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***Climate Change-Induced Bias in Turtle Populations with
Temperature-Dependent Sex Determination***

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Abstract

Temperature-dependent sex determination (TSD) in turtles is an adaptive strategy that causes an increase in the production of female hatchlings when eggs are exposed to warmer incubation temperatures. Under the influence of anthropogenic climate change and its rapidity, this adaptation may become threatening, as turtle populations are affected by high levels of feminization. In this study, I use an agent-based modeling (ABM) approach to determine which percentage of female hatchlings would cause a turtle population to become unstable in its growth, decline, or even go extinct over time, if all temperature-induced effects other than sex ratio biases are disregarded. In my simulation, a fictional sea turtle model population, starting at a 50:50 sex ratio, undergoes a simplified reproductive cycle, which produces hatchlings at a pre-determined primary sex ratio, varied for each scenario. Additionally, I vary the number of females one male turtle can mate with during one season to test how the sensitivity of the model population towards skewed sex ratios changes under different levels of polygyny. I found that at the lowest simulated level of polygyny, a female hatchling ratio of 85% is enough to destabilize population dynamics in my model. Under the same conditions, a female bias of 94% causes extinction in all simulated runs. Scenarios with low female biases lead to population increase and stabilizations at constant levels that are not influenced by the female ratio or level of polygyny. At sex ratio biases with the potential to cause population decline or extinction, increased polygyny proves to make the model population more resilient and results in the persistence of the population over the simulated time frame. The female ratio under which all runs end in extinction amounts to 97% instead of 94% for these high-polygyny scenarios. Based on the limitations of this study, these numbers are to be understood as overall trends rather than actual thresholds and are not sufficient to determine whether sea turtle populations can persist under climate change conditions. However, the model suggests that TSD can become problematic if female biases exceed certain levels. Positive effects of TSD that increase resilience towards changing climates could not be shown in this study but may become effective in the model if other temperature-based threats are included in the simulation.

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1. Introduction

As global warming progresses, the many aspects of our changing climate threaten biodiversity globally (Jensen et al., 2018). One characteristic that makes animal species especially vulnerable to temperature increases is temperature-dependent sex determination (TSD) (Hays et al., 2014). In over 400 species of fish and reptiles, the sex of hatchlings depends on the temperature that eggs are exposed to during incubation (Lockley & Eizaguirre, 2021), more specifically during the thermosensitive period, which at constant temperatures is found in the middle third of incubation (Girondot et al., 2018). If temperature conditions deviate from what the respective species have adapted to, this environmental change has the potential to heavily skew sex ratios, an effect that may put species at risk of extinction (Bleichschmidt et al., 2020).

There are three different types of TSD, based on the effect of different temperatures on the sex of hatchlings. The three types, as derived by Lockley & Eizaguirre (2021), are described as follows: Type Ia produces primarily females at a higher temperature, Type Ib is characterized by a higher number of males at higher temperatures, and Type II produces females at both the cooler and warmer thresholds of the temperature range. In all cases, there is a pivotal temperature (PT) at which the sex ratio is 1:1 and a transitional range of temperature (TRT) that produces both sexes with a bias towards males or females based on the TSD type and incubation temperature. Outside the transitional range of temperature, only one sex develops (Hulin et al., 2009). Among the species with TSD are most turtles worldwide (Tezak et al., 2020), including all seven species of sea turtles (Lockley & Eizaguirre, 2021). Most turtle species show TSD type Ia, meaning that with increasing incubation temperatures, the sex ratio is biased towards females. Slight temperature increases of under 2°C have been shown to be sufficient to cause drastic female biases in hatchling sex ratios, and temperature increases of 4°C are enough to cause female-only offspring in painted turtles (*Chrysemys picta*) (Janzen, 1994). For leatherback turtles (*Dermochelys coriacea*), an increase in incubation temperature of just 1°C was linked to hatchling sex ratios of 0.92 to 0.96, compared to 0.86 and 0.76 during the reference period (Santidrián Tomillo et al., 2015). One of the largest populations of green sea turtles (*Chelonia mydas*), native to the northern Great Barrier Reef (GBR), Australia, already shows sex ratios of up to 99.1% females in juvenile turtles. With temperatures rising even further, this population may produce only female offspring in the future (Jensen et al., 2018).

However, seeing TSD as merely a threat may be inaccurate for two reasons. First, when considering hatchling sex ratios alone, the important factor of the breeding cycle characteristic of sea turtles is left out. Breeding and nesting mean a lot more energy expense for female sea turtles. Therefore, they usually nest in intervals of several years, while their male counterparts may return to the breeding grounds as often as annually. This results in an operational sex ratio (OSR) that is significantly less female-biased than primary or hatchling ratios. In fact, a certain female bias in the hatchling sex ratio might be the reason that optimal OSRs can be maintained (Hays et al., 2014). Second, recent research suggests that TSD, rather than being a disadvantage, might be an evolutionary mechanism that has allowed reptiles to persist in the face of climate variability in the past (Santidrián Tomillo & Spotila, 2020). Considering that not only sex ratios are affected by temperature changes but that there is a negative impact on both egg viability and hatchling success correlated with higher temperatures, TSD could make turtles more resilient to climate change, as shown by a model-based study by Santidrián Tomillo et al. in 2015.

Nevertheless, at the current rate of global warming, the positive effects of TSD are likely to be outbalanced by the repercussions and complete feminization of populations, as well as extinction due to TSD and other temperature-related influences remain considerable threats, especially if turtles do not manage to adapt to the rapid change (Santidrián Tomillo et al., 2015). Over long periods of time, turtles have evolutionarily adapted to different pivotal temperatures and transitional ranges of temperature. Both the values for PT and TRT vary not only between species but also between different populations of one species, as derived by Hulin et al. (2009). One behavioral adaptation observed in hawksbill turtles (*Eretmochelys imbricata*) is an increased level of polygyny, meaning that one male mates with several females during one breeding season and, therefore, sires more nests. Reports of polygyny in sea turtle populations are rare and proposedly coincide with shortages of male mates that result from high female biases in hatchling sex ratios (Gaos et al., 2018).

Mathematical models have been described to link incubation temperatures and sex ratios (e.g., Hulin et al., 2009). For this study, however, the research question shall focus on the effect of offspring sex ratios on a population's development, rather than the temperatures, that cause those ratios. I use an agent-based modeling (ABM) approach to examine the effect of female-biased sex ratios of different severity on turtle populations, not considering other significant consequences of high temperatures, like decreased egg viability and hatchling survival. My aim is to test the sensitivity of a turtle population regarding different degrees of

feminization brought about by skewed hatchling sex ratios that persist over a long period of time. Additionally, I analyze the possibly balancing effects of increased levels of polygyny as an example of behavioral adaptation.

