existence condition found here is equivalent to that previously found with the A_M equilibrium.

Since the expression on the right needs to be greater than 0, for the inequality to hold the following must be true.

$$\frac{\mu_E + \alpha_M}{p} \left(\frac{1}{\frac{\alpha_M}{\mu_M}} + \frac{a}{\frac{\alpha_F}{\mu_F}L}\right) \frac{1}{r'} > 0, \tag{23}$$

Which is equivalent to

$$(\mu_E + \alpha_M)\left[\frac{\mu_M}{\alpha_M} + a\left(\frac{\mu_F}{\alpha_F}\right)\frac{(\alpha_F + \mu_E)}{(\alpha_M + \mu_E)}\left(\frac{p}{1-p}\right)\right] < r'p.$$

Solving the inequality in terms of p gives the following results

$$\left(\mu_E + \alpha_M\right)\left[\frac{\mu_M}{\alpha_M} + a\left(\frac{\mu_F}{\alpha_F}\right)\frac{\left(\alpha_F + \mu_E\right)}{\left(\alpha_M + \mu_E\right)}\left(\frac{p}{1-p}\right)\right] < r'p$$

$$\left(\alpha_M + \mu_E\right)\left[\frac{\alpha_F}{\mu_F}\cdot\frac{\left(\alpha_M + \mu_E\right)}{\left(\alpha_F + \mu_E\right)}\cdot\frac{(1-p)}{p} + a\left(\frac{\alpha_M}{\mu_M}\right)\right] < r'p\cdot\frac{\left(\alpha_M + \mu_E\right)}{\left(\alpha_F + \mu_E\right)}\cdot\frac{(1-p)}{p}\cdot\left(\frac{\alpha_M}{\mu_M}\right)$$

Bringing p to one side, we get

$$\begin{aligned} p &> \frac{\left(\alpha_M + \mu_E\right)\mu_M}{r'\alpha_M} + \frac{a\cdot\left(\alpha_M + \mu_E\right)}{r'\cdot\frac{\alpha_F(\alpha_M+\mu_E)(1-p)}{\mu_F(\alpha_F+\mu_E)p}} \\ p &> \frac{\left(\alpha_M + \mu_E\right)\mu_M}{br\alpha_M} + \frac{a\mu_F\left(\alpha_F + \mu_E\right)p}{br\alpha_F\left(1-p\right)} \\ p &> \frac{\left(\mu_E + \alpha_M\right)\mu_M}{\alpha_M br} + \frac{a\mu_F\left(\mu_E + \alpha_F\right)}{\alpha_F br}\frac{p}{1-p} \end{aligned}$$

Inequality condition (20) now is explicitly given inters of original model parameters.

7.3. *Range for temperature*

By substituting function (7) into inequality (4), we get

$$\begin{aligned} p_1 < p(T) &< p_2 \\ p_1 < \frac{1}{1+e^{-\frac{1}{S}(\beta-T)}} &< p_2 \\ \frac{1}{p_1} > 1 + e^{-\frac{1}{S}(\beta-T)} &> \frac{1}{p_2} \\ \frac{1}{p_1} - 1 > e^{-\frac{1}{S}(\beta-T)} &> \frac{1}{p_2} - 1 \\ \ln\left(\frac{1}{p_1} - 1\right) > -\frac{1}{S}(\beta - T) &> \ln\left(\frac{1}{p_2} - 1\right) \\ \ln\left(\frac{1}{p_1} - 1\right)S > -(\beta - T) &> \ln\left(\frac{1}{p_2} - 1\right)S \\ \ln\left(\frac{1}{p_2} - 1\right)S + \beta < T &< \ln\left(\frac{1}{p_1} - 1\right)S + \beta \end{aligned}$$