

Modeling the effects of crab potting and road traffic on a population of diamondback terrapins

Sarah Gilliland¹, Randolph M. Chambers^{1,2}, and M. Drew LaMar¹

¹Department of Biology,
College of William and Mary

²Keck Environmental Field Lab,
College of William and Mary

Abstract

Diamondback terrapins are a species of turtle found along the coast of the United States from Massachusetts to Texas. Many of the states in this range list the terrapins as endangered, threatened, or a species of concern. However, little is known about their actual population sizes across the range. Mitro (2003) created a linear age class model for a terrapin population in Rhode Island. Here we examine the effects on the same population of human-related threats such as crab pots and road traffic using a nonlinear, stage-based model. This model shows that crab potting has a larger negative effect on the population (which causes a population decline occurring at 6.6% mortality of affected stages) than road mortality (with a population decline at 10.6% mortality of affected stages). We conclude that, in areas of existing crab potting, conservation efforts should focus on reducing terrapin mortality through the use of bycatch reduction devices.

Keywords: diamondback terrapin, *Malaclemys terrapin*, bycatch reduction device

1 Introduction

Diamondback terrapins are the only North American turtles living exclusively in brackish water. They can be found along the east and gulf coasts of the United States from Cape Cod, Massachusetts to Corpus Christi, Texas. *Malaclemys terrapin terrapin* is one of seven subspecies and has a range extending from Massachusetts to North Carolina. There are conflicting reports as to how long a terrapin can live; some suggest the oldest terrapins are over 40 years old, while more conservative estimates fall around 20 years [2]. We assume that 40 years is the maximum lifespan. Diamondback terrapins feed on a variety of invertebrates including snails, clams, mussels, crabs, worms, and small fish [2]. They also incidentally consume a good deal of plant matter [20].

Adult terrapins are sexually dimorphic, with females reaching a maximum plastron length of about 15 to 20 centimeters and males growing to roughly 10 to 13 centimeters. Females also have larger heads and shorter, thinner tails. The opening of the female cloaca is located on the portion of the tail that falls under the carapace, whereas the male cloaca can be found slightly closer to the tip of the tail [2].

Relatively little is known about the status of terrapin populations. Massachusetts and Rhode Island list terrapins as “threatened” and “endangered”, respectively. In states such as New Jersey and Virginia, however, they are listed as a “species of concern” due to lack of adequate population

data on which to base a decision [2]. Due to the number of threats of mortality in a terrapin's environment, there is good reason to believe that the more relaxed listings should be amended.

1.1 Crab Potting and Road Mortality

Many terrapins are caught every year in crab pots. Attracted by the bait or curious about the pot, those terrapins that can fit enter the trap and drown when they are not able to find their way out. When one individual enters a pot, it becomes more likely that others will as well [2]. Hatchlings are small enough to swim out through the gaps in the traps, and adult females are too large to enter in the first place. Thus, juveniles of both sexes and adult males are disproportionately affected [17]. The threat to the population is exacerbated in the presence of "ghost pots," which are abandoned, unbaited crab pots that still manage to attract and drown terrapins [2].

Bycatch reduction devices (BRDs) can be attached to crab pots to exclude terrapins from the harvest. Developed by Roger Wood in 1992, these wire or plastic frames fit over the openings of the pots, reducing the size enough to prevent most terrapins from squeezing through while still allowing crabs to enter [2]. Although BRDs are quite effective at excluding terrapins, the catch of the target species in crab pots fitted with BRDs is variable by study and location. To date, four states (NY, NJ, DE, and MD) have regulations requiring the use of BRDs on crab pots [4].

Even though they cannot fit into crab pots, adult females are far from safe from human influences. Upon coming ashore to lay their eggs, terrapins may be run over by cars as they attempt to cross roads in search of a suitable nesting site [2]. Some of these females are attempting to lay their eggs right next to the road, while others are simply exploring the area as they look for an ideal nesting location [19]. The sandy beaches they once preferred may now lie under buildings and houses. Thus, some of the only lands left available to them are the grassy areas next to highways [21]. When females are killed by vehicles, the eggs can sometimes be salvaged from the remains of the mother and brought to term in a laboratory, but this requires timely action by an individual familiar with terrapin biology [2].

We will examine the effects of crab potting and road mortality on the long-term dynamics of the terrapin population. The results will demonstrate the levels of mortality at which a terrapin population reaches a tipping point between growth and decline. Based on the findings, we will suggest the type of conservation actions that need to be taken in order to protect the population.

1.2 Classic Loggerhead Turtle Study

In 1987, Crouse et al. studied loggerhead sea turtles (*Caretta caretta*) using a stage-based population model. The female loggerheads were divided into seven stage classes based on similarities in life history traits: eggs/hatchlings, small juveniles, large juveniles, subadults, novice breeders, first-year remigrants, and mature breeders. A population matrix was constructed that included fecundity terms (the number of individuals produced per breeder per year), persistence terms (the fraction of a stage class that remains in that stage class from one year to the next), and growth terms (the fraction of a stage class that moves to the next stage class in a given year). This matrix was used to predict the future behavior of a theoretical loggerhead population, and to determine the sensitivity of the model to changes in the various parameters [6].

They found that the theoretical female population responded more drastically to changes in survival of juvenile and subadult stages than to increases in survival of the other stage classes, implying that conservation efforts ought to be focused on these intermediate stages [6]. This is not to say that nest site conservation efforts should be abandoned, but the same amount of effort directed towards the juvenile stage class, for instance, should yield better results.