2. Methods

To examine how persisting degrees of feminization would affect a turtle population, I use an agent-based model that I developed using the programming language NetLogo (Willenski, 1999) and conduct a sensitivity analysis regarding different primary sex ratios and levels of polygyny. I derive setup parameters and the concept of the life cycle from sea turtle studies, focusing on green sea turtles (*Chelonia mydas*), as this species is one of the best studied (Robinson et al., 2023), and data is therefore readily available. To keep my model simple, I do not explicitly simulate temperatures, as it is, for instance, done in a detailed individual-based analysis by Blechschmidt et al. (2020) or calculate sex ratios as a function of temperatures, as, for example, described by Massey et al. (2019). Instead, I implement hatchling sex ratios as input parameters, thereby aiming to analyze the effect of a certain degree of feminization, rather than the temperature that causes it. I abstract from other temperature-related phenomena like decreased egg viability and hatchling survival under high-temperature conditions (Santidrián Tomillo et al., 2015) or loss of nesting habitat due to rising sea levels (Fuentes et al., 2010) to solely focus on the effects of different hatchling sex ratios.

The model consists of a finite world, representing an isolated ecosystem with limited resources and without migration from or to other populations. The turtles are created as one type of agent and differentiated regarding their respective sex and age variables, thereby dividing them into mature, juvenile, male, and female turtles. The group of juveniles here includes all turtles before reaching sexual maturity, from the neonate stage up to the maturity age of 35 years in the model, with this group being excluded from the reproductive process and subject to a different mortality rate than adults. The model is spatially explicit.

2.1. Model Initialization and Life Cycle

A time step in the model represents one year. In each year, every turtle in the model undergoes the following steps:

1. First, the age of all turtles increases by one. If a turtle reaches the maturity age of 35 years in the current time step, it now counts towards the adult population and can mate.
2. The turtles then move one step in a random direction.
3. Within the assigned radius, every male turtle mates with up to a maximum number of females according to the scenario ($mates_{max} = 4, 5, \text{ or } 6$).

4. Any female that mates with a male produces hatchlings. The number of hatchlings is based on the average number of eggs a female turtle lays in one season, the fraction of eggs that statistically survive, and a calculated chance to reach maturity (see Chapter 2.2 *Parametrization*). The hatchling sex is determined by the chance of producing females according to the hatchling sex ratio of the respective scenario. A female that mates in time step t_i is excluded from the mating and breeding procedure in the two consecutive years t_{i+1} and t_{i+2} .
5. In each time step, adult turtles die with a probability of $p_m = 0.05$. To ensure compliance with the model's carrying capacity, an additional mortality rate m_K is calculated based on the current number of turtles in the population and becomes effective if the carrying capacity K is surpassed (see Equation 1).

Following this yearly cycle, the number of males available for mating becomes the limiting factor in the model. In a first analysis, I run experiments with combinations of 4, 5, or 6 mates per male and season, and female hatchling ratios ranging from 0.5 to 1.0 in increments of 0.1 over a time span of 600 steps, representing 600 years. For each parameter combination, I simulate the outcome 1000 times and calculate the number of all male and female turtles, as well as the number of mature males and females, to measure population developments under the respective conditions. If a run leads to extinction, meaning that the total number of turtles in timestep $t = 600$ is zero, I mark this run as an extinction run and count it towards the proportion of runs within a certain scenario that bring about this outcome. By doing this, I can identify a range of hatchling sex ratios that would possibly lead to extinction for each scenario regarding the maximum number of mates per male. From these first runs, I derive scenarios in which the number of mature individuals stabilizes, scenarios that show considerable variability in adult turtle numbers, and scenarios in which the population would go extinct in most or all runs. I use those results to deduce ranges of hatchling sex ratios that need further assessment. In additional experiments, I examine those ranges in increments of 0.01 to identify thresholds of when extinction would become a threat in the simulations. For a conclusive assessment of the average number of adult turtles at the end of a simulation run, I compare average turtle numbers of the runs that do not lead to extinction and compare the population levels and extinction chances separately. Additionally, I run simulations for the opposite effect, a higher proportion of males, to test the model's functionality and see if a certain degree of feminization would be beneficial in the model compared to masculinization.

2.2. Model Parametrization

In the following, I describe the parameters used in the model in more detail. I initially test the model for and adjust it to stable conditions at pivotal temperature, resulting in a baseline scenario at a 1:1 sex ratio with a starting population of $N_0 = 200$ turtles, a carrying capacity of $K = 300$, and individuals being able to consider turtles within a radius of 5 in a world of 36 x 36 patches as mates. A model by Blechschmidt et al. (2020) also uses an initial population of 200 and sets the carrying capacity to this number, as well. However, in my study, I use a higher value for K , as allowing for initial population growth under the restriction of the carrying capacity serves as a stabilizing factor in my model. Additionally, this model attribute allows me to determine whether population growth would happen under the given conditions.

I differentiate between adult and non-adult or juvenile turtles. In the time steps following its initialization, the model only considers adult turtles for assessing the population in regard to its carrying capacity, assuming that neonate and juvenile turtles need fewer resources than mature and reproducing ones. In accordance with the minimum breeding age used in the individual-based model by Mazaris et al. (2006), I set the age of sexual maturity at 35 years, with a turtle reaching this age in a time step counted towards the breeding population from that point on.

In the initialization step, each turtle is assigned a random age between one and 40 years. The agents are not limited by a maximum age but are rather subjected to an annual adult mortality of $p_m = 0.05$, based on the annual survival chance for turtles in this life stage of 0.9482 as derived by Chaloupka (2002), the probability that is also used in the modeling approaches of Mazaris et al. (2006) and Blechschmidt et al. (2020). I ensure that the population remains within the bounds of the carrying capacity K by adding an additional mortality rate that increases based on the number of adult turtles present and becomes effective if K is surpassed. Equation 1 shows how this additional mortality rate m_K is calculated based on N_i , the current number of mature individuals, and K , the carrying capacity (Wilensky, 1997). This function results in the population being able to increase beyond the number of K yet ensures a capped population development with the carrying capacity representing limited availability of resources within an ecosystem.

