

FRESHWATER TURTLES AS A RENEWABLE RESOURCE: USING THE
RED-EARED SLIDER (*TRACHEMYS SCRIPTA ELEGANS*)
AS A MODEL SPECIES

by

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ABSTRACT

Freshwater turtles have a long history of utilization by humans. For centuries, turtles have been used as a protein resource and in traditional medicine, playing an important role in people's cultures across the globe. Wild turtle harvest has historically and currently been unsustainable. Recently, habitat alterations and the popularity of turtles as pets have contributed to overharvest and population declines. While some regulatory regimes have been implemented in different regions, many taxa remain unprotected and there is a need for improving current regulations.

The objectives of this dissertation is to assess the problem of freshwater turtle harvest and trade in the United States of America (US), focusing first on the entire southeast region and then specifically on the Texas harvest paradigm. This dissertation also examines turtle farming as an alternative to wild population harvest.

The first study reported the evidence of large, unsustainable exports of freshwater turtles out of the US, despite recently implemented restrictions on turtle harvest in several states of the Southeast US. Moreover, I provided evidence for negative consequences of non-uniform harvest regulations across the Southeast US. For example, harvest can continue illegally in the states that provide protection, with these turtles being exported from the states that provide no legal protection. This study suggests necessity of establishing guidelines mandating the labeling of sources for all exported turtles. Better control and law enforcement during shipping operations can be attained by requiring

legal certification and documentation of turtles exported from unregulated states by the shipping agent.

In my second study, I examined patterns of overland movements across the landscape by adult red-eared sliders (*Trachemys scripta elegans*). I also developed a novel method of monitoring the movement at a higher resolution than previously reported. This study is directly related to establishing buffer zones as well as establishing potential harvest seasons. It also allowed me to test the source-sink harvest paradigm applied to Texas freshwater turtle populations. The study provided the evidence of different seasonal patterns between male and female red-eared sliders. It also provided evidence for flaws in the current management regime in Texas, but also gave a direction for future studies that might improve this management.

Finally, I tested alternative options for harvesting adults from wild populations, such as freshwater turtle farming. Specifically, I developed a biological and economic model for farming red-eared sliders in Louisiana. This model demonstrated the economic challenges of farming red-eared sliders for meat markets. However, it gives a perspective on what the future market may develop. Future studies should focus on modifying this model to fit more desirable and rare taxa.

CHAPTER I

GENERAL INTRODUCTION

Unlimited harvest of a wildlife resource is not sustainable for any taxa.

Freshwater turtles represent one such example, where unregulated take has led to severe declines of numerous species across the globe. While Asia and China are often used as examples, the United States (US) continues this failed management paradigm even today. Asia is a unique region of the world because turtles have not only been valued as a protein resource but have also been an important part in traditional medicine. According to ancient Chinese medical books, consuming turtles confers longevity and cures numerous diseases. Today, China remains the leading consumer of turtles primarily for meat, traditional medicine, and the pet trade. Historically, a lack of harvest regulations and current lack of law enforcement in Asia represent probably the most extreme example of how unconstrained exploitation of wild turtle populations leads to severe depletion, extirpation, and even extinction. As a consequence, wild populations from other regions of the world have been experiencing increased harvest pressures in order to meet high demands for depleted Asian turtle populations. Shortly after the Asian market collapse in the 1990s, the US became one of the leading turtle exporters in the world, with a majority of the exported turtles being shipped to Asia. The magnitude of trade in the US has been documented in several reports and peer reviewed articles (Reed and Gibbons 2003, Telecky 2001). However, wild harvest regulations were first implemented in the early 2000s, as a response to petitions signed by conservation groups to end

commercial harvest (Association of Fish and Wildlife Agencies 2011). The main concern is the Southeast US (i.e., Florida, Alabama, Mississippi, Louisiana, etc.), the region with the greatest diversity and abundance of freshwater turtles in the US (Buhlmann et al. 2009). Currently, harvest regulations across US are state specific and the level of protection ranges from complete harvest bans to no protection (unlimited take).

Unlimited harvest of adult turtles is exceptionally hard on wild turtle populations because of turtle life history and demography. Under normal conditions, turtle populations are characterized by low survivorship of eggs and hatchlings and high survivorship of adults (Ernst and Lovich 2009). Stage-based life history models show that the adult life stage is the most sensitive to additive mortality (i.e., Congdon et al. 1994). For example, reducing adult survivorship of alligator snapping turtles, *Macrochelys (Macroclemys) temminckii*, (i.e., due to harvest) by two percent has the potential to reduce the population by half in 50 years (Reed et al. 2002). Since adult turtles, females in particular, have been the primary targets of commercial harvesters, the decrease in abundance of free-ranging populations due to harvest was foreseeable and reported in several studies across North America (Gamble and Simons 2004, Brooks et al. 1991). However, many natural resource agencies still argue that the harvest in the US is not an actual threat to widely distributed and non-listed species. The argument often comes from a belief that, although turtles are not particularly vagile animals, their ability to migrate among harvested water bodies will act as a buffer for harvested regions. This strategy has been specifically incorporated in Texas, where the ban on harvest has been placed only on public water bodies, leaving private water bodies open to unlimited harvest. Although, it is known that freshwater turtles make overland movements, there are no studies that

specifically examined landscape heterogeneity and the likelihood of increased immigration of turtles into harvest-depleted regions. Therefore, scientific evidence for effectiveness to buffer declines from harvests by implementing spatially controlled harvest management regimes is still lacking. Moreover, information on conditions under which protected water bodies would act as buffers (e.g. landscape connectivity and weather conditions) as well as the ratio of protected vs unprotected regions required to achieve a sustainable system is also lacking. For example, under our current management regime in Texas, only ~2% of water bodies are protected by the law, but no scientific evidence exists that 2% will be sufficient to replenish unprotected water bodies (Brown et al. 2011). Much of the missing information is due to limitations in movement monitoring techniques for freshwater turtles. Methods such as drift fences, traditional hoop net traps, and radio telemetry have all been implemented, but each lack the resolution necessary to answer questions such as under what circumstances, biotic (e.g., population density) and abiotic (e.g., temperatures, rainfall, etc.) are turtles likely to make overland movements.

As an alternative to wild population harvest, turtle farming was considered one way to meet high market demands. Incorporating turtles into a large scale aquaculture has been developed in Asia since the 1980s (Haitao et al. 2008), and well developed and successful in the southeastern US since the 1990s (Hughes 1999). For example, Louisiana is the leading exporter of farm-raised turtles in the US, bringing millions of dollars to the economy of this state. However, despite the development of farming operations, pressures on wild populations have persisted. Many well-recognized farms initially established their facilities by harvesting turtles from free-ranging stock, and this practice continues in certain states such as Florida. Secondly, established farms focus mainly on

raising hatchlings for the pet trade or for export to Asian turtle farms. Therefore, traditional turtle aquaculture in the US has not directly addressed the demands from meat markets that still require the harvest of large adults taken from the wild.

In recent years, US turtle farms are being outcompeted by more prevalent Asian turtle farms, causing the number of farms and the total production of hatchlings in Louisiana to decrease. Given that harvest of wild adults is unsustainable, the demand for turtles on meat markets in Asia will continue. With the demand for farmed raised hatchlings decreasing, there is a need for developing novel strategies in turtle aquaculture that would enable production of marketable size turtles for meat markets. Realistically, the new management would have to, at a minimum, result in even profit when compared with strictly hatchling production, but also out produce the wild turtle harvest economy by decreasing the prices of adult turtles.

Captive farming of wildlife in order to decrease pressures on wild populations has been successful for the American alligator (*Alligator mississippiensis*). The American alligator has a similar life history to turtles, with low survivorship of eggs and hatchlings but high survivorship of adults. Collecting eggs from the wild, raising hatchlings under farmed conditions, and returning a portion of the young back to the wild and raising the rest to adulthood proved to be a profitable aquaculture enterprise as well as a the key feature in the recovery and delisting of this species from the endangered species list. Therefore, the commercial utilization of the alligator and its subsequent delisting is a good example of the farming potential of reptiles as well as evidence of how farming can contribute directly to conservation. However, in several ways, the American alligator model cannot be directly applied to conservation of freshwater turtles.

Despite similar life histories, there are fundamental differences in behavior under farmed conditions between alligators and turtles. These differences generally make turtles potentially an even better farmed reptile. Alligators are extremely hard to breed under farmed conditions, therefore farmers depend on wild eggs. In addition, large males tend to become territorial, making it nearly impossible to keep alligators in high density aggregations on the farms. On the other hand, turtles on farms can be kept in high densities and breeding under farmed conditions is easily accomplished. Therefore, while freshwater turtles have even better farming potential than alligators, there is a disconnect between farming and conservation because turtle farms do not depend on wild populations.

The purpose of my dissertation research was to address the issue of freshwater turtle vulnerability to direct anthropogenic impacts and evaluate potential solutions to global declines of freshwater turtle taxa. To reach my goals, I examined harvest, collected novel data to contribute to modeling turtle farming, and sought to confront harvest management regimes to these new analyses. The first portion of this research focuses specifically on the issue of harvest management in the Southeast US. This region is unique due to its freshwater turtle biodiversity and history of exploitation. The Southeast US also represents a region with various, recently implemented, and state specific harvest management regimes. I assessed the outcomes of different law enforcement strategies by evaluating trends in the export of freshwater turtles from the US before and after regulation implementations, with the focus on the southeast. I specifically considered any trend changes in magnitude of exports between states that recently implemented bans on commercial harvest to states with no harvest regulations.

In the second portion of my work, I evaluated the rationale behind the harvest regime in Texas, where overland movements are crucial for population persistence since only public waters are protected from commercial harvest (Texas Parks and Wildlife 2007). This chapter consists of three major components. First, I developed and tested the efficacy of using a stationary microchip reader to provide very high resolution monitoring of turtle overland movement. Secondly, I examined the patterns of overland movements and their direct correlations with environmental factors. Thirdly, I simulated harvest of a water body and examined how movement patterns changed due to this additive mortality.

In the final portion of my dissertation, I turned from analyzing wild turtle populations/harvest regimes to focusing on alternative solutions to meet high market demands. To do so, I evaluated turtle farming operations that only produce hatchling turtles. Based on the biology of farmed turtles and the economic aspects of production, I tested the potential for these same farms to shift into production of adult turtles for meat markets.

While the second chapter of this dissertation addresses the global issue of harvest pressures on non-listed North American freshwater turtles, in the third and fourth chapters I focused mainly on one species of freshwater turtle, the red-eared slider (*Trachemys scripta elegans*). The red-eared slider is one of the most studied and widely distributed turtle species in the world (Gibbons 1990). On the other hand, red-eared sliders have been heavily harvested in Texas (Ceballos and Fitzgerald 2004), have the longest history of being farmed in the US, and are a species commonly found in Asian food markets. Red-eared sliders are known to be one of the most vagile freshwater species, making the species an optimal choice to test a spatially distributed harvest

regime. Because the red-eared slider is also the species for which the life history parameters under farmed conditions are most recognized, using this turtle enabled me to create the most complete model for turtle farming. While currently species specific, this model can be used as a baseline for evaluating farming of other species.

Overall, my dissertation binds together the consequences of changed harvest management regimes in the Southeast US (Chapter II) and the rationale behind two potential solutions to what currently seems an unsustainable harvest: spatially distributed harvest based on movement patterns (Chapter III) and innovation in farming approaches (Chapter IV).

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CHAPTER II

MAGNITUDE OF THE FRESHWATER TURTLE EXPORTS FROM THE US: LONG TERM TRENDS AND EARLY EFFECTS OF NEWLY IMPLEMENTED HARVEST MANAGEMENT REGIMES¹

Abstract

Unregulated commercial harvest remains a major threat for turtles across the globe. Due to continuing demand from Asian markets, a significant number of turtles are exported from the United States of America (US). Beginning in 2007, several southeastern states in the US implemented restrictions on the commercial harvest of turtles in order to address the unsustainable take. I have summarized freshwater turtle exports from the US between 2002 and 2012 and demonstrated that although the exports decreased throughout the decade, the magnitude of turtle exports from the US remained high. Louisiana and California were the major exporters. The majority of exports were captive bred, and from two genera, *Pseudemys* and *Trachemys*. I review the changes over the decade and speculate that the increase in export of wild turtles out of Louisiana after 2007 could be a consequence of strict regulations in surrounding states (e.g., Alabama, Florida). I suggest that if wild turtle protection is a goal for conservation efforts, then these states should work together to develop comprehensive regulatory reforms pertaining to the harvest of wild turtles.

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Introduction

Turtles are a substantial commodity in the global market of wildlife commercial goods and sustenance. For example, in 1995 the estimated value of freshwater turtle exports from Vietnam to China exceeded 1 million US dollars [1]. Recent and historic over harvest led to severe declines and even subsequent extinctions of several freshwater turtle, sea turtle, and tortoise species [2], [3]. Today chelonians represent one of the most endangered taxonomic groups on the planet [4]. China is the world's largest consumer of turtles, where meat and shells are believed to have medicinal value [5], [6], [7]. High demands from the Asian turtle markets resulted in a depletion of wild Asian turtle populations [8], [9], [10], and in turn, led to an increased demand for imported US species [11], [12]. As wild populations of large turtle species (e.g., green sea turtle and alligator snapping turtle) declined due to over harvest, commercial trappers focused on smaller non-listed species [13]. In turn, turtle farming has become a booming aquaculture business in the southeastern US, especially Louisiana, in response to these demands [14]. However, even with extensive farming operations, the harvest pressures on wild turtle populations remain high [15], [16].

Turtle exports from the US have increased in recent decades. Telecky (2001) [17] reported the number of exported native and non-native turtle and tortoise species rose by 257% between 1989 and 1997, from 3,485,136 to 8,990,699 individuals per year, respectively. Reed and Gibbons (2003) [15] specifically examined US native turtles and found an increase in the turtle trade from 7,044,951 turtles exported in 1996 to 13,661,976 individuals exported in 2000, effectively doubling of exports within a 5 year period (Fig. 2.1). Ceballos and Fitzgerald (2004) [18] reported an average increase of

approximately 18,000 turtles per year between 1995 and 2000. Asian countries were the major importers and the top species exported belonged to three genera of common freshwater turtle species: *Trachemys*, *Chrysemys*, and *Pseudemys*.

Large adults, females in particular, are the most valuable on the meat market and therefore a primary target of commercial trappers [19]. The adult life stage is also the most sensitive to harvest [20], [21], [22]. Research has shown harvest pressures can cause population declines in some of the most common freshwater turtle species [23]. In the US, harvest pressure has been most noticeable in the southeastern United States, an ecoregion of “further conservation consideration” for freshwater turtles [24]. Scientists raised a concern for wild turtle populations and warned that the magnitude of take exceeds sustainable levels [25], [15]. The Center for Biological Diversity, with a coalition of more than 20 conservation and health groups, took action in 2007 by submitting regulatory petitions to the states of the southeast to end commercial harvest of freshwater turtles [26]. Contemporaneously, several states in the southeast US increased their restrictions on commercial take of non-listed or previously unprotected wild turtle populations.

While individual state laws control the harvest of non-threatened species, the U.S. Fish and Wildlife Service Office of Law Enforcement (USFWS) is in charge of overseeing the export shipments. Definitions were developed by CITES and used by the USFWS in all states to identify and record the harvest source of individual animals or shipments. Potential sources include wild, captive bred, farmed, ranched, or turtles of unknown source; our interpretation of source definitions can be found in Supplemental Table S1. However, these definitions can be vague and unclear. For example, farmed

turtles are defined as being born in captivity yet farmed individual can also represent F1+ generations of wild caught turtles. Ranched individuals can be defined as wild caught but reared in a controlled environment. There are no guidelines regarding the time in captivity required for wild caught turtles to produce “captive-bred” offspring or time in captivity before wild caught turtles can be sold as “ranched” turtles. The magnitude of these discrepancies, if any, is impossible to track. According to the source, a working group in CITES has been reviewing the source code definitions for several years, but a clear conclusion has not been reached yet (Peter Paul van Dijk, pers. comm).

Evaluations of turtle exports are seldom reported in the peer reviewed literature, especially the trends in more recent years subsequent to wild harvest regulations in production states. My goal here was to analyze the magnitude of turtle exports from the US between 2002 and 2012, the period that includes the years prior to and after the implementation of commercial harvest regulations among the states in the southeastern US. I sought to 1) quantify and examine trends in the volume of live freshwater turtle exports from 2002-2012, 2) characterize the exports in terms of species, ports of export, and sources, specifically focusing on the relative magnitude of exports from wild caught individuals, and 3) review the laws in the Southeast US regarding commercial harvest and examine the possible effects they might have on the exports. I was interested in determining if closed markets influenced the magnitude of trade from adjacent exporting ports. That is, whether strict harvest regulations in one state affected the exports not only in that state, but also the surrounding states. I acknowledge that this analysis excludes any domestic trade and that the total trade numbers are much larger, but I consider this to be a

sufficient proxy of the general trends for this commercial trade and its potential impacts to native populations of freshwater turtles in the Southeast US.

Methods

Data

The US Fish and Wildlife Service (USFWS) maintains the records of all the shipments of turtles in and out of the US in the Law Enforcement Management Information System (LEMIS) database. These records can be accessed by making a request to USFWS based on the Freedom of Information Act. I queried the records of turtle shipments out of the United States between 2002 and 2012. Each shipment record contains the species being shipped, the source (wild caught, captive bred, ranched, farmed, or turtles of an unknown source), description (live specimens, or bodily remains), units (number or mass of shipment in kg), purpose of trade (commercial, scientific, captive propagation purposes etc.) and the port of export. Species were recorded by the four letter codes, which were often incomplete and only reported the genus; therefore I analyzed the data at the generic level. In addition, the LEMIS data only reports the ports of export, and thus not necessarily the state the individuals were collected or originated. The LEMIS data is the only resource available that provides detailed description of export shipments and therefore the best available data from which to conduct analyses and evaluations. I also included data from the Louisiana Agriculture Center [27] that keeps records of total production of freshwater turtles under farmed operations. I used this data to corroborate turtle farm production with turtle exports from this state.

I reviewed the commercial harvest management policies of freshwater turtles in the nine states of the southeast US: Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, Oklahoma, South Carolina, and Texas. The Association of Fish and Wildlife Agencies has assembled the state laws regarding amphibians and reptiles in a State of the Union report, last updated in December 2011 [28]. I also include regulations implemented after 2011.

Analyses

From the LEMIS database, I sought only the exports for commercial purposes, as the shipments for scientific and conservation purposes were not our primary interest here. I only focused on the number of exported live, native, freshwater species. I summarized the total yearly exports and used least squares simple linear regression to investigate relationships between year and total amount of export [29]. I used F-tests to conduct hypothesis tests on regression coefficients, inferring significance at $\alpha = 0.05$. I then classified the exports by each state. For the top four exporting states, I used a model selection approach by conducting a likelihood ratio test for two mixed effects models treating years as fixed and states as random factors. I tested the intercept only model versus the intercept and slope model. A small p-value (<0.05) indicates significant differences between the two models and the model including intercept and slope is preferred while a large p-value indicates no significant results and the model including intercept only is chosen. In the same manner, I then tested the winning model versus the same model with lag 1 temporal autocorrelation factor. For the winning model I estimated significance of the parameters. In addition, for the top four exporting states, we: 1) partitioned the taxa being exported by genus, and 2) partitioned the exports by

source. For these analyses, I estimated regression coefficients across the states in order to infer any significant trends. Further, for those genera representing the majority of exported individuals, I examined the proportion of wild caught turtles. I performed statistical analyses using R version 2.10.1 (The R Foundation for Statistical Computing, Vienna, Austria). Once the data were analyzed, I linked the export trends with the management regimes implemented in each state.

Results

Overall Trends

Between 2002 and 2012, a total of 126,600,529 individual freshwater turtles were exported from the USA. Based on the marginally significant simple linear regression ($F = 3.91$; $df = 1,9$; $p = 0.08$), the number of exported turtles decreased on average 500,000 turtles per year over the 11 year period. However, in 2007, the residual standard deviation was 2.5 times higher than the average residual standard deviation. In 2007, there was a 79% increase (18,457,520 individual turtles) compared to 2006 (Fig. 2.1). Overall, 53% were commercially bred, 28% were classified as farmed or ranched, and 19% were classified as wild caught individuals. When I partitioned the total exports by source, the number of captive bred exports declined after 2007 while wild caught exports increased after 2009 (Supplemental Fig. S1).

