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Population dynamics of *Ctenosaura bakeri*

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Abstract

The Ctenosaura bakeri is an iguana species endemic to the island of Utila, a small island off the eastern coast of Honduras. It is currently one of the species of the genus Ctenosaura most threatened with extinction, having its conservation status labelled as "Critically Endangered" by the IUCN Red List.

The goals of this paper are to give some mathematical insights on the intrinsic trend of the whole population and to analyse the influence of the greater threats to the survival of the species (such as sex dependent hunting and habitat destruction).

We will use a transition matrix approach to investigate the intrinsic trend of the population and we will provide arguments for the estimation of the different parameters.

For the influence of the threats we will take a deterministic approach using systems of ODEs and DDEs, investigating the stationary points and their stability and giving prediction through simulations for the evolution of the population.

We will also introduce a first model for the occurence of hybridization with another iguana species of the island.

The achieved results are summarized and still open questions stated at the end.

Population dynamics of *Ctenosaura bakeri*

Contents

Chapter 1

Introduction

As we will see in Chapter 2 the problem of predicting the dynamics of a system, let it be demographical, economical or biological has fascinated humans for centuries. In 1798 Thomas Malthus gave birth to a first approach to model a real world situation to describe the evolution of the demographics of a population. Of course it was a primitive model and quite unrealistic but it was a beginnig.
Since then, many progresses have been made starting from the logistic equation (the improvement of Malthus approach) arriving to more recent approaches which include a time delay.

With this elaborate we want to give some predictions on the population dynamics of an endangered species of Iguana (see below for further details). We will use different models to approach the study of the dynamics but what is in common to the models we used is that they are all deterministic: since we are studying a population with a relatively large number of individuals we can neglect the stochastic effects.

However, we will start using a linear discrete time model and we will focus on the analysis of the eigenvalues of the corresponding matrix for our model. After that, we will use a linear continuous time model (via ODEs and DDEs) and we will focus on the study of the stability of the trivial stationary point. Lastly, we will formulate a nonlinear continuous model (via ODEs and DDEs) and we will study the stability of the stationary points (the trivial and the nontrivial one) for both the ODEs approach and the DDEs one.

It is important to stress that most of the models we made up were solved through numerical methods.

1.1 Biological background

The *Ctenosaura bakeri* (commonly known as Utila Spiny-tailed Iguana) is an iguana species endemic to the island of Utila (i.e., it can only be found there), a small island off the eastern coast of Honduras. It is currently one of the species of the genus *Ctenosaura* most threatened with extinction, having its conservation status labelled as "Critically Endangered" (which is just above being "Extinct in the Wild") by the IUCN (International

Union for Conservation of Nature) Red List.

This iguana appears from dark brown to black in its earliest stages (this help the hatchlings and the juveniles to blend in with the vegetation and the soil of the swamps this species inhabits) and it brightens with age to a blue or light grey.
After hatching and until sexual maturity the *Ctenosaura bakeri* will grow linearly in total length and Snout-Vent length (or SVL, which is the typical way of measuring one iguana's length, especially if this one can willingly lose its tail) and exponentially in weight. It is interesting to see how the relative tail length (when the tail is present) changes while growing: it decreases with increasing SVL, which results in hatchlings with a tail length almost equals to four times their SVL, while adults have a tail length almost equals to 1.5 times their SVL ([9], [12]).
This species also shows sexual dimorphism with males larger and heavier than females, with the former ones exhibiting "comblike" dorsal crests (the genus *Ctenosaura* was named after the latter ones since it derives from two Greek words: *ctenos* meaning "comb" and *saura* meaning "lizard").

This reptile can be considered strictly stenoecious (i.e., it has a very restricted range of habitats): it is the only iguana species that lives almost its whole life in mangrove swamps of the island (the *Ctenosaura bakeri* is called "Swamper" by the locals because of this). It is thought that this species took the swamps as its habitat because of the competition with the other larger and more agressive local (but not endemic) iguana species belonging to the same genus: the *Ctenosaura similis* (which is also the fastest lizard on Earth reaching up to 35 km/h). Yet the swamp's soil is not very suitable for egg laying, let alone for digging nesting burrows since it is muddy and frequently submerged, so when the laying season approaches the pregnant females migrate to Utila's beaches and dig there the nests. Once the eggs hatch the newborns will in turn migrate back to the swamps ([9], [12]).
The mangroves in the swamps (whose species are the *Rhizophora mangle*, the *Avicenna germinans* and the *Laguncularia racemosa* also known as Red mangrove, Black mangrove and White mangrove, respectively) provide retreats and shelters with their cavities to the *Ctenosaura bakeri*. It has been observed that the different mangrove species are preferred by different age classes: hatchlings prefer the red mangroves, juveniles the black ones, while adults the white ones ([31], [8]).

The *Ctenosaura bakeri* like most of the iguana species is primarily herbivorous, eating flowers, leaves, stems and fruits, but (just like many species of the Iguanidae family) it is also an opportunistic carnivore (especially in its early stages) preying upon arthropods (mainly termites and fiddler crabs) and other small animals (cannibalism has also been recorded).

The mating season begins with the dry season (roughly from mid-January to early August) which starts when both the frequency and the quantity of the rainfall of the previous months decrease (it will be interesting to study how the current climate crisis will affect that). Usually mating reaches its peak at mid-February while egg laying is at its highest intensity from early April to mid-April. As mentioned before gravid females will migrate

from the swamps they inhabit to the beaches of the Island and there will start looking for a suitable place for nesting (they can be very ”picky”, looking for spots clear from vegetation and debris). Nest burrows vary in depth from 200 mm to 600 mm also depending on the material composition of the substarte.
The average temperature in the nesting burrows ranged from 29.1°C to 30.8°C in a study dated 2000 ([9], [12]). Because of this short range of temperatures it is not clear whether the *Ctenosaura bakeri* is a species with temperature-dependent sex determination (TSD) like many other reptiles and lizards or not, nevertheless because of the reported sex ratio of males to females of 1:1.2 (taken from a study dated 2000, [12]) it can be considered a Fisherian species (the *Alligator missisippiensis* is an example of a reptilian species which is non-Fisherian, having a sex ratio of males to females of roughly 1:5 because of its TSD). The incubation period lasts from 85 to 99 days, after that the newly hatched iguanas will migrate back to the swamps, as previously mentioned ([9], [12], [18]).

There are not many species that prey on adults of *Ctenosaura bakeri*, some of the ones that have been observed are: the Common Black Hawk (*Buteogallus anthracinus*), Great Egret (*Ardea alba*) and Boa Constrictor(*Boa imperator*). In the earliest stages of an iguana's life it is a completely different matter, though: hatchlings are preyed upon by many more species than the previously mentioned, including but not limited to birds like the Great-tailed Grackle (*Quiscalus mexicanus*) and the Green Heron (*Butorides virescens*); snakes like the Salmon-bellied Racer (*Mastigodryas melanolomus*), the Mexican Parrot Snake (*Leptophis mexicanus*), the Mexican Vine Snake (*Oxybelis aeneus*) and the Green Vine Snake (*Oxybelis fulgidus*) and, finally, lizards too like the Brown Basilisk (*Basiliscus vittatus*), the Common Spiny-tailed Iguana (*Ctenosaura similis*) and, as previously mentioned, the very *Ctenosaura bakeri*.
The above mentioned predators are autochtonous to Utila, nevertheless there are some allochthonous (i.e., which have been introduced by humans) like rats and free-roaming dogs and cats ([18]).

As for many other species whose population is decreasing (which is the current trend of *Ctenosaura bakeri*) there are many contributory causes behind the decision of labelling this iguana species as ”Critically Endangered”.

The main threat to the survival of this species is the habitat degradation and destruction of both the swamps and the beaches. Causes of destruction and degradation of swamps are attributable to infrastructure development for the tourism industry; mangrove swamps are used as garbage dumping sites and there is a potential risk posed by water contamination from terrestrial landfills and agricultural chemicals (fertilisers and pesticides). There is also an extensive deforestation of mangrove habitat for housing and marina construction and for future potential crop plantations (this could become a more prevalent threat in the future, since cattle have been observed trampling over nests). Mangroves near developed areas and roads are also becoming isolated from their water sources, causing the trees to die and leaving large patches of dead mangrove in dry lagoons. While taking into consideration the beaches, causes of destruction and degradation of them are mainly oceanic and local pollution (mainly plastics) which affect the nesting sites by obscuring laying sites and also potentially affecting sand and incubation temperatures. Other factors of degradation of nesting beaches are the intensive removal of vegetation in preparation for development and the presence of invasive plant species which contribute to the impracticability of nesting sites. Because of the increasing loss of shelters due to the mangrove forests deforestation the previously mentioned predators may become a greater threat to the survival of the *Ctenosaura bakeri* (since they do not feed exclusively on it).

The second main threat is local hunting: even though the *Ctenosaura bakeri* is protected by Honduran law through a ban on hunting, in place since 1994, the actual enforcement of the law is inadequate and both locals and inlanders are still poaching this species primarly for meat consumption. While this species is not specifically targeted by hunters, it is clear that if you have to choose between a rather slow and sedentary iguana and the fastest lizard on Earth you would go for the former as chances of catching it are significantly higher. To make things worse gravid females are considered a delicacy for the Easter's meals (which coincidentially occurs during the period of migration from the swamps to the nesting beaches): this habit is utterly devastating since by doing this two generations are wiped out at once.

This practice further jeopardizes the survival of the species not only because specifically targeting gravid females is detrimental for the well being of the yearly reproductive output but also because it could lead to a male-biased population which is not optimal for an overall growth of the whole population (especially for nonmonongamous species, like the *Ctenosaura bakeri*), while, on the countrary, having a female-biased population is excellent for the continuity of the species.

Even though *Ctenosaura bakeri* and *Ctenosaura similis* are not so closely related (with the former genetically closer to the species *Ctenosaura oedirhina*, endemic to Roatán, another Honduran island, and *Ctenosaura melanosterna*) it has been observed (in areas of habitat niche overlap) that they can mate and produce fertile hybrids.

While not a threat to the survival of *Ctenosaura bakeri* per se, in the future it can become one in combination with its habitat destruction: with fewer hectars at *Ctenosaura bakeri* disposal, the interactions between it and *Ctenosaura similis* will significantly increase, which will lead to a greater number of fertile hybrids. It has been observed that the hybrids have a greater clutch size than *Ctenosaura bakeri* and thus a greater fitness: this would lead to the complete eradication of *Ctenosaura bakeri* where the hybrids are present (since they compete for the same resources).

It is still unclear whether the hybrids' spawn (in the long run and after multiple generations) can fall back into one of the two species or not.

Another potential threat linked to habitat destruction is the fragmentation of the population: even though *Ctenosaura bakeri* is a sedentary species, subpopulations are not present, meaning the population is homogeneous from a genetic point of view. Habitat destruction is likely to cause a segregation of two or three different subpopulations which would result in a lower biodiversity and higher chances of extinction: isolated subpopulations could present higher cases of inbreeding and would face stronger threats (because of their smaller number of individuals).

1.2 Approach

As for many other realistic situations, there are almost countless approaches to study the population dynamics of *Ctenosaura bakeri*. In this paper we will focus on four different aspects.

We will firstly study the intrinsic trend of the whole population via a Transition Matrix approach, i.e. a discrete model,: we will take into consideration its growth without considering habitat destruction and poaching, so we will only look at survival rates and preying by both locals and exotic predators. We will study the dominating eigenvalue to check whether the population would intrinsically grow or not.

Secondly, we will take a closer look to the effects of human hunting (not taking into consideration habitat destruction) on the population sex ratio: we will try to fit data and analyse the qualitative behaviour. We will use a linear continuous model to tackle this problem thus we will focus on the stability of the trivial stationary point. We will first assume the hunting effort to be constant and we will set up two models to study the dynamics: first without delay and afterwards with a delay factor. Then, we will assume the hunting effort not to be constant and we will repeat the process we did for the constant hunting effort: first we will consider our model without delay and then with delay.

Thirdly, we will look at the consequences of habitat destruction (this time not directly taking into consideration poaching) of both the mangrove forests and the nesting beaches. We will use a nonlinear continuous time model, and first we will study the stationary points of the models and their stability. Then we will introduce the factors of habitat destruction and we will make some predictions for both a nondelayed approach and a delayed on. Furthermore, we will add a response type death rate to better reflect the effects of habitat destruction on the population.

Lastly, even though it has not been well understood yet from a biological point of view, we will try to give a model for the hybridization effects on the populations of *Ctenosaura bakeri* and *Ctenosaura similis* for future research.

The main goal of this thesis is trying to understand which is the current greater threat to the survival of the *Ctenosaura bakeri* and see what actions could be taken to reverse the trend of population decrease.

Chapter 2

Mathematical instruments and theorems

In this chapter we will focus on the mathematical theory behind the arguments of the next chapters (see [14] for further details). As mentioned in the in Introduction we will use a deterministic approach only, since we can assume the population we are considering to be large enough to consider stochastic effects to be negligible.

Historically, the first approach to describe the evolution of a population was the one made by Thomas Malthus in 1798, which in its discrete form reads:

$$x_{n+1} = x_n + rx_n$$

where x_n is the population we are considering at time n and r is the net growth rate per individual. We can easily see that, given a starting population x_0, we can compute an explicit solution which reads:

$$x_n = (1 + r)^n x_0$$

For biological models it makes sense to consider $1 + r \geq 0$, thus we can split the solution in two (main) cases (omitting the case for $r = -1$ and for $r = 0$):

- $-1 < r < 0$, we have a strictly monotone decreasing sequence, with $x_n \to 0$.
- $r > 0$, we have a strictly monotone increasing sequence, with $x_n \to \infty$.

We can see that the main problem with this model is that it can predict an infinite growth of a population. This is not realistic since every population needs resources to grow and there are no such things as infinite resorces. Nevertheless, it can still be used both in its discrete form and in its continuous form (which reads $\dot{x}(t) = rx(t)$) to describe the growth of a relatively small population which has access to abundant resources (like the first phases of bacterial growth).

Verhulst in 1838 proposed a variation of the Malthus model, which in its continuous form reads:

$$\dot{x}(t) = rx(t)\left(1 - \frac{x(t)}{K}\right)$$

where r is again our growth rate which now is slowed down by the factor $\left(1 - \frac{x(t)}{K}\right)$. K is the so called carrying capacity, which represents the maximum number of individuals that our system can sustain. We can see that this model does not consider an infinite growth over time since, if $r > 1$ (and our starting population $x(0) << K$) we will have at first a growth similar to exponential but afterwards the population will tend to K.

From the approaches of both Malthus and Verhulst we can see that the deterministc models can be discrete or continuous in time. In this study we will use both the approaches and in the next sections we will focus on the theory and instruments needed for the following chapters (we will omit all the proofs of the following mentioned theorems or propositions).

2.1 Discrete time models

Discrete time models to describe the dynamics of a population are mainly used when the previously mentioned population has a fixed time interval between generations, due to, for example, breeding seasons which occur in regular time interval. Furthermore we will consider only linear discrete time model, since we will use only this kind of approach in the next chapter.
Thus, the idea is to generalize the Malthus approach, by having, as population a vector and as growth rate a matrix rather than a number:

$$\vec{x}_{n+1} = L\vec{x}_n \tag{2.1}$$

where $\vec{x}_n \in \mathbb{R}^m$ and $L \in \mathbb{R}^{m \times m}$. Thus, $\vec{x}_n = L^n\vec{x}_0$ is the solution of (2.1) where $\vec{x}_0$ is our starting population.
$\vec{x}_0$ can be represented by using a basis $(\vec{v}_1, \vec{v}_2, ..., \vec{v}_m)$ of eigenvectors of L:

$$\vec{x}_0 = b_1\vec{v}_1 + b_2\vec{v}_2 + ... + b_m\vec{v}_m$$

Let λ_1,λ_2,..., λ_m be the corresponding eigenvalues to $\vec{v}_1, \vec{v}_2, ..., \vec{v}_m$, then we get:

$$\vec{x}_n = L^n\vec{x}_0 = L^n(b_1\vec{v}_1 + ... + b_m\vec{v}_m) = b_1L^n\vec{v}_1 + ... + b_mL^n\vec{v}_m = b_1L^{n-1}(L\vec{v}_1) + ... + b_mL^{n-1}(L\vec{v}_m) =$$

$$= b_1L^{n-1}(\lambda_1\vec{v}_1) + ... + b_mL^{n-1}(\lambda_m\vec{v}_m) = b_1\lambda_1^n\vec{v}_1 + ... + b_m\lambda_m^n\vec{v}_m$$

We can see that the long term behaviour is mainly determined by the eigenvalues and their corresponding eigenvectors. In particular we will look at the so called Dominating Eigenvalue.

Definition 2.1 (Dominating Eigenvalue)**.** Let L be a matrix, f a polynomial and $\lambda_1 \in \mathbb{R}$.

1. λ_1 is called simple zero of $f(\lambda)$, if $f(\lambda) = 0$ and $f'(\lambda) \neq 0$.

2. λ_1 is called simple eigenvalue of L, if λ_1 is simple zero of $det(L - \lambda_1 I)$ (characteristic polynomial).

3. λ_1 is called dominating eigenvalue of L, if the following conditions are satisfied:
   (a) λ_1 is simple eigenvalue
   (b) λ_1 is real and nonnegative
   (c) $\lambda_1 >\mid \lambda \mid$ for all other eigenvalues λ of L.

Then the following proposition tells us explicitely how the long term behaviour of 2.1 looks like.

Proposition 2.1.1 (Dominating Eigenvalue)**.** *Suppose matrix L has a dominating eigenvalue λ_1. Let $\vec{v}$ be the corresponding eigenvector. Then, there exists an $a \in \mathbb{R}$ with*

$$\lim_{j\to\infty} \frac{\vec{x}(j)}{\lambda_1^j} = a\vec{v},$$

i.e., for large j we have $\vec{x}(j) \approx \lambda_1^j a\vec{v}$.
(Assuming that $\vec{x}(0)$ can be represented as $\vec{x}(0) = a\vec{v} + b\vec{w} + \dots$ in the basis of eigenvectors, where $a \neq 0$).

We can easily see that if our dominating eigenvalue is smaller than 1 the solution will tend to 0 while, if it is larger than 1 the population will grow to infinity.

2.2 Continuous time models

In this section we will take a look at the theory we will need for the continuous time models we will use in the next chapters. We will first look at linear ODE systems, which are of the form:

$$\dot{x} = Ax$$

Similar to the discrete systems, to learn about the behaviour of the linear continuous system we will look at the eigenvalues and the eigenvectors. In particular we will focus on the special case of $A \in \mathbb{R}^{2\times 2}$, i.e.,

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = A \begin{pmatrix} x \\ y \end{pmatrix}$$

We know that the characteristic equation reads $\lambda^2 - tr(A) + det(A) = 0$, thus in this special case the eigenvalues read $\lambda_{1,2} = \frac{tr(A) \pm \sqrt{tr^2(A) - 4det(A)}}{2}$. Thus calling $\Delta = tr^2(A) - 4det(A)$, we have the so called trace determinant graph which is useful to determine the nature of the stationary points, which in the linear case is only 0.

The main cases are:

- Sources, given by the fact that both λ_1 and λ_2 are positive.
- Saddles, given by the fact that one among λ_1 and λ_2 is positive while the other is negative.
- Sinks, given by the fact that both λ_1 and λ_2 are negative.

Furthermore we have a useful criterion to decide for or against stability in a linear system:

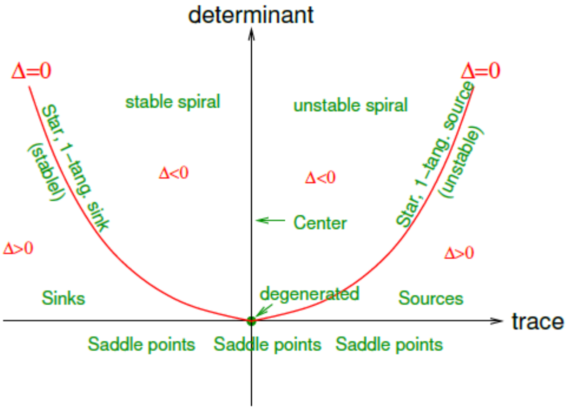


Figure 2.1: Picture taken from [14].

Proposition 2.2.1 (Linear case). *Consider the linear case* $\dot{x} = Ax$, $A \in \mathbb{C}^{n\times n}$. *Let* $\sigma(A)$ *be the spectrum of* A.

1. *0 is asymptotically stable* $\Leftrightarrow$ *Re* $\sigma(A) < 0$.
2. *0 is stable* $\Leftrightarrow$ *Re* $\sigma(A) \leq 0$ *and all eignevalues* λ *with Re* $\lambda = 0$ *are semi-simple.*
3. *If there is a* $\lambda \in \sigma(A)$ *with Re* $\lambda > 0$, *then 0 is unstable.*

2.2.1 Nonlinear systems

For the nonlinear system, to analyze the behaviour around the stationary points, we will proceed through the so called linearization process.

Let $\dot{x} = f(x)$, with $f \in C^1(\mathbb{R}^n, \mathbb{R}^n)$, $f(\bar{x}) = 0$, (i.e., $\bar{x}$ is a stationary point) $\bar{x} \in \mathbb{R}^n$. We consider the solutions $x(t)$ of $\dot{x} = f(x)$ in the neighbourhood of $\bar{x}$, $x(t) = \bar{x} + z(t)$, then

$$\dot{z}(t) = f'(\bar{x})z(t) + o(\|z\|)$$

The corresponding linearised system is $\dot{z} = Az$, $A = f'(\bar{x}) = \left(\frac{\partial f_i}{\partial x_k}(\bar{x})\right)$, being based on the Jacobian matrix of the right hand side function.

Proposition 2.2.2. *If the real parts of all eigenvalues of* $A = f'(\bar{x})$ *are negative, then* $\bar{x}$ *is exponentially asymptotically stable, i.e., there are constants* $\delta, C, \alpha > 0$, *such that* $\|x(0) - \bar{x}\| < \delta$ *implies*

$$\|x(t) - \bar{x}\| < Ce^{-\alpha t} \quad \text{for } t \geq 0$$

Addendum:
From Re $\sigma(A) \cap (0, \infty) \neq \emptyset$ *it follows that* $\bar{x}$ *is unstable.*

Definition 2.2 (Hyperbolic point). $\bar{x}$ is called hyperbolic, if $0 \notin \text{Re}\ \sigma(f'(\bar{x}))$.