$$m_K = \frac{(N_i - K)}{N_i} \quad (1)$$

Regarding the spatial dimension, each turtle is first assigned a random location from which it will later move, with the interactions with other turtles being based on spatial proximity. As male turtles are the limiting factor for reproduction in this model, they serve as the starting point of the mating function. In each time step, each male turtle mates with up to 4, 5, or 6 females, with the maximum number of female mates implemented according to the scenario. The number of hatchlings produced by each female is calculated based on the following assumptions: Sea turtles lay several clutches of eggs within one season and can store sperm so that females can lay clutches months after mating (Fitzsimmons, 1998). Based on this, a female turtle in the model can only mate once in a season, as this is sufficient for several clutches of eggs. In the first step, I calculate the mean number of eggs per female and season based on the values derived by Chaloupka (2002), resulting in an annual clutch size of $C = (575 \pm 140)$ eggs per female. A random number following these values for the mean and standard deviation of a normal distribution is created for each gravid female and multiplied with a chance to hatch $p_h = 0.44$, based on egg and hatchling survival rates (Chaloupka, 2002). For computational reasons, I then calculate a combined chance to reach maturity based on the chance of survival for all life stages before maturity as derived by Chaloupka (2002) and used, for example, in the model by Blechschmidt et al. (2020) rather than creating several hundred hatchlings in each time step and applying an annual mortality rate to them. This probability of surviving to the state of an adult turtle amounts to $p_a = 0.0018$ and is applied to every potential hatchling by randomly sampling from a uniform probability distribution. Only the surviving hatchlings are introduced to the population as new agents and do not undergo any mortality rates until they reach the age of maturity, from when the adult mortality becomes effective.

If a female turtle mates with a male, it enters a state of gravidity and produces hatchlings according to the above-described hatching function. Of the hatchlings that survive and are included in the model population, each one gets assigned a sex according to the new sex ratio of the respective scenario, representing the primary sex ratio under different temperature conditions. The fact that male turtles breed more frequently than females (Hays et al., 2014) is implemented as a period for which a female remains unable to mate after breeding. I set this period to three years, according to green sea turtle data that suggests their returning to breeding grounds every two to five years, depending on the specific population (Witherington et al., 2006).

3. Results

Running simulations for hatchling female ratios between 0.5 and 1.0 in increments of 0.1 revealed that for scenarios with 50% to 80% female hatchlings, the model population would first increase and then stabilize at an end population of between 280 and 285 mature individuals on average. As the size of the mean end population is limited by the carrying capacity K in this model, the level of polygyny could not be related to higher final population numbers but only to changing sensitivity towards female biases. An example of the population development measured in terms of the average and variation in the number of mature turtles per time step can be seen in Figure 1, where the mean number of adult turtles over 1000 runs is presented as a line, and the variations with a 0.95 confidence interval illustrated as a green area around the mean curve.

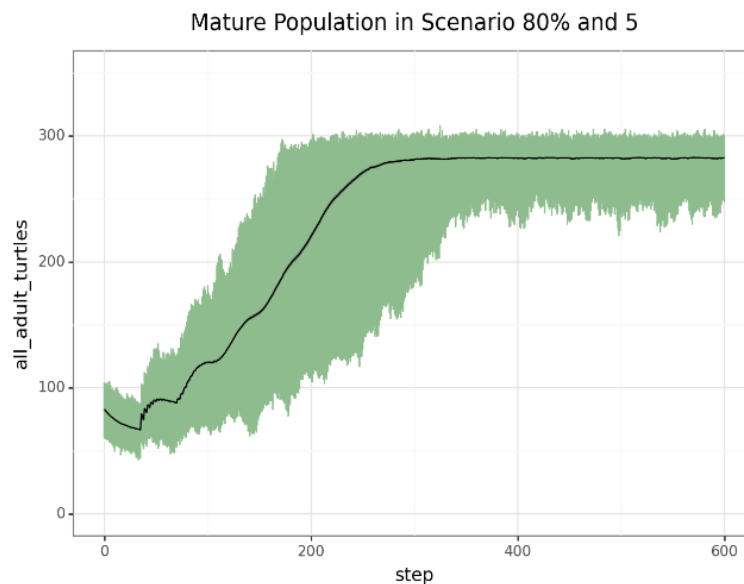


Figure 1: Mean population development (black line) and variation (green) in the scenario 80% female hatchlings and a maximum of five mates per male and season. On average, the population stabilizes around the carrying capacity.

To avoid overlooking variations or noticeable developments that might be lost by accessing the mean data, I chose random simulations for each scenario and compared them with the graphs of the statistical outcome over 1000 runs. Figure 2 shows a randomly chosen example experiment for the same parameter combination as illustrated in Figure 1, with 80% female hatchlings and $mates_{max} = 5$. In contrast to the statistical overview in Figure 1, the single experiment illustration shows significant fluctuations in turtle numbers between time steps. These are caused by the model design, which limits the population size through mortality rather than controlled birth rates. Generally, however, the statistical analysis graphs

prove to be an applicable portrayal of the population development for the respective scenarios.

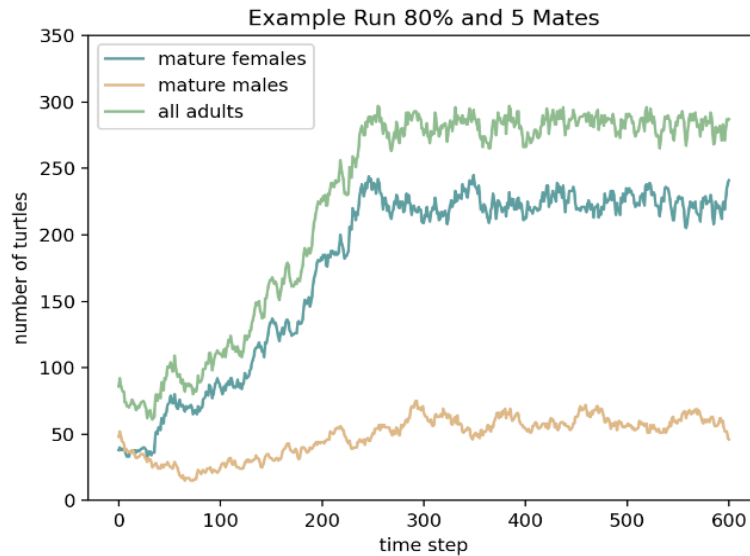


Figure 2: Exemplary run of the scenario 80% females and five mates. Fluctuations that are the result of the specific model assumptions and seasonal cycle are visible in both male and female turtle numbers.

