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A COMPUTATIONAL STUDY OF THE EFFECTS OF TEMPERATURE VARIATION ON TURTLE EGG DEVELOPMENT, SEX DETERMINATION, AND POPULATION DYNAMICS.

by

Amy Parrott

A DISSERTATION

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Major: Mathematics

Under the Supervision of Professor J. David Logan

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August, 2009

A COMPUTATIONAL STUDY OF THE EFFECTS OF TEMPERATURE VARIATION ON TURTLE EGG DEVELOPMENT, SEX DETERMINATION, AND POPULATION DYNAMICS.

Amy Parrott, Ph.D.

University of Nebraska, 2009

Adviser: J. David Logan

Climate change and its effects on ecosystems is a major concern. For certain animal species, especially those that exhibit what is known as temperature-dependent sex determination (TSD), temperature variations pose a possibly serious threat

(Valenzuela and Lance, 2004). In these species, temperature, and not chromosomes, determines the sex of the animal (Valenzuela and Lance, 2004). It is conceivable therefore, that if the temperature changes to favor only one sex, then dire consequences for their populations could occur. In this dissertation, we examine possible effects that climate change may have upon Painted Turtles (Chrysemys picta), a species with TSD. We investigate the magnitude and type of change required to have an adverse effect upon its population. We look at both the effects caused by an increase in average temperature and an increase in daily temperature variance. To examine these effects, we develop a computational model that connects daily ambient air temperature and solar radiation readings to the sex of the turtles in the nests and to the male/female population structure. We show that an increase in both temperature or variance may cause a decline in the population, but an increase in both temperature and variance produces the greatest decline.

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Chapter 1

Introduction

Climate change and its effects on ecosystems is a major concern. The 2007 Intergovernmental Panel on Climate Change (IPCC) reports that climate change is evident worldwide. They report the frequency of heat waves and heat extremes is likely to increase (Bernstein, 2007). For certain animal species, especially those that exhibit what is known as temperature-dependent sex determination (TSD), temperature variations pose a possibly serious threat (Valenzuela and Lance, 2004). In these species, temperature, and not chromosomes, determines the sex of the animal (Valenzuela and Lance, 2004). It is conceivable therefore, that if the temperature changes to favor only one sex, then dire consequences for their populations could occur.

In this dissertation, we examine possible effects that climate change may have upon Painted Turtles (*Chrysemys picta*), a species with TSD. We investigate the magnitude and type of change required to have an adverse effect upon its population. We look at both the effects caused by an increase in average temperature and an increase in daily temperature variance. We chose to observe the effects of changing average temperature and daily amplitude because Shine and Harlow (1996) found that both the mean temperature and the variance of temperature influenced the development rates and thus incubation periods of skinks (*Bassiana duperreyi*).

To examine these effects, we develop a computational model that connects daily ambient air temperature and solar radiation readings to the sex of the turtles in the nests and to the male/female population structure. There seems to be no detailed population model in the literature that incorporates effects of climate change on populations and gender structure of any species with TSD. In one related study the author correlated the average air temperature in July to the sex of the turtles, and then they extrapolated the result to determine that an increase of $4^{\circ}C$ could effectively eliminate the population (Janzen, 1994). However, only the average monthly temperature was considered, and the author did not to take into account the possible insulating effects that air may have around the eggs. As part of our study, we model the temperature profile in a nest, given ambient air temperature and solar radiation; we include the effects of variable heat conduction properties in the nest, specifically of the air and soil effects in the egg layer. In contrast to Janzen (1994), we show that a global increase of $4 \circ C$ is not enough to eliminate the population, but that an increase of 4°C coupled with an increase of 4°C in average temperature amplitude is necessary for the population to decrease.

Woodward and Murry (1993) construct a model that describes dynamics for a population with TSD, but in their model they assume that the proportion of females each year is constant. In our model, we use a stochastic temperature profile inside the nest to determine the proportion of females each year. The proportion of females is calculated using a degree-hour approach. Georges (1989; 2005 and Valenzuela and Lance (2004)) has developed a model for determining the sex of the nest based upon the temperature profile inside the nest, but his model is only valid for species with one temperature threshold. Because northern painted turtles have both upper and lower temperature thresholds, we cannot use Georges' model. We use a degree hour model instead. Schwarzkopf et. al. (1987) found that degree-hours best predicted the sex of the nest in northern painted turtles.

1.1 Temperature-Dependent Sex Determination

Temperature-dependent sex determination (TSD) is a life history strategy in which the temperature during development of the organism determines the sex of the animal, in contrast to other organisms which determine sex through chromosomes. There are three major types of TSD: male-female where males are produced at cooler temperatures and females at warmer temperatures, female-male where females are produced at cooler temperatures and males at warmer temperatures and female-male-female where females are produced at both temperature extremes and males are produced in between. TSD is seen in crocodilians, lizards, turtles, some fish and even in some birds. (Valenzuela and Lance, 2004)

There have been many studies performed in laboratory settings on the effects of temperature on sex (Demuth, 2001; Chevalier et al., 1999; Du and Ji, 2003) (Shine and Harlow, 1996; Janzen and Morjan, 2002; Schwarzkpf and Brooks, 1985; Bull et al., 1982). The majority of the laboratory studies involve incubating the eggs at a constant temperature. However, there have been very few studies on the influence of temperature in actual nests (Bull, 1985; Georges, 1992; Shine and Harlow, 1996; Janzen, 1994).

While painted turtles in southern latitudes of the United States exhibit the malefemale type of TSD, (Bull et al., 1982), Schwarzkopf et. al. (1985) and Gutzke et. al. (1984) have shown that northern populations of painted turtles produce females at both cooler and very warm nest temperatures. The upper and lower thresholds for producing males show some variation among the populations. The upper threshold was found to be $27.5^{\circ}C$ in Tennessee (Bull et al., 1982) and in Ontario (Schwarzkpf and Brooks, 1985), $28^{\circ}C$ in Nebraska (Gutzke and Paukstis, 1984) and 28.5 in Wisconsin (Bull et al., 1982). In Nebraska, the lower threshold was found to be $22^{\circ}C$ (Gutzke and Paukstis, 1984) and in Ontario $20^{\circ}C$ (Schwarzkpf and Brooks, 1985). It is speculated that the lower threshold evolved because the ground temperature in northern climates seldom reaches a temperature above $28^{\circ}C$

(Gutzke and Paukstis, 1984). In this study, we use the threshold temperatures for the Nebraska turtles (Fig. 1.1).



Figure 1.1: Temperature thresholds for the Nebraska population of painted turtles.

The sex of a painted turtle is determined during the middle-third of its developmental period (Valenzuela and Lance, 2004). If the majority of development during this time period occurs within the male temperature range, the nest will be male. If the majority of the development occurs within the female temperature range, the nest will produce females, and if the temperature fluctuates about a threshold cutoff, the nest will produce both males and females (Valenzuela and Lance, 2004).

The evolutionary benefit of TSD remains uncertain. There are four widely accepted reasons for TSD persistence in reptiles, which are reviewed in

(Janzen and Phillips, 2006; Murry, 2002; Valenzuela and Lance, 2004). First, fitness levels may be optimal for each sex at these temperatures; that is, males are produced if the eggs develop under conditions favorable to post-hatching males and females are produced if the eggs develop under conditions favorable to post-hatching females

(Warner and Shine, 2008) although, Janzen et. al. (2006) downplay the significance of this hypothesis, stating that the research confirming this view conflicts with other research. There have been studies with the same experimental design as well as studies on the same species but with different experimental designs that have produced both results for and against this hypothesis (Janzen and Phillips, 2006). Second, "TSD promotes adaptive control of sex ratio to promote group fitness" (Janzen and Phillips, 2006). Third, "TSD minimizes inbreeding by producing single-sex clutches" (Janzen and Phillips, 2006). Fourth, there is no adaptive advantage to evolving from TSD, so it is just maintained.

1.2 Painted Turtle Life History

Chrysemys picta, the painted turtle, is characterized by a dark green to black carapace, and the plastron ranges in color from yellow to a dark red with black ink-blot type markings. The head, neck, and limbs are generally dark green in color and can be striped with yellow or red lines. There are several distinguishing features between the sexes. Mature males have longer fore claws and longer, thicker tails than those of females, and mature females are generally larger in overall size than males (Bartlett and Bartlett, 2006; Ernst et al., 1994).

There are four subspecies of painted turtles which are determined according to the region of North America it occupies. *C. picta picta* resides from southeastern Canada down the coast to Georgia or Florida. *C. picta marginata* resides from the southern Quebec and Ontario south through Illinois and east through Tennessee, West Virginia, Virginia, and the Carolinas. *C. picta dorsalis* resides in southern Illinois and Missouri, down both sides of the Mississippi River to the Gulf of Mexico. *C. picta belli* resides from western Ontario to British Columbia, down through northern Oregon to Oklahoma. The differences between the subspecies are small, the main difference being the number and size of the clutches (Ernst et al., 1994; Cagle, 1954).

The habitat of the painted turtle consists primarily of slow moving waters such as lake coastlines, ponds, marshes, and creeks. The turtles generally begin their day around sunrise when they bask out of the water for several hours before foraging. After eating, they continue to bask in the sun until late afternoon or early evening when they again forage for food before spending the night sleeping in the water. Painted Turtles are opportunistic omnivores. Diet consist of plant matter, algae, leaches, crayfish, spiders, mosquitoes, fish, frogs, and various other insects and bugs. Younger painted turtles tend to be mostly carnivorous while adults are primarily herbivores (Ernst et al., 1994).

Painted turtles have three general age classes: hatchlings (1 year olds), juveniles (2-7 year olds), and adults (2-8+ year olds) (Cagle, 1954; Ernst et al., 1994). Hatchling refers to the first year after emergence from the nest. During the first year after emergence from the nest, hatchling growth is very rapid and they may double in size (Cagle, 1954; Ernst et al., 1994). The age at which the turtles move from the juvenile to adult age class depends upon both the sex of the turtle and the geographical location of the turtle (Gibbons, 1968; Ernst et al., 1994; Wilbur, 1975a; Iverson and Simith, 1993). Juveniles grow at a steady rate until maturity is reached; then they grow at a much slower rate (Gibbons, 1968; Wilbur, 1975b). Males reach maturity after one to five years, while females require five to nine years (Gibbons, 1968; Ernst et al., 1994). Painted turtles in northern climates reach maturity later than those in southern climates (Wilbur, 1975a; Iverson and Simith, 1993). Male painted turtles for at least six years, and females generally have a life

span of at least 12 years. Many of both gender live for 15 years, and it has been reported that painted turtles can live for 30 to 40 years. However, the upper limit on life span is unknown (Gibbons, 1968).

The predators of the painted turtle are dependent upon the size of the turtle. Hatchlings and juveniles are preyed upon by rice rats, muskrats, mink, raccoons, snapping turtles, snakes, bullfrogs, large fish, herons, and water bugs, while predators of adult turtles consist of alligators, raccoons, bald eagles, osprey, red-shouldered hawks, and other birds. Humans and their automobiles contribute to the death of many turtles, especially adults. Overall, raccoons are assumed to be the major predator (Ernst et al., 1994).

Generally, reproduction occurs in late May through mid-July (Iverson and Simith, 1993; Rowe et al., 2003; Cagle, 1954; Tinkle et al., 1981). Temperature strongly influences the beginning of the nesting season, although how temperature determines the beginning may depend on the location and, hence, subspecies of turtle. Ernst (1994) reports that in Quebec, the beginning is positively correlated with the average previous year's temperature. But, in the Nebraska sand-hills (Iverson and Simith, 1993) and in Michigan (Rowe et al., 2003), the onset of nesting is correlated with the average maximal temperature in March through May of the current year, and the previous year's temperature is unrelated to the onset of nesting .

Most nests are constructed in the late afternoon or early evening. They are dug in sandy soil and are flask shaped. Generally, nests are "dug within 200m of water, but may be as far away as 600m" (Ernst et al., 1994). After depositing and covering the eggs with soil, the female often wets the soil with bladder water to moisten the nest. The nests are often dug out in the open where the soil covering the nest is exposed to direct sunlight. If weather conditions are not favorable, either too hot or too dry, the female may delay nesting for up to three weeks (Ernst et al., 1994). A female will lay from one to five clutches per season, although two to three clutches are common (Ernst et al., 1994). The number of eggs per clutch varies among the subspecies. *C. picta bella* lays the most with 6 to 21 eggs, (Iverson and Simith, 1993) while *C. picta picta* lays 2-10 eggs and *C. picta marginata* lays 3-14 eggs. *C. picta dorsalis* lays the fewest number with 1-7 eggs on average per clutch (Ernst et al., 1994).