Since the publication of Crouse's findings, conservation efforts aimed at loggerhead sea turtles have become much more prevalent. Turtle excluder devices (TEDs) are called for everywhere by federal regulations, and there are now signs on beaches educating visitors about how to avoid dis-

turbing nesting loggerheads [13]. We use a model similar to that used by Crouse and colleagues [6] for the Rhode Island diamondback terrapin population, and hope that the results will contribute to conservation efforts as well.

2 Model Development

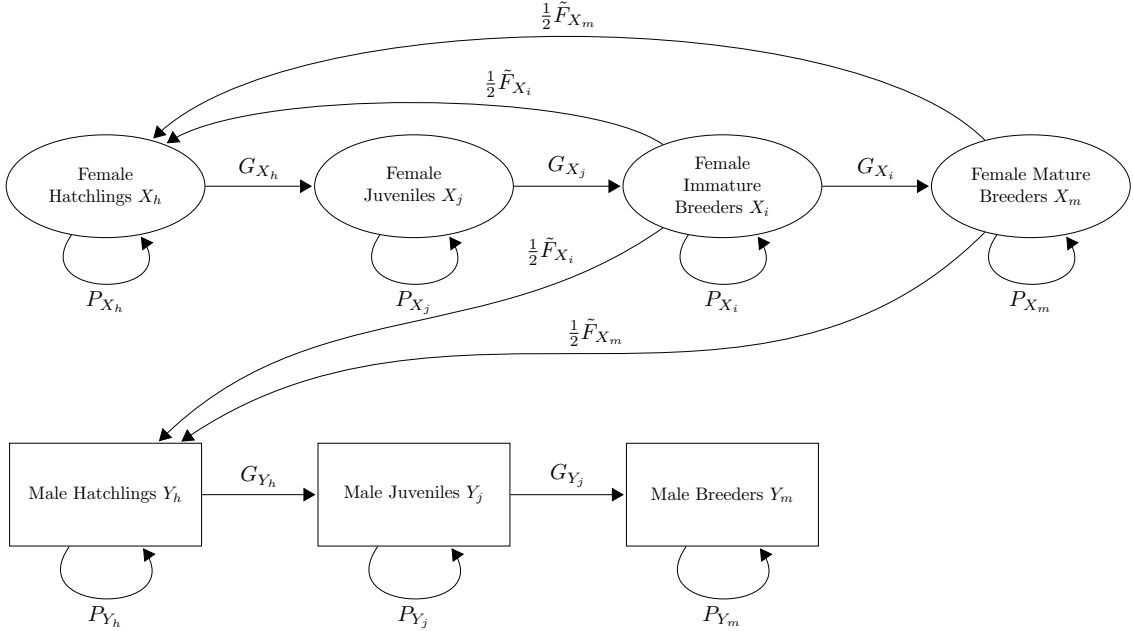


Figure 1: Life cycle graph for diamondback terrapins (similar to [1]). Parameters in Table 2.

We consider both a modified linear model from [1] and a nonlinear model that replaces the fecundity term with a frequency dependent mating function to account for decreased matings with skewed sex ratios. Unlike Crouse's paper [6], these models include the male stages and fecundity contributions. Male terrapins face different pressures than the females, and it is not reasonable to assume that the behavior of the female portion of the population accurately represents the trends in the male portion, especially considering the skewed effects of crab potting and road mortality. The terrapins are divided up into seven stage classes [1]: female hatchlings (X_h ; ages 1-2), female juveniles (X_j ; ages 3-7), immature female breeders (X_i ; ages 8-11), mature female breeders (X_m ; ages 12-40), male hatchlings (Y_h ; ages 1-2), male juveniles (Y_j ; age 3-4), and male breeders (Y_m ; ages 5-40) (see Figure 1). The probability of the survival of an individual from year n to year $n + 1$ (σ) and the probability of a surviving individual progressing to the next stage class in year $n + 1$ (γ) were calculated based on parameters found in [11] and are given in Table 1. The hatchling survival rates were the only parameters not taken directly from [11]. The hatchling survival rates and number of clutches per year for the mature breeders were adjusted so that the population growth rate was $\lambda = 1.034$ and the average fecundity (see (8)) was equal to 19.0706 eggs per female [11]. Our hatchling survival $\sigma_{X_h} = \sigma_{Y_h} = 0.5545$ for the linear model was slightly different than that reported in [11] ($\sigma = 0.565$). This difference is slight, however, with the population growth rate and stable age/stage distributions a very close match. Finally, with Z denoting an arbitrary stage class, the growth parameters are given by (see [3])

$$\gamma_Z = \frac{\left(\frac{\sigma_Z}{\lambda}\right)^{T_Z} - \left(\frac{\sigma_Z}{\lambda}\right)^{T_Z-1}}{\left(\frac{\sigma_Z}{\lambda}\right)^{T_Z} - 1}, \quad (1)$$

with T_Z the stage duration for each class, given by

$$T_Z = \begin{cases} 2, & Z = X_h, Y_h, Y_j \\ 5, & Z = X_j \\ 4, & Z = X_i \\ 29, & Z = X_m \\ 36, & Z = Y_m. \end{cases}$$

As mentioned previously, the growth parameter γ_Z is the proportion of individuals developing to the next stage class from those individuals that have survived to the next year. For the mature stage classes X_m and Y_m , this corresponds to surpassing the maximum life span of 40 years.