While the 80% female hatchling scenarios all end in a stable final population, simulations with primary sex ratios of $r_f = 0.9$ result in very different average model behavior depending on the parameter $mates_{max}$, with some simulations leading to the extinction of the model population. For low levels of polygyny ($mates_{max} = 4$), a drastic population decline with an average end population close to extinction can be observed. I then excluded runs that end in extinction from the calculation. In this case, the average final population amounts to $N_{final} = (17 \pm 22)$ mature turtles, a number that is still low enough to cause the population to die out likely and that is affected by a wide standard deviation (SD). In 71.2% of runs for this parameter combination ($r_f = 0.9$ and $mates_{max} = 4$), the population dies out in the model. An increase in the number of mates per male and season by just one ($mates_{max} = 5$ and $r_f = 0.9$) leads to an average outcome that still shows population decline yet at a much slower rate and an average population of $N_{final} = (92 \pm 73)$ turtles, calculated without the runs ending in extinction. Six mates per male turtle are enough, in this model, to cause a population increase rather than decrease up to an average end population of $N_{final} = (222 \pm 76)$ for the given sex ratio of $r_f = 0.9$. In this last case, specifically, the population keeps increasing and does not reach a stable

condition within the simulated time steps. Figure 3 shows the average model behavior for the three different scenarios with a 90% female hatchling ratio.

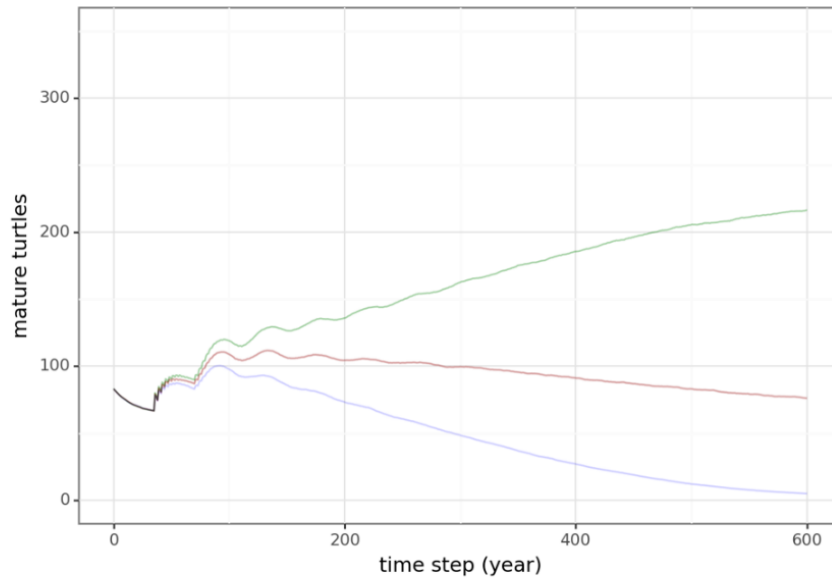


Figure 3: Population development over time for scenarios with 90% female hatchlings and four (blue graph), five (brown graph), or six (green graph) mates per male turtle and year.). Note that these scenarios are subject to significant standard deviations and that a differentiation between runs that end in extinction and others must be considered.

All runs with a female ratio of 1.00 or 100% lead to a population crash or, rather, to the population's inability to grow in the first few time steps, as it was observed in all scenarios that result in stable population sizes. This means that for my simulated parameter range of polygyny, there is a range of hatchling ratios between $r_f = 0.80$ and $r_f = 1.00$, in which the given degree of feminization causes the model population to decline rather than grow, and eventually die out. Figure 4 shows the population developments in scenarios with female-only offspring, measured in the total population number, rather than just the number of adults, as in the previous graphs.

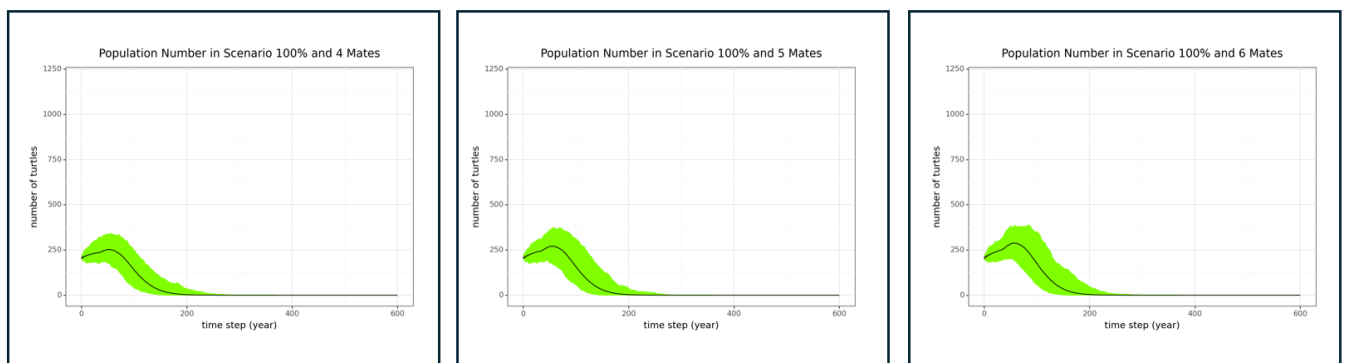


Figure 4: Population development measured in terms of the number of all turtles as a function over time for the scenarios with 100% female hatchlings and the different levels of polygyny.

To examine which ratio would be the threshold between population growth and stabilization on the one end and the inability to grow, leading to population decline and eventually extinction, I carry out additional experiments in the previously defined critical range of primary sex ratios between $r_f = 0.80$ and $r_f = 1.00$. Figure 5 illustrates the outcome by graphing the mean and standard deviation of the simulated scenarios with 70% to 100% female hatchlings.