Female painted turtles store sperm of their mates. They can use this sperm to fertilize multiple clutches within a single season and over multiple seasons. Females may also mate with another male even if they have stored sperm from a previous copulation. In this case, the most recent sperm is used in fertilizing the eggs first. Larger clutches (more than 12 eggs) have a higher frequency of multiple paternity than smaller clutches (Pearse et al., 2001, 2002).

Both the rate at which the soil conducts heat and the level of humidity play a role in the hatching rate of the eggs. Eggs that are incubated in moist soil tend to take longer to hatch, but have a greater hatching rate than those in dryer soil. Also, eggs that are incubated in soil with higher thermal conductivity absorb more water than those that are incubated in soil with lower thermal conductivity (Ernst et al., 1994).

The eggs hatch, on average, after a 76-day incubation period (Ernst et al., 1994). In colder climates, the turtles hibernate in the nest and emerge in the spring. Painted turtles have the ability to be frozen in the nest over winter and can survive temperatures as cold as -8.9° C (Cagle, 1954; Ernst et al., 1994). Cagle (1954) reports that during the first 10 days after emergence from the eggs, the turtles change greatly in appearance, and by the tenth day they take on the size and proportions of small juveniles.

According to Gibbons (1968), there are three major causes of mortality in the nest. The first is infertility; that is, the eggs that are laid are not viable and will

never hatch. Also, environmental conditions, such as extreme heat, cold, moisture, or dryness may cause mortality. Finally, predation of the nests causes the failure of many nests. The majority of predation is by raccoons, but other small rodents, foxes, snakes and humans also contribute to failure of some nests (Ernst et al., 1994).

1.3 Model Overview

We develop a computational model to examine the potential effects that climate change may have upon painted turtles. A computational model a model "whose complexity puts [it] beyond the reach of mathematical analysis" (Ellner and Guckenheimer (2006) p. 243). That is, the model contains a large number of interacting processes with a large parameter set. Each part the model is modeled explicitly with a set of rules governing the interactions between the parts.Because of their complexity, these models must be analyzed by computer simulation. One criticism of this type of a model is that one is replacing a complex biological process with a complex computer system. However, a computer system does have its benefits because it can be studied in a much shorter amount of time than the actual biological system.Also, a computer model allows the experimenter to change whichever parameters he or she sees fit without disturbing the actual biological system.

A second criticism is that because the models are so complex, it is difficult to determine exactly why an outcome occurs. While this criticism cannot be completely remedied, one can perform a local sensitivity analysis on the parameters whereby one only considers small perturbations of each parameter, while holding the other parameters constant. This allows the researcher to rank the parameters in order of impact and it aids in the implementation of biological experiments. However, this does not allow the researcher to discern possible interactions between the parameters. Here we use a stage structured population model to explore the effects of climate change. We examine the effects that various temperature scenarios have upon the population of painted turtles. Specifically, we examine the effects of increases in average temperature and the effects of increases in daily temperature variance.

We increment the model yearly. That is, in each year we first determine stochastic temperature and solar radiation profiles. For each female in the population, we determine a first and second nesting date from a truncated normal distribution. Next we calculate the temperature profile inside the egg layer of each nest from the heat, or diffusion, equation. Then we determine the sex of the nest using a degree-hour approach. Finally, we update the population projection matrix and compute the population vector for the year. We repeat this process for a 30-year time period. A flow chart of the model process is shown in Fig. 1.2.

1.4 Model Assumptions

We make several assumptions to simplify the model.

- 1. Heat flow occurs only in the vertical direction. Because the computational model is as complex as it is, we do not consider the geometry of the nest.
- 2. The metabolic heat created by the eggs is negligible. In a study on parchmentshelled reptile eggs, such as for the painted turtle, Ackerman et. al. (1985b) found that the eggs of three species of reptiles would be, on average, $0.18^{\circ}C$ warmer than the air temperature. Because the clutch size of the painted turtle is small (< 20 eggs) (Iverson and Simith, 1993; Ernst et al., 1994), and because the temperature increase is minimal, we do not include the metabolic heat created by the eggs in determining the nest temperatures. This assumption



Figure 1.2: Flow chart for the computational model.

would not be valid for species of reptiles that have large clutches, such as the sea turtle (Crouse et al., 1987).

3. Moisture levels remain constant in the nest. Water potential inside the nest is very important for embryonic survival (Cagle et al., 1993; Ackerman et al., 1985b; Gutzke et al., 1987; Ackerman et al., 1985a; Rimkus et al., 2002). We assume that the moisture level remains constant and sufficient for development. Thus we ignore the effect of rainfall on egg development. This assumption simplifies the model in that the diffusivity of the soil and egg layers remain

constant instead of variable.

- 4. Turtles only store sperm for at most one year, even though there is evidence that, on occasion, sperm is stored for more than one year (Pearse et al., 2001, 2002). We also assume that the stored sperm does not lose its viability. Pearse et. al. (2001) found that the hatchling success of turtles from stored sperm was not significantly different from the hatchling success of turtles from new sperm.
- 5. Each female adult turtle nests twice a year and produces a nest every year. Iverson et al. (1993), report that painted turtles in Nebraska generally produce two nest each year. There is no indication of senescence. Wilbur (1975a) record females over 30 years old still reproducing. We make the simplifying assumption that the number of eggs laid by each adult is the same regardless of the age of the female turtle.
- 6. The only environmental stochasticity is temperature. While other aspects of environmental stochasticity (e.g., predators, food availability) may have an impact upon turtle mortality and egg production, we consider only the effects of temperature.

Chapter 2

Model Derivation

2.1 Nest Temperature Model

We now examine the nest temperature part of our model. A diagram of the nest setup is shown in Fig. 2.1. We begin by deriving the equation governing the flow of heat through the nest. Then we discuss the conditions on the surface and at the top and bottom of the nest. Finally, we discuss exact and numerical solutions to this part of the model.

2.1.1 Diffusion Equation

In this section derive the heat equation, which describes the vertical flow of heat through the nest. We follow the derivation given in (Logan (1987) Ch. 4). We assume the egg layer begins at some depth a and ends at depth b, with 0 < a < b. Let u(x,t) be the temperature at depth x at time t, and let A be the cross-sectional area of the layer. Then for any depth x within the layer, the flux at x is given by Fourier's Law

flux at
$$x = -K(x)u_x(x,t)$$



Figure 2.1: Schematic of a turtle nest below a ground area A.

where

$$K(x) = \begin{cases} K_s & 0 \le x < a \text{ and } b \le x \le L \\ K_e & a \le x < b \end{cases}$$

is the thermal conductivity in the soil and egg layers. Let η and ζ be two points in the soil or egg layer with $\zeta < \eta$. Then the total energy in the region is

$$A\int_{\zeta}^{\eta} c(x)\rho(x)u(x,t)dx$$

where

$$c(x) = \begin{cases} c_s & 0 \le x < a \text{ and } b \le x \le L \\ c_e & a \le x < b \end{cases} \text{ and } \rho(x) = \begin{cases} \rho_s & 0 \le x < a \text{ and } b \le x \le L \\ \rho_e & a \le x < b \end{cases}$$

are the specific heat and density, respectively. Then the time rate of change of energy in the region is equal to the heat entering at ζ minus the heat exiting at η . That is,

$$\frac{d}{dt} \int_{\zeta}^{\eta} c(x)\rho(x)u(x,t)dx = K(\eta)u_x(\eta,t) - K(\zeta)u_x(\zeta,t).$$

Then, assuming that u is smooth in the layer (soil or egg), the Fundamental Theorem of Calculus gives

$$\frac{d}{dt} \int_{\zeta}^{\eta} c(x)\rho(x)u(x,t)dx = \int_{\zeta}^{\eta} \frac{d}{dx}(K(x)u_x(x,t))dx.$$

Pulling the time derivative under the integrand and rearranging yields

$$\int_{\zeta}^{\eta} \left(\frac{d}{dt} (c(x)\rho(x)u(x,t)) - \frac{d}{dx} (K(x)u_x(x,t))dx \right) = 0.$$

Therefore, as η and ζ are arbitrary, the integrand is zero and thus we have

$$c(x)\rho(x)u_t(x,t) = \frac{d}{dx}(K(x)u_x(x,t)).$$

Because c, ρ and K are constant in each zone (soil or egg), we can write

$$u_t = k(x)u_{xx},\tag{2.1}$$

where

$$k(x) = \begin{cases} k_s & 0 \le x < a \text{ and } b \le x \le L \\ k_e & a \le x < b \end{cases}$$

with $k_s = \frac{K_s}{c_s \rho_s}$ and $k_e = \frac{K_e}{c_e \rho_e}$.

The diffusivity is equal to the ratio of the thermal conductivity, K_s or K_e , to the product of the density, ρ_s or ρ_e , and the specific heat, c_s or c_e , where the subscripts denote the soil and egg layer values respectively.

2.1.2 Boundary Conditions

We now examine the condition at the boundaries: the surface, the interfaces, and lower boundary. We consider a patch of ground of area A. At the surface, the flux in at x = 0 is equal to the flux due to the temperature difference between the surface and the ambient temperature plus the flux due to radiation. From Fourier's law, the flux in at x = 0 is

$$-AK_s u_x(0^+, t),$$

where K_s is the thermal conductivity of the soil. The flux due to temperature differences is

$$Ah(U_{amb}(t) - u(0^+, t)),$$

where h is the heat transfer coefficient from Newton's law of cooling and $U_{amb}(t)$ is the ambient air temperature at time t. The radiation flux is

$$A\alpha W(t),$$

where W(t) is the solar radiation at time t, and α is the proportion of the solar energy absorbed. Putting this all together, we have

$$-AK_s u_x(0^+, t) = Ah(U_{amb}(t) - u(0^+, t)) + A\alpha W(t).$$

Dividing by A and rearranging, we obtain the boundary condition at the surface,

$$u(0^+, t) - \frac{K_s}{h} u_x(0^+, t) = U_{amb}(t) + \frac{\alpha}{h} W(t).$$
(2.2)

To calculate the boundary conditions at the interfaces, the top and bottom of the nest layer, we let a be the depth where the egg layer begins and b be the depth where the egg layer ends, with 0 < a < b. We require that the flux across each boundary interface is constant. That is

$$K_s u_x(a^-, t) = K_e u_x(a^+, t) \qquad K_e u_x(b^-, t) = K_s u_x(b^+, t) \qquad (2.3)$$

In our model, we will also assume that we know the temperature profile at some depth L. That is,

$$u(L,t) = g(t).$$
 (2.4)

This is a reasonable assumption because the earth's temperature is relatively constant at 9.76m below the surface (web, a). Note that this depth is much deeper than the nest which is between 8cm to 12cm below the surface.

Therefore, we have that 2.1, 2.2, 2.3 and 2.4 form a BVP for the temperature in 0 < x < L, t > 0.