Let $\vec{X}_n = [X_{h,n} \ X_{j,n} \ X_{i,n} \ X_{m,n} \ Y_{h,n} \ Y_{j,n} \ Y_{m,n}]^T$ be the vector of stage class abundances at year n . We will compare the results of a linear and nonlinear model, starting with the linear model given by $\vec{X}_{n+1} = A\vec{X}_n$, where

$$A = \begin{bmatrix} P_{X_h} & 0 & \frac{1}{2}\tilde{F}_{X_i} & \frac{1}{2}\tilde{F}_{X_m} & 0 & 0 & 0 \\ G_{X_h} & P_{X_j} & 0 & 0 & 0 & 0 & 0 \\ 0 & G_{X_j} & P_{X_i} & 0 & 0 & 0 & 0 \\ 0 & 0 & G_{X_i} & P_{X_m} & 0 & 0 & 0 \\ 0 & 0 & \frac{1}{2}\tilde{F}_{X_i} & \frac{1}{2}\tilde{F}_{X_m} & P_{Y_h} & 0 & 0 \\ 0 & 0 & 0 & 0 & G_{Y_h} & P_{Y_j} & 0 \\ 0 & 0 & 0 & 0 & 0 & G_{Y_j} & P_{Y_m} \end{bmatrix}. \quad (2)$$

Each of the persistence (P_Z) and growth (G_Z) parameters for stage class Z are given by

$$\begin{aligned} P_Z &= \text{Prob}[\text{survive and not develop}] &= \sigma_Z(1 - \gamma_Z), \\ G_Z &= \text{Prob}[\text{survive and develop}] &= \sigma_Z\gamma_Z. \end{aligned} \quad (3)$$

For the mature stage classes $Z = X_m$ and $Z = Y_m$, the growth parameters G_Z give the proportion that survive past the maximal life span of 40 years. In this situation, we effectively remove this portion from the population and consider them having died from old age.

The ‘‘fecundity’’ terms \tilde{F}_{X_i} and \tilde{F}_{X_m} give the number of hatchlings that survived to year 1,

$$\begin{aligned} \tilde{F}_{X_i} &= F_{X_i} h \sigma_e \sigma_h^{(3/4)}, \\ \tilde{F}_{X_m} &= F_{X_m} h \sigma_e \sigma_h^{(3/4)}, \end{aligned} \quad (4)$$

where $\sigma_h = \sigma_{X_h} = \sigma_{Y_h}$ and the $3/4$ corresponds to a 3 month incubation period, so that the hatchlings must survive for $3/4$ of the remaining year. The number of eggs per immature and mature female are given by $F_{X_i} = k u_i$ and $F_{X_m} = k u_m$, respectively, with the remaining parameters described in Table 1.

For the nonlinear model, all parameters are the same except for σ_{X_h} , σ_{Y_h} , u_m , and the fecundity terms, with the fecundity terms now density dependent (more precisely, they are *frequency dependent* [3]). As in the linear model, we adjusted hatchling survival and u_m so that the population growth rate $\lambda = 1.034$ and the average fecundity was equal to 19.0706 eggs per female, as in [11]. To derive the new fecundity terms, we start with the *marriage function* $B \equiv B(X_i, X_m, Y_m)$ given by

$$B(X_i, X_m, Y_m) = \frac{2Y_m(X_i + X_m)}{Y_m + X_i + X_m},$$

which gives the number of matings as a function of breeding males and females. This choice of marriage function represents the harmonic mean of $X_i + X_m$ and Y_m and is believed to be the most biologically accurate representation of density dependent mating [3]. Some of the important properties of this function that are inherited from the properties of the harmonic mean include:

- $B = X_i + X_m = Y_m$ when $X_i + X_m = Y_m$

Parameter	Value	Description	Source
λ	1.034	Population growth rate	[11]
$\sigma_{X_h}, \sigma_{Y_h}$	0.5545	Probability of survival for hatchlings (Linear)	Calculated
$\sigma_{X_h}, \sigma_{Y_h}$	0.528371	Probability of survival for hatchlings (Nonlinear)	Calculated
σ_Z	0.944	Probability of survival for stage class $Z \neq X_h, Y_h$	[11]
σ_e	0.097	Probability of survival of eggs	[11]
h	0.8735	Probability of hatching of surviving eggs	[11]
u_i	1	Clutches per year per immature breeding female	Assumed
u_m	2.3362	Clutches per year per mature breeding female (Linear)	Calculated
u_m	2.33625	Clutches per year per mature breeding female (Nonlinear)	Calculated
k	10	Number of eggs per clutch	[18]
l	40	Longevity	[11]

Table 1: Table of parameters used for the linear and nonlinear model.