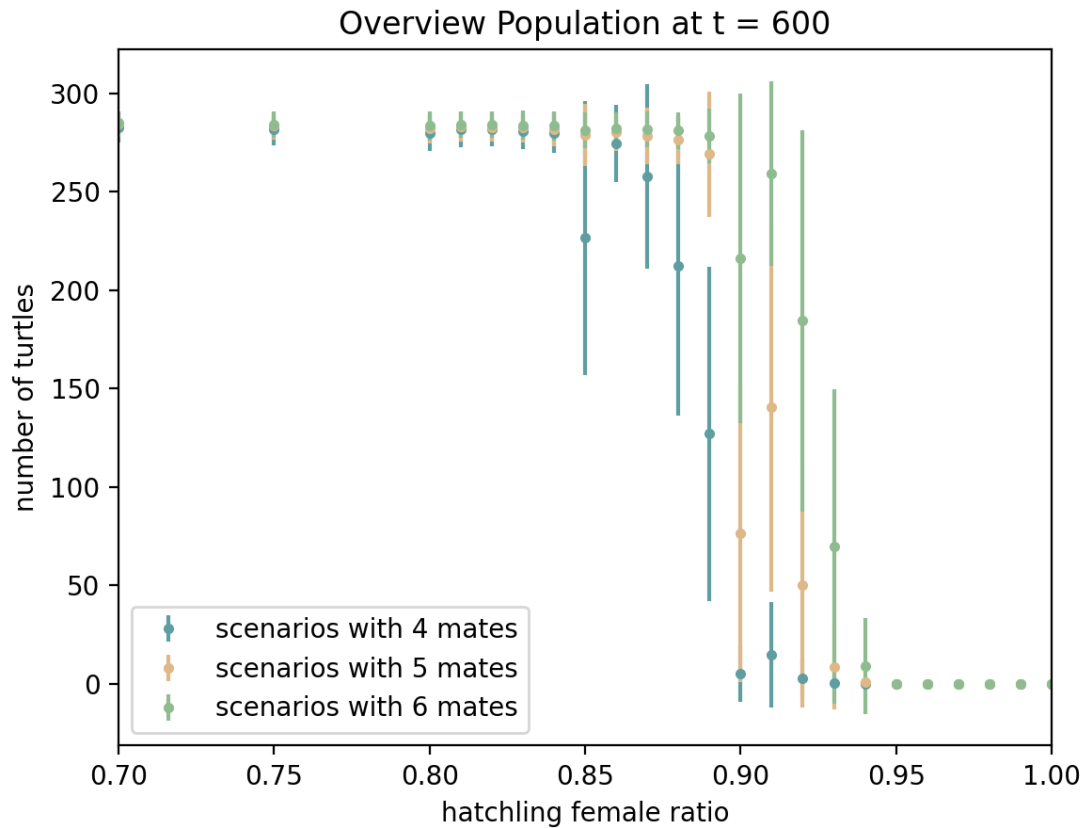


Figure 5: Average numbers and standard deviations of the end population over 1000 runs for different scenarios of hatchling female ratios between 0.70 and 1.00, and the different levels of polygyny expressed as colors.

For scenarios with $mates_{max} = 4$, the population development starts to deviate from the stable final population conditions at 89% female hatchlings. At this ratio, an equilibrium is still reached, yet at a significantly lower population level than for all lower female ratios. For $r_f = 0.90$ or higher, the mean final population is zero. All 1000 simulation runs end in the model population's extinction at a sex ratio of $r_f = 0.94$, and the highest average final population correlated with just a slight female ratio of 60% for the four polygyny scenarios. For experiments with five mates per male and season, the average final population reaches a stable level for ratios of up to $r_f = 0.90$, and at $r_f = 0.95$, all runs lead to extinction. The highest simulated polygyny level, $mates_{max} = 6$, remains stable for hatchling sex ratios of up

to 92% females. Table 1 summarizes the above-described indicator values of the highest female hatchling ratios that lead to stable end populations $r_{f_{\max}(\text{stabilization})}$ and the lowest ratios that lead to at least one run ending in extinction $r_{f_{\min}(\text{extinction})}$. It also shows the ratios at which more than 90% of runs end in extinction $r_{f(>90\% \text{ extinction})}$, and those ratios that result in a 100% chance of extinction $r_{f(100\% \text{ extinction})}$ are also shown. Additionally, the maximum population size N_{\max} , measured in terms of the mature population, and responding hatchling sex ratios $r_{f(N_{\max})}$ are listed.

Table 1: Summary of the simulation results

\max_{mates}	$r_{f_{\max}}(\text{stabilization})$	$r_{f_{\min}}(\text{extinction})$	$r_{f(>90\% \text{ extinction})}$	$r_{f(100\% \text{ extinction})}$	$r_{f(N_{\max})}$	N_{\max}
4	0.89	0.87	0.93	0.94	0.6	283.12 ± 7.29
5	0.90	0.85	0.94	0.95	0.7	284.52 ± 6.40
6	0.92	0.90	0.95	0.97	0.7	284.94 ± 5.98

There proved to be a span of hatchling sex ratios that would lead to extinction in some, yet not all scenarios. This share of extinction runs per scenario is summarized in Figure 6, expressed as the respective absolute number of runs out of $n = 1000$ simulations in which the model population reached $N_{\text{final}} = 0$ within the simulated time frame. Note that scenarios in which the final population was very small but not yet zero, could potentially become extinction runs over a longer modeling period (see average end populations for scenarios with four mates in Figure 5).

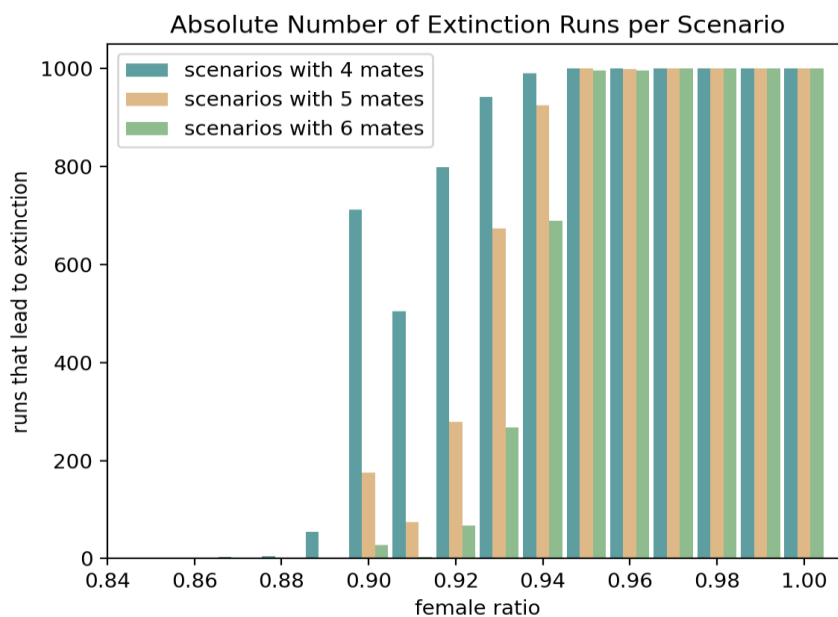


Figure 6: Absolute number of runs that led to extinction in the respective scenarios ($n = 1000$ per parameter combination).

This study aimed to focus not merely on the possibility of extinction, but also possible effects on the population size aside from that, like an increase or decrease of the number of turtles at equilibrium. Therefore, I also analyzed the mean and standard deviation of population sizes if the scenarios that led to extinction were excluded from the calculation. The results for the relevant parameter combinations are displayed in Figure 7. It can be seen that the average population size is subject to great variation in those runs in between the lower threshold that marks the end of the one stable state, which means that the population is reaching an equilibrium only limited by the carrying capacity and the second stable state, which is the dying out of the population and a final population of zero. Generally, the mean population size decreases with increasing female biases in between those two extreme outcomes. For scenarios with 91% female hatchlings, however, there is an interesting increase in the average population, compared to 90%. This is true for all three levels of polygyny.