2.1.3 Numerical Solution

We now turn our attention to the numerical solution to the BVP for the nest temperature. The temperature model solution is calculated numerically by a backward implicit method (Logan, 1987). We use this method because it converges for all choices of step size (Logan, 1987). We will calculate the numerical solution to the related BVP:

$$c\rho(x)u_t = \frac{d}{dx}(K(x)u_x(x,t))$$
(2.5)

where

$$c\rho(x) = \begin{cases} c_s\rho_s & 0 \le x < a - \varepsilon \text{ and } b + \varepsilon \le x \le L \\ c_e\rho_s & a + \varepsilon x < bx < b - \varepsilon \\ \frac{c_e\rho_e - c_s\rho_s}{2\varepsilon}(x - a + \varepsilon) + c_s\rho_s & a - \varepsilon \le x \le a + \varepsilon \\ \frac{c_s\rho_s - c_e\rho_e}{2\varepsilon}(x - b - \varepsilon) + c_s\rho_s & b - \varepsilon \le x \le b + \varepsilon \end{cases}$$

and

.

$$K(x) = \begin{cases} K_s & 0 \le x < a - \varepsilon \text{ and } b + \varepsilon \le x \le L \\ K_e & a + \varepsilon x < bx < b - \varepsilon \\ \frac{K_e - K_s}{2\varepsilon} (x - a + \varepsilon) + K_s & a - \varepsilon \le x \le a + \varepsilon \\ \frac{K_s - K_e}{2\varepsilon} (x - b - \varepsilon) + K_s & b - \varepsilon \le x \le b + \varepsilon \end{cases}$$

with $0<\varepsilon\ll 1$ with boundary conditions

$$u(0^+, t) - \frac{K_s}{h} u_x(0^+, t) = U_{amb}(t) + \frac{\alpha}{h} W(t)$$
(2.6)

$$u(L,t) = g(t) \tag{2.7}$$

It is well-known in the literature that as $\varepsilon \to 0$, the related BVP (2.5-2.7) con-

verges to our BVP derived earlier (2.1, 2.2, 2.3, 2.4). Note that as $\varepsilon \to 0$, the solution to the related BVP does satisfy the boundary conditions at *a* and *b*. Observe that, by the Fundamental Theorem of Calculus,

$$\int_{a-\varepsilon}^{a+\varepsilon} c\rho(x)u_t dx = \int_{a-\varepsilon}^{a+\varepsilon} \frac{d}{dx} (K(x)u_x) dx$$
$$= K(a+\varepsilon)u_x(a+\varepsilon,t) - K(a-\varepsilon)u_x(a-\varepsilon,t).$$

Evaluating the limit as $\varepsilon \to 0$, we have

$$0 = K(a^{+})u_{x}(a^{+},t) - K(a^{-})u_{x}(a^{-},t).$$

That is,

$$K_e u_x(a^+, t) = K_s u_x(a^-, t).$$

Similarly, as $\varepsilon \to 0$,

$$K_e u_x(b^-, t) = K_s u_x(b^+, t).$$

Now, a solution to the BVP exists and is unique. Indeed, assume there are two solutions u_1 and u_2 of 2.5 with associated boundary conditions. Then, letting $w = u_1 - u_2$, we have that w solves the BVP

$$w_{t} = \frac{d}{dx}k(x)w_{x} \qquad 0 \le x \le L, \ 0 \le t$$

$$w(0^{+}, t) - \frac{K_{s}}{h}w_{x}(0^{+}, t) = 0,$$

$$w(a^{-}, t) = w(a^{+}, t) \qquad w(b^{-}, t) = w(b^{+}, t)$$

$$K_{s}w_{x}(a^{-}, t) = K_{e}w_{x}(a^{+}, t) \qquad K_{e}w_{x}(b^{-}, t) = K_{s}w_{x}(b^{+}, t)$$

$$w(L, t) = 0$$

$$w(x, 0) = 0$$

We set $E(t) = \int_0^L w^2 dx$, which is the energy. Then, $E(t) \ge 0$ and E(0) = 0. Now,

$$\begin{aligned} E'(t) &= \int_0^L 2w w_t dx \\ &= \int_0^L 2w \frac{d}{dx} (k(x)w_x) dx \\ &= 2k(L)w(L,t)w_x(L,t) - 2k(0)w(0,t)w_x(0,t) - \int_0^L 2k(x)(w_x)^2 dx \\ &= 0 - \frac{2k_s h}{K_s} (w_x(0,t))^2 - \int_0^L 2k(x)(w_x)^2 dx. \end{aligned}$$

The final line in the inequalities is less than zero as $\frac{2k_sh}{K_s} > 0$ and k(x) > 0 for $0 \le x \le L$. Hence, E(t) is a non-increasing function, and because E(0) = 0 and $E(t) \ge 0$, we must have that E(t) = 0. Therefore, w(x,t) = 0 and the solution is unique. Hence, the BVP is a well posed problem and so our numerical solution, which approximates the solution to 2.5-2.7 with $\varepsilon \ll 1$, will converge to the actual solution.

Assume that $\varepsilon < 0.001$ and let Δx and Δt be the space and time steps respectively with $\Delta x > \varepsilon$. We set up a grid (x_j, t_n) , j = 1, 2, ..., J, n = 1, 2, ..., N, of points with $t_1 = x_1 = 0$, and where $x_{j+1} = x_j + \Delta x$ and $t_{n+1} = t_n + \Delta t$. Note that we start our counter at 1 instead of the conventional 0 to be consistent with the notation in our Matlab program. Then, $u(x,t) \approx U(x_j, t_n)$ for some j, n. For simplicity of notation, we write $U(x_j, t_n)$ as $U_{j,n}$. The implicit method uses the backward approximation for the time derivative,

$$u_t \approx \frac{U_{j,n} - U_{j,n-1}}{\Delta t},$$

and the second derivative is approximated by

$$u_{xx} \approx \frac{U_{j+1,n} - 2U_{j,n} + U_{j-1,n}}{(\Delta x)^2}$$



Figure 2.2: A computational molecule for the implicit scheme.

Thus, to leading order, the heat equation can be approximated by

$$\frac{U_{j,n} - U_{j,n-1}}{\Delta t} - k(x)\frac{U_{j+1,n} - 2U_{j,n} + U_{j-1,n}}{(\Delta x)^2} = 0$$

which simplifies to

$$-rU_{j-1,n} + (1+2r)U_{j,n} - rU_{j+1,n} = U_{j,n-1}$$

where $r = \frac{k(x)\Delta t}{(\Delta x)^2}$. This leads to the system of equations for each time n

$$\begin{bmatrix} U_{1,n-1} + rU_{0,n} \\ U_{2,n-1} \\ \vdots \\ \vdots \\ U_{J-2,n-1} \\ U_{J-1,n-1+rU_{J,n}} \end{bmatrix} = \begin{bmatrix} 1+2r & -r & & & \\ -r & 1+2r & -r & & \\ & -r & \ddots & \ddots & \\ & & \ddots & \ddots & \ddots & \\ & & & & -r \\ & & & & -r & 1+2r \end{bmatrix} \begin{bmatrix} U_{1,n} \\ U_{2,n} \\ \vdots \\ \vdots \\ \vdots \\ U_{J-1,n} \end{bmatrix}.$$
(2.8)

Note that here $U_{0,n}$ is a false boundary point as we are indexing beginning at 1. The computational molecule is shown in Fig. 2.2.

The surface boundary condition is discretized as follows. We have $u(0+,t) \approx U_{1,n}$

and $u_x(0+,t) \approx \frac{U_{2,n}-U_{0,n}}{2\Delta x}$. Again, here $U_{0,n}$ refers to a false boundary point and not to the ambient air temperature above the ground. We then obtain

$$U_{1,n} - \frac{K_s}{h} \left(\frac{U_{2,n} - U_{0,n}}{2\Delta x} \right) = U_{\text{amb}}(t_n) + \frac{\alpha}{h} W(t_n).$$

This equation simplifies to

$$U_{0,n} = \frac{1}{\beta} \left(U_{\text{amb}}(t_n) + \frac{\alpha}{h} W(t_n) - U_{1,n} \right) + U_{2,n},$$
(2.9)

where $\beta = \frac{K_s}{2h\Delta x}$.

Now, the first row in the matrix equation (2.8) is

$$U_{1,n-1} + rU_{0,n} = (1+2r)U_{1,n} - rU_{2,n}$$

Using (2.9), we then have

$$U_{1,n-1} + \frac{r}{\beta} \left(U_{\text{amb}}(t_n) + \frac{\alpha}{h} W(t_n) \right) = (1 + 2r + \frac{r}{\beta}) U_{1,n} - r U_{2,n}$$

At the lower boundary, or at depth $L = x_J$ we have that u(L,t) = g(t) so we set $U_{J,n} = g(t_n).$

Recall that the boundary conditions at the interfaces, or at the top and bottom of the egg layer, require that the flux is assumed constant. These may be discretized as

$$-K_s\left(\frac{U_{a,n}-U_{a-1,n}}{\Delta x}\right) = -K_e\left(\frac{U_{a+1,n}-U_{m,n}}{\Delta x}\right)$$
(2.10)

and

$$-K_e\left(\frac{U_{b,n}-U_{b-1,n}}{\Delta x}\right) = -K_s\left(\frac{U_{b+1,n}-U_{b,n}}{\Delta x}\right).$$
(2.11)

Here a and b depend upon the location of the egg layer as well as the choice of step size. Hence, from (2.10) and (2.11), at depth a the corresponding row in the matrix equation becomes

$$K_s U_{a-1,n} - (K_s + K_e) U_{a,n} + K_e U_{a+1,n} = 0,$$

and at depth b the corresponding row is

$$K_e U_{b-1,n} - (K_s + K_e) U_{b,n} + K_s U_{b+1,n} = 0.$$

2.1.4 Parameter Values

In our model, we assume that all nests are laid at the same depth. We assume that the egg layer begins 8cm below the surface and ends 12cm below the surface. These values are those given by Larson (2004), who observed Painted turtles in Nebraska. According to Ernst, the average dimensions of nests in Pennsylvania were between 9.9cm and 11.1cm deep (Ernst et al. (1994) p.291). We will use the temperature profile obtained from 10cm below the surface as the egg depth to calculate the sex of the nest.

The thermal conductivity of the egg layer was calculated by estimating the effective thermal conductivity. As the specific geometry of the egg, air and soil arrangements is unknown, we choose a model that takes this into consideration. There are many methods for estimating the effective thermal conductivity of heterogeneous media. Several of these have been reviewed in Floury et. al. (2008). The model we have chosen was first given by Landour (1952) and expanded upon by Davis et. al. (1975). An overview of many widely used models is available in (Floury et al., 2008). We choose this particular model because it assumes that the air-egg media are randomly dispersed within the volume where as other models do not allow for this random dispersion. The effective thermal conductivity is found by solving

$$\sum_{j} v_j \frac{K_j - K_e}{K_j + 2K_e} = 0$$

for K_e , where v_j is the fractional volume of the *j*th medium with thermal conductivity K_j .

To determine the possible values for the fractional volumes of the eggs and the air within the nest, we examine ellipsoid packings because Painted turtle eggs are ellipsoidal. Indeed, Iverson et. al. (1993) reported that Nebraska Painted turtles eggs measured on average 30.14 ± 2.14 mm in length and 18.31 ± 1 mm in width. Experimentally, it has been determined that the most efficient packing will result in approximately 74% of the volume filled with eggs (Donev et al., 2004). Thus, 74% is taken to be an upper bound on the fractional volume of the eggs as it is unlikely that the turtle will lay her eggs in a most efficient packing. We choose 60% to be the default fractional volume of the eggs.

Because painted turtle eggs contain about 75% water Deeming (2004), we use the values of water for the specific heat, density and thermal conductivity of the eggs. Again, this is consistent with the literature Edwards et al. (2003). The values of these parameters were obtained from web (2008) as well as the parameter values for air. The specific heat and the density of the egg layer were obtained by multiplying the fractional volume of the eggs by the specific heat (density) of water and then adding this to the product of the fractional volume of the air (default is 40%) by the specific heat (density) of air. The absorption coefficient, α , is taken to be 0.8, which is the value used in Buonanno et al. (1995). The heat transfer coefficient, h, is estimated using the method given in Kreith (1965) and Buonanno et al. (1995).

We used Soil Climate Analysis Network (SCAN) data (web, b) taken at Rogers Farm southeast of Lincoln, NE to estimate the parameter values used for the soil layer. At this site, the air temperature, solar radiation, and soil temperature at depths of 2in, 4in, 8in, 20in and 40in as well as other constants are observed every hour. We estimated the soil layer parameter values by solving an inverse problem as follows. We define the function *soilTemps* which takes as input two values: one for the soil thermal conductivity and one for the product of the specific heat and density. The function then returns the 2-norm difference between the numerical calculation of the soil temperature and the actual data values of the soil temperature. We then apply the Nelder-Mead method to minimize *soilTemps*. The starting values were taken from Ramold (1996), who give a survey of the literature of acceptable values. The numerical solution to the inverse problem gave $K_s = 14.6$ and $c_{soil}\rho_{soil} = 3.8$. The thermal conductivity value is close to those for dry-sandy soil given in the literature (Buonanno et al., 1995; Ramold, 1996), but gives a higher value for the product of the specific heat and density than those given in the literature. However, we feel our solution is reasonable because the SCAN data includes bouts of moisture that are not included in our model; including moisture would cause the difficulty in modeling to increase. Buonanno et. al. (1995) lists thermal conductivities ranging from 14.4-21.6 $\frac{W}{cmC}$ and the product of the density and specific heat to be 1.121.36 $\frac{J}{cm^3C}$ for dry-sandy soil.