Proposition 2.2.3 (Hartman and Grobman)**.** *Let $\bar{x}$ be hyperbolic. Then, there is a neighbourhood U of $\bar{x}$ and a homeomorphism $H : U \longrightarrow \mathbb{R}^n$ with $H(\bar{x}) = 0$, which maps the trajectories of $\dot{x} = f(x)$ one-to-one into trajectories of $\dot{z} = Az$, with respect to the time course.*

Thus, thanks to the proposition of Hartman and Grobman, if the hypotheses are satisfied, i.e. if our stationary point is hyperbolic, we are able to use the tools of the analysis of the linear systems for the analysis of the nonlinear ones.

Another tool for the analysis of the nonlinear 2D systems, something we will use in chapter 5 is the following criterion:

Proposition 2.2.4. *Let $D \subseteq \mathbb{R}^2$ be a simply connected region and $(f, g) \in C^1(D, \mathbb{R})$ with $div(f, g) = \frac{\partial f}{\partial x} + \frac{\partial g}{\partial y}$ being not identically zero and without change of sign in D. Then the system*

$$\dot{x} = f(x, y)$$
$$\dot{y} = g(x, y)$$

has no closed orbits lying entirely in D.

which gives us insights on the solution curves of our system without directly studying it.

2.2.2 DDEs systems

The basic idea of delay models is the change of a variable may depend not only on its current state but also on its state some time in the past (for further details see [32]).
Thus we will have a so called (discrete time) delay differential equation (with $f \in C^1(\mathbb{R}^n, \mathbb{R}^n)$ and $x(t) \in \mathbb{R}^n$), like the following:

$$\dot{x}(t) = f(x(t), x(t - \tau))$$

where $\tau > 0$, here is a parameter.
It is important to note that instead of the initial value in the case of an ODE, $x(t)$ needs to be given for all $t \in [-\tau, 0]$, which is called history function.

The approach to study the stability of the stationary points is the same as for the ODEs (furthermore, the stationary points are the same as for an ODE system): we first perform a Taylor expansion around our stationary point $(\bar{x})$, dropping all terms of second or higher order (i.e., we linearize the system).

Our linearized system in matrix notation is slightly different by the usual ODE system because of the presence of a delay and it reads:

$$\dot{x}(t) = Ax(t) + Bx(t - \tau)$$

where $A = \left(\frac{\partial f_i}{\partial x_k(t)}(\bar{x})\right)$ and $B = \left(\frac{\partial f_i}{\partial x_k(t-\tau)}(\bar{x})\right)$. Thus, A contains the non-delayed and B the delayed terms.
The characteristic equation in terms of A and B is given by:

$$det(\lambda I - A - Be^{-\lambda}) = 0$$

This equation usually leads to a transcendental equation, but luckily in our case, in chapter 5 we will have back a ”normal algebraic” equation, as for the ODEs case.

Chapter 3

Transition Matrix approach

3.1 Introduction and assumptions

In this chapter we will study the population dynamics of the *Ctenosaura bakeri* through the analysis of the eigenvalues of the transition matrix. This approach will give us an insight to the intrinsic well-being of the population: we will be able to understand whether the population could survive on its own if we are not considering hunting and habitat destruction and in case of a negative answer, we will be able to determine which stage is best to intervene on in order to reverse an intrinsic extinction trend.

First we need to make the following assumptions, keeping the model as simple as possible, but with most important properties for a realistic situation:

- We consider the population to be uniformly distributed across its habitat.
- We divide the population into 4 different non overlapping age classes:
  - Eggs and Hatchlings (from ”-0.5” to 0.5 years old)
  - Juveniles or sub adults (from 0.5 to 2.0 years old)
  - Novice breeders (from 2.0 to 2.5 years old)
  - Mature breeders (from 2.5 years old on)
- We consider the male-female ratio to be 50:50.
- Once an individual reaches sexual maturity they mate every year until their natural death.
- Mating (and thus egg laying) occurs at the same time for every sexual mature individual.
- We consider the incubation period to be 6 months.
- We consider the survival probability in the Hatchling and Juvenile age class to increase linearly in time.
- We consider the survival probability in the adult age classes to be constant in time.
- We are not considering (human) hunting and habitat destruction to occur.

3.2 The model

This is the core section of this chapter; our main goals here are: setting up a transition matrix for our population and giving an estimation of the different parameters (average of eggs laid every year per individual, survival probabilities for each age class, etc.). After that we will compute the eigenvalues of our transition matrix and we will focus on the Dominating Eigenvalue in order to see which will be the predicted population trend. It is important to consider that this approach is primarily used for asexually reproducing species, while we are considering the *Ctenosaura bakeri* which is a sexually reproducing reptile. Because of that (and thanks to the 50:50 sex ratio assumption), we will need to keep in mind that we are only considering the female individuals out of our total population with all of the implications this will raise (halving the initial population of each age class, halving the average of eggs laid per female, etc.).

3.2.1 The approach

The transition matrix (from one year to the following) for a four-stage model (with stages as introduced before) reads in general form:

$$L = \begin{pmatrix} p_1 + e_1 & e_2 & e_3 & e_4 \\ q_1 & p_2 & 0 & 0 \\ 0 & q_2 & p_3 & 0 \\ 0 & 0 & q_3 & p_4 \end{pmatrix}$$

where e_i denotes the eggs laid per female iguana of stage i per year, p_i the proportion of individuals that remain in stage i in the following year and q_i the proportion of individuals that survive and move into stage $i+1$. It is important to note that $p_i + q_i$ yields the annual survivorship of stage i (s_i).

In our scenario we will further split the age classes from four to seven:

- Eggs from "-0.5" to 0 years old (E)
- Hatchlings from 0 to 0.5 years old (H)
- Juveniles or sub adults from 0.5 to 1.0 year old (J_1)
- Juveniles or sub adults from 1.0 to 1.5 years old (J_2)
- Juveniles or sub adults from 1.5 to 2.0 year old (J_3)
- Novice breeders (NB)
- Mature breeders (MB)

We did this so that the p vector will consist only of the p_{MB} component while all the other ones will be 0 (for the other classes we have transition only) and thus the estimation of the q components will be easier.

The "problem" is that in our model we have transitions between two stages that occur every six months while reproduction (and thus egg laying) occurs once a year. We can tackle this problem by considering our transition matrix to be the product of two other different matrices: L_e which is the transition matrix when the egg laying occurs and L_h which is the transition matrix when the hatching of the eggs occurs (this is also the matrix which represents the transition of the just hatched hatchlings to the J_1 class). So our transition matrix reads:

$$L = L_h L_e$$

where:

$$L_e = \begin{pmatrix} \tilde{p}_1 + e_1 & e_2 & e_3 & e_4 & e_5 & e_6 & e_7 \\ \tilde{q}_1 & \tilde{p}_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & \tilde{q}_2 & \tilde{p}_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & \tilde{q}_3 & \tilde{p}_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & \tilde{q}_4 & \tilde{p}_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & \tilde{q}_5 & \tilde{p}_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & \tilde{q}_6 & \tilde{p}_7 \end{pmatrix} \text{ and } L_h = \begin{pmatrix} \tilde{p}_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ \tilde{q}_1 & \tilde{p}_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & \tilde{q}_2 & \tilde{p}_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & \tilde{q}_3 & \tilde{p}_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & \tilde{q}_4 & \tilde{p}_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & \tilde{q}_5 & \tilde{p}_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & \tilde{q}_6 & \tilde{p}_7 \end{pmatrix}$$

Here the $\tilde{p}$ and the $\tilde{q}$ vectors have the same role of the previous p and q vectors, but this time over a period of six months rather than one year. We can then drop the tildes and use the observation we made after the splitting into seven age classes so that the matrices read:

$$L_e = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & e_{NB} & e_{MB} \\ q_{E\to H} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & q_{H\to J_1} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & q_{J_1\to J_2} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & q_{J_2\to J_3} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & q_{J_3\to NB} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & q_{NB\to MB} & p_{MB} \end{pmatrix}$$

$$L_h = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ q_{E\to H} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & q_{H\to J_1} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & q_{J_1\to J_2} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & q_{J_2\to J_3} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & q_{J_3\to NB} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & q_{NB\to MB} & p_{MB} \end{pmatrix}$$

It is important to highlight that we are considering an incubation period of six months instead of 3 months (which is generally what happens in nature) in order not to further split the age classes and by doing so complicating our transition matrix. We can interpret this by also considering the mating season to be in the same time frame.
Also, we will not have all the eggs turning into hatchlings, so we will consider $q_{E\to H} =$

$r_h < 1$, where r_h is the natural hatching rate of *Ctenosaura bakeri*'s eggs. Keeping this in mind, then our matrix L will read:

$$\begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & r_h e_{NB} & r_h e_{MB} \\ r_h q_{H\to J_1} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & q_{H\to J_1} q_{J_1\to J_2} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & q_{J_1\to J_2} q_{J_2\to J_3} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & q_{J_2\to J_3} q_{J_3\to NB} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & q_{J_3\to NB} q_{NB\to MB} & q_{NB\to MB} p_{MB} & p_{MB}^2 \end{pmatrix}$$

It is worth noting that the first row of our matrix is a null vector and this is due to the fact that the eggs' age class lasts only 6 months and we are considering the situation where the egg laying season occurs at the beginning of our one year cycle, so by the end of the latter all the eggs which have hatched transit to the next age classes.
This means that we will always have at least a null age class among E, H, J_1, J_2, J_3 and NB every six months.

3.2.2 Parameter estimation and generation time

Now that we have set up our transition matrix we need to give an estimation for the different parameters. Unfortunately, there is not much data on the survival probability for the different age classes, especially for the hatchlings and the subadults since it appears they are very hard to detect to begin with ([12]), let alone being able to monitoring them. Nevertheless we can try giving some realistic estimation based on observations of similar species in similar habitats.

Let us start with the hatching rate (r_h): one statistical study ([9]) gave us the natural hatching rate of *Ctenosaura bakeri* to be 92.3%. Another study ([12]) gave us the mean clutch size (i.e., the mean number of eggs laid per female iguana) for both Novice Breeders and Mature Breeders, which respectively are $\tilde{e}_{NB} = 8.7$ and $\tilde{e}_{MB} = 11.2$. It is interesting to see that the difference of eggs laid form one age class to the other one is due to the fact that there is a linear correlation between the mean Snout-Vent length (SVL) and the mean clutch size.
It is also important to notice, as we said previously, that we are considering only the females in our model, so since not all the hatchlings coming out the eggs laid will be females, we will have $e_{NB} = \frac{\tilde{e}_{NB}}{2} = \frac{8.7}{2} = 4.35$ and $e_{MB} = \frac{\tilde{e}_{MB}}{2} = \frac{11.2}{2} = 5.6$ i.e., since we are assuming the ratio between males and females to be 50:50, the eggs that will carry female individuals should be half the total of eggs laid per female.

Now we need to estimate $q_{H\to J_1}$. Luckily enough there was a study made specifically to give an estimation for the survival rate of hatchlings of *Cyclura cornuta stejnegeri* on the Mona Island ([25]). Of course this is a completely different species (it does not even share the same genus with *Ctenosaura bakeri*) but at the initial stages most iguanas share the same size and appearance. Furthermore, both species live on a caraibic island and share almost the same predators so it is fair to assume a similar survival rate for the *Ctenosaura bakeri* hatchlings. The survival rate the study provided us is 0.22 over the first five months of life, but we need a survival rate over the first six months. If the survival rate was to stay constant we would have a survival rate of 0.7387 per month but we are assuming that the survival rate grows linearly over time (this assumption makes sense if we are considering that the hatchlings are linearly increasing in length, thus we are assuming the threats to them to decrease linearly) so we are assuming a survival rate of 0.72 for the first month, 0.73 for the second, 0.74 for the third, 0.75 for the fourth and 0.76 for the fifth. These rates are realistic indeed since they give us back a survival rate over 5 months of 0.22. With this procedure in mind, we can assume a survival rate of 0.77 for the sixth month and this will give us a total suvival rate of 0.17 over the first six months, i.e., $q_{H\to J_1} = 0.17$.

Now we will give an estimation for $q_{NB\to MB}$ and p_{MB}. We are assuming the survival probability for adults to be constant in the age class, rather than increasing (linearly) as we assumed for the sub adults and the hatchlings. This is mainly due to the fact that the threats to the adults will not significantly decrease with the increase of size since, for example, the few species which still prey upon the *Ctenosaura bakeri* at this stage of its life, will do regardless of the bulk of the iguanas (individuals of *Ctenosaura bakeri* are considered adults when they reach the "critical" SVL of 150 mm so we assume that, by then, the predators of the juveniles are no longer able to prey upon the adults).
We also assumed a mean lifespan (or, more likely, the average upper age limit for an individual to reproduce) of a specimen which reached sexual maturity to be around 10 years. This is due to the fact that the mean lifespan of two similar species (*Iguana iguana* and *Ctenosaura similis*) are, respectively, 9 years ([4], though in this case, it is probably the average upper age limit for an individual to reproduce, since we found other articles, like [37], that give us estimations of an average lifespan of 20 years) and 5-20 years ([36]). We also found a report of a *Ctenosaura bakeri* which lived in captivity up to 13.8 years ([35]).
This being said we call $x = q_{NB\to MB} = p_{MB}$ and we set

$$\begin{cases} (x^2)^8 \geq 0.5 \\ (x^2)^9 < 0.5 \end{cases}$$

i.e., the probability (starting from the beginning of adulthood) to reach 10 years (or a less than 10 years age) should be greater than 0.5, while the probability to reach the eleventh year should be less than 0.5. This yields:

$$\begin{cases} x \geq 0.95760 \\ x < 0.96222 \end{cases}$$

So we will take $x = 0.96$ so $q_{NB\to MB} = p_{MB} = 0.96$ and this result is consistent with the observations ([12]) where it was found that all the marked adult individuals survived after one year from the first capture.

Now we will give an estimation for $q_{J_1\to J_2}$, $q_{J_2\to J_3}$ and $q_{J_3\to NB}$. Just like we assumed a linear increase of the survival probability for the hatchlings, we will assume the same for the sub adults. We start giving an estimation of the survival probability for the first month of the age class: we assumed it to be 0.81 (which is slightly larger than the survival probability for the last month of the hatchling age class). Then we proceed to give an estimation of the survival probability for the eighteenth month (the last one): we assumed it to be 0.98 (which is slightly smaller than the adult class survival probability per month, which is $\sqrt[6]{q_{NB\to MB}} = \sqrt[6]{p_{MB}} > 0.99$). Having fixed the range boundaries we are able to calculate the increase of the survival probability per month: $\frac{0.98-0.81}{17} = 0.1$. This will lead us to the calculation of $q_{J_1\to J_2}$, $q_{J_2\to J_3}$ and $q_{J_3\to NB}$:

$$q_{J_1\to J_2} = (0.81)(0.82)(0.83)(0.84)(0.85)(0.86) = 0.34$$

$$q_{J_2\to J_3} = (0.87)(0.88)(0.89)(0.90)(0.91)(0.92) = 0.51$$

$$q_{J_3\to NB} = (0.93)(0.94)(0.95)(0.96)(0.97)(0.98) = 0.76$$

With the survival probabilities we want to see whether the age structure we chose is relevant. We will do it via calculating the generation time G given by the following:

$$G = \frac{\sum_{k=0}^{n} l(k)b(k)k}{\sum_{k=0}^{n} l(k)b(k)}$$

where k is the number of the age class (starting to enumerate from the youngest), $l(k)$ is the proportion of those individuals that survive until the beginning of age k (or, equivalently, the probability that an individual survives from birth to the beginning of age k) and $b(k)$ is the average number of (in our case again, female) offspring born by an individual of the corresponding age class.

Since

$$g(k) = \frac{l(k+1)}{l(k)}$$

we can calculate $l(k)$ knowing $g(k)$ (the survival probability):

$l(0) = 1.0$

$l(1) = l(0)g(0) = l(0)q_{H\to J_1} = (1.0)(0.17) = 0.17$

$l(2) = l(1)g(1) = l(1)q_{J_1\to J_2}q_{J_2\to J_3}q_{J_3\to NB} = (0.17)(0.34)(0.51)(0.76) = 0.02$

$l(3) = l(2)g(2) = l(2)q_{NB\to MB} = (0.02)(0.96) = 0.02$

So now we can build the corresponding life table:

Age Class	k	$l(k)$	$b(k)$
Hatchlings	0	1.0	0
Juveniles	1	0.17	0
Novice breeders	2	0.02	4.35
Mature breeders	3	0.02	5.6

Now we are able to calculate G:

$$G = \frac{\sum_{k=0}^{n} l(k)b(k)k}{\sum_{k=0}^{n} l(k)b(k)} = \frac{(0.02)(4.35)(2) + (0.02)(5.6)(3)}{(0.02)(4.35) + (0.02)(5.6)} \approx 2.56 > 1.0$$

Since our generation time is greater than 1.0, the age structure we chose to represent the *Ctenosaura bakeri* population is relevant.

Having checked the generation time, we can put the estimations we found earlier into our matrices L_e, L_h and L so that they finally read:

$$L_e = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 4.35 & 5.6 \\ 0.923 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.17 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.34 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.51 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.76 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.96 & 0.96 \end{pmatrix}$$

$$L_h = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0.923 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.17 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.34 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.51 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.76 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.96 & 0.96 \end{pmatrix}$$

$$L = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 4.02 & 5.17 \\ 0.16 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.06 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.17 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.39 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.73 & 0.92 & 0.92 \end{pmatrix}$$

3.2.3 Study of the eigenvalues and population estimation

Now that we have the transition matrix L we want to study its eigenvalues by studying the roots of its characteristic polynomial:

$$det(L-\lambda I) = det(\begin{pmatrix} -\lambda & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -\lambda & 0 & 0 & 0 & 4.02 & 5.17 \\ 0.16 & 0 & -\lambda & 0 & 0 & 0 & 0 \\ 0 & 0.06 & 0 & -\lambda & 0 & 0 & 0 \\ 0 & 0 & 0.17 & 0 & -\lambda & 0 & 0 \\ 0 & 0 & 0 & 0.39 & 0 & -\lambda & 0 \\ 0 & 0 & 0 & 0 & 0.73 & 0.92 & 0.92-\lambda \end{pmatrix}) = \lambda^7 - \frac{92}{10^2}\lambda^6 - \frac{941}{10^4}\lambda^4 - \frac{248}{10^4}\lambda^3$$

Thus the eigenvalues are:

$$\lambda_{1,2,3} = 0, \quad \lambda_4 \approx -0.1867, \quad \lambda_{5,6} \approx 0.0378 \pm 0.3567i \quad \text{and} \quad \lambda_7 \approx 1.0311$$

Then we can find the matrix V of the corresponding eigenvectors (to be read in columns):

$$\begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.7321 & 0.9569 & 0.9569 & -0.9819 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -0.2353 & 0.0169 + 0.1592i & 0.0169 - 0.1592i & -0.0571 \\ 0.2161 & -0.2161 & 0.2161 & 0 & 0 & 0 & 0 \\ -0.7708 & 0.7708 & -0.7708 & 0.4916 & -0.1702 + 0.0365i & -0.1702 - 0.0365i & -0.0216 \\ 0.5993 & -0.5993 & 0.5993 & -0.4087 & 0.1393 - 0.0944i & 0.1393 + 0.0944i & -0.1790 \end{pmatrix}$$

We can see that we have a pair of complex eigenvalues (and corresponding eigenvectors) and their presence could lead to an oscillatory behaviour, but most importantly, we can see that λ_7 is the dominating eigenvalue of L since it is a simple eigenvalue, it is real and non-negative and $\lambda_7 >\mid \lambda \mid$ for all other eigenvalues λ of L ($\mid \lambda_{5,6} \mid \approx \sqrt{(0.0378)^2 + (0.3567)^2} \approx 0.3581 < \lambda_7$). As for the usage of the proposition of the dominating eigenvalue (see **??**), we need an expression of the form:

$$N(0) = \delta_1 v_1 + \delta_2 v_2 + \delta_3 v_3 + \delta_4 v_4 + \delta_5 v_5 + \delta_6 v_6 + \delta_7 v_7 \tag{3.1}$$

where $N(0)$ is the vector of the starting population and v_i is the i-th column of the matrix V. The parameter a dominating the long-term behaviour that we are looking for is $a := \delta_7$ (v_7 is the eigenvector corresponding to the dominating eigenvalue).

Before proceeding calculating a we need to give an estimation of $N(0)$. We can assume without loss of generality (we will justify it later in this subsection) that our starting population will be of the type: $N(0) = (0, H(0), 0, J_2(0), 0, NB(0), MB(0))^T$ i.e., we start just before the eggs are laid and this makes sense since our transition matrix L is thought to be starting just after the mating period.
From [9] and [12] we can take the statistical data from on-field observations done in three different spots on the island ("Blue Bayou", "Big Bight Pond" and "Iron Bound") and make an estimation for the total population:

Location	J	NB	MB	Total
Blue Bayou	4	9	11	24
Big Bight Pond	2	6	32	40
Iron Bound	40	34	33	107
Σ	46	49	76	171

The study from [12] gives us an estimation of the density of adult iguanas per hectare

which ranges from 53 adults/ha to 86 adults/ha according to different the different models employed in the previously mentioned study ([33]).
From the previous table, since we are assuming the population to be uniformly distributed, we can find the densities of J, NB and MB:

Juveniles

$$125 : 53 = 46 : j_- \longrightarrow j_- = 19.5$$

$$125 : 86 = 46 : j_+ \longrightarrow j_+ = 31.65$$

Novice breeders

$$49 : 125 = nb_- : 53 \longrightarrow nb_- = 20.78$$

$$49 : 125 = nb_+ : 86 \longrightarrow nb_+ = 33.71$$

Mature breeders

$$76 : 125 = mb_- : 53 \longrightarrow mb_- = 32.22$$

$$76 : 125 = mb_+ : 86 \longrightarrow mb_+ = 52.29$$

It is important to consider that the study stated that the actual density of the juveniles is likely to be five times greater than what the data suggested and this is mainly due to the sub adults' small size and ability to camouflage with the vegetation of their habitat. This consideration leads us to a juveniles' density that ranges from 98 individuals/ha to 158 individuals/ha. This estimation is a realistic one since the highest density of subadults recorded was 20 juveniles/(10^3 m^2) (=200 juveniles/ha).