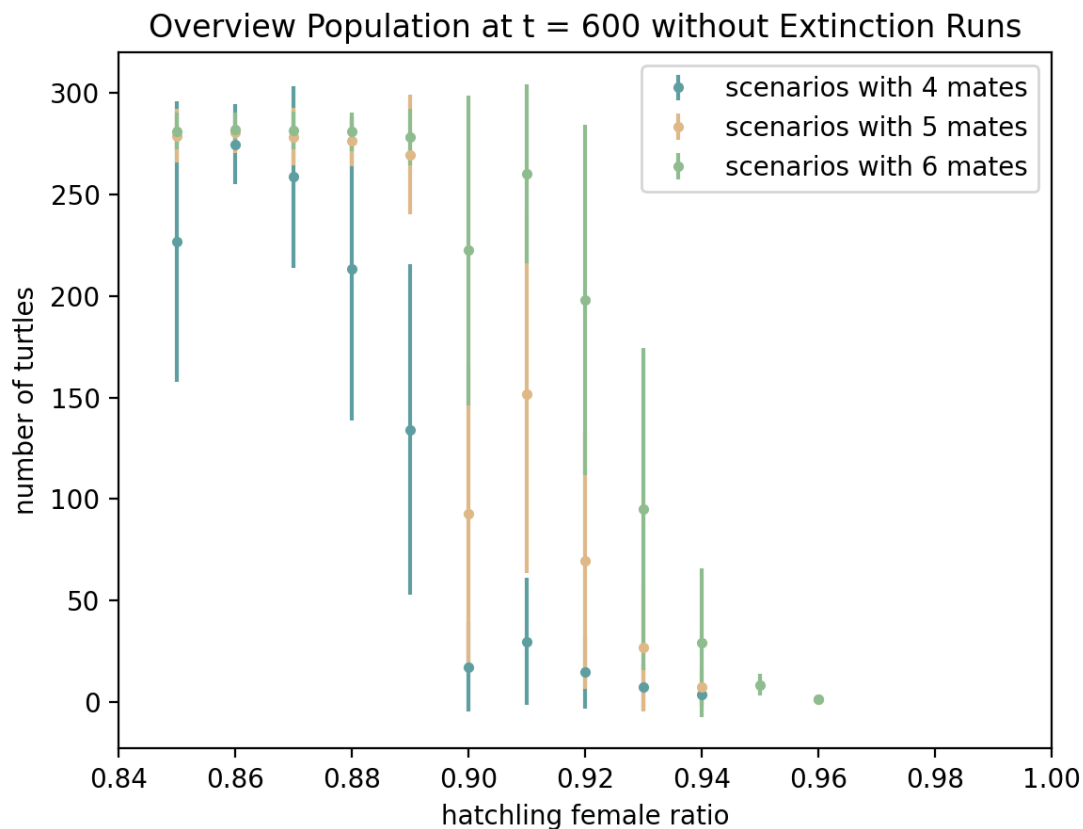


Figure 7: Mean and standard deviation of the model population over $n = 1000$ runs for the scenarios with female ratios between 85% and 100% if runs that end in extinction are excluded from the calculation.

4. Analysis/Discussion

There are two different views on TSD in sea turtle populations: On the one hand, increasing temperatures may be a considerable threat as they cause skewed sex ratios to the point of complete feminization (Jensen et al., 2018) and cause extinction as a shortage of male mates arises (Blechs Schmidt et al., 2020). On the other hand, TSD causes the production of more females under extreme conditions, which leads to increased future breeding potential and has been suggested to make turtle populations more resilient towards changing climates (Santidrián Tomillo & Spotila, 2020; Santidrián Tomillo et al., 2015). For some sea turtle populations, like the green sea turtle population at the Northern Great Barrier Reef, female-only offspring is predicted for rising temperatures (Jensen et al., 2018), while for one of the biggest loggerhead turtle (*Caretta caretta*) populations in the Cape Verde Islands, complete feminization is not expected in the near future (Laloë et al., 2014). Nevertheless, it is generally agreed that the currently predicted temperature increases associated with anthropogenic climate change will outweigh the adaptive significance of TSD as temperature increases are too drastic in terms of both magnitude and speed (Santidrián Tomillo et al., 2015).

4.1. Feminization and Population Development

The results of this study suggest that in a turtle population that can be portrayed by a simulation such as the described model, high levels of female bias may cause population decline and eventually, extinction, even when other temperature-related effects are disregarded. The threshold of the critical ratio, where populations decline instead of reaching an equilibrium close to the carrying capacity, amounts to between 89% and 92% females in this model, depending on the level of polygyny. The parameter combinations at which at least one out of 1000 runs led to extinction were even lower than that at 85%, 87%, and 90%. At 94%, 95%, and 97% for the respective numbers of mates, all 1000 runs in an experiment led to extinction (see Table 1). Based on that, an increase in the share of female hatchlings from 0.86 and 0.76 to 0.92 and 0.96, as has been linked to a temperature increase of 1°C by Santidrián Tomillo et. al (2015), would be enough to shift a population's development from an equilibrium to a decline resulting in extinction. This is only true, however, if the number of mates per male is similar to the numbers used in this study and if other population characteristics are adequately approximated. According to the representative concentration pathways (RCPs) as predicted by the Intergovernmental Panel on Climate Change (IPCC), a

temperature increase of 1°C in the mean global temperature, compared to today's level, is not unlikely, and regional warming might be higher in critical areas. Compared to the reference period 1850 to 1900, we have already experienced a global mean temperature increase of 1.1°C for the period 2011 to 2020. For the less optimistic pathways (RCP 8.5), 4°C warming is predicted (IPCC, 2023). This degree of global warming resembles what Janzen (1994) identified as the global mean temperature increase sufficient to cause 100% female offspring in painted turtles, a freshwater turtle species. In my model, female-only hatchlings led to a crash of the model population within just 200 years, with the mature population number reaching zero or a level close to zero in this interval. More importantly, the initial growth that characterized all scenarios that ended in a stable population size was not reached in the 100% female hatchling scenarios in the first place.

