

Homework 1: Deterministic Matrix Models

1 Background

In their seminal work, that has since accumulated over 1000 citations, Deborah Crouse and her colleagues present a Lefkovich stage class matrix model of loggerhead sea turtles (*Caretta caretta*) in the southwest United States, aiming to test current estimates of population vital rates and to inform conservation management practices for these endangered populations (Crouse et al., 1987). These turtles are iteroparous with a slow life history, meaning they are long-lived and take many years before their first reproductive bout. These particular life history characteristics make estimating their survival and fecundity relatively difficult. Individuals must be followed for a long time, and very few individuals make it to the most highly reproductive ages, making following an individual to maturity very logistically challenging. Further, they are also difficult to observe, given that only nesting females, eggs and hatchlings spend time on land and individual turtles can travel long distances.

Despite these observational challenges, Richardson (1983) collected data that could be used to estimate fecundity and survival over the course of 20 years of surveying. With that data, as well as other observations, Frazer (1983) then created an age-based life table. The values in these tables assume a closed population, a 1:1 sex ratio, an age of first reproduction of 22 years and a maximum life span of 54 years old, and a rate of population decline of 3% per year. Crouse et al. (1987) then grouped Frazer's life table of 54 stages (1 year each) into 7 broader stages based on the turtles' observed sizes (Fig. 1). They calculated the transition probabilities between the 7 stages and the probability of staying in each of the given classes using Fraser's annual survival probabilities (See the resultant Matrix 2).

As one might expect for a long-lived species with a slow life history, they found the stable age distribution of the population is biased towards more individuals of younger age classes (Fig. 2), and that these immature age classes contribute far less to the total fecundity of the population than their mature counterparts. Their subsequent analysis showed that it is precisely these classes for whom conservation efforts aiming to increase their *survival* to the later adult, more fecund stages, would have the greatest effect. In fact, increasing survival of any of stage 2, 3, or 4 (Small juveniles, large juveniles or subadults) to 100% would be sufficient to reverse the current decline of this population, whereas increasing the *fecundity* of adult turtles would not. In their sensitivity analysis, they identified that it is generally changes the probability of survival in the same stage (Fig. 1 purple arrows a_{22}, a_{33}, a_{44} , & a_{77}), specifically those in the juvenile, subadult and mature stages, that has the greatest ability to change population growth rate (Fig. 3 & Fig. 4c,d). This means that increasing survival within a stage is potentially the most fruitful conservation goal, but also means that these parameters are the most important to get right if we are to estimate the true population growth rate.

$$A_{i,j} = \begin{bmatrix} a_{1,1} & a_{1,2} & \cdots & a_{1,j=7} \\ a_{2,1} & a_{2,2} & \cdots & a_{2,j=7} \\ \vdots & \vdots & \ddots & \vdots \\ a_{i=7,1} & a_{i=7,2} & \cdots & a_{i=7,j=7} \end{bmatrix}$$

$$A_{i,j} = \begin{bmatrix} 0 & 0 & 0 & 0 & 127 & 4 & 80 \\ 0.67 & 0.73 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.04 & 0.66 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.01 & 0.69 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.05 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.80 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.80 & 0.80 \end{bmatrix}$$