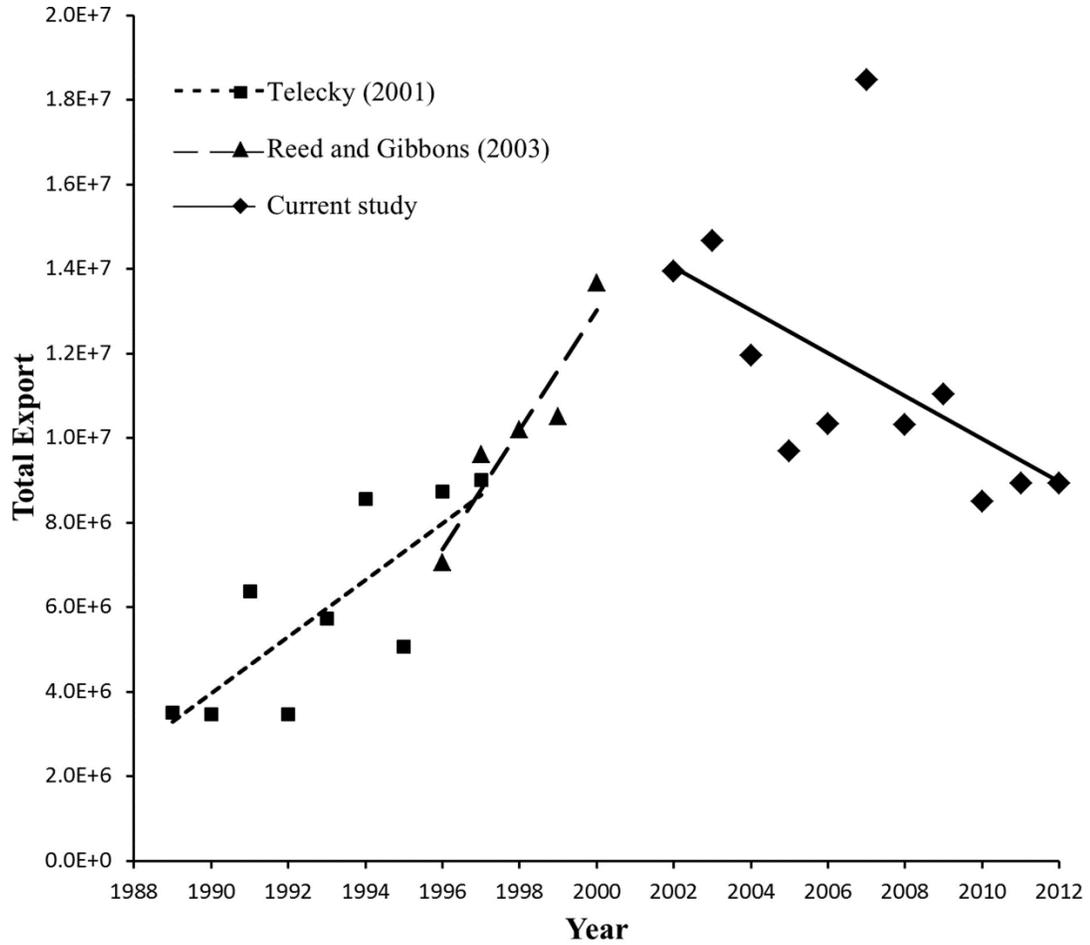


Figure 2.1: Yearly number of individual turtle exports (y-axis) from the United States as reported by Telecky (2001) [17], Reed and Gibbons (2003) [15], and what I reported for purposes of this study, including the linear trend lines. The first two studies show trending exponential increase in exports from 1989-2000 while our study shows the overall decrease for the period from 2002-2012. However, the magnitude of exports remained high (within millions) with significant increase in exports in 2007 (residual standard deviation 2.5 times higher than the average residual standard deviation), the year when the implementation of the new harvest regimes began in the Southeast US.

Exported Taxa

The following genera were exported: *Apalone*, *Chelydra*, *Chrysemys*, *Clemmys*, *Deirochelys*, *Emydoidea*, *Graptemys*, *Kinosternon*, *Macrochelys*, *Malaclemys*, *Pseudemys*, *Sternotherus*, *Terrapene*, and *Trachemys*. Combined, *Pseudemys* and *Trachemys* represented between 61% (Florida; 1,321,202 individual turtles) and 96% (Louisiana; 81,404,579 individual turtles) of all species traded from the top four exporting states (Fig. 2.2). *Chelydra* consisted of 12% (4,248,913 individuals) of the exports from California, 5% (99,846 individuals) of the exports from Texas, and 5% (125,276 individuals) of the exports from Florida. *Apalone* consisted of 25% (540,815 individuals) of all exports from Florida and 5% (99,024 individuals) from Texas. For the top four exported genera (*Apalone*, *Chelydra*, *Pseudemys*, and *Trachemys*), regression coefficients showed significant increase in traded *Trachemys* in Louisiana ($p = 0.02$) and significant decrease in traded *Trachemys* in California ($p < 0.01$). Traded *Apalone* significantly increased in Florida and California ($p < 0.01$) while traded *Chelydra* increased in Louisiana and California ($p < 0.01$).

Considering the high magnitude of exports from Louisiana and California, it is worth reporting the totals among all exported genera (Table 2.1).

Table 2.1: Total number of exported freshwater turtles from the top two exporting states from 2002-2012 sorted by genus.

<i>Genus</i>	Louisiana	California
<i>Pseudemys</i>	59,240,411	3,108,013
<i>Trachemys</i>	22,154,168	26,154,972
<i>Graptemys</i>	1,822,122	132,684
<i>Chelydra</i>	664,912	4,348,913
<i>Sternotherus</i>	325,238	337,397
<i>Apalone</i>	300,679	1,806,493
<i>Chrysemys</i>	217,519	132,684
<i>Macrolemys</i>	73,602	233,916

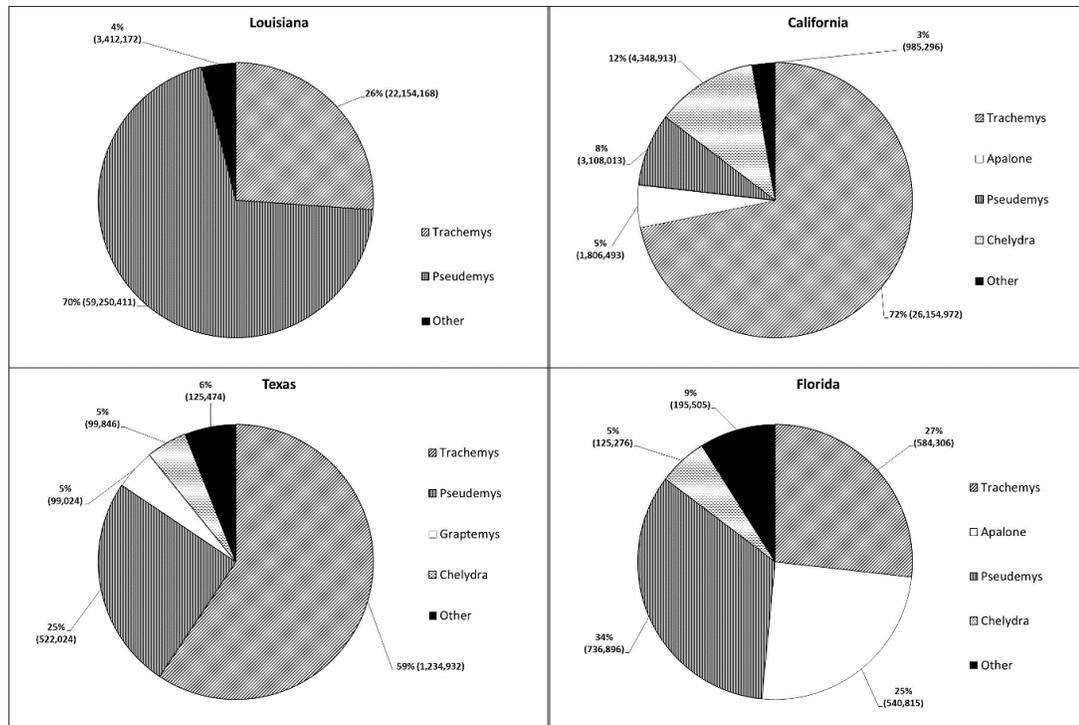


Figure 2.2: Percentage of different genera of native freshwater turtles exported from Louisiana, California, Texas, and Florida from 2002-2012. The majority of exports belonged to the genera *Pseudemys* and *Trachemys*.

Exporting States

I broke the data set down into the number of exports in each state. Turtles were exported out of California, Florida, Georgia, Hawaii, Illinois, Louisiana, New Jersey, New York, Texas, and Washington (Fig. 2.3A). Overall, Louisiana and California accounted for 96% of the exports (67% and 29% respectively), followed by Texas and Florida (2% each; Fig. 2.4). The model containing intercept only was superior to the intercept slope model ($p = 0.28$) and the model containing lag 1 autocorrelation factor was superior to the intercept only model ($p < 0.01$). The winning model showed no significant trend in exports over the 11 year period among the states ($p = 0.49$), but the correlation parameter estimate of 0.75 indicated high temporal autocorrelation within the dataset.

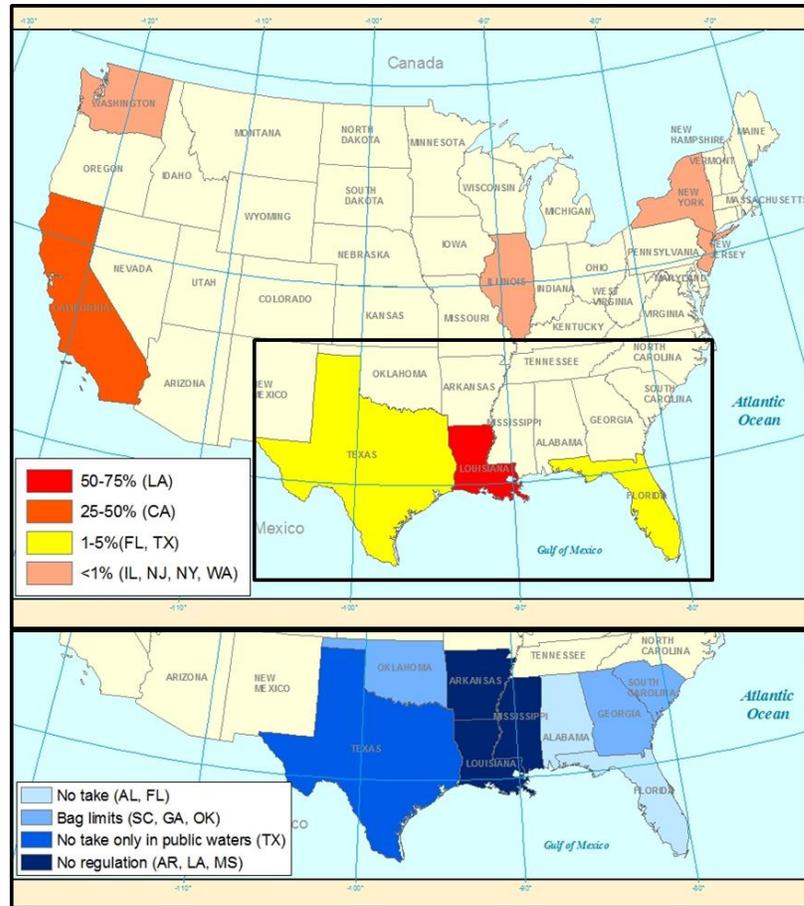


Figure 2.3: Proportion of freshwater turtles exported from the US in the period from 2002-2012, partitioned by the exporting state (A), and an overview of state regulations in the southeast US (B), the region with the greatest conservation concern regarding freshwater turtles. Four states (Louisiana, California, Texas, and Florida) account for 96% of all exports. On the other hand, Louisiana, Arkansas, and Mississippi still allow unlimited take while Alabama and Florida banned commercial harvest from all water bodies and therefore represent two states with the strictest laws regarding commercial turtle harvest.

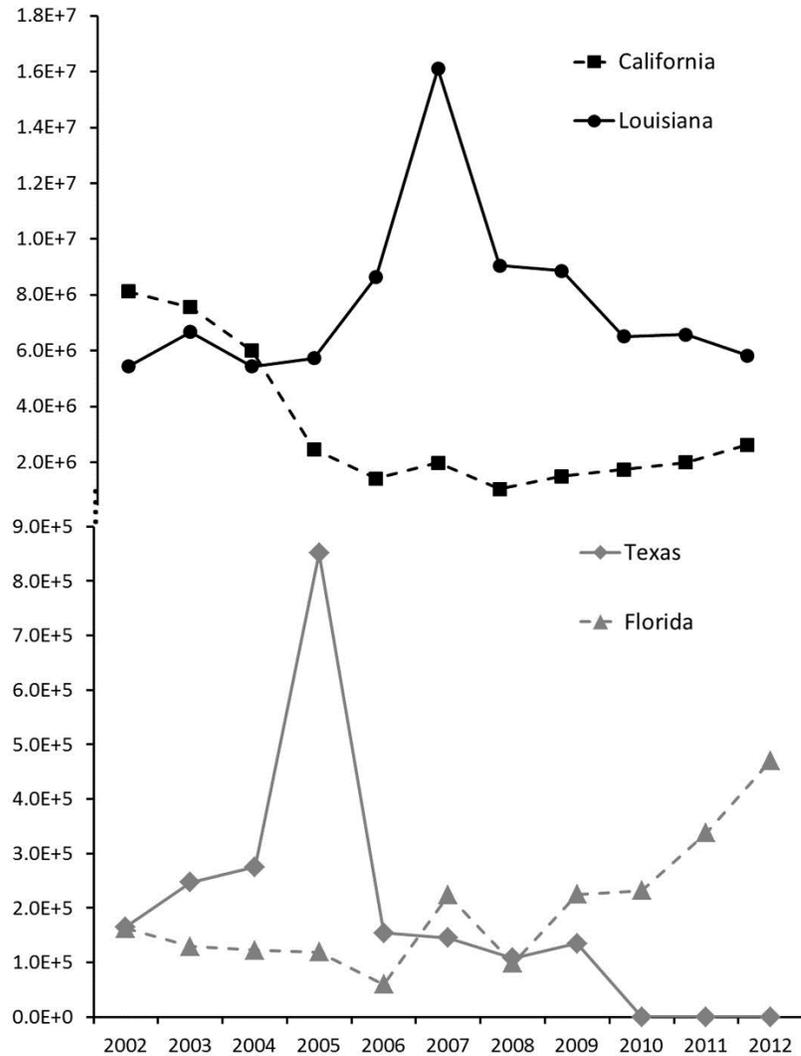


Figure 2.4: Number of native freshwater turtles (y-axis) exported from Louisiana, California, Texas, and Florida from 2002-2012 (x-axis). Louisiana and California accounted for 96% of the overall export from the US. Texas and Florida accounted for 2% each of the overall export from the US.

On average, 7,710,614 and 3,309,426 turtles/year were exported from Louisiana and California, respectively. Across all years, Louisiana exported the most turtles in 2007 (16,105,077 turtles). Exports out of California gradually decrease between 2002 and 2005, and throughout the next seven years approximately 2 million turtles were exported per year. Although Texas and Florida account for a small proportion of total exports,

there was an increase in exports from Texas in 2005 (850,940 individual turtles exported) and an increase in exports from Florida in 2007 (223,895 individual turtles). In all cases except Florida, the number of exports decreased dramatically after these peaks and continued to slowly decrease. However, exports out of Florida have steadily increased since 2008.

Turtle Sources among States

In Louisiana, Texas, and Florida captive bred individuals comprised the majority of exports (65%, 85%, and 86%, respectively) while in California, farmed/ranched individuals composed the majority of exports (75%; Fig. 2.5). Regression coefficients showed significant increase in exported wild individuals in Louisiana ($p < 0.01$) and a significant decrease in exported farmed/ranched individuals in Louisiana and California ($p = 0.01$ and $p < 0.01$, respectively).

For each of the top four states, any change in exports among the years corresponds with the change in exports of captive bred individuals. Comparatively, wild caught turtles were exported in much smaller quantities than captive bred individuals. In Louisiana, however, the number of exported wild caught turtles increased from 80,050 in 2008 to 6,386,030 in 2009 and remained high the following 3 years and exceeded the number of captive bred turtles exported.

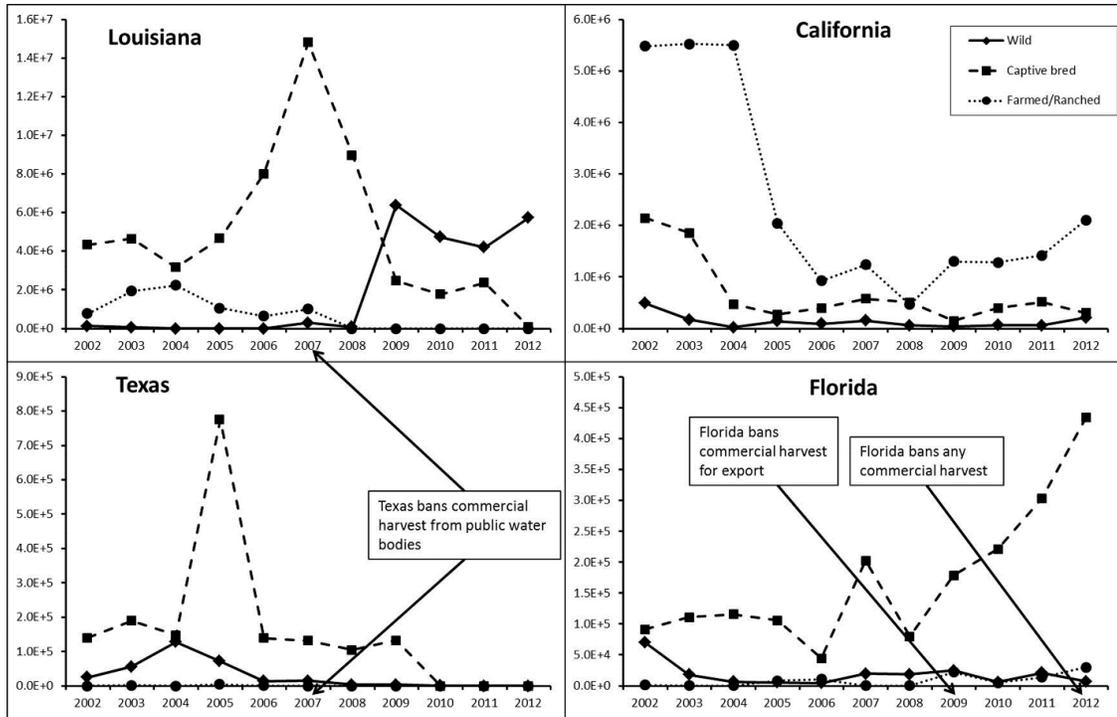


Figure 2.5: Numbers of native freshwater turtles (y-axis) exported from Louisiana, California, Texas, and Florida from 2002-2012 (x-axis), separated by sources.

Wild Turtle Exports

Louisiana reportedly exported the wildest caught individuals of any state (Fig. 2.6). The number of wild exports significantly increased for *Apalone*, *Chelydra*, *Pseudemys*, and *Trachemys* ($p < 0.01$) while California increased exports of wild *Chelydra* ($p < 0.01$). Most wild caught *Trachemys* were exported from Louisiana. However, prior to 2009, the number of exported *Trachemys* from Louisiana was trivial in contrast to 2009 when over a million wild caught turtles were exported. Since then, the number of turtles exported steadily rose, achieving 5,288,482 individuals in 2012. Louisiana was also a primary exporter of wild *Pseudemys*, but like *Trachemys* exports were negligible until 2009. In 2009, over four million *Pseudemys* were exported yet the numbers gradually declined as the number of *Trachemys* exported increased (Fig. 2.6).

Since the definition of wild caught can include F1 hatchlings from wild caught brood stock, I also gathered information from Louisiana Department of Agriculture and examined the number of captive bred turtles over the same period. I noticed the number produced after 2009 closely matched the captive bred reported in the LEMIS data (Supplemental Fig. S2). This observation suggests the wild exports out of Louisiana were most likely turtles directly harvested from wild populations.