The effect of a certain female bias being beneficial for population numbers can barely be shown in this study. While the highest population numbers occurred at female ratios of 60% and 70%, depending on the scenario, those numbers were insignificantly higher than for a 1:1 primary sex ratio. Figure 5 and Figure 7 show how the population sizes for all scenarios leading to stable populations are very similar. This stable population size across scenarios is slightly lower than the carrying capacity, which is likely caused by the averaging of 1000 runs to access these numbers. In single-run graphs, the population number does show to reach K , or rather, oscillate around it, with the oscillations based on the mortality rate that becomes effective if the population number exceeds the carrying capacity. For $mates_{max} = 4$, 86% female hatchlings resulted in a higher average population than an 85% female ratio and all 91% female hatchling scenarios showed higher average population numbers than their counterparts at 90%. As there are also less extinction runs for 91% female hatchlings, compared to 90% female hatchling ratio scenarios, a survivorship bias based on the average population calculation, is unlikely. The findings might therefore suggest that there might be a better-balanced operational sex ratio in scenarios with a slightly higher female hatchling ratio. In this case, a further decrease correlating with higher female ratios could be interpreted as exceeding the adaptive potential of TSD. Alternatively, there could be an unknown bias that would need to be identified in future experiments and assessments of this model. Especially interesting is the observation that the parameter combination of 90% female hatchlings and six mates per male and season led to continued population growth beyond the time frame of this experiment, on average. The mean population size was smaller than for lower female ratio scenarios, but instead of stabilizing, the population continued to grow even after 600

simulated years. To understand whether this effect is caused by slowed growth to an equilibrium that is just reached later or if said equilibrium would be at a higher level than in other scenarios, an extension of the time frame in the model would be needed.

4.2. Adaptation and Effects of Increased Polygyny

If female biases beyond the adaptive benefit of TSD are assumed, there are still possibilities for turtles to adapt to warmer temperatures and the resulting sex ratios. Pivotal temperatures and TRTs vary between species and between populations of the same species (Hulin et al., 2009). As female hatchling ratios and incubation temperatures differ significantly between regions and rookeries, changing nesting locations might be a solution to not only balance sex ratios but also mitigate other temperature-related impacts. The sex ratios for green sea turtles at the Northern Great Barrier Reef, for example, are already as high as 99.1%, while the cooler counterpart at the Southern GBR produces just 68% females (Jensen et al., 2018). Similarly, in a loggerhead turtle study in the Cape Verde Islands, light-colored beaches produce 70% female hatchlings while eggs from nests in darker sands turn out more female-biased (> 93%) (Laloë et al., 2014). If turtles can change their behavior and align their choice of nesting habitat, they may be successful in balancing out general warming effects, as has been observed in the semi-aquatic spotted turtle (*Clemmys guttata*). For species or populations that are found in warm climates and areas, that option might not be available, as they are already possibly nesting at the coolest possible sites (Roberts et al., 2023). For green sea turtles, the life cycle is typically characterized by high nest site fidelity (Patrício et al., 2018). If, however, different nesting beaches are utilized by nesting sea turtles, this has the potential to increase the survival chance of populations (Blechschmidt et al., 2020).

Whether or not turtles will be able to adapt to increased incubation temperatures remains to be seen. The fact that large populations with a strong female bias already exist suggests that there is a chance that these biases are less problematic than previously thought, although complete feminization would lead to extinction (Hays et al., 2014). Those species that have broader transitional temperature ranges are at an advantage in terms of adapting to warmer temperatures, while others may already nest under conditions that are close to the outer temperatures in their respective TRTs (Hulin et al., 2009). Increased levels of polygyny have been reported in hawksbill turtle populations with lowered shares of males in the population (Gaos et al., 2018). Laloë et al. (2014) report operational sex ratios of only 3.95 - 16.74% males in a loggerhead sea turtle population, with the percentage being that low

having the potential to affect the population's clutch fertility and state that these males can probably breed with multiple females to make up for the strong male bias. In my simulations, the level of polygyny increased the population's resilience towards higher levels of feminization. Even if for six mates, the population only endured a 2-3% higher female ratio than for four-mate scenarios, this correlation already illustrates the potential of polygynous behavior and that the TSD species that already show this mating strategy may be better adapted to high sex ratios than others. In other words, if males sire more nests in one season, the reproductive cycle is not limited by the availability of males as quickly. Interestingly, higher levels of polygyny did not lead to larger model populations. This may be explained again by the way the carrying capacity was implemented. Or the effect may be attributed to the fact that if enough mates are available, at low female biases, the maximum number of mates would not be exhausted. Similarly, a first decrease in the share of males did not lead to population decline, straight away, as there was less competition between males in the model and one male turtle would have the chance to reach the maximum number of female mates it was limited by.

4.3. Limitations

For species like turtles with long generation times and already threatened populations, modeling approaches can be a valuable tool to assess potential dangers and inform management decisions. A model, however, is always a simplified portrayal of the natural system and must be understood that way. To interpret the results from this particular study, a couple of limitations need to be addressed.

Firstly, the reproductive cycle in this model does include female breeding intervals as a rough estimate, yet the spatial dimension does not account for breeding grounds, nesting habitats, and feeding grounds. Males being able to sire nests from four, five, or six females is an assumption based on data for hawksbill sea turtles, while green sea turtle males may have more female mates within one season. The conclusion that a higher level of polygyny may serve as an advantage when facing high female-biased sex ratios may still be generally true for sea turtles. This is in accordance with Laloë et al. (2014), who state that the question of how many males a population needs to be fertile is central to conservation efforts.

Secondly, natural sea turtle populations are much larger than the model population. At a starting population of just 200 turtles and the highest numbers amounting to 285 mature turtles or just above 1000 turtles, including hatchlings and juveniles, are much lower than the

actual numbers. Estimates for just the female breeding population of green sea turtles at the Northern GBR, for example, are as high as 200,000 individuals (Jensen et al., 2018). This must be considered when looking at illustrations based on single simulation runs, where high numbers of hatchlings, representing literature data, in combination with a comparatively very small model population result in high fluctuations in the mature population size in each modeled year. Starting the population at 200 turtles and allowing for initial population growth does also not portray real-life conditions and was merely used to differentiate between the potential of a population at a specific parameter combination to grow, stabilize, or crash, which made the model more stable and the interpretation more distinct. This, however, resulted in a longer time frame where the first 200 to 300 years of a simulation were needed to see if a population would stabilize or not manage to grow initially. The idea was to examine whether a population at this rate of feminization would be able to persist or even grow if the carrying capacity was not already a limiting factor. Other individual-based models in turtle research like Blechschmidt et al. (2020), Mazaris & Matsinos (2006), Massey et al. (2019), and Mazaris et al. (2006) have not used this approach and are therefore closer to the current actual circumstances and may be used to inform management decisions on a timely basis, while my study merely allows for a general sensitivity analysis towards female biases, without a realistic portrayal of the time frame of a potential population decline.