Before giving an estimation for the hatchlings' density, we must remember that our model works with the number of females (or the number of couples) so our densities in order to be used need to be halved, so that they read:

Juvenile : from 49/ha to 79/ha;

Novice breeders : from 10/ha to 19/ha;

Mature breeders : from 16/ha to 26/ha.

Now we can proceed to give an estimation of the hatchlings' densities. We take the previously found Novice and Mature breeders' densities, we multiply them by the hatching rate and by the respective average eggs laid (considering the female hatchlings only) and then we sum up the results.

$$h_- = ((nb_-)(e_{NB}) + (mb_-)(e_{MB}))r_h = ((10)(4.35) + (16)(5.6))(0.923) \approx 112.85 \approx 113$$

$$h_+ = ((nb_+)(e_{NB}) + (mb_+)(e_{MB}))r_h = ((19)(4.35) + (26)(5.6))(0.923) \approx 210.68 \approx 211$$

So we have an estimation of the hatchlings' densities. It is important to highlight that this estimation is for the following year and not the one we are considering to be the year of our initial population. Our transition matrix L is not invertible, so we cannot

properly calculate the hatchlings' density of our initial population but since the dominating eigenvalue is bigger than 1, we know that the total population is increasing thus we can assume, without any loss of generality, the starting hatchlings' density to be slightly smaller than the one we have found.
Then, we can assume our densities for the H age class to read:

$$h_- = 105 \text{ and } h_+ = 200$$

Now, since there are three age classes to represent the more general juveniles' age class and since we have the estimated densities of the sub adults starting population, we need to figure out how the found densities are distributed throughout the J_1, the J_2 and the J_3 age classes.
Let $N(0)$ be the general vector of our starting population (or starting densities):

$$N(0) = (e(0), h(0), j_1(0), j_2(0), j_3(0), nb(0), mb(0))^T$$

Now we can calculate $N(1)$ (which is the population after one year):

$$N(1) = LN(0) = \begin{pmatrix} 0 \\ (4.02)nb(0) + (5.17)mb(0) \\ (0.16)e(0) \\ (0.06)h(0) \\ (0.17)j_1(0) \\ (0.39)j_2(0) \\ (0.73)j_3(0) + (0.92)(nb(0)mb(0)) \end{pmatrix} =: \begin{pmatrix} 0 \\ h(1) \\ j_1(1) \\ j_2(1) \\ j_3(1) \\ nb(1) \\ mb(1) \end{pmatrix}$$

With $N(1)$ we can calculate $N(2)$:

$$N(2) = LN(1) = \begin{pmatrix} 0 \\ (4.02)nb(1) + (5.17)mb(1) \\ 0 \\ (0.06)h(1) \\ (0.17)j_1(1) \\ (0.39)j_2(1) \\ (0.73)j_3(1) + (0.92)(nb(1) + mb(1)) \end{pmatrix} =: \begin{pmatrix} 0 \\ h(2) \\ 0 \\ j_2(2) \\ j_3(2) \\ nb(2) \\ mb(2) \end{pmatrix}$$

So we can find $N(3)$:

$$N(3) = LN(2) = \begin{pmatrix} 0 \\ (4.02)nb(2) + (5.17)mb(2) \\ 0 \\ (0.06)h(2) \\ 0 \\ (0.39)j_2(2) \\ (0.73)j_3(2) + (0.92)(nb(2) + mb(2)) \end{pmatrix} =: \begin{pmatrix} 0 \\ h(3) \\ 0 \\ j_2(3) \\ 0 \\ nb(3) \\ mb(3) \end{pmatrix}$$

By the same reasoning we calculate $N(4)$:

$$N(4) = LN(3) = \begin{pmatrix} 0 \\ (4.02)nb(3) + (5.17)mb(3) \\ 0 \\ (0.06)h(3) \\ 0 \\ (0.39)j_2(3) \\ (0.92)(nb(3) + mb(3)) \end{pmatrix} =: \begin{pmatrix} 0 \\ h(4) \\ 0 \\ j_2(4) \\ 0 \\ nb(4) \\ mb(4) \end{pmatrix}$$

We can now easily see by induction (see A.1.1) that, for a large enough $n \in \mathbb{N}$, we have:

$$N(n+1) = LN(n) = \begin{pmatrix} 0 \\ (4.02)nb(n) + (5.17)mb(n) \\ 0 \\ (0.06)h(n) \\ 0 \\ (0.39)j_2(n) \\ (0.92)(nb(n) + mb(n)) \end{pmatrix} =: \begin{pmatrix} 0 \\ h(n+1) \\ 0 \\ j_2(n+1) \\ 0 \\ nb(n+1) \\ mb(n+1) \end{pmatrix}$$

This observation allows us to take (without loss of generality) our initial population (or density) vector the like:

$$N(0) = (0, h(0), 0, j_2(0), 0, nb(0), mb(0))^T$$

This makes sense since the matrices which our transition matrix is made up of are ordered in a way that first we have the egg laying and then we have the hatching of the eggs previously laid. This means that in our transition matrix the transit through the egg stage is not esplicitly shown.

So, since j_2 is the only density for the juvenile's age class, the starting vectors of our densities will be of the form:

$$N_-(0) = (0, h_-(0), 0, j_{2-}(0), 0, nb_-(0), mb_-(0))^T = (0, h_-(0), 0, j_-(0), 0, nb_-(0), mb_-(0))^T$$

$$N_+(0) = (0, h_+(0), 0, j_{2+}(0), 0, nb_+(0), mb_+(0))^T = (0, h_+(0), 0, j_+(0), 0, nb_-(0), mb_-(0))^T$$

which read:

$$N_-(0) = (0, 105, 0, 49, 0, 10, 16)^T$$

$$N_+(0) = (0, 200, 0, 79, 0, 19, 26)^T$$

Now, going back to (3.1) we need to find a_- and a_+, which are respectively δ_{7-} and δ_{7+} of the following equations:

$$N_-(0) = \delta_{1-}v_1 + \delta_{2-}v_2 + \delta_{3-}v_3 + \delta_{4-}v_4 + \delta_{5-}v_5 + \delta_{6-}v_6 + \delta_{7-}v_7$$

$$N_+(0) = \delta_{1+}v_1 + \delta_{2+}v_2 + \delta_{3+}v_3 + \delta_{4+}v_4 + \delta_{5+}v_5 + \delta_{6+}v_6 + \delta_{7+}v_7$$

This means:

$$N_-(0) = \begin{pmatrix} 0 \\ 105 \\ 0 \\ 49 \\ 0 \\ 10 \\ 16 \end{pmatrix} = V \begin{pmatrix} \delta_{1-} \\ \delta_{2-} \\ \delta_{3-} \\ \delta_{4-} \\ \delta_{5-} \\ \delta_{6-} \\ \delta_{7-} \end{pmatrix} \quad \text{and} \quad N_+(0) = \begin{pmatrix} 0 \\ 200 \\ 0 \\ 79 \\ 0 \\ 19 \\ 26 \end{pmatrix} = V \begin{pmatrix} \delta_{1+} \\ \delta_{2+} \\ \delta_{3+} \\ \delta_{4+} \\ \delta_{5+} \\ \delta_{6+} \\ \delta_{7+} \end{pmatrix}$$

where V is the eigenvectors' matrix introduced at the beginning of this subsection. The problem with this matrix is that it is not invertible. So we can reduce it by erasing the first and third rows (which are null ones) and the first and the third columns (which are linearly dependent with v_2, i.e. the second column of V and one of the eigenvectors corresponding to the null eigenvalue). By doing so and considering the vectors $\tilde{N}_\pm(0) = (h_\pm(0), j_{2\pm}(0), 0, nb_\pm(0), mb_\pm(0))^T$ we can solve the following system:

$$\begin{pmatrix} h_\pm(0) \\ j_{2\pm}(0) \\ 0 \\ nb_\pm(0) \\ mb_\pm(0) \end{pmatrix} = \begin{pmatrix} 0 & 0.7321 & 0.9569 & 0.9569 & -0.9819 \\ 0 & -0.2353 & 0.0169 + 0.1592i & 0.0169 - 0.1592i & -0.0571 \\ -0.2161 & 0 & 0 & 0 & 0 \\ 0.7708 & 0.4916 & -0.1702 + 0.0365i & -0.1702 - 0.0365i & -0.0216 \\ -0.5993 & -0.4087 & 0.1393 - 0.0944i & 0.1393 + 0.0944i & -0.1790 \end{pmatrix} \begin{pmatrix} \delta_{2\pm} \\ \delta_{4\pm} \\ \delta_{5\pm} \\ \delta_{6\pm} \\ \delta_{7\pm} \end{pmatrix}$$

Solving these two systems will yield:

$$a_- = \delta_{7-} = -190.31$$

$$a_+ = \delta_{7+} = -321.99$$

Thus, for large t thanks to 2.1.1, we have:

$$N_-(t) \approx \lambda_7^t a_- v_7 \approx (1.0311)^t \begin{pmatrix} 0 \\ 186.87 \\ 0 \\ 10.87 \\ 0 \\ 4.11 \\ 34.07 \end{pmatrix} \quad \text{and} \quad N_+(t) \approx \lambda_7^t a_+ v_7 \approx (1.0311)^t \begin{pmatrix} 0 \\ 316.16 \\ 0 \\ 18.39 \\ 0 \\ 6.99 \\ 57.64 \end{pmatrix}$$

3.3 Conclusions

After having set up a model for the population of *Ctenosaura bakeri* focussing on an age structured approach we managed to find the dominating eigenvalue of the transition matrix associated to the model. This dominating eigenvalue being $\lambda_7 \approx 1.0311 > 1$ tells us that, with the given assumptions, the population should be growing. This is factually not the case, though: in 2000 (the year of the study we took our data for the initial population had taken place) the estimated total adult population ranged from 57823 to 93826 individuals while in 2017 ([18]) it ranged from 3000 to 6000 individuals.

These data, with the given assumptions, can be converted in adults' densities which for the year 2000 will be given by $nb_{-}(0) + mb_{-}(0) = 26$ adults/ha and $nb_{+}(0) + mb_{+}(0) = 45$ adults/ha (for the lower and the upper estimations, respectively). In the year 2017 we do not have the adults' densities explicitly shown, but we can easily figure them out: since we are assuming habitat destruction processes not to occur we will have the same area of habitat we had in 2000 i.e., 1091 ha. So we take the estimation boundaries, we half them (it is important to remember that, in this model, we are considering the population of female individuals only) and then we divide the result by the habitat area. This give us the observed (female) adults' densities which are 1.38 adults/ha and 2.75 adults/ha .

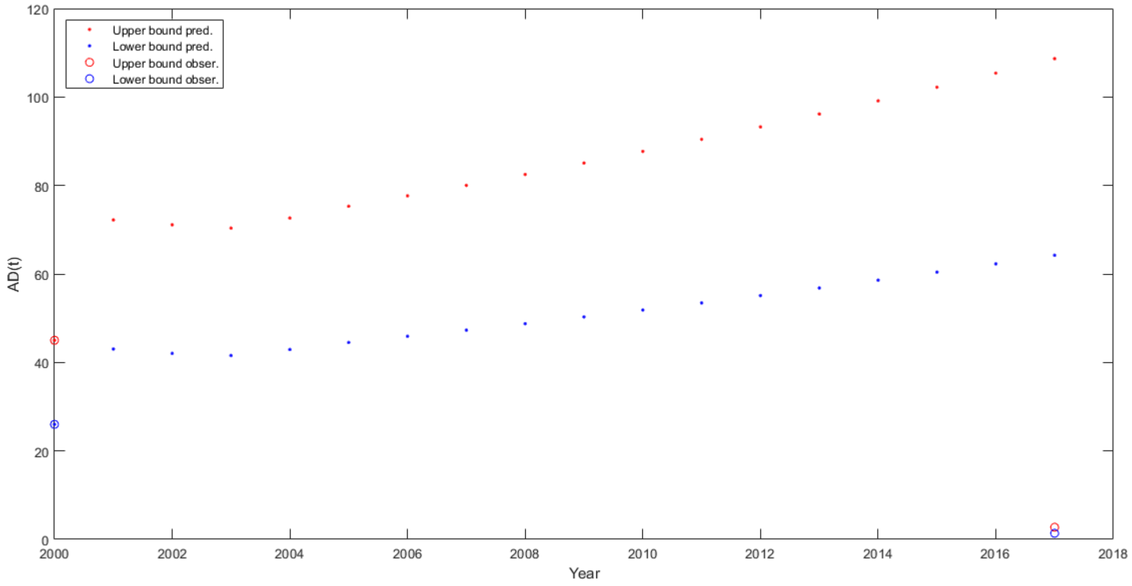


Figure 3.1: Estimations of predicted and observed female adults' densities in comparison.

This result can be read in two ways (which are not mutually esclusive):

1. We have that our dominating eigenvalue $\lambda_7 \approx 1.0311$ is indeed larger than 1 (which leads our population in the long term to grow) but it is only slightly larger than 1. Because of this (and having rough estimates anyway), if one or more parameters in our transition matrix L are perturbed by a small $\epsilon > 0$, our dominating eigenvalue could turn into a value smaller than 1. This could lead to a different outcome and an actual decrease of the estimated densities (and so of the estimated population) rather than an increase.

2. Factors we excluded in the assumptions for this model, like habitat destruction and intensive hunting (which are known to occur), greatly affect the population dynamics of *Ctenosaura bakeri.* It is also worth noting that in our calculation for the observed adults' densities in 2017, we divided the observed adults' populations by the habitat surface in 2000 (since we had assumed no habitat destruction events to occur), this most likely yielded to lower densities than the actual ones since in 2017 we actually have a smaller habitat surface than the one in 2000.

If the first case is to happen a possible, doable and currently implemented solution would be trying to increase one or more of the parameters of the transition matrix L and thus increasing the value of the dominating eigenvalue (which would eventually increase the population's growth). in practical terms this is currently impelmented by Útila Iguana Research and Breeding Station (IRBS): the foundation coordinates a breeding program with captive and wild female iguanas. Captive-hatched juveniles are released after one year on the beaches where the females were captured and in other suitable areas. This increses the mean hatchlings' survival rate ($q_{H \to J_1}$) and thus increases the dominating eigenvalue.
Nevertheless, such a steep drop in the recorded adults' densities and (mostly) such a difference between the predicted densities and the recorded ones cannot be justified by a small perturbation of the dominating eigenvalue, so the second case most likely has a greater impact on the population dynamics of the species.

The second case is considering the fact that factors like hunting and habitat destruction are actually playing a massive role on the population dynamics and then on the decline of the total population. We will further investigate these factors in the next chapters.

From a biological point of view the situation is indeed critical but we can say that hope still sparks: if factors like habitat destruction and hunting could be mitigated to the point of having a negligible influence to the population dynamics (also thanks to the efforts of the IRBS), the *Ctenosaura bakeri* would thrive, since from the proposition 2.1.1 we know that the population would grow.

Chapter 4

Sex dependent hunting

4.1 Introduction and assumptions

In this chapter we will focus on the effects of sex selective hunting on the population dynamics of *Ctenosaura bakeri*. As mentioned in the introduction, one of the main threat to the survival of this species is the human poaching, especially if it specifically targets gravid females. The biologists first arrived to the conclusion that the females were the preferred targets of the poachers because of the incongruity of the recorded sex ratios in comparsion with other species closely related to the *Ctenosaura bakeri* (for example, in *Ctenosaura similis* was found a ratio of 0.63 males to 1 female, in *Ctenosaura oedirhina* a ratio of 0.61 males to 1 female, while in Colombia for *Iguana iguana* there was found a ratio of 0.40 males to 1 female).

We will approach this problem in two ways: at first we will consider the hunting effort parameter to be constant, while secondly we will consider it to be dependent on time to reflect the observed trend of increased number of poachers, mostly coming from the mainland (see [12] and [23]).

Our main goals in this chapter are: showing how the sex dependent hunting affects the change of the sex ratio of the iguana population switching from a slight female dominance to a relevant male dominance over the years ([23]) and giving realistic predictions of the evolution of the sex ratio (and of the total male and female populations) in the next years.

For the next models we will make the following assumptions:

- We consider the population to be uniformly distributed across its habitat.
- We consider all adult females to become gravid after every mating season.
- We consider the male and female death rates to be the same.
- We consider the whole sexually mature population to consist of mature breeders only.
- We consider the *Ctenosaura bakeri* to be a Fisherian species (the ratio of the newborn males to the newborn females is 1:1).
- We consider the hunting efforts occurring during the whole year to be negligible.

- Mating (and thus egg laying) occurs at the same time for every sexual mature individual.
- We consider the incubation period to be 6 months.
- When iguanas are 2.5 years they reach sexual maturity.
- We are not considering habitat destruction to occur.
- We consider the adult population to be far from its maximum, i.e., we consider the carrying capacity of the system to be much bigger than the total adult population.

4.2 The model(s)

In this section we will set up the models to describe the dynamics of the population of *Ctenosaura bakeri* starting from the Kendall and Goodman approach (see [13]), which, in its simplest form reads (omitting the dependence on time):

$$\begin{cases} \dot{m} = -\mu_m m + b_m \Lambda(f,m) \\ \dot{f} = -\mu_f f + b_f \Lambda(f,m) \end{cases}$$

where m and f are the male and female populations, respectively, μ_f and μ_m are the death rates of the female and male populations, respectively, b_f and b_m are the female and male births per pregnancy (or more generally the female and male individuals that reach sexual maturity) and $\Lambda(f,m)$ are the successful matings.
We are using this kind of approach because a classical growth model in our case would not be sufficient: those are mainly used for a population which reproduces asexually or, in the case of a sexually reproducing population, only the female population or the couple population are considered. In this chapter we want to understand better how the dynamics of both sexes are affected differently by the hunting efforts. So we will mainly use the above mentioned approach and since we are assuming the carrying capacity of our system to be much bigger than the total adult population, we will not use a logistic model, as our situation can be read to be in the first part of the curve (where the growth is close to exponential).

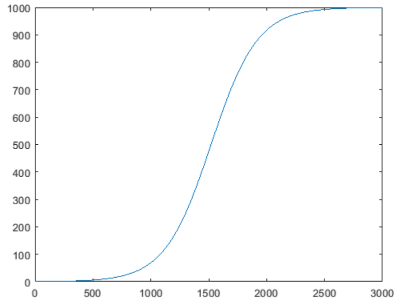


Figure 4.1: Example of logistic growth.

The reasons behind this assumption are mainly due to the intention of focussing more on the effects of hunting to the survival of the population rather than studying the stationary points of "coexistence" with the poachers.

4.2.1 First approach: constant hunting effort (I)

As previously mentioned, we start from the the Kendall and Goodman approach, leading to the following system (omitting the dependence on time):

$$\begin{cases} \dot{m} = b_m \Lambda(f,m) - \mu_m m \\ \dot{f} = b_f \Lambda(f,m) - \mu_f f \end{cases}$$

$\Lambda(f,m)$ can assume different functions, depending on the situation. In [13], there are some like: $\Lambda(f,m) = \sqrt{fm}$ (the geometric mean), $\Lambda(f,m) = \min(f,m)$ or $\Lambda(f,m) = \frac{2fm}{f+m}$ (the harmonic mean).
In our case, since we are starting from a 1.2 females to 1 male ratio and since the collected data ([23]) tell us that as time progresses the ratio tends to a male dominance, considering that the *Ctenosaura bakeri*, as many other reptile species, is polygamous and that we are assuming that all the female adults successfully mate at every mating season; we will consider $\Lambda(f,m) = f$.

$$\begin{cases} \dot{m} = b_m f - \mu_m m \\ \dot{f} = b_f f - \mu_f f \end{cases}$$

Now we introduce the hunting efforts in our system, which now reads:

$$\begin{cases} \dot{m} = b_m(1 - \hat{h}_f)f - \mu_m m - \tilde{h}_m m \\ \dot{f} = b_f(1 - \hat{h}_f)f - \mu_f f - (h_f + \tilde{h}_f)f \end{cases}$$

where $\tilde{h}_m$ and $\tilde{h}_f$ are the hunting efforts for both the male and female populations, respectively (hunting which occurs during the whole year), while h_f is the hunting effort targetting the pregnant females which are migrating from the swamps to the nesting sites on the beaches of Utila. This is also reflected on the growth rate where it is included the fraction of survived gravid females: $(1 - \hat{h}_f)$.
It is worth noting that we are taking 1 year as time unit so $\hat{h}_f = h_f \cdot 1$ year and we have that $0 < h < 1$ since, otherwise it would lead to a nonpositive solution, thus a biologically non relevant case. So we can drop the hat and consider the model to be non-dimensionalised.

Since we are assuming the hunting efforts $\tilde{h}_m$ and $\tilde{h}_f$ to be negligible (so we can consider $h_f = h$, omitting the subscript) and the natural mortality rates to be the same for both the male and the female population ($\mu_m = \mu_f = \mu$) the system reads:

$$\begin{cases} \dot{m} = b_m(1 - h)f - \mu m \\ \dot{f} = b_f(1 - h)f - \mu f - hf \end{cases}$$

Finally, since we are assuming the *Ctenosaura bakeri* to be a Fisherian species, we have $b_m = b_f = b$, the system reads:

$$\begin{cases} \dot{m} = b(1 - h)f - \mu m \\ \dot{f} = b(1 - h)f - \mu f - hf = f(b(1 - h) - \mu - h) \end{cases} \tag{4.1}$$

Before looking at the stationary points, we want to look at the consistency of the model, i.e. we want to look at the positivity of the solutions (see [32] for more details):

$$m = 0 \Longrightarrow \dot{m} = b(1-h)f \geq 0$$

so the solution for m will not become negative. Now we consider the second equation:

$$f = 0 \Longrightarrow \dot{f} \geq 0$$

thus, also for f the solution will not become negative. Then our system is consistent.