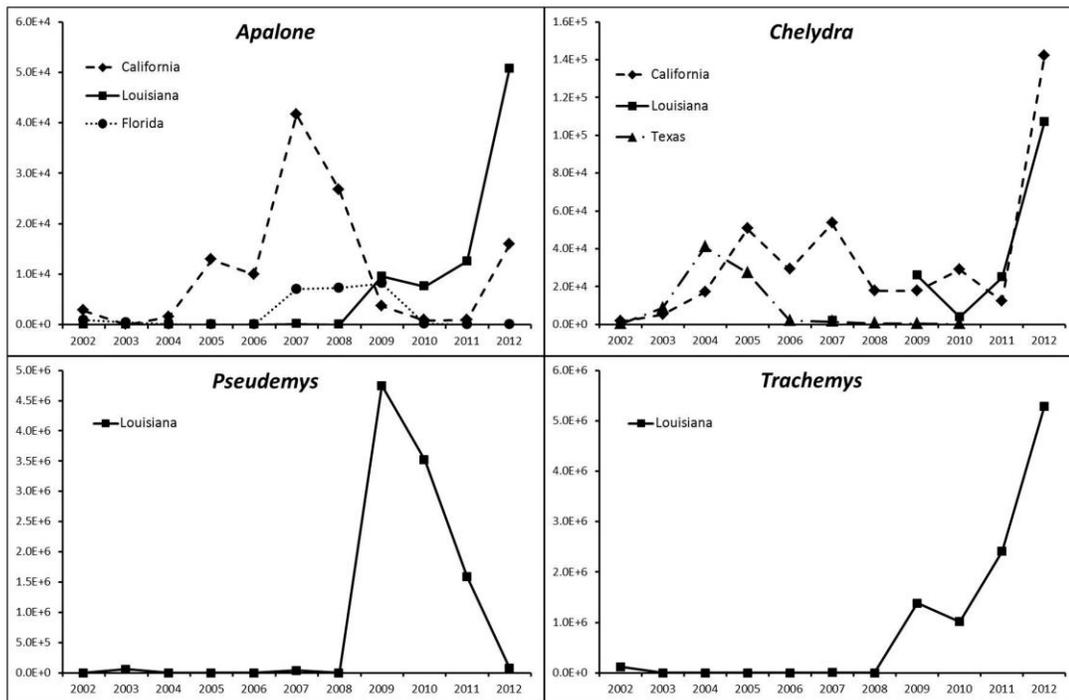


Figure 2.6: Numbers of wild caught *Apalone*, *Chelydra*, *Pseudemys*, and *Trachemys* (y-axis) shipped from the major exporting states from 2002–2012 (x-axis). Louisiana was a major exporter of *Pseudemys* and *Trachemys* while Louisiana and California were the major exporters of *Apalone* and *Chelydra*.

Harvest Management Regimes

As a response to submitted petitions to ban commercial harvest, six out of nine states in the southeast US provide different levels of protection (Fig. 2.3B). Alabama and Florida now have the strictest laws on commercial take (Table 2.2), prohibiting any

commercial harvest from public and private water bodies. While Alabama implemented its laws for the first time in 2012, Florida began implementing the new regulations three years prior. In 2009, Florida banned commercial harvest for export, but turtle farmers were allowed to continue harvesting essentially unlimited numbers of wild turtles for aquaculture with appropriate permits [28]. These permits expired in April of 2012, with Florida then implementing a prohibition of commercial harvest. After Florida banned commercial harvest for export, exports of captive bred individuals increased, but there was no apparent change in wild caught turtle exports after the ban (Fig. 2.4). Texas provided some level of harvest management beginning in 2007 with a ban of commercial harvest from public water bodies. By 2010, zero wild caught turtles were exported out of Texas. South Carolina established daily and annual bag limits in 2009 while Georgia and Oklahoma established daily and bag limits in 2012.

Table 2.2: Summarized commercial collection limits within each state in the southeast US and its legal and regulatory provisions.

State	Regulation	Daily/annual bag	Size restrictions	Source
Alabama	No take			Alabama Department of Conservation and Natural Resources (2012) [33]
Arkansas	Open season	Unlimited	Any	Association of Fish and Wildlife Agencies (2011) [28]
Florida	No take		Any	Association of Fish and Wildlife Agencies (2011) [28]
Georgia	Open season	10 turtles/day	Any	Georgia Department of Natural Resources (2012) [34]
Louisiana	Open season	Unlimited	Any	Association of Fish and Wildlife Agencies (2011) [28]
Mississippi	Open season	Unlimited	At least 12 inch carapace length for common snapping turtles	Association of Fish and Wildlife Agencies (2011) [28]
Oklahoma	Open season	6 turtles/day	Any	Association of Fish and Wildlife Agencies (2011) [28]
South Carolina	Open season	10 turtles/vehicle 20 turtles/year		Association of Fish and Wildlife Agencies (2011) [28]
Texas	Private waters only	Unlimited	Any	Texas Parks and Wildlife (2007) [35]

The remaining three states, Arkansas, Louisiana, and Mississippi permit essentially unlimited take. Until 2009, the vast majority of exports from Louisiana were captive bred individuals. While the number of captive bred exported turtles slowly decreased after 2007, export of wild caught turtles from Louisiana has since steadily increased. According to the LEMIS and Louisiana Department of Agriculture data, wild caught turtles now make up the largest portion of the total exports from Louisiana (Fig. 2.5). The Louisiana Department of Agriculture (2012) reported that competition among turtle farms eventually led to a decrease in the number of total farms in the state. It is

possible that this decline in turtle farms could account for the decrease in farmed exports out of Louisiana.

Discussion

Turtles are an important part of the aquatic ecosystems. While relatively little work has been published directly seeking their contributions to food webs or ecosystem function, their contribution to these functions is important [30]. Over harvest can cause population declines in even the most common species, and subsequently cause changes in energy flow, nutrient cycling, and food web structure. In the last three decades, the US became a major turtle exporter that has supplied the otherwise depleted Asian food markets [15]. In response to concerns raised by researchers and biodiversity groups, alongside increased awareness of the magnitude of this harvest by state regulatory agencies, several states in the southeast have banned commercial harvest of freshwater turtles within the past 5 years.

I summarized freshwater turtle exports from the US across the past 11 years and found that the magnitude of export has remained high when compared with previous reports [17], [15] (Fig. 1). However, the overall exported quantity has been decreasing, with marginal statistical support (Fig. 1). Also, the proportion of wild caught individuals (19%) was less than previously reported (34%) [15]. The decrease could potentially be a positive outcome from the new management regimes. However, if the harvest effort has remained the same over the past 11 years, this may alternatively, indicate a decline in freshwater turtle numbers as fewer individuals are found to bring to market.

The vast majority of exports belonged to common species of the genera: *Trachemys*, *Pseudemys*, *Chelydra*, and *Apalone*. Although these are not protected under CITES, research has shown that populations of some of the most utilized taxa, such as *Trachemys scripta elegans*, can become significantly depleted under intense harvest pressures, taking these populations decades to recover [23]. Although statistical analysis failed to detect significant differences in the exportation trends, states with harvest regulations decreased wild turtle exports and states without harvest regulations increased wild turtle exports.

I did observe short term responses to regulation within states that have emplaced changes to commercial utilization of turtles. I am particularly referring to Texas, where, at least according to LEMIS, commercial harvest is no longer occurring. After Florida first implemented harvest regimes in 2009, this state continued to export wild caught individuals. It is of my further interest to continue monitoring exports from Florida especially after the complete harvest ban in 2012. The results also indicate that these regimes could have potential negative effects on wild turtle harvest in the surrounding states, potentially placing extreme harvest pressure on Louisiana's wild turtle populations. Ultimately, the lack of clear data describing the actual origin of exported turtles enables more than one interpretation of the data.

First, commercial trappers from the states with new harvest management regimes may have simply shifted their exportation ports to nearby states (e.g., Louisiana). Large scale turtle harvest is organized as a pyramid scheme including trappers, middlemen, and dealers. Turtle dealers usually have an interstate network of several hundred employees and are capable of exporting hundreds of thousands of turtles a year (Texas Parks and

Wildlife Department, pers. comm.). It is less likely that harvest regulations in one state could impact this business network. There are currently no laws in place to declare the state of origin of wild caught turtles, aside from obtaining state harvesting permits, nor are there any interstate trade regulations for non CITES listed species. Therefore, perhaps wild caught turtles from the surrounding regulated states are now being exported through Louisiana. This alternative hypothesis is further supported by the numbers of exported turtles out of California, a state with only one native freshwater turtle species, the western pond turtle *Actinemys marmorata* [31].

California has remained a top exporter of turtles, matching the magnitude of turtles shipped from Louisiana. The majority of exported turtles from California are farmed or ranched individuals. I was not able to find information on extensive turtle farming operations in California, certainly not at the scale of the Louisiana Turtle Farmer's association (California Aquaculture Association, pers. comm.). Therefore, I am confident that exported *Apalone*, *Chelydra*, and *Trachemys* did not originate from California, and this makes any assessment of the origin for these California exports difficult to track. In 2012 the owner of a turtle aquaculture facility in Florida was convicted of illegally marking wild caught turtles as captive bred and attempting to export these turtles out of the Los Angeles International Airport [32]. Understanding the domestic origin of these shipments or the domestic origin of the turtles themselves is crucial to our understanding of the commercial trade of freshwater turtles in the US, and the lacking public information at hand is worrisome.

Management Recommendations

To improve our understanding of temporal trends in turtle exports, I recommend establishing better guidelines for labeling the sources of exported turtles. Clear and reliable standards set for all turtle exports from the US would include required confirmation of captive bred versus wild animals and reporting of originating states, not just the port of export. Moreover, animals that are directly taken from the wild and being exported immediately (e.g., the same year) must be clearly separated from any other category. In addition, I recommend developing a new category for the shipments that would classify exported turtles as hatchlings (juveniles less than 1 year since hatching) or adult turtles. That would provide better understanding of whether the turtles are being exported for food markets (adult turtles) or possibly pet markets (hatchlings). The LEMIS database had previously included values per shipment which did enable inference as to whether the shipment includes low priced hatchlings that are most likely coming from farming operations or higher price adult turtles. I strongly recommend re-establishing this category. With these improvements of shipment recording, LEMIS database could be more useful in evaluating the trends and consequences of harvest regimes.

Based on my findings, I have shown that the strict regulations in one state may well have a negative harvesting influence in surrounding states with and without regulatory laws. The reasons are twofold. Primarily, this could act to drive increased harvest in unregulated states. Secondly, harvest in regulated states could illegally continue if turtles can be exported from a neighboring state. Arkansas, Louisiana, Mississippi, and Georgia are in the center of the freshwater biodiversity hotspot for the US and all still lack strict regulatory legislation (i.e., prohibition of harvest from the wild)

on the commercial harvest of the most utilized taxa. Regulating commercial harvest by implementing a ban on the most sensitive life stages (adults, specifically adult females) in these states, especially exporting states (e.g. Louisiana) would also strengthen the laws previously established in surrounding states. The simple requirement of legal certification and documentation by the shipping agent that all turtles exported from these unregulated states, originated there, would enable better control and law enforcement during shipment operations. For example, under current circumstances, a turtle dealer residing in Louisiana could be harvesting turtles from Texas or Florida but reporting them as Louisiana turtles. There are currently no requirements to verify the origin or category of turtles exported.

There are several variations of harvest regulation currently in place: complete ban, establishing season and bag limits, or complete ban in certain areas (e.g., public waters) and no season or bag limits for the utilized taxa in the rest (e.g., private waters). As a complete ban is certainly the strictest possible law and the hardest to pass, I recommend establishing seasons and bag limits as a first step toward protection. Within a state, I do not recommend protection of certain areas while leaving the other areas open to unlimited harvest, because there is no supporting evidence that protected populations would replenish the harvested areas.

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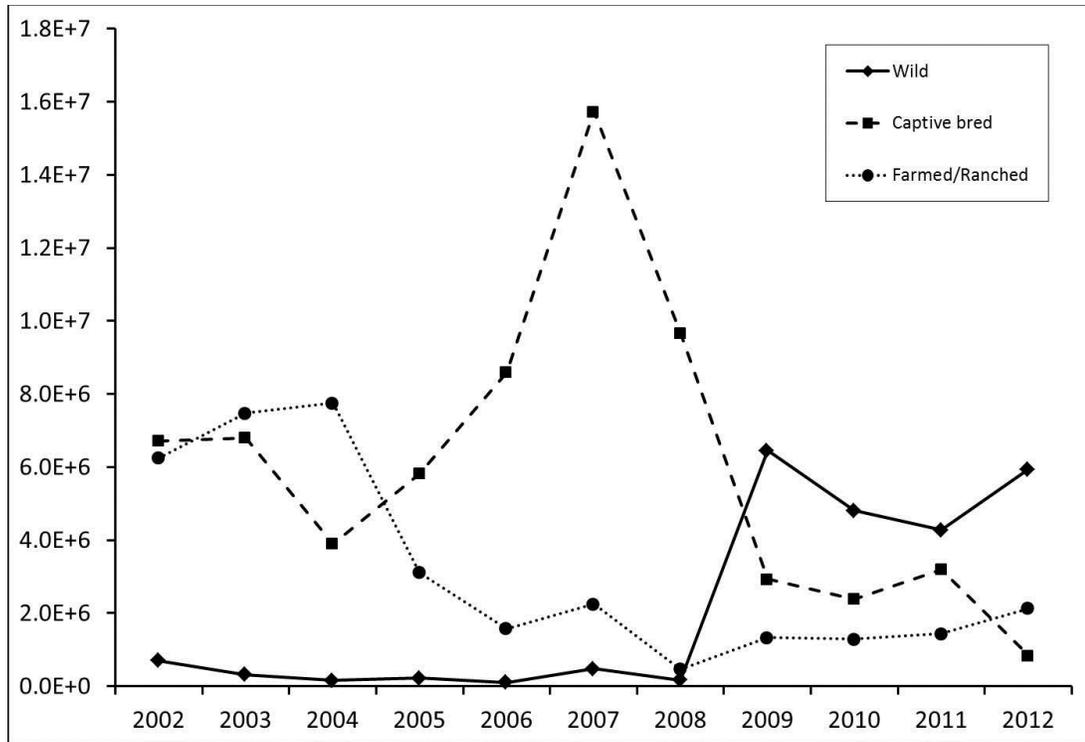
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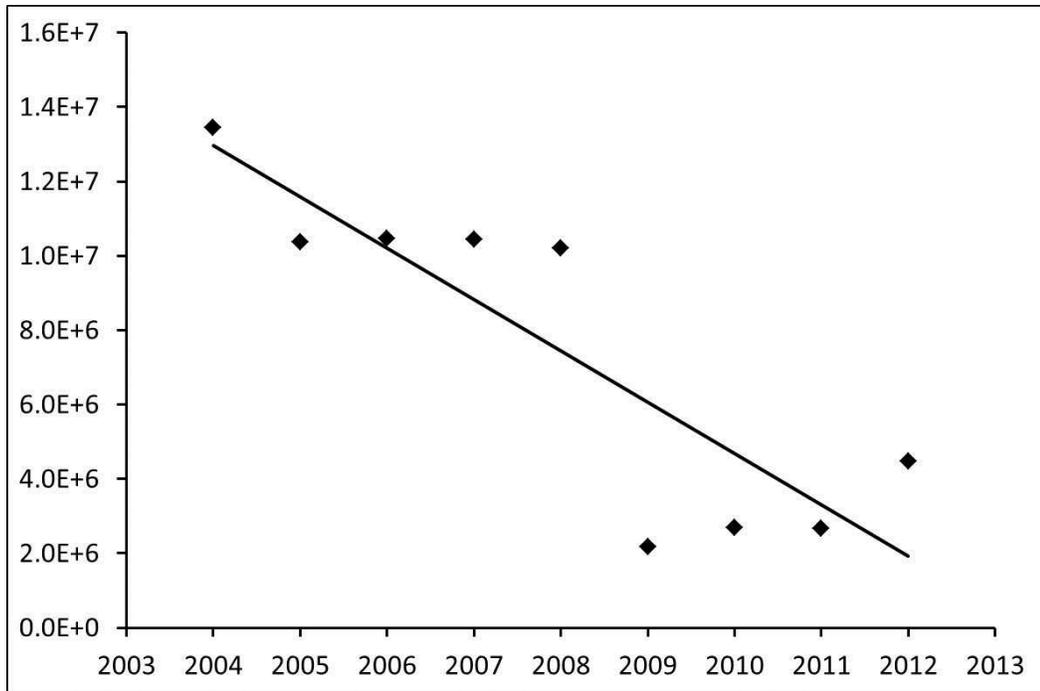
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Supplemental Figure S1. Total number of exported turtles (y-axis) from 2002-2012 (x-axis) partitioned by the source of turtles.



Supplemental Figure S2. Total production of freshwater turtles (y-axis) on Louisiana farms from 2002-2012 (y-axis).

Supplemental Table S1. Definitions of the sources of exported freshwater turtles used by the USFWS during the inspection of shipments.

Source of specimen	Description
Bred-in-captivity	The specimen was born to parents that either mated or transferred gametes in a controlled environment
F1 (farmed)	Born in captivity to wild-caught parents but are not considered as captive bred under CITES
Ranched	Directly removed from the wild and reared in a controlled environment or are progeny from gravid females captured from the wild
Wild	Specimen taken from the wild or specimen born in captivity from an egg collected in the wild

CHAPTER III

SPATIAL AND TEMPORAL MOVEMENT DYNAMICS OF SEMI-AQUATIC TURTLES IN AN ENCLOSED POND SYSTEM ACROSS A SMALL LANDSCAPE

Introduction

An important part of applying proper conservation strategies for species management is to recognize the significance of population dynamics across the landscape because many game species occur as metapopulations in spatially heterogeneous environments (Pulliam and Danielson 1991, Dias 1996, Ritchie 1997). For semi-aquatic species, dispersal among wetlands is vital for maintaining regional population stability (Harrison 1991, Thomas et al. 1999). Such dispersal is dependent on the availability, proximity, quality, and heterogeneity of wetlands in the landscape and the facility with which individuals can travel among them- landscape connectivity (Thomas et al. 1999, Gibbs 2000, Marsh and Trenham 2001). Recent studies have recognized that management schemes directed at wetlands as individual units with only narrow terrestrial buffer zones do not adequately capture the mosaic of habitats used by the semi-aquatic species and that the inclusion of wide terrestrial buffer zones in wetland management is recommended (Joyal et al. 2001, Roe and Georges 2008).

Freshwater turtles are taxa dependent on pond ecosystems and surrounding landscapes (Pitman and Dorcas 2009). Wetland connectivity and the overland

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composition are essential for successful dispersal of freshwater turtles. Semi-aquatic turtles move across landscapes in search of mates, suitable aquatic habitats, new resources, nesting sites, or in response to drought conditions (Parker 1984, Tuberville et al. 1996, Doody et al. 2002, Bowne et al. 2006, Steen et al. 2012). Costs associated with such movements include increased risk of predation, dehydration, and increased mortality due to vehicular traffic (Aresco 2005). As different species vary in their physiology, home range sizes, and habitat requirements, the amount of time spent overland can also be species specific. The decision to leave an aquatic habitat can be influenced by environmental factors such as hydro-period, water temperatures, air temperatures, and rainfall (Litzgus et al. 2004). In addition, variable responses may exist between individuals of the same species that differ in age, sex, or body size (Roe and Georges 2008, Pittman and Dorcas 2009, House et al. 2010).

The patterns in which size and sex affect turtle overland movements vary among different studies (Thomas et al. 1999, Carter et al. 2000, Litzgus et al. 2004, Bowne et al. 2006). While some studies concluded that males move more frequently than females (Morreale et al. 1984, Tuberville et al. 1996) others found that females moved more often due to nesting migrations (Steen and Gibbs 2004, Aresco 2005, Gibbs and Steen 2005). Based on “reproductive strategies hypothesis”, it is generally believed that females are more likely to make terrestrial movements during the nesting season while males usually make overland movements during mating season (Litzgus et al. 2004). Also, juvenile turtles are less likely to move overland because they are not reproductively active and because they face a higher risk of predation and dehydration (Gibbons 1990). However,

some studies have found no sex or size specific bias to inter-pond movements (Carter et al. 2000, Ryan et al. 2008, House et al. 2010).

It has been documented that anthropogenic alterations of the landscape can jeopardize successful dispersal of freshwater turtles (i.e., Areso 2005, Gibbs and Steen 2005). For example, turtles are thought to be particularly vulnerable to road mortality because of their relatively slow travel speeds (Ashley and Robinson 1996, Steen and Gibbs 2004, Szerlag and McRobert 2006). However, to my knowledge, no one has documented how direct human actions such as harvest pressures affect dispersal rates. This issue is vital due to recent changes in turtle harvest management regimes in the United States of America (US). Texas in particular protects commercial freshwater turtle harvest in public but not private water bodies (Texas Parks and Wildlife 2007). This regime operates under a major assumption that protection of public waters should buffer the remaining regions against overexploitation (McCullough 1996). In other words emigration from non-harvested private and public waters acts to replenish harvested ponds and keep the populations sustainable. Thus, all harvest is drawn from private water and the public waters act as source populations for impending commercial harvests. However, no one has validated the effectiveness of this management regime.