Table 2.1: Parameter values used in the model.

Parameter	Value
K_{soil}	14.6
K_{egg}	21.7875
$c_{soil}\rho_{soil}$	3.8
$c_{egg}\rho_{egg}$	1.7449

2.2 Degree Hour Model

Recall from section 1.2 that painted turtles have two thresholds for determining sex. Painted turtles produce exclusively males if the eggs are incubated between 22C and 28C. Eggs incubated at temperatures below 22C or above 28C produce females. However, if the temperature fluctuates about one of these thresholds, a mixed nest will be produced (Fig. 2.3) Gutzke and Paukstis (1984) Schwarzkpf and Brooks (1985). Schwarzkopf et. al. found that degree hours best predicted the sex of the nest Schwarzkopf and Brooks (1987). Thus, in our model, we determine the sex of each nest based upon the proportion of development achieved within each temperature range.





Figure 2.3: Temperature thresholds for each sex.

Let $d(\theta)$ be the development rate, given in degree-days per day, at temperature θ . Note that θ is a function of time t. Then, the total development, from time t = 0 to
$t = t^*$ is given by

$$\int_0^{t^*} d(\theta(t)) dt.$$

In our model we assume that the development rate is linear, and we use data from Cagle et al. (1993) and Gutzke et al. (1987) to parameterize the development function. Following the method in Shine and Harlow (1996), we divide the shortest incubation time, 41 days, by the incubation time for each temperature (Ta 2.2). We then calculate the least squares regression line with these points. Thus, the development function is

$$d(\theta) = \begin{cases} .05\theta - .6068 & 12.136 \le \theta \\ 0 & \theta < 12.136 \end{cases}$$

This line has an R^2 value of .9075.

Recall that the sex of the turtle is determined during the middle third of their development; this is referred to as the thermal sensitive period. To determine the thermal sensitive period, we determine the starting time,

 TSP_{begin} , and the ending time, TSP_{end} , of the middle third of the development period by solving

$$\int_{0}^{TSP_{begin}} d(\theta(t))dt = 0.\overline{33}$$

and

$$\int_{0}^{TSP_{end}} d(\theta(t))dt = 0.\overline{66}$$

for TSP_{begin} and TSP_{end} respectively.

We do this numerically by calculating the sum

$$\sum_{n=0}^{n^*} d(\theta(t_n)) \Delta t,$$

Temperature (C)	Incubation Period (days)	Development Rate
22	97.9	.4188
22	97.9	.4188
22	100	.41
23.4	72.3	.5671
23.6	68.7	.5968
23.6	65.4	.6269
23.9	66.9	.6129
24	68.8	.5959
24.7	60.6	.6766
24.8	56.3	.7282
26	57.8	.7093
26.2	61.1	.671
27	53.5	.7664
27	52.7	.778
27	51.4	.7977
32	45.4	.9031
32	42	.9762
32	41	1

Table 2.2: The incubation period is the number of days until pipping. Data from Gutzke et al. (1987) has temperature readings of 22, 27 and 32, all other readings are from Cagle et al. (1993).

where Δt is the time increment between time t_n and t_{n+1} , until we have reached one-third and two-thirds of the total development, respectively.

Next, we determine the proportion of development within each temperature range. Let $\Theta = [\theta_1, \theta_2]$ be a temperature interval and $\mathfrak{T} = [TSP_{begin}, TSP_{end}]$. Then, numerically, the total development achieved within that range is given by

$$\sum_{\{t \in \mathfrak{T}: \theta(t) \in \Theta\}} d(\theta(t)) \Delta t.$$

We then compare the total development in the female range, the male range, and the mixed range. The range that has the highest cumulative development gives the sex of the nest. Note that we are combining the total development in both female tem-

perature ranges together and the development in both of the mixed ranges together when determining the sex of the nest. If the largest proportion of development is in the male temperature range, the program deems that nest to be male and returns a 0 as the proportion of females. If the largest proportion of time is spent in the mixed range, the program returns 0.5 as the proportion of females in that nest, and if the proportion is in the female range, it returns a 1.

2.3 Two-Sex Model

We model the population dynamics of the system with a two-sex model. The reasons are two-fold. First, males reach maturity at a faster rate than females. Males reach maturity after one to five years, while females require five to nine years (Gibbons, 1968; Ernst et al., 1994). Second, besides being polyandrous, female turtles also can store the sperm of their mates (Pearse and Avise, 2001; Pearse et al., 2002). It has been shown they use this sperm even if they mate again the subsequent year, employing a "last in first out" fertilization scheme (Pearse and Avise, 2001; Pearse et al., 2002). That is, they use the most recent sperm first and then the stored sperm. In this population, it is possible that reproduction could be sperm limited if the temperature increase puts the population to be very female dominated. In Fig. 2.5, we plot the total number of eggs as a function of the number of adult males in the population with the number of adult females being held constant at 100 individuals. Notice that once the ratio of adult males to adult females is less than 1:2, the number of eggs declines dramatically. The ratio of adult males to adult females is generally 1:1, although skewed sex ratios of 1.36:1 (male dominate) and 1:1.39 (female dominate) have been reported (Ernst et al. (1994) p. 295).

The life cycle graph of the system is shown in Fig. 2.4. In this model, turtles



Figure 2.4: Two-sex model of a painted turtle population incremented yearly.



Figure 2.5: The number of eggs as a function of the number of males. Here the number of females is held at a constant 100 individuals.

are divided into five age classes. Because of the variability of the age at maturity, we could have done a stage structured model instead. However, according to Iverson et. al.(1993), "age and size at maturity are about equally variable" Iverson and Simith (1993). Because Painted turtles in northern climates reach maturity later than those in southern climates (Wilbur, 1975a; Iverson and Simith, 1993), we use the later ages for reaching adulthood. For males the classes are hatchlings (year 1), juveniles (years 2-3) and three adult stages, 4-5 years, 6-7 years and 8+ years. For females the classes are hatchlings (year 1), three juvenile classes, 2-3 years, 4-5 years and 6-7 years, and adults. Recall that in northern climates, the painted turtle eggs are laid from May to mid July and the turtles overwinter in the nests emerging in the spring, so we give them their own age class (Ernst et al., 1994).

We set s_i , i = 1, ..., 5 and g_i , i = 1, ..., 4 to be the survivorship and graduation rates respectively, and p is the proportion of eggs that are male. The annual survivorship of both males and females is similar within each age class (Mitchell, 1988; Tinkle et al., 1981; Heppell, 1998). Thus, we assume that the survivorship and graduation rates are the same for males and females within an age class. Note that s_1 and s_5 represent true annual survivorship rates, but s_2 , s_3 and s_4 are not true annual survivorship rates since the turtles remain in the age classes they represent for two years.

We define the variables E, eggs, H_m and H_f , male and female hatchlings, J_m , J_{f1} , J_{f2} , J_{f3} , male and female juveniles, A_{m1} , A_{m2} , A_{m3} , A_f , male and female adults. Each variable is a function of time. That is, $J_{f1}(n)$ is the number of female juveniles age 2-3 years at year n. From Fig. 2.4, we deduce the equations

$$H(n+1) = s_1 p E(n),$$

$$J(n+1) = s_2 J(n) + g_1 H(n),$$

$$A_{m1}(n+1) = s_3 A_{m1}(n) + g_2 J(n),$$

$$A_{m2}(n+1) = s_4 A_{m2}(n) + g_3 A_{m1}(n),$$

$$A_{m3}(n+1) = s_5 A_{m3}(n).$$

The female cycle is done similarly. In all, the equations can be written in matrix form as

Note that this matrix does not give the number of eggs at time n+1. This is because the number of eggs at time n is determined by the number of adults at time n and number females at time n-1. We deduce this equation later.

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Age Class	Tinkle et. al. (1981)	Mitchell (1988)	Wilbur (1975)	Model
Eggs and 1yr	0.67	0.19	0.08	.33
2-3 yrs	0.76	0.46	0.82	.6
4-7 yrs	0.76	0.94	0.82	.7
8+ yrs	0.76	0.96	0.82	.9

Table 2.3: True annual survivorships for both males and females found in literature and used in model.

We assume that the annual survivorship rates within each age class is the same for the male and female populations. This is consistent with findings in the literature (Tinkle et al., 1981; Wilbur, 1975a; Mitchell, 1988). The values chosen for each age class are shown in Ta. (2.3). There is much uncertainty in the annual survivorship for the egg and 1 year old range. This is mainly due to the difficulty in finding and capturing this age group because of how small they are. Thus, we chose 0.33 for the eggs and 1 year olds because it allows for the model to approach a stable state.

We determine the survivorship proportion and graduation rate for age classes that last for more than one year by using the method given in Crouse et al. (1987) and Caswell (2001). We assume that the proportion of individuals in their first year in the age class is 1 and let q be the probability of surviving one year. Note that for each two year age class, q is the model proportion given in Ta. 2.3. Then, the relative abundance of individuals is 1 + q. Hence, the proportion of individuals in the first year of the age class is $\frac{1}{1+q}$, and therefore the probability of surviving and remaining in the age class is $\frac{q}{1+q}$. The proportion of individuals in their second year is $\frac{q}{1+q}$, and so the graduation probability is $\frac{q^2}{1+q}$. The survivorship and graduation rates used in the model are shown in Ta. 2.3.

The number of eggs, E(n), is determined by a mating function. We let $a_m(n)$ represent the sum of all adult males at time n. We assume that the number of mating episodes is the harmonic mean of the number of adult males and adult fe-

Age Class	Survivorship	Graduation
Egg & 1yr	.33	.33
2-3 yrs.	.375	.225
4-5 yrs.	.4118	.2882
6-7 yrs.	.4118	.2882
8+ yrs.	.9	

Table 2.4: The survivorship proportion and graduation rate for both males and females used in the matrix model.

males. Although the harmonic mean was first used to model human populations, it has since been applied to several non-human populations (Sundelöf and Åberg, 2006; Ranta and Kaitala, 1999; Ranta et al., 1999; Lindström and Kokko, 1998; Engel et al., 2001). Thus, the total number of episodes is

$$\frac{2a_m(n)A_f(n)}{a_m(n) + A_f(n)}$$

We now adjust to include the average number of eggs laid by each female per year, k, and the number of females, h, mated with per male. We get the total number of eggs laid each year:

$$E(n) = \frac{2a_m(n)kA_f(n)}{a_m(n) + h^{-1}A_f(n)}$$

Finally, we let r be the probability of using the sperm from the current year n. Then 1-r is the probability of using the sperm from last year. Recall that we are assuming that females do not store sperm for more than one year. Thus, the total number of eggs is the number of eggs fertilized from the current year's sperm plus the number of eggs fertilized from the previous year's sperm; therefore,

$$E(n) = r \frac{2a_m(n)kA_f(n)}{a_m(n) + h^{-1}A_f(n)} + (1-r)\frac{2a_m(n-1)kA_f(n-1)s_5}{a_m(n-1) + h^{-1}A_f(n-1)s_5}.$$
 (2.13)

Note that we have multiplied only the total number of females by the survivorship probability because to produce eggs in the current year they must be alive, but males do not need to be alive in the current year to use their sperm from the previous year. Figure 2.5 shows a graph of the number of eggs as a function of the number of males in the population.

In turtles, where higher temperatures often favor female offspring, it has been speculated that higher temperatures favor the expression of the gene for the femaledetermining factor (Valenzuela and Lance, 2004; Janzen and Phillips, 2006; Murry, 2002). Further, in a warm nest, eggs develop faster (Gutzke et al., 1987; Cagle et al., 1993). For certain species this may mean that adult females are larger and can lay more eggs, and therefore have a higher fitness. Others speculate that it is density dependence that governs the sex ratio rather than individual fitness (Valenzuela and Lance, 2004; Janzen and Phillips, 2006; Murry, 2002). Temperature changes in the environment may lead to dynamics that favor one sex or the other in the birth function of a two-sex model. In different words, when the male population is low, there is an increase in contribution that males make in the birth function. For example, in the case here, the female may use stored sperm more frequently if the male population is small.