Now, going back to our system (4.1), we want to study the stationary points: we can easily see that (0,0) is the only stationary point for our model, alternatively the population grows unlimitedly, since we decided not to consider the carrying capacity of our system. Now, we want to study its stability.
We write down the Jacobian associated to the system which reads:

$$J_{(m,f)} = \begin{pmatrix} -\mu & b(1-h) \\ 0 & b(1-h)-(\mu+h) \end{pmatrix} = J_{(0,0)}$$

We can see that the eigenvalues of the Jacobian matrix are:

$$\lambda_1 = -\mu$$

$$\lambda_2 = b(1-h) - (\mu + h)$$

With little calculation we can see that $\lambda_2 < 0$ for $h > \frac{b-\mu}{b+1}$ and, of course, $\lambda_2 > 0$ for $h < \frac{b-\mu}{b+1}$. It is worth noting that all the parameters are positive and $\mu = 1 - p_{MB} = 0.04$, while $b = e_{MB} r_h l(3) \approx 0.11$ (where p_{MB}, e_{MB}, r_h and $l(3)$ are the parameters we have calculated in the previous chapter).It is important to note that since we are considering one year to be our time unit the yearly adult survivorship (p_{MB}) can be taken as a "survival" rate, thus our death rate μ will be as above mentioned.
Keeping this in mind we can see that (0,0) is a stable node for $h > \frac{b-\mu}{b+1} \approx 0.074$ and a saddle for $h < \frac{b-\mu}{b+1} \approx 0.074$.

Now we want to see the evolution of the female to male ratio in time:

$$\left(\frac{f}{m}\right)' = \frac{\dot{f}m - f\dot{m}}{m^2} = \frac{mf(b(1-h)-\mu-h) - f(bf(1-h)-\mu m)}{m^2} =$$

$$= \frac{mf(b(1-h)-h) - f^2 b(1-h)}{m^2} = \frac{f}{m}(b(1-h)-h) - \frac{f^2}{m^2}b(1-h)$$

So we have that:

$$\left(\frac{f}{m}\right)' = (b(1-h)-h)\left(\frac{f}{m}\right) - b(1-h)\left(\frac{f}{m}\right)^2 \tag{4.2}$$

Before looking at the explicit solution we study the stationary points of this ODE and their stability. So we rewrite it in the following way:

$$\left(\frac{f}{m}\right)' = (b(1-h)-h)\left(\frac{f}{m}\right)\left(1-\frac{b(1-h)}{b(1-h)-h}\left(\frac{f}{m}\right)\right)$$

.

The stationary points read $\left(\frac{f}{m}\right)^* = 0$ and $\left(\frac{f}{m}\right)^* = \frac{b(1-h)-h}{b(1-h)}$.
Now we look at their stability. Calling $r := \left(\frac{f}{m}\right)$ and $r' = g(r)$ we have:

$$g(r)' = b(1-h) - h - 2b(1-h)r = b(1-h)(1-2r) - h$$

For the trivial one, $r^* := \left(\frac{f}{m}\right)^* = 0$, we have:

$$g(r^*)' = b(1-h) - h - 2b(1-h)r^* = b(1-h) - h$$

We have that if $g(r^*)' > 0$, $r^* = 0$ is an unstable stationary point, on the other hand, if $g(r^*)' < 0$, $r^* = 0$ is a stable stationary point. With some calculation we have that if $h < \frac{b}{b+1}$ we have that 0 is an unstable stationary point and if $h > \frac{b}{b+1}$ 0 is a stable stationary point.
Since we have slightly different conditions for the stability of the stationary points of (4.2) compared to the conditions for stability of the stationary point of (4.1), we can take a closer look especially to the conditions of stability of (0,0) and $r^* = 0$:

- $h < \frac{b}{b+1} - \frac{\mu}{b+1}$, then (0,0) and $r^* = 0$ are unstable.
- $\frac{b}{b+1} - \frac{\mu}{b+1} < h < \frac{b}{b+1}$, then (0,0) is stable, while $r^* = 0$ is still unstable.
- $h > \frac{b}{b+1}$, then (0,0) and $r^* = 0$ are stable.

It is interesting to see that we have an "intermediate" case for $\frac{b}{b+1} - \frac{\mu}{b+1} < h < \frac{b}{b+1}$ in which we have (0,0) stable and $r^* = 0$ unstable. This can be interpreted as h being strong enough to lead the male and female adult populations to extinction but at almost the same speed for both the males and females (hence the $r^* = 0$ is unstable).

Now, looking at the nontrivial stationary point of (4.1), $r^* := \left(\frac{f}{m}\right)^* = \frac{b(1-h)-h}{b(1-h)}$, we have:

$$g(r^*)' = b(1-h) - h - 2b(1-h)r^* = -(b(1-h) - h)$$

Repeating the previous argument we have that $r^* = \frac{b(1-h)-h}{b(1-h)}$ is an unstable stationary point if $h > \frac{b}{b+1}$, while it is stable if $h < \frac{b}{b+1}$.

Now we calculate the explicit solution of the ODE (4.2) (see A.2) which reads, calling $r(t) := \left(\frac{f}{m}\right)(t)$ and $r(0) = r_0 := \left(\frac{f}{m}\right)_0$:

$$r(t) = \frac{(b(1-h)-h)r_0}{e^{-(b(1-h)-h)t}\,(b(1-h)(1-r_0) - h) + b(1-h)r_0}$$

where r_0 is the initial value of our female to male ratio.

In [23] we have the collected data of the female to male ratio in 2000, 2006 and 2011 which read 1.2, 0.96 and 0.60, respectively. So if we set the starting point to be 1.2 and the passage to the other two points at time 6 and 11 we can figure out two values for h:

$$h_1 \approx 0.031$$

$$h_2 \approx 0.081$$

In order to further use the few data we have and to better the estimation of h we set the starting point to be 0.96 and the passage to 0.60 with a proper time rescaling, so we have:

$$h_3 \approx 0.118$$

If we do the mean of these values we find $h \approx 0.077$.

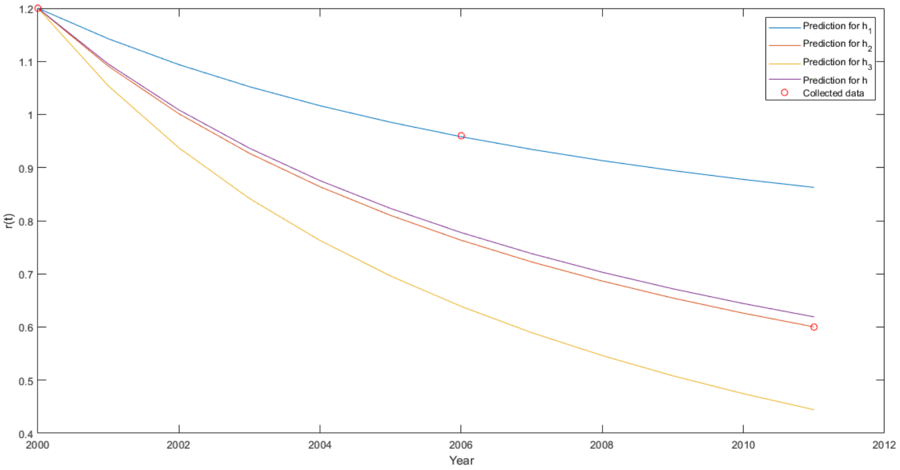


Figure 4.2: Estimated evolution of sex ratios r(t) varying h.

Calculating $\frac{b}{b+1}$ with our parameters, we have $\frac{b}{b+1} \approx 0.099$. Hence we have:

- For h_1 we have that (0,0) for (4.1) is a saddle and $r^* = \frac{b(1-h_1)-h_1}{b(1-h_1)}$ for (4.2) is a stable point. This means that for h_1 the population will grow anyway and the ratio of females to males will tend to $\frac{b(1-h_1)-h_1}{b(1-h_1)}$.
- For h_2 we have that (0,0) is a stable point, while the nontrivial point r^* is stable. This means that the population will die out but the ratio will tend to $\frac{b(1-h_2)-h_2}{b(1-h_2)}$.
- For h_3 we have that both (0,0) and $r^* = 0$ are stable, i.e., both the populations will die out and the female population will go exitinct faster than the male one.
- For the mean h, we are in the situation of h_2.

With this result we have that the population will die out, since (0,0) under those conditions is stable.

We want now to take a look at the evolution of the male, female and total populations affected by the previously calculated hunting efforts. The total population estimated in year 2000 (see [12]) ranges from 57823 to 93826 mature individuals. Keeping in mind that our starting sex ratio is 1 male to 1.2 females we can find the estimations of the starting male and female populations:

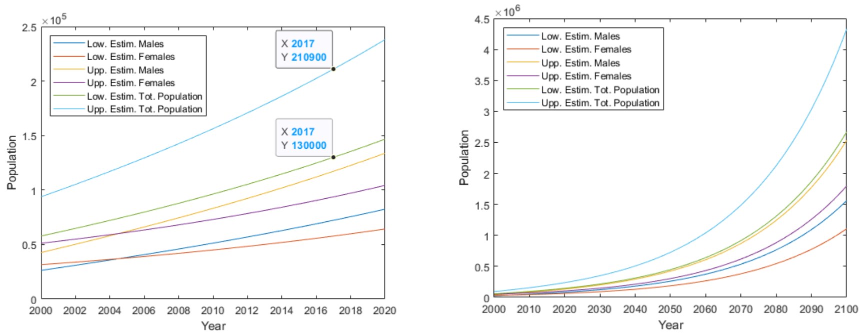
$$m_{0_+} : (f_{0+} + m_{0+}) = 1 : (1 + 1.2) \Longrightarrow m_{0+} : 93826 = 1 : 2.2 \Longrightarrow m_{0+} \approx 42648$$

$$m_{0_-} : (f_{0-} + m_{0-}) = 1 : (1 + 1.2) \Longrightarrow m_{0-} : 57823 = 1 : 2.2 \Longrightarrow m_{0-} \approx 26283$$

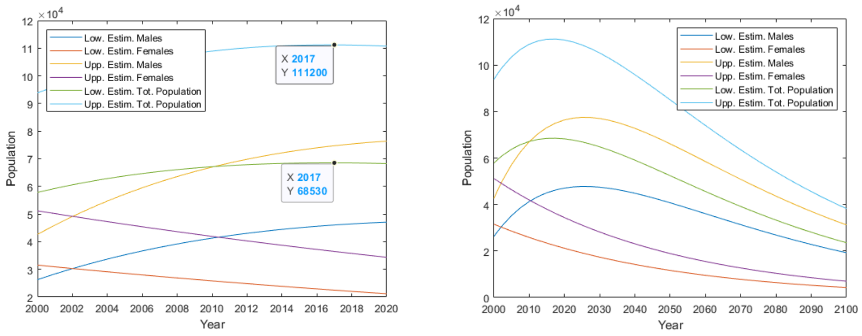
$$f_{0+} : (f_{0+} + m_{0+}) = 1.2 : (1 + 1.2) \Longrightarrow f_{0+} : 93826 = 1.2 : 2.2 \Longrightarrow f_{0+} \approx 51178$$

$$f_{0_-} : (f_{0-} + m_{0-}) = 1.2 : (1 + 1.2) \Longrightarrow f_{0-} : 57823 = 1.2 : 2.2 \Longrightarrow f_{0-} \approx 31540$$

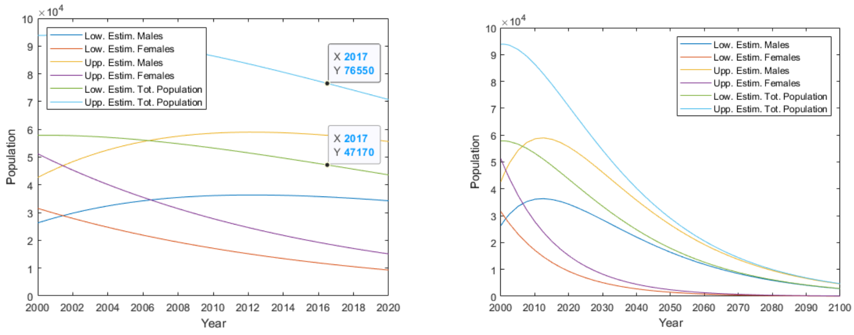
So for h_1, h_2 and h_3 we have the following prediction graphs:



(a) *Hunting effort* h_1 *(2000-2020)* (b) *Hunting effort* h_1 *(2000-2100)*



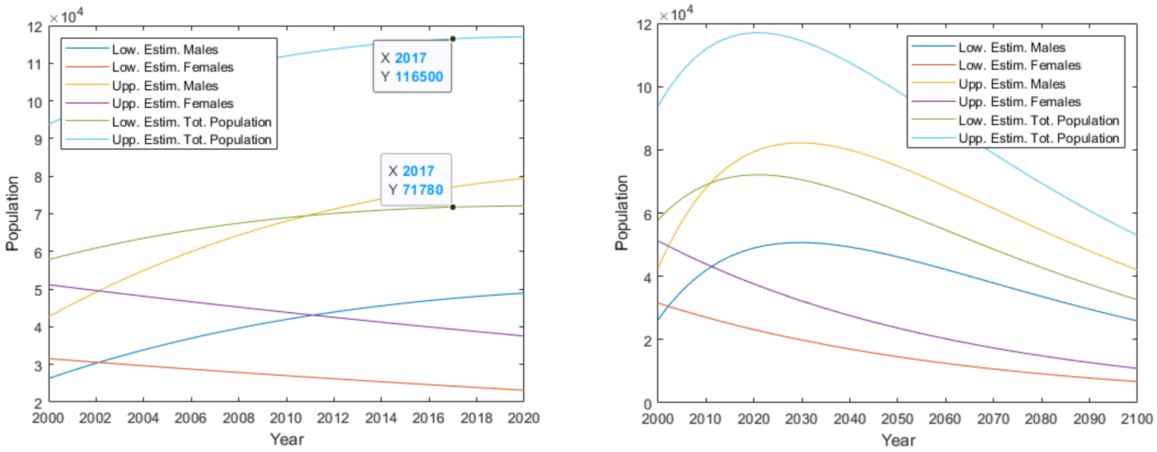
(c) *Hunting effort* h_2 *(2000-2020)* (d) *Hunting effort* h_2 *(2000-2100)*



(e) *Hunting effort* h_3 *(2000-2020)* (f) *Hunting effort* h_3 *(2000-2100)*

Figure 4.3: Estimated evolution of populations varying the hunting efforts.

While for h we have:



(a) *Hunting effort h (2000-2020)*

(b) *Hunting effort h (2000-2100)*

Figure 4.4: Estimated evolution of populations for the mean of the hunting efforts.

We can then compare the estimated values of the populations of our model with the values of the populations estimated by the biologists in [18]. Our model for the mean value of the hunting effort h gives us back an increased population compared to the starting one (even though we know from the previous analysis that it will eventually die out), ranging from 71780 to 116500 mature individuals, while the actual situation gives us a population ranging from 3000 to 6000 mature individuals.
Thus it is likely that either a constant hunting effort approach is not very realistic or some factors we omitted with our assumptions (like habitat destruction) play a greater role in the dynamics of the population of *Ctenosaura bakeri*.

4.2.2 First approach: constant hunting effort (II)

Now we want to take a more realistic approach since it takes some time to the newly hatched iguanas to reach sexual maturity. Thus we will introduce a delay τ in the growth term of both equations of (4.1) which yields:

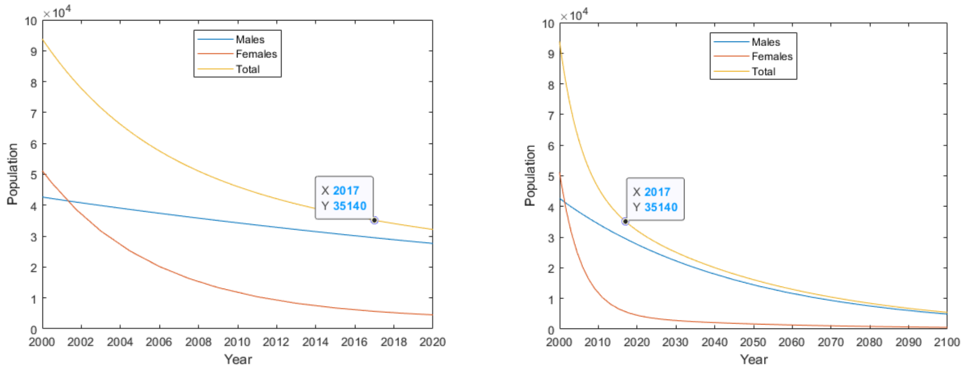
$$\begin{cases} \dot{m}(t) = b(1-h)f(t-\tau) - \mu m(t) \\ \dot{f}(t) = b(1-h)f(t-\tau) - (\mu + h)f(t) \end{cases}$$

In this section we will not delve into the analysis of the stationary points and their stability since it will give us back the same results as for the nondelayed case (our model only have the trivial stationary case).
We will take as our delay $\tau = 3$ years, since he are assuming the *Ctenosaura bakeri* reaches sexual maturity at 2.5 years old and has an incubation time of 6 months, thus it takes 3 years to form an adult individual from the moment the egg it hatched from had been laid.

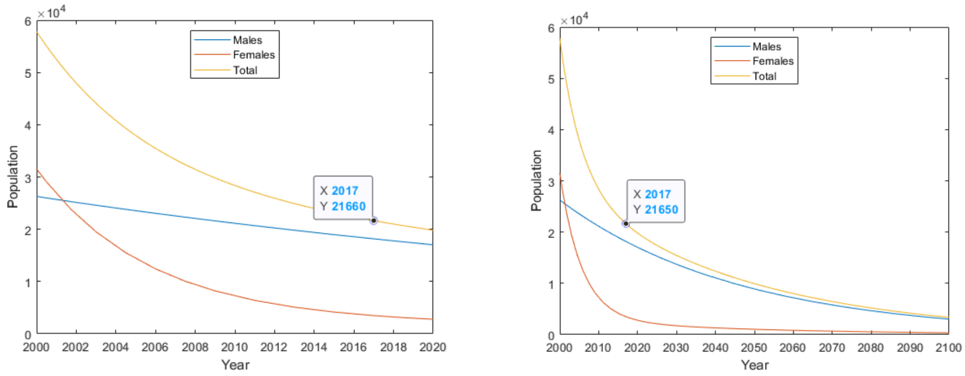
We take as our history functions the following:

$$\begin{cases} m_+(t) = 42648, \text{ for } -\tau \leq t \leq 0 \\ f_+(t) = 51178, \text{ for } -\tau \leq t \leq 0 \end{cases} \qquad \begin{cases} m_-(t) = 26283, \text{ for } -\tau \leq t \leq 0 \\ f_-(t) = 31540, \text{ for } -\tau \leq t \leq 0 \end{cases}$$

Furthermore, knowing $b = 0.11$, $r(0) = 1.2$, $r(6) = 0.96$, $r(11) = 0.6$ we can use a least square minimum approach to give an estimation for h which reads $h \approx 0.1386$. Thus we have the following prediction graphs:



(a) *Upper estimation (2000-2020)* (b) *Upper estimation (2000-2100)*



(c) *Lower estimation (2000-2020)* (d) *Lower estimation (2000-2100)*

Figure 4.5: Estimated evolution of populations with delay for h constant.

These results, in contrast with the ones calculated in the previous section, give us back a lower total population than the starting one. Even though it is still greater than the estimated population calculated by the biologists, having introduced a delay let us see a stronger impact of the poaching activity compared to the model without delay. This is probably due to the fact that the hunting effort we calculated is bigger than the hunting effort h_3 we had calculated for the model without delay. Indeed, that hunting effort in the model without delay would lead our starting populations to extinction in a very short period of time, something that is exasperated in our delayed model, because of a greater hunting effort and as a consequence of the delay (it takes longer for an individual to be able to mate and thus reproduce).

So, like for the nondelayed model, the starting population will be driven to extinction, only that with this model in a shorter period of time.

In the next sections we will repeat the process of modelling a system for hunting starting with a nondelayed one and then adding a delay, but this time we will take our hunting effort to be time dependent.

4.2.3 Second approach: time dependent hunting effort (I)

In this section we will give a more realistic approach dropping the assumption of the hunting effort to be constant in time. Indeed, over the years an increasing number of hunters (mainly coming from the inland) was recorded, thus we will take $h(t)$ to be time dependent.
Because of the arguments previously stated in this chapter we assume that $0 \leq h(t) \leq 1$. Furthermore, to reflect the competition among the poachers we will use a logistic approach to describe the hunting effort:

$$\dot{h}(t) = ah(t)(1 - h(t))$$

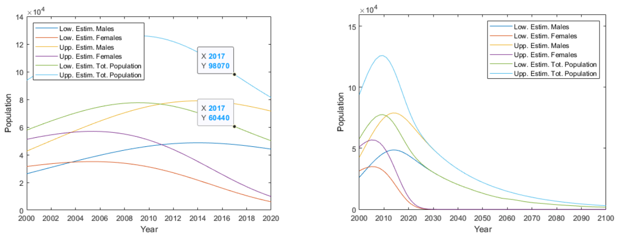
where a is an opportune constant which reflects the increase of the hunting effort in time. Recalling the argument for (4.2) we can give an explicit solution for $h(t)$ which reads:

$$h(t) = \frac{h_0}{e^{-at}(1 - h_0) + h_0}$$

as for h_0 we take h_1 calculated in section 3.2.1, i.e., $h_0 = 0.031$. So we can set the following system of two equations:

$$\begin{cases} \dot{r}(t) = (b(1 - h(t)) - h(t))r(t) - (b(1 - h(t)))r^2(t) \\ h(t) = \frac{h_0}{e^{-at}(1-h_0)+h_0} \end{cases}$$

where the first equation is (4.2) with a time dependent hunting effort and $r(t) = \frac{f(t)}{m(t)}$.
Knowing $b = 0.11$, $h(0) = 0.031$, $r(0) = 1.2$, $r(6) = 0.96$ and $r(11) = 0.6$, we can use a least square minimum approach to give an estimation for a which reads $a \approx 0.1384$.
Our system of two equations for the male and female populations is the same as (4.1) but this time we have h to be time dependent, thus a non-autonomous system. Thus we have the following prediction graphs:



(a) *Evolution of populations from 2000 to 2020.* (b) *Evolution of populations from 2000 to 2100.*

Figure 4.6: Estimated evolution of populations for the time dependent hunting effort.