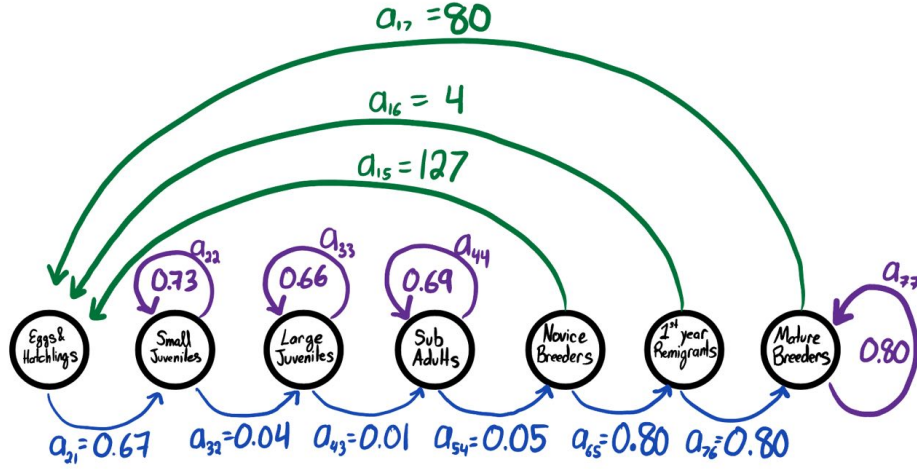


Figure 1: The lifecycle of loggerhead sea turtles (*Caretta caretta*). Black bubbles represent the various life stages, and numbered arrows represent the probability of a given individual in a given stage transitioning from one state to another. Parameter names and values can be seen in their matrix context with in Matrix 1 and 2 in the text. Decimal places have been truncated for ease of reading.

2 Methods

I re-ran the analyses of Crouse et al. with matrix projection via the ‘popbio’ package (Stubben and Milligan, 2007) in R version 4.2.1 (R Core Team, 2019). The exact stage class population matrix is shown above in Matrix 2. From this matrix, I calculated the population growth rate (the leading eigenvalue), the stable age distribution (the right eigenvector), and the reproductive value of each stage (the left eigenvector), and the sensitivity and elasticity matrices. Next, I projected the population matrix forward in time, again with the ‘popbio’ package using a starting population size of 20 individuals in each class.

3 Results & Discussion

From my analysis, I was successfully able to replicate the results of Crouse et al’s population growth rate ($\lambda = 0.9450$), stable age distribution (Fig. 2c; Egg/hatchling: 20.65%, Small Juveniles: 66.97%, Large Juveniles: 11.45%, Subadults: 0.66%, Early Breeders: 0.03%, Remigrants:

0.03, and Mature: 0.18%), and reproductive value (Fig. 2d, Egg/hatchling: 1.00, Small Juveniles: 1.40, Large Juveniles: 6.00, Subadults: 155.84, Early Breeders: 568.78, Remigrants: 507.37, and Mature: 587.67). Elasticities also matched between the two analyses (see Fig. 3 and Crouse et al. (1987) Fig. 3). This is because as a deterministic model, there is only one possible outcome for each calculation and there is no random draw being done to incorporate stochasticity that would lead to slightly different results in each run.

Using the population projection, I plotted the total number of individuals through time in each class and in total (Fig. 2a). This shows that for a population starting at 20 individuals per class, there is a sudden spike in growth, at which point the population is close to the stable age distribution (compare with Fig. 2b), followed by decline. This is consistent with our population rate of growth being less than one ($\lambda = 0.9450$).