The model we develop in this dissertation does not take into account possible effects when the male population is small. However, it can be adapted to address some of the issues involving natural selection and density dependence. Conducting numerical simulations under various scenarios in a modified model may lead to a better understanding of the possible role of these influences. These are problems we point to for further study and analysis (2).

In summary, we use a two-sex model because the males and females have different maturity rates and the females store sperm from one year to the next. The yearly dynamics are determined by the matrix 2.12 and the egg equation 2.13. Each year, we first calculate the number of hatchlings, juveniles and adults and then we calculate the total number of eggs laid.

2.4 Stochastic Air Temperature Model

We generate stochastically the daily ambient temperature profile following the method given in Logan and Wolesensky (2007). The temperature profile, $\theta_y(t)$, for each Julian day, y, is given by the sinusoidal curve

$$\theta_y(t) = \Theta_y - \phi_y \cos\left(\frac{\pi}{12}(4-t)\right),$$

where $0 \le t < 24$. Here Θ_y is the stochastic average daily temperature and ϕ_y is the stochastic daily amplitude. The average daily temperature is given by

$$\theta_{avg}(y) = Y_{avg} - Y_{amp} \cos\left(\frac{2\pi}{365}(35-y)\right)$$

where Y_{avg} is the yearly average temperature and Y_{amp} is the yearly average amplitude and y is the Julian day of the year. Then, the stochastic daily temperature is given by the autoregression

$$\Theta_{y+1} = \theta_{avg}(y) + Y_{cor}(\Theta_y - \theta_{avg}(y)) + \sigma_y \sqrt{1 - Y_{cor}^2} Z$$

where Y_{cor} is the autocorrelation of the current day's temperature with the previous day's temperature, σ_y the standard deviation of the temperature and Z a normal random variable with mean 0 and standard deviation 1.



Figure 2.6: A sample 20 day run of the temperature program.

The temperature amplitude for each day is determined by

$$\phi_{y+1} = Y_{amp} + \Phi_{cor}(\phi(y) - Y_{amp}) + \sigma_{\phi}\sqrt{1 - \Phi_{cor}^2}Z$$

where Φ_{cor} is the autocorrelation of the current day's amplitude with the previous day's amplitude and σ_{ϕ} is the standard deviation of the amplitude.

The baseline values used for the temperature profile are:

$$Y_{avg} = 10, \ Y_{amp} = 13.5, \ Y_{cor} = .9, \ \sigma_y = 4.4, \ \Phi_{cor} = .9, \ \sigma_{\phi} = 4.4.$$

A sample of a temperature run is shown in Fig. 2.6.

2.5 Stochastic Solar Radiation Model

We use average monthly data from the National Renewable Energy Laboratory (web, c) to calculate the daily solar radiation. We assume that the solar radiation is zero between the hours of 8:00p.m. and 6:00 a.m.. We also assume that the most intense rays occur at 2:00p.m.. We assume that the daily solar radiation is given by a piecewise cubic equation

$$W(t) = \begin{cases} 0, & 0 \le t \le 6 \text{ and } 18 \le t < 24 \\ At^3 + Bt^2 + Ct + D & 6 \le t \le 18 \end{cases}$$

For each Julian day, y, we choose a value, r_y , from a uniform distribution between 0 and 0.8 to be the maximum solar radiation given in W/cm^2 , where 0.8 comes from the solar radiation data for Nebraska, web (c). Because W(t) must pass through the points, (6,0), (14, r_y) and (20,0) and since (14, r_y) is a local maximum, we are able to solve for the coefficients of the cubic equation uniquely. Note that in our model, we have not correlated the daily temperature to the solar radiation to simplify our calculations. A sample of 20 days of a solar radiation run is shown in Fig. 2.7.

2.6 Computational Model

We combine the models in the previous sections together to examine the dynamics in the turtle population based upon various changes in the temperature profile. A flow chart of this process is shown in Fig. 2.6.

Each year, we determine the temperature and solar radiation profiles. We choose a first nesting date for each female from a truncated-normal random distribution, with mean June 1 and standard deviation of 7 days. The distribution is truncated at



Figure 2.7: A sample 20 day run of the solar radiation program.

May 1 and June 30. These dates are those given in Iverson and Simith (1993) and similar to those given in Rowe et al. (2003). According to Iverson et. al. (1993), the second nest occurs, on average, 16 days after the first nest. Thus, we assume that the turtle lays a second nest 16 days after her first nest. Next, we calculate the temperature profile inside the nest for each nesting episode. Once we have determined the temperature profile inside the nest, we then use the degree hour model to find the sex of each nest. We then calculate the overall sex ratio for the eggs that year by averaging the outcomes of each nest. We finally update the population projection model.

We repeat this process for a period of thirty years, and observe the outcome of



Figure 2.8: A flow chart of the computational model's yearly process.

the population vector. We repeat this process for 50 total runs for each change in the temperature model. After the baseline runs, we increase the average temperature by $2^{\circ}C$ and then $4^{\circ}C$. We also observed the change in the dynamics when we change the daily amplitude variation. We chose to observe the effects of changing average temperature and daily amplitude because Shine and Harlow (Shine and Harlow, 1996) found that both the mean temperature and the variance of temperature influenced the development rates and thus incubation periods of skinks (*Bassiana duperreyi*).

Chapter 3

Results

3.1 Numerical Solution of the Nest Temperature Model

In this first section we examine the diffusion problem and demonstrate the comparison between the numerical solution for the temperature in the nest and experimental data. We simulated the model using as input the SCAN data gathered from Roger's farm web (b) for the surface boundary condition. We then compared the calculated result using the diffusion model at 10cm below the surface to the data taken with temperature sensors from the farm. Because the data from Roger's farm does not include a nest, we assumed that the nest in the numerical simulation began and ended at the same depth of 9.14m. Both experimental and computed temperature profiles are shown in Fig. 3.1. Overall, the numerical solution closely approximates the experimental temperature profile. However, when there are large changes in the surface temperature, the numerical solution seems to slightly exaggerate these changes. Episodes of rain are not included in the numerical model, which may also



explain some of the differences in the two profiles.

Figure 3.1: Actual temperature data taken from Roger's Farm compared to the numerical approximation at 10 cm below the surface.

In summary, the numerical solution provides a good approximation to the actual experimental temperature profile. While we have not shown the convergence of the numerical scheme, the accuracy is good evidence that the numerical solution converges to the unique solution.

3.2 Parameter Sensitivity

Next we test the parameter sensitivity of the nest temperature model by adjusting each parameter individually and comparing the resultant temperature profiles with that of the baseline profile. In the baseline simulation, we set the ambient air temperature at $10\cos(\pi t/12) + 25$ and we assume that the solar radiation is 0. Choosing these values, rather than a more random input, allows us to discern the effects of each parameter with a minimum of computation. The baseline parameter values are

Parameter	Value
K_{soil}	14.6 $\frac{W}{cmhC}$
K_{egg}	$21.7875 \ \frac{W}{cmhC}$
$c_{soil} \rho_{soil}$	$3.8 \frac{\mathrm{J}}{\mathrm{cm}^{3}\mathrm{C}}$
$c_{egg} ho_{egg}$	$1.7449 \ \frac{\mathrm{J}}{\mathrm{cm}^{3}\mathrm{C}}$

Table 3.1: Parameter values used in the nest temperature baseline simulation.

shown in Ta. 3.1.

• Soil Thermal Conductivity

For soil conductivity we ran the model with K_s values between 9.3191 and 59.3191 $\frac{W}{\text{cmhC}}$, incrementing by 5 each on each run. These values are within the typical range of soil thermal conductivities (Buonanno et al., 1995). All simulations produced temperatures within 3.2918°C of the baseline temperature. Plots of these solutions are shown in Fig. 3.2. As expected, the higher the thermal conductivity of the soil, the greater the amplitude of the temperature.

• Egg Layer Thermal Conductivity

For the egg layer's thermal conductivity, we considered test values between 50% above and below the baseline value. All simulations produced temperatures within 0.1914°C of the baseline value (Fig. 3.3).

• Egg Versus Air Ratio



Figure 3.2: Temperature profiles for different soil thermal conductivities.



Figure 3.3: Temperature profiles for the egg layer thermal conductivity.

Next, we increment the ratio between egg and air ratio in the egg layer. We consider values between 15% and 75% incrementing by 5%. The simulations produced temperatures within 0.2821° C of the baseline (Fig. 3.4).

• Density and Specific Heat in Soil Layer

The product of density and specific heat in the soil layer was incremented be-



Figure 3.4: Temperature profiles for the egg versus air ratio.

tween 50% above and below the baseline value. Temperature profiles were all within 0.7365° C of the baseline run (Fig. 3.5).



Figure 3.5: Temperature profiles for the product of the density and specific heat in the soil layer.

• Density and Specific Heat in Egg Layer

Within the egg layer, the values for the product of the density and specific



Figure 3.6: Temperature profiles for the product of the density and specific heat in the egg layer.

heat were incremented between 50% below and above the baseline value. All simulations produce temperatures within 0.0983°C of the baseline value (Fig. 3.6).

• Heat Transfer Coefficient

The heat transfer coefficient is perhaps the most uncertain parameter in the model, and it is often difficult to determine in heat transfer models. To examine sensitivity, values of the heat transfer coefficient were taken between 5 and 30 $(ds \frac{J}{cm^2hC})$, incrementing by 5. The temperature profiles differs from the baseline profile by at most 1.1425°C which occurred using the smallest value, 5 (Fig. 3.7).

We now examine the sensitivity of the parameters in our two-sex model. Recall that the matrix is not a Leslie matrix and that the egg population equation is nonlinear with a two-year recurrence relation; therefore, the population growth rate is not know a priori. Hence, to examine the sensitivity of the parameters in the two-sex model, we adjust each parameter individually, calculate the geometric mean of the year-to-year



Figure 3.7: Temperature profiles for the heat transfer coefficient.

Table 3.2: Parameter values in the two-sex model baseline run.

Parameter	Value
s_1 and g_1	.33
s_2	.375
g_2	.225
s_3 and s_4	.4118
g_3 and g_4	.2882
s_5	.9
p	.5
q	.7
k	14
h	1.7

growth rate, and then compare the results to the baseline run. The baseline values are shown in Ta. 3.2. We adjust each parameter within biologically measured values (Ta. 3.3).

The baseline simulation is shown in Fig. 3.8. In the baseline plot, although it appears at first that the population is rapidly increasing (because of the scale), it is actually remaining nearly constant with an average growth rate of 1.0012. The female population only increases by about 40 individuals and the egg population only

Table 3.3: Biologically measured values for each two-sex model parameter

Parameter	Tinkle et. al. (1981)	Mitchell (1988)	Wilbur (1975)
s_1 and g_1	0.67	0.19	0.08
s_2 and g_2	0.76	0.46	0.82
s_3, s_4, g_3 and g_4	0.76	0.94	0.82
S_5	0.76	0.96	0.82



Figure 3.8: Two-sex model baseline run.

increases by 100 eggs. Note that, because we are using 0.5 as the proportion of males, the male and female populations will be the same; so, we only show the plot of the female population.

• Egg Survivorship and Hatchling Graduation

We adjust both the annual egg survivorship, s_1 , and hatchling graduation rates, g_1 , between 0.06 and 0.6 incrementing by 0.06. The growth rates for egg survivorship are shown in Ta. 3.4, and the growth rates for hatchling graduation are shown in Ta. 3.5.

• Survivorship and Graduation Rates for 2-3 Year-olds

Egg Survivorship	Growth Rate
.06	0.9179
.12	0.9425
.18	0.9625
.24	0.9795
.30	0.9944
.36	1.0077
.42	1.0197
.48	1.0308
.54	1.0410
.6	1.0506

Table 3.4: Egg survivorship growth rates.

Table 3.5: Hatchling graduation growth rates.