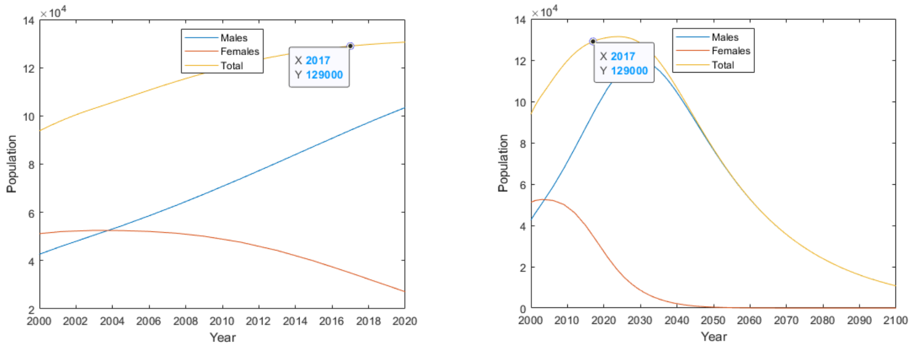
Again, as for the constant h approach (without delay) the model gives us back an increased total population in year 2017 compared to the starting one, ranging from 60440 to 98070 mature individuals. Nevertheless, the population will soon die out because of the hunting effort and the disproportionated sex ratio caused by the former.

4.2.4 Second approach: time dependent hunting effort (II)

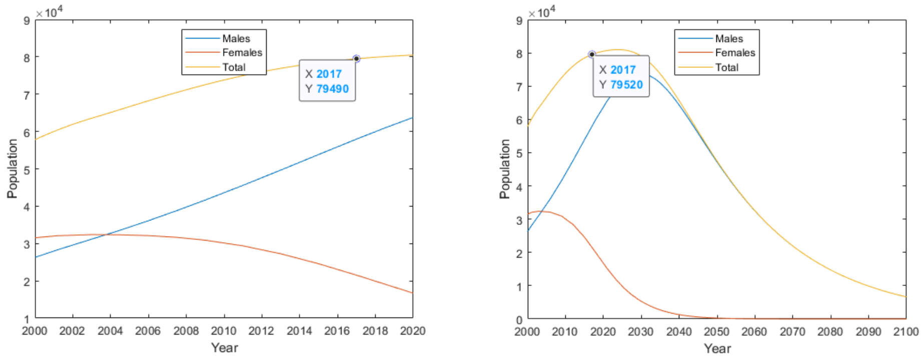
Now, repeating the argument given in section 4.2.2 and keeping the $h(t)$, we will introduce a delay in the growth term of the equations for the dynamics of both the male and the female populations, thus yielding:

$$\begin{cases} \dot{m}(t) = b(1 - h(t))f(t - \tau) - \mu m(t) \\ \dot{f}(t) = b(1 - h(t))f(t - \tau) - (\mu + h(t))f(t) \end{cases}$$

where our hunting effort is the same of the previous section: $h(t) = \frac{h_0}{e^{-at}(1-h_0)+h_0}$.
Setting $h(0) = 0.031$ (like in the previous section) and knowing $b = 0.11$, $r(0) = 1.2$, $r(6) = 0.96$ and $r(11) = 0.6$, we can use a least square minimum approach to give an estimation for a which reads $a \approx 0.1747$.
With such results we have the following prediction graphs:



(a) *Upper estimation (2000-2020)* (b) *Upper estimation (2000-2100)*



(c) *Lower estimation (2000-2020)* (d) *Lower estimation (2000-2100)*

Figure 4.7: Estimated evolution of populations with delay for the time dependent hunting effort.

Here, the model gives us back an increased total population in year 2017 compared to the starting one, just like the previous nondelayed model with a time dependent hunting

effort. In this case it is even greater than the predicted population of the nondelayed model: here we have a total population ranging from 79490 to 129000 mature individuals, in contrast with the population of the previous model which ranged from 60440 to 98070 mature individuals. This is due to the fact that the females have to reach sexual maturity before being hunted, since we are assuming the poachers target sexual mature female individuals only.
However, like the previous cases, we have again the total population to die out in the near future because of the hunting pressure and the disproportionated sex ratio caused by the former.

4.3 Conclusions

In this chapter we have analyzed the population dynamics of the *Ctenosaura bakeri* focussing on the hunting effects on the whole population and the sex ratio of the latter. Our most realistic models (the last two) gave us back an increased total population in year 2017 compared to the starting one (dated year 2000). This is in contrast with what was found by the biologists in [18], where the estimated population ranged from 3000 to 6000 mature individuals which is much less than the one predicted by our models.
This can be explained by the fact that we probably have not considered other effects in our initial assumptions (most likely the habitat destruction effect, which we will further investigate in the next chapter).

Nevertheless, all the models we have considered in this chapter lead to the extinction of the total population because of the pressure of poaching itself and mostly because of the induced disproportion in the sex ratio because of the latter.

The models we have considered can, of course, be modelled by, for example in the time dependent hunting effort, taking a, the growing parameter of the hunting effort, to be itself time dependent (or other parameter dependent, like the female population).

Chapter 5

Habitat destruction and Carrying Capacity

5.1 Introduction and assumptions

In this chapter we will focus on how the habitat destruction affects the population dynamics of *Ctenosaura bakeri*. As mentioned in the introduction, the most likely main threat to the survival of this species is the habitat destruction of both the mangrove forests and swamps (the juveniles and adults habitat) and the beaches (which are the nesting sites). By habitat destruction we do not only mean the actual levelling of both the swamps and nesting sites but we also take into consideration the use of the formers as dumpsites and the oceanic plastic pollution and the invasion of allochthonous plants of the latters (see [9], [12] and [18]).
In the year 2000 it was predicted that the realization of the development plans on Utila would have lead to a 50% decrease in the mangrove area (which at the time measured 10.91km^2) and to a loss of around 80% of all nesting sites (which at the time measured 1.09km^2) (see [12]). Even though a more recent study dated 2017 (see [18]) reports the mangrove area to be less than 8km^2 (so it might be that the previous predictions were slightly exaggerated), in this chapter we will consider the habitat destruction to be as it was predicted in 2000.
Furthermore, the degradation of the swamps due to the development plans, for example the building of the island airport, could lead to the fragmentation of the habitat and consequently to different subpopulations (which jeopardizes the genetic pool of *Ctenosaura bakeri*).

From a mathematical point of view, we will approach this problem setting up a continuous model with a system of two ordinary differential equations. Firstly, we will check the consistency of the model and we will study the stationary points and their stability. Secondly, we will give some estimations for the habitat degradation and the carrying capacity, comparing them with the observed data. Afterwards, we will give predictions for the dynamics of the populations and lastly we will introduce a delay in our model in order to give a more realistic prediction taking into account the time an newly hatched iguana takes to become sexually mature and we will esimate the dynamics of the population with such delay.

For the next models in this chapter we will make the following assumptions:

- We consider the population to be uniformly distributed across its habitat.
- We consider all adult females to become gravid after every mating season.
- Mating (and thus egg laying) occurs at the same time for every sexual mature individual.
- We consider the incubation period to be 6 months.
- When iguanas are 2.5 years they reach sexual maturity.
- We consider the whole sexually mature population to consist of mature breeders only.
- We consider the male-female ratio to be 1:1.
- We consider the *Ctenosaura bakeri* to be a Fisherian species (the ratio of the newborn males to the newborn females is 1:1).
- We are not considering (human) hunting to occur.
- We consider the habitat destruction to occur uniformly (it does not create isolated habitats).
- We consider the habitats (swamps and beaches) not to overlap.
- Once an individual reaches sexual maturity they mate every year until their natural death.
- We consider the habitat destruction to be linear in time (from 2000 to 2020).
- We consider the densities of both the adults and the nests to be constant in time.

5.2 The model(s)

In this section we will set up the models to describe the dynamics of the population of *Ctenosaura bakeri* starting from a simple logistic model approach:

$$\dot{u}(t) = r(t)u(t)\left(1 - \frac{u(t)}{K(t)}\right)$$

where $u(t)$ is the total population or the population's density, $r(t)$ is the growth rate and $K(t)$ is the carrying capacity. Since we are considering a sexually reproducing species we will only consider the female population instead of the toal population.

In this chapter the habitat destruction effect will be reflected on the carrying capacity, since the latter can be interpreted as $D \cdot A$ where D is the maximum density of a population in the habitat taken into consideration, while A is the total area of the habitat.

In our case we are considering two different and non overlapping habitats: the swamps and the beaches. So our model will consist of a system of two different logistic equations (taking now the r and the K as costants):

$$\begin{cases} \dot{x} = r_1 x \left(1 - \frac{x}{K_S}\right) \\ \dot{e} = r_2 e \left(1 - \frac{e}{K_B}\right) \end{cases}$$

where x is the adult female population, r_1 is the growth rate of former and K_S is the carrying capacity of the swamps, while e is the number of eggs laid, r_2 is the growth rate of the egg "population" and K_B is the carrying capacity of the beaches.

Of course, it does not make much sense to consider an egg "population", let alone consider a growth rate of such egg population. Moreover, the growth rate of the adult female population must depend on the number of eggs laid.
So for the second equation we will set $r_2 e = rx$, where r is the yearly rate of eggs laid per individual. For the first equation we will split the growth rate into the death rate of the adult population (μx) and the "birth" rate of the adult population (which of course depends on the egg "population"). We set the latter to be be, where b is the rate of hatchlings (dependent on the number of eggs) which reach adulthood.

Thus our system reads:

$$\begin{cases} \dot{x} = be \left(1 - \frac{x}{K_S}\right) - \mu x \\ \dot{e} = rx \left(1 - \frac{e}{K_B}\right) \end{cases} \tag{5.1}$$

It is worth noting that all the parameters b, r, μ, K_S and K_B are strictly positive. As we did in the previous chapter, we look at the consistency of the model:

$$x = 0 \Longrightarrow \dot{x} = be \geq 0$$

so the solution for x will not become negative. Now we consider the second equation:

$$e = 0 \Longrightarrow \dot{e} = rx \geq 0$$

so, also in this case, the solution for e will not become negative.
Thus, if our initial conditions are positive (and they should be positive to be biologically relevant), then our solutions cannot become negative.

5.2.1 Stationary points and their stability

Before we start studying the stationary points and their stability we want to exclude the existence of closed orbits using the negative criterion of Bendixson (see 2.2.4).
We take as $BM := \{(x, e) \in \mathbb{R}^2;\ x, e \geq 0\}$ which is the set of the biologically meaningful points of our system (this set is simply connected), thus setting:

$$\begin{cases} \dot{x} = f(x, e) \\ \dot{e} = g(x, e) \end{cases}$$

we look at the $div(f,g)$:

$$div(f,g) := \frac{\partial f}{\partial x} + \frac{\partial g}{\partial e} = -\frac{be}{K_S} - \mu - \frac{rx}{K_B}$$

we can easily see that $div(f,g)$ is not identically zero and it does not change sign in $\{(x,e) \in \mathbb{R}^2;\ x,e \geq 0\}$, then our system has no closed orbits lying entirely in BM.

Now, going back to (5.1) we study its stationary points and their stability, setting:

$$\begin{cases} 0 = be\left(1 - \frac{x}{K_S}\right) - \mu x \\ 0 = rx\left(1 - \frac{e}{K_B}\right) \end{cases}$$

Thus this leads us to two biologically meaningful stationary points: (0,0) and $(\bar{x}, \bar{e})$, where $\bar{x} = \frac{bK_SK_B}{bK_B+\mu K_S}$ and $\bar{e} = K_B$ (both the stationary points are biologically relevant regardless of the values of the parameters).
Their stability is determined by calculating the Jacobian matrix at the respective points. The general Jacobian reads:

$$J_{(x,e)} = \begin{pmatrix} -\frac{be}{K_S} - \mu & b\left(1 - \frac{x}{K_S}\right) \\ r\left(1 - \frac{e}{K_B}\right) & -\frac{rx}{K_B} \end{pmatrix}$$

For (0,0) the Jacobian reads:

$$J_{(0,0)} = \begin{pmatrix} -\mu & b \\ r & 0 \end{pmatrix}$$

and its eigenvalues read $\lambda_{1,2} = \frac{-\mu \pm \sqrt{\mu^2+4rb}}{2}$. We can easily see (since all the parameters are strictly positive) that $0 \notin \text{Re}\ \sigma(J_{(0,0)})$, thus we can apply 2.2.3. Then, again, because all the parameters are strictly positive, the eigenvalues are discordant, thus (0,0) is a saddle.
(0,0) being a saddle means that if we have our starting population being of 0 females (or couples) and 0 eggs, if we slightly perturbate it, like (idealistically speaking) with the introduction of an adult subpopulation or some eggs we will have our solution curve step away from (0,0). Furthermore, because of this, our model does not include the possibility (if at least one between the starting x and e is strictly positive) of the population going extinct.

For the nontrivial stationary point $(\bar{x}, \bar{e}) = \left(\frac{bK_SK_B}{bK_B+\mu K_S}, K_B\right)$ the Jacobian reads:

$$J_{(\bar{x},\bar{e})} = \begin{pmatrix} -\mu - \frac{bK_B}{K_S} & b\left(1 - \frac{bK_B}{bK_B+\mu K_S}\right) \\ 0 & -r\frac{bK_S}{bK_B+\mu K_S} \end{pmatrix}$$

its eigenvalues read $\lambda_1 = -\frac{\mu K_S + bK_B}{K_S}$ and $\lambda_2 = -r\frac{bK_S}{bK_B+\mu K_S}$. Both are negative and real, which means, by applying 2.2.3, that the nontrivial stationary point $(\bar{x}, \bar{e})$ is a stable node.

We can conclude that the trivial point $(0,0)$ is always a saddle point, while $(\bar{x},\bar{e})$ is always an exponentially asymptotically stable point.

If we assume our starting egg "population" $e_0 = e(0) \leq K_B$, recalling that $K_B = D_B \cdot A_B$ (where D_B is the maximum density of eggs in the beaches and A_B is the total surface of the nesting sites) we can give an estimation of the maximum density of the nests $D_{Nest} = \frac{D_B}{r}$, where r is the number of eggs laid per individual which will give birth to a female individuals.
To calculate the starting egg "population" we need to take the hatchling densitiy estimated in Chapter 2 which ranges from 105/ha $= 10500/\text{km}^2$ to 200/ha $= 20000/\text{km}^2$. If we multiply the densities $(h(0)_\pm)$ by the surface of the mangrove areas (A_S) we get the estimations for the hatchlings' population (which we call H_- and H_+):

$$H_- = h(0)_- \cdot A_S = (10500)(10.91) = 114555$$

$$H_+ = h(0)_+ \cdot A_S = (20000)(10.91) = 218200$$

Then, if we multiply them by $\frac{1}{r_h}$, where r_h is the hatching rate we find the estimations for the starting population:

$$e_{0-} = \frac{H_-}{r_h} \approx 124111$$

$$e_{0+} = \frac{H_+}{r_h} \approx 236403$$

Recalling that $r = 5.6$ (calculated in Chapter 2) and since we have $A_B = 1.09\text{km}^2$ (from [12]), we can give an estimation of D_{Nest}:

$$\frac{e_{0\pm}}{rA_B} \leq D_{Nest}$$

thus splitting the cases we have the ranges of the estimations of D_{Nest}:

$$D_{Nest-} \geq \frac{e_{0-}}{rA_B} = \frac{124111}{(5.6)(1.09)\text{km}^2} = \frac{124111}{(5.6)(1.09)10^6\text{m}^2} \approx 0.02/\text{m}^2$$

$$D_{Nest-} \geq \frac{e_{0+}}{rA_B} = \frac{236403}{(5.6)(1.09)\text{km}^2} = \frac{236403}{(5.6)(1.09)10^6\text{m}^2} \approx 0.04/\text{m}^2$$

We have, then, as lower estimations for D_B, $0.02/\text{m}^2$ and $0.04/\text{m}^2$. The data collected from biologists point to a lower statistical estimation of $0.02/\text{m}^2$ (see [12]). This estimation is consistent with the estimation from the model; thus we can conclude that the estimations of $e_{0\pm}$ are realistic.

5.2.2 Time dependent carrying capacity

In this section we will consider the habitat destruction to occur which means that our carrying capacities are time dependent, i.e., $K_B = K_B(t)$ and $K_S = K_S(t)$. So our previous system (5.1) now reads:

$$\begin{cases} \dot{x} = be\left(1 - \frac{x}{K_S(t)}\right) - \mu x \\ \dot{e} = rx\left(1 - \frac{e}{K_B(t)}\right) \end{cases} \tag{5.2}$$

Since we are assuming habitat destruction to occur linearly from 2000 to 2020 and the densities to be constant in time we can rewrite the carrying capacities in the following way:

$$K_S(t) = D_S \cdot A_S(t) = D_S(A_S(0) + c_S t)$$
$$K_B(t) = D_B \cdot A_B(t) = D_B(A_B(0) + c_B t)$$

The study [12] (dated year 2000) gave us a prediction of how much surface of both habitats would be lost (because of Utila's development plans) in the following years: 50% decrease in the mangrove area and the loss of around 80% of all nesting sites.
This can give us an estimation of both c_S and c_B (having assumed a linear destruction in time):

$$c_S = \frac{A_S(20) - A_S(0)}{20} = \frac{\frac{1}{2}A_S(0) - A_S(0)}{20} = -\frac{10.91}{40} \approx -0.27\text{km}^2/\text{year}$$
$$c_B = \frac{A_B(20) - A_B(0)}{20} = \frac{\frac{1}{5}A_B(0) - A_B(0)}{20} = -\frac{1.09}{25} \approx -0.0436\text{km}^2/\text{year}$$

Hence our system (5.2) reads:

$$\begin{cases} \dot{x} = be\left(1 - \frac{x}{D_S(A_S(0)+c_S t)}\right) - \mu x = be\left(1 - \frac{x}{D_S(A_S(0)-(0.27)t)}\right) - \mu x \\ \dot{e} = rx\left(1 - \frac{e}{D_B(A_B(0)+c_B t)}\right) = rx\left(1 - \frac{e}{D_B(A_B(0)-(0.0436)t)}\right) \end{cases} \tag{5.3}$$

It is important to note that the stationary points we calculated in the previous section are not stationary points for this model, but the point $(\bar{x}(t), \bar{e}(t)) = \left(\frac{bK_S(t)K_B(t)}{bK_B(t)+\mu K_S(t)}, K_B(t)\right)$ acts as an attractor for the solution curve of the system (5.2), because its corresponding point for the system (5.1) is a stable node.

Now, before giving the predictions for the evolution of the population we need to find some estimations for the parameters in (5.3). For this purpose we will assume that $(x(0), e(0)) = (\bar{x}(0), \bar{e}(0)) = \left(\frac{bK_S(0)K_B(0)}{bK_B(0)+\mu K_S(0)}, K_B(0)\right)$.
We have already calculated the values in which the total eggs range, thus we can have the estimations for $K_B(0)$, which are:

$$K_{B-}(0) = e_-(0) = 124111$$

$$K_{B+}(0) = e_+(0) = 236403$$

Now, knowing $x_+(0) = 46913$ and $x_-(0) = 28912$ (we calculated those values in Chapter 2) we can give an estimation for $K_{S\pm}(0)$, since $x_\pm(0) = \bar{x}_\pm(0) = \frac{bK_{S\pm}(0)K_{B\pm}(0)}{bK_{B\pm}(0)+\mu K_{S\pm}(0)}, K_{B\pm}(0)$, thus:

$$K_{S-} = \frac{bK_{B-}x_-}{bK_{B-} - \mu x_-} = \frac{71765944.64}{2482.22 - 1156.48} = \frac{71765944.64}{1325.74} \approx 54132.8$$

$$K_{S+} = \frac{bK_{B+}x_+}{bK_{B+} - \mu x_+} = \frac{221807478.78}{4728.06 - 1876.52} = \frac{221807478.78}{2851.54} \approx 77785.15$$

We know $A_S(0) = 10.19\text{km}^2$ and $A_B(0) = 1.09\text{km}^2$ thus we can give estimations for D_S and D_B:

$$D_{B+} = \frac{K_{B+}}{A_B} = \frac{236403}{1.09\text{km}^2} \approx 216884/\text{km}^2 \quad D_{B-} = \frac{K_{B-}}{A_B} = \frac{124111}{1.09\text{km}^2} \approx 113863/\text{km}^2$$

$$D_{S+} = \frac{K_{S+}}{A_S} = \frac{77785.15}{10.91\text{km}^2} \approx 7130/\text{km}^2 \quad D_{S-} = \frac{K_{S-}}{A_S} = \frac{54132.8}{10.91\text{km}^2} \approx 4962/\text{km}^2$$

We already know from previous calculations $b = 0.02$ and $\mu = 0.04$. Thus we have the following prediction graph:

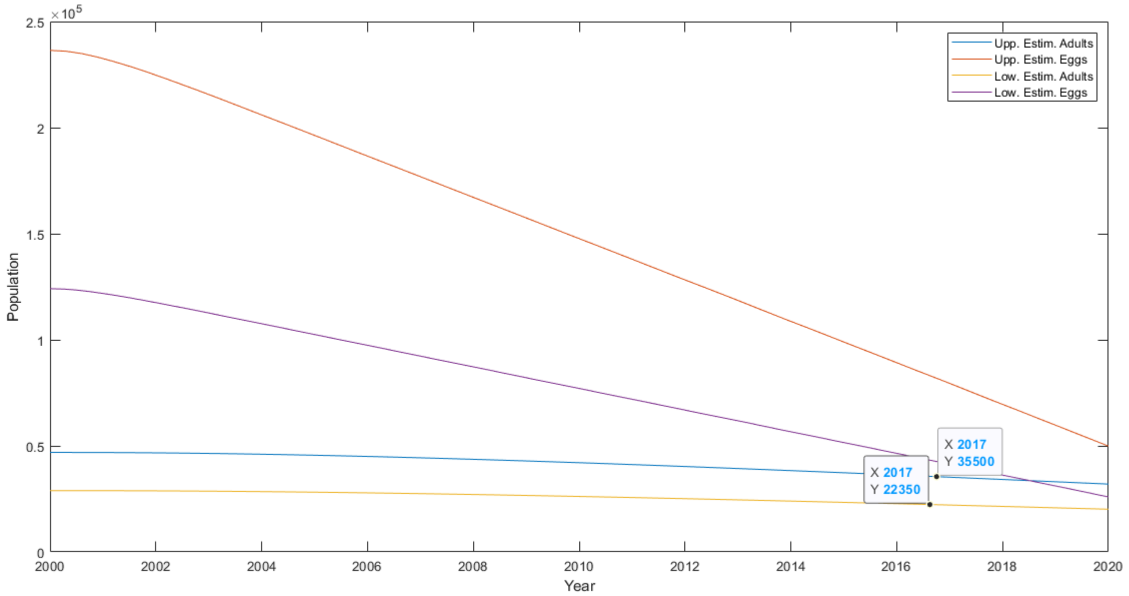


Figure 5.1: Evolution of adult and egg populations with habitat destruction occuring.