In this chapter, I investigated spatial and temporal freshwater turtle movement in an enclosed pond system across a smaller landscape but with higher resolution than previously reported studies. My goals were three-fold:

1. To design an innovative method to study inter-pond movement of freshwater turtles

2. To determine under which environmental cues are freshwater turtles likely to make terrestrial movements across the landscape
3. To determine whether the pond that has been depleted (simulated harvest) of turtles is likely to be repopulated by turtles from surrounding ponds

Previous studies used various methods to investigate different aspects of movement patterns for freshwater turtles: pitfall traps (Gibbons 1990, Roe et al. 2009), radio telemetry (e.g., Forsythe et al. 2004, Litzgus et al. 2004), and traditional aquatic trapping methods (e.g., crab pots and hoop nets; Thomas and Parker 2000, Roe and Georges 2008, House et al. 2010). Trapping methods are based on capture-mark-recapture techniques that rely on the ability to recapture marked turtles. Trapping is usually seasonal or done at intervals, but rarely conducted continuously, or if so, not on a long-term basis (e.g., every day of the year during multiple years). Traps are usually checked daily, but information on specific times of the day that turtles are likely to be active is lacking. In addition, captured individuals remain in traps until traps are checked, preventing movement or dispersal data aside from differing points of recapture. Radio telemetry can give more precise data on overland movements and correlate such activity to environmental factors (Roe and Georges 2008). However, the radio tracking period affects such models (Roe and Georges 2008) and high-resolution monitoring of overland activity using radio telemetry would require locating turtles several times/day for extended periods of time. In this study, I designed a method to study the inter-pond movement by using the PIT (Passive Integrated Transponders) tags and a stationary PIT tag reader. This is a non-invasive stationary reader system, including the addition of camera traps for determining direction of movement alongside detection of individuals.

Although overland dispersal of freshwater turtles may appear to be well studied, my research project was unique for several reasons. The study design allowed me to monitor not only the day of the movement but the time of the day as well. The uniqueness of the system also allows us to test the source-sink theory. The pond invasion of freshwater turtles has been documented in previous studies (i.e., Tuberville et al. 1996), but to my knowledge no one has addressed movement patterns in the light of harvest. My goal was first to assess harvest intensity, observe if the population can recover, and if so, evaluate in what time frame the harvested pond can be repopulated. Although previously published studies on inter-pond turtle movement were able to encounter seasonality patterns, the studies were usually unable to establish the time of the day turtles moved. On the other hand, I was able to monitor the time of the day when movements occur, every day, regardless of the time or conditions. Also, I am not aware of any published study that examined turtle dynamics in the light of harvest. Results of these studies can be used when writing policies and making managerial decisions in order to protect freshwater turtles from overharvest.

Methods

Study Site

This set of studies was conducted in a complex of ponds within a private property parcel in Guadalupe County, Texas. The site contains three ponds completely fenced to prevent turtle immigration/emigration from outside of the system (Fig 3.1). In addition, one of the ponds is fully enclosed and has a “gate” built into the fence which facilitates monitoring turtle movement between Enclosure Pond 1 and the other two ponds. The

second enclosure contains two ponds, called the Lake and the House Pond which originally were not fenced separately. In no-drought conditions, the Enclosure Pond 1 and House Pond have perimeters of 96 and 87 meters, respectively. The Lake is unique, because, in a sense, it represents two ponds connected by a 5m wide and 45m long canal. During droughts or the typical Texas summer, this canal dries, splitting the Lake into two separate ponds. In the severe 2011 drought, not only did the canal dry, but water had to be pumped from the east side of the Lake to the west side and to the House Pond in order to prevent them from drying out. The Enclosure Pond 1 was pumped dry in 2009 in order to allow complete removal of turtles to enable this investigation. After turtles were removed, water was replaced in Enclosure Pond 1 water was replaced and a single turtle released into it. The turtle gate remained closed throughout 2010 to confirm that the pond perimeter fencing was “turtle-proof”.

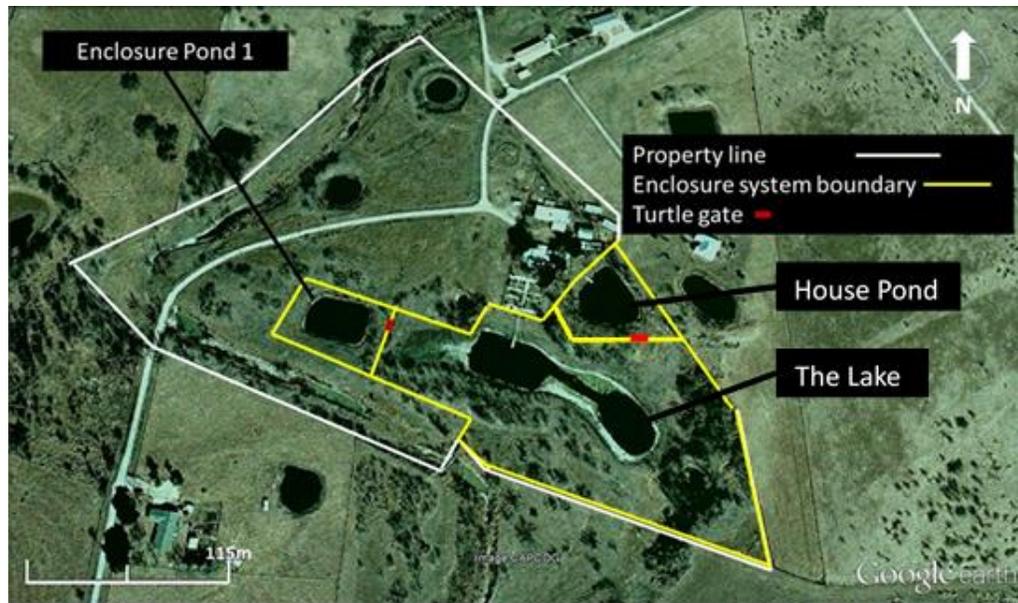


Figure 3.1: Aerial image of the study area used to monitor the interpond movement of freshwater turtles. The image shows the enclosure system boundary (primary system) that includes 4 ponds that are completely fenced off with a 2 cm × 4 cm horse fence panels to restrict global overland movement of turtles in and out of the system. Originally, Enclosure Pond 1 was fenced off from the remaining ponds, with a single opening allowing movement (turtle gate). This gate was opened on July 2011. Later, an additional gate was crated between the Lake and the House pond in February 2013.

Study Design

In the spring of 2011, I populated the Enclosure Pond with PIT tagged turtles that I trapped in the Lake and House Pond. To increase sample size, I also included turtles trapped from ponds on a private property in Blanco County, Texas. I finished populating Enclosure Pond 1 on June 4th, 2011, with a total of 63 PIT tagged turtles and 1 male untagged red-eared slider (*Trachemys scripta elegans*) representing the original single male stocked to test the fencing in 2009. Of the 64 turtles in the Enclosure pond, two were softshells (*Apalone spinifera guadalupensis*), four were Texas river cooters (*Pseudemys texana*) and the rest (58) were red-eared sliders. Out of 58 red-eared sliders, 29 were females, 25 were males, and four were hatchlings, and since they were the most

abundant species in the pond I primarily focused on this species. I allowed ~a month long “cool down” period before opening the turtle gate in order to prevent any movement simply due to turtle displacement into the new environment. I opened the gate on July 14th, 2011. Additionally, throughout the year of 2011, 19 additional turtles that were found in the Lake portion of the system were chipped and returned to the Lake.

The movement of turtles in and out of the Enclosure Pond 1 was monitored in two different ways: ISO-2001 (Biomark©) chip reader and RECONYX© game camera (Fig 3.2). The reader antenna was placed just below the surface at the turtle gate, and the reader was connected to the power supply at all times reading the chip numbers and the date and time turtles cross the gate. Stored data can be downloaded on a computer at any time. The game camera is placed just above the gate capturing the photographs of not only marked individuals but also any non-chipped individuals in the Lake and House Pond moving between the ponds. This detection array provides an opportunity to follow the number of adults in the Enclosure Pond 1 from day to day and to evaluate the parameters affecting movement into and out of the pond. Later in the study, a second monitoring system identical to the original one was placed between the House Pond and the Lake, monitoring movement from 1 February 2013 to 31 October 2013.



Figure 3.2: Stationary reader system placed at the only opening (turtle gate) of otherwise enclosed area (Enclosure Pond 1). While the reader scanned PIT-tagged turtles that pass through the gate, the game camera recorded the images and the direction of the movement.

I first monitored inter-pond turtle movement between the Enclosure Pond 1 and the rest of the system until harvest season of the following year, May 2012, in order to investigate environmental cues that trigger overland activity. In May 2012, I simulated a harvest event in the Enclosure Pond 1 by trapping the pond using 76.2 cm diameter hoop nets baited with canned sardines - the traditional method used by commercial turtle harvesters (Fig 3.3). The first harvest event lasted from 18 May 2012 to 26 May 2012 with a total of 140 trap days. I continued to monitor the inter-pond movement after the harvest for the following 12 months and simulated the second harvest event from 9 June to 16 June 2013 with a total of 140 trap days, and continued to monitor the system for the following six months.



Figure 3.3: A “typical” hoop net trap used by commercial trappers for collecting freshwater turtles from the wild. (Photo by Jaqueline Ferrato)

Data Analyses

As evidence for the effectiveness of the monitoring system, I first represented an overview of the individual movement events per week based solely on the chip reader data, for the period from July 2011 to May 2012, which included multiple movement events of the same individuals during the same week. I also included examples of game camera images capturing the movement events.

To correlate activity events to environmental factors, I used logistic Generalized Linear Mixed Effects Modeling (GLMM; Zuur et al. 2009). In this modeling approach, I used only chipped adult red-eared sliders as a subset of the total number of red-eared sliders within the entire system, and treated each individual chip number as a random effect since the movement events by the same turtle may not be independent. The response variable was binary- the presence or the absence of activity. In other words, if an animal was recorded on the chip reader at a particular day of the year, the response variable took the value of 1 and 0 if an individual was not detected by the reader. The full model included the following factors: turtle size- straight line carapace length (CL) measured in millimeters, maximum daily temperature, season, rain event, and the number of days since the last rain event. Maximum daily temperatures were obtained from the National Oceanic and Atmospheric Administration (NOAA) weather station, located in New Braunfels, Texas (29.704N, 98.029W). The data were freely available on the NOAA website. Rainfall data was obtained directly from an on-site rain gauge. However, the rain event in the model was presented as a binary variable with values 0 (representing no rain event) and 1 (representing rain event of > 1 mm). The factor “season” included calendar seasons: spring (March-May), summer (June-August), autumn (September-November),

and winter (December-February), and autumn was used as a reference category. The full model also included an interaction term between the season and maximum daily temperature and an interaction term between the season and rain event. I then compared the full model to alternative models using Akaike's information criteria (AIC; Burnham and Anderson 1998). To conduct the analyses, I used the `glmmML` function in R programming language because it estimates the model parameters by maximum likelihood and allows AICs to be calculated (Zuur et al. 2009). To choose the best model, I calculated the Akaike weights for each model, which represents the relative probability of each model being the best model. Two sets of models were conducted, one for each sex, because the preliminary data exploration showed lower AIC values for full model (AIC = 600) for male and female separately than when both sexes were pulled together (AIC = 1252).

Based on the chip reader data and additionally the game camera data, I evaluated the total number of turtles in the Enclosure Pond 1 just prior to the first harvest event. While the chip reader recorded only PIT tagged individuals, the game camera recorded additional non-chipped turtles that were originally present in the Lake or House Pond. However, based solely on the images, it was not possible to distinguish each individual non-chipped turtle. Therefore, I only recorded the daily number of turtles entering/exiting the Enclosure Pond 1, with the total number of non-chipped turtles in the Enclosure Pond 1 representing the difference between the number of turtles entering and the number of turtles exiting the pond. Based on this simple calculation, I was able to determine the total number of turtles in the Enclosure Pond 1 at any given time and therefore the harvest intensity for both harvest events. I calculated the total number of turtles at the end

of every month post-harvest to demonstrate the migration patterns and potential invasions into the depleted stock. In order to assess population growth rates following the harvest events, I evaluated the relationship between the total numbers of individuals at each month. Specifically, a total number of turtles was calculated at the end of each time period- month. I used segmented regression (Muggeo 2003, Ricca et al. 2014) to describe population growth patterns within the 12 months following the first simulation event. I conducted the model selection approach by using the Akaike Information Criterion corrected for small sample size to test a linear and two-slope model (AIC_c; Burnham and Anderson 1998). The significance of each slope was based on 95% confidence intervals. For this analysis, I used segmented package in Program R (Muggeo 2008).

Results

An Overview of the Efficiency of the Monitoring System

The stationary chip reader proved to be a reliable method for recording passage of turtles through the gate. For example, within the first 9 months, 46 PIT-tagged turtles (73% of all chipped turtles) passed through the gate and were recorded by the reader on 105 different occasions. Movement did not appear to be sex biased: 23 females, 22 males, and one juvenile passed through the gate. The number of individual's movements varied from 1–12. Twenty-eight turtles moved on only one occasion while 18 moved more than once. Six individuals moved in and out of the system on several occasions during a single day (range = 2–4, mean = 2.3). Preliminary results revealed predictable seasonal activity in winter, with 0–1 movement events per week, and highest activity in the spring, with up to 37 passages per week (Fig 3.4). All turtles were active during the day, with no

nocturnal activities recorded. Out of 105 movement events, 42 were recorded in the morning (0630 to 1200 hours DST) and 63 in the afternoon (1200 to 2030 hours DST). Based on the original placement of tagged turtles (Enclosure Pond 1), I could speculate on the direction of the movement. However, because the reader was set to continuously record the tags, the data often consisted of numerous readings of the same tag within a short period of time (several minutes), which created some level of uncertainty of the final direction of the movement using the reader alone. However, the combination of the chip reader and the camera time stamp enabled us to determine the direction of the movement of each tagged turtle using the camera images (Fig 3.5-3.8).

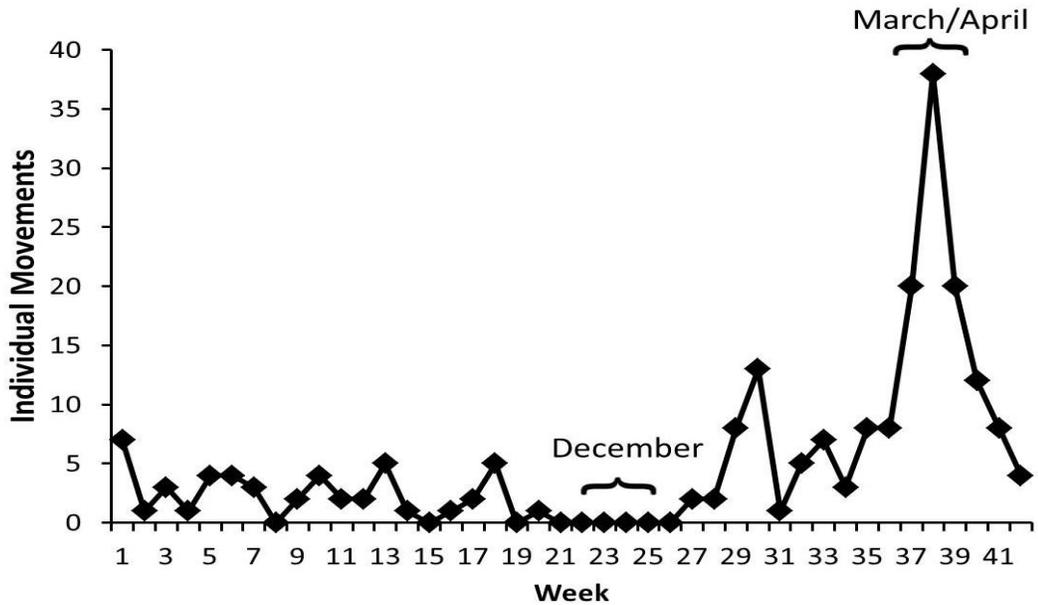


Figure 3.4: Number of individual movements recorded by the stationary chip reader placed between the Enclosure Pond 1 and the rest of the system. The data were sorted by the week from time of the opening the turtle gate in July 2011 throughout May 2012. The movement activity was seasonal, with very few movements in the winter and the highest activity in spring.



Figure 3.5: Red-eared slider (*Trachemys scripta elegans*) passing through the turtle gate. The image was captured with a RECONYX[®] game camera that was mounted 1 m vertically above the gate opening.



Figure 3.6: Common snapping turtle (*Chelydra serpentina*) passing through the turtle gate. The image was captured with a RECONYX[®] game camera that was mounted 1 m vertically above the gate opening.



Figure 3.7: Guadalupe spiny softshell (*Apalone spinifera guadalupensis*) passing through the turtle gate. The image was captured with a RECONYX[®] game camera that was mounted 1 m vertically above the gate opening.



Figure 3.8: Texas river cooter (*Pseudemys texana*) passing through the turtle gate. The image was captured with a RECONYX[®] game camera that was mounted 1 m vertically above the gate opening.

Environmental Factors Influencing Turtle Overland Activity

To test which environmental cues triggered overland movement, I used only adult chipped red-eared sliders that were stocked in the Enclosure Pond 1 because they represented the vast majority of the total chipped individuals ($n = 53$). In the GLMM models, I used the period from July 2011 to May 2012, the period prior to the first harvest simulation.

In the case of females, the best fit model included: season, rain, the number of days since the last rain event, and the maximum daily temperature as explanatory variables ($w_i = 0.403$; Table 3.1). Females were significantly more active during spring

season ($P < 0.01$). Individuals were more active during rain events ($P = 0.04$) and the activity decreased as the days since the last rain event increased ($P < 0.01$). However, maximum daily temperatures did not significantly influence the movement patterns ($P = 0.13$).

For males, the best fit model included: season, rain, the number of days since the last rain event, maximum temperature, and the interaction term between the season and the temperature ($w_i = 0.284$; Table 3.2). In particular, there was a significant positive interaction between the winter season and the temperature ($P = 0.04$). This suggested that male movement during winter is more likely to occur on warm days. In addition, the rain event was not a significant factor in overland activity ($P = 0.1$). The number of days since the last rain event factor was not significant based on our statistical inference cut off, but it can be seen as trending toward significance ($P = 0.07$).

Table 3.1: Results from a model selection analysis using Akaike Information Criterion (AIC), to test the influence of turtle size and various environmental factors on overland activity of female red-eared sliders (*Trachemys scripta elegans*). The model containing season, the event of rain, number of days since the last rain event, and maximum daily temperature as predictors ranked highest.

Predictor	# of parameters	AIC	Delta AIC	AIC Weight
Season+Size+RainDay+DaysSinceRain+MaxT+Season:MaxT+Season:RainDay	9	627.3	6.0	0.02
Season+RainDay+DaysSinceRain+MaxT+Season:MaxT	7	624.1	2.8	0.10
Season+Size+RainDay+DaysSinceRain+MaxT	7	623.1	1.8	0.16
Season+RainDay+DaysSinceRain+MaxT	6	621.3	0	0.40
Season+RainDay+DaysSinceRain	5	621.8	0.5	0.31

Table 3.2: Results from a model selection analysis using Akaike Information Criterion (AIC), to test the influence of turtle size and various environmental factors on overland activity of male red-eared sliders (*Trachemys scripta elegans*). The model containing season, the event of rain, number of days since the last rain event, maximum daily temperature, and interaction between the season and maximum daily temperature as predictors ranked highest.

Predictor	# of parameters	AIC	Delta AIC	AIC Weight
Season+Size+RainDay+DaysSinceRain+MaxT+Season:MaxT+Season:RainDay	9	634.6	2	0.10
Season+RainDay+DaysSinceRain+MaxT+Season:MaxT	7	632.6	0	0.28
Season+RainDay+DaysSinceRain+MaxT	6	633.5	0.9	0.18
Season+RainDay+DaysSinceRain	5	632.9	0.3	0.24
Season+DaysSinceRain	4	634.3	1.7	0.12
Season+RainDay	4	635.6	3	0.06

Harvest Intensity, Post-harvest Events, and Movement Patterns

Based on the chip reader and game camera data at the beginning of the first harvest event, the estimated number of adult red-eared sliders in the pond was 42. Of these, 22 were originally chipped turtles that were placed in the Enclosure Pond 1, two that were found around the lake and chipped after the experiment started, and 18 non-chipped turtles. During the first harvest event from 18-26 May 2012, 16 red-eared sliders were harvested with 0.11 capture per unit effort (CPUE). Of these, six were the original stock turtles from Enclosure Pond 1 while the rest (10) were non-chipped turtles. Based on the abundance estimation, the harvest intensity was 38.1%, leaving the population at 26 turtles. By the end of August, the estimated abundance in the turtle depleted pond was back to 41, by the end of September it was 47, and remained relatively constant until the second harvest simulation in June 2013.