Hatchling Graduation Rate	Growth Rate
.06	0.9236
.12	0.9462
.18	0.9648
.24	0.9808
.30	0.9948
.36	1.0073
.42	1.0187
.48	1.0291
.54	1.0387
.6	1.0477

The annual survivorship and graduation rates in the 2-3 year age class were examined within the interval 0.46 to 0.82, incrementing by 0.04. We adjusted for the 2 year time period as described in section 2.3. The growth rates ranged from 0.995 to 1.0102 (Ta. 3.6). The growth rates for the graduation are given in Ta. 3.7.

• Survivorship and Graduation Sensitivity for 4-5 and 6-7 Year-olds

The annual survivorship and graduation rates for the 4-5 and 6-7 year age classes were examined within an interval 0.76 to 0.92, incrementing by 0.04,

Yearly Survivorship	Growth Rate
.46	0.9950
.50	0.9968
.54	0.9986
.58	1.0004
.62	1.0021
.66	1.0038
.7	1.0054
.74	1.0070
.78	1.0086
.82	1.0102

Table 3.6: 2-3 year olds survivorship growth rates.

Table 3.7: 2-3 year olds graduation growth rates

Yearly Survivorship	Growth Rate
.46	0.9753
.5	0.9830
.54	0.9904
.58	0.9977
.62	1.0047
.66	1.0116
.7	1.0183
.74	1.0248
.78	1.0311
.82	1.0373

again adjusting for the two year time period as described in section 2.3. The growth rates are shown in Tables 3.8, 3.9, 3.10 and 3.11.

• 8+ Year-Old Survivorship Sensitivity

The annual survivorship rates for the 8+ year age classes were examined within the interval 0.76 to 0.96, incrementing by 0.04. The growth rates are given in Ta. 3.12.

• Probability of Using Current Year's Sperm Sensitivity

Table 3.8: 4-5 year olds survivorship growth rates.

Yearly Survivorship	Growth Rate
.76	1.0035
.80	1.0050
.84	1.0064
.88	1.0078
.92	1.0092

Table 3.9: 4-5 year olds graduation growth rates.

Yearly Survivorship	Growth Rate
.76	1.0093
.80	1.0146
.84	1.0196
.88	1.0246
.92	1.0294

Table 3.10: 6-7 year olds survivorship growth rates.

Yearly Survivorship	Growth Rate
.76	1.0033
.80	1.0047
.84	1.0061
.88	1.0074
.92	1.0087

Table 3.11: 6-7 year olds survivorship growth rates.

Yearly Survivorship	Growth Rate
.76	1.0091
.80	1.0141
.84	1.0190
.88	1.0238
.92	1.0284
I	

Growth Rate
0.9364
0.9610
0.9865
1.0127
1.0398
1.0677

Table 3.12: 8+ years survivorship growth rate.

Table 3.13: Probability of using current year's sperm growth rates.

Probability of Using Current Year's Sperm	Growth Rate
.1	1.0003
.2	1.0005
.3	1.0006
.4	1.0008
.5	1.0009
.6	1.0011
.7	1.0012
.8	1.0014
.9	1.0015
1	1.0017
	-

We adjusted the probability of using the current year's sperm between 10% and 100% incrementing by 10%. The growth rates vary from 1.0003 to 1.0017 (Ta. 3.13).

• Total Eggs Laid Per Female Sensitivity

The total eggs laid per female per year is examined for 6 to 24 eggs. The growth rates vary between 0.9506 and 1.0447 (Ta. 3.14).

• Number of Females Mated With Per Male Sensitivity

We examine the average number of females mated with per male for values between 1.2 to 3 incrementing by 0.2. The growth rates range between 0.9954 and 1.0077 (Ta. 3.15).

Total Eggs Laid	Growth Rate
6	0.9506
8	0.9655
10	0.9787
12	0.9905
14	1.0012
16	1.0111
18	1.0203
20	1.0289
22	1.0370
24	1.0447
	•

Table 3.14: Total eggs laid sensitivity growth rates.

Table 3.15: Number of females mated with per male sensitivity growth rates

Females per Male	Growth Rate
1.2	0.9954
1.4	0.9982
1.6	1.0003
1.8	1.0020
2.0	1.0034
2.2	1.0046
2.4	1.0056
2.6	1.0064
2.8	1.0071
3.0	1.0077

• Proportion of Male Eggs

We look at the proportion of male eggs in the range of 20% to 80% incrementing by 10%. The growth rates varied from 0.9656 to 1.0078 (Ta. 3.16). We have included the graph of the population curves for this case (Fig. 3.9). Notice in this case that as the proportion of male eggs increases, the male population acutally decreases. This is due to the fact that the total number of eggs depends upon the number of females as well as the number of males. The fewer females there are to lay eggs, the fewer males there will be in the long term.



Figure 3.9: Two-sex model proportion of male eggs sensitivity.

Proportion of Males	Growth Rate
0.2	1.0010
0.3	1.0078
0.4	1.0067
0.5	1.0012
0.6	0.9925
0.7	0.9808
0.8	0.9656
	1

Table 3.16: Proportion of male eggs sensitivity growth rates.

To further complete our analysis, we look at the population growth rates when we parameterize the model using each set of data individually (Wilbur, 1975a; Tinkle et al., 1981; Mitchell, 1988). These values are given in Ta. 3.3. In the cases of Tinkle et. al. (1981) and Mitchell (1988), the population is increasing with growth rates of 1.1597 and 1.0074 respectively. In contrast, using the values given in Wilbur (1975), the population is decreasing with a growth rate of 0.8628.

3.3 Model Results

Now we examine the behavior of the population under nine different scenarios. In the baseline run, the average year temperature is 10°C and the average year amplitude is 13.75°C. In the remaining scenarios, we increase the average temperature and amplitude by $2^{\circ}C$ and $4^{\circ}C$, and for each average temperature, we increase the amplitude by 0, 2, and 4°C. We denote each scenario by the temperature followed by the amplitude increase from the baseline run. For example, T4A2 has the average year temperature 4°C above the baseline temperature and the average year amplitude 2°C above the baseline amplitude. Recall that for each scenario, we observe the population dynamics over a period of thirty years and make 50 total observations. In each scenario, we assume that the mean of the data for each year is normally distributed. We feel that this is an appropriate assumption because the median and the mean for each year within a scenario were approximately the same, differing at most by 43.24 individuals (in T4A4 year 19) and on average differing by fewer than 14 individuals. For each scenario, two plots are shown. The first shows the total sample average (not including the eggs) of the 50 runs as a solid line along with dotted lines showing two sample standard deviations away from the sample mean. The second shows the average male and average female population profiles. The male population is shown with a dashed line and the female population is shown with a solid line. One should note that the first few years for each run look similar because it takes 5 years for the temperature variations to affect the whole population. As with the sensitivity profiles, we compute the growth rate for the total population average by calculating the geometric mean of the year-to-year growth rate. The growth rates are shown in table 3.17.



Figure 3.10: Population profile for the baseline scenario (T0A0).



Figure 3.11: Population profile for average yearly temperature 10° C and average yearly amplitude 15.75° C (T0A2).

Scenario	Growth Rate
T0A0	0.99943
T0A2	0.99205
T0A4	0.99569
T2A0	0.98836
T2A2	0.99544
T2A4	1.00039
T4A0	0.99299
T4A2	1.00019
T4A4	0.97942

Table 3.17: The mean growth rate for each scenario.

1 -



Figure 3.12: Population profile for average yearly temperature 10° C and average yearly amplitude 17.75° C (T0A4).



Figure 3.13: Population profile for average yearly temperature 12°C and average yearly amplitude 13.75°C (T2A0).



Figure 3.14: Population profile for average yearly temperature 12°C and average yearly amplitude 15.75°C (T2A2).



Figure 3.15: Population profile for average yearly temperature $12^{\circ}C$ and average yearly amplitude $17.75^{\circ}C$ (T2A4).



Figure 3.16: Population profile for average yearly temperature 14°C and average yearly amplitude 13.75°C (T4A0).



Figure 3.17: Population profile for average yearly temperature 14°C and average yearly amplitude 15.75°C (T4A2).



Figure 3.18: Population profile for average yearly temperature $14^{\circ}C$ and average yearly amplitude $17.75^{\circ}C$ (T4A4).

Chapter 4

Discussion

4.1 Conclusions

Finally, we discuss the implications of the sensitivity analysis and computational model cases. From the analysis of the nest temperature model, we find that it is most sensitive to the change in the thermal conductivity of the soil (Fig. 3.2) and the heat transfer coefficient (Fig. 3.7). It follows from the fact that these two parameters have the greatest impact on the nest temperature because these parameters greatly affect the rate at which the heat is transfered through the soil to the nest. We expected that the model would be sensitive to the ratio of air-to-egg thermal conductivity (Fig. 3.4) inside the egg layer because of the very low thermal conductivity of air, however the model showed only a change of at most 0.2821°C from the baseline run.

In the two-sex model the parameters most sensitive to change were the total eggs laid, k (Ta. 3.14), adult survivorship, s_5 (Ta. 3.12), egg survivorship, s_1 (Ta. 3.4) and hatchling graduation rate, g_1 (Ta. 3.5). We also observe that in the analysis done using each set of data (Wilbur (1975a), Tinkle et al. (1981), Mitchell (1988)) separately (3.2), that the egg survivorship and hatchling graduation rates seem to strongly influence the survival of the population because they are the only rates that differ significantly among the data sets.

Next, we can make three important observations about the behavior of the computational model (Figs: 3.10-3.12):

- 1. As the male population increases or decreases, the female population decreases or increases the exact same amount respectively. The reason for this is an artifact of the model. Each year the proportion of males is determined from the nest temperature profile; then, as this proportion increases, the proportion of females decreases. Hence, we would expect to see similar trends in real data.
- 2. The first five years' output is similar in all cases because it takes five iterations for the effects of the varying temperature profiles to transfer through all five age classes.
- 3. Even in the most severe case (T4A4), the population growth rate is very close to one; this may explain the buffering of temperature effects and why the species has survived so long.

We now turn our attention to the individual cases. Observe that in our baseline run (T0A0 Fig. 3.10), the growth rate is essentially one. Perturbations from the steady state cause the population to return to the steady state. Hence, if the temperature trajectory remains at its current levels, the painted turtle population will continue in its steady state.

In contrast to Janzen (1994), our model requires not just an increase of 4°C, but also an increase in temperature variance of 4°C. The case T4A4 is the only case where we suggest there is a good possibility of extinction (Fig. 3.18). In this case, approximately 95% of the runs were at or below the steady state. The growth rate for
T4A4 is 0.97942. Neither the cases of T4A0 or T4A2 (Figs. 3.16 and 3.17), produced a growth rate small enough to consider it significant. Infact, the case of T4A2 has growth rate above one (1.00019).

4.2 Future Directions

There are several problems that may be the focus of further investigation:

1. Variable thermal conductivity with soil moisture

In the model herein the effects of variable soil moisture were not included, nor were rain events. The moisture content of the soil changes the thermal conductivity of the soil (Buonanno et al., 1995) as well as the development time of the eggs (Ackerman et al., 1985a). Thus, the effects of moisture may play a role in the population dynamics of the painted turtles.

2. Variable sperm storage

Several questions concerning sperm storage remain unanswered at this time because there is little information or data concerning the storage of sperm. We do not know if the sperm becomes less viable over time or if the use of stored sperm is greater if the population is male limited. We tested the second hypothesis crudely by assuming that the proportion of stored sperm usage is large when the male population is small. We adjusted our two-sex model such that the proportion of sperm used from the current year is a function of the male population. That is,

$$q(m_n) = 1/(1 + e^{-10(\frac{m}{200} - .5)}),$$

where m_n is the number of males in year n. Because there is no data available, we chose a function that satisfies two criteria; first, it is an increasing function with range [0, 1] and second, we require that it give an output of approximately 0.7 at the baseline steady state.

In this scenario, to cause a population to crash, we need to resort to extreme cases. The proportion of males in the starting population needs to be less than 30% and the percentage of males from each clutch must be less than 20%. In the case where the starting male to female ratio is 30 : 70 and the percentage of males from each clutch is 10%, the average growth rate of the male population is 0.96665 and the average growth rate of the female population is 0.98018.