- $B \leq \max(X_i + X_m, Y_m)$
- $\lim_{Y_m \rightarrow 0} B = 0$
- $\lim_{X_i + X_m \rightarrow 0} B = 0$

The fraction of matings coming from immature and mature females, denoted by B_{X_i} and B_{X_m} , respectively, are given by

$$\begin{aligned}
 B_{X_i} &\equiv \frac{X_i}{X_i + X_m} B = \frac{2Y_m X_i}{Y_m + X_i + X_m} \\
 B_{X_m} &\equiv \frac{X_m}{X_i + X_m} B = \frac{2Y_m X_m}{Y_m + X_i + X_m},
 \end{aligned} \tag{5}$$

so that $B = B_{X_i} + B_{X_m}$. This can be used to define the fecundities for the nonlinear model as

$$\begin{aligned}
 F_{X_i} &\equiv \frac{k u_i B_{X_i}}{X_i} = \frac{2k u_i Y_m}{Y_m + X_i + X_m} \\
 F_{X_m} &\equiv \frac{k u_m B_{X_m}}{X_m} = \frac{2k u_m Y_m}{Y_m + X_i + X_m}
 \end{aligned} \tag{6}$$

which give the number of eggs produced per breeding immature and mature female, respectively. These fecundities are then substituted into (4) to arrive at the hatchling fecundity terms. Simulation of the nonlinear model is the same as the linear model, with the added step of updating the ‘‘fecundity’’ terms (4) in the matrix A in (2) at each time step.

Note that the linear model is equivalent to using a marriage function B that is *female dominant* [3], given by

$$B(X_i, X_m, Y_m) = X_i + X_m.$$

In this case, we can use (5) to show $B_{X_i} = X_i$ and $B_{X_m} = X_m$, as well as (6) to show $F_{X_i} \equiv k u_i B_{X_i} / X_i = k u_i$ and $F_{X_m} \equiv k u_m B_{X_m} / X_m = k u_m$. Thus, the linear and nonlinear models are derived from the same equations with an appropriate choice of marriage function.

Using the appropriate marriage function for the linear and nonlinear models, we can write the total number of eggs per year (*total birth*) as

$$X_i F_{X_i} + X_m F_{X_m} = k(u_i B_{X_i} + u_m B_{X_m}), \tag{7}$$

and the average number of eggs per mating pair per year (*average fecundity*) as

$$\frac{X_i F_{X_i} + X_m F_{X_m}}{B} = k u_i \left(\frac{B_{X_i}}{B_{X_i} + B_{X_m}} \right) + k u_m \left(\frac{B_{X_m}}{B_{X_i} + B_{X_m}} \right). \tag{8}$$

Thus, the average fecundity gives an indication of the relative proportion of immature to mature breeders in the population as a weighted average of the number of eggs produced per year by the immature and mature breeders.

2.1 Modeling crab potting and road mortality

We make the following assumptions on crab-potting and road mortality:

- Both male and female hatchlings are too small to be affected by crab pots.
- Immature and mature breeding females are too large to be affected by crab pots.
- Male juveniles and breeders, as well as female juveniles, are affected equally by crab pots.
- Both immature and mature breeding females are the only stage classes affected by road mortality, as they are the only classes to cross roads to build nests.
- Immature breeding females are less affected by road mortality as they have fewer clutches per season ($u_i < u_m$).

Letting c and r denote the proportion killed by crab potting and roads, respectively, where $0 \leq c, r \leq 1$, we modify the survival terms as follows:

$$\hat{\sigma}_Z = \begin{cases} \max(\sigma_Z - c, 0), & \text{for } Z = X_j, Y_j, Y_m, \\ \max(\sigma_Z - (u_i/u_m)r, 0), & \text{for } Z = X_i, \\ \max(\sigma_Z - r, 0), & \text{for } Z = X_m. \end{cases} \quad (9)$$

Whenever new values σ_Z for the survival terms are used, an iterative technique must be performed to calculate the other parameters in the system, as the growth terms γ_Z in (1) depend implicitly on the unknown population growth rate λ . To illustrate, first initialize the sequence $\lambda^{(n)}$ such that $\lambda^{(0)} = \lambda_0$. This initial value λ_0 could for example correspond to some previous growth rate before an incremental change in σ_Z occurred. Now repeat the following until $\lambda^{(n)}$ has converged:

1. Update γ_Z using equation (1) with σ_Z and $\lambda^{(n)}$.
2. Update P_Z and G_Z using equation (3) with σ_Z and the updated γ_Z from Step 1.
3. Calculate $\lambda^{(n+1)}$ using equation (2) with the updated P_Z and G_Z from Step 2.

After convergence in N steps, set $\lambda = \lambda^{(N)}$. For the nonlinear model, linearization at the origin is ill-defined, and so to calculate the population growth rate (and stable stage distribution), we iterate the model until the stage distribution and growth rate stabilizes (which is guaranteed to occur since the model is frequency dependent [14, 15, 16]).

3 Results

We obtained parameter values for the growth, persistence, and fecundity terms from the calculations described above, based on the parameters in [11] (Table 2). In the stable Rhode Island population with a growth rate of $\lambda = 1.034$, the distribution of terrapins in the linear and nonlinear models is very similar (Fig. 2), and matches closely the stable age distribution in [11]. The plurality of the population falls in the male breeder stage, and the female mature breeder stage is also fairly large, as these final stages accumulate terrapins that remain there for the rest of their lives. The hatchling stages also contain a high proportion of the individuals, but then the proportion declines throughout the intermediate stages as mortality takes its toll.

Parameter	Linear	Nonlinear
P_{X_h}	0.3609	0.3497
P_{X_j}	0.7879	0.7879
P_{X_i}	0.7392	0.7392
P_{X_m}	0.9371	0.9371
P_{Y_h}	0.3609	0.3497
P_{Y_j}	0.4935	0.4935
P_{Y_m}	0.9405	0.9405
G_{X_h}	0.1935	0.1787
G_{X_j}	0.1561	0.1561
G_{X_i}	0.2048	0.2048
G_{Y_h}	0.1935	0.1787
G_{Y_j}	0.4505	0.4505
\bar{F}_{X_i}	0.2722	–
\bar{F}_{X_m}	0.6360	–

Table 2: Calculated persistence P and growth G parameters from (3), and constant “fecundity” terms from (4) used in the model (2).