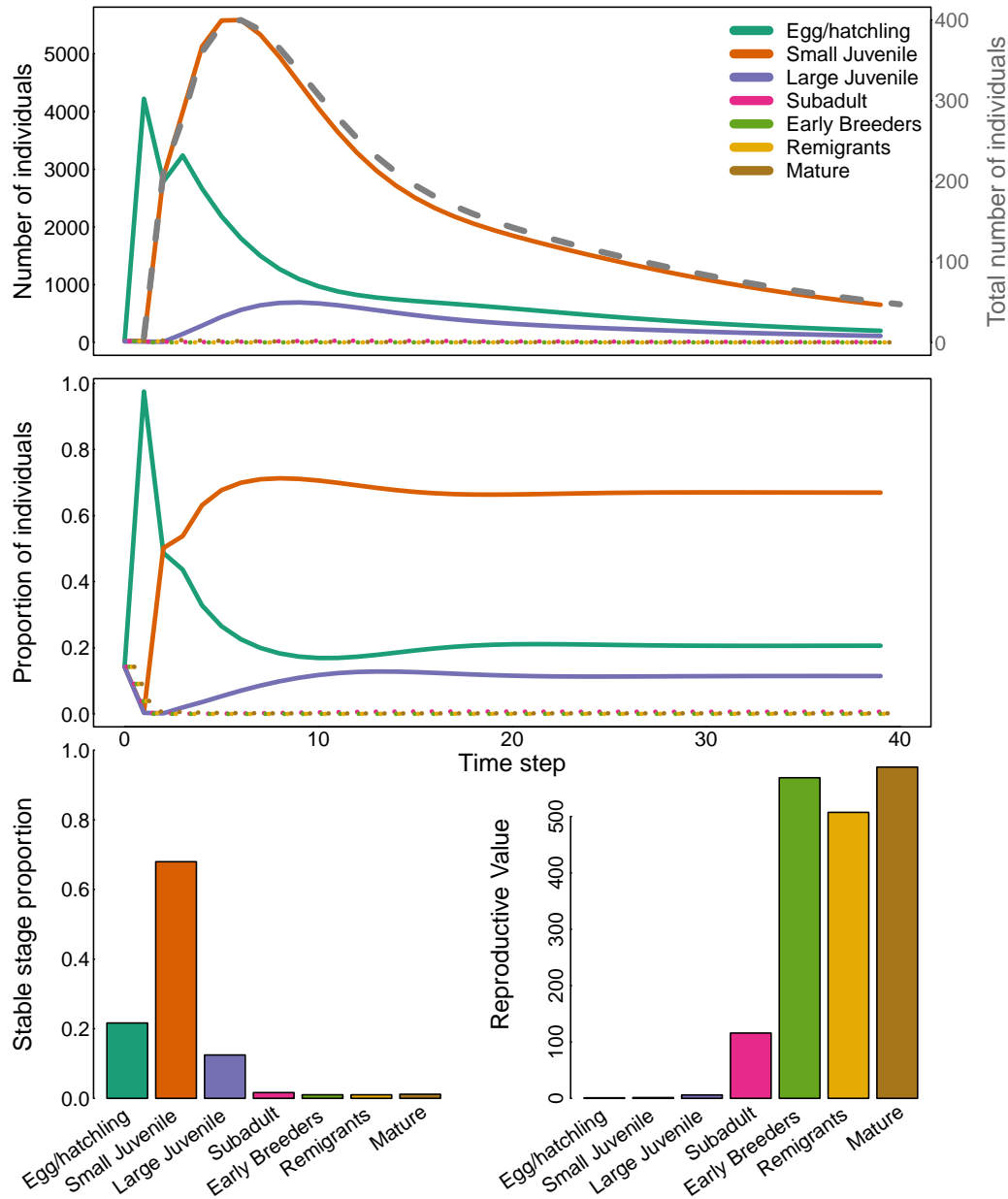


Figure 2: Figures representing the abundance and relative abundance of turtles in the south-eastern United States starting from 1 individual in each age class projected forward by iterating the projection matrix. Panel 1 shows the raw number of individuals through time on by class on the left axis with the solid and dotted lines. The grey dashed line is plotted on the right hand axis and represents the sum of the other lines, the total number of individuals in the population. Panel 2 shows the relative proportions of individuals in each class, and panel 3 represents the stable age distribution.