We also examined what would happen if there were no sperm storage. Using the same starting ratios as above (male to female ratio of 30 : 70 and the percentage of males from each clutch being 10%), we have that the average growth rate of the male population is 0.96333 and the female average growth rate is 0.97687. Thus the computational model supports the hypothesis that there is an adaptive advantage to sperm storage.

In these test simulations we ignored the survivorship of the eggs as accounting for the possibility of less viability in the older sperm. Much more experimental research in this area is needed to provide accurate models of population dynamics.

3. Variable absorption of solar radiation

We assumed that the nest was on flat ground and the soil absorbed 80% of the solar radiation. We could make our model more realistic by assuming that the ground is not flat, that the soil has more reflective properties, or the nest is shaded. Either of these cases would change the absorption coefficient. We could also assume variations for each nest in the multiple simulations.

4. Nest geometry, metabolic heat and clutch size

In our model, we assumed that the soil inside and outside the nest had the same porosity and that the heat traveling horizontally between the nest and the surrounding soil does not affect the temperature of the nest. Thus, for example, we could change the geometry of the nest to be a bounded cylinder and then perform the calculations; however, the determination of heat flow in three dimensions, and time, would be computationally intensive.

If we take into account the metabolic heat generated by the eggs, which is a source term in the diffusion equation, the temperature inside the nest would be affected. As we noted earlier, the nest temperature in this case is more likely to be effected when the clutch size is larger. Also, we may want to consider that the sex of the turtle eggs depend upon not only the depth of the egg, but also upon the location within the nest. The eggs near the center may be warmer than those on the outer edges.

5. Different birth function

We have chosen a birth function given by a harmonic mean. Equally, we could investigate the affects of using a different birth function on population growth. We would be interested to see if this change causes a significant difference in the results.

6. Female choice in nest site and nesting time selection

In all of the cases, we assume that the female does not consider the sex of her offspring when choosing her nesting site and that the mean date of first nest is June 1. It is hypothesized that if the average temperature shifts that the females may be able to nest earlier or later in the season or that they may choose different nesting sites to compensate for the thermal shift and thus maintain the current nest temperature conditions (Valenzuela and Lance, 2004).

Finally, because of its flexibility, the model we present in this dissertation can also be of great benefit to other researchers in the field who want to examine the effects of different temperatures and their variations on other species with TSD, e.g., crocodilians, as well as other turtle species. For example, the temperature, solar radiation, and conductivity are inputs into the model, and they can be adapted to specialized environmental conditions, including temperature levels, nest location, soil type, and rain events. The TSD model easily accommodates different temperature ranges that apply to other species during their egg incubation period. The model also offers the opportunity to study density effects, for example, the dependence of the mating function on the ratio of males to females and each's contribution to the sex of the hatchlings. Other modifications of the two-sex population model are possible as well, in order to fit the species life history traits. The model is a beginning step in understanding the long term high fitness shown by many species with TSD.

Appendix A

Parameter Descriptions

Parameter	Description	Units
A	cross-sectional area	cm^2
a	depth	cm
b	depth	cm
C_e	specific heat egg layer	$\frac{J}{kaC}$
C_S	specific heat soil layer	$\frac{J}{kaC}$
h	heat transfer coefficient	$\frac{J}{cm^2hC}$
K_e	thermal conductivity egg layer	$\frac{W}{cmhC}$
K_s	thermal conductivity soil layer	$\frac{W}{cmhC}$
L	depth	cm
α	heat absorption proportion	
$ ho_e$	density egg layer	$\frac{kg}{cm^3}$
ρ_s	density soil layer	$\frac{kg}{cm^3}$

Table A.1: Diffusion Equation and Boundary Conditions

Parameter/Function	Description
d(heta)	development rate function
heta(t)	temperature function
TSP_{begin}	beginning of thermal sensitive period
TSP_{end}	end of thermal sensitive period

Table A.2: Degree Hour Model

Parameter	Description
A_f	adult females
A_{m1}	adult males 4-5 years
A_{m2}	adult males 6-7 years
A_{m3}	adult males 8+ years
$a_m(n)$	total number of males in year n
E	eggs
g_i	graduation proportion
H_m	male hatchlings
H_f	female hatchlings
h	number of females mated with per male
J_{f1}	juvenile females 2-3 years
J_{f2}	juvenile females 4-5 years
J_{f3}	juvenile females 6-7 years
J_m	juvenile males
k	number of eggs laid by a female
p	proportion male
s_i	survivorship proportion
	Table A.3: Two-Sex Model

Parameter/Function	Description
Y_{amp}	yearly average amplitude
Y_{avg}	yearly average temperature
Y_{cor}	temperature autocorrelation
Z	normal random variable
Φ_{cor}	amplitude autocorrelation
ϕ_y	stochastic daily amplitude
σ_y	temperature standard deviation
σ_{ϕ}	amplitude standard deviation
Θ_y	stochastic daily temperature average
$\theta_{avg}(y)$	average daily temperature
$\theta_y(t)$	temperature profile on day y

 Table A.4: Stochastic Temperature

Appendix B

Programs

B.1 Nest Temperature Model

%This program calculates the temperature at requested depth given the %surface temperature and solar radiation. This function solves the %one dimensional case of Ut=KUzz z>0 U(0,t)+aUz(0,t)=h(t) where K %depends upon depth using an implicit scheme. It takes as imput the %surface temperature,solar radiation and the depth inside the nest one %wants the temperature profile of.

function nestTemp=nestTemperature(surfaceTemp, solarRad,NestDepth,day2start,startValue)

Pair=.4; %volume percentage for the air in the egg layer Pegg=.6; %volume percentage for the eggs in the egg layer ThermAir= .9252; %thermal conductivity of air ThermEgg=21.5424;%thermal conductivity of the eggs %calculate effective thermal conductivity of the egg layer Kegg=(Pair*(2*ThermAir-ThermEgg)+Pegg*(2*ThermEgg-ThermAir) +sqrt((Pair*(2*ThermAir-ThermEgg)+Pegg*(2*ThermEgg-ThermAir)) ^2+8*ThermAir*ThermEgg))/4; %effective thermal conductivity of egg layer

Ksoil=14.6; %thermal conductivity of soil layer cegg=Pegg*4181.8+Pair*1005; %specific heat of egg layer cRhoSoil=3.8; %specific heat times density of soil rhoEgg=Pegg*.00099821+Pair*.000001205; %density of egg layer cRhoEgg=cegg*rhoEgg;

h=30; %heat transfer coefficient
alpha=.8; %percent of solar radiation abosrbed.
ke=Kegg/(cRhoEgg); %diffusivity of egg layer
ks=Ksoil/cRhoSoil; %diffusivity of soil layers

deltaT=.25; %change in time (hours) deltaX=.5; %change in space N=length(surfaceTemp); %number of time steps after start T=deltaT*N; %number of hours total depth=101;%915; %total depth in centimeters depthS2E=6; %depth (cm) at which ks changes to ke depthE2S=10; %depth (cm) at which ke changes back to ks

```
beta=Ksoil/(2*h*deltaX);
```

```
rS=ks*deltaT/(deltaX^2);
```

```
rE=ke*deltaT/(deltaX^2);
```

J=1+depth/deltaX; %number of total space steps
JE=1+floor(depthS2E/deltaX); %space step where ks changes to ke
JS=1+floor(depthE2S/deltaX); %space step where ke changes back to ks
U=25*ones(J,N);

U(:,1)=startValue;%initial condition

t=[0:deltaT:T];

Uamb=surfaceTemp; %temperature profile on surface

W=solarRad;%.001*cos(pi.*t./12); %solar energy on surface

```
g=(rS/beta).*(Uamb+(alpha/h).*W);
```

```
%iii=fortyTemp(day2start,N/96);
```

```
%size(iii)
```

```
%size(U(J,:))
```

U(J,:)=fortyTemp(day2start,N/96);%15; %boundry condition at depth

```
A(ii,ii-1)=-rS;
```

```
A(ii,ii+1)=-rS;
```

 end

A(JE,JE-1)=Ksoil;

A(JE,JE)=-(Ksoil+Kegg);

A(JE,JE+1)=Kegg;

for ii=JE+1:JS-1

A(ii,ii)=1+2*rE;

A(ii,ii-1)=-rE;

A(ii,ii+1)=-rE;

end

A(JS,JS-1)=Kegg;

```
A(JS,JS)=-(Kegg+Ksoil);
```

A(JS,JS+1)=Ksoil;

for ii=JS+1:J-2

A(ii,ii)=1+2*rS;

```
A(ii,ii-1)=-rS;
```

A(ii,ii+1)=-rS;

end

```
A(J-1,J-1)=1+2*rS;
```

A(J-1, J-2) = -rS;

for n=2:N

```
f=U(1:J-1,n-1);
f(1)=f(1)+g(n);
%f(1)=f(1)+rS*g(n);
%f(1)=f(1);
f(J-1)=f(J-1)+rS*U(J,n);
f(JE)=0;
f(JS)=0;
U(1:J-1,n)=A\f;
```

 end

```
nestTemp=U(1+floor(NestDepth/deltaX),:);
```

B.2 Inverse Program

%This solves the inverse problem for K and k in the soil temperature %profile.

```
function inverseSoilProbMess
clear all
tic
global AirTemp
global Solar07
global Two
global Four
global Eight
```

global Twenty

global Forty

load AirTemp

load Solar07

load Two

load Four

load Eight

load Twenty

load Forty

global dataVec

global h

global alpha

global deltaT

global deltaX

global depth

global depthS2E

global depthE2S

dataVec=[Two; Four; Eight; Twenty; Forty]; h=30; %heat transfer coefficient alpha=.8; %percent of solar radiation abosrbed. deltaT=1; %change in time (hours) deltaX=.5; %change in space depth=915; %total depth in centimeters
depthS2E=914; %depth at which ks changes to ke
depthE2S=914; %depth at which ke changes back to ks

```
yy=[14.4,3.6];
theNorm=soilTemps(yy)
toc
end
```

%%%%%%%	///////////////////////////////////////	soilTemps	°/°/°/°/°/°/°/°/°/°/°/°/°/°/°/°/°/°/°/
function	on vecNorm=soil	lTemps(yy)	
global	AirTemp		
global	Solar07		
global	dataVec		
global	h		
global	alpha		
global	deltaT		
global	deltaX		
global	depth		
global	depthS2E		
global	depthE2S		
Ksoil=	yy(1);		

```
cRhoSoil=yy(2);
Kegg=Ksoil;
cRhoEgg=cRhoSoil;%cegg*rhoEgg
```

ke=Kegg/(cRhoEgg); %diffusivity of egg layer
ks=Ksoil/cRhoSoil; %diffusivity of soil layers

N=length(AirTemp); %number of time steps after start T=deltaT*N; %number of hours total

```
beta=Ksoil/(2*h*deltaX);
```

```
rS=ks*deltaT/(deltaX^2);
```

```
rE=ke*deltaT/(deltaX^2);
```

```
J=1+depth/deltaX; %number of total space steps
JE=1+floor(depthS2E/deltaX); %space step where ks changes to ke
JS=1+floor(depthE2S/deltaX); %space step where ke changes back to ks
```

```
U=AirTemp(1)*ones(J,N+1);%initial condition
t=[0:deltaT:T];
Uamb=AirTemp; %temperature profile on surface
W=Solar07;%.001*cos(pi.*t./12); %solar energy on surface
g=(rS/beta).*(Uamb+(alpha/h).*W);
U(J,:)=11.7; %boundry condition at depth
```

```
%Initialize matrix "A"
```

```
A=zeros(J-1,J-1);
```

```
A(1,1)=1+2*rS+(rS/beta);
```

```
A(1,2)=-2*rS;
```

```
for ii=2:JE-1
```

```
A(ii,ii)=1+2*rS;
```

```
A(ii,ii-1)=-rS;
```

```
A(ii,ii+1)=-rS;
```

end

```
A(JE,JE-1)=Ksoil;
```

```
A(JE,JE)=-(Ksoil+Kegg);
```

```
A(JE,JE+1)=Kegg;
```

```
for ii=JE+1:JS-1
```

```
A(ii,ii)=1+2*rE;
A(ii,ii-1)=-rE;
A(ii,ii+1)=-rE;
```

end

```
A(JS,JS-1)=Kegg;
```

```
A(JS,JS)=-(Kegg+Ksoil);
```

```
A(JS,JS+1)=Ksoil;
```

```
for ii=JS+1:J-2
```

```
A(ii,ii)=1+2*rS;
A(ii,ii-1)=-rS;
```

```
A(J-1,J-1)=1+2*rS;
A(J-1,J-2)=-rS;
```

```
for n=2:N
```

```
f=U(1:J-1,n-1);
f(1)=f(1)+g(n);
%f(1)=f(1)+rS*g(n);
%f(1)=f(1);
f(J-1)=f(J-1)+rS*U(J,n);
f(JE)=0;
f(JS)=0;
U(1:J-1,n)=A\f;
end
```

```
vector=(Uvec-dataVec);
vecNorm=norm(vector,inf);
end
```