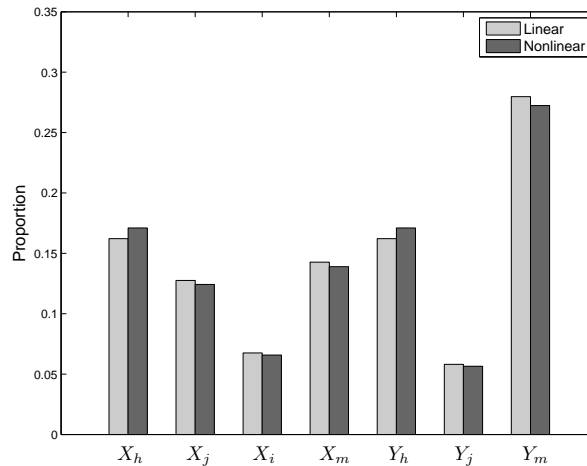


Figure 2: The stable stage distribution for both the linear and nonlinear model.

Figure 3 shows the change in the population growth rate as a function of the crab potting (left) and road mortalities (right). In the nonlinear model, the point at which the terrapin population begins to experience decline due to crab potting happens at a level of mortality of the affected stages of 6.6%. In the linear model, this tipping point does not occur until 11.6% mortality (close to 12% found in [1]). These results illustrate the possible benefit of using a nonlinear model, as it is more sensitive to changes that affect male portions of the population. The linear model has no way to account for the decrease in the number of males or the decrease in the male contribution to fecundity. As the adult males are killed off, only the nonlinear model reflects the resulting decline in egg number due to the shortage of breeding males. Note that a modification to the linear model was performed in [1] to account for a female:male sex ratio of 10:1, giving a critical point of crab potting at 9%.

Road mortality does not have as detrimental an effect on the growth of the population (Fig. 3). The linear model predicts a shift from population growth to decline at a lower level of mortality (7.6% of mature female breeders and 3.3% of immature female breeders) than does the nonlinear model (10.6% of mature female breeders and 4.5% of immature female breeders). The values for the

two models are fairly close together, as both models are taking female survival into account. These results are supported by the findings of Gibbs and Steen (2005), who saw that the female to male ratio of terrapins decreases in areas with more roads [7]. In [1], the critical point for road mortality was found to be approximately 10% for immature and mature female breeders.

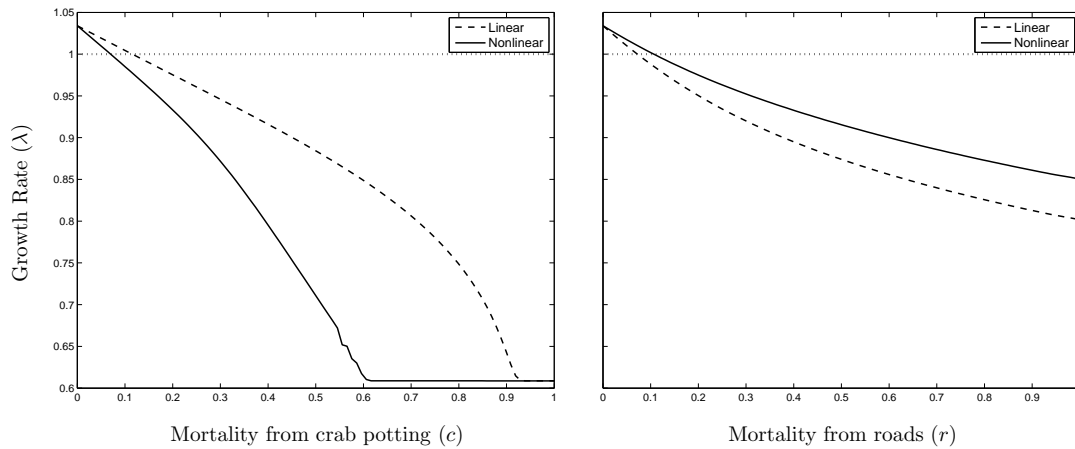


Figure 3: Population growth rate λ as a function of both crab potting c (left plot) and road mortality r (right plot) for both the linear (dashed line) and nonlinear (solid line) models. Dotted line denotes $\lambda = 1$, the critical value separating growth and decline. Critical point for crab potting: $c = 0.116$ (linear) and $c = 0.066$ (nonlinear). Critical point for road mortality: $r = 0.076$ (linear) and $r = 0.106$ (nonlinear)

The ratio of female breeders to male breeders is greatly affected by both crab potting mortality and road mortality (Fig. 4). As the amount of mortality from crab potting increases, so does this ratio. The increase occurs much faster under the nonlinear model, as it directly addresses male mortality, as discussed above. The rate of decrease in the ratio of female to male breeders due to road mortality is similar in both the models, although the linear model appears to be slightly more sensitive to the effects of such mortality.