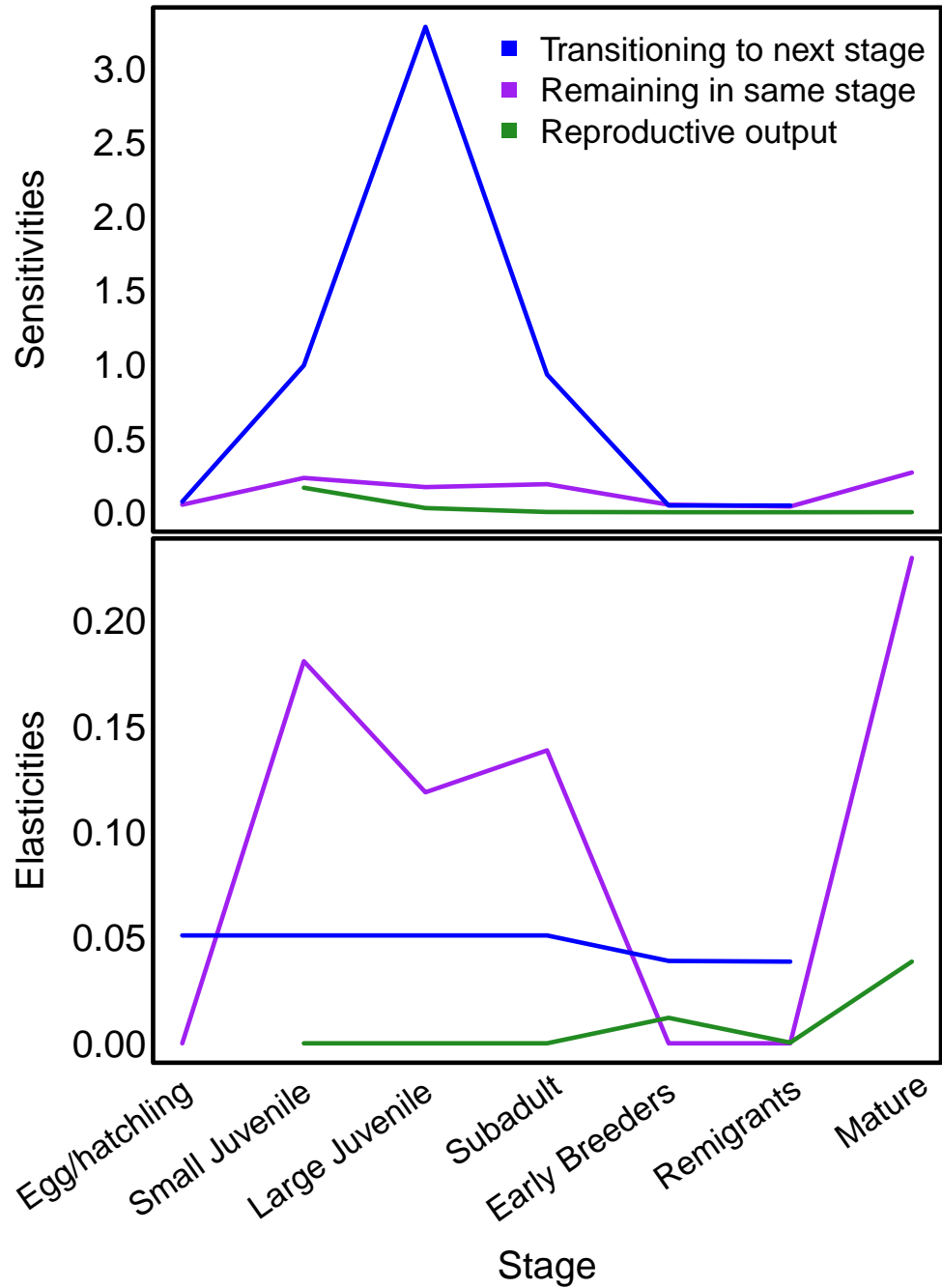


Figure 3: Sensitivities and elasticities of lambda to changes in all parameters of the model. Colours correspond to the matrices and to figure 1.