As we can see the predicted adult population in year 2017 ranges from 22350 to 35500 (female) individuals which is far from the observed data (the total adult population in year 2017 ranged from 3000 to 6000 mature individuals).
In the next section we will implement the model including a time delay and we will see whether this approach can lead us to a more realistic result.

5.2.3 Time dependent carrying capacity with delay

Now we want to implement our model (5.1) including a time delay which reflects the years needed to reach adulthood starting as eggs. Thus we have:

$$\begin{cases} \dot{x}(t) = be(t-\tau)\left(1 - \frac{x(t)}{K_S}\right) - \mu x(t) \\ \dot{e}(t) = rx(t)\left(1 - \frac{e(t)}{K_B}\right) \end{cases} \tag{5.4}$$

Before linearizing the system, it is worth noting that the stationary points of the delayed system are the same of the nondelayed one: (0,0) and $(\bar{x}, \bar{e}) = \left(\frac{bK_SK_B}{bK_B+\mu K_S}, K_B\right)$.

Now to linearize the system, we first perform a Taylor expansion around the nontrivial stationary point , dropping all terms of second or higher order, which yields as for the nondelayed case (calling $\dot{x} = f(x,e)$ and $\dot{e} = g(x,e)$):

$$\begin{cases} f(x,e) \approx f(\bar{x},\bar{e}) + (x-\bar{x})\frac{\partial f}{\partial x}(\bar{x},\bar{e}) + (e-\bar{e})\frac{\partial f}{\partial e}(\bar{x},\bar{e}) = (x-\bar{x})\left(-\frac{b\bar{e}}{K_S} - \mu\right) + (e-\bar{e})\left(b - \frac{b\bar{x}}{K_S}\right) \\ g(x,e) \approx g(\bar{x},\bar{e}) + (x-\bar{x})\frac{\partial g}{\partial x}(\bar{x},\bar{e}) + (e-\bar{e})\frac{\partial g}{\partial e}(\bar{x},\bar{e}) = (x-\bar{x})\left(r - \frac{r\bar{e}}{K_B}\right) + (e-\bar{e})\left(-\frac{r\bar{x}}{K_B}\right) \end{cases}$$

Since, by definition, $f(\bar{x},\bar{e}) = 0 = g(\bar{x},\bar{e})$.
Now putting these results back in our system (5.4) and expliciting again the time delay:

$$\begin{cases} \dot{x}(t) = \left(-\frac{b\bar{e}}{K_S} - \mu\right)x(t) + \left(b - \frac{b\bar{x}}{K_S}\right)e(t-\tau) + 2\frac{b\bar{x}\bar{e}}{K_S} + \mu\bar{x} - b\bar{e} \\ \dot{e}(t) = \left(r - \frac{r\bar{e}}{K_B}\right)x(t) - \frac{r\bar{x}}{K_B}e(t) + \frac{2r\bar{x}\bar{e}}{K_B} - r\bar{x} \end{cases}$$

Our linearized system in matrix notation reads:

$$\begin{pmatrix} \dot{x}(t) \\ \dot{e}(t) \end{pmatrix} = A\begin{pmatrix} x(t) \\ e(t) \end{pmatrix} + B\begin{pmatrix} x(t-\tau) \\ e(t-\tau) \end{pmatrix}$$

where A and B are the following:

$$A = \begin{pmatrix} -\frac{b\bar{e}}{K_S} - \mu & 0 \\ r - \frac{r\bar{e}}{K_B} & -\frac{r\bar{x}}{K_B} \end{pmatrix} \qquad B = \begin{pmatrix} 0 & b - \frac{b\bar{x}}{K_S} \\ 0 & 0 \end{pmatrix}$$

where A contains the non-delayed and B the delayed terms.
The characteristic equation in terms of A and B is given by:

$$det(\lambda I - A - Be^{-\lambda}) = 0$$

The matrix $\lambda I - A - Be^{-\lambda}$ is the following:

$$\begin{pmatrix} \lambda + \frac{b\bar{e}}{K_S} + \mu & (\frac{b\bar{x}}{K_S} - b)e^{-\lambda} \\ \frac{r\bar{e}}{K_B} - r & \lambda + \frac{r\bar{x}}{K_B} \end{pmatrix}$$

recalling that $(\bar{x}, \bar{e}) = \left(\frac{bK_SK_B}{bK_B+\mu K_S}, K_B\right)$ we have:

$$\begin{pmatrix} \lambda + \frac{bK_B}{K_S} + \mu & \left(\frac{b^2K_B}{bK_B+\mu K_S} - b\right) e^{-\lambda} \\ \frac{rK_B}{K_B} - r & \lambda + \frac{rbK_S}{bK_B+\mu K_S} \end{pmatrix} = \begin{pmatrix} \lambda + \frac{bK_B}{K_S} + \mu & \left(\frac{b^2K_B}{bK_B+\mu K_S} - b\right) e^{-\lambda} \\ 0 & \lambda + \frac{rbK_S}{bK_B+\mu K_S} \end{pmatrix}$$

which yields the following characteristic equation:

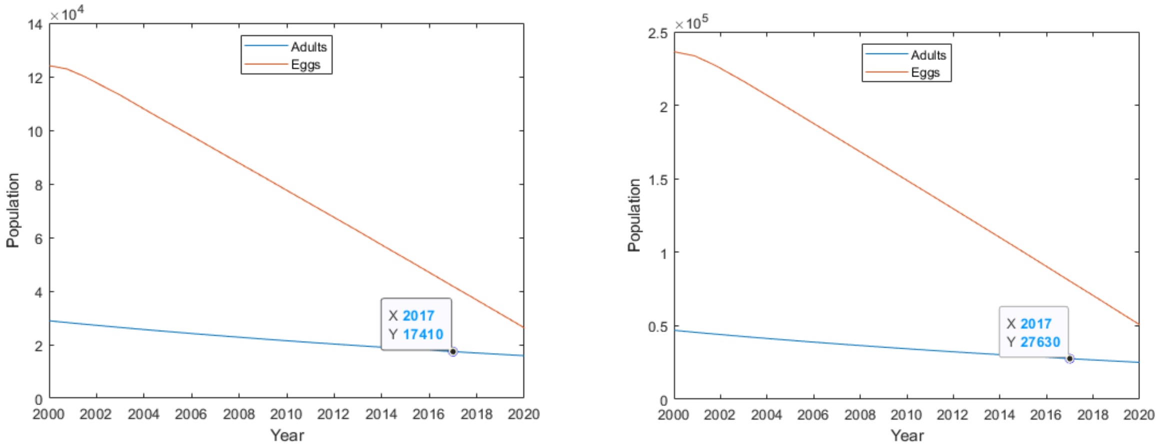
$$\left(\lambda + \frac{bK_B}{K_S} + \mu\right)\left(\lambda + \frac{rbK_S}{bK_B + \mu K_S}\right) = 0$$

In contrast to most other DDE systems, it's still a polynomial, not a transcendental equation and so we can easily read out the eigenvalues which are $\lambda_1 = -\frac{bK_B}{K_S} - \mu$ and $\lambda_2 = -\frac{rbK_S}{bK_B+\mu K_S}$. Since, all parameters are strictly positive we have that $\lambda_{1,2} < 0$, thus $(\bar{x}, \bar{e})$ is a stable node as for the nondelayed model.

Just like in chapeter 3 we will take as our delay $\tau = 3$ years, since he are assuming the *Ctenosaura bakeri* reaches sexual maturity at 2.5 years old and has an incubation time of 6 months, thus it takes 3 years to form an adult individual from the moment the egg it hatched from had been laid.
Now, taking the parameters we calculated in the previous section and taking as history functions the following:

$$\begin{cases} x_+(t) = 46913, \text{ for } -\tau \leq t \leq 0 \\ e_+(t) = 236403, \text{ for } -\tau \leq t \leq 0 \end{cases} \qquad \begin{cases} x_-(t) = 28912, \text{ for } -\tau \leq t \leq 0 \\ e_-(t) = 124111, \text{ for } -\tau \leq t \leq 0 \end{cases}$$

This gives us the following prediction graph for both the lower and the upper estimations:



(a) *Lower estimation for the starting population.* (b) *Upper estimation for the starting population.*

Figure 5.2: Evolution of adult and egg populations with habitat destruction occuring (with delay included).

The predicted adult population in year 2017 ranges from 17410 to 27630 (female) mature individuals. This result, even though is lower than the nondelayed case (whose predicted population ranged from 22350 to 35500 female mature individuals), it is still much greater than the observed data (the total adult population in year 2017 ranged from 3000 to 6000 mature individuals). Thus other effects may be relevant and should be included into the model approach.
We will introduce a different approach in the next section.

5.2.4 Response type death rate

The problem with the previous models was mainly due to the fact that the death rate stayed constant in time which, if we have a situation where habitat destruction is occurring (and thus we have a decrease of the carrying capacity), is not very realistic.
Thus, if we have $\dot{K}(t) = f(t)$, where $K(t)$ is the carrying capacity of an habitat and f is a continuous function we can define the following:

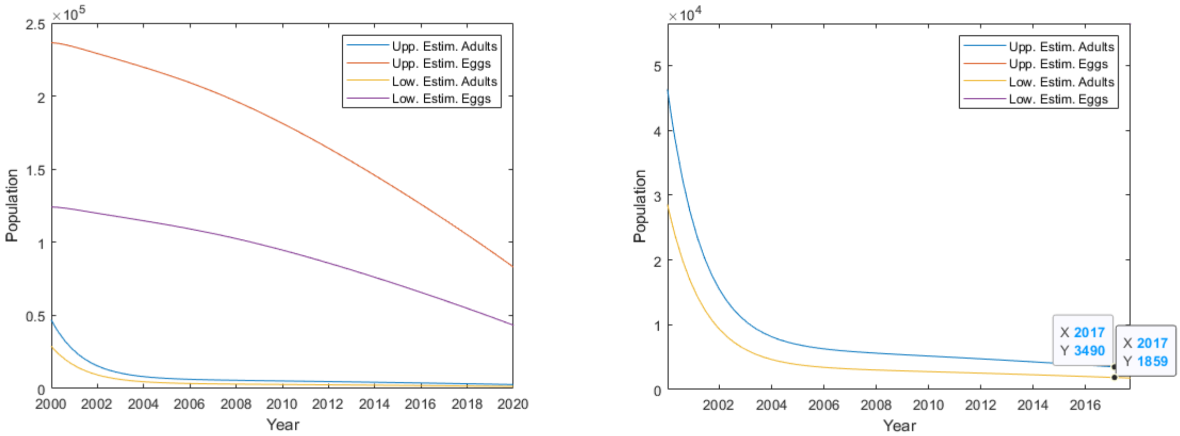
$$\bar{\mu}(t) = \mu e^{-\gamma(t,x(t))f(t-\tau)} \tag{5.5}$$

Where $\gamma(t, x(t))$ is an opportune function which should depend on the fraction $\frac{x(t)}{K(t)}$. Indeed, if we have the number of individuals $x(t)$ to be much smaller than the carrying capacity they should not be too bothered by events of habitat destruction.
We can easily see that if $K(t)$ is constant in time we have back our old death rate μ. Furthermore we put a delay for it seems more realistic: for example, if we have a large area of habitat destroyed the survived individuals will need some time to adapt (including a decrease of the population) to the new habitat.
Hence our systems (5.2) and (5.4) read:

$$\begin{cases} \dot{x}(t) = be(t)\left(1 - \frac{x}{K_S(t)}\right) - \mu e^{-\gamma(t,x(t))f(t)}x(t) \\ \dot{e}(t) = rx(t)\left(1 - \frac{e}{K_B(t)}\right) \end{cases} \qquad \begin{cases} \dot{x}(t) = be(t-\tau)\left(1 - \frac{x(t)}{K_S}\right) - \mu e^{-\gamma(t,x(t))f(t-\tau_1)}x(t) \\ \dot{e}(t) = rx(t)\left(1 - \frac{e(t)}{K_B}\right) \end{cases}$$

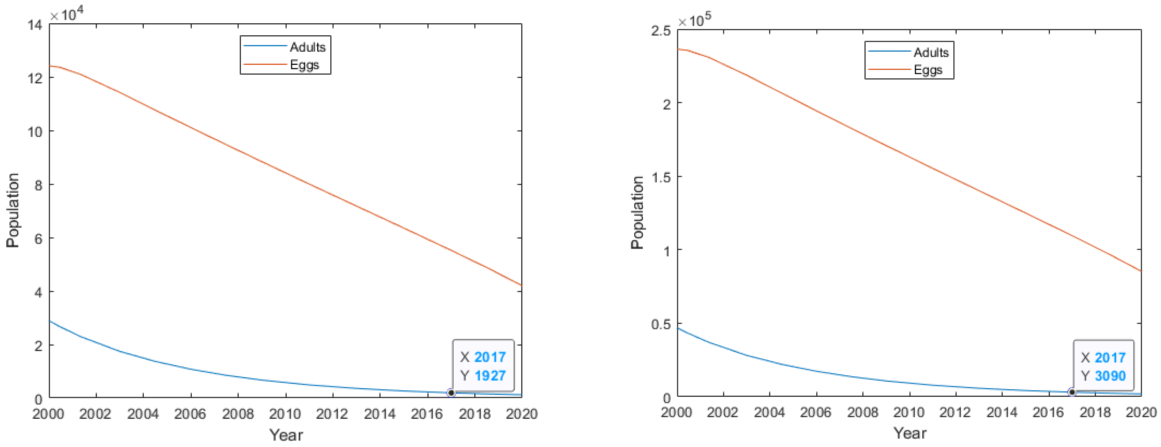
without and with delay, respectively (which is not necessarily the same as the delay τ for the population growth).
In our case, since we do not have a huge gap between the values of the carrying capacity and the total population, we can assume γ to be locally constant. We will take $\gamma \approx \frac{10.5}{D_S}$ for our nondelayed system and $\gamma \approx \frac{5.65}{D_S}$ for the delayed one. Furthermore, since we are assuming the habitat destruction to occur linearly we have $f(t) = (D_S)(c_s) = f(t - \tau_1)$. Thus, taking all the parameters we used for our previous models, as history functions the same we took for (5.4) and as starting points the same we took for (5.2) we have the prediction graphs (Figure 5.3 and Figure 5.4).

We can see that with this response type death rate approach we get as predicted female adult populations values that range from 1859 to 3490 individuals (for the nondelayed model) and values that range from 1927 to 3090 individuals (for the model with delay).
Compared to the biologists' estimations (the total adult population was estimated to range from 3000 to 6000 individuals in 2017) we have that these models' estimations are



(a) *Overall look at the total populations.* (b) *Focus on the adult population.*

Figure 5.3: Evolution of adult and egg populations with habitat destruction occuring.



(a) *Lower estimation for the starting population.* (b) *Upper estimation for the starting population.*

Figure 5.4: Evolution of adult and egg populations with habitat destruction occuring (with delay included).

very realistic.

Nevertheless, assuming our function γ to be a constant can be quite reductive, thus it is something that needs to be further investigate on in order to have a more generalized formulation of the previously mentioned function.

5.3 Conclusions

In this chapter we have investigated the effects of habitat destruction only on the overall adult population of *Ctenosaura bakeri*, not taking into cosiderations other factors like sex selective hunting.
Our last approach in this chapter gave us estimations very close to the ones observed by biologists and compared to the the models of the previous chapter (which gave us a

greater total population in 2017 than the starting one) we can conclude that the major factor that caused this decrease of the population is attributable to the habitat loss. However, it is interesting to stress that this model, in contrast with the sex dependent models, does not directly lead to the extinction of the whole population since $(\bar{x}(t), \bar{e}(t)) \neq (0, 0)$ acts as an attractor for our solution curve. Nevertheless, this should not lead to the false belief that the habitat destruction effects cannot push the population to extinction for the following reasons:

- If $\lim_{t\to\infty}(K_S(t), K_B(t)) = (p, q)$, where at least one between p and q is 0, we will have $\lim_{t\to\infty} \bar{x}(t) = \lim_{t\to\infty} \frac{bK_S(t)K_B(t)}{bK_B(t)+\mu K_S(t)} = 0$, which means that our solution curve $(x(t), e(t))$ will tend to (0,0).
- If we will have a relatively small population, then stochastic effects (which we did not take into consideration since all the models we have considered so fare are deterministic ones) will play a major role and could lead to the extinction of the population even if it is not predicted by our model.
- Lastly, the lack of genetic variance in the population, if the latter is small, jeopardies the survival of the species since it becomes more vulnerable to possible drastic changes (like climate change).

Hence it is vital to preserve the habitat of *Ctenosaura bakeri* if we want to see them bouncing back to healthier numbers.

Chapter 6

Hybridization

6.1 Introduction and assumptions

As mentioned in the Introduction chapter the *Ctenosaura bakeri* is one the few saurian species to produce fertile hybrids when mating with the other native iguana species of the island: the *Ctenosaura similis*. This event is not usual since the two species share different ecological niches but where the two habitats overlap, at the niches' borders, matings between the two species are observed.

This chapter will only provide a first approach to the problem by giving a general model based on the theory of compartment models (see [20]). We will take a system of two ordinary differential equations which will describe the dynamics of the three different species, by looking at their growth rate and the competition among themselves in the area of the overlapping habitats.
However, we will not deepen the analysis of possible stationary points and their stability and we will not provide simulations like we did in the previous chapter mainly because many aspects of this phenomenon are still unclear from a biological point of view, like: are the offsprings of the hybrids fertile too? Can an hybrid individual mate with a non hybrid individual? Are hybrids whose mother is a *Ctenosaura bakeri* and whose father is a *Ctenosaura similis* different from hybrids whose mother *Ctenosaura similis* is a and whose father is a *Ctenosaura bakeri*?

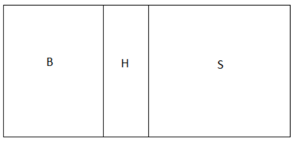
That being said we will make the following assumptions:

- We consider the populations to be uniformly distributed across their habitats.
- We consider all adult females to become gravid after every mating season.
- Mating (and thus egg laying) occurs at the same time for every sexual mature individual.
- We consider the whole sexually mature populations to consist of mature breeders only.
- We are not considering (human) hunting and habitat destruction to occur.

- Once an individual reaches sexual maturity they mate every year until their natural death.
- We consider the densities of both the adults and the nests to be constant in time.
- We consider the hybrids only to mate with hybrids.
- We consider hybrid individuals not to leave the overlapping habitats.
- *Ctenosaura bakeri* individuals can move from their habitats to the overlapping one and back.
- *Ctenosaura similis* individuals can move from their habitats to the overlapping one and back.

6.2 The model

With the given assumptions we can sketch a simple draw to represent the situation of the different habitats with the overlapping ones, which can be summarized in the following way:



- The "B" labelled habitat is the one for *Ctenosaura bakeri* only.
- The "H" labelled habitat is the one for the overlapping habitats, thus hybrids can only appear and live here.
- The "S" labelled habitat is the one for *Ctenosaura similis* only.

Having this in mind we can give the following system to model our problem:

$$\begin{cases} \dot{b}_1 = r_b b_1(1 - \frac{b_1}{K_b}) - t_{1\to 2} b_1 + t_{2\to 1} b_2 \\ \dot{b}_2 = (r_b - \epsilon) b_2 (1 - \frac{b_2 + k_h h + k_s s_2}{K_h}) + t_{1\to 2} b_1 - t_{2\to 1} b_2 \\ \dot{h} = r_h h (1 - \frac{h + k_b b_2 + k_s s_2}{K_h}) + \epsilon b_2 s_2 \\ \dot{s}_2 = (r_s - \epsilon) s_2 (1 - \frac{s_2 + k_h h + k_b b_2}{K_h}) + v_{1\to 2} s_1 - v_{2\to 1} s_2 \\ \dot{s}_1 = r_s s_1 (1 - \frac{s_1}{K_s}) - v_{1\to 2} s_1 + v_{2\to 1} s_2 \end{cases}$$

We have that b_1 stands for the *Ctenosaura bakeri* population living in habitat B, b_2 stands for the *Ctenosaura bakeri* population living in the overlapping habitat H, h is the hybrid population (of course living in the overlapping habitat H), s_2 stands for the *Ctenosaura similis* population living in the overlapping habitat H, while s_1 stands for the *Ctenosaura similis* population living in habitat S.

K_b, K_h and K_s are respectively, the carrying capacities of habitat B, H and S.

The first and the fifth equations have a logistic growth term and two other terms, characterized by the parameters t and v which describe the movement of the subpopulations, respectively of the *Ctenosaura bakeri* and the *Ctenosaura similis*, from the original habitat to the overlapping one and back ($1 \rightarrow 2$ indicates the movement the former while $2 \rightarrow 1$ indicates the latter).