In this model, I completely disregard genetic effects and solely focus on the availability of male mates as a limiting factor. As green sea turtles have high breeding ground fidelity (Patrício et al., 2018), the chance to encounter males might be higher in nature than in the model, where no breeding or feeding grounds are incorporated in the spatial dimension of the model. When males become scarce, however, fertility might be affected not just because they are unable to mate with enough female turtles but also because genetic diversity may decrease. The number of individuals that is necessary for a population's long-term persistence is usually estimated to be in the hundreds or thousands. A study on bog turtles, a freshwater species, however, states that a population of as few as 15 females at breeding age has a fair chance of survival within a 100-year time frame and suggests, that minimum viable population numbers may generally be smaller than previously expected for long-lived species that reproduce multiple times in a lifetime. Such considerations are important as management and conservation decisions are often limited by resources and therefore moved away from populations or species that have been rated as less likely to survive (Shoemaker et al., 2013).

Lastly, the temperature effects in this model are approximated through an average chance of a hatchling becoming a male or female turtle in each year, resulting in a share of males and females in the newborn population of each year. In reality, nests are often unisex and for painted turtles, a study has shown that some years produced only female hatchlings while others produced only male individuals (Janzen, 1994). It may therefore be more accurate to implement the chance of an entire nest to turn out as males or females based on their nest site and the temperature condition in the nesting season than to apply the chance to individual hatchlings based on the overall ratio within a population.

4.4. Conservation Conclusion and Future Research

The results of this study suggest that depending on other factors like polygyny or adult mortality, temperature-induced female biases will become a threat for the persistence of sea turtle populations under conditions of global warming. Similar individual-based modeling approaches have also led to this conclusion, and while TSD potentially increases the resilience of species towards climatic extremes, the speed at which our climate is warming may overrun those advantages. Since the outcomes of skewed sex ratios are not to be seen until years in the future, more refined modeling approaches that also consider the dangers of genetic bottlenecks may be a valuable contribution to finding out at which rate the number of males in a population may fall below a critical number or percentage. With this knowledge, manipulation of primary sex ratios in the form of nest shading or incubation under controlled conditions may be implemented at their maximum efficiency. When shading nests, it must be considered, however, that this interference may prevent the turtles from adapting to higher temperature levels (Santidrián Tomillo & Spotila, 2020). Skewed sex ratios are, unfortunately, by far not the only factor that threatens turtle populations worldwide. As crucial as future research on the potential of feminization is, it is therefore also vital to focus on other ways to contribute to the research and conservation of turtle species that are endangered today or may become threatened in the future.

List of Abbreviations

ABM	<i>agent-based modeling</i>
GBR	<i>Great Barrier Reef</i>
IPCC.....	<i>Intergovernmental Panel on Climate Change</i>
OSR.....	<i>operational sex ratio</i>
PT	<i>pivotal temperature</i>
RCPs	<i>representative concentration pathways</i>
SD	<i>standard deviation</i>
TRT	<i>transitional range of temperature</i>
TSD.....	<i>temperature-dependent sex determination</i>

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List of Variables

Variable	Description	Unit
N_i	Population size in a certain time step	turtles
N_0	Initial population	turtles
N_{final}	Final population	turtles
p_h	Chance to hatch	-
p_a	Chance to reach maturity/adult stage	-
p_m	Mortality chance	-
r_f	Primary sex ratio expressed as ratio of females in a clutch	-
C	Annual clutch size	eggs
K	Carrying capacity	-
t	Time	years
$mates_{max}$	Maximum number of female mates per male	turtles
$r_{fmax(stabilization)}$	Maximum female ratio that leads to stabilization	
$r_{fmin(extinction)}$	Minimum female ratio that causes extinction runs	
$r_{f(>90\% extinction)}$	Female ratio at which >90% of runs lead to extinction	
$r_{f(>100\% extinction)}$	Female ratio at which 100% of runs lead to extinction	
$r_{f(N_{max})}$	Female ratio that leads to the highest population number	

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Appendix

Table 2: Final population mean and standard deviation for scenarios with $mates_{max} = 4$

Female Ratio	Final Mature Population Mean	Final Mature Population SD	Extinction Percentage
0.50	282.29	7.70	0.0
0.60	283.12	7.29	0.0
0.70	282.80	7.47	0.0
0.75	281.82	8.29	0.0
0.80	280.06	9.47	0.0
0.85	226.82	69.31	0.0
0.86	274.78	19.70	0.0
0.87	258.77	44.86	0.3
0.88	213.53	74.66	0.5
0.89	134.23	81.57	5.4
0.90	17.08	22.06	71.2
0.91	29.68	31.41	50.5
0.92	14.51	17.73	79.9
0.93	7.19	11.32	94.3
0.94	3.33	5.27	99.1
0.95	0.00	0.00	100.0
0.96	0.00	0.00	100.0
0.97	0.00	0.00	100.0
0.98	0.00	0.00	100.0
0.99	0.00	0.00	100.0
1.00	0.00	0.00	100.0

Table 3: Final population mean and standard deviation for scenarios with $mates_{max} = 5$

Female Ratio	Final Mature Population Mean	Final Mature Population SD	Extinction Percentage
0.50	282.92	7.20	0.0
0.60	284.15	6.57	0.0
0.70	284.52	6.40	0.0
0.75	283.58	6.94	0.0
0.80	282.45	7.77	0.0
0.85	279.01	13.09	0.1
0.86	280.53	9.82	0.0
0.87	278.54	14.24	0.0
0.88	276.54	12.62	0.0
0.89	269.71	29.57	0.2

0.90	92.47	73.44	17.5
0.91	151.71	88.19	7.5
0.92	69.54	63.37	27.9
0.93	26.57	31.17	67.4
0.94	7.08	8.97	92.5
0.95	0.00	0.00	100.0
0.96	1	0.00	99.9
0.97	0.00	0.00	100.0
0.98	0.00	0.00	100.0
0.99	0.00	0.00	100.0
1.00	0.00	0.00	100.0

Table 4: Final population mean and standard deviation for scenarios with $\text{mates}_{\max} = 6$

Female Ratio	Final Mature Population Mean	Final Mature Population SD	Extinction Percentage
0.50	282.99	7.42	0.0
0.60	284.63	6.53	0.0
0.70	284.94	5.98	0.0
0.75	284.24	6.51	0.0
0.80	283.59	7.41	0.0
0.85	281.28	8.99	0.0
0.86	282.19	8.31	0.0
0.87	281.74	9.23	0.0
0.88	281.10	9.47	0.0
0.89	278.29	13.93	0.0
0.90	222.51	76.26	2.8
0.91	260.32	44.18	0.4
0.92	197.97	86.26	6.7
0.93	95.15	79.35	26.7
0.94	29.19	36.70	68.9
0.95	8.25	5.36	99.6
0.96	1.33	0.47	99.7
0.97	0.00	0.00	100.0
0.98	0.00	0.00	100.0
0.99	0.00	0.00	100.0
1.00	0.00	0.00	100.0