Although the population in the Enclosure Pond 1 seemed to recover relatively quickly by immigration from the Lake, few chipped individuals moved through the gate after the first harvest simulation. Six of the 18 chipped stock turtles that stayed in the Enclosure Pond 1 after the first harvest simulation moved through the gate in the following 12 months. Out of the rest of the original stock that was in the Lake prior to harvest, only six made overland movements in the following 12 months. Finally, out of additionally marked turtles during the first year of the study, seven were recorded by the chip reader in the following year. However, 16 additional non-chipped turtles were recorded by the game camera in the Enclosure Pond 1 by June 2013. At the beginning of the second harvest simulation in June 2013, the estimated number of turtles in the pond was 49; 25 chipped turtles and 24 non-chipped turtles.

The depleted population ($N = 26$) grew to 47 individuals by the end of September, which was six individuals higher than what was considered stable prior to harvest (Fig 3.9). After September, population size fluctuated between 47 and 49 turtles until June 2013. For the period between the two harvest events, the relationship between the population size and month was described by a two-slope model rather than a single slope model ($AIC_c = 68.12$ and 89.87 , respectively). Significant population growth occurred within the first four months after the harvest ($r = 0.47$, 95% CI = 2.86–4.92). For the rest of the period, population was considered stable ($r = 0.25$, 95% CI = -0.42–0.66; Fig 3.10).

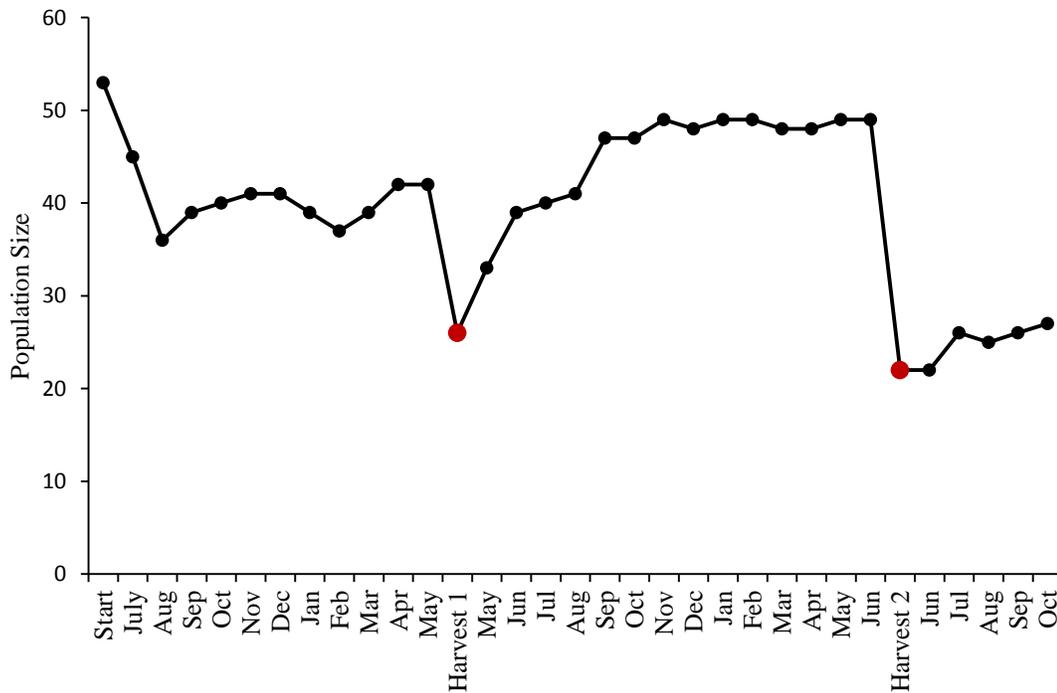


Figure 3.9: The number of red eared sliders (*Trachemys scripta elegans*) in the Enclosure Pond 1 at the end of each month from July 2011 to October 2013. The population size was calculated based on the chip reader data and the game camera data recording the movement. Two harvest simulations took place: in May 2012 and June 2013, and the graph also presents the number of turtles immediately before and after harvest events.

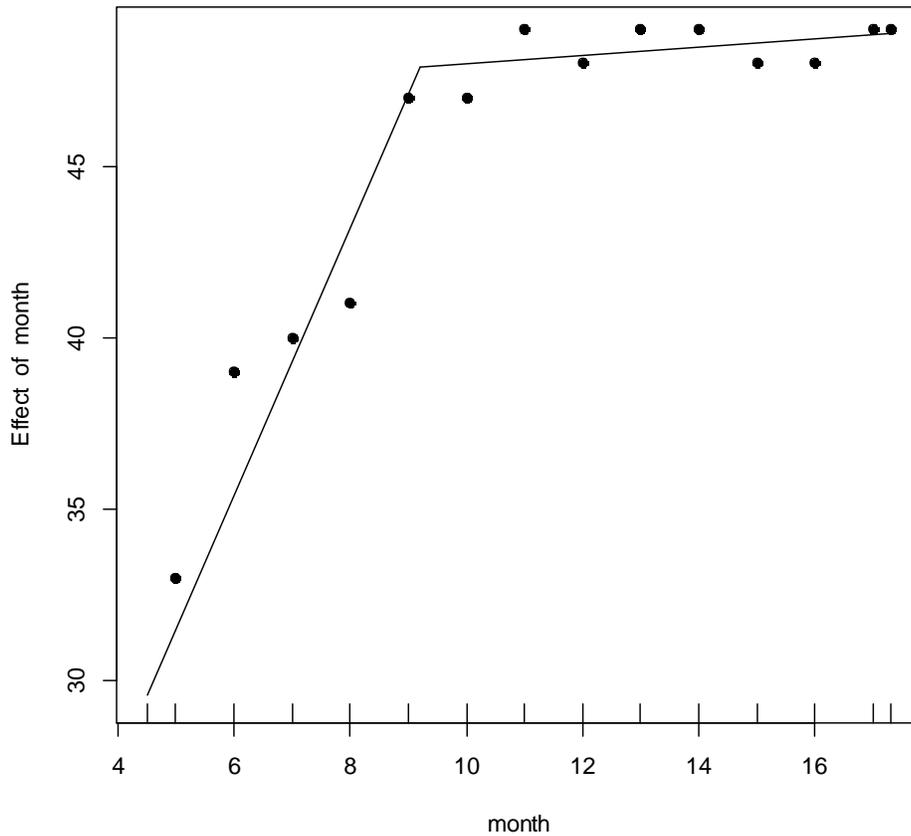


Figure 3.10: Segmented regression of red eared slider (*Trachemys scripta elegans*) population size after the first harvest simulation (May 2012) against month. Regression illustrates two significantly different slopes from May 2012 to June 2013.

In the second harvest event, from June 9nd to June 16th 2013, I captured 24 red-eared sliders, with 0.19 CPUE. Six turtles were previously chipped while 18 were non-chipped turtles. The harvest intensity was 49.0%. I monitored the movement throughout October 2013. Similarly to the first post-harvest event, the population experienced a growth within the following months. However, by the end of October, the population recovered to only 27 individuals, which is approximately 55% of the pre- second harvest population size and 64.3% of the pre-first harvest population size.

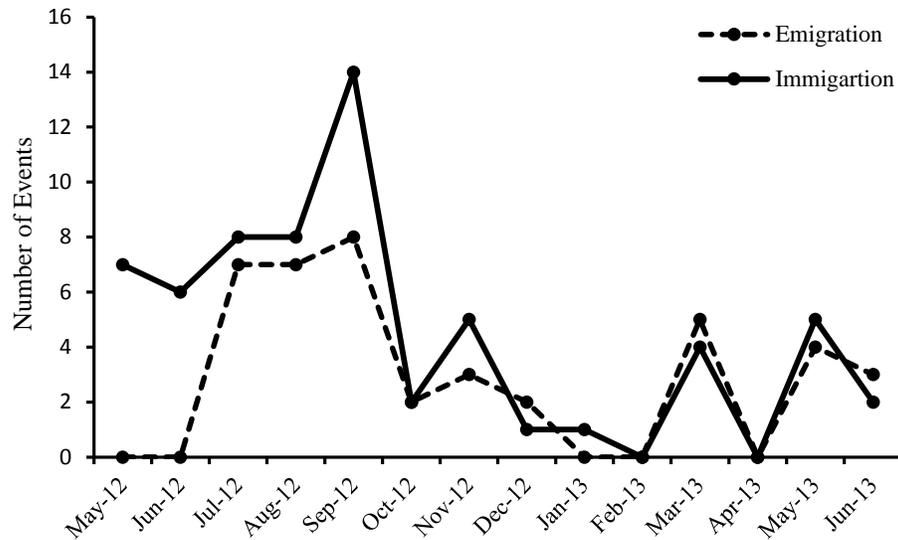


Figure 3.11: Number of immigration and emigration events in Enclosure Pond 1 from May 2012 to June 2013, the period between two harvest events.

Figure 3.11 enables visualization of turtle immigration and emigration dynamics after the first harvest event, the data indicate higher immigration rates during the first four months. However, emigration rates were also quite high between July and September of 2012. For the rest of the period, immigration and emigration rates were relatively balanced. In February 2013, I opened the second monitoring system between the House Pond and the Lake. Interestingly, for the period when both monitoring systems were operating, from February 2013 to November 2013, the activity was continuously higher at the Gate 1 than at the Gate 2 (Figure 3.12). Even after the second harvest event in June 2013, when turtles harvested from Enclosure Pond 1 were released into the House Pond, Gate 2 showed little activity in comparison to activity at Gate 1.

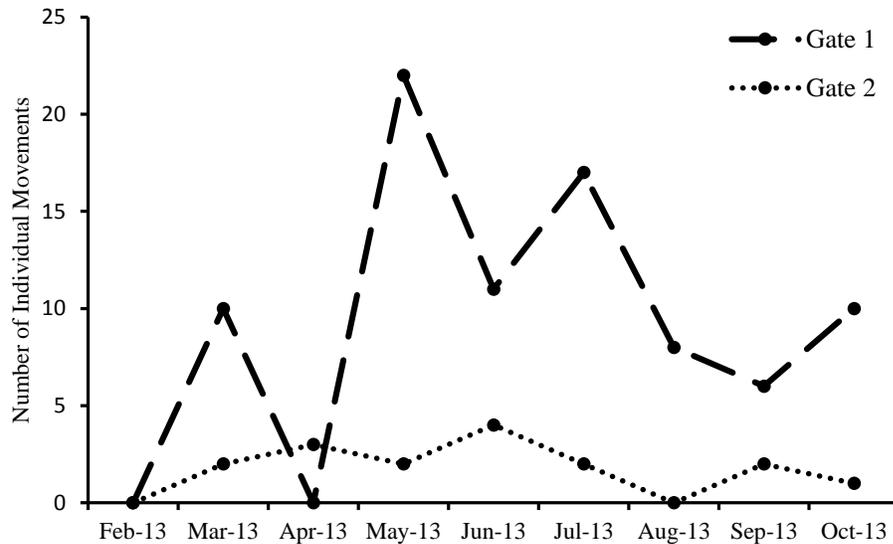


Figure 3.12: Number of individual turtle movement events recorded by two monitoring systems: Gate 1- linking the Enclosure Pond 1 and the Lake, and Gate 2- linking the House Pond and the Lake.

Discussion

I demonstrated that it is simple to convert a portable Biomark[®] PIT tag reader system into a stationary PIT tag reader system enabling us to monitor freshwater turtle interpond movement. This technique requires initial trapping and PIT tagging individual turtles. However, after initial handling there is no more need to handle animals. It is less labor intensive than either trapping constantly or long-term radio telemetry. Furthermore, if the equipment is maintained, the system can run for several years. Although the reader did not record the exact times turtles exited the water bodies but rather the times of the passage through the gate, this method is likely to be a suitable way to link weather conditions and periods of the day to the turtle movement patterns.

My study was conducted on private property with nearby access to an electric power grid. The use of solar panels as the source of power would improve the system,

especially for monitoring projects in more remote areas. At the beginning of the experiment, I constructed only one reader station and used a relatively small enclosed area for proof of concept testing. The second reader between the House pond and the Lake was constructed approximately a year and a half after the experiment began. Therefore, the second reader was not included in the analyses of environmental factors on the movement.

The results show that the first reader (i.e. Gate 1) recorded considerably more activity than the second reader (i.e. Gate 2). For example, for the period from February to October 2013, the period throughout which the second reader was active, 83.5% of the overall movement was made between the Enclosure Pond 1 and the Lake while only 16.5% of movements were made between the House Pond and the Lake (Figure 3.12). This is particularly interesting because the population in the House Pond has increased subsequent to harvested turtles from the Enclosure Pond 1 being released into the House Pond. Therefore, I expected movement through the second gate to be higher than movement through the first gate, particularly after the harvest events. I speculate that this result was due to a different topography, with the House Pond having steep sides, potentially making it difficult for turtles to exit. Also, the House Pond is located in a more open area with limited shade availability, potentially influencing movement. Therefore, future studies should include larger landscapes with a variety of topographical features to more clearly capture the nuances in freshwater turtle movement dynamics.

My study potentially underestimated the magnitude of movement, due to the possibility that some individuals did not walk along the fence but rather returned to the water. I believe that such occurrences were minimal due to the small scale of the

experiment (e.g., small fence perimeter) and the fence was simply serving the role of the aluminum flashing in commonly used drift fences (Gibbons 1990). This system was designed to be expanded using additional gates to open the three ponds to allow movement between the ephemeral creek and the additional ponds. On a larger landscape level, monitoring movement in this manner would be costly, because it would require enclosing larger sections and purchasing additional chip readers and PIT tags. However, high-resolution interpond movement dynamics of freshwater turtles on a larger landscape level are still poorly understood and expanding this approach to a larger scale would contribute to the understanding of these movement patterns.

For the resolution I sought on movement dynamics, alternative methods are actually more expensive. For example, while radio telemetry would address these same questions, the labor costs and necessity for shift work across 24-hr, daily schedules would be dramatically (and prohibitively) more costly. One way to reduce the cost for a larger scale study would be to use flashing to enclose the movement areas. Gibbons (1990) used aluminum flashing to enclose several kilometers of perimeter of experimental water bodies in order to study the interpond movement of slider turtles. Therefore, instead of using a costly fence system, one could use aluminum flashing that is commonly used to construct drift fences, with pitfall buckets being replaced with reader systems. Unfortunately, this alternative has its own trade-offs. I consider flashing to be very disadvantageous in its relative vulnerability to tree fall, livestock, and vehicular passage. Further, the urban wildland interface in many states provides an opportunity to create larger scale studies that follow our new approach with relatively minor changes to existing fencing systems (bottom integrity, gate installation, and readers). All methods

seeking to document wild animal movements in real time have tradeoffs. I consider this new approach to minimize several negative aspects of radio telemetry costs and provide data at a finer resolution than can be achieved by other methods. Even in the study by Gibbons (1990), once trapped, the animals were contained until release, while in our system they are constrained in an exit point but not in movement beyond that single constraint. While this too is a tradeoff, I argue that it is a lesser one than daily point observations from telemetry or daily capture locations in a large field enclosure with pitfalls.

Environmental factors play important roles in the overall activity of wildlife. For aquatic turtles, overland activity increases the risk of dehydration and predation, but these excursions are made in search for mates, better resources, or nesting sites (Milam and Melvin 2001, Bowne et al. 2006, Steen et al. 2012). In my study, I directly showed that females and males use different cues for making decisions on exiting the pond. The rain event significantly stimulated activity of females while longer dry periods significantly decreased the activity of females; temperatures, however, do not seem to affect the movement. However, females are more active during spring months, which is probably related to their nesting migrations (Steen et al. 2012). For males, the patterns were not as clear due to a significant positive interaction term between the winter season and temperatures. This suggests that males could potentially start being active before females within a given year, but that such activity occurs only on warmer days. If the mating season begins just prior to nesting season, my findings are consistent with the “reproductive strategies hypothesis”, which states that females are more likely to make

terrestrial movements during the nesting season while males usually make overland movements during mating season (Litzgus et al. 2004).

Other environmental factors that might influence overland movements. For example, it has been documented that the hydro-period of wetlands play an important role as freshwater turtles respond to the drying periods (Roe and Georges 2008). In my study, I measured the depth of the ponds once a month. None of our ponds completely dried out during the study period because water was pumped into the ponds from the nearby creek in the dry months. As an indirect indication of the drying period, I used the number of days since the last rain event as our factor variable. As the number of days since the last rain event increased, the activity of turtles decreased probably due to the increased risk of dehydration. Although I can assume that the hydro-period is negatively related to the number of days since last rain event, it did not appear that the hydro-period of the ponds decreased to the threshold that would trigger movement due to a completely dry pond. Also the quality of the pond can play an important role (Roe and Georges 2008), such as the physical and chemical properties of the water itself. I tested the pH and DO (dissolved oxygen) of the ponds, using HANNA[®] instrument, but found that neither of these two properties differed between the Enclosure Pond 1, the Lake pond, and the House Pond. Additionally, all ponds consisted of similar aquatic and land vegetation; therefore, movement and the final destination of turtles is less likely to be caused due to better resources in one vs other ponds.

Significance of seasonality but not air temperatures in the female model is likely due to female physiology and nesting migrations. Alternatively, one can measure the actual water temperatures and estimate correlations with air temperatures. For example,

more turtles are likely to bask in the early spring months when water temperatures are substantially cooler than the air temperatures (Harless and Morlock 1979), but how these relationships between water and air temperatures relate to overland movement requires further exploration.

My last goal for this chapter was to describe how the system would behave after a single pond (Enclosure Pond 1 in this case) was directly depleted by simulating a harvest event. Although this entire set of studies was conducted in a small landscape, this last portion of the study is directly relevant to the current harvest management regimes in Texas. Since 2007, Texas allows unlimited harvest in private water bodies while protecting only the public water bodies. This harvest strategy assumes that the protected populations will act as a buffer and replenish depleted populations. However, this assumption has no scientific evidence, and, to my knowledge, my study was the first attempt to justify this assumption. Although one flaw of this study is that it was done on a small landscape comparing to the overall ability of turtles to travel longer distances (Schubauer et al. 1990, Ernst and Lovich 2009), the experimental design has allowed me to study the population dynamics in a single pond on a much higher resolution. I was able to know the exact size of the population in the Enclosure Pond 1 at any given time, which allowed me to determine the harvest intensity and to describe how the model/population behaves after it was directly depleted by harvest. However, the information presented in this portion of my study should be taken with caution as the level of immigration into sink population is directly related to turtle abundance in the source population. In my study, I was only measuring turtle abundance in the sink population (Enclosure Pond 1) while the abundance of turtles in the source (Lake) was unknown. However, based on the

sink population as well as the second chip reader data, I was able to indirectly evaluate the source-sink management of freshwater turtles. According to my study, the level of freshwater turtle movement is not sufficient to maintain sink populations. Consequently, in Texas, this means harvest is essentially unlimited for turtles and by no means sustainable.

At the beginning of the experiment in July 2011, I observed a slight drop in the population size which was expected as the turtles were reaching an equilibrium between the two ponds. However, I did not expect the fast recovery that I observed after the harvest in 2012. Moreover, the fast recovery within the next 3-4 months was mostly due to non-chipped turtles entering the depleted pond. This suggested that although turtles will use the density independent factors such as the environmental cues for leaving the water, their final destination within the system would appear to be density dependent from these data. In other words, once a turtle inhabited the depleted pond, it was likely to stay there for the extended period of time due to lower overall population density. The segmented regression shows that the population is in a sense resembling the logistic curve, as the population stabilizes at the beginning of the winter and remains constant even throughout the following spring months when the overland activity is more frequent.

There is a likelihood that the unexpected rapid repopulation of Enclosure Pond 1 occurred due to overcrowding of turtles in the rest of the system. Although I cannot entirely rule out the possibility of overcrowding, the data from the second gate suggests that overcrowding was not the primary reason for this immigration event into the harvested pond. Unfortunately, the second gate had not been established in 2012, when

the first harvest event occurred, but the data from 2013 suggests that the addition of turtles into the House Pond did not result in higher migration activity when turtles added to the system created higher densities. Anecdotally, throughout course of the experiment, only one harvested turtle subsequently found crossing the first gate.