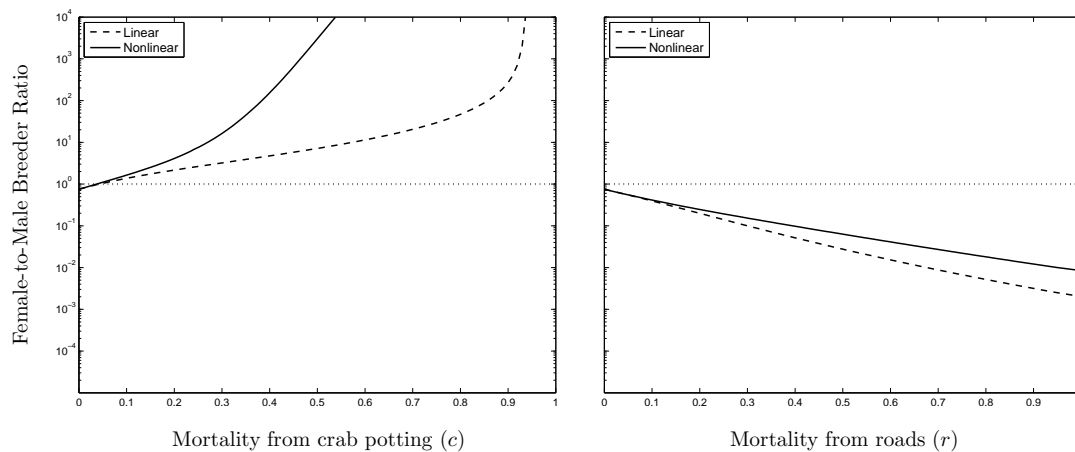


Figure 4: Female-to-male ratio of breeders as a function of crab potting c (left plot) and road mortality r (right plot) for both the linear (dashed line) and nonlinear (solid line) models. Dotted line denotes a ratio of 1, representing equal proportions of males and females.

The average fecundity, or number of eggs produced per breeding pair per year (see (8)), of terrapin populations that experience crab potting is actually higher than that of populations free from the negative influences of crab potting (Fig. 5). The decline in the size of the juvenile female

stage caused by crab potting in turn diminishes the size of the immature breeding female stage. Those terrapins that survive to the mature breeding female stage begin to accumulate, as they are safe from the crab pots. These mature breeders produce greater numbers of eggs than the immature breeders, and do so for the remainder of their potentially long lives. This accounts for the increase in average fecundity that approaches $ku_m \approx 23.3625$, or the number of eggs produced per mature breeding female per year. However, the total birth, or total number of eggs produced per year (see (7)), declines at high levels of crab potting in the nonlinear model, as the total number of breeders is declining. This decline in the birth term does not happen to a great extent in the linear model, as it doesn't include male stages, as discussed above.

Both the average fecundity and the birth term decline as the level of road mortality increases (Fig. 5). The fecundity approaches $ku_i = 10$, or the number of eggs produced per immature breeding female per year. This happens because road mortality disproportionately affects mature breeding females. The birth term for both models approaches 0 as road mortality increases, because in both models a complete lack of females results in no new hatchlings.

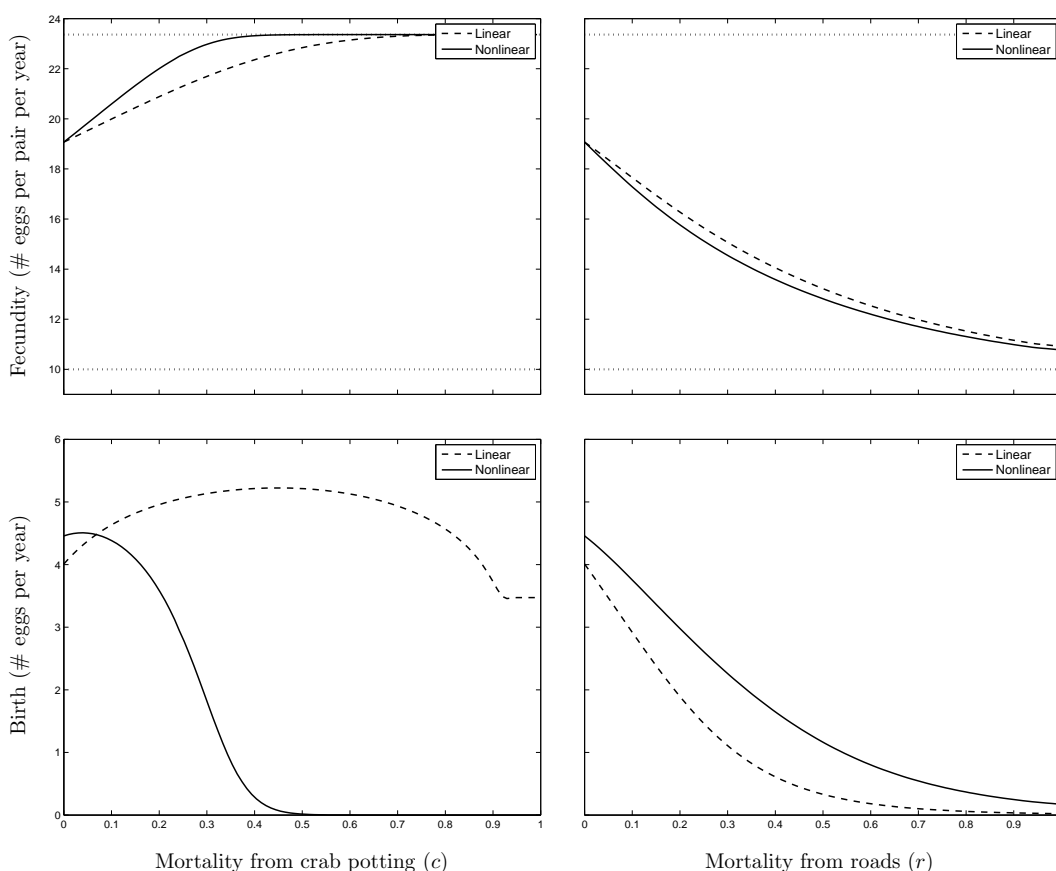


Figure 5: Average fecundity (8) (top) and total birth (7) (bottom) as a function of both crab potting c (left) and road mortality r (right). For fecundity, the dotted lines denote the fecundities for populations whose female breeders are either all immature (lower value) or all mature (upper value).

