ABSTRACT

Basking Dynamics among Sympatric Turtle Species (*Trachemys scripta elegans*, *Pseudemys texana*, and *Graptemys pseudogeographica kohnii*) in Waco Creek, Texas

Jeff H. Bardwell, Ph.D

Committee Chairperson: Richard E. Duhrkopf, Ph.D

The premise of this manuscript condenses into three words: turtles on logs. Turtles splaying their limbs and sunning themselves on emergent deadwood is commonly known as basking. Basking involves ectotherms taking advantage of solar radiation to boost their core temperature and fuel metabolic processes. This study examines a community assemblage of three turtle species within the Family Emydidae—*Trachemys scripta elegans*: Red-eared Slider, *Pseudemys texana*: Texas River Cooter, and *Graptemys pseudogeographica kohnii*: False Map Turtle—in Waco Creek, Texas, a tributary of the Brazos River, from 2010-2012. Turtles were collected daily via specialized traps which take advantage of repetitive basking habits, individually marked, measured, identified, and then released from June to October 2010, April to October 2011, and April to October 2012. Multiple recaptures allowed for observation of individual, population, and community progression over time. This manuscript asks three fundamental questions about the role of basking behavior in the Waco Creek emydid turtles: 1) What is the significance of the basking community assemblage composition in

Waco Creek, 2) How do basking trap modifications and population demographic selection affect group trap response, and 3) How do polynomial and k-growth mixed models describe juvenile turtle logistic growth?

Trachemys scripta elegans comprise 46%, *Pseudemys texana* 32%, and *Graptemys pseudogeographica kohnii* 23% sample composition within the Waco Creek basking turtle assemblage. All mature populations were significantly male skewed and turtle demographics exhibited several expected seasonal behavior patterns. The community has a large abundance of juveniles, young males, and immature females regardless of species. In addition, juvenile *T. scripta* appear to be the most actively basking demographic. Between individual demographic behavior and trap design as predictors for trap response, demographic behavior was significant across most response variables whereas trap design variables were not. This study pioneered a new technique for comparing turtle logistic growth models using a polynomial mixed model as a control. With an adequate sample size and consistent seasonal dispersal, results from this technique agree with reports from the literature and look promising.

Basking Dynamics among Sympatric Turtle Species (*Trachemys scripta elegans*, *Pseudemys texana*, and *Graptemys pseudogeographica kohnii*) in Waco Creek, Texas

by

Jeff H. Bardwell, B.S., M.S.

A Dissertation

Approved by the Department of Biology

Robert D. Doyle, Ph.D., Chairperson

Submitted to the Graduate Faculty of
Baylor University in Partial Fulfillment of the
Requirements for the Degree
of

Doctor of Philosophy

Approved by the Dissertation Committee

Richard E. Duhrkopf, Ph.D., Chairperson

Joseph D. White, Ph.D.

Darrell S. Vodopich, Ph.D.

Stephen J. Trumble, Ph.D.

Joe C. Yelderman, Ph.D.

Accepted by the Graduate School
August 2013

J. Larry Lyon, Ph.D., Dean

Page bearing signatures is kept on file in the Graduate School.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

GLOSSARY

Additive	adj	pertaining to system interactions in which one component increases the effect of another
Allopatric	adj	describing geographically isolated populations
Antagonistic	adj	pertaining to system interactions in which one component decreases the effect of another
Bask	v	behavior by which poikilotherms attain optimal body temperature while lying prostrate on a surface via radiation, convective, and conductive energy transfer
Conduction	n	energy transfer via direct surface contact
Convection	n	Forced – energy transfer via flowing medium (wind or water) Free – energy transfer via molecular kinetics
Corning	v	the process during gunpowder manufacture when each separate component is integrated into a uniform product via pressing mixed powder into cakes, then grinding it again to a finer consistency
Determinism	n	the philosophy that any complex process is inherently unpredictable and cannot be deconstructed into basal components, whose interactions introduce an intangable system stochasticity
Diel	adj	per daily basis
Ecology	n	the study of how organisms interact with their environment
Ectotherm	n	an animal which is dependent on supplemental environmental energy sources rather than internal metabolism to maintain optimal temperature
Endotherm	n	an animal which does not rely upon environmental energy sources, but rather internal metabolism to maintain optimal temperature
Handling	v	expending time and energy absorbing, digesting, metabolizing, and egesting prey

Homeotherm	n	an animal which regulates and maintains a stable body temperature
Lentic	adj	pertaining to a still body of water
Limnology	n	the study of inland freshwater systems
Lotic	adj	pertaining to a flowing body of water
Mean	n	arithmetic mean, average, sum divided by the number of replicates Symbol – $\bar{x}$
Metabolism	n	Part 1 – Catabolism: the process by which organisms oxidize hydrocarbon polymers to generate energy (ATP) and byproducts such as carbon dioxide, heat, and water Part 2 – Anabolism: the process by which organisms construct compounds, tissues, and organs from basal molecular components utilizing ATP
Niche	n	an organism's role in the environment
Poikilotherm	n	an animal incapable of internally regulating body temperature, which fluctuates with the environment
Population	n	A census of every individual of a particular species in a given area
Proximate	adj	factoring individual physiological or genetic behavioral stimuli
Radiation	n	Long wave – radiant energy emitted from the earth and living organisms Short wave – radiant energy emitted from the sun
Reductivism	n	the philosophy that any complex process can be predictably deconstructed into basal components, whose sum of parts strictly define the system
Sample	n	A proportion of individuals from a population within a given area
Synergistic	adj	pertaining to components achieving a greater system effect than can be explained by the sum of individual contributions
Sympatric	adj	describing geographically cohabiting populations
Trophic	adj	pertaining to hierarchal dietary guild levels
Ultimate	adj	factoring mutigenerational evolutionary behavioral stimuli

ACKNOWLEDGMENTS

I am indebted to many countless individuals investing both time and effort into this project. For helping me formulate my ideas and thoughts into a solid, defensible work I'd like to thank my advisor Dr. Richard E. Duhrkopf and the rest of my committee: Dr. Joseph D. White, Dr. Darrell S. Vodopich, Dr. Stephen J. Trumble, and Dr. Joe C. Yelderman.

I'd like to thank Nora Schell and Tom Connery at Lake Waco Wetlands for assisting with a portion of this project which, while ultimately not coming to fruition, still offered many learning experiences. I'm also grateful to the multitude of grade school children passing through the wetlands educational center who rekindled my notion of dry facts as things of awe and wonder. If listening to my ramblings about basking or examining live turtles inspired young students to go out and explore the natural world or better appreciate their own unique niches, then I celebrate the intrinsic value of science beyond numbers and data points.

Lastly, where would I be without my field crew? That wasn't a rhetorical question; I'm sure I'd still be elbow deep in halfway built basking traps. I'd like to thank Katelyn Blankenship, Colin Carrol, Andrew Cheung, Caitlin Kyle, Austin Leone, Katie Lloyd, Chi Nguyen, Clinton Trimble, Jonathan Nguyen, Lesley Nguyen, Hemali Patel, Son Pham, Tracy Pinney, Stephanie Schroeder, James Yian, and Rebecca York who all helped bend wires, notch turtles, and haul traps, and probe turtles.

DEDICATION

To my family

For their unquestioning love and support

CHAPTER ONE

Introduction

Jeff H. Bardwell claims sole authorship of this manuscript and responsibility for any errors or mistakes. This dissertation contains original research data which have not been previously published. Internal citation and unit abbreviation formatting conform to the standardized guidelines for *Journal of Herpetology, Herpetologica,* and *Herpetological Monographs*. All other formatting conforms to the 2013 Baylor Graduate School guidelines.

Subsequent chapters examine ecological facets of ectothermal basking behavior within the emydid assemblage inhabiting the mouth of Waco Creek from 2010-2012. This manuscript includes the following topics: reviewing turtle evolution, emydid turtle life history, basking-related literature, relevant field techniques, and a study site description (Chapter 2); utilizing emydid turtle demography as a model system to examine community assemblages (Chapter 3); quantifying the effects of individual selection and trap design on trap capture response (Chapter 4); and examining k-growth mixed models among second season juvenile turtles (Chapter 5). The manuscript ends with a conclusion which highlights four biologically significant trends among the three preceding chapters (Chapter 6). Supplementary materials include a statistical programming guide for r and python with illustrated examples of pertinent analyses found within main body of the dissertation (Appendix A).

CHAPTER TWO

Turtles on Logs

Background

According to classical ecological theory, animals divide into two primary categories based on their population life history traits, relative survivorship curves, and dipolar reproductive strategies: r versus K (Pianka, 1970). In population ecology symbology, r refers to fecundity or a population's reproductive rate whereas K refers to carrying capacity or the number of individuals within a population which their habitat can support. R species (i.e., dragonflies) live fast and die young: early sexual maturity, high fecundity, no maternal investment, and short-lived. By contrast, K species (i.e., whales) take their time: late sexual maturity, low fecundity, high maternal investment, and long-lived. Either strategy is effective producing the next generation. Each shows high taxonomic fidelity. Most insects exhibit r specificity and most mammals K specificity. However, this theory has been largely superseded by more complex models (Kuno, 1991; Getz, 1993). Several unique animal life histories (i.e., turtles) refuse to fit neatly into either r or K strategies (Shine and Iverson, 1995), exhibiting late sexual maturity, high fecundity, no maternal investment, and long lives. Turtles also possess a unique evolutionary history, morphology, and metabolic behavior.

Once animals crawled from the seas and evolved four limbs capable of supporting their weight, encased their bodies with dry skin and their embryos in amniotic eggs, these amniotes began to diversify and fill largely untapped habitat and unexplored niches. This evolutionary branching is most evident in the bones, especially skulls. If you examine turtle skulls you will note they have a solid cranium with no temporal fenestrae, or apses. Four lineages of amniotes arose, each identifiable by their pattern of temporal holes: Anapsids-none, Diapsids-two, Euryapsids-one small, and Synapsids-one large (Osborn, 1903). Turtles represent the last remaining Anapsids. Some believe Anapsids evolved before Diapsids, others think they arose from early Diapsids after secondarily losing their cranial apses and teeth (Modesto and Anderson, 2004; Harding, 2006). The absence of derived traits can be posed as either evidence of ancestral morphotypes (limbless fish evolved into limbed amphibians) or progenitorial specialization (limbed lizards evolved into limbless snakes). However, loss of traits through specialization is usually more common in parasites (Price, 1980). Whether Diapsids gave rise to Anapsids or arose from them, other amniote lineages evolved into mammals (Synapsids) or dinosaurs, lizards, crocodilians, tuatara, and avians (Diapsids) or ichthyosaurs, nothosaurs, placodonts, and plesiosaurs (Euryapsids). The turtle bauplan remains unchanged since they emerged 200 million years ago: a top shell (carapace) and bottom shell (plastron) comprised of individually sutured bony plates (scutes) covered with skin; a keratinized beak-like mouth; and a set of four limbs, tail, and telescopic neck with head all of which retract into the shell cavity. Such evolutionary conservation and worldwide propagation argues well for the success of their life history (Ernst and Lovich, 2009).

Evolutionary conservation is not meant to suggest turtles, Order Chelonia, represent an undiversified, monolithic group; though unlike the mollusks none have lost their shells. The order spans every continent except Antarctica with almost 320 species, divided among two classes: lateral-neck folding Pleurodira and vertical-neck folding Cryptodira. Over the millennia, various North American Cryptodiran turtle families returned to the sea, only emerging again to nest on the beaches (Cheloniidae and Dermochelyidae), others adapted to dry terrestrial habitats (Testudinidae and two species of Emydidae), while others balanced between freshwater and land (Chelydridae, Emydidae, and Trionychidae) (Ernst and Lovich, 2009).

Basking Turtles

Turtles within the family Emydidae are particularly interesting because they engage in a behavior known as basking. This behavior is not unique to turtles. Anyone who has seen a lizard sitting on a rock has observed reptilian basking behavior, but the most common instance cited for this behavior involves turtles on logs (Boyer, 1965; Congdon et al., 1982). Basking serves several purposes. It exposes the large carapace surface area to warm air and sunlight, which increases turtle metabolic rates and facilitates digestion and hindgut fermentation. Many turtles carry algae and entire invertebrate communities upon their carapaces and leeches within their shell cavities; basking desiccates and alleviates this parasitic load. Lastly, direct sunlight exposure allows vitamin D synthesis, which facilitates calcium uptake. Turtles with poor calcium uptake develop weak, spongy shells, a condition exacerbated by rapid growth, poor diet, or egg production (Kass et al., 1982; Lindeman, 1999a; Ernst and Lovich, 2009).

Freshwater turtle (family Emydidae) growth, or ontogeny, has been examined empirically (Cagle, 1946; Avery et al., 1993; Tucker et al., 1995) and using models (Frazer at al., 1990b; Stamps, 1995; Kennett, 1996). Relative measurements of growth include mouth gape, carapace length, and most commonly plastron length. Freshwater turtles are sexually dimorphic, with males maturing faster than females and the female sex growing to mature sizes 1.5-3.0 times as large as males. The pattern of growth in turtles is continuous and seasonally dependent on resource availability. The myth that turtles "stop" growing upon reaching maturity is still prevalent due to incremental annual changes among adults: growth is sigmoidal, with fast hatchling and juveniles slowing to reach an asymptotic adult plateau (Ernst et al., 1994; Parker, 1996; Congdon et al., 1999).

Dietary Ontogeny

Emydid turtle diets range across the scale from herbivory to omnivory to carnivory depending on species and ontogeny. Dietary composition often comprise such variety as fruits, leaves and shoots from aquatic and terrestrial vegetation, invertebrates, and small fish (Dreslik, 1999; Lindeman, 2003; Ernst and Lovich, 2009). Often large adult turtles were observed grazing rooted littoral vegetation; these same turtles were not above scavenging a dead, floating catfish carcass for extra protein (pers obs).

Ontogenous dietary thresholds are the growth points within a population at which significant changes in prey selection occur along a continuous gradient from hatchling to mature adults based on a common measurement of size (i.e., carapace length, plastron length, or mouth gape.) The effect of predator ontogeny upon prey selection has been studied among many different turtles (Ernst and Lovich, 2009); however, ontogenous thresholds are often arbitrary, predetermined before analysis, and dependent on discrete categories such as age groups or size classes.

Several Emydidae genera: *Chrysemys*, *Trachemys*, and *Pseudemys* have all demonstrated omnivorous diets and similar analogous prey bases among the aquatic invertebrates and vegetation within their respective freshwater habitats (Clark and Gibbons, 1969; Parmenter, 1980; Hart, 1983; Dreslik, 1999; Lindeman, 2003; Bouchard and Bjorndal, 2006). An ontogenous shift from juvenile carnivory to adult herbivory was reported in *Trachemys scripta scripta* (Clark and Gibbons, 1969; Bouchard and Bjorndal, 2006). Similarly, *T. s. elegans* showed transition from juvenile insectivorous to adult herbivorous diet (Hart, 1983; Dreslik, 1999).