After the second harvest in June 2013, the population in the Enclosure Pond 1 was not able to recover to its pre-harvest size. Within the following five months, the time period for recovery after the first harvest, I observed similar immigration patterns but at a much lower magnitude, bringing the population only to 55% of its original pre-harvest size. This suggested that although immediate immigration will occur, the source population will eventually not be sufficient to replenish the sink. It would be particular relevant to know, how many turtles in the Lake remained after immigration events into the Enclosure Pond 1, and is the equilibrium reached within the first six months post-harvest. This study demonstrates that turtles' ability to move to depleted pond is misleading evidence that spatially defined harvest management will ensure sustainability.

The current turtle harvest management regime in Texas may be sufficient to keep populations sustainable on the short term due to reported turtle movements and invasions into the newly established water bodies. My study calls for caution of continuous use of such a management regime absent additional regulations that would prevent harvesting of the same ponds or landscapes on a repeated basis. Although, superficially, it appears that this regime is efficient, in the longer run such practice can be disastrous even if wetland connectivity is high. In the simple design, I demonstrated that the continuous harvest of a single water body can very quickly result in significant changes that deplete the

population despite immigration patterns and apparent population growth (within a single pond population) after the first harvest event.

Because there is no harvest quota in Texas, the harvest intensity can be high. Since commercial trappers focus on adults only, setting no quota on the harvest of particular water bodies is a serious problem due to the nature of chelonian life histories and sensitivity of the adult age class (Congdon et al. 1994). Chelonian life histories characterized by slow generation time aid to conclusions presented in my study. For example, red-eared sliders in the wild mature at age seven (Gibbons 1990). Therefore, for Texas harvest management regime to be sustainable, harvest events should occur on a minimum of seven year cycles. The rapid, initial replenishment in the first post-harvest period did not account for other sources of mortality. In my study, the mortality was negligible since the system was fenced with predator exclusion fencing resulting in minimal natural predation, and there was no vehicular traffic, both of which are well known sources of mortalities. Therefore, even the first post-harvest immigration would be expected to be lower than what is reported here. If the source-sink management theory remains the basis for the harvest of freshwater turtles, future studies should focus on testing the different harvest quotas and establishing the proportion of source versus sink water bodies in order to maintain sustainable populations.

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CHAPTER IV

MODELING DYNAMICS OF FRESHWATER TURTLE FARMING IN THE SOUTHEAST US: PRODUCTION, PROFIT, AND CONSERVATION

Introduction

Harvest of wildlife on commercial levels without regard for sustainability can lead to declines of populations of species and species extinction (Halliday 1980; Heinsohn et al. 2004; Jonzen et al. 2001). Freshwater turtle populations have suffered from such declines and extinctions because of a long history of being exploited for meat, eggs, traditional medicine, and more recently the demands of the pet trade (Alves and Santana 2008; Chen et al. 2009; Enge 2005; Fordham et al. 2007; Nijman and Shepherd 2007). Harvest levels of wild populations have mostly been excessive and unsustainable (Eisemberg et al. 2011; Nijman and Shepherd 2007). Asia, China in particular, is the leading consumer of turtles in the world (Cheung and Dudgeon 2006; Gong et al. 2009; Xianlin et al. 2002). High demands for freshwater turtles for food has placed significant negative pressures on wild populations not only in Asia but also in other regions of the world (Brown et al. 2011; Ceballos and Fitzgerald 2004; Mali et al. 2014). For example, many North American species are being targeted to supply depleted Asian food markets (Ceballos and Fitzgerald 2004). To meet demand, captive breeding of turtles has expanded in the last two decades in China and other Southeast Asian countries (Haitao et al. 2008; Haitao et al. 2007; Pongtanapanich 2001), and freshwater turtle farming is a booming aquaculture business in the southeast United States of America (US; Hughes 1999).

In the US, Louisiana is a leading freshwater turtle exporter of both wild caught individuals and captive bred individuals (Mali et al. 2014). For export to Asian food markets, turtle trappers focus on harvesting the largest individuals from wild populations (Close and Seigel 1997), while US turtle farmers rear hatchlings for the pet trade and for export to Asian turtle farms (Hughes 1999; Jesse Evans- Concordia Turtle Farm, pers. comm.). While newborn hatchlings can be exported to foreign countries, the pet trade in the US is restricted to a minimum turtle size of 4 in (101.6 mm carapace length) specifically tied to turtle associated human *Salmonella* infections (Harris et al. 2010). Four inch turtles are sold to US pet stores, but according to turtle farmers there is currently no market in the US for turtles > 4 in (Jesse Evans- Concordia Turtle Farm, pers. comm.). Every year, turtle farms bring millions of dollars to the economy of Louisiana (Louisiana Department of Agriculture 2012). However, the number of hatchlings produced has decreased from 13.4 million in 2004 to 4.5 million in 2012 (Louisiana Department of Agriculture 2012; Figure 4.1). The Louisiana Department of Agriculture and turtle farmers speculate that the decline is due to lack of demand for hatchling turtles due to competition because of well-established Asian turtle farms (Jesse Evans- Concordia Turtle Farm, pers. comm.).

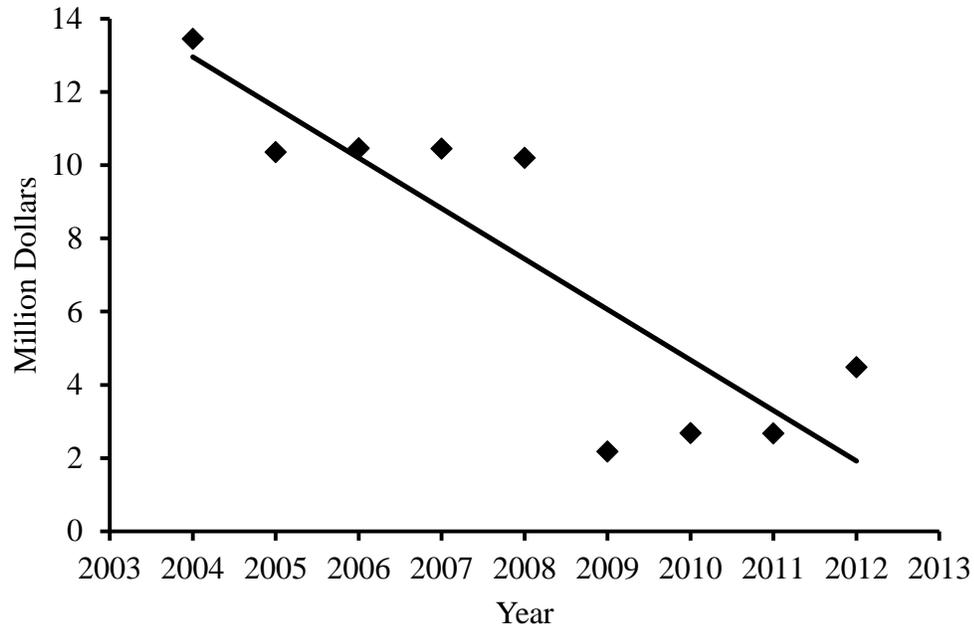


Figure 4.1: Annual production of hatchling turtles on Louisiana turtle farms from 2004-2012 reported by turtle farms to the Louisiana Department of Agriculture.

Apart from reports on annual hatchling production on farms, there are no models that describe biological and economic dynamics for this type of farming operation in the US. Traditionally, turtle farmers operated on a “trial and error” basis, slowly improving conditions (i.e., cleanness of the ponds) on the farms and modernizing the practices (i.e., using machines for cleaning the ponds; Jesse Evans- Concordia Turtle Farm, pers. comm.). The purpose of this study was threefold: 1) to use information and knowledge currently available for freshwater turtle biology under farmed conditions and develop a biological model that describes the dynamics of turtle production on a representative farm in Louisiana, 2) to modify this model and test production of adults on the farm by harvesting adult turtles from the stock for foreign meat markets in addition to raising and harvesting hatchling and 4 in turtles; and 3) based on the model developed above,

conduct sensitivity and break even analyses and describe profit requirements needed to be collected per adult turtle in order to make the same profit as traditional farming.

I sought to provide insights on the economy of farming operations by summarizing the cost, price, and demand for turtles in the past, but also by creating predictive models about future demand. I developed these models in order to explore the possibility of decreasing pressures on wild turtle populations by creating a supply of turtle meat through farming operations. The future of turtle farming is not only important for the economy of the region, but also has potential to serve as the foundation for conservation and recovery of wild turtle populations. For example, the rapid growth of the salmon aquaculture industry has outcompeted the fishing industry in some regions of the world (e.g., Alaska; Eagle et al. 2003). More relevant, farming and head-starting of the once endangered American Alligator (*Alligator mississippiensis*) not only enabled its recovery from endangered to delisted, but also enabled the current sustainable harvest of wild populations (Heykoop and Frechette 2001).

I chose the red-eared slider (*Trachemys scripta elegans*) as a model species. The red-eared slider has a large geographic range in North America (Ernst and Lovich 2009) and is one of the most commonly farmed freshwater turtles in the US. Although red-eared sliders are still considered common in the wild, declines due to unregulated harvest in the southeast have been reported (Brown et al. 2011). On US farms, red-eared sliders are produced and sold as hatchlings or 4 in turtles (i.e., yearlings); however, adult red-eared sliders are often found on Asian meat markets (Nijman and Shepherd 2007). I chose the red-eared slider due to its long tradition of being farmed in the US, resulting the greatest amount of knowledge about their life history and requirements under farmed conditions.

The majority of farming parameters (i.e., fecundity, stock density, etc.) were acquired from personnel at a representative turtle farm in Louisiana, which is one of the oldest and most successful turtle farms in the US. For the information that remained unknown (i.e., relationship between female size and her reproductive output), I incorporated a few simplifications in my models based on knowledge about these parameters for wild populations. Therefore, our quantitative results at this stage must remain a tentative approximation.

Materials and Methods

Traditional Turtle Farming in the Southeast US

Farms usually consist of a number of artificial ponds containing stock turtles, with enclosed sand beaches surrounding the ponds. Under current management regimes, ideally, all turtles are in the adult life stage. On well-established farms, adult turtles are wild caught. In order to maintain the stock, turtles are occasionally added either from the wild or from farmed hatchlings. Adults are not harvested, but maintained for egg production. Every year, gravid females nest on the pond beaches, and eggs are collected and incubated in indoor facilities. Females usually lay in the spring and summer months. The majority of turtles, including red-eared sliders, have temperature dependent sex determination, with higher incubation temperatures producing females (Ewert et al. 1994; Wibbels et al. 1998). Since eggs are incubated indoors, the sex of the hatchlings can be directly manipulated. Under current regimes, however, farmers produce only female hatchlings in order to keep the electricity costs low during summer months. Eggs hatch within the same year that the eggs are collected, usually a couple of months after being laid. After hatching, a portion of healthy newborns are sold the same year to foreign

markets. A portion of healthy hatchlings and the non-healthy looking individuals (i.e., shell deformations are common due to difficulty of coming out of the shell) are transferred to enclosed ponds (e.g., green houses). Ponds in the green houses are heated during winter months and turtles are artificially fed, which in turn results in faster growth rates. Turtles remain in the green-houses until the following year when they reach four inches in size, which is the only marketable size for sale to US markets. Turtles with shell deformations are placed in the stock ponds because they will produce viable offspring, once they reach reproductive stage (Figure 4.2).

Two factors appear to be important for the overall health of the stock population: freshness of the ponds and stock density. Survivorship is usually high if the ponds are cleaned every 2-3 years. The greatest source of mortality occurs in early spring after the hibernation period, when a lack of oxygen due to unclean ponds or warm winters is thought to cause mass mortalities. Stock density represents the maximum number of turtles the pond can hold without compromising survivorship. Relationship between turtle density, survivorship, and growth rates is unknown, but because the turtles are artificially fed, the assumption is that growth rates are not compromised as long as the density is below the disease threshold and the ponds are sufficiently turbid prevent the turtles from seeing each other. In clear water ponds, turtles tend to become territorial and aggressive often causing turtle injury and decrease in reproductive output (Jesse Evans- Concordia Turtle Farm, pers. comm.).

Sex ratio is another potential parameter important for overall production. However, for many farmed turtle species, the optimal sex ratio (i.e., minimum proportion of males necessary to inseminate 100% of females) is currently unknown. The real sex

ratio on farms is also not often known. Farmers generally add females to the stock with a belief that there will always be enough males to inseminate females.

Conceptual Model

I constructed the models using STELLA, graphical dynamic simulation software (Deanton and Winebrake 2000). The initial step was to construct a conceptual diagram representing major farming operations. First, I created an age-structured matrix population model for females and for males. Each parameter was assigned superscript F or M , representing females and males, respectively, while the subscript i represented the age class. The number of individuals in each age class was represented as N_i^F or N_i^M and survivorship in each age class as S_i^F or S_i^M . The number of age classes depended on the age at maturity for males (m) and females (f) because I grouped all mature individuals into one age class, therefore $i = 0-m$ or $0-f$. I defined the time (t) interval as a one year. Because the young hatch in the same year the eggs are laid, I did not create a separate age class representing eggs; rather, N_0 represents the number of hatchlings.

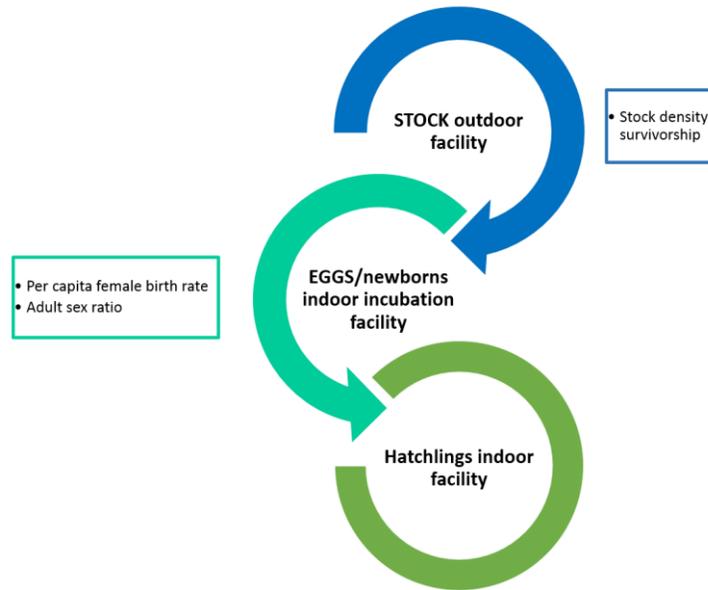


Figure 4.2: Farming operations illustrated by the flow diagram. Stock pond is a mixture of turtles >1 years of age. Hatchling production depends on nesting activity of adult females in a stock pond. The eggs are picked up, incubated, and hatched in the same year (t) that the eggs were laid. In the following year (t+1), the hatchlings are either sold for profit or released into the stock pond.

I assumed no density dependent growth rates so long as the stock density is equal or less than the threshold, labeled as SD . This is based on the assumption that competition does not occur for food or space among stock individuals as long as the pond is dark enough and turtles cannot see each other (Jesse Evans- Concordia Turtle Farm, pers. comm.). I defined the optimal sex ratio, SR_o , as the minimum number of sexually mature, adult males to number of sexually mature, adult females required to inseminate 100% of the adult females in the population. Average per capita birth rate (BR) is the product of average clutch size (CS) and number of clutches per season per female (NC), and proportion of eggs that hatch (HR). I also created birth rate adjustment parameter (ADJ) that controls for proportion of female vs male hatchlings produced. The summary of the baseline parameters is presented in Table 1. Based on the values for SD, SR_o, S_i, f , and m ,

I created a model that represents the dynamics of freshwater turtle biology under farmed conditions.

Under current management regimes, stock turtles are not sold, at least not on commercial levels. Currently, only hatchlings and 4 in turtles are being sold. I created two harvest rate parameters, h_0^M and h_0^F representing harvest rates of hatchlings and h_1^M and h_1^F representing harvest of 4 in turtles. To test the possibility and profitability of selling adults (i.e., for meat markets, etc.), I also created h_m^M and h_f^F as the harvest rates of adult males and females, respectively.

Total hatchling production (N_0^F and N_0^M) depends not only on the number of reproductively active females and per capita birth rate, as well as the proportion of adult males vs adult females in a population, or the sex ratio (SR). As long as $SR \leq SR_o$, 95% of adult females will lay fertile eggs in a given season. Otherwise, the percentage of fertile eggs will linearly decline. In addition, total female and male hatchling production is separated by the birth adjustment rate (ADJ):

$$N_0^F(t) = IF (SR(t) \leq SR_o) THEN (N_f^F(t) * BR * ADJ) ELSE (\frac{1}{SR_o} * SR(t) * N_f^F(t) * BR * ADJ)$$

$$N_0^M(t) = IF (SR(t) \leq SR_o) THEN (N_f^F(t) * BR * (1 - ADJ)) ELSE (\frac{1}{SR_o} * SR(t) * N_f^F(t) * BR * ADJ)$$

Young turtles are sold either shortly after hatching or kept in green-house ponds until the following year, when they are either sold for profit or added to the stock population. The farmer's goal is to sell all turtles that are marketable, which is dependent on both production and demand. Turtles with undesirable phenotypes (non-uniform scutes) are usually added to the brood stock. In order to keep farms self-sustaining (i.e., not adding wild caught adults to the stock), I made an assumption that 4 in turtles are primarily used to repopulate the stock up to the threshold size, and the surplus is then

available to be sold. Therefore, the number of hatchlings that will be added to the stock is:

$$G_0^F(t) = G_0^M(t) = IF \left(\sum_{i=1}^f N_i^F(t-1) \geq Max^F \right) THEN (0) ELSE$$

$$IF (N_0^F(t-1) * S_0^F) \\ \geq \left(Max^F - \sum_{i=1}^f N_i^F(t-1) \right) THEN \left(Max^F - \sum_{i=1}^f N_i^F(t-1) \right) ELSE (N_0^F(t-1) * S_0^F)$$

for females, and

$$G_0^M(t) = IF \left(\sum_{i=1}^m N_i^M(t-1) \geq Max^M \right) THEN (0) ELSE$$

$$IF (N_0^M * S_0^M)(t-1) \\ \geq \left(Max^M - \sum_{i=1}^m N_i^M(t-1) \right) THEN \left(Max^M - \sum_{i=1}^m N_i^M(t-1) \right) ELSE (N_0^M(t-1) * S_0^M)$$

for males, where Max^F and Max^M represent maximum allowable number of females and males in a stock, and their values depend on the optimal stock density and optimal sex ratio. In the stock population, survivorship rates determine the number of individuals entering the next age group:

$$G_i^F(t) = N_i^F(t-1) * S_i^F, \text{ where } (i=1-f)$$

and,

$$G_i^M(t) = N_i^M(t-1) * S_i^M, \text{ where } (i=1-m)$$

The list of parameters and their symbols is presented in Table 4.1 and the summary of the dynamics between age classes and production is presented in Table 4.2. Additionally, an illustration of STELLA model created to fit the farming operations of red-eared sliders is presented in Supplemental Figure 4.1.

Table 4. 1: The list of the baseline parameters for development of the population dynamics model for freshwater turtles under farmed conditions. Parameter values are associated with red-eared slider production and were acquired either: from the personnel on the farms, based on independent experiment, or by parameter calibration.

PARAMETERS	Symbol	Value	Reference
Max stock density (per acre)	SD	5,000	Concordia turtle farm (pers. comm.)
Optimal adult sex ratio (M:F)	SR_o	1:3	Unpubl. data
Max proportion of total females	p	0.75	Managed
Max number of females (Max^F)	$SD * acres * p$	3,350	
Max number of males (Max^M)	$SD * acres * (1 - p)$	1,650	
Female Survivorship	$S_i^F (i=0-f)$	0.97	Concordia turtle farm (pers. comm.)
Male Survivorship	$S_i^M (i=0-m)$	0.97	Concordia turtle farm (pers. comm.)
Clutch size	CS	8-22 (10)	Concordia turtle farm (pers. comm.)
Number of clutches per season	NC	3-5 (3)	Concordia turtle farm (pers. comm.)
Hatch rate	HR	0.85	Concordia turtle farm (pers. comm.)
Per capita birth rate ($CS * NC * HR$)	BR	24.2	
Year at maturity (females)	f	5	Concordia turtle farm (pers. comm.)
Year at maturity (males)	m	4	Concordia turtle farm (pers. comm.)
Female stock	$N_i^F (i=0-f)$		
Male stock	$N_i^M (i=0-m)$		

Table 4. 2: Summary of the dynamics between age classes and turtle production in a conceptual model of freshwater turtle farming.