We also examined the effects of egg survival on the Rhode Island population to determine the value of conservation measures aimed at nests. The egg survival obtained from [11] had a value of 0.097. As this value is increased, the values of crab potting and road mortality at which the population begins to decline also increase (Fig. 6). For instance, when the egg survival is doubled to 0.194 and road mortality is non-existent, the value of c at which $\lambda = 1$ roughly doubles. With that value for egg survival and no crab potting, the value of r at which $\lambda = 1$ more than doubles. The

line along which $\lambda = 1$ shifts even farther when the original value for egg survival is quadrupled.

Egg survival does play a definite role in determining the rate of population growth, but it is much easier to reduce the rate of population decline by cutting down on the number of terrapins that drown in crab pots. As can be seen in Figure 6, increases in crab pot mortality more rapidly lead to smaller values of λ than increases in road mortality. Although compliance and enforcement issues may limit the effectiveness of BRD regulations, it is much less time consuming and costly to affix BRDs to crab pots than it is to protect nests full of eggs on beaches from threats such as predation by raccoons and erosion by storm surges [2].

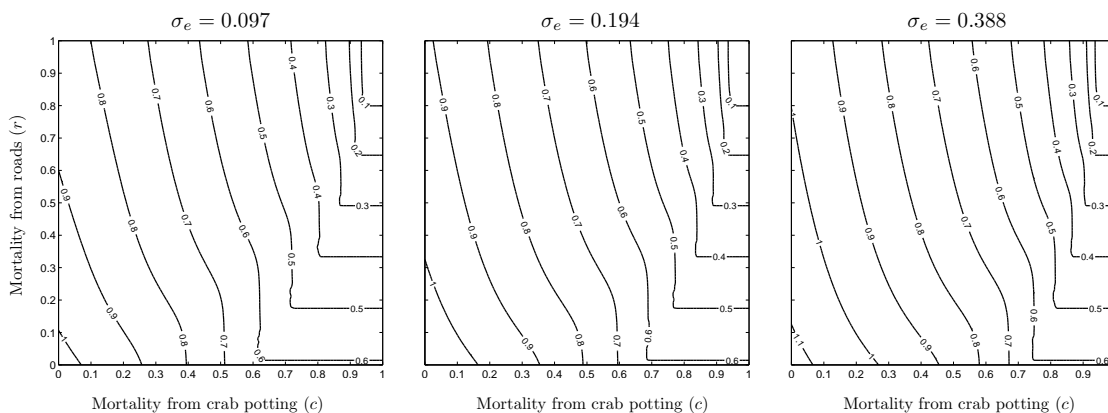


Figure 6: Population growth λ in the nonlinear model versus both crab potting c and road mortality r for three levels of egg survivorship: $\sigma_e = 0.097$ (baseline), 0.194 (double baseline) and 0.388 (quadruple baseline).

4 Conclusions

As we have not validated the linear and nonlinear models against actual population data, we cannot conclusively determine which better predicts the behavior of terrapin populations. We would need a population that has been studied over multiple years (as in [11]), that we know to have been affected by a certain degree of crab potting and road mortality, in order to see which model better represents the dynamics that are occurring. The importance of collecting data for model validation is strengthened by the different level of importance each model attributes to crab potting versus road mortality: critical values for population decline are nearly opposite in each case ($c = 6.5\%$, $r = 10.6\%$ for the nonlinear model; $c = 11.6\%$, $r = 7.6\%$ for the linear model). However, the nonlinear model has the potential to be a more accurate depiction of the dynamics, as it takes the male contribution to fecundity into account. This could be especially important in populations that experience crab potting.

Diamondback terrapin populations can benefit from measures to protect the terrapins from both crab pot and road mortalities. The modeled Rhode Island population was growing, but at a slow rate ($\lambda = 1.034$) [11], and both models suggest a relatively small push could send it into decline. Crab potting is theoretically an easier problem to fix, which the nonlinear model suggests would have a larger effect on an affected population. Unfortunately, there can be much resistance to the use of BRDs, as they are viewed as potentially harmful to the crabbing industry. Educating both recreational and commercial crabbers about the benefits of BRDs could have a positive effect on the terrapin population.

A study performed in Georgia in an area with low levels of road traffic found that road mortalities did not contribute to population decline [8]. This illustrates the importance of tailoring conservation efforts to the specific locations where they will be applied. In this situation, it would be more effective

to focus on promoting the use of BRDs in the marsh around this Georgia population, but in highly developed areas with frequently used roads, it could be more effective to look into a long-term management plan to reduce road mortality.