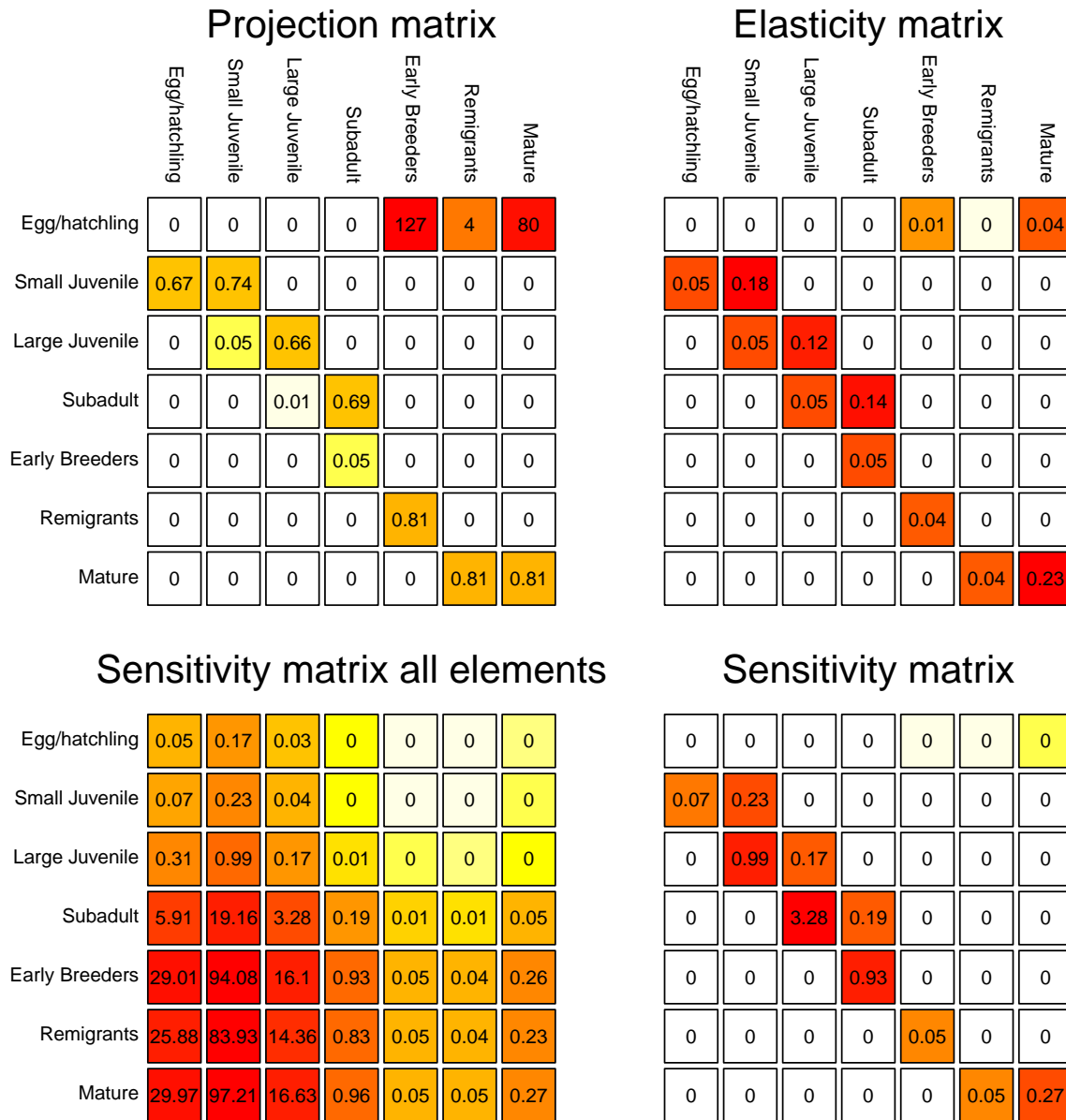


Figure 4: Matrices output from my analysis. Grid cells are colored by value, with red being the highest and white/light yellow being the lowest. Sensitivity matrix 1 contains the sensitivity to all parameters of the model, whereas sensitivity matrix 2 contains sensitivity only for parameters that are able to be varied in nature in this system.

References

- Crouse DT, Crowder LB, Caswell H (1987) A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68(5):1412–1423
- Frazer NB (1983) Demography and life history evolution of the Atlantic loggerhead sea turtle, *Caretta caretta* (Georgia). University of Georgia
- R Core Team (2019) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL <http://www.R-project.org/>
- Richardson JI (1983) A population model for adult female loggerhead sea turtles (*Caretta caretta*) nesting in Georgia.
- Stubben CJ, Milligan BG (2007) Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software* 22(11)