System of Interest	Conceptual Formula
Total Female Hatchling Production $N_0^F(t)$	$IF (SR \leq SR_o) THEN (N_f^F(t) * BR * ADJ) ELSE (\frac{1}{SR_o} * SR * N_f^F(t) * BR * ADJ)$
Total Male Hatchling Production $N_0^M(t)$	$IF (SR \leq SR_o) THEN (N_f^F(t) * BR * (1 - ADJ)) ELSE (\frac{1}{SR_o} * SR * N_f^F(t) * BR * ADJ)$
Female hatch growth $G_0^F(t)$	$G_0^F(t) = IF \left(\sum_{i=1}^f N_i^F(t-1) \geq Max^F \right) THEN (0) ELSE$ $IF (N_0^F(t-1) * S_0^F) \geq \left(Max^F - \sum_{i=1}^f N_i^F(t-1) \right) THEN \left(Max^F - \sum_{i=1}^f N_i^F(t-1) \right) ELSE (N_0^F(t-1) * S_0^F)$
Male hatch growth $G_0^M(t)$	$G_0^M(t) = IF \left(\sum_{i=1}^m N_i^M(t-1) \geq Max^M \right) THEN (0) ELSE$ $IF (N_0^M(t-1) * S_0^M) \geq \left(Max^M - \sum_{i=1}^m N_i^M(t-1) \right) THEN \left(Max^M - \sum_{i=1}^m N_i^M(t-1) \right) ELSE (N_0^M(t-1) * S_0^M)$
Female stock growth $G_i^F(t) (i=1-f)$	$N_i^F(t-1) * S_i^F$
Male stock growth $G_i^M(t) (i=1-m)$	$N_i^M(t-1) * S_i^M$
Female hatch harvest $H_0^F(t)$	$(N_0^F(t-1) * S_0^F) - G_0^F(t)$
Male hatch harvest $H_0^M(t)$	$(N_0^M(t-1) * S_0^M) - G_0^M(t)$
Female adult harvest $H_f^F(t)$	$(N_f^F(t) * S_f^F) * h_f^F$
Male adult harvest $H_m^M(t)$	$(N_m^M(t) * S_m^M) * h_m^M$

Applying the Model to Farmed Red-eared Sliders

To put my conceptual model into practice, I used parameters for farmed red-eared sliders. I obtained values for the baseline parameters by interviewing personnel on a representative turtle farm in Louisiana, based on independent unpublished data (i.e., optimal sex ratio), or by actively managing the parameter values (i.e., birth adjustment rate). Red-eared sliders stock density can reach the extremes of 37,500 individuals per hectare; however, 12,500 individuals per hectare is a preferred healthy stock density. Therefore, I treat the maximum capacity- threshold at 12,500 turtles per hectare. At my representative farm, a total of ~12.5 hectares contains red-eared sliders, making a total stock density of 25,000 turtles. In a good year, survivorship of the stock is high (~0.97). However, in an event of warm winters, a mass mortality of up to 10% can result, with these events occurring, on average, every six years (Jesse Evans- Concordia Turtle Farm, pers. comm.).

Optimal sex ratio for the adult turtles is estimated to be 3:1, female: male, and it enables 95% of the females to lay fertile eggs. The nesting season lasts from April through August, but the egg collection usually ends in July. Red-eared sliders are known to produce 3-5 clutches per season and 8-22 eggs per clutch. For farmed red-eared sliders, clutch size is weakly correlated to the size of the adult females (i.e., $r^2 = 0.2$, unpubl. data). However, the same data shows that across all females, clutch size is normally distributed with mean of 10 ± 2.8 SD. Under farmed conditions, females mature at the age of 5 years when they start laying ~8 eggs per clutch. Incubation period is ~60 days, with a hatch rate of 85%. Upon hatching, the young are either sold to foreign markets or

kept in green house ponds for ~eight months until they reach 4 in in size. Turtles that are transferred to the green house ponds include not only healthy looking individuals, but also turtles with shell defects due to improper emergence from the shell and turtles with genetic defects. Therefore, despite the fact that the green house is heated during winter and the turtles are artificially fed, the mean mortality rate approaches 15%.

I created six age classes for females (N_t^F): hatchlings, 1-, 2-, 3-, 4, and 5+ year olds. All reproductively active females, 5+ years old, were classified in one age group (N_5^F). The male portion of the model was created in a similar manner, but since males mature earlier, I created five age classes (N_t^M): hatchlings, 1-, 2-, 3-, and 4+ year olds. I ran several simulation models using average parameter values for survivorship and per capita birth rate and tested the production under different harvest rates of hatchlings and 4 in turtles, and also by adding different harvest regimes for adult stock. I also ran a series of stochastic models in order to describe the uncertainty of production. In all models, I maintained the optimal sex ratio and the threshold stock density.

Economy

In general, annual profit on farms depends on the annual cost of farming operations and annual revenue of sold individuals:

$$\text{Annual Profit} = \text{Annual Revenue} - \text{Annual Cost}$$

The annual cost can be separated into three components:

$$\begin{aligned} \text{Annual Cost} = & \text{Annual cost (HATCHLINGS)} + \text{Annual cost (4 INCH TURTLES)} \\ & + \text{Annual Cost (STOCK)} \end{aligned}$$

The annual revenue is separated into two components:

Annual Revenue

$$\begin{aligned} &= \text{Annual revenue (HATCHLINGS)} + \text{Annual revenue (4 INCH TURTLES)} \\ &+ \text{Annual revenue (ADULTS)} \end{aligned}$$

Hatchling red-eared slider prices in the past decade varied from \$0.35-0.50 (mean = 0.41) although, in 2014 the prices rose to \$0.70/hatchling; the production cost per hatchling is usually ~\$0.25. Competition due to growing numbers of farms in the US as well as hatchling production from now well established Asian turtle farms caused not only a decrease in price but also market saturation. The price for 4 in turtles is usually \$7.50-8.00, with a higher cost of production of ~\$4.00/capita due to heating cost of green house ponds. Turtle values are affected by market demands, which varied greatly across past decades. For example, demand from Asian markets and turtle popularity as pets is driving the hatchling production for foreign markets while demand from domestic markets currently includes only 4 in turtles for pet trade. However, the demand for 4 in turtles seems to be more stable than the demand for hatchlings (Jesse Evans- Concordia Turtle Farm, pers. comm.).

It is important to note that all farms raise a mixture of species (i.e., not solely red-eared sliders) and it is often difficult to separate costs by species. In addition to uncertainties of demand, cost uncertainties also affect overall profit. Costs of operating a turtle farm include: feed, fuel, personnel (i.e., seasonal egg collectors, full time employees, etc.), egg/hatchling cleaning, packaging, and shipping materials. The costs of feed can vary greatly depending on the usage and the cost of different food types. For example, turtles are fed pellets, fresh carp, and corn for 9 months/year. The cost of feed was reduced by incorporating cheap fresh fish (i.e., carp) or by growing corn themselves (Jesse Evans- Concordia Turtle Farm, pers. comm.).

Results

Red-eared Slider Production

Assuming a healthy stock (i.e., no stock mortalities) and average per capita birth rates, my model shows an annual production of 454,219 hatchling turtles, which is in close agreement with actual production of ~425,000 hatchlings, based on our interviews with the farm owners. I then ran a series of simulation models, using average survivorship rates (0.97 for stock and 0.85 for green house turtles) and mean per capita birth rate (24.2), changing the proportion of hatchlings sold and assuming that green house turtles are primarily used to repopulate stock and the rest is potentially sold on domestic markets as 4 in turtles. I ran a total of six simulations, with the proportion of hatchlings sold varying from 0.78 to 0.88. I ran simulations for 100 year and used the numerical outcomes of the models post initial oscillations, when production stabilized to constant values. The number of hatchlings available for sale varied from 300,000 to 345,000 while the number of yearlings available for sale varied from 40,000 to 70,000, which matches the current demand for yearling turtles on domestic markets (40-60,000 yearling turtles are usually sold annually on the farm; Figure 4.3). In order for the farm to operate sustainably, approximately 182 male and 546 female head-starts (yearlings) must be released into the stock ponds annually.

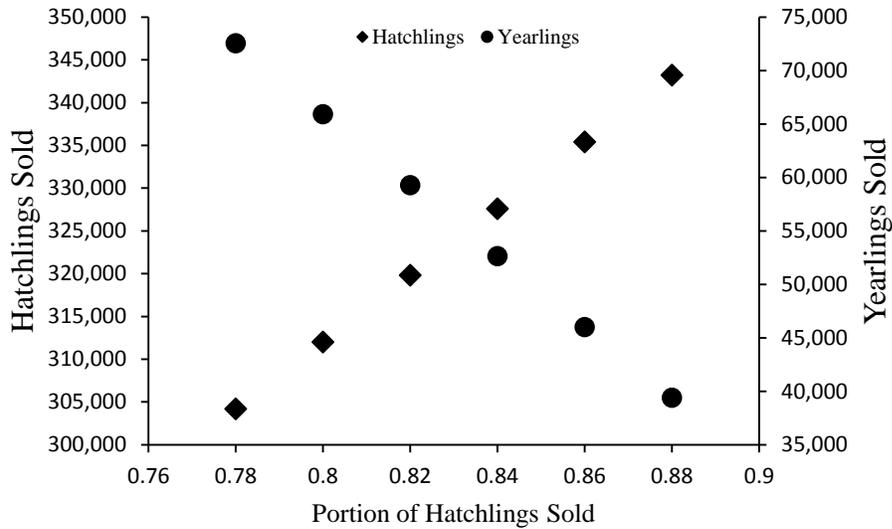


Figure 4.3: Annual production of hatchling and yearling red-eared sliders (*Trachemys scripta elegans*) depending on the proportion of hatchlings sold and assuming the green-house turtles are primarily used to repopulate the stock and the rest is sold on domestic markets as four inch turtles (yearlings). I conducted a 100 year simulations and used the numerical outcomes of the models post the initial oscillations, when the production stabilized to constant values.

Uncertainty

Occasional winter/early spring stock die-offs will decrease overall profit due to lower egg production and an increased number of head-starts that must be returned to the ponds the following year. Assuming 55,000 yearlings are sold annually, approximately 324,400 hatchlings would be sold in the best case scenario. That number can drop to 295,855 immediately following a one year die-off or even 243,700 in case of die-offs in three consecutive years (Figure 4.4).

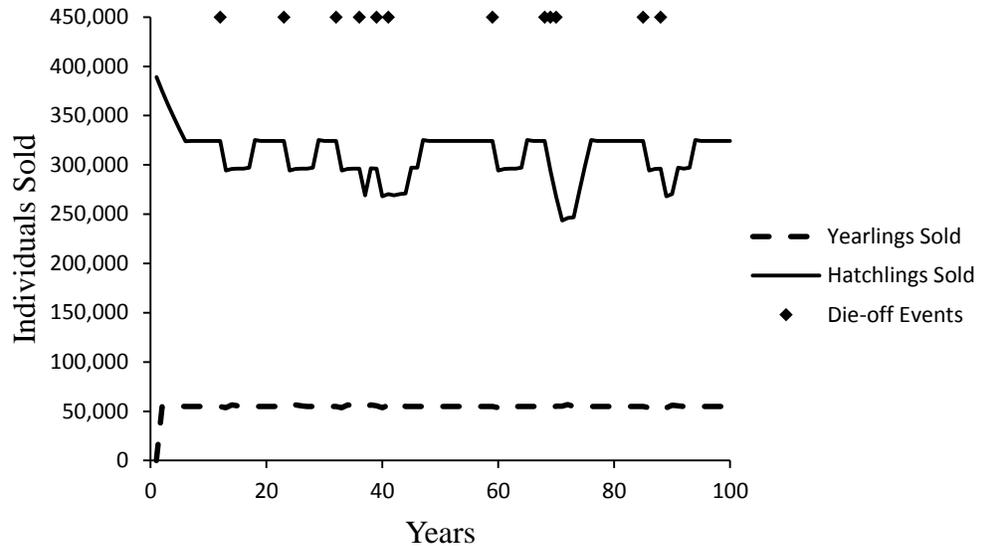


Figure 4.4: A 100 year simulation model showing hatchling and yearling production where mass die-offs (~10%) occur on average every six years, and assuming a constant demand for yearling turtles (~55,000).

Finally, I also incorporated number of eggs per clutch produced as a function of normal distribution with a mean of 10 and standard deviation of 2.8, based on data collected from the farm. A 100 year simulation model showed great variation in hatchling and yearling production. For example, under 82% harvest rate of hatchlings (in a non-stochastic model, this is the rate at which farmers can meet the demand for yearling turtles), 5,000 – 80,000 yearlings and 33,000 – 400,000 hatchlings can be sold annually. Assuming the demand for pet turtles on domestic markets remains constant (~55,000), I modified the stochastic model to meet this demand. That means that despite the variation in egg production in a given year (due to mortalities as well as variation in female fertility between years), the number of hatchlings transferred to the green house equals the number of 4 in turtles that can be sold (~55,000) and the number necessary to replenish the stock pond (actually 15% more turtles are transferred to account for

mortality in the green house). The model shows that the number of hatchlings sold can vary between 65,500 and 542,280, with an average of 308,800 (Figure 4.5).

Conservative estimates of profit (assuming \$0.35 price per hatchling and \$7.50 price per yearling) vary between \$171,553 and \$219,228 (mean = \$195,976; Figure 4.5).

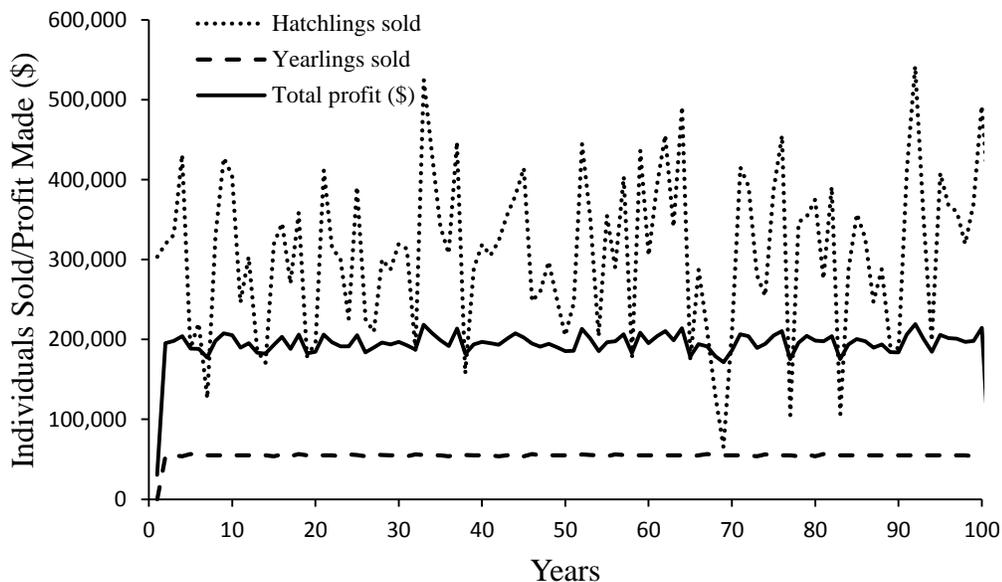


Figure 4.5: A 100 year simulation of a stochastic model that takes into account variation in egg production and occasional die-offs, showing a variation in hatchling production and total profit, assuming the demand for hatchling turtles remains the same (~55,000).

Adult Harvest

For the non-stochastic model, I incorporated harvest of the adult stock at the following rates: 0.1, 0.2, 0.3, 0.4, 0.5, and 0.6, to determine number of adults, yearlings, and hatchlings that can be sold annually. I tested each harvest rate against three different hatchling harvest rate simulations (Figure 4.6). Depending on the adult harvest rates, 520-1000 male and 1600-3000 female head-starts should be released into the stock ponds,

annually. As expected, harvesting the adult portion of the stock population will decrease egg production and therefore decrease profit made from hatchling and yearling exports. Therefore, loss of profit should be offset by profit made from selling adults, which varies between 1450 and 3500 total individuals in the case of 0.1 and 0.6 harvest rates, respectfully.

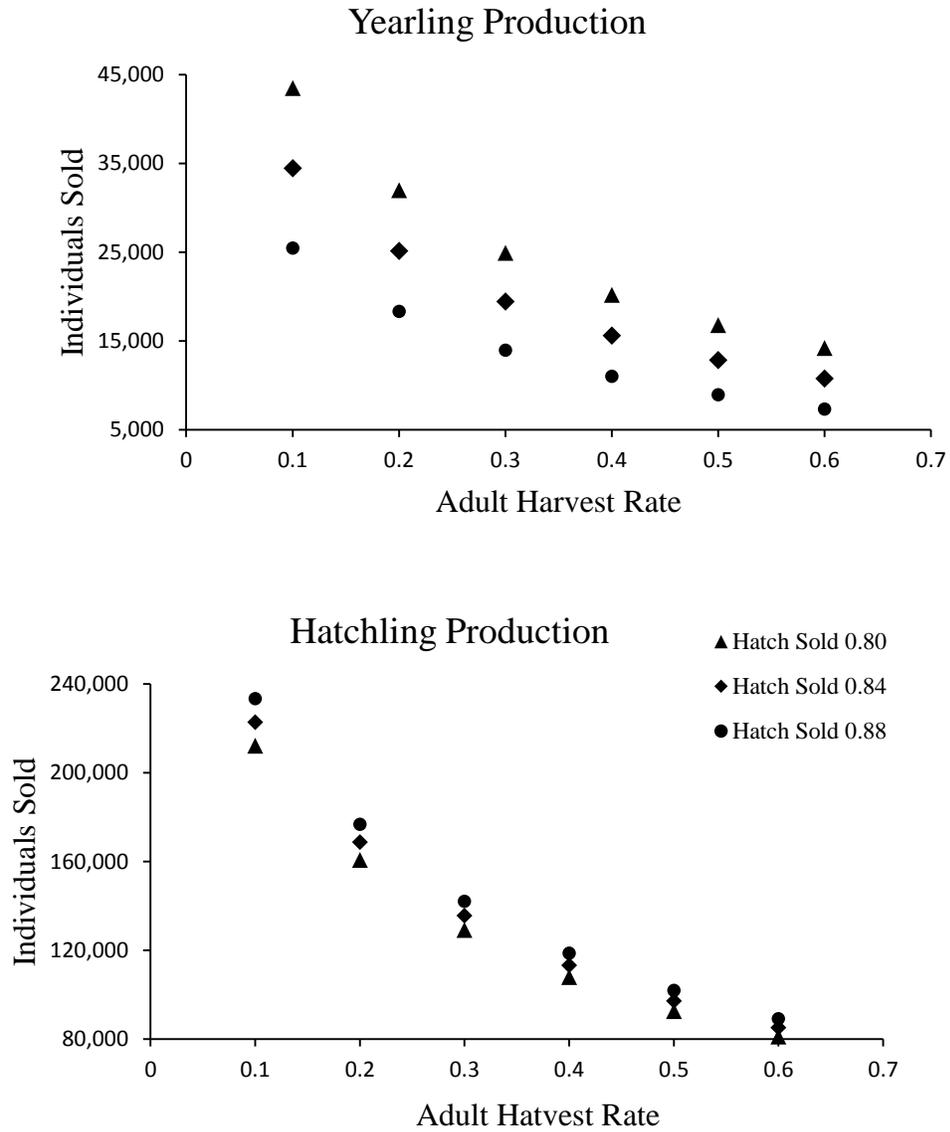


Figure 4.6: Annual hatchling (top) and yearling (bottom) red-eared slider (*Trachemys scripta elegans*) production as a function of different adult stock harvest rates (0.1-0.6) and under three different portions of hatchlings sold. The model runs under assumption that turtles not sold as hatchlings (green-house turtles) are primarily used to repopulate the stock and the rest is sold on domestic markets as four inch turtles (yearlings). I ran 100 year simulations and used the numerical outcomes of the models post the initial oscillations, when the production stabilized to constant values.

Profit- break Even Analysis

Although profit is higher for 4 in turtles, current market demands in the US allow for only ~60,000 individuals to be sold. To meet this demand, approximately 82% of hatchling turtles (~320,000) can be sold to foreign markets, while the rest of the hatchlings must be transferred to the green-houses for yearling production and future stock. A conservative approximation of annual profit (assuming \$0.35 price per hatchling and \$7.50 price per yearling) is ~\$240,000. I performed a break even analysis and evaluated the profitability of selling adults on the commercial levels. For example, assuming a constant demand for yearling turtles (~55,000 yearling turtles/year) and 40% adult harvest rate (~3000 adults), 50% of hatchlings could be sold annually (~67,500). Assuming above per capita profit for hatchlings and yearlings and continuing demand for 4 in turtles, per capita profit for adult turtles would have to be ~\$8.50 in order to break even with the profit made from traditional hatchling and four inch turtle based farming. In the case of increasing prices of hatchling turtles, the profit required from adult turtles would also increase in order to motivate sale of adult turtles. For example, for a hatchling price of \$0.5, the adult profit would have to be ~\$21, and for hatchling price of \$0.7, which is the current market price for hatchling red-eared sliders, adult profit would have to be ~\$38.5 per adult turtle (Figure 4.7). Under other adult harvest rates and different yearling demands, the break even analyses showed similar results, assuming that all hatchlings can be sold for profit.