Future research will focus on altering the model to add detail to the fecundity terms. The addition of a term for the size of a harem (the number of females one male will mate with) could be included. This value could be set to 5, because farm raised terrapins produce the most offspring under a female:male ratio of 5:1 [9]. If this is also the case for terrapin populations in the wild, certain levels of crab potting would actually increase the fecundity of the population, if it pushed the ratio of females:males closer to 5:1. Also, a parameter for the proportion of eggs that are female (or male) could be included, as terrapin eggs undergo temperature-dependent sex determination (TSD) [2]. Temperatures of at least 31 degrees Celsius lead to female hatchlings, while temperatures of less than 27 degrees Celsius lead to male hatchlings [10].

Other directions for future research could include examining demographic stochasticity, as well as the sensitivities and elasticities of the various parameters in the linear and nonlinear models. As in the loggerhead turtle study [6], a sensitivity analysis would more conclusively determine how the population would respond to changes in survivability across different stages, as well as changes in crab potting and road mortality. Terrapin conservation efforts would benefit from the knowledge of exactly how responsive each stage class is to boosts or declines in survival, as they would be able to allocate their resources and funds accordingly to counteract effects of human influences on terrapin populations.

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References

- [1] C. Ayers, 2010. A population model for the diamondback terrapin: Implications for conservation management. Honors Thesis. College of William and Mary.
- [2] B. Brennessel, 2006. *Diamonds in the Marsh: A Natural History of the Diamondback Terrapin*. Lebanon, NH: University Press of New England.
- [3] H. Caswell, 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sunderland, MA: Sinauer Associates.
- [4] R.M. Chambers, J.C. Maerz, R.E. Wood. Terrapin Bycatch in the Blue Crab Fishery. Under Review.
- [5] D. Crews, J.M. Bergeron, J.J. Bull, D. Flores, A. Tousignant, J.K. Skipper, T. Wibbels, 1994. Temperature-dependent sex determination in reptiles: Proximate mechanisms, ultimate outcomes, and practical applications. *Developmental Genetics*, **15**, 297-312.
- [6] D.T. Crouse, L.B. Crowder, H. Caswell, 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology*, **68(5)**, 1412-1423.
- [7] J.P. Gibbs, D.A. Steen, 2005. Trends in sex ratios of turtles in the United States: Implications of road mortality. *Conservation Biology*, **19(2)**, 552-556.

- [8] A.M. Grosse, J.C. Maerz, J. Hepinstall-Cymerman, M.E. Dorcas, 2011. Effects of Roads and Crabbing Pressures on Diamondback Terrapin Populations in Coastal Georgia. *Journal of Wildlife Management*, **75(4)**, 762-770.
- [9] S.E. Hildebrand, 1932. Growth of diamond-back terrapins: Size attained, sex ratio, and longevity. *Zoologica* **IX(15)**, 551-563.
- [10] P. Jeyasuria, W.M. Roosenburg, A.R. Place, 1994. Role of P-450 aromatase in sex determination of the diamondback terrapin, *Malaclemys terrapin*. *The Journal of Experimental Zoology*, **270**, 95-111.
- [11] M.G. Mitro, 2003. Demography and viability analyses of a diamondback terrapin population. *Canadian Journal of Zoology*, **81(4)**, 716-726.
- [12] A.S. Morris, S.M. Wilson, E.F. Dever, R.M. Chambers, 2011. A test of bycatch reduction devices on commercial crab pots in a tidal marsh creek in Virginia. *Estuaries and Coasts*, **34(2)**, 386-390.
- [13] S. Murphy, D. Griffin. Loggerhead turtle: *Caretta caretta*. *South Carolina Department of Natural Resources*. Web 12 Dec. 2013. <http://www.dnr.sc.gov/cwcs/pdf/Loggerheadturtle.pdf>.
- [14] R.D. Nussbaum, 1986. Convexity and log convexity for the spectral radius. *Linear Algebra and its Applications*, **73**, 59-122.
- [15] R.D. Nussbaum, 1988. Iterated nonlinear maps and Hilbert's projective metric. *Memoirs of the American Mathematical Society*, **75(391)**, Providence, Rhode Island, USA.
- [16] R.D. Nussbaum, 1989. Iterated nonlinear maps and Hilbert's projective metric, II. *Memoirs of the American Mathematical Society*, **79(401)**, Providence, Rhode Island, USA.
- [17] M.A. Rook, R.N. Lipcius, B.M. Bronner, R.M. Chambers, 2010. Bycatch reduction device conserves diamondback terrapin without affecting catch of blue crab. *Marine Ecology Progress Series*, **409**, 171-179.
- [18] W.M. Roosenburg, A.E. Dunham, 1997. Allocation of reproductive output: Egg- and clutch-size variation in the diamondback terrapin. *Copeia*, **2**, 290-297.
- [19] S. Szerlag, S.P. McRobert, 2006. Road occurrence and mortality of the northern diamondback terrapin. *Applied Herpetology*, **3(1)**, 27-37.
- [20] D.C. Tulipani, 2013. Foraging ecology and habitat use of the northern diamondback terrapin (*Malaclemys terrapin terrapin*) in southern Chesapeake Bay. Dissertation. Virginia Institute of Marine Science.
- [21] R.C. Wood, R. Herlands, 1997. Turtles and Tires: The impact of roadkills on northern diamond-back terrapin, *Malaclemys terrapin terrapin*, populations on the Cape May peninsula, southern New Jersey, USA. *Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles - An International Conference*, 46-53.