The second, the third and the fourth equations describe the situation in the overlapping habitats where we have competition among the three populations (like in a Lotka-Volterra competition model).
In the second and fourth equations we have, as for the first and fifth equations the parameters t and r which describe the movement of the subpopulations with opposite sign compared to the latters.

The parameters r_b, r_h and r_s are the growth rates for the population of *Ctenosaura bakeri*, the hybrids and *Ctenosaura similis*, respectively.

The ϵ parameter describes the mating rate between the *Ctenosaura bakeri* and the *Ctenosaura similis* at which hybrids are generated. It is worth noting that we have considered the growth rate of the hybrids due to the mating of the different species to follow the law of mass action. Furthermore, we can see that the growth rate of the subpopulations of *Ctenosaura bakeri* and *Ctenosaura similis* living in the overlapping habitats is lower than that of the populations living in their own habitats, because of that.

As mentioned in the introduction we will not study this model, nevertheless it is important to stress that hybridization combined with habitat loss could pose a threat in the future for the *Ctenosaura bakeri*, for this species will likely be forced to live in the overlapping niche, thus competing with two other populations of iguanas (the *Ctenosaura similis* and the hybrids) and having a lower growth rate as a direct consequence of hybridization.

Chapter 7

Conclusions and open questions

We formulated and studied three different models to approach the study of the population dynamics of *Ctenosaura bakeri*.

We first studied the intrinsic growth of the *Ctenosaura bakeri*, i.e. excluding hunting and habitat destruction, via a discrete time linear model, using a transition matrix approach. We gave estimations for the parameters and we calculated the dominating eigenvalue which we saw it was bigger than 1. Thus we concluded that, if both hunting and habitat destruction would cease the population would bounce back in numbers.

Secondly, we approached the effects of sex selective huning on the dynamics of the species. We mainly used this time a contiunous time linear model, i.e. we did not consider the carrying capacity of the system, since we wanted to focus more on the effects that hunting has on the growth term of the population (being far away from any limitation of growth). We started considering our hunting effort to be constant and we studied the stability of the trivial stationary point and we also gave an estimation of the hunting effort knowing the evolution of sex ratio over the years. Then we gave a prediction for the population dynamics having calculated the hunting effort, before. We repeated the same procedure for the same model (with a constant hunting effort), this time including a delay in our model (to reflect the time needed for an individual to reach sexual maturity).
Afterwards, we changed the model not considering our hunting effort to be constant anymore, rather than we considered it to be time dependent. At first we thought about considering it being dependent on the population of the hunted individuals (i.e. the females of *Ctenosaura bakeri*), but then, since the number of poachers was reported to be increasing in the years and also considering the illegal market behind the trade of this iguana's meat, we decided to move to a time dependent hunting effort. This unfortunately is more detrimental to the iguana's population than a female population dependent hunting effort, since in the latter case we could reach an equilibrium like in the Lotka Volterra predator prey model and grant the survival of the species. However, historically this is not true, since many times numerous animal species have been driven to extinction also because of economic interests (thus independently from the number of animals left of the species).
We approached this problem as we did for the constant hunting effort: we first take a nondelayed model and then we considered the same model with delay. We assumed our

hunting effort to be less than 1 and to follow a logistic growth over time (this also to reflect the competition between hunters). What was left to estimate was the growth rate of the hunting effort and we did it using a least square sum approach, then we gave a prediction for dynamics of the total population.
It is worth noting that as history functions, because of the lack of older data, we took the starting populations as constants for the interval $-\tau \leq t \leq 0$ (where τ is our delay). However, it is likely that the females of *Ctenosaura bakeri* have been heavily poached even before the year 2000, since if we compare the sex ratio of this species in the year 2000 with that of other similar species we can see that for the *Ctenosaura bakeri* the sex ratio was slightly biased towards a female dominance, while for the other species it is heavily biased towards a female dominance. Having said so, it could be that our predictions are more optimistic than what the situation actually is.
However, we were quite surprised on how greatly hunting impacts on the dynamics of *Ctenosaura bakeri*, since for all the four approaches we got as results that the population will die out due to overhunting.

Thirdly, we approached the effects of habitat destruction (without considering hunting to occur) on the survival of the species. We first approached this problem setting up a model consisting of two logistic like differential equation, with two different carrying capacities: one for the nesting beaches and the other for the mangrove forests (the habitat of the adult iguanas). We decided that the effects of habitat destruction would have affected the carrying capacity, considering it to be the product of the maximum density of the habitat by the surface of the same.
We first studied the stationary points and their stability and we found out that extinction was not contemplated by the model.
Then we set the habitat destruction to occur linearly and after having estimated the parameters we gave the predictions for the population dynamics. We repeated the same process but considering a delayed model (again taking into consideration the time needed for an individual to reach sexual maturity).
Both these approaches failed to give us a prediction coherent with the collected data, thus we introduced a response type death rate, dependent on the variation of the carrying capacity and this approach granted predictions consistent with the estimated data.
It is worth noting that it is realistic to assume this type of death rate to exist, furthermore having considered that the hunting models gave us an increased population and thus, for at least this near future the huge decrease of the numbers of the *Ctenosaura bakeri* should be blamed on the habitat destruction effect.

Finally we set a basic model for the hybridization effects and we left it still to be studied. This lead us to start stating the open questions left by this study of the population dynamics of *Ctenosaura bakeri*. Firstly, of course this model for the hybridization should be studied.

Secondly, it should be worth if some biologists and real world observationscould give us insights on the estimations of the parameters for the intrisic growth of the population.

Then, for the sex dependent hunting model, it could be interesting to delve into the study of the growth parameter for the time dependent hunting effort: we considered it to be a constant but it could also be time dependent to reflect possible measure to fight illegal poaching.

For the habitat destruction model, it could be very interesting to further analyse the response type death rate and to see whether it could be bettered or applied to other situations.

Also, we used only determinsitic models to study these problems and it could be interesting to see if a stochastic approach would lead to different results or if it could give us different insights.

Finally, our predictions for the population dynamics of *Ctenosaura bakeri* are very dire and something should be done as soon as possible, since we predicted a great decrease in the total population in the next years, a population which is already small in numbers. If through law enforcement and sensibilisation, this situation could be reversed we will see the population to bounce back at greater numbers, since we know that it would intrinsically grow.

Indeed the mathematical models, in this case applied to study the population dynamics of an endangered species, provied possibilities to better estimate the effects of certain actions, even quantitatively and by that, can help the biologists and the politicians to decide which actions maybe should be taken first or where to put effort in most efficiently.From this point of view, our wish is that this study could help the fight for the survival of this species.

Appendix A

Basic proofs

A.1 Starting population

The following proposition is needed for giving insights to the structure of the starting population in section 3.2.3

Proposition A.1.1. *For large enough $n \in \mathbb{N}$ we have*

$$N(n) = (0, h(n), 0, j_2(n), 0, nb(n), mb(n))^T$$

Proof. As we have already seen in the latter part of section 3.2.3 if we start with $N(0) = (e(0), h(0), j_1(0), j_2(0), j_3(0), nb(0), mb(0))^T$ we will have that $N(4)$ is already of the form $(0, h(n), 0, j_2(n), 0, nb(n), mb(n))^T$, so we want to prove that for every $n \geq 4$ we have $N(n) = (0, h(n), 0, j_2(n), 0, nb(n), mb(n))^T$. We will prove it by induction:

1. (Base case) We have already seen that (in 3.2.3) for $n = 4$ we have $N(4) = (0, h(4), 0, j_2(4), 0, nb(4), mb(4))^T$
2. (Inductive step) Now we suppose (for every $n \in \mathbb{N}$ greater or equal than 4) that we have $N(n) = (0, h(n), 0, j_2(n), 0, nb(n), mb(n))^T$ and we have to show that $N(n+1)$ is of the form $N(n+1) = (0, h(n+1), 0, j_2(n+1), 0, nb(n+1), mb(n+1))^T$.

$$N(n+1) = LN(n) = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 4.02 & 5.17 \\ 0.16 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.06 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.17 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.39 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.73 & 0.92 & 0.92 \end{pmatrix} \begin{pmatrix} 0 \\ h(n) \\ 0 \\ j_2(n) \\ 0 \\ nb(n) \\ mb(n) \end{pmatrix} =$$

$$= \begin{pmatrix} 0 \\ (4.02)nb(n) + (5.17)mb(n) \\ 0 \\ (0.06)h(n) \\ 0 \\ (0.39)j_2(n) \\ (0.92)(nb(n) + mb(n)) \end{pmatrix} =: \begin{pmatrix} 0 \\ h(n+1) \\ 0 \\ j_2(n+1) \\ 0 \\ nb(n+1) \\ mb(n+1) \end{pmatrix}$$

□

A.2 Ratio equation for costant hunting effort (I)

We will refer to $\frac{f}{m}(t)$ as $r(t)$, from now on.

$$\dot{r}(t) = (b(1-h)-h)r(t) - b(1-h)r(t)^2 = (b(1-h)-h)r(t)(1-\frac{b(1-h)}{b(1-h)-h}r(t))$$

So we can write this equation in the following way, calling $a = b(1-h)-h$ and $K = \frac{b(1-h)-h}{b(1-h)}$:

$$\dot{r}(t) = ar(t)(1-\frac{r(t)}{K})$$

We introduce a new variable (assuming that the population never vanishes) $v(t) = \frac{1}{r(t)}$. Without loss of generality let $t_0 = 0$, $v_0 = \frac{1}{u_0}$. Hence we get:

$$\dot{v}(t) = -\frac{\dot{r}(t)}{r(t)^2} = -\frac{ar(t)(1-\frac{r(t)}{K})}{r(t)^2} = -a\left(\frac{1}{r(t)} - \frac{1}{K}\right) = -av(t) + \frac{a}{K}$$

This is a linear inhomogeneous ODE, so we apply the variation of costants which yields:

$$v(t) = v_0 e^{-A(t)} + \textstyle\int_0^t e^{-(A(t)-A(s))} \frac{a}{K}\, ds \qquad \text{where} \quad A(t) = \textstyle\int_0^t a\, ds = at$$

Returning to the variable $r(t) = \frac{1}{v(t)}$ we get:

$$r(t) = \frac{r_0}{e^{-A(t)} + r_0 \int_0^t e^{-(A(t)-A(s))} \frac{a}{K}\, ds} = \frac{r_0 e^{A(t)}}{1 + r_0 \frac{a}{K} \int_0^t e^{A(s)}\, ds}$$

So, since we have a and K constant, we get the following explicit solution:

$$r(t) = \frac{r_0}{e^{-at} + r_0 \frac{a}{K} e^{-at} \int_0^t e^{as}\, ds} = \frac{r_0}{e^{-at} + \frac{r_0}{K}(1-e^{-at})} = \frac{r_0}{e^{-at}(1-\frac{r_0}{K}) + \frac{r_0}{K}}$$

Thus, our solution reads:

$$r(t) = \frac{r_0 K}{e^{-at}(K-r_0) + r_0} = \frac{r_0 \frac{(b(1-h)-h)}{b(1-h)}}{e^{-(b(1-h)-h)t}\left(\frac{b(1-h)-h}{b(1-h)} - r_0\right) + r_0}$$

$$r(t) = \frac{r_0(b(1-h)-h)}{e^{-(b(1-h)-h)t}(b(1-h)(1-r_0)-h) + r_0 b(1-h)}$$

Appendix B

Code

B.1 Calculation of characteristic polynomial and eigenvalues and corresponding eigenvectors of the Transition matrix

```
>> L=[0 0 0 0 0 0 0; 0 0 0 0 0 4.02 5.17; 0.16 0 0 0 0 0 0; 0 0.06 0 0 0 0 0; 0 0 0.17 0 0 0 0; 0 0 0 0.39 0 0 0;
 0 0 0 0 0.73 0.92 0.92]

L =

         0         0         0         0         0         0         0
         0         0         0         0         0    4.0200    5.1700
    0.1600         0         0         0         0         0         0
         0    0.0600         0         0         0         0         0
         0         0    0.1700         0         0         0         0
         0         0         0    0.3900         0         0         0
         0         0         0         0    0.7300    0.9200    0.9200

>> charpoly(L)

ans =

    1.0000   -0.9200         0   -0.0941   -0.0248         0         0         0

>> [V,D]=eig(L)

V =

  Columns 1 through 6

   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i
  -0.9819 + 0.0000i   0.9569 + 0.0000i   0.9569 + 0.0000i   0.7321 + 0.0000i   0.0000 + 0.0000i  -0.0000 + 0.0000i
   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i
  -0.0571 + 0.0000i   0.0169 - 0.1592i   0.0169 + 0.1592i  -0.2353 + 0.0000i  -0.0000 + 0.0000i   0.0000 + 0.0000i
   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.2161 + 0.0000i  -0.2161 + 0.0000i
  -0.0216 + 0.0000i  -0.1702 - 0.0365i  -0.1702 + 0.0365i   0.4916 + 0.0000i  -0.7708 + 0.0000i   0.7708 + 0.0000i
  -0.1790 + 0.0000i   0.1393 + 0.0944i   0.1393 - 0.0944i  -0.4087 + 0.0000i   0.5993 + 0.0000i  -0.5993 + 0.0000i

  Column 7

   0.0000 + 0.0000i
   0.0000 + 0.0000i
   0.0000 + 0.0000i
  -0.0000 + 0.0000i
   0.2161 + 0.0000i
  -0.7708 + 0.0000i
   0.5993 + 0.0000i


D =

  Columns 1 through 6

   1.0311 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i
   0.0000 + 0.0000i   0.0378 + 0.3567i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i
   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0378 - 0.3567i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i
   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i  -0.1867 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i
   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i
   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i
   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i

  Column 7
```

```
   0.0000 + 0.0000i
   0.0000 + 0.0000i
   0.0000 + 0.0000i
   0.0000 + 0.0000i
   0.0000 + 0.0000i
   0.0000 + 0.0000i
   0.0000 + 0.0000i
```

B.2 Calculation of $a_\pm$ of 2.1.1

```
>> N0min=[105;49;0;10;16]
N0max=[200;79;0;19;26]
Vtilde=[0 0.7321 0.9569 0.9569 -0.9819; 0 -0.2353 0.0169+0.1592i 0.0169-0.1592i -0.0571; -0.2161 0 0 0 0;
0.7708 0.4916 -0.1702+0.0365i -0.1702-0.0365i -0.0216; -0.5993 -0.4087 0.1393-0.0944i 0.1393+0.0944i -0.1790]
solvecmin=linsolve(Vtilde, N0min)
solvecmax=linsolve(Vtilde, N0max)

N0min =

   105
    49
     0
    10
    16


N0max =

   200
    79
     0
    19
    26


Vtilde =

  Columns 1 through 3

   0.0000 + 0.0000i   0.7321 + 0.0000i   0.9569 + 0.0000i
   0.0000 + 0.0000i  -0.2353 + 0.0000i   0.0169 + 0.1592i
  -0.2161 + 0.0000i   0.0000 + 0.0000i   0.0000 + 0.0000i
   0.7708 + 0.0000i   0.4916 + 0.0000i  -0.1702 + 0.0365i
  -0.5993 + 0.0000i  -0.4087 + 0.0000i   0.1393 - 0.0944i

solvecmin =

   1.0e+02 *

  -0.0000 + 0.0000i
  -0.2615 + 0.0000i
  -0.3277 - 1.0392i
  -0.3277 + 1.0392i
  -1.9031 + 0.0000i


solvecmax =

   1.0e+02 *

  -0.0000 + 0.0000i
  -0.3386 + 0.0000i
  -0.4774 - 1.7042i
  -0.4774 + 1.7042i
  -3.2199 + 0.0000i
```

B.3 Plot of Figure 3.1

```
function [N_tp1] = transition_matrix(L, N_t)
%product of L and N(t) to get N(t+1)
N_tp1=L*N_t;
end
```

```
Nmin_0=[0; 105; 0; 49; 0; 10; 16];
Nmax_0=[0; 200; 0; 79; 0; 19; 26];
L=[0 0 0 0 0 0 0; 0 0 0 0 0 4.02 5.17; 0.16 0 0 0 0 0 0; 0 0.06 0 0 0 0 0; 0 0 0.17 0 0 0 0;
 0 0 0 0.39 0 0 0; 0 0 0 0 0.73 0.92 0.92];
tmax=18;
Nmin_t=zeros(7,tmax);
```

```
Nmax_t=zeros(7,tmax);
Nmin_t(:,1)=Nmin_0;
Nmax_t(:,1)=Nmax_0;

for t=1:tmax-1
Nmin_t(:,t+1)=transition_matrix(L, Nmin_t(:,t));
Nmax_t(:,t+1)=transition_matrix(L, Nmax_t(:,t));
end

%Calculation of adult's densities per year
ADmin_t=zeros(1,tmax);
ADmax_t=zeros(1,tmax);

ADmin_t(1)=Nmin_0(6)+Nmin_0(7);
ADmax_t(1)=Nmax_0(6)+Nmax_0(7);

for t=1:tmax-1
ADmin_t(t+1)=Nmin_t(6,t+1)+Nmin_t(7,t+1);
ADmax_t(t+1)=Nmax_t(6,t+1)+Nmax_t(7,t+1);
end

figure

plot(2000:2017,ADmax_t(1,:), 'r.', 2000:2017,ADmin_t(1,:), 'b.', 2000,ADmax_t(1), 'ro',
 2000,ADmin_t(1), 'bo', 2017,2.75, 'ro', 2017,1.38, 'bo')
xlabel('Year')
ylabel('AD(t)')
legend({'Upper␣bound␣pred.','Lower␣bound␣pred.','Upper␣bound␣obser.', 'Lower␣bound␣obser.'},'Location','northwest')
```

B.4 Plot of Figure 4.1

```
t=[1:3000];
tmax=length(t);
r=zeros(1,tmax);
r(1)=0.5;
for t=2:tmax
r(t)=(0.5*1000)/((exp(-(0.005)*(t)))*(1000-0.5)+0.5);
end
figure

plot(1:3000, r(1,:))
```

B.5 Calculation of the hunting effort in 4.2.1

```
>> vpasolve(((0.11*(1-x)-x)*1.2)/((exp(-(0.11*(1-x)-x)*6))*(0.11*(1-x)*(1-1.2)-x)+0.11*(1-x)*1.2)-0.96)

ans =

0.030568593480773906424046634600962

>> vpasolve(((0.11*(1-x)-x)*1.2)/((exp(-(0.11*(1-x)-x)*11))*(0.11*(1-x)*(1-1.2)-x)+0.11*(1-x)*1.2)-0.60)

ans =

0.081067205595275305846646984307853

>> vpasolve(((0.11*(1-x)-x)*0.96)/((exp(-(0.11*(1-x)-x)*5))*(0.11*(1-x)*(1-0.96)-x)+0.11*(1-x)*0.96)-0.60)

ans =

0.11777132821752242227578714112776
```

B.6 Plot of Figure 4.2

```
function [r] = sexconstratio(b,r_0,h,t)
r=((b*(1-h)-h)*r_0)/((exp(-(b*(1-h)-h)*(t)))*(b*(1-h)*(1-r_0)-h)+b*(1-h)*r_0)
end
```

```
t=[2000:2011];
tmax=length(t);
b=0.11;
r_0=1.2;
h_1=0.031;
```

```
h_2=0.081;
h_3=0.118;
h=0.077;
r_1=zeros(1,tmax);
r_2=zeros(1,tmax);
r_3=zeros(1,tmax);
r=zeros(1,tmax);
r_1(1)=r_0;
r_2(1)=r_0;
r_3(1)=r_0;
r(1)=r_0;
for t=2:tmax
r_1(t)=sexconstratio(b,r_0,h_1,t-1);
r_2(t)=sexconstratio(b,r_0,h_2,t-1);
r_3(t)=sexconstratio(b,r_0,h_3,t-1);
r(t)=sexconstratio(b,r_0,h,t-1);
end

figure

plot(2000:2011,r_1(1,:),2000:2011,r_2(1,:),2000:2011,r_3(1,:),2000:2011,r(1,:), 2000,1.2, 'ro', 2006,0.96,'ro', 2011,0.6, 'ro' )
xlabel('Year')
ylabel('r(t)')
legend({'Prediction␣for␣h_1','Prediction␣for␣h_2','Prediction␣for␣h_3', 'Prediction␣for␣h', 'Collected␣data'},'Location','northeast')
```

B.7 Plot of Figure 4.3

```
function yp = huntingconsth(t,y)
b=0.11;
h=0.031;
mu=0.04;
yp =[ b*(1-h)*y(2)-mu*y(1); (b*(1-h)-h-mu)*y(2)];
end
```

```
function yp = huntingconsth(t,y)
b=0.11;
h=0.081;
mu=0.04;
yp =[ b*(1-h)*y(2)-mu*y(1); (b*(1-h)-h-mu)*y(2)];
end
```

```
function yp = huntingconsth(t,y)
b=0.11;
h=0.118;
mu=0.04;
yp =[ b*(1-h)*y(2)-mu*y(1); (b*(1-h)-h-mu)*y(2)];
end
```

```
t0=0;
tfinal=20;
y0max=[42648;51178];
y0min=[26283;31540];
[t,y1]=ode45(@huntingconsth, [t0 tfinal], y0min);
[t,y2]=ode45(@huntingconsth, [t0 tfinal], y0max);
t=t+2000;
figure
plot(t,y1,t,y2,t,y1(:,1)+y1(:,2),t,y2(:,1)+y2(:,2))
xlabel('Year')
ylabel('Population')
legend('Low.␣Estim.␣Males','Low.␣Estim.␣Females','Upp.␣Estim.␣Males', 'Upp.␣Estim.␣Females', 'Low.␣Estim.␣Tot.␣Population',
'Upp.␣Estim.␣Tot.␣Population','Location','Northeast')
```

```
t0=0;
tfinal=100;
y0max=[42648;51178];
y0min=[26283;31540];
[t,y1]=ode45(@huntingconsth, [t0 tfinal], y0min);
[t,y2]=ode45(@huntingconsth, [t0 tfinal], y0max);
t=t+2000;
figure
plot(t,y1,t,y2,t,y1(:,1)+y1(:,2),t,y2(:,1)+y2(:,2))
xlabel('Year')
ylabel('Population')
legend('Low.␣Estim.␣Males','Low.␣Estim.␣Females','Upp.␣Estim.␣Males', 'Upp.␣Estim.␣Females', 'Low.␣Estim.␣Tot.␣Population',
'Upp.␣Estim.␣Tot.␣Population','Location','Northeast')
```