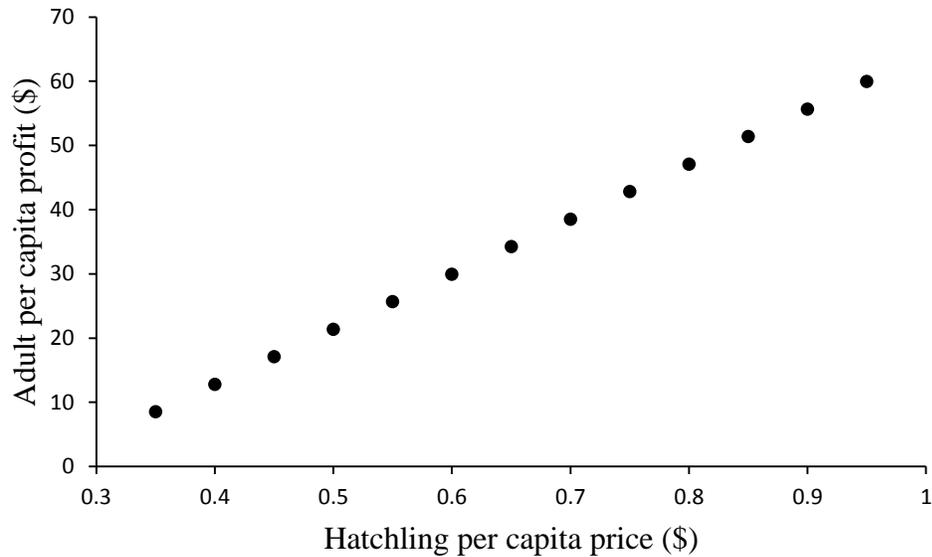


Figure 4.7: An example of economic analysis showing a profit that must be made per adult red eared slider (*Trachemys scripta elegans*) under varying hatchling prices in order to break-even with traditional farming where only hatchlings and yearlings are sold. The model assumes a constant demand for yearling turtles (~55,000) and that all hatchlings can be sold for profit. This example illustrates conditions where 40% of adult stock is sold for profit. However, other adult harvest rates show similar result.

Discussion

In recent decades, the southern US has played an important role in supplying wild caught freshwater turtles to Asia (Ceballos and Fitzgerald 2004; Mali et al. 2014). To meet demands, turtle farming became a common practice on Asian farms but also a booming aquaculture business in the southern US (Haitao et al. 2008; Hughes 1999). Yet, farming practices in the US have been narrowed to commercially raising hatchlings for either the pet trade or to supply Asian turtle farms, which provides no competition to wild turtle collectors. In this paper, I described the dynamics and challenges of freshwater turtle farming on a representative farm in Louisiana by using red-eared sliders as a model species. I evaluated the possibilities of using turtle farms for commercially

raising and harvesting adults from the stock, in order to decrease pressures on wild populations.

Financial analyses showed that in order to break even by selling hatchlings and yearlings, the profit per adult must be ~\$8.5 in the best case scenario (\$0.35 per hatchling price) and ~\$38.5 in the case of \$0.7/hatchling price, which is the current (2014) hatchling value on the market (Jesse Evan- Concordia Turtle Farm, pers. comm.; Figure 4.7). Unfortunately, the dramatically lower current price for adult wild caught red-eared sliders (~\$0.60) in the US (Jesse Evans- Concordia Turtle Farm, pers. comm.) currently makes selling adult turtles from stock un-profitable. Louisiana is one of several states in the southeast US that still allows unlimited take of freshwater turtles from the wild (Mali et al. 2014). Because of high costs associated with commercially producing adult red-eared sliders on the farms, commercial harvest of wild adults in unprotected states is likely to continue and even increase due to recently implemented regulations in surrounding states (Association of Fish and Wildlife Agencies 2011) exacerbating the threat to wild populations.

Because the current market/demand is more stable for 4 in red-eared sliders than hatchling turtles, our model operates under the assumption that demand and prices for 4 in turtles will remain constant and that all hatchling turtles produced will be sold. Price and demand for hatchling turtles that are exported overseas have varied in past years (Jesse Evans- Concordia Turtle Farm, pers. comm.). Louisiana Department of Agriculture and farm owners speculate that the decrease in demand is due to Asian farms becoming self-sustaining and Asian farmers exporting hatchlings for the pet trade. Competition within the US also plays an important role. In the early 2000s, when popularity and

demand for turtles on foreign markets was high, many farms were established in Louisiana, which might have caused the decrease in hatchling prices (Louisiana Department of Agriculture 2012). In more recent years, many farms went out of business either due to competition or poor design of the farms themselves (Louisiana Department of Agriculture 2012; Jesse Evans- Concordia Turtle Farm, pers. comm.). I speculate that the reason for the current rise in price of hatchlings is due to this collapse. However, a continuing decrease in demand for hatchling red-eared sliders and also future lack of wild individuals due to overharvest may shift farm operations towards production of larger turtles, especially for more desirable species on the meat markets.

Such a shift in production goals can be enabled by decreasing the cost of farming operations. The cost of maintaining green-houses and stock is a crucial part of making a profit from adult turtles. The cost of raising head-start red-eared sliders is particularly expensive (~\$4.0 per turtle) mainly due to costs associated with heating the ponds. However, future improvements and changing the approach by which farms are maintained can lower costs. Already, many innovations have been implemented, such as adding cheap fresh fish (e.g., an exotic invasive species like carp) into the diet and raising corn, instead of using the more expensive commercial pellets in turtle diet. Although not yet implemented, switching to solar energy would decrease the costs of greenhouse maintenance. On the other hand, increasing fuel costs for machinery (i.e., for feeding and cleaning the ponds) and inflation rates will impact future costs as well.

I modeled the dynamics on the farm by using one of the most common species of freshwater turtles in the wild and one of most commonly and successfully farmed species in the US. I chose this species because of the extensive knowledge about their life

histories in the wild and their requirements and life histories on farms. Red-eared sliders also represent ~50% of all turtles on the farm while the rest is a mix of other species such as yellow-bellied sliders (*Trachemys scripta scripta*), snapping turtles (*Chelydra serpentina*), softshell turtles (*Apalone sp.*), etc. Although harvesting adult red-eared sliders from stock is not profitable under current market conditions, this model can be modified to fit other species that are currently more desirable for the pet trade or meat markets. For example, snapping and softshell turtles are desirable on the Asian meat markets and have higher values than red-eared sliders, but are currently only exported as hatchlings. I am interested in continuing to modify the existing model when more knowledge is acquired about species life histories and space requirements on the farms, and I intend to test the possibilities of raising snapping and softshell turtles to adulthood and selling them directly to the meat markets.

Acknowledgments

Special thanks go to Jesse and Dave Evans, the owners of the Concordia Turtle Farm who were welcoming to my research ideas and provided an overview of the past and current turtle market situation. I also thank Dr. Mark Feldman, whose knowledge about the turtle biology at Concordia farm was useful in developing the model for this chapter.

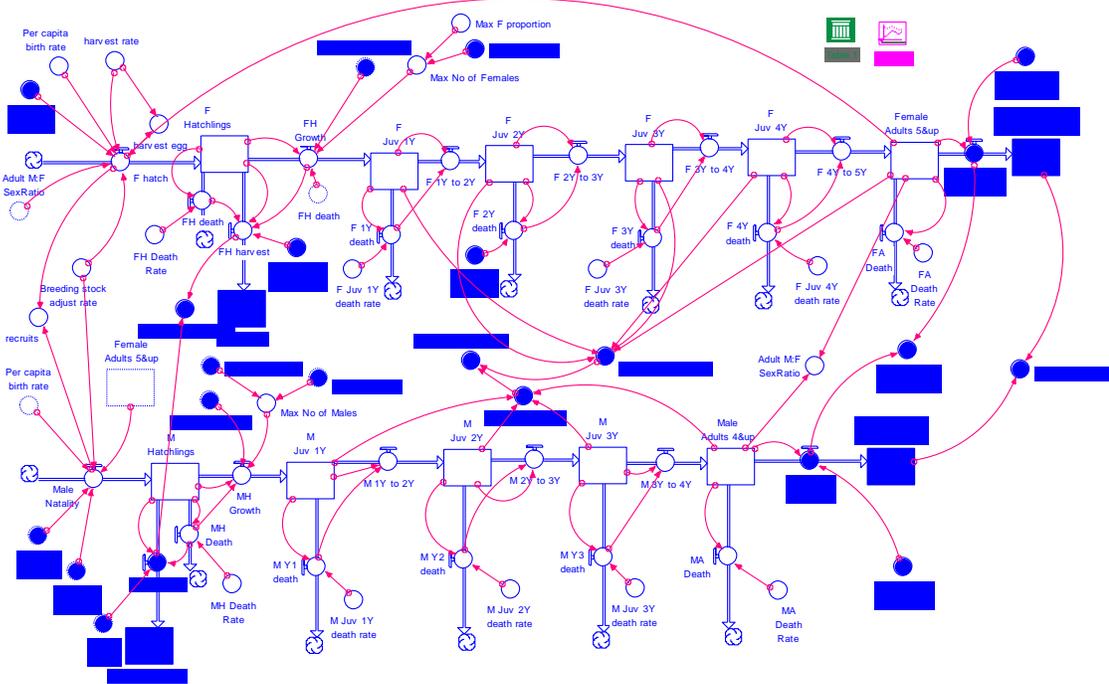
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Supplemental Figure 4.1: An illustration of STELLA model created to fit the farming operations of red-eared sliders.

CHAPTER V

CONCLUSIONS

Unregulated harvest is one of the major threats to wild freshwater turtle populations across the globe. The demand for turtle meat, particularly in China, has not only depleted Asian wild turtle populations, but has also impacted wild populations across North America. Turtles from the United States of America (US) are being exported in large numbers to supply depleted Asian stocks (Ceballos and Fitzgerald 2004; Brown et al. 2011). Only recently, however, have state agencies begun implementing harvest regulations, specifically in the southeast US, the region with the highest species richness of freshwater turtles in North America (Buhlmann et al. 2009). In my dissertation, I addressed the issues and concerns associated with sustainability of wild freshwater turtle populations in the US. I sought to correlate the magnitude and sources of exports of live turtles from the US on commercial levels with recently implemented harvest management regimes in the southeast US. I specifically focused on the state of Texas due to its unique harvest management theory and tested the main assumption under which this regime operates (Texas Parks and Wildlife Department 2007). However, I also examined the potential future solutions and the logistics of such solutions that could potentially decrease the harvest pressures from the wild.

Despite the apparent decrease in the overall exports of freshwater turtles in the past decade, the LEMIS data analyses completed for each exporting state revealed troublesome results. I specifically refer to California that has remained a top exporter of larger, more valuable species on the meat markets, such as snapping turtles. There was a noticeable increase in *Chelydra* exports in the past five years, and the latest LEMIS data

shows over one million individuals shipped in 2013. The primary destination of exports from California was Asia, and turtles were being shipped by only a few exporters. These corporations established in California are not turtle farms or individual exporters, which makes tracking the actual geographic origin of these turtles from the data recorded by the USFWS, effectively impossible. This is an obvious issue and should be resolved by immediate legislation or regulatory changes that require listing the origins of turtles exported not only from Californian ports, but from all US transit ports. While exporting states like Louisiana and Florida can seemingly claim that all turtles originated within the exporting state, California is home to only one freshwater turtle species, the western pond turtle. Moreover, commercial turtle collectors have an interstate network of several hundred employees and is organized as a pyramid scheme, suggesting that even from shipping ports in Louisiana and Florida, turtles were not reared or caught in that state. No laws currently demand a declaration of the geographic origin of wild caught turtles, aside from obtaining state harvesting permits, and there are currently no interstate trade regulations for non-CITES listed species. The LEMIS data provides the column for the name of the exporter, but such data is often missing or the list contains only the names of the exporting company.

Further, there is a need for stricter harvest regulations, specifically in the states that provide no levels of protection (i.e., Louisiana, Mississippi, and Arkansas) (Association of Fish and Wildlife Agencies 2011). In addition, southeastern states must work together to establish better guidelines for labeling the sources of exported turtles (i.e., wild caught vs farmed individuals) in order to more accurately evaluate export trends and levels of threat to wild populations. Close analyses of the LEMIS data

revealed that the strict regulations in one state can have negative consequences on harvest pressures in the surrounding states that provide no protection for freshwater turtles. Such speculation is based primarily on the observed increase in exports out of Louisiana after 2009, when several harvest restrictions came into place in surrounding states.

Secondarily, the attempts to export wild caught turtles, originating from the states where harvest is illegal, as captive bred through the shipping ports located in states with no harvest regulations is alarming.

In conclusion, strict harvest regulations even when enforced in several states are not a permanent solution to the problem of high numbers of exported turtles. Although some states recently implemented a ban on commercial harvest, the strictest level of protection, large scale turtle harvest continues through an interstate network including trappers, middlemen, aggregators, and dealers, which only emphasizes the necessity for regulation of commercial harvest for freshwater turtles in all the states of the Southeast US. Understanding the domestic origin of turtle exports or the domestic origin of the turtles themselves is thus crucial to our understanding of the commercial trade in freshwater turtles in the US, and the lack of publicly available information for evaluation is at odds with the conceptual framework for wildlife management and for the sustainable use of natural resources.

Among the states of the southeast that recently implemented harvest regimes is the state of Texas. Texas has a unique harvest management regime: populations are protected only in public water bodies while the harvest of all major commercial taxa remains unlimited in private water bodies (Texas Parks and Wildlife Department 2007). I did observe some short term response to this regulation in the LEMIS data as the number

of turtles exported from the Texas ports essentially decreased to negligible numbers; however, subsequent exports have significantly increased in Louisiana. In the third chapter of my dissertation, I designed a method to monitor the inter-pond movement of freshwater turtles in order to test the main assumption under which the harvest management regime in Texas operates: the source-sink theory. Understanding population dynamics across the landscape is crucial in making harvest management decisions such as the current regime in Texas. While it is known that many species occur as metapopulations in spatially heterogeneous environments (Pulliam and Danielson 1991, Dias 1996, Ritchie 1997), no one has tested how the dispersal of freshwater turtles between wetlands justifies the spatially controlled harvest management regime in Texas. My findings showed that the apparent ability of turtles to invade depleted water bodies can be misleading, and the source-sink theory is not an appropriate model for harvest of freshwater turtles.

Based on the results of Chapter 3 of my dissertation, I can conclude that density dependent factors do play an important role in population dynamics. However, the immediate population growth observed after the first harvest simulation was not a product of higher fecundities or higher survivorships, but rather strictly the product of the ability of adult turtles to emigrate into the “newly” depleted water bodies with lower turtle densities. This became obvious after the second harvest treatment, when I observed lower levels of post-harvest recovery, however, due to the overall depletion of turtles in the entire system, the population was unable to recover to its original size. Only one turtle species, the Australian sideneck turtle (*Chelodina rugosa*), shows signs of density dependent population growth by decreasing the age at maturity during “bad” years, as a

sign of adaptation to wet-dry Australian seasons (Fordham et al. 2007). Therefore, although at first glimpse it might seem that the source-sink theory is a good basis for harvest, I demonstrated how this theory is misleading in the case of freshwater turtle populations in only two harvest treatment steps, and that in a long run, this level of protection will not provide a sufficient to sustainably manage the commercial utilization of freshwater turtles.

Moreover, in my experimental design additive mortalities were managed to minimize additional mortality effects beyond the harvest events. Therefore, immigration rates were higher than what would be expected in a more realistic landscape level system. Besides natural predators, vehicular traffic is an additional source of mortality that was not accounted for in my experiment. Thus, the rate of population recovery is also more likely to be slower than what was reported in Chapter 3. In conclusion, there is no evidence that the spatially controlled harvest management regime for freshwater turtles in Texas provides sufficient levels of protection. To reach a level of sustainability, more detailed guidelines must be developed. For example, future studies should focus on determining the proportions of source versus sink water bodies on a spatially explicit (regional or even county specific basis) basis and then use these data to inform the establishment of harvest quotas. My experiment showed that harvest intensity during a commercial harvest can be as high as 55% of the adults. This is high for taxa that rely on high survivorship of adults to maintain the population (Congdon et al. 1994). Moreover, only 2% of water bodies in Texas are considered public (Brown et al. 2011), which is highly unlikely to serve as a sufficient source for unprotected areas. Establishing protected zones and zones open for harvest based on the region and wetland connectivity

is also another way to improve Texas freshwater turtle management. However, further studies seeking to test and justify these alternative suggestions are needed in order to provide a scientific evidence of their validity.

Generally, in Chapter 3, I demonstrated that it is possible to monitor the overland movement of freshwater turtles at a higher resolution than what was previously reported, which opened the opportunity to explicitly test the source-sink theory as applied to freshwater turtles. Additionally, I provided evidence of seasonality of movement and general patterns of overland activity for semi-aquatic turtles, which could potentially serve as a basis for establishing wetland buffer zones and season limits to harvest.

In Chapter 4, I tested alternatives to the wild population harvest by applying a method that previously proved to be successful for a once seriously endangered reptile, the American alligator (*Alligator mississippiensis*). Due to successful farming and headstarting practices (Heykoop and Frechette 2001), the American alligator was not only delisted in 1979 from the endangered species list, but continues to be harvested in a sustainable manner. Turtle farms in the US currently produce only hatchlings that are being exported to Asian turtle farms or to pet markets. Based on interviews with turtle farm owners, I modeled the production of hatchlings under current farming practices and then modified this basic model to test the possibilities of farming adult turtles for meat markets.

Based on the current costs associated with farming and current prices for hatchlings and wild caught adults, farms would need to make \$8.00 profit off of every adult red-eared slider (*Tracemys scripta elegans*) sold in order to break even with their traditional farming practices. Currently the price of wild caught adult red-eared sliders is

approximately \$0.60, making farming of adults for meat markets unprofitable. However, the demand for hatchling red-eared sliders has dramatically decreased in the past decade and will most likely continue to decrease due to new, well established Asian farms that not only no longer demand hatchlings from US farms but also are becoming competitors in the world pet turtle market. This competition is worrisome and I predict that US farms will have to modify their practices in order to remain competitive with Asia. Asian farms are currently able to profit from selling the adults due to lower costs of maintaining their farms: low labor costs, a warmer climate that does not require additional heating of the ponds, and low feed costs (Jesse Evans- Concordia Turtle Farm, pers. comm.).

I focused on the red-eared slider, a species that is still considered common in the wild and also commonly farmed in the US. My future goals are to further modify and expand my model to consider more desirable taxa on the meat markets, such as soft-shell turtles and snapping turtles. It is obvious that extrapolating the model and approaches to address the commercial value and conservation nexus for rare taxa remains a future goal. A mixture of turtle farming for world markets that incorporates conservation practices such as head-starting, and that would provide some level of profit to the farms might soon become the only option for US farms. In turn, head-starting turtles on turtle farms and releasing them in the wild can help depleted wild populations, and also could help establish and maintain sustainable harvest seasons and quotas. Conservation groups working with turtle farmers would benefit from the decreased costs compared to establishing new head-start facilities and simultaneously provide access to the depth of knowledge available for raising turtles at a scale relevant to wild population supplementation. Collaboration among farmers, conservation groups, and wildlife

agencies can ensure the future of not only wild turtle populations but also the economic stability of turtle farms in the US.

In recent decades, numerous anthropogenic pressures on freshwater turtles have led to worldwide declines of wild populations. One of the key problems with threats continuing to rise is the lack of wildlife management programs that focus on different aspects of turtle life histories as well as different turtle taxa. In the Southeast US, in the last decade, different management policies have been implemented to a series of non-CITES listed freshwater species. However, the difficulty remains in creating informed detailed scientific basis for different management paradigms. In my dissertation, I demonstrated the evidence of continuous exports of wild freshwater turtles at high levels despite the changes in harvest regimes. I also developed a technique for testing the management paradigm in Texas that can be used in future studies to help improve currently unsustainable harvest regime. Finally, I created the basic model for turtle farming that can be used in the future for different taxa and help develop innovative farming practices that can be used as an aid for decreasing pressures on wild populations.

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