B.3 Degree Hour Model

 $\% This \ensuremath{\text{This}}$ program calculates the total degree hours accumulated

%within each class: [aa,bb]=female, [cc,dd]=mixed-low, %[bb,ee]=male, [ff,gg]=mixed-high, [ee,40]=female. The program %returns either 0, .5 or 1 depending on if it is an all male, % mixed or female nest respectively

```
function female=degreeHours(TemperatureTrace)
Temp=TemperatureTrace;
deltat=1/96; %this assumes that the temperature trace
%gives values every 15 minutes
aa=19;
bb=22;
cc=21;
dd=23;
ee=28;%30;
ff=27.5;%29;
gg=28.5;%31;
```

devRate=.0544.*Temp-.6068;%.07251.*Temp-1.1818;

```
%identify the Thermal Sensitive Period (TSP)
```

S=0;

count=1;

while (S<33.3 && count<length(Temp))</pre>

%count=count+1;

RateEval=devRate(count)*deltat;

```
S=S+RateEval;
```

count=count+1;

end

```
TSPbegin=count;
```

```
while (S<66.7 && count<length(Temp))
```

count=count+1;

RateEval=devRate(count)*deltat;

S=S+RateEval;

end

```
TSPend=count;
```

%length(Temp)

countF=0; %female count

countM=0; %male count

countX=0; %mix count

```
for ii=TSPbegin:TSPend
```

```
if (Temp(ii)>=aa && Temp(ii) <=bb)</pre>
```

```
countF=countF+devRate(ii);
```

end

```
if (Temp(ii)>=cc && Temp(ii) <=dd)</pre>
```

```
countX=countX+devRate(ii);
```

end

if (Temp(ii)>=bb && Temp(ii)<=ee)</pre>

```
countM=countM+devRate(ii);
```

end

```
if (Temp(ii)>=ff && Temp(ii) <=gg)</pre>
```

```
countX=countX+devRate(ii);
```

end

```
if (Temp(ii)>=ee)
```

```
countF=countF+devRate(ii);
```

end

end

```
if (countF>countM && countF>=countX)
    female=1;
elseif (countM>countF && countM>=countX)
    female=0;
else
```

```
female=.5;
```

end

end

B.4 Daily Temperature Model

function DTemp=DailyTemp(day2Start,NumDays,t,r)
%Gives a stochastic daily temperature profile starting on
%the specified Julian calendar date (day2Start), extending

%for NumDays days, with t being the time incriments during %each day, and r is the seededrandom number to start with

```
d=[0:NumDays-1];
```

d=d+day2Start;

```
AvgDailyTemp=12-13.75*cos((2*pi/365)*(35-d));
```

```
%Baseline: 10-13.75*cos((2*pi/365)*(35-d))
```

```
%Avg Temp Up 2C: 12-13.75*cos((2*pi/365)*(35-d))
```

AvgAmp=13.75;

```
TempAutoCor=.9;
```

TempStdev=4.4;

randn('state',r);

```
Temp=AvgDailyTemp(1);
```

Temphist=Temp;

```
Amp=AvgAmp(1);
```

```
Amphist=Amp;
```

```
AmpAutoCor=.9;
```

```
AmpStdev=4.4;
```

```
\ calculate random daily temperature average
```

```
for nn=2:NumDays
```

```
Temp=AvgDailyTemp(nn)+TempAutoCor*
```

```
(Temp-AvgDailyTemp(nn))+
```

```
TempStdev*randn*sqrt(1-TempAutoCor^2);
```

```
Temphist=[Temphist,Temp];
```

```
%calculate random daily amplitude
```

for nn=2:NumDays

Amp=AvgAmp+AmpAutoCor*(Amp-AvgAmp)+AmpStdev

*randn*sqrt(1-AmpAutoCor^2);

Amphist=[Amphist,Amp];

end

%calculate daily stochastic temperature

DTemp=[];

for nn=1:NumDays

Temp=Temphist(nn)-Amphist(nn)*cos((pi/12)*(4-t));

DTemp=[DTemp,Temp];

end

B.5 Solar Radiation Model

%This program calculates the daily solar radiation. %It takes as input the number of days to calculate %and a number to seed the random number generator with function dailyRadiation=solarRadiation(NumDays,r)

deltaT=.25; %fifteen minute incriments
Time=0:deltaT:23.75; %will need to change if delta T chages
a=6/deltaT+1;

```
b=14/deltaT+1;
d=20/deltaT+1;
```

```
rand('state',r)
```

```
dailyRadiation=[];
for ii=1:NumDays
    c=.8*rand;
    RadToday=zeros(size(Time));
    Matrix=[a^3, a^2, a, 1; b^3, b^2, b, 1; d^3, d^2, d, 1;
        3*b^2, 2*b, 1, 0];
        column=[0;c;0;0];
        xx=Matrix\column;
        for jj=a:d
            RadToday(jj)=xx(1)*jj^3+xx(2)*jj^2+xx(3)*jj+xx(4);
        end
        dailyRadiation=[dailyRadiation,RadToday];
```

end

B.6 Computational Model

%This is the big massive program which calls all the smaller programs: %DailyTemp - gives a stochastic daily temperature profile %solarRadiation - gives a stochastic solar radiation profile %nestTemperature - gives the temperature profile at the %requested depth truncNorm - picks a random date to lay the nest %from a trucated distribution %- determines the sex of the nest %

function turtlePop
clear all

diary('TurtlePopStocAvgUp4')

NumYears=30;

NumRuns=25;

%Tpiv=27;

firstDay=121; %first day to lay eggs (May 1)
lastDay=197; %last day to lay eggs (July 15)
n=lastDay-firstDay+1; %number of days to lay eggs
t=96*n; %total number of time increments (96 quarter hours in a day)
dayT=0:.25:23.75; %a single day's worth of time increments

gestationPeriod=150; %"maximum" number of days in gestation period

s1=.33;	%egg	survivorship		
s2=.375;	%age	class	2-3	survivorship
s3=.4118;	%age	class	4-5	survivorship

...

- s4=.4118; %age class 6-7 survivorship
- s5=.9; %age class 8+ survivorship
- g1=.33; %age class 1 graduation rate
- g2=.225; %age class 2-3 graduation rate
- g3=.2882; %age class 4-5 graduation rate
- g4=.2882; %age calss 6-7 graduation rate

q=.7;	%probability of using sperm from this year
k=14;	%number of eggs per female (2 clutches total)
h=1.7;	%number of females mated with by one male
recH=1/h;	

```
%The matrix
projMatrix=zeros(10,11);
projMatrix(2,2)=g1;
projMatrix(2,3)=s2;
projMatrix(3,3)=g2;
projMatrix(3,4)=s3;
projMatrix(4,4)=g3;
projMatrix(4,5)=s4;
projMatrix(5,5)=g4;
projMatrix(5,6)=s5;
projMatrix(7,7)=g1;
projMatrix(7,8)=s2;
projMatrix(8,8)=g2;
```

```
projMatrix(8,9)=s3;
projMatrix(9,9)=g3;
projMatrix(9,10)=s4;
projMatrix(10,10)=g4;
projMatrix(10,11)=s5;
```

```
endingValues=[];
```

allValues=[];

```
for kk=1:NumRuns
```

kk

```
%start values
```

```
EHJA=ones(11,1);
```

```
EHJA(1)=1221;
```

```
EHJA(2)=197;
```

```
EHJA(3)=101;
```

```
EHJA(4) = 38;
```

```
EHJA(5)=19;
```

```
EHJA(6)=55;
```

```
EHJA(7)=197;
```

```
EHJA(8)=101;
```

```
EHJA(9) = 38;
```

EHJA(10)=19;

EHJA(11)=55;

```
for ii=1:NumYears
```

```
count=0;
```

%calculate the daily temperature and solar radiation r=ceil(1000000*rand*kk+ii); %number to seed the generator with Temp=DailyTemp(firstDay-20,n+gestationPeriod+20,dayT,r);

%n+gestationPeriod is the total number of days Rad=solarRadiation(n+gestationPeriod+20,r); %mmm=size(Rad) %nnn=size(Temp) NestProfileTemp=[]; MF=[];

%this calculates the initial temperature of the soil soilTemp=soilTemperature(Temp,Rad,firstDay-20);

```
%this calculates the temperature inside the nest at 10cm when
%evaluated at different days
for jj=1:n
    NestTemp=
    nestTemperature(Temp(96*(jj-1)+1921:96*
    (jj+gestationPeriod)+1920),
```

```
Rad(96*(jj-1)+1921:96*(jj+gestationPeriod)+1920),
```

10,firstDay+jj-1,

```
soilTemp(:,96*(jj-1)+1921));
```

```
NestProfileTemp=[NestProfileTemp;NestTemp];
end
```

%these calculate the male/female ratio for this year

```
%this gives the first nest date for each female
numbFemales=yy(11);
nestDate=truncNorm(numbFemales);
```

```
%determines if it is a male or female nest for each day
%of the nesting period
for jj=1:n
   [MorF,countMortality]=degreeHours(NestProfileTemp(jj,:));
   MF=[MF,MorF];
end
```

counter=0;

for jj=1:numbFemales

```
MFDay=nestDate(jj);
```

```
if isnan(MF(MFDay))==0
```

```
count=count+MF(MFDay);%first nest M/F
```

```
counter=counter+1;
```

```
if ((MFDay+17)<length(MF)&&isnan(MF(MFDay+17))==0)
    count=count+MF(MFDay+17); %second nest M/F
    counter=counter+1;
end</pre>
```

end

end

```
percentFemale=count/(counter)
```

```
if isnan(percentFemale)==1
```

percentFemale=1;

 end

end

```
%this calculates the populations for the year
projMatrix(1,1)=s1*(1-percentFemale);
projMatrix(6,1)=s1*(percentFemale);
```

```
xx=projMatrix*yy;
adultm1=xx(3)+xx(4)+xx(5);
adultm2=yy(3)+yy(4)+yy(5);
E=q*(2*adultm1*xx(10)*k/(adultm1+xx(10)*recH))
        +(1-q)*(2*adultm2*yy(11)*s5*k/(adultm2+yy(11)*s5*recH));
yy=[E;xx];
EHJA=[EHJA,yy];
```

```
endingValues=[endingValues,EHJA(:,NumYears+1)];
```

```
allValues=[allValues;EHJA];
```

end

endingValues

allValues

%size(allValues(:,1))

figure

```
plot(endingValues')
```

```
for jj=1:11
  figure
  for kk=0:NumRuns-1
  plot(allValues(jj+11*kk,:)')
  hold on
  title(jj)
  end
  hold off
end
```

B.6.1 First Nesting Date Program

%This function takes as input the number of females and %returns the date of first egg laying date drawn from a %trucated normal distribution. May 1 -June 30 function date=truncNorm(numFemales)

XX = 1:61;

mu=32;

sigma=7;

```
%calculate pdf
pdfTrunc=normpdf(XX,mu,sigma)./(normcdf(92,mu,sigma)
-normcdf(1,mu,sigma));
```

%calculate cdf

```
for jj=2:length(XX)
    trunCdf(jj)=sum(pdfTrunc(1:jj));
```

end

```
%subplot(1,2,1),plot(pdfTrunc)
%subplot(1,2,2),plot(trunCdf)
```

rand('twister',100) % picks the starting random value % f(x) = 0

```
date=[];
for ii=1:numFemales
rn=rand;
index=find(trunCdf>rn);
date=[date,index(1)];
end
```

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