Thermoregulation

The link between diet and thermoregulation has been noted in a variety of ectotherms, including fish, toads, salamanders, lizards, and turtles (Spotila et al., 1989; Avery et al., 1993; Angilletta, 2001; Secor and Faulkner, 2002; Roe et al., 2005). Dietary thermoregulation may specifically address components, quality, digestibility, or correlations among these factors. Turtles offer a unique opportunity for examining this interplay through basking. As Spotila (et al. 1989) noted, turtles must balance a relatively stable aquatic foraging environment with a highly variable terrestrial environment after dietary consumption. If environmental conditions are held stable, or experimentally manipulated, this more directly links dietary quality, thermoregulatory behavior, and physical expression such as growth.

While most behavioral studies have focused on turtle foraging (Schoener, 1971; Gatten, 1980; Parmenter, 1980) or digestive components (Roe et al., 2005), ectotherms offer the opportunity to integrate behavior directly with bioenergetic processes. These organisms vary their body temperature by moving along microclimate thermogradients, thus potentially adjusting metabolic rates based on dietary quality through behavioral rather than endothermic physiological means.

Turtles are poikilothermic ectotherms, meaning they require an environmental energy source (usually radiant or conductive heat exchange) to metabolize and their core body temperatures modulate with the environment. Many freshwater turtles engage in basking behavior, often congregating at prime basking sites in high abundances (Zimmerman and Tracy, 1989; Manning and Grigg, 1997; Lindeman, 1999a). Experiments comparing fasted and fed individuals show the latter *Trachemys scripta* bask higher along a thermogradient, raising body temperature 4.5 degrees Celsius to facilitate digestion (Gatten, 1974); compensate for foraging (Schoener, 1971); and season permitting promote egg gestation, nesting behavior, and oviposition (Krawchuk and Brooks, 1998).

Environmental criterion concerning turtle thermoregulation (Lucey, 1974; Foley and Spotila, 1978; Hutchinson, 1979; Crawford et al., 1983; Spotila et al., 1984) and basking behavior (Lucey, 1974; Crawford et al., 1983) have often been examined in tandem (Lucey, 1974; Schwarzkopf and Brooks, 1985). However, dietary bioenergetics studies (Schoener, 1971; Gatten, 1974; Schubauer and Parmenter, 1981; Spotila et al., 1989; Knight et al., 1990; Avery et al., 1993; Koper and Brooks, 2000) rarely link these potential factors driving net metabolic conservation (Hennemann, 1979; Tracy, 1982; Spotila and Standora, 1985; Krawchuk and Brooks, 1998). Turtles tradeoff between basking energy gain and metabolic cost, both related to organism size. Size therefore influences both sides of the energetic equation. While shell surface area controls absorbed radiation and relative energy gain, dietary foraging and metabolic energetics accumulate energy loss (for ectotherms, metabolic heat production is minimal.)

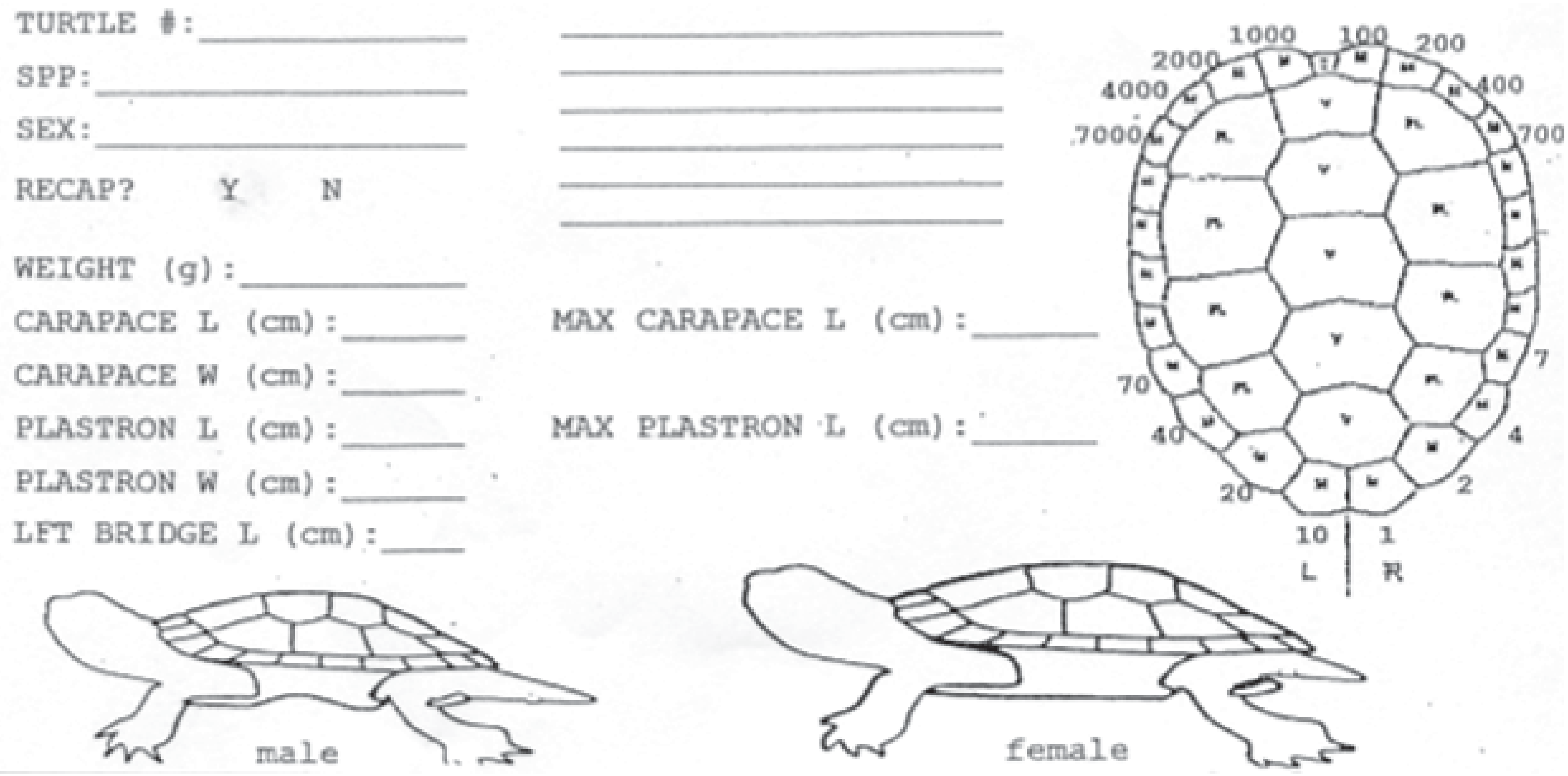
Dietary quality is primarily expressed by two metrics: nutrients or calories. Several ectotherm physiology studies have examined the importance of diet nutrient composition, in particular protein (Avery et al., 1993; Bjorndal and Bolten, 1993), while others have examined dietary energetics (Angilletta, 2001; Roe et al., 2005). Few have examined the tandem effects of nutrition and energetics (Secor and Faulkner, 2002), and none have examined these covariant dietary qualities using quantified thermoregulatory selective behavior such as basking.

Shell Notching

Any study involving monitoring individuals requires a method of differentiating one conspecific animal from another. Aside from birds—which require an additional federal permit due to the Migratory Birds Act—most wild animals can be legally marked with a state wildlife department scientific collection permit. Neck collars, belts, or leg bands offer many advantages: tough plastic construction, bright colors, and an attachment platform for tags, sensors or radio transmitters. Streamers may be attached to ears, fins, or shells, particularly useful for monitoring underwater activity. Subcutaneous implanted PIT tags even allow for physiological data collection (Nietfeld et al., 1996).

Biologists have devised many clever methods for marking individual turtles, including toe clipping, branding, floating streamers, metal tags, and PIT tagging, but most involve defacing the shell. Painting numerals offers a unique advantage of identifying turtles at a distance without having to recapture them and etching has been documented to last several decades, but carapace notching is the most common (Cagle, 1939; Ernst, 1972; Loncke and Obbard, 1977; Plummer, 1979; Nietfeld et al., 1996; Kornilev et al., 2012).

The author developed a modified shell notching pattern variant in 2009 capable of marking sizes ranging from hatchlings to large females with equal ease (Fig. 2.1). The system divides the shell into quadrants of four marginal scutes, each representing the number 1, 2, 4, or 7 orienting outwards from the center of the shell: upper left is the



TURTLE #:__________

SPP:__________

SEX:__________

RECAP? Y N

WEIGHT (g):__________

CARAPACE L (cm):______

CARAPACE W (cm):______

PLASTRON L (cm):______

PLASTRON W (cm):______

LFT BRIDGE L (cm):____

MAX CARAPACE L (cm):______

MAX PLASTRON L (cm):______

Figure 2.1 – Turtle collection datasheet showing individual identification system using marginal scute notching

thousands place, upper right hundreds, lower left tens, lower right ones. With practice any number can be assigned and later read from 1 to 9,999 by notching no more than eight scutes. In practice, it's better to start with 1,001 rather than 1 so that each individual turtle has at least two notches in case of future shell malformation.

Study Site

All subsequent chapters in this dissertation document studies utilizing turtles collected from Waco Creek, Texas from 2010 to 2012 (Fig. 2.2). Waco Creek is part of the Brazos River watershed. The Brazos River is the longest in Texas, with headwaters in New Mexico and mouth emptying into the Gulf of Mexico.

The specific study site was the mouth of Waco Creek upstream from South University Parks Drive and confluence with the Brazos River Reservoir in McLennan County, Texas (31° 32' 59.5231" N, 97° 6' 44.6505" W). The Waco Creek confluence is upriver of the Lake Brazos Dam on the Brazos River, turning the mouth of the creek into an arm of the Brazos River Reservoir. Severe water level drop within the reservoir empties the creek bed; however the creek is still subject to spring runoff flooding events (pers obs). Several floating basking traps were placed along a 270 m transect at 50 – 60 m intervals of the NW facing creek bank from June to October 2010, April to October 2011, and April to October 2012. While a single basking trap was placed in the creek October to November 2009 as part of a pilot study, and fifteen turtles captured, these data were not included in any analyses.

Basking trap design underwent several progressive modifications. Traps were constructed around square 7.62 cm diameter polyvinyl chloride (PVC) pipe floats, foam core filled (2012). An open basket was attached under each float, either 1.35 cm

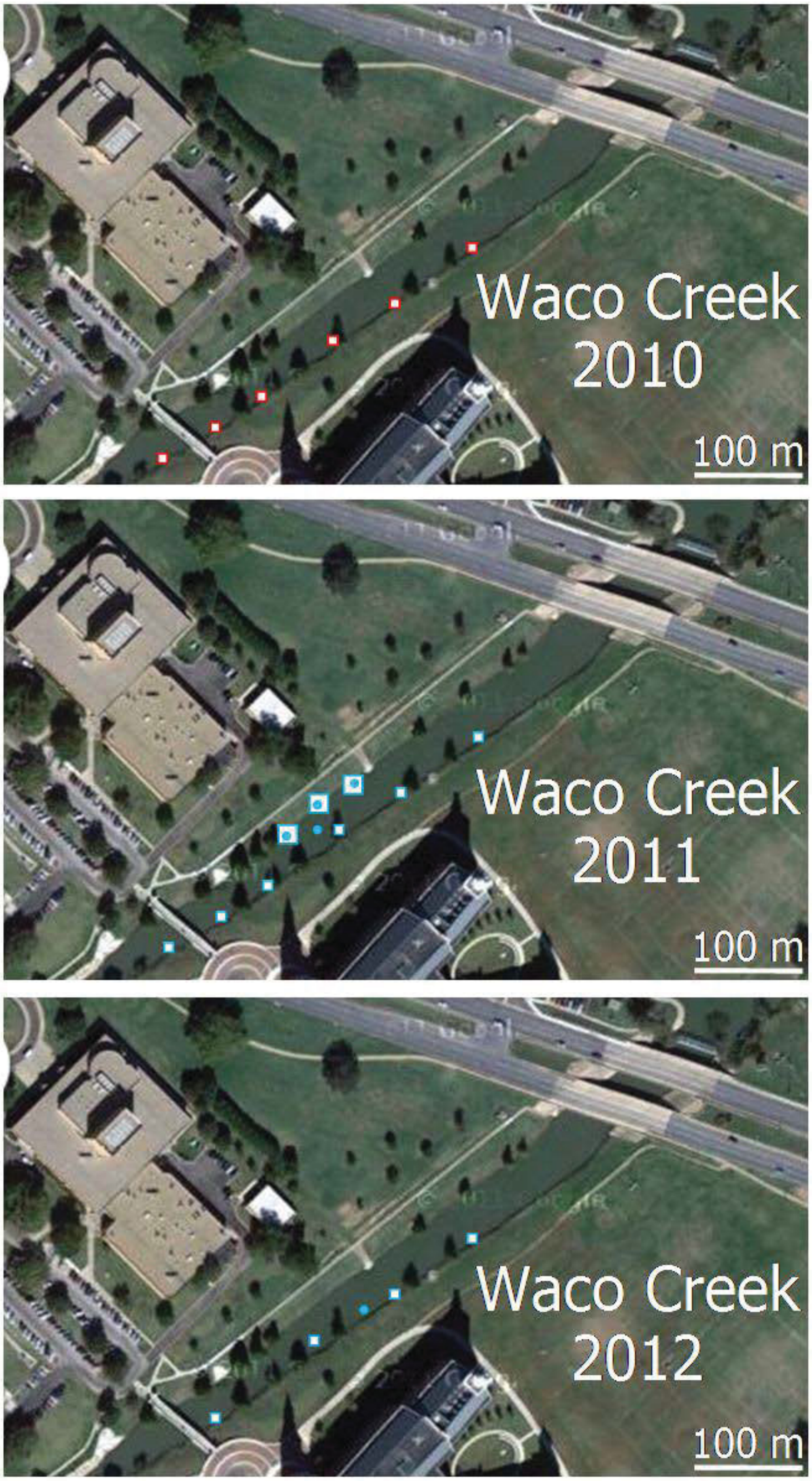


Figure 2.2 – Waco Creek, McLennan County, Texas with small red squares representing metal basking traps, small blue squares representing wooden/plastic basking traps, large blue squares representing cages, and small blue circles representing sensor platforms

galvanized metal mesh (2010) or stiff 0.635 cm plastic mesh walls (2011) and weighted bottoms (2012). Traps utilized metal mesh ramps (2010), no ramps (2011), or a combination of no ramps, half-ramped, and plywood ramps (2012). PVC pipe floats were 60.68 cm length squares (2010 and 2011) or 60.68 cm and 91.44 cm squares (2012).

CHAPTER THREE

Basking Turtle Assemblage Demographics within a Central Texas Creek

Abstract

This study examined the demographic composition of a central Texas emydid assemblage from 2010 to 2012 using basking traps. Species proportions included *Trachemys scripta elegans* (46%), *Pseudemys texana* (32%), and *Graptemys pseudogeographica kohnii* (23%). Larger males and females were conspicuously absent, *T. scripta* and *P. texana* male:female ratios were significantly male skewed, although none of the species' gender proportions shifted significantly from year to year. Comparing ontogenous variation among annual samples, only *T. scripta* (all and male) and *P. texana* (all) demographics showed significant plastron length change from year to year. Male activity showed few consistent annual seasonal trends, female activity was typically minimal and absent during summer 2011, and juvenile activity rose in August to September. Some results statistically varied between analyzing individuals and capture events per demographic.