B.8 Plot of Figure 4.4

```
function yp = huntingconsth(t,y)
b=0.11;
h=0.077;
mu=0.04;
yp =[ b*(1-h)*y(2)-mu*y(1); (b*(1-h)-h-mu)*y(2)];
end
```

```
t0=0;
tfinal=100;
y0max=[42648;51178];
y0min=[26283;31540];
[t,y1]=ode45(@huntingconsth, [t0 tfinal], y0min);
[t,y2]=ode45(@huntingconsth, [t0 tfinal], y0max);
t=t+2000;
figure
plot(t,y1,t,y2,t,y1(:,1)+y1(:,2),t,y2(:,1)+y2(:,2))
xlabel('Year')
ylabel('Population')
legend('Low.␣Estim.␣Males','Low.␣Estim.␣Females','Upp.␣Estim.␣Males', 'Upp.␣Estim.␣Females', 'Low.␣Estim.␣Tot.␣Population',
'Upp.␣Estim.␣Tot.␣Population','Location','Northeast')
```

```
t0=0;
tfinal=20;
y0max=[42648;51178];
y0min=[26283;31540];
[t,y1]=ode45(@huntingconsth, [t0 tfinal], y0min);
[t,y2]=ode45(@huntingconsth, [t0 tfinal], y0max);
t=t+2000;
figure
plot(t,y1,t,y2,t,y1(:,1)+y1(:,2),t,y2(:,1)+y2(:,2))
xlabel('Year')
ylabel('Population')
legend('Low.␣Estim.␣Males','Low.␣Estim.␣Females','Upp.␣Estim.␣Males', 'Upp.␣Estim.␣Females', 'Low.␣Estim.␣Tot.␣Population',
'Upp.␣Estim.␣Tot.␣Population','Location','Northeast')
```

B.9 Estimation of hunting effort in section 4.2.2

```
function dmfdt = mfequation(t,mf,Z)
%function to evaluate trajectories
global h b mu
%first component: dm/dt, m is mf(1)
%second component: df/dt, f is mf(2)

mf_lag2 = Z(:,1); %lag for f
dmfdt = [(b*(1-h))*mf_lag2(1)-mu*mf(1); (b*(1-h))*mf_lag2(1)-(mu+h)*mf(2)];
end
```

```
function [leastsquare_rh] = compute_least_squares(x0)
%here we compute the least square of the data points and the function
%values.
global h b mu
%given values:
h=x0;
b=0.11;%fixed
mu = 1;
tau=3;
m_0=42648;
f_0=51178;
tmax=11;%end of observation (locked here as it is the last observation time)

%m is mf(1)
%f is mf(2)
%solve the ODE system. I used a stiff solver, could also try different solvers here
sol = dde23(@mfequation,tau,@ddex1hist,[0 tmax]);

%the problem now is that the solution values are on a non-integer
%timescale. We need to shift them to be able to compare computed values
%with the data points. This happens in the following:
t=sol.x;
y=sol.y;
new_amountscale = zeros(tmax+1,2);%"new" population matrix with r in the first row and h in the second row
%shift solution time course to integer time values
for i=0:tmax
    [minValue,closestIndex] = min(abs(i-t));
    new_timescale(i+1) = t(closestIndex);
    new_amountscale(i+1,:) = y(:,closestIndex);
    closestValue(i+1) = t(closestIndex);
end

%compute least squares (as we have only three values, I did not set up a
%sum. The first square is zero, as we start our computations with that value
meas1=new_amountscale(6,2)/new_amountscale(6,1);
meas2=new_amountscale(11,2)/new_amountscale(11,1);
```

```

leastsquare_rh = (meas1-0.96)^2+(meas2-0.60)^2;

end


function s = ddex1hist(t)
% Constant history function for DDEX1.
s = [42648 51178];
end
```

```
%clean up
clear all
close all
clc
%a is adjusted in the computations. Set as global to make those
%computations faster and easier. Cave: Can cause errors though.
global h b mu
tic

%starting value for the algorithm. This is the initial value of a to be
%"tested"
x0 = 0.5;

lb = [0.000001]; %lower boundary of rate to be tested
ub = [1]; %upper boundary of rate to be tested

%some settings, also to visualize what happens.
options = optimoptions(@fmincon,'Algorithm','sqp','StepTolerance',1e-20,'ConstraintTolerance',1e-15,
'MaxFunctionEvaluations',5000,'PlotFcn',@optimplotfval);
nonlcon = [];
[x,fval,exitflag,output]=fmincon(@compute_least_squares,x0,[],[],[],[],lb,ub,nonlcon,options)
toc

%compute ODE system with found value
%given values:
h=x;
b=0.11;%fixed
mu = 1;
tau=3;
m_0=42648;
f_0=51178;
tmax=11;%end of observation (locked here as it is the last observation time)

%m is mf(1)
%f is mf(2)
%solve the ODE system. I used a stiff solver, could also try different solvers here
sol = dde23(@mfequation,tau,@ddex1hist,[0 tmax]);

%the problem now is that the solution values are on a non-integer
%timescale. We need to shift them to be able to compare computed values
%with the data points. This happens in the following:
t=sol.x;
y=sol.y;

%plot results
figure
plot(t,y)
hold on
%plot(0,r_0,'b*',6,r_6,'b*',11,r_11,'b*')
legend('m(t)','f(t)')
xlabel('time')
ylabel('value')

fraction_y = zeros(1,length(y));
for i=1:length(y)
    fraction_y(i) = y(2,i)./y(1,i);
end

figure
plot(t,fraction_y)
hold on
plot(0,1.2,'b*',6,0.96,'b*',11,0.60,'b*')
legend('f(t)/m(t)','Data')
xlabel('time')
ylabel('value')

%save all the results.
save('results_h')


function s = ddex1hist(t)
% Constant history function for DDEX1.
s = [42648 51178];
end
```

B.10 Plot of Figure 4.5

```
function dydt = ddehuntingconst(t,y,Z)
b=0.02;
h=0.1386;
mu=0.04;
ylag2=Z(:,1);
dydt =[ b*(1-h)*ylag2(1)-mu*y(1);
   b*(1-h)*ylag2(1)-(mu+h)*y(2)];
end
```

```
function s = historyhuntingmin(t)
  s = [26283;31540];
end
```

```
function s = historyhuntingmax(t)
  s = [42648;51178];
end
```

```
t0=0;
tfinal=20;
lags=[3];
sol = dde23(@ddehuntingconst, lags, @historyhuntingmax, [t0 tfinal]);
a=linspace(t0,tfinal,(tfinal-t0)*5);
b=deval(sol,a,1);
c=deval(sol,a,2);
d=deval(sol,17,1);
e=deval(sol,17,2);
figure
plot(sol.x, sol.y);
hold on
plot(a, b+c)
hold on
plot(17, e+d, ’bo’)
legend(’Males’,’Females’,’Total’,’Location’,’North’)
xlabel(’Year’)
ylabel(’Population’)
```

B.11 Plot of Figure 4.6 and estimation of a

```
function drhdt = rhequation(t,rh)
%function to evaluate trajectories
global a b
%first component: dr/dt, r is rh(1)
%second component: dh/dt, h is rh(2)
drhdt = [(b*(1-rh(2))-rh(2))*rh(1) - (b*(1-rh(2)))*rh(1)*rh(1); a*rh(2)*(1-rh(2))];
end
```

```
function [leastsquare_rh] = compute_least_squares(x0)
%here we compute the least square of the data points and the function
%values.
global a b
%given values:
a=x0;
b=0.11;%fixed
h_0=0.031;%fixed
r_0=1.2;%fixed
r_6=0.96;%fixed
r_11=0.6;%fixed
tmax=11;%end of observation (locked here as it is the last observation time)

%r is rh(1)
%h is rh(2)
[t,y] = ode23s(@rhequation,[0 tmax],[r_0 h_0]);

%the problem now is that the solution values are on a non-integer
%timescale. We need to shift them to be able to compare computed values
%with the data points. This happens in the following:

new_amountscale = zeros(tmax+1,2);%"new" population matrix with r in the first row and h in the second row
%shift solution time course to integer time values
for i=0:tmax
    [minValue,closestIndex] = min(abs(i-t));
    new_timescale(i+1) = t(closestIndex);
    new_amountscale(i+1,:) = y(closestIndex,:);
    closestValue(i+1) = t(closestIndex);
end

%compute least squares (as we have only three values, I did not set up a
%sum. The first square is zero, as we start our computations with that value
leastsquare_rh = (r_0-new_amountscale(1,1))^2+(r_6-new_amountscale(7,1))^2+(r_11-new_amountscale(12,1))^2;

end
```

```
%clean up
clear all
close all
clc
%a is adjusted in the computations. Set as global to make those
%computations faster and easier. Cave: Can cause errors though.
global a
tic

%starting value for the algorithm. This is the initial value of a to be
%"tested"
x0 = 0.00005;

lb = [0.000001]; %lower boundary of rate to be tested
ub = [1]; %upper boundary of rate to be tested

%some settings, also to visualize what happens.
options = optimoptions(@fmincon,’Algorithm’,’interior-point’,’StepTolerance’,1e-20,
’ConstraintTolerance’,1e-15,’MaxFunctionEvaluations’,5000,’PlotFcn’,@optimplotfval);
nonlcon = [];
[x,fval,exitflag,output]=fmincon(@compute_least_squares,x0,[],[],[],[],lb,ub,nonlcon,options)
toc

%compute ODE system with found value
%given values:
a=x;
b=0.11;
h_0=0.031;
r_0=1.2;
r_6=0.96;
r_11=0.6;
t0=0;
tmax=11;

%r is rh(1)
%h is rh(2)

[t,y] = ode23s(@rhequation,[t0 tmax],[r_0 h_0]);

%plot results
figure
plot(t+2000,y)
hold on
plot(2000,r_0,’bo’,2006,r_6,’bo’,2011,r_11,’bo’)
legend(’r(t)’,’h(t)’,’Collected␣data’)
xlabel(’Year’)
ylabel(’Value’)

%save all the results.
save(’results_a’)
```

B.12 Estimation of a in section 4.2.4

```
function dmfdt = mfequation(t,mf,Z)
%function to evaluate trajectories
global a h0 b mu
%first component: dm/dt, m is mf(1)
%second component: df/dt, f is mf(2)

mf_lag2 = Z(:,1); %lag for f
h = h0/((exp(-a*t))*(1-h0)+h0);
dmfdt = [(b*(1-h))*mf_lag2(1)-mu*mf(1); (b*(1-h))*mf_lag2(1)-(mu+h)*mf(2)];
end
```

```
function [leastsquare_rh] = compute_least_squares(x0)
%here we compute the least square of the data points and the function
%values.
global a b mu h0
%given values:
h0=0.031;
a=x0;
b=0.11;%fixed
mu = 0.04;
tau=3;
m_0=42648;
f_0=51178;
tmax=11;%end of observation (locked here as it is the last observation time)

%m is mf(1)
%f is mf(2)
%solve the ODE system. I used a stiff solver, could also try different solvers here
sol = dde23(@mfequation,tau,@ddex1hist,[0 tmax]);

%the problem now is that the solution values are on a non-integer
%timescale. We need to shift them to be able to compare computed values
%with the data points. This happens in the following:
```

```
t=sol.x;
y=sol.y;
new_amountscale = zeros(tmax+1,2);%"new" population matrix with r in the first row and h in the second row
%shift solution time course to integer time values
for i=0:tmax
    [minValue,closestIndex] = min(abs(i-t));
    new_timescale(i+1) = t(closestIndex);
    new_amountscale(i+1,:) = y(:,closestIndex);
    closestValue(i+1) = t(closestIndex);
end

%compute least squares (as we have only three values, I did not set up a
%sum. The first square is zero, as we start our computations with that value
meas1=new_amountscale(6,2)/new_amountscale(6,1);
meas2=new_amountscale(11,2)/new_amountscale(11,1);

leastsquare_rh = (meas1-0.96)^2+(meas2-0.60)^2;

end

function s = ddex1hist(t)
% Constant history function for DDEX1.
s = [42648 51178];
end
```

```
%clean up
clear all
close all
clc
%a is adjusted in the computations. Set as global to make those
%computations faster and easier. Cave: Can cause errors though.
global a b mu h0
tic

%starting value for the algorithm. This is the initial value of a to be
%"tested"
x0 = [0.02];

lb = [0.000001]; %lower boundary of rate to be tested
ub = [1]; %upper boundary of rate to be tested

%some settings, also to visualize what happens.
options = optimoptions(@fmincon,’Algorithm’,’interior-point’,’StepTolerance’,
1e-20,’ConstraintTolerance’,1e-15,’MaxFunctionEvaluations’,5000,’PlotFcn’,@optimplotfval);
nonlcon = [];
[x,fval,exitflag,output]=fmincon(@compute_least_squares,x0,[],[],[],[],lb,ub,nonlcon,options)
toc

%compute ODE system with found value
%given values:
h0=0.031;
a=x;
b=0.11;%fixed
mu = 0.04;
tau=3;
m_0=42648;
f_0=51178;
tmax=11;%end of observation (locked here as it is the last observation time)

%m is mf(1)
%f is mf(2)
%solve the ODE system. I used a stiff solver, could also try different solvers here
sol = dde23(@mfequation,tau,@ddex1hist,[0 tmax]);

%the problem now is that the solution values are on a non-integer
%timescale. We need to shift them to be able to compare computed values
%with the data points. This happens in the following:
t=sol.x;
y=sol.y;

%plot results
figure
plot(t,y)
hold on
%plot(0,r_0,’b*’,6,r_6,’b*’,11,r_11,’b*’)
legend(’m(t)’,’f(t)’)
xlabel(’time’)
ylabel(’value’)

fraction_y = zeros(1,length(y));
for i=1:length(y)
    fraction_y(i) = y(2,i)./y(1,i);
end

figure
plot(t,fraction_y)
hold on
plot(0,1.2,’b*’,6,0.96,’b*’,11,0.60,’b*’)
legend(’f(t)/m(t)’,’Data’)
xlabel(’time’)
ylabel(’value’)

%save all the results.
```

```
save(’results_h’)

function s = ddex1hist(t)
% Constant history function for DDEX1.
s = [42648 51178];
end
```

B.13 Plot of Figure 4.7

```
function s = historyhuntingmax(t)
  s = [42648;51178];
end
```

```
function s = historyhuntingmin(t)
  s = [26283;31540];
end
```

```
function dmfdt = delhuntinghnonconst(t,mf,Z)
h0=0.031;
a=0.1334;
b=0.11;
mu=0.04;
mf_lag2 = Z(:,1); %lag for f
h = h0/((exp(-a*t))*(1-h0)+h0);
dmfdt = [(b*(1-h))*mf_lag2(1)-mu*mf(1); (b*(1-h))*mf_lag2(1)-(mu+h)*mf(2)];
end
```

```
t0=0;
tfinal=20;
lags=[3];
sol = dde23(@delhuntinghnonconst, lags, @historyhuntingmax, [t0 tfinal]);
a=linspace(t0,tfinal,(tfinal-t0)*5);
b=deval(sol,a,1);
c=deval(sol,a,2);
d=deval(sol,17,1);
e=deval(sol,17,2);
figure
plot(sol.x, sol.y);
hold on
plot(a, b+c)
hold on
plot(17, e+d, ’bo’)
legend(’Males’,’Females’,’Total’,’Location’,’North’)
xlabel(’Year’)
ylabel(’Population’)
```

B.14 Plot of Figure 5.1

```
function yp = habitatmax(t,y)
b=0.02;
r=5.6;
mu=0.04;
k=10.5;
D=[7130;216884];
A=[10.91; 1.09];
yp =[ b*y(2)*(1-y(1)/(D(1)*(A(1)-0.27*t)))-mu*y(1); r*y(1)*(1-y(2)/(D(2)*(A(2)-0.0436*t)))];
end
```

```
function yp = habitatmin(t,y)
b=0.02;
r=5.6;
k=10.5;
mu=0.04;
D=[4962;113863];
A=[10.91; 1.09];
yp =[ b*y(2)*(1-y(1)/(D(1)*(A(1)-0.27*t)))-mu*y(1); r*y(1)*(1-y(2)/(D(2)*(A(2)-0.0436*t)))];
end
```

```
t0=0;
tfinal=20;
y0max=[46913;236403];
y0min=[28912;124111];
Dmax=[7130;216884];
[t1,y1]=ode45(@habitatmax, [t0 tfinal], y0max);
[t2,y2]=ode45(@habitatmin, [t0 tfinal], y0min);
```

```
t1=t1+2000;
t2=t2+2000;
plot(t1,y1,t2,y2)
xlabel('Year')
ylabel('Population')

legend('Upp.␣Estim.␣Adults','Upp.␣Estim.␣Eggs','Low.␣Estim.␣Adults','Low.␣Estim.␣Eggs','Location','Northeast')
```

B.15 Plot of Figure 5.2

```
function s = historyhabitmin(t)
  s = [28912;124111];
end
```

```
function dydt = ddehabitatmin(t,y,Z)
b=0.02;
r=5.6;
mu=0.04;
D=[4962;113863];
A=[10.91; 1.09];
ylag2=Z(:,1);
dydt =[ b*ylag2(1)*(1-y(1)/(D(1)*(A(1)-0.27*t)))-mu*y(1);
    r*y(1)*(1-y(2)/(D(2)*(A(2)-0.0436*t)))];
end
```

```
t0=0;
tfinal=20;
tspan=[t0 tfinal];
lags=[3];
sol= dde23(@ddehabitatmin, lags, @historyhabitmin, tspan);
a=deval(sol,17,1);
figure
plot(sol.x, sol.y);
hold on
plot(17, a,'bo')
xlabel('Year');
ylabel('Population');
legend('Adults','Eggs','Location','North')
```

```
function s = historyhabitmax(t)
  s = [46913;236403];
end
```

```
function dydt = ddehabitatmax(t,y,Z)
b=0.02;
r=5.6;
mu=0.04;
D=[7130;216884];
A=[10.91; 1.09];
ylag2=Z(:,1);
dydt =[ b*ylag2(1)*(1-y(1)/(D(1)*(A(1)-0.27*t)))-mu*y(1);
    r*y(1)*(1-y(2)/(D(2)*(A(2)-0.0436*t)))];
end
```

```
t0=0;
tfinal=20;
tspan=[t0 tfinal];
lags=[3];
sol= dde23(@ddehabitatmax, lags, @historyhabitmax, tspan);
a=deval(sol,17,1);
figure
plot(sol.x, sol.y);
hold on
plot(17, a,'bo')
xlabel('Year');
ylabel('Population');
legend('Adults','Eggs','Location','North')
```

B.16 Plot of Figure 5.3

```
function yp = habitatmax(t,y)
b=0.02;
r=5.6;
k=10.5;
mu=0.04;
```

```
D=[7130;216884];
A=[10.91; 1.09];
yp =[ b*y(2)*(1-y(1)/(D(1)*(A(1)-0.27*t)))-mu*exp(k*0.27)*y(1); r*y(1)*(1-y(2)/(D(2)*(A(2)-0.0436*t)))];
end
```

```
function yp = habitatmin(t,y)
b=0.02;
r=5.6;
k=10.5;
mu=0.04;
D=[4962;113863];
A=[10.91; 1.09];
yp =[ b*y(2)*(1-y(1)/(D(1)*(A(1)-0.27*t)))-mu*exp(k*0.27)*y(1); r*y(1)*(1-y(2)/(D(2)*(A(2)-0.0436*t)))];
end
```

```
t0=0;
tfinal=20;
y0max=[46913;236403];
y0min=[28912;124111];
Dmax=[7130;216884];
[t1,y1]=ode45(@habitatmax, [t0 tfinal], y0max);
[t2,y2]=ode45(@habitatmin, [t0 tfinal], y0min);
t1=t1+2000;
t2=t2+2000;
plot(t1,y1,t2,y2)
xlabel('Year')
ylabel('Population')

legend('Upp.␣Estim.␣Adults','Upp.␣Estim.␣Eggs','Low.␣Estim.␣Adults','Low.␣Estim.␣Eggs','Location','Northeast')
```

B.17 Plot of Figure 5.4

```
function s = historyhabitmin(t)
  s = [28912;124111];
end
```

```
function dydt = ddehabitatmin(t,y,Z)
b=0.02;
r=5.6;
mu=0.04;
k=5.65;
D=[4962;113863];
A=[10.91; 1.09];
ylag2=Z(:,1);
dydt =[ b*ylag2(1)*(1-y(1)/(D(1)*(A(1)-0.27*t)))-mu*exp(0.27*k)*y(1);
    r*y(1)*(1-y(2)/(D(2)*(A(2)-0.0436*t)))];
end
```

```
t0=0;
tfinal=20;
tspan=[t0 tfinal];
lags=[3];
sol= dde23(@ddehabitatmin, lags, @historyhabitmin, tspan);
a=deval(sol,17,1);
figure
plot(sol.x, sol.y);
hold on
plot(17, a,'bo')
xlabel('Year');
ylabel('Population');
legend('Adults','Eggs','Location','North')
```

```
function s = historyhabitmax(t)
  s = [46913;236403];
end
```

```
function dydt = ddehabitatmax(t,y,Z)
b=0.02;
r=5.6;
mu=0.04;
k=5.65;
D=[7130;216884];
A=[10.91; 1.09];
ylag2=Z(:,1);
dydt =[ b*ylag2(1)*(1-y(1)/(D(1)*(A(1)-0.27*t)))-mu*exp(0.27*k)*y(1);
    r*y(1)*(1-y(2)/(D(2)*(A(2)-0.0436*t)))];
end
```

```
t0=0;
tfinal=20;
tspan=[t0 tfinal];
lags=[3];
sol= dde23(@ddehabitatmax, lags, @historyhabitmax, tspan);
a=deval(sol,17,1);
figure
plot(sol.x, sol.y);
hold on
plot(17, a,'bo')
xlabel('Year');
ylabel('Population');
legend('Adults','Eggs','Location','North')
```

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