Keywords: gender, *Graptemys*, population, *Pseudemys*, *Trachemys*

Introduction

A community is an artificial organizational construct which solely examines an ecological system in terms of interspecies relationships. Ecological studies often attempt to reduce a complex community into a series of interconnected groups using descriptive characteristics such as species composition, niches, trophic levels, or assemblages. A subset based upon taxonomic or ecological distinctions, contemporary studies often use assemblages to describe community structure. Studies may also describe this structure via component populations grouped into common assemblages. Populations are comprised of individuals, so individual behavior and success are a foundation of assemblage dynamics (Schulter and Ricklefs, 1993; Morin, 1999; Dreslik et al., 2005).

Freshwater turtle communities offer a ready opportunity to examine ecologically distinct assemblages through individual group behavior—those which bask versus those which do not—based upon trap designs used to sample the community. This behavioral distinction also follows a parallel taxonomic split; most North American basking species fall within the family Emydidae whereas sympatric species which typically do not bask fall without (Chelydridae, Kinosternidae, and Trionychidae). During basking behavior, turtles emerge on rocks, logs, and embankments, splay their limbs, and sun themselves, often vying for prime sites (Zimmerman and Tracy, 1989; Manning and Grigg, 1997; Lindeman, 1999a). This behavior boosts core temperature, fueling metabolic processes. Not only can specific basking trap designs target this behavior, but several studies have shown multiple concurrent trap designs such as basking, fyke, and hoop traps are required to fully sample a turtle community due to bias inherent in each sampling method (Cagle and Chaney, 1950; Ream and Ream, 1966; Dunham et al., 1988; Burke et al., 1995; Dreslik et al., 2005).

Emydid turtle population demographics are often quantified in terms of mature males, mature females, and juveniles; occasionally the latter is subcategorized into hatchlings, immature males, and immature females. Gender may be determined by anatomical features, dissecting matured sexual organs, or using x-rays to reveal egg production (Gibbons and Greene, 1979; Ewert and Nelson, 1991; Readel et al., 2008). Turtle embryos exhibit temperature dependent sex-linked determination. Incubation temperatures above 29.2 °C will produce more female turtles and temperatures falling below will produce more male turtles on a sliding proportional scale (Willingham, 2005). While turtle samples are usually compared to a hypothetical balanced 1.00 sex ratio, due to environmental microclimate variation this convention does not hold to empirical nest observations (Bull and Vogt, 1979; Vogt and Bull, 1982; Vogt and Bull, 1984; Janzen, 1994). Faster male maturity, aquatic trapping techniques, and road density produce a male bias while seasonal nesting and terrestrial trapping produce a female bias (Gamble and Simons, 2004; Gibbs and Steen, 2005). Population sample sex ratios (male:female) range from 0.50 to 13.00 across North American emydid species and geographical boundaries (Gibbons, 1990; Parker, 1990; Burke et al., 1995; Congdon and Gibbons, 1996; Litzgus and Mousseau, 2004; Conner et al., 2005; Hays and McBee, 2010).

The goal of this study is to examine basking turtle demographics within a central Texas community. Objectives include 1) quantifying physical attributes of each species' demographics, 2) examining annual shifts in sex ratios and demographic size variation among different species, and 3) examining seasonal sampling trends.

Methods and Materials

The study site was the mouth of Waco Creek upstream from South University Parks Drive and confluence with the Brazos River Reservoir in McLennan County, Texas (31° 32' 59.5231" N, 97° 6’ 44.6505” W). The Waco Creek confluence is upriver of the Lake Brazos Dam on the Brazos River, turning the mouth of the creek into an arm of the Brazos River Reservoir. Severe water level drop within the reservoir empties the creek bed; however the creek is still subject to spring runoff flooding events (pers obs). Several floating basking traps were placed along a 270 m transect at 50 – 60 m intervals of the NW facing creek bank from June to October 2010, April to October 2011, and April to October 2012.

Traps were checked at 24 hr intervals. Turtles were measured, identified, sexed, individually marked with marginal scute notches, and then released within three meters of the original capture site. Measurements included weight, carapace length, carapace width, plastron length, and plastron width. Age as a function of scute rings was not examined due to the unreliability of this methodology and the worn, pitted shells of many larger turtles. The only verifiable ages were those hatchling turtles clutched during the sampling period. Mature males were identified by relatively longer claws, thicker tails, and the position of the cloacal vent beyond the edge of the carapace. All other turtles were deemed juveniles or females with the species specific plastron length (PL) demarcation between the two deriving from prior conspecific studies: *Trachemys scripta elegans* 15.9 cm PL, *Pseudemys texana* 21.3 cm PL, and *Graptemys pseudogeographica kohnii* 12.0 cm PL (Timken, 1968; Lindeman, 2005; Lindeman, 2007; Perez-Santigosa et al., 2008; Ernst and Lovich, 2009).

Sex ratio data were subjected to a chi-squared analysis (χ^2) to compare male:female frequencies to an expected 1:1 ratio and Fisher's exact test (P) to compare proportions among annual samples. Annual ontogenous variation among species demographics was assessed with individual annual first capture plastron length data using a Kruskal-Wallis test (χ^2) with Dunn's posthoc. Nonparametric tests were used on account of the skewed nature and small sample size of most demographics. Unless otherwise noted, all statistical analyses set p-value significance using α = 0.05 (Zar 1999). All qualitative data analyses, figures, and tables were generated using open office and all quantitative analyses used the R 2.15.2 analytical software package stat (R Core Team 2012).

Results

Several species were collected throughout the study's three year period. Emydid basking species included (individuals / total capture events) the Red-eared Slider *Trachemys scripta elegans* (282/529), Texas River Cooter *Pseudemys texana* (192/308), and False Map Turtle *Graptemys pseudogeographica kohnii* (139/288). Per annum, these data partition into *T. scripta*: 2010 (98/136), 2011 (92/154), and 2012 (92/229); *P. texana*: 2010 (35/42), 2011 (89/129), and 2012 (68/133); and *G. pseudogeographica*: 2010 (15/22), 2011 (44/90), and 2012 (80/175). All records concerning two outliers were omitted before tabulating the total sample (613/1125) and all subsequent analyses—a juvenile *G. pseudogeographica* T1224 and juvenile *T. scripta* T1360, both captured during 2012—due to excessive 18 and 70 capture events per season, respectively.

Other species included the Spiny Softshell Turtle *Apalone spinifera* (5 capture events), Harris Mud Crab *Rithropanopeus harrisii* (8 capture events), and several unidentified, unquantified fish. It is interesting to note that while catfish *Icturus sp*. were routinely observed within the creek, only bass *Micropterus sp.* and sunfish *Lepomis sp.* were collected from the basking traps. Several photographs were taken to substantiate species identifications and document injuries—several turtles still managed to bask and climb into the traps despite missing feet or limbs—however, museum specimens were not collected so as to not permanently remove individuals from their respective populations.

Because of its planar surface, the most common unit of turtle measurement is plastron length (PL), sometimes called midline plastron length, but other common metrics were recorded for each species demographic (Table 3.1). For the largest species *Pseudemys texana*, PL ranged 3.1 – 24.4 cm with juveniles averaging 7.0±2.4 cm, males averaging 13.2±2.4, and females averaging 20.0±3.4 cm. *Trachemys scripta elegans* PL ranged 3.0 – 23.1 cm with juveniles averaging 6.6±2.5 cm, males averaging 12.3±2.3 cm, and females averaging 18.1±3.2 cm. For the smallest species, *Graptemys pseudogeographica kohnii*, PL ranged 2.8 – 17.5 cm with juveniles averaging 7.1±2.9 cm, males averaging 8.7±1.1 cm, and females averaging 12.9±2.0 cm.

Species sex ratios ranged from 2.54 to 11.00, ranking in descending order of male skewedness (individuals/total capture): *P. texana* (8.50/11.00), *T. scripta* (5.59/8.33), and *G. pseudogeographica* (2.54/5.25). Sex ratios were all compared to an expected 1.00 ratio using a chi-squared test (χ^2) among both individuals and total captures for each species demographic sampled from 2010 to 2012 (Table 3.2A). All demographic chi-squared values were statistically significant at $\alpha = 0.01$, evincing male skewed ratios except individually captured *G. pseudogeographica*, whose test results show that group's balanced male:female ratio of 33:13 did not statistically differ from the 23:23 expected ratio.

Annual gender proportions were compared across subsequent years for each demographic using a Fisher exact test (P) to determine if sex ratios changed significantly year to year (Table 3.2B). Due to lack of female captures in 2010, *G. pseudogeographica* ratios were omitted that year. Despite changing ratios, none of the gender proportions changed to a statistically significant degree at $\alpha = 0.05$.

Table 3.1 – Descriptive statistics for *Trachemys scripta elegans* (TRSC), *Pseudemys texana* (PSTE), and *Graptemys pseudogeographica kohnii* (GRPS) frequency (n), mass, plastron length (PL), and carapace length (CL)

Species	n	Mass (g) mean±sd	Mass (g) min	Mass (g) max	PL (cm) mean±sd	PL (cm) min	PL (cm) max	CL (cm) mean±sd	CL (cm) min	CL (cm) max
TRSC M	153	394.4±236.7	115.0	1349.0	12.3±2.3	8.2	18.4	13.6±2.6	9.2	20.8
TRSC F	20	1241.8±539.8	311.0	2137.0	18.1±3.2	11.6	23.1	19.5±3.2	12.8	24.4
TRSC J	356	90.8±119.9	8.0	944.0	6.6±2.5	3.0	15.3	7.1±2.8	3.1	17.0
PSTE M	70	448.3±226.6	80.0	1304.0	13.2±2.4	6.8	19.4	14.7±3.0	1.6	21.5
PSTE F	6	1346.7±646.4	792.0	2184.0	20.0±3.4	17.0	24.4	21.4±3.5	18.1	26.1
PSTE J	232	94.1±85.4	11.0	629.0	7.0±2.4	3.1	15.8	7.8±2.7	3.5	16.8
GRPS M	85	128.8±43.1	37.0	261.0	8.7±1.1	5.4	11.2	10.0±1.3	6.1	12.9
GRPS F	16	419.7±242.6	251.0	1080.0	12.9±2.0	11.2	17.5	14.2±2.3	12.2	19.7
GRPS J	187	101.3±88.7	6.0	370.0	7.1±2.9	2.8	12.6	7.9±3.2	3.0	13.5

Table 3.2 – Sex ratios for three sympatric Waco Creek turtle species with the top row showing individuals captured and the bottom total captured A) cumulative ratios with a chi-squared test (χ^2) comparing to an expected 1.00 ratio and B) annual ratios with the Fisher exact test (P) comparing successive years with * denoting significance at α = 0.05 and ** significance at α = 0.01

A

Species	Male	Female	Ratio	χ^2
Trachemys scripta elegans	95	17	5.59	29.34**
	150	18	8.33	59.58**
Pseudemys texana	51	6	8.50	19.21**
	66	6	11.00	28.27**
Graptemys pseudogeographica kohnii	33	13	2.54	3.70
	84	16	5.25	24.63**

B

Species	2010	P	2011	P	2012
Trachemys scripta elegans	4.78	0.68	7.00	0.66	10.67
	5.44	0.53	10.33	0.79	13.00
Pseudemys texana	10.00	0.81	12.33	2.24	5.50
	10.00	0.68	14.67	2.44	6.00
Graptemys pseudogeographica kohnii	-	-	2.25	0.75	3.00
	-	-	5.50	1.12	4.92

Annual demographic ontogenous variation was assessed using a Kruskal-Wallis test (χ^2) for twelve demographic groups using plastron length as the metric and sample year as grouping factor (Table 3.3). Of these groups, only *T. scripta* (χ^2 = 22.26, df = 2, p-value < 0.000), *T. scripta* males (χ^2 = 18.89, df = 2, p-value < 0.000), and *P. texana* (χ^2 = 10.52, df = 2, p-value = 0.005) were significant at α = 0.05 and *P. texana* males (χ^2 = 4.92, df = 2, p-value = 0.085) significant at α = 0.10 evincing mean plastron length

Table 3.3 – Annual demographic ontogenous variation using a Kruskal-Wallis test with Dunn's procedure ($\alpha = 0.05$) to compare individual turtle plastron lengths among sample years for *Trachemys scripta elegans* (TRSC), *Pseudemys texana* (PSTE), and *Graptemys pseudogeographica kohnii* (GRPS)

Sample	χ^2	df	p-value	Year
TRSC (ALL)	22.26	2	< 0.000	2012 < 2011 < 2010
TRSC (M)	18.89	2	< 0.000	2012 < 2011 < 2010
TRSC (F)	2.76	2	0.252	
TRSC (J)	3.02	2	0.221	
PSTE (ALL)	10.52	2	0.005	2012 < 2010 < 2011
PSTE (M)	4.92	2	0.085	
PSTE (F)	0.21	2	0.901	
PSTE (J)	2.40	2	0.301	
GRPS (ALL)	1.88	2	0.390	
GRPS (M)	1.30	2	0.523	
GRPS (F)	0.29	1	0.588	
GRPS (J)	1.44	2	0.486	

variation between one or more years. A Dunn's posthoc was run on the three groups significant at $\alpha = 0.05$ to assess rank among annual PL demographic samples. Both *T scripta* and *T. scripta* male PL ranked 2012 < 2011 <2010 while *P. texana* PL ranked 2010 < 2010 < 2011. Turtle demographic capture activity showed interesting seasonal variation from 2010 to 2012 (Fig. 3.1). Although no months showed matching annual patterns, several descriptive trends still emerged. Every year, juvenile and male activity increased in September during both 2010 and 2011 and August in 2012, however juvenile:male ratios were higher during the spring and summer months and lower in the autumn. Female activity was minor and periodic throughout the entire sampling period except May to August 2011 which showed an absence of female activity.

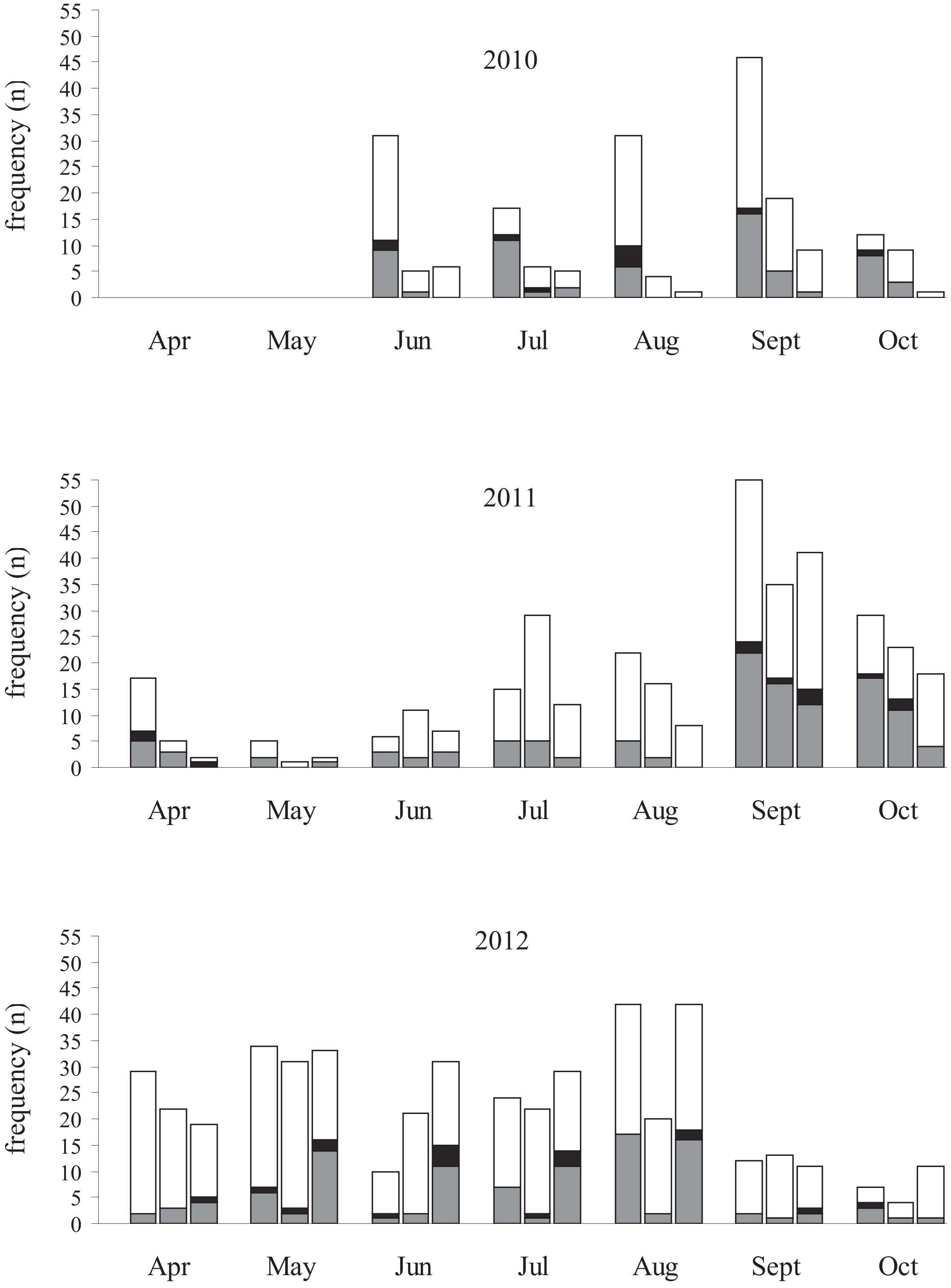


Figure 3.1 – Demographic seasonal activity for *Trachemys scripta elegans* (left column), *Pseudemys texana* (central column), and *Graptemys pseudogeographica kohnii* (right column) including males (gray bars), females (black bars), and juveniles (white bars)

Discussion

Several studies have examined North American freshwater turtle assemblage abundances using aquatic trap techniques in which most component species are within the family Emydidae. These species—with prior publications updated to reflect current taxonomy—include *Apalone muticus* (APMU), *Apalone spinifera* (APSP), *Chelydra serpentina* (CHSE), *Chrysemys picta* (CHPI), *Deirochelys retucularia* (DERE), *Emydoidea blandingii* (EMBL), *Graptemys geographica* (GRGE), *Graptemys ouachitensis* (GROU), *Graptemys pseudogeographica* (GRPS), *Kinosternon subrubrum* (KISU), *Pseudemys concinna* (PSCO), *Pseudemys floridana* (PSFL), *Pseudemys texana* (PSTE), *Sternotherus odoratus* (STOD), and *Trachemys scripta* (TRSC).

This study examined a 4 species community assemblage from 2010-2012 at Waco Creek, Texas with the following abundances: TRSC 46%, PSTE 31%, GRPS 22%, and APSP < 1%. Several other studies have previously examined turtle assemblages with at least four species among both lotic and lentic wetlands systems within North American watersheds. Lotic (flowing water) assemblages include Barko et al. 2004 examining a 7 species assemblage from 1996-2001 in the upper Mississippi River adjacent to Missouri and Illinois: GRPS 83%, TRSC 10%, APMU 5%, APSP 2%, CHSE < 1%, and STOD < 1%. A study from Indiana in 2002 examined a 6 species assemblage at Central Canal, which originates from the White River: GRGE 40%, STOD 34 %, CHSE 14%, TRSC 5%, CHPI < 4%, and APSP 3% (Conner et al., 2005). A 2005-2007 study at the Brazos River reservoir, Texas examined a 5 species assemblage: PSTE 66%, TRSC 29%, GRPS 3%, APMU 1%, and APSP 1% (Hill, 2008).

Lentic (still water) assemblages have also been examined. From 1994-1999 at Round Pond, Illinois Dreslik (et al. 2005) sampled a 10 species assemblage: TRSC 67%, PSCO 15%, APSP 13%, CHSE 9%, STOD 4%, GROU 3%, APMU < 1%, CHPI < 1%, GRGE < 1%, and GRPS < 1%. A study at Dewart Lake, Indiana documented a 7 species turtle assemblage from 1995-1997: CHPI 73%, STOD 17%, GRGE 6%, TRSC 2%, APSP < 1%, CHSE < 1%, and EMBL < 1% and 6 species assemblage from 1993-2002: CHPI 61%, STOD 26%, GRGE 4%, TRSC 4%, CHSE 4%, and EMBL < 1% (Smith and Iverson, 2004). Conner (et al. 2005) examined a 6 species assemblage in Indiana during 2002 at Indianapolis Museum of Art Lake: TRSC 67%, STOD 21%, GRGE 5%, CHPI 3%, CHSE 3%, and APSP 2%.

Several trends appear after examining these turtle assemblages. Lentic systems have higher mean turtle species richness than lotic systems. The piscivorous *Apalone spp* and *Chelydra* do not show high trap abundance in this or any cited studies—even those which utilized baited hoop traps (APMU 1-5%, APSP < 1 – 13%, and CHSE 3-14%). Genera like *Kinosternon* and *Sternotherus* are benthic foragers, whereas most of the other genera are pelagic or littoral foragers, and appear less in rivers (<1%) than canals (34%) or ponds (17-21%). Riverine systems like the Mississippi are dominated by *Pseudemys* (83%) or *Graptemys* (66%) and sparsely populated by *Trachemys* (5-10%) or *Chrysemys* (4%). Ponds and lakes are dominated by *Trachemys* (67%) or *Chrysemys* (61-73%) and show limited *Pseudemys* (15%) or *Graptemys* (4-5%). These trends match the respective lotic or lentic habitat preferences of these four genera (Bodie and Semlitsch, 2000; Anderson et al., 2002; Ernst and Lovich, 2009). However, artificially constructed lotic systems like the Brazos River reservoir (*Pseudemys* 66%, Graptemys 3%, and *Trachemys*

29%) or Central Canal (*Graptemys* 40%, *Trachemys* 5%, and *Chrysemys* 4%) show less riverine species dominance. The mouth of Waco Creek (*Pseudemys* 31%, *Graptemys* 22%, and *Trachemys* 46%) is almost 1:1 codominant between riverine and pond species, suggesting intermediate habitat characteristics or a possible niche overlap.

Mean, range plastron length and maximum carapace length for mature individuals (Table 3.1) included *P. texana* males (13.2, 6.8-19.4 cm PL and 21.5 cm CL) and females (20.0, 17.0-24.4 cm PL and 26.1 cm CL), *T. scripta* males (12.3, 8.2-18.4 cm PL and 20.8 cm CL) and females (18.1, 11.6-23.1 cm PL and 24.4 cm CL), and *G. pseudogeographica* males (8.7, 5.4-11.2 cm PL and 12.9 cm CL) and females (12.9, 11.2-17.5 cm and 19.7 cm CL). Compared to previously sampled demographics, Waco Creek turtles encompass a smaller, restricted upper limit size range irrespective of different maturation rates affecting the lower limit size range. Hill (2008) sampled *P. texana* males (14.7, 10.0-29.9 cm PL) and *P. texana* females (18.0, 8.0-28.4 cm PL). Lindeman (2001) documented males (17.8-16.2 cm PL) and females (21.2-23.4 cm PL). Maximum CL recorded for this species are male (25.3 cm CL) and female (33.0 cm CL) as reported by Ernst and Lovich (2009). Cagle (1950) measured *T. scripta* males (9.0-19.6 cm PL) and *T. scripta* females (15.3-22.0 cm PL). Maximum CL recorded for this species are male (23.0 cm CL) and female (30.2 cm CL) as reported by Ernst and Lovich (2009). Timken (1968) recorded *G. pseudogeographica* males (10.3-13.4 cm PL) and females (7.8-25.5 cm PL). Maximum CL recorded for this species are male (15.0 cm CL) and female (27.0 cm CL) as reported by Ernst and Lovich (2009).

Among Waco Creek emydid species captured from 2010-2012 (Table 3.2A), the two larger turtles' male:female sex ratios statistically varied from a balanced 1.00 ratio at α = 0.05(*) whereas the smallest turtle species did not: *Trachemys scripta elegans* (5.59*), *Pseudemys texana* (8.50*), and *Graptemys pseudogeographica kohnii* (2.54). Additional ratios for North American *T. scripta* include 0.31*, 0.69*, 0.91, 1.09, 1.12, 1.21, 1.23, 1.49*, 1.74*, 2.05*, 2.28*, 2.37*, 2.48*, 3.54* (Viosca, 1933; Cagle, 1942; Cagle, 1950; Webb, 1961; Parker, 1984; Gibbons, 1990). *P. concinna, P. floridana,* and *P. texana* ratios include 1.16, 1.31, and 1.70*, respectively (Jackson, 1970; Gibbons, 1990; Hill, 2008). *G. geographica* ratios include 1.40, 1.67*, 1.74*, and 3.00*, and *G. ouachitensis* ratios include 0.26* and 0.56*, and *G. pseuodogeographica* ratios include 0.62*, 1.00, and 4.29* (Timken, 1968; Gordon and MacCulloch, 1980; Vogt, 1980a; Shively and Jackson, 1985; DonnerWright et al., 1999; Anderson et al., 2002).

If the cited examples are representative of their respective taxa, Waco Creek *Trachemys* and *Pseudemys* are severely male skewed while the *Graptemys* fall within an expected range. This is expected if—as the smaller ranged sizes for males and females suggest—larger turtles including much of the female population inhabit the adjacent Brazos River (*Pseudemys*) or floodplains, ponds, and marshes (*Trachemys*), making Waco Creek a metapopulation of males and juveniles for the two larger turtle species. The smallest species, riverine *Graptemys pseudogeographica kohnii*, does not evince a skewed sex ratio, indicating either a greater rate of female migration to Waco Creek or less basking trap bias due to smaller female turtles. Bodie and Semlitsch (2000) documented gender based disproportionate habitat use in female *G. pseudogeographica* preference for rivers and male *G. pseudogeographica* and *T. scripta* preference for scoured wetlands as well as sedentary behavior in male *T. scripta*. Despite annual shifts in sex ratios (Table 3.2B), gender proportions did not significantly change from year to year, which shows stable sampling bias or more likely indicates a stable population within Waco Creek.

Gender plastron length variation remained constant for most Waco Creek demographics throughout the sampling period (Table 3.3). Exceptions included *T. scripta* males and total sample and *P. texana* total sample, with PL significantly shifting from year to year. These data are likely more due to demographic changes rather than weather or trap-influenced bias; else one might expect corresponding changes in the juvenile demographic of both species. Whether due to changes in population growth, immigration, or emigration, there is no ready explanation as to why turtles among the two larger basking species in Waco Creek decreased in size during this study while most of the demographic groups showed no statistically significant change in size.

Seasonally, one would expect male turtle activity to rise in the spring and fall to reflect courtship and mating behavior, female activity to rise in May-June to coincide with nesting season, and juvenile activity to rise in the fall (southern latitudes) or early spring (northern latitudes) to coincide with hatchling emergence (Ernst and Lovich, 2009). Male behavior does not show any predominant seasonal trend from 2010 to 2012 (Fig. 3.1). While nesting behavior was observed along the banks of Waco Creek mid May (pers obs), this behavior is not reflected in comparative seasonal capture rates. Juvenile capture rates do follow seasonal expectations by rising in September (2010 and 2011) and August (2012) to reflect hatchling emergence from their nests. The early emergence in 2012 perhaps reflects the local drought conditions of the previous year.

To conclude, the mouth of Waco Creek appears to offer habitat conducive to both lotic and lentic turtle species, showing marked male skewed populations among larger turtle species as evinced by sex ratios and a lack of female captures. The site also evinces a decreased range of larger turtles, suggesting that while nesting may occur, resources are too limited to support larger male and female turtles, leaving Waco Creek a shelter for hatchlings, juveniles, and young males. Biological significances of these conclusions are that the unique Waco Creek mouth habitat conditions foster species diversity, weaken sympatric competition, and attract juvenile congregation or provide limited resources for larger individuals. Large scale comparative analyses encompassing adjacent ponds and rivers and further trap diversity would better examine habitat partitioning and trap bias among different size demographics and place Waco Creek within the larger landscape. Further study is required to fully resolve these questions.

Acknowledgments

I thank my main field crew Rebecca York, Johnathan Nguyen, and Hemali Patel for coming back year after year and appreciate the many helpful suggestions from Robert Baldridge during the genesis and execution of this project. I would also like to thank the Baylor University Biology department and Graduate School for support. This study was funded in part by the Jack G. and Norma Jean Folmar grant. Turtles were sampled under Texas Parks and Wildlife Scientific Permit #SPR-0609-127. This project was reviewed and approved by Baylor University's Institutional Animal Care and Use Committee.

CHAPTER FOUR

Target Demographic: Factors Driving Basking Response

Abstract

This study examines the impact of demographic selection and trap modification on sample capture statistics from April to October 2012 among three species within a central Texas creek community. Plotting individual plastron length over the entire trapping season, the community divides into three distinct ontogenous temporal strata: late emerging hatchling/juveniles (2.9-4.3 cm PL), rapidly growing juveniles/immature males (2.8-7.5 cm PL), and maturing males/immature females/young mature females (7.5-15.8 cm PL). Comparing species and sex demography to population estimate ratios, species samples were less variable and more representative of the population. This was due to the large number of repeating basking juveniles/immature males. Nine linear mixed models were used to account for individual repeated measures, individual size, and microclimate variation over the course of the study to generate an analysis of variance for each trapday capture response statistic: plastron length mean, plastron length range, capture density, conspecific frequency, consexual frequency, condemographic frequency, species richness, species evenness, and species diversity. Among the factorial fixed predictors for the response variables, sex showed significance for nine responses ($F_{(df=2)} = 3.691\text{-}180.068$, $p < 0.000\text{-}0.026$), trap position was significant for eight ($F_{(df=3)} = 2.802\text{-}7.488$, $p = 0.000\text{-}0.024$), species was significant for five ($F_{(df=2)} = 5.002\text{-}7.911$, $p = 0.000\text{-}0.007$), and trap size significant for one ($F_{(df=2)} = 5.440$, $p = 0.020$).

Keywords: *Graptemys*, *Pseudemys*, *Trachemys*, trap, turtle

Introduction

Traps take advantage of individual repetitive behavior among wildlife and researchers have long used these observed patterns to ensnare herpetofaunal species. Pitfall, funnel traps, and drift fences exploit terrestrial movement (Corn and Bury, 1990); hoop, fyke nets, trammel nets, and turtle blinds, aquatic movement; baited traps, foraging (Lagler, 1943; Ream and Ream, 1966; Bider and Hoek, 1971; Vogt, 1980b); and basking traps and bal-chatri, thermoregulation (Ream and Ream, 1966; Braid, 1974).

Several studies document an inherent bias for many of these trapping methods, with one exception (Bider and Hoek, 1971). Multiple pitfall and funnel trap positions and configurations induce herpetofaunal community sample variation (Greenberg et al., 1994; Enge, 2001; Todd et al., 2007). Ream and Ream (1966) demonstrate how five dissimilar concurrent trap techniques yield different demographic ratios within a single *Chrysemys picta* population. Initial individual captures also influence subsequent capture rates, with snapping turtles negatively and conspecific emydid turtles positively influencing trap success (Cagle and Chaney, 1950; Plummer, 1979; Dunham et al., 1988; Frazer et al., 1990c). Bider and Hoek (1971) claim an apparent unbiased technique using a turtle blind apparatus, citing criteria (Ream and Ream, 1966) including juvenile to adult ratios, male to female ratios, percent population capture, and capture efficiency. However, these criteria do not demonstrate turtle blinds offer more representative population demographics sampling than any other technique nor do any other studies utilizing turtle blinds purport a lack of sampling bias (Robinson and Murphy, 1975). Without conducting a complete census on a closed habitat system to establish population parameters for comparison, bias can only reasonably be assessed among different sampling methods. Several studies have used population estimation techniques using basking sample data (Tinkle, 1958; Wilbur and Landwehr, 1974; Lindeman, 1990; Burke et al., 1995), however to date nobody has examined trap sample bias and population estimation in tandem.

Freshwater turtles in the Family Emydidae are often sampled to infer population dynamics using floating basking traps. Turtles sun themselves on any emergent surface such as shallow embankments, floating driftwood, logs, and car tires (Gibbons, 1990; Ernst and Lovich, 2009). Targeting this behavior, classical basking traps utilize ramps mounted to a square float constructed from large diameter polyvinylchloride pipes with a trap body submerged underwater. Turtles bask on the ramps, a portion of which fall into the trap. Such traps are often used to examine population growth (Frazer et al., 1990a; Frazer et al., 1990b; Gamble and Simons, 2004) and compare population or community assemblage demographics (Cagle and Chaney, 1950; Tinkle, 1958; Dunham et al., 1988; Frazer et al., 1990c; Burke et al., 1995).

Most demographic basking turtle studies focus on adult behavior such as invasive interspecies competition (Cadi and Joly, 2003; Polo-Cavia et al., 2010), native interspecies competition (Lindeman, 1999a; Carriere et al., 2008; Coleman and Gutberlet, 2008; Peterman and Ryan, 2009), intraspecific competition (Lovich, 1988), implications of basking habitat conditions (Moore and Seigel, 2006; Peterman and Ryan, 2008; Lindeman, 1999b; Hays and McBee, 2010), or the physiological significance of sexual dimorphism among mature individuals (Hammond et al., 1988; Lefevre and Brooks, 1995; Lindeman, 1999a; Bulté and Blouin-Demers, 2009). Basking among hatchlings and juveniles has largely been ignored (Hennemann, 1979; Janzen et al., 1992).

Traps provide a demographic sample from within a given population. Utilizing sample bias due to individual selection, it is possible to infer community demographic behavior patterns of the dominant repetitive trait used to entrap them. Instead of using multiple trap types to infer demographic sampling bias, conversely focusing on variations within a single basking trap design allows for examination of the effect of trap features and individual bias on capture demographics. This study seeks to examine how various predictors influence trap capture response. Objectives include determining how 1a) individual demographics and 1b) trap design factors affect trap capture 2a) morphometrics and density, 2b) demographic attraction, and 2c) community measurements among the Waco Creek basking turtle assemblage.

Methods and Materials

The study site was the mouth of Waco Creek upstream from South University Parks Drive and confluence with the Brazos River Reservoir in McLennan County, Texas (31° 32' 59.5231" N, 97° 6’ 44.6505” W). The Waco Creek confluence is upriver of the Lake Brazos Dam on the Brazos River, turning the mouth of the creek into an arm of the Brazos River Reservoir. Severe water level drop within the reservoir empties the creek bed; however the creek is still subject to spring runoff flooding events (pers obs). Four basking traps were placed at 54 m equidistant positions tethered along the NW facing bank and sampling occurred April-October 2012 among successive downstream positions: alpha, beta, gamma, and delta.

All traps possessed foam core filled 7.62 cm diameter square PVC pipe floats, stiff plastic fence walls with 0.635 cm width holes and weighted bottoms, and all material connections made using zip ties to facilitate rapid modifications. Trap design factorial variations included size (two small traps using 60.68 cm length and two large using 91.44 cm length PVC square floats) and the absence, presence of two parallel, or presence of four 30.48 cm width 1 cm ply laminate platform ramps attached at a 45 degree angle extending the length of each PVC segment.

Traps were checked at 24 hr intervals. Trials lasted 120 hrs with random trap design variation shuffling at each position, selecting one of three ramp variants for each pair of small and large traps at each position along the creek per each trial. Ramp platforms were rotated into storage after every trial to limit algal growth and warping. Turtles were measured, identified, sexed, and individually marked, then released the same day at the capture site. Creek microclimate variables—air temperature, water temperature, and relative humidity—were measured at 600 s intervals (iButton, Embedded Data Systems) with daily statistics calculated using a mean 7:00 am sample time to mark each day (i.e., each morning turtle sample is associated with the previous day's microclimate data.) Sensors were replaced every ten days to accommodate iButton datalogger storage capacity.

For the data analysis matrix, each row represented a daily individual turtle capture event and each column associated variables. Due to the longitudinal, nonparametric, zero inflated, disproportional replicate nature of the data, analysis utilized a linear mixed model regression, which examined the effects of fixed and random predictive variables upon a single response variable. Fixed predictors included the factorial variables: turtle species, gender, trap position, trap size, and trap ramps. Random predictors (per trapday) included capture date, turtle identification, turtle plastron length, mean daily air temperature, water temperature, and relative humidity. Response variable categories included morphometric and density measurements (plastron length mean, plastron length range, and capture density), demographic capture proportions (conspecific frequency, consexual frequency, and condemographic frequency), and community measurements (richness, evenness, and Shannon Diversity Index.)

Demographic data were compared among samples and population estimates using chi-squared analysis. Each mixed model was examined for regression assumption violations and then subjected to an analysis of variance. All data analyses and graphics were generated using R 2.15.2 statistical software: car, ggplot2, lme4, and stats packages (Nobre et al., 2007; Hothorn et al., 2008; Wickham, 2009; Fox and Weisberg, 2011; Bates et al., 2013).

Results

Turtle trapping occurred from April 16, 2012 to October 22, 2012 with a gap from July 1, 2012 to July 6, 2012 or 740 trapdays (185 days). Microclimate variables air temperature, water temperature, and relative humidity were recorded and daily means generated (Fig. 4.1). Daily air temperature mean ranged 19.7-36.6 ^{o}C while averaging 28.99±3.94 ^{o}C, water temperature mean ranged 21.12-32.95 ^{o}C, averaging 27.72±3.33 ^{o}C, and relative humidity mean ranged 56.72-103.14 %RH, averaging 73.78±9.38 %RH. After comparing AIC numbers among various polynomial degree model versions to establish the most parsimonious fit—air and water, second power and humidity seventh order polynomial—mixed model orthogonal polynomial regressions were assessed for microclimate variables over time while using turtle identification as a random variable to account for repeated measures. Model adjusted r-square values included air temperature ($r^2 = 0.51$), water temperature ($r^2 = 0.83$), and relative humidity ($r^2 = 0.14$).

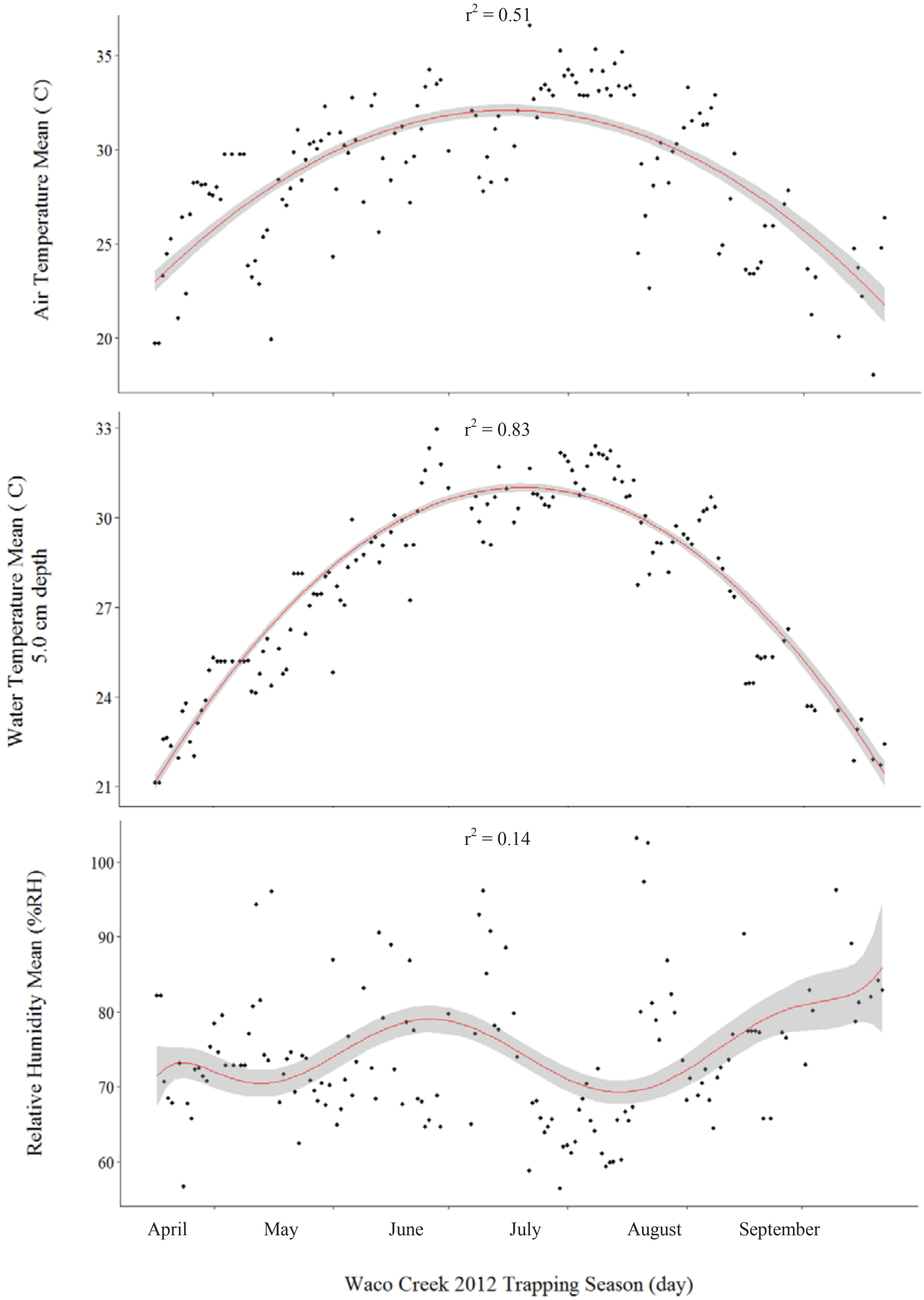


Figure 4.1 – Microclimate daily measurements for Waco Creek April-October 2012 overlaid with mixed model orthogonal polynomial trendline (red) with 95% CI (gray shading) and adjusted r-square using turtle identification as a random predictor

Of the 740 trapdays, 584 trapdays (146 days) yielded successful turtle capture events. Turtle frequency included 240 marked individuals among 537 total capture events. Three turtles were subsequently omitted as outliers. T1385, a *Pseudemys texana* female, was omitted due to her large 23.0 cm plastron length (PL). A juvenile *Graptemys pseudogeographica kohnii* T1224 and juvenile *Trachemys scripta elegans* T1360 were omitted due to excessive 18 and 70 capture events per season, respectively. Omitting data from these three turtles reduced the number of successful trapdays to 548 trapdays (137 days) and turtle frequency to 237 marked individuals among 448 total capture events.

Several trends were apparent examining turtle capture demographics over the entire 2012 trapping season (Fig 4.2). Male and female/immature female capture density was consistent from April to June, highest in July after the traps were pulled for repairs and again in August, and then began to wane in September. Juvenile/immature male density was highest in April and consistent May-October. The scatter plot shows three distinct strata, representing years of successive growth among individuals. Hatchlings emerged September-October at the first stratum (2.9-4.3 cm PL), juvenile and immature males exhibited rapid sigmoid growth for the second stratum (2.8-7.5 cm PL), but not maturity, with the exception of two isolated *Graptemys pseudogeographica*. Growth rate decreased as the sexes diverged and males began maturing during the third stratum (7.5-15.8 cm PL).

Immature sexes remained externally morphologically indistinguishable before the emergence of secondary male traits and among sexually dimorphic species, juveniles larger than the demarcation established by the smallest male conspecifics within their

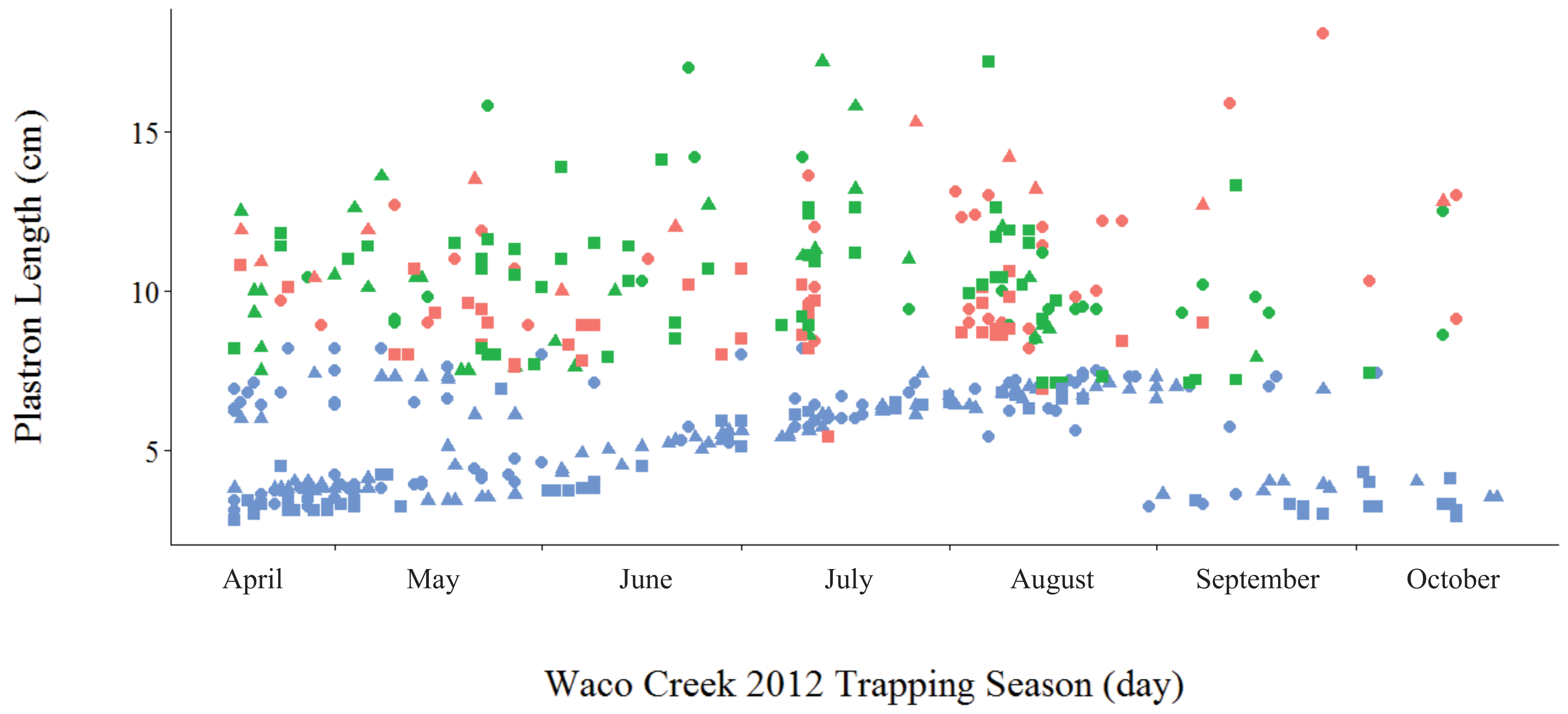


Figure 4.2 – Turtle demographic capture per trapday from Waco Creek April-October 2012, showing plastron length change over time among *Trachemys scripta elegans* (circle), *Pseudemys texana* (triangle), *Graptemys pseudogeographica kohnii* (square) juvenile and immature male (blue), male (ochre), and female and immature female (green) individuals

respective populations—*Trachemys scripta elegans*: 8.2 cm PL, *Pseudemys texana*: 7.4 cm PL, and *Graptemys pseudogeographica kohnii*: 6.9 cm PL—were deemed immature females. Immature versus mature females were also indistinguishable without verifying the presence of eggs or internal dissection of sexual organs and the onset of female sexual maturity varied dependent on latitude and climate (Timken 1968, Lindeman 2007, Perez-Santigosa et al 2008, Ernst and Lovich 2009). Since male maturity was the only established demographic onset for this community, demographic categories were lumped as juvenile and immature males (JIM), mature males (M), and mature and immature females (FIF). The absence of larger mature females > 15.8 cm PL within the community was notable.

Monthly demographic trap capture records were compared to Lincoln-Peterson estimates to assess how trap success reflected the parent population and both compared to a 1:1:1 ratio to examine relative component ratios among species and sexes (Table 4.1). Mark-recapture models used sample data to generate a hypothetical population values and like any statistic failing their assumptions precluded validity. The Lincoln-Peterson assumed no additions (birth or immigration) or deletions (death or emigration), every random individual had equal catchability, and no marks were lost during the sampling period (Seber 1982). This modified Lincoln-Peterson model reduced bias and used an intuitive ratio which compared the total sample collected (n_1), the number of individuals collected (n_2), and the number of recaptured marked individuals (m_2) to derive a population estimate ($\hat{N}$):

$$\hat{N} = \left[\frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} \right] - 1$$

Table 4.1 – Comparing April-August 2012 monthly demographic trap capture event sample ratios to a 1:1:1 ratio and to Lincoln-Peterson (L-P) estimate ratios among A) turtle species: *Trachemys scripta elegans* (TRSC), *Pseudemys texana* (PSTE), and *Graptemys pseudogeographica kohnii* (GRPS) and B) turtle sexes: males (M), females and immature females (FIF), and juveniles and immature males (JIM) using a chi-squared test (χ^2): significance ($\alpha = 0.10$) *, ($\alpha = 0.05$) **, and ($\alpha = 0.001$) ***

A

	Species	April	May	June	July	Aug	$\bar{x}$
χ^2					**	*	
Trap	TRSC	29	34	10	24	42	27
	PSTE	22	30	21	22	20	23
	GRPS	17	29	26	26	38	27
	χ^2					*	
L-P	TRSC	106	133	54	209	165	133
	PSTE	119	106	51	56	59	78
	GRPS	51	155	75	90	84	91
	χ^2	***	*		***	***	**

B

	Sex	April	May	June	July	Aug	$\bar{x}$
χ^2			***	***	***	***	***
Trap	M	7	18	9	17	32	16
	FIF	10	25	18	19	30	20
	JIM	51	50	30	36	38	41
	χ^2	***	**	**			**
L-P	M	27	170	26	152	216	118
	FIF	54	207	107	189	123	136
	JIM	142	128	36	73	64	88
	χ^2	***	**	***	***	***	*

Brief sample periods best simulated closed population conditions, however one month was the smallest time segment which produced at least one recapture per demographic. The months of September and October were omitted due to hatchling emergence and low sample sizes. Multiple recaptures were only counted once per individual to tally n_1.

Comparing species samples to population estimates using a chi-squared test (χ^2), $\alpha = 0.05$, only July and sum ratios significantly differed. No sample demographic components deviated from a 1:1:1 ratio. Population estimate components for April, July, August, and mean significantly differed from a 1:1:1 ratio. Comparing sex samples to population estimates, May, June, July, August, and mean ratios significantly differed. Sample demographic components for April, May, June, and mean, and population estimation components for April, May, June, July, and August statistically deviated from a 1:1:1 ratio.

Nine linear mixed models examined the effects of predictive fixed captured turtle species, sex, trap capture density, and trap design variables while using turtle identification, capture date, plastron length, and mean daily microclimate measurements as random predictors. The nine group response variables included plastron length mean (plastron length mean of captured turtles/trapday), plastron length range (plastron length range of captured turtles/trapday), capture density (number of turtles captured/trapday), conspecific frequency (proportion of captured turtles matching individual turtle's species/trapday), consexual frequency (proportion of captured turtles matching individual turtle's gender/trapday), condemographic frequency (proportion of captured turtles matching individual turtle's demographic/trapday), species richness (number of captured species/trapday), species evenness (Shannon evenness index of captured turtle species/trapday), and species diversity (Shannon diversity index of captured turtle species/trapday).

Linear mixed models followed the same assumptions as all least squares linear regressions with a few caveats. Predictor independence, homoscedasticity, nonlinearity, and error normality were assumed. However, response samples may be a nonlinear function of predictors, provided the population interactions are linear and mixed models may be forgiving of statistical assumptions like replication independence. Examining model homoscedasticity (Fig. 4.3) showed all models bias and homoscedastic with the exception of the Plastron Length Mean Model, which was unbias and homoscedastic. Examining model error normalcy (Fig 4.4), all models showed normal linear residuals.

After running an analysis of variance on each mixed model, examining the significance ($\alpha = 0.05$) of fixed factorial predictors among morphological and density (Table 4.2), demography (Table 4.3), and community measure (Table 4.4) response variables, sex showed significance for the following response variables: plastron length mean ($F_{(df=2)} = 180.068$, $p < 0.000$), plastron length range ($F_{(df=2)} = 19.984$, $p < 0.000$), capture density ($F_{(df=2)} = 9.547$, $p < 0.000$), conspecific frequency ($F_{(df=2)} = 4.073$, $p = 0.018$), consexual frequency ($F_{(df=2)} = 48.356$, $p < 0.000$), condemographic frequency ($F_{(df=2)} = 18.424$, $p < 0.000$), richness ($F_{(df=2)} = 5.316$, $p = 0.005$), evenness ($F_{(df=2)} = 3.691$, $p = 0.026$), and diversity ($F_{(df=2)} = 4.498$, $p = 0.012$). With the Tukey posthocs, females/immature females and males significantly grouped while juvenile/immature males separated.

Trap position was significant for plastron length range ($F_{(df=3)} = 6.410$, $p = 0.000$), capture density ($F_{(df=3)} = 7.488$, $p < 0.000$), conspecific frequency ($F_{(df=3)} = 3.446$, $p =$

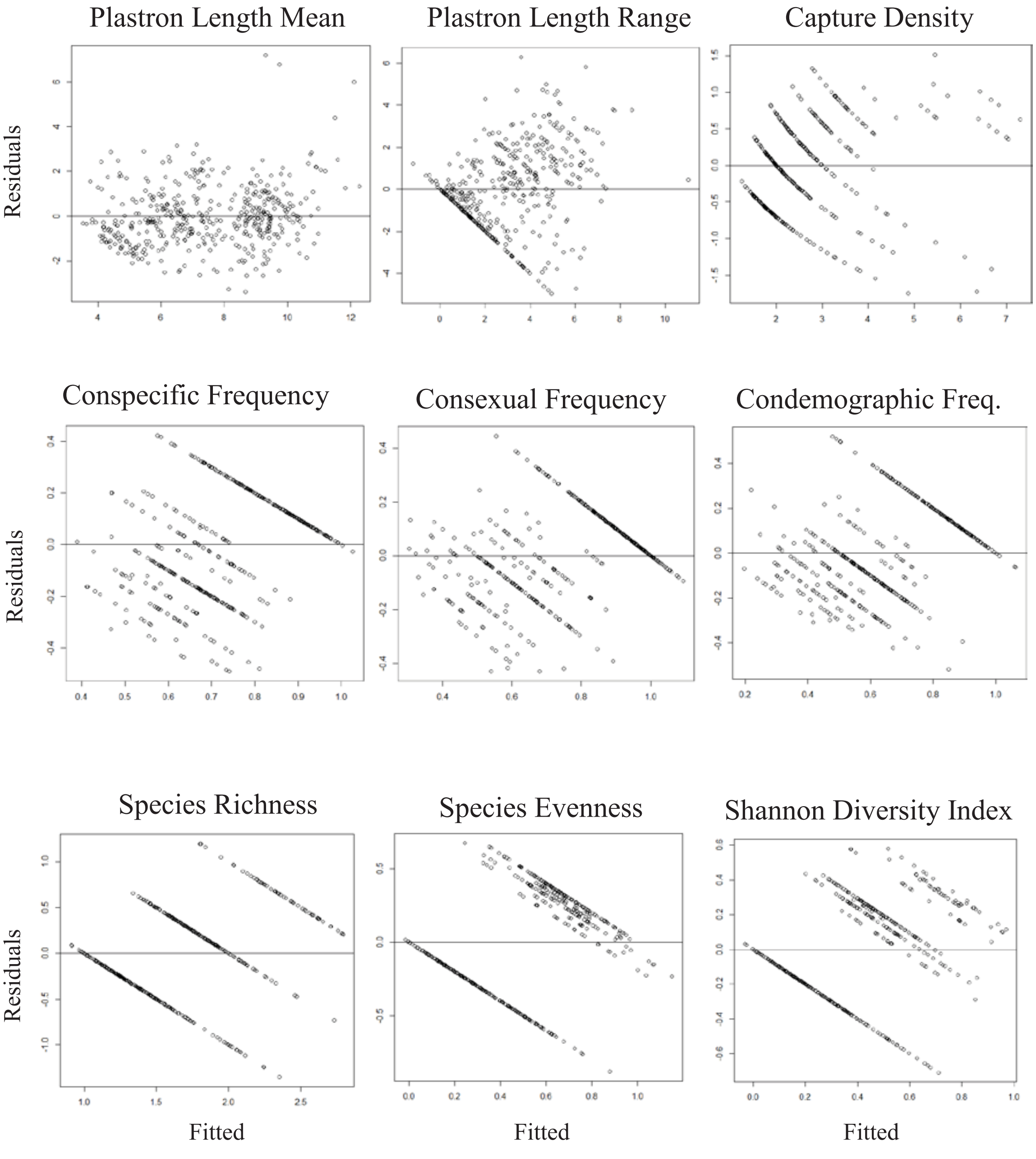


Figure 4.3 – Linear mixed model fitted vs residual plots labeled via response variable

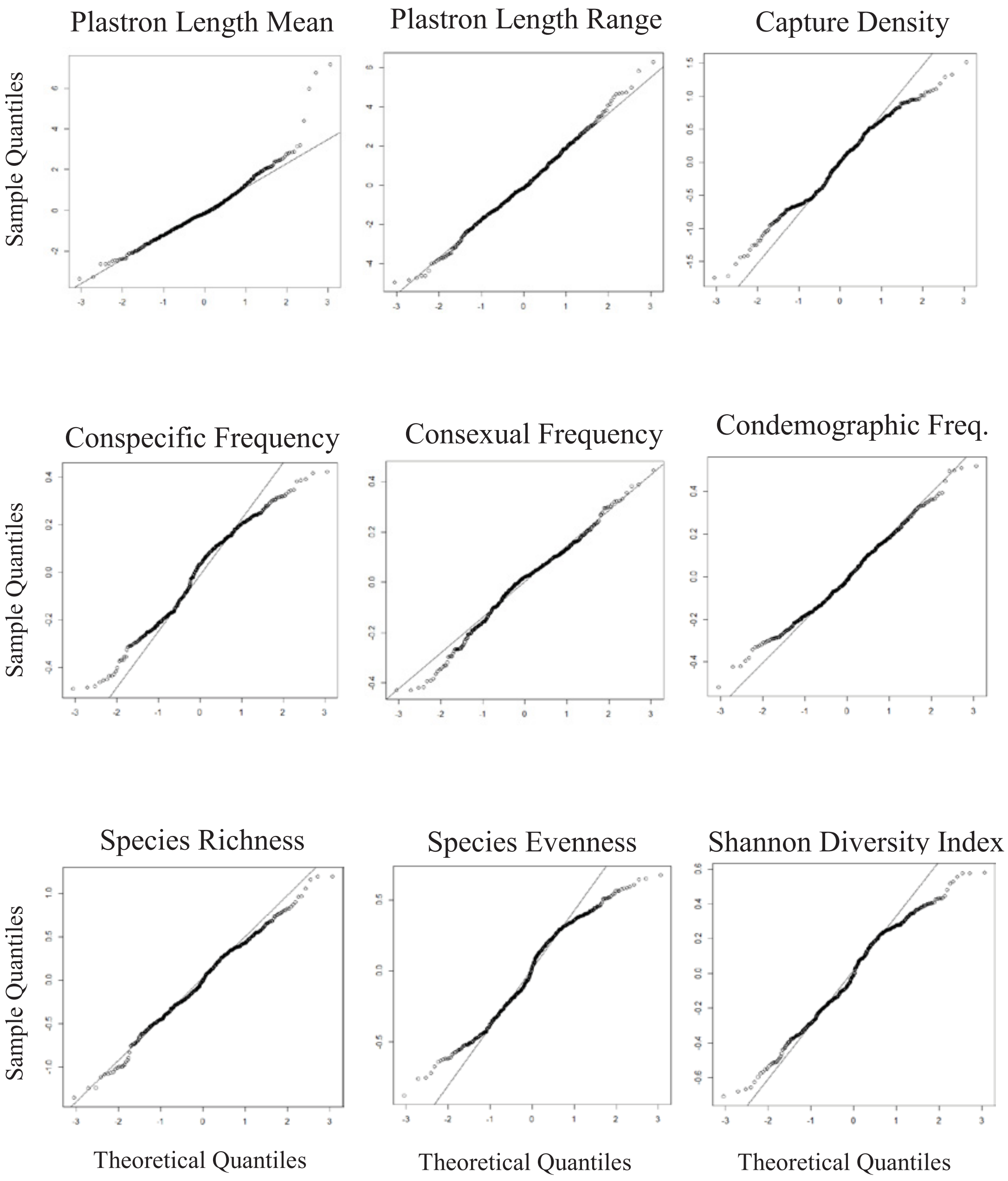


Figure 4.4 – Linear mixed model Q-Q residual plots labeled via response variable

Table 4.2 – The effects of factorial fixed predictors on A) plastron length mean, B) plastron length range, and C) capture density responses using a linear mixed model ANOVA with Tukey posthoc (α = 0.05) among the following demographics: *Trachemys scripta elegans* (TRSC), *Pseudemys texana* (PSTE), *Graptemys pseudogeographica kohnii* (GRPS), male (M), female and immature female (FIF), and juvenile and immature male (JIM) with < denoting an insignificant group split and << a significant group split

A

Source	df	SS	MS	F	P-value	Category
Species	2	16.400	8.200	2.224	0.109	
Sex	2	1327.400	663.700	180.068	< 0.000	JIM << M, FIF
Trap position	3	23.100	7.700	2.078	0.102	
Trap size	1	0.900	0.900	0.254	0.615	
Trap ramps	2	14.500	7.200	1.962	0.142	
Residuals	436	1607.000	3.700			

B

Source	df	SS	MS	F	P-value	Category
Species	2	8.260	4.130	0.493	0.611	
Sex	2	502.080	167.360	19.984	< 0.000	JIM << FIF, M
Trap position	3	161.040	53.680	6.410	0.000	alpha < gamma < delta, beta
Trap size	1	16.870	16.870	2.010	0.157	
Trap ramps	2	14.940	7.470	0.892	0.410	
Residuals	436	3651.000	8.370			

C

Source	df	SS	MS	F	P-value	Category
Species	2	3.288	1.644	0.544	0.581	
Sex	2	57.704	28.852	9.547	< 0.000	JIM << FIF, M
Trap position	3	67.887	22.629	7.488	< 0.000	gamma, alpha << beta, delta
Trap size	1	0.023	0.023	0.007	0.931	
Trap ramps	2	8.472	4.236	1.409	0.245	
Residuals	436	1317.600	3.022			

Table 4.3 – The effects of factorial fixed predictors on A) conspecific frequency, B) consexual frequency, and C) condemographic frequency responses using a linear mixed model ANOVA with Tukey posthoc ($\alpha = 0.05$) among the following demographics: *Trachemys scripta elegans* (TRSC), *Pseudemys texana* (PSTE), *Graptemys pseudogeographica kohnii* (GRPS), male (M), female and immature female (FIF), and juvenile and immature male (JIM) with < denoting an insignificant group split and << a significant group split

A

Source	df	SS	MS	F	P-value	Category
Species	2	0.937	0.468	6.715	0.001	PSTE << GRPS, TRSC
Sex	2	0.568	0.284	4.073	0.018	M, FIF << JIM
Trap position	3	0.720	0.240	3.446	0.017	delta << gamma, alpha, beta
Trap size	1	0.176	0.176	2.517	0.113	
Trap ramps	2	0.020	0.011	0.154	0.857	
Residuals	436	30.383	0.069			

B

Source	df	SS	MS	F	P-value	Category
Species	2	0.072	0.036	0.555	0.574	
Sex	2	6.243	3.121	48.356	< 0.000	M, FIF << JIM
Trap position	3	0.617	0.206	3.184	0.024	delta, beta << gamma, alpha
Trap size	1	0.000	0.000	0.005	0.945	
Trap ramps	2	0.018	0.009	0.142	0.867	
Residuals	436	28.143	0.065			

C

Source	df	SS	MS	F	P-value	Category
Species	2	0.812	0.406	5.002	0.007	PSTE << GRPS, TRSC
Sex	2	2.990	1.495	18.424	< 0.000	M, FIF << JIM
Trap position	3	1.110	0.370	4.558	0.004	delta << gamma, beta, alpha
Trap size	1	0.047	0.047	0.583	0.446	
Trap ramps	2	0.030	0.015	0.181	0.834	
Residuals	436	35.370	0.081			

Table 4.4 – The effects of factorial fixed predictors on species A) richness, B) Shannon evenness, and C) Shannon diversity index responses using a linear mixed model ANOVA with Tukey posthoc (α = 0.05) among the following demographics: *Trachemys scripta elegans* (TRSC), *Pseudemys texana* (PSTE), *Graptemys pseudogeographica kohnii* (GRPS), male (M), female and immature female (FIF), and juvenile and immature male (JIM) with < denoting an insignificant group split and << a significant group split

A

Source	df	SS	MS	F	P-value	Category
Species	2	4.757	2.374	5.243	0.006	TRSC, GRPS << PSTE
Sex	2	4.814	2.407	5.316	0.005	JIM << M, FIF
Trap position	3	8.016	2.672	5.902	0.001	beta, alpha, gamma << delta
Trap size	1	2.463	2.463	5.440	0.020	small << large
Trap ramps	2	1.594	0.797	1.759	0.173	
Residuals	436	197.370	0.453			

B

Source	df	SS	MS	F	P-value	Category
Species	2	3.380	1.690	7.911	0.000	TRSC, GRPS << PSTE
Sex	2	1.576	0.788	3.691	0.026	JIM < M < FIF
Trap position	3	1.797	0.599	2.802	0.040	beta, alpha, gamma << delta
Trap size	1	0.109	0.109	0.511	0.475	
Trap ramps	2	0.362	0.181	0.846	0.430	
Residuals	436	93.130	0.214			

C

Source	df	SS	MS	F	P-value	Category
Species	2	1.906	0.953	6.510	0.002	TRSC, GRPS << PSTE
Sex	2	1.316	0.658	4.498	0.012	JIM << M, FIF
Trap position	3	2.004	0.668	4.567	0.004	beta, alpha, gamma << delta
Trap size	1	0.481	0.481	3.289	0.070	
Trap ramps	2	0.102	0.051	0.348	0.707	
Residuals	436	63.810	0.146			

0.017), consexual frequency ($F_{(df=3)} = 3.184$, $p = 0.024$), condemographic frequency ($F_{(df=3)} = 4.558$, $p = 0.004$), richness ($F_{(df=3)} = 5.902$, $p = 0.001$), evenness ($F_{(df=3)} = 2.802$, $p = 0.040$), and diversity ($F_{(df=3)} = 4.567$, $p = 0.004$). For the Tukey posthocs, two scenarios occurred: alpha grouped with gamma and beta grouped with delta or alpha, beta, and gamma grouped with delta separated.

Species showed significance among the following responses: consexual frequency ($F_{(df=2)} = 6.713$, $p = 0.001$), condemographic frequency ($F_{(df=2)} = 5.002$, $p = 0.007$), richness ($F_{(df=2)} = 5.243$, $p = 0.006$), evenness ($F_{(df=2)} = 7.911$, $p = 0.000$), and diversity ($F_{(df=2)} = 6.510$, $p = 0.002$). For all Tukey posthocs, *G. pseudogeographica* and *T. scripta* grouped significantly while *P. texana* remained separated.

Trap size showed significance for response variable richness ($F_{(df=2)} = 5.440$, $p = 0.020$). For the Tukey posthoc, small and large traps were significantly distinct.

Discussion

Several basking patterns become apparent examining microclimate (Fig. 4.1) and turtle demographic capture records (Fig. 4.2) from the Waco Creek community. Dense clusters of individuals were observed in April, July, and August; if lack of traps precipitated the first two clusters, low relative humidity and a lack of precipitation through the month of August likely precipitated the last. Neither daily air nor water temperature means appeared to have an impact on demographic basking patterns beyond an apparent threshold of 20 ^{o}C below which basking activity dwindled.

Daily weather means were incorporated in the mixed model as random variables to account for microclimate variability as plastron length was included for ontogenous variability and turtle identification for individual replication and thus not expressed within the analysis of variance, which only analyzed fixed variables. As the ANOVA statistic was run from a regression and did not have a declared grouping factor, nonfactorial predictor variables also would have presented a statistical fallacy. Prior studies examining the effects of climate on turtle activity were conducted at multiannual (Frazer et al., 1993) or diel scales (Spotila et al., 1984; Spotila et al., 1989); mean daily climate variation warrants further study.

While there is a strong case to be made for September and October as the end of the basking season due to decreasing capture events, the season begins in medias res without a corresponding capture increase and the basking season likely initiated in February or March. This projected eight month basking season coincides with other central Texas congeneric studies (Craig, 1992; Lindeman, 1999c) and would result in more rapid annual growth and faster onset of maturity than conspecific northern populations.

The stratification among the demographic data (Fig 4.2) presents an interesting puzzle. If one takes a logistic curve and breaks it into three equal parts, each part would overlap a comparable stratum with lower asymptote growth increasing during the first strata, slope rising, passing inflection point, and then decreasing during the second strata, and then a succession of flatter and flatter curves as maturing turtles progress up through the third strata year after year. This matches expected patterns for asymptotic, logistic growth reaching inflection within the second season as previously reported in emydid freshwater species (Ernst, 1971; Frazer et al., 1990; Lindeman, 1999c). There also appears to be a lack of growth during the cool season from October-April as plastron lengths remain consistent from the end of one stratum to the beginning of another. It is interesting to note that JIM comprise all of the turtles within the first autumn and most within the second year, but disappear before the end of the third spring. While successive years overlap among the third stratification, it appears males within these populations mature within two to three years with *G. pseudogeographica* maturing before *T. scripta* or *P. texana* due to smaller body size (Ernst and Lovich, 2009). This progression was difficult to determine with certainty as multiple individual captures documenting sexual demographic transitions were rare with no hatchling to male event observed over the entire extended three year sampling of the larger umbrella study.

It is difficult sometimes to separate basking trap capture success as an indicator of relative demographic activity versus an indicator of relative demographic presence (Table 4.1). Interpreting the data, species samples (2/5 months statistically differing) were more representative of population patterns than gender samples (4/5 months statistically differing). Trap sample proportions among species (1/5 months statistically differing at $\alpha = 0.10$) and sexes (3/5 months statistically differing at $\alpha = 0.01$-0.05) suggest intraspecific basking competition (Lovich, 1988) was much more aggressive than the interspecific competition (Lindeman, 1999; Cadi and Joly, 2003; Polo-Cavia et al., 2010) widely reported in the literature. For much of the sample period, all three species shared baking sites in statistically equal proportions. Population proportions were equally significantly proportionately heterogeneous among both species (4/5 months) and sex (5/5 months). Among the species, *T. scripta* individuals were recaptured more often than *P. texana* of *G. pseudogeographica* as evinced by the skewed L-P ratio and among the sexes, JIM were recaptured more often than M or FIF. This would suggest within the Waco Creek emydid community, *T. scripta* juveniles are either the most actively basking, actively migratory, or abundant demographic. I would argue based on the frequency range of *T. scripta* (54-209) and JIM (36-142) “population” estimates over such a short, static five month period, L-P is most likely an indicator of relative basking activity and secondarily abundance. This makes sense in an ecological context as juveniles and young males require faster metabolisms to fuel their rapid growth (Gatten, 1974; Hennemann, 1979) and thus repeated frequent basking events; however studies have confirmed that basking event length is inversely proportional to turtle length (Lefevre and Brooks, 1995; Bulté and Blouin-Demers, 2010). Examining how the ontogenous tradeoff between basking event frequency and duration affects basking capture frequency remains to be seen as well as either closed system experiments or model simulations to parse the effects of demographic abundance, migration, and activity on basking capture frequency.

With their inclusion in most every classic and commercial basking trap design (Cagle and Chaney, 1950; Ream and Ream, 1966; Frazer et al., 1990c), I would have expected the lack or presence of basking ramps to have more of an impact on turtle capture statistics than this study demonstrated (Table 4.2, 4.3, 4.4). The lack, partial, or total presence of ramp platforms available on these basking traps failed to exert any significant effect whatsoever, suggesting that with a sufficiently wide PVC float, these accoutrements were superfluous for maintaining a functional basking trap design. Any hypothetical advantages conferred by the presence of platforms such as increased surface area or ease of access did not matter. Turtles apparently scaled vertically up the side of the trap netting and perched on top of the float, falling into traps with equal frequency as those that crawled halfway up the ramps and lounged. Lack of ramps made traps more portable, manageable and several kilograms lighter—especially for larger sizes—so unless basking surface variability was of interest, there seems little future benefit to them.

Trap size was another variable noted for its lack of effect (Table 4.4). Large traps attracted a more species rich sample than smaller traps. However, no other responses showed any significance for this predictor variable. This was especially surprising among response variables such as plastron length range and capture density.

The only trap-associated variable with any wide ranging impact on capture event statistics was trap position (Table 4.2, 4.3, 4.4), and that more linked to spatial orientation than structural design. The trap furthest downstream, delta, appeared to capture significantly less conspecific and condemographic, but more rich, even, and diverse, individual compositions than the other trap placements. For plastron length range, capture density, and consexual frequency, delta and beta significantly grouped away from the others. With trap placement exerting these effects within such a narrow transect (216 m), this suggests copious movement between traps (supported by the large recapture rate of individuals among different trap placements).

Among turtle species, *T. scripta* and *G. pseudogeographica* were statistically similar and *P. texana* grouped apart (Table 4.3, 4.4). For conspecific and condemographic frequency, *P. texana* was significantly less and for richness, eveness, and diversity, *P. texana* was significantly greater than the other two species. With the sample and population estimates previously examined (Table 4.1), I would have expected *T. scripta* or *G. pseudogeographica* to significantly separate from the other species based on their relative size or abundance.

Turtle gender (Table 4.2, 4.3, 4.4) had a similar significance across eight response variables: M and FIF clustered together with JIM apart. For plastron length mean, plastron length range, and capture density, JIM were significantly less than FIF and M which makes sense given the relative gender morphometrics, but not for expected relative abundances. JIM also comprised significantly less rich and diverse capture groups. However, JIM were statistically more conspecific, consexual, and condemographic, which argued for concentrated group juvenile basking. Evenness had no significant pleural groups, though JIM and FIF were statistically separate, sharing M between them. One must remember interpreting these results that the effects of extreme sexual dimorphism reported in other studies (Hammond et al., 1988; Lefevre and Brooks, 1995; Bulté and Blouin-Demers, 2010) had no discernable effect in a metapopulation comprised largely of immature turtles—there was a distinct lack of dimorphism between male and female individuals (Fig. 4.2), which perhaps explained the uncharacteristic statistical clumping of M and FIF demographics.

In conclusion, mixed model regressions offer a unique methodology for running an analysis of variance on recalcitrant, nonparametric, repeated measures, unbalanced longitudinal data which ecological field experiments routinely provide. The data reveal several significant trends for demographic basking trap capture behavior of a community comprised of immature and young male individuals, different trap capture affinities among species, and varied sex and species ratios comparing sample to Lincoln-Peterson monthly estimates. Biological significance of these conclusions: while individual selection is the root of all sampling bias—which affects estimates of true population activity and size—demographic behavior partially explains individual behavior. The data also offered several useful efficient basking trap configuration results, but designing expressly to target particular demographics may require a more diverse community.

Acknowledgments

I thank Kevin Gutzwiller for helpful analytical advice. I would also like to thank the Baylor University Biology department and Graduate School for their support. This study was funded in part by the Jack G. and Norma Jean Folmar grant. Turtles were sampled under Texas Parks and Wildlife Scientific Permit #SPR-0609-127. This project was reviewed and approved by Baylor University's Institutional Animal Care and Use Committee.

CHAPTER FIVE

Growth Pattern Mixed Modeling among Juvenile Basking Turtles

Abstract

This study pioneers a new method for using third order polynomial mixed models as a null scenario to compare k-growth logistic models using successive daily recapture data over the trapping season as well as presenting growth curve data for second season juvenile emydid turtles within a central Texas creek. Fitting growth models using linear mixed models rather than regressions or linear fixed models allows for turtle identification to be assessed as a random variable, which accounts for individual pseudoreplication among multiple individual recaptures. Given a requisite minimal sample size, lack of dataset gaps, and a continuous sample dispersal over time, growth model comparisons and control growth model agree with reports in the literature, from best to worst at predicting plastron length: Polynomial Model, Fabens Logistic Growth Model, and von Bertalanffy Logistic Growth Model. This technique offers unique possibilities for future growth modeling endeavors.

Keywords: k, logistic

Introduction

Ubiquitous and long-lived, growth among turtles has long been the subject of scientific curiosity and ecological study. All growth energetic processes from bacterial fermentation (Bjorndal and Bolten, 1990), cellular metabolism (Gatten, 1974), individual biomass accumulation (Jackson, 1970), morphology (Davis and Grosse, 2008), egg production (Congdon and Gibbons, 1983), population fluctuation (Frazer et al., 1993; Lefevre and Brooks, 1995), and community assemblage interaction (DonnerWright et al., 1999) have all been studied for these ectothermal organisms. While all scales within the preceding hierarchy are inexorably intertwined, the most commonly linked applications of turtle growth involve individuals, which comprise populations (Shine and Iverson, 1995).

Among freshwater turtles, growth is sigmoid and asymptotic, with the fastest rate occurring over the second season (Ernst, 1971). Upon reaching maturity, growth rates begin to decline with males maturing within three years and females within eight (Cagle, 1946). Turtle aging involves counting scute annuli, however turtles may accumulate more than one annulis per season and shell deterioration and algal growth after several years increases difficulty and no consensus exists in the literature as to the technique's reliability estimating age (Wilson et al., 2003). Growth has been documented among wild sampled (Cagle, 1946; Jackson, 1970; Ernst, 1971; Frazer et al., 1990) and laboratory raised (Allen and Littleford, 1955; Avery et al., 1993; Koper and Brooks, 2000) populations. Growth patterns among emydid turtles have been linked to dietary nutrition (Avery et al., 1993), seasonal climate constraints (Frazer et al., 1993; Koper and Brooks, 2000), and sexual dimorphic variation (Congdon and Gibbons, 1983; Gibbons and Lovich, 1990; Shine and Iverson, 1995; Stamps, 1995; Lindeman, 1997).

Growth models are typically derivations of the Logistic Model (Zar, 1999):

$$f\left(t\right)=\frac{1}{e^{-rt}} \qquad \text{(Eq.1)}$$

A common equation where organism age is known at the sampling time is the von Bertalanffy Model (Frazer et al., 1990):

$$PL_t = PL_A\left(1 - be^{-rt}\right) \quad \text{(Eq. 2)}$$

$$b = e^r\left(1 - PL_H / PL_A\right) \quad \text{(Eq.3)}$$

$$r = \frac{\log\left(PL_1\right) - \log\left(PL_0\right)}{t_1 - t_0} \quad \text{(Eq. 4)}$$

and a modification where organism age is unknown, the Fabens Model, (Fabens, 1965):

$$PL_R = PL_A - \left(PL_A - PL_C\right)e^{-kt} \quad \text{(Eq. 5)}$$

$$k = \frac{\log\left(PL_2\right) - \log\left(PL_1\right)}{t_2 - t_1} \quad \text{(Eq. 6)}$$

In all three models and derivative equations, b represents a turtle hatchling constant relative to PL_H, (Eq. 3) e equals Euler's constant, PL plastron length: PL_A the upper asymptotic growth limit for the turtle demographic of concern, PL_C size at capture, PL_H demographic hatchling size, PL_R size at recapture, PL_t size a time t, k the geometric instantaneous growth rate, r the intrinsic growth rate, and t represents time. Most other logistic-derived growth models fall into either the ages known, single capture von Bertanalanffy model type: Sine-wave von Bertalanffy (Moreau, 1987), Richards model (Richards, 1959), and Gompertz (Moreau, 1987) or ages unknown, multiple capture Fabens model type: logistic growth rate (Schoener and Schoener, 1978) and instantaneous relative growth rate (Brody, 1945).

One major weakness of growth models involves the requisite recapture of individuals to utilize instantaneous geometric growth (k) rather than intrinsic growth (r), the former yielding a more accurate, realistic model (Lindeman, 1997). However, this constraint eliminates the proportion of individuals only captured once, typically ignores multiple recaptures, and reduces sample variability from the subsequent analysis. This study seeks to examine an alternate nonlinear regression modeling approach which allows for single-captured individuals of unknown age. Second season juveniles were selected as the target demographic due to their high basking activity, abundance, and rapid seasonal growth rate. Objectives include examining juveniles from three sympatric species over a period of two years using 1) Polynomial, 2) von Bertalanffy growth, or 3) Fabens growth mixed models provide the best fit for truncated recapture k-growth datasets with time set on a continuous scale.

Methods and Materials

The study site was the mouth of Waco Creek upstream from South University Parks Drive and confluence with the Brazos River Reservoir in McLennan County, Texas (31° 32' 59.5231" N, 97° 6’ 44.6505” W). The Waco Creek confluence is upriver of the Lake Brazos Dam on the Brazos River, turning the mouth of the creek into an arm of the Brazos River Reservoir. Severe water level drop within the reservoir empties the creek bed; however the creek is still subject to spring runoff flooding events (pers obs). Several floating basking traps were placed along a 270 m transect at 50 – 60 m intervals of the NW facing creek bank from April to October 2011 and April to October 2012. Traps were checked at 24 hr intervals. Turtles were measured, identified, sexed, individually marked with marginal scute notches, and then released back into the creek within three meters of the original capture site.

All model parameters were derived using instantaneous k-growth (Eq. 6) estimates from recaptured individuals, using time as a continuous variable (units: days from prior individual capture event). PL_A was estimated using the mean of the five largest capture event PLs per demographic per season while PL_H was the smallest condemographic hatchling captured in April during the entire 2010-2012 Waco Creek sampling period.

Analysis utilized a linear mixed model regression, which examined the effects of fixed and random predictive variables upon a single response variable. Fixed predictors included the capture date, and PL_t, and PL_R for the third order Polynomial, von Bertalanffy Growth, and Fabens Growth Models, respectively. The random predictor for each model was turtle identification to account for the pseudoreplication inherent from sampling multiple recaptured individuals per demographic. The response variable for each model was the measured plastron length that corresponded with the capture date or PL estimate for the given individual turtle at time t. All data analysis and graphical generation was conducted with R 2.15.2 statistical software: ggplot2, lme4, and stats packages (Wickham, 2009; Fox and Weisberg, 2011; Bates et al., 2013).

Results

Turtles were only utilized for this study if their plastron length (PL) at time t conformed to second season growth patterns, i.e. all turtles were hatched the previous autumn season. This was done to eliminate discrete annual age as a variable so that time could be expressed as a continuous variable: days and emphasize logistic growth patterns. To avoid the issue of interrupted growth presented by the intervening winter season, t_0 was set to the beginning of the spring 2011 and 2012 sampling seasons and PL_H taken from an April, not September or October, capture event.

Two *T. scripta* individuals' capture events—T1360 and T1600—were omitted due to excessive capture frequency and stunted growth, respectively. T1360 was recaptured 70 times from April to July 2012. While this presented a wonderful example documenting individual sigmoid growth, this turtle dominated any dataset using it, reducing all other individuals to residuals and outliers. Removal of T1360 reduced the r^2 value for the *Trachemys scripta elegans* 2012 polynomial model from 0.51 to 0.35 after all records of its capture were removed. T1600 was only captured three times July to August; however this turtle's growth fell below established juvenile trends.

For comparative purposes, data were examined using the classical technique of generating k and b using only the initial capture and final recapture events per individual (Table 5.1A). This technique tends to increase k, while decreasing n, relative to using all available sequential recapture events. The author wishes to reiterate the mixed model analysis data analyzed every recapture event sequentially to derive the k and b values used for the subsequent data analyses (Table 5.1B).

The nature of the sigmoid, or logistic, second season growth among Waco Creek emydid turtles is evident with individual captures plotted over the course of 2011 and 2012 seasons (Fig 5.1, Fig 5.2). Third order polynomial mixed models were fit to the data and species adjusted r^2 values either increased from 2011 to 2012: *T. scripta* (2011 $r^2 = 0.13$, 2012 $r^2 = 0.33$) and *P. texana* (2011 $r^2 = 0.20$, 2012 $r^2 = 0.26$) or decreased *G. pseudogeographica* (2011 $r^2 = 0.29$, 2012 $r^2 = 0.21$). Comparing species values per annum to a 1:1 ratio using a chi-square test yielded *T.scripta* ($\chi^2 = 0.087$, 0.768), *P. texana* ($\chi^2 = 0.008$, p-value = 0.930), and *G. pseudogeographica* ($\chi^2 = 0.013$, p-value = 0.909). Setting $\alpha = 0.05$, no annual changes were significant.

Each of the three model types was compared per species per sample year (Table 5.2). Examining the Akaike Information Criterion (AIC) and the Bayesian Information

Table 5.1 – Parameter estimates for von Bertalanffy and Fabens K-Growth Models (mean±95% CI) for sampled second season juvenile turtles from 2010-2012: *Trachmeys scripta* elegans (TRSC), *Pseudemys texana* (PSTE), and *Graptemys pseudogeographica kohnii* (GRPS) using A) capture and last recapture events per individual and B) capture and sequential recapture events per individua

A

	n	k	b	PL_A
TRSC 2011	18	0.0013±0.0004	0.5887±0.0003	7.2800
TRSC 2012	14	0.0021±0.0006	0.5970±0.0004	7.4200
PSTE 2011	8	0.0017±0.0009	0.5716±0.0005	7.2200
PSTE 2012	12	0.0017±0.0004	0.5786±0.0002	7.3400
GRPS 2011	6	0.0010±0.0006	0.6592±0.0004	8.2000
GRPS 2012	9	0.0017±0.0007	0.6143±0.0004	7.2400

B

	n	k	b	PL_A
TRSC 2011	35	0.0011±0.0004	0.5886±0.0002	7.2800
TRSC 2012	37	0.0020±0.0006	0.5968±0.0004	7.4200
PSTE 2011	16	0.0015±0.0007	0.5714±0.0004	7.2200
PSTE 2012	49	0.0016±0.0005	0.5786±0.0003	7.3400
GRPS 2011	15	0.0007±0.0004	0.6590±0.0003	8.2000
GRPS 2012	35	0.0016±0.0006	0.6143±0.0004	7.2400

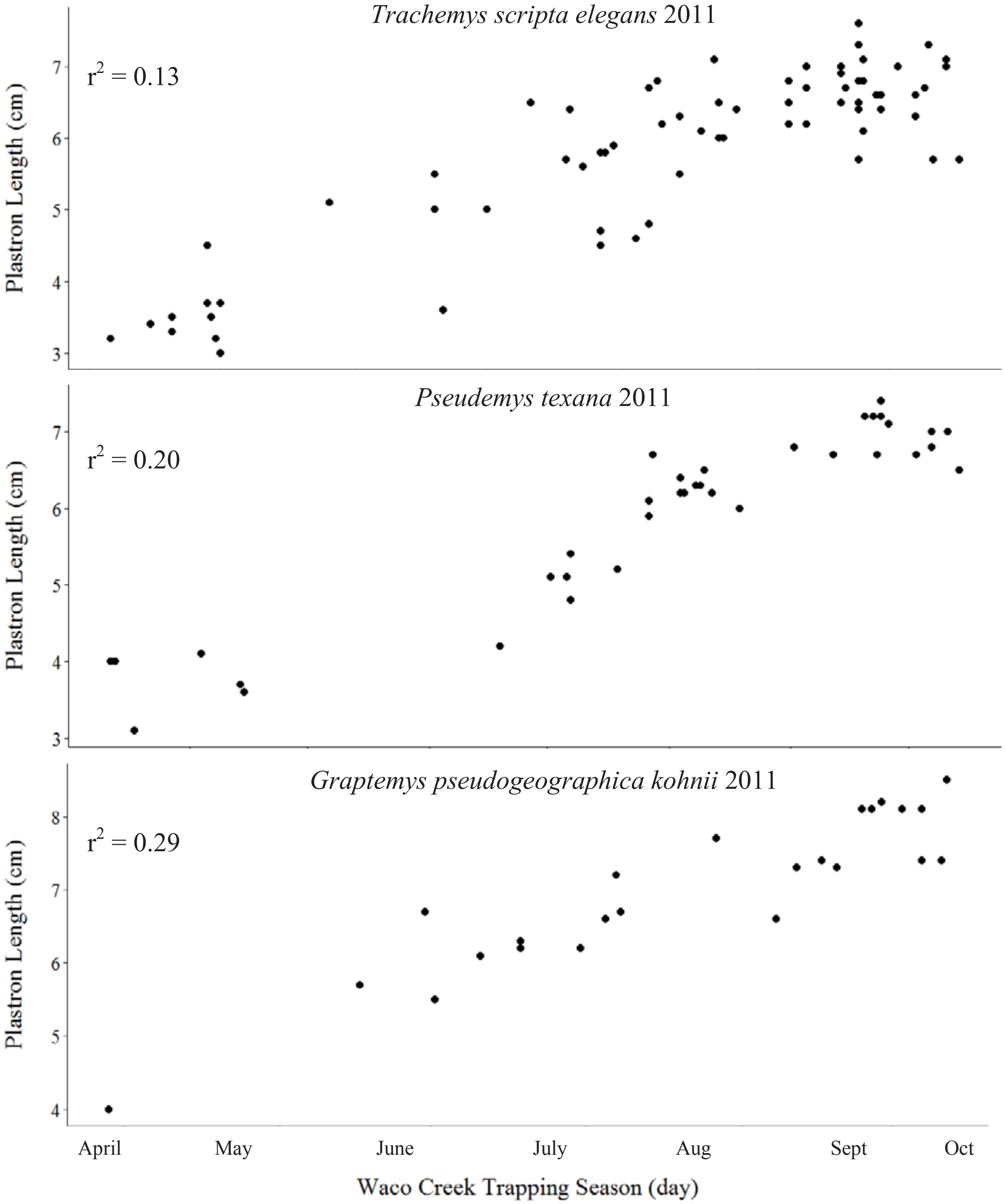


Figure 5.1 – Second season juvenile growth records for Waco Creek, 2011 with adjusted r-square values using third order orthogonal polynomial mixed models with individual identification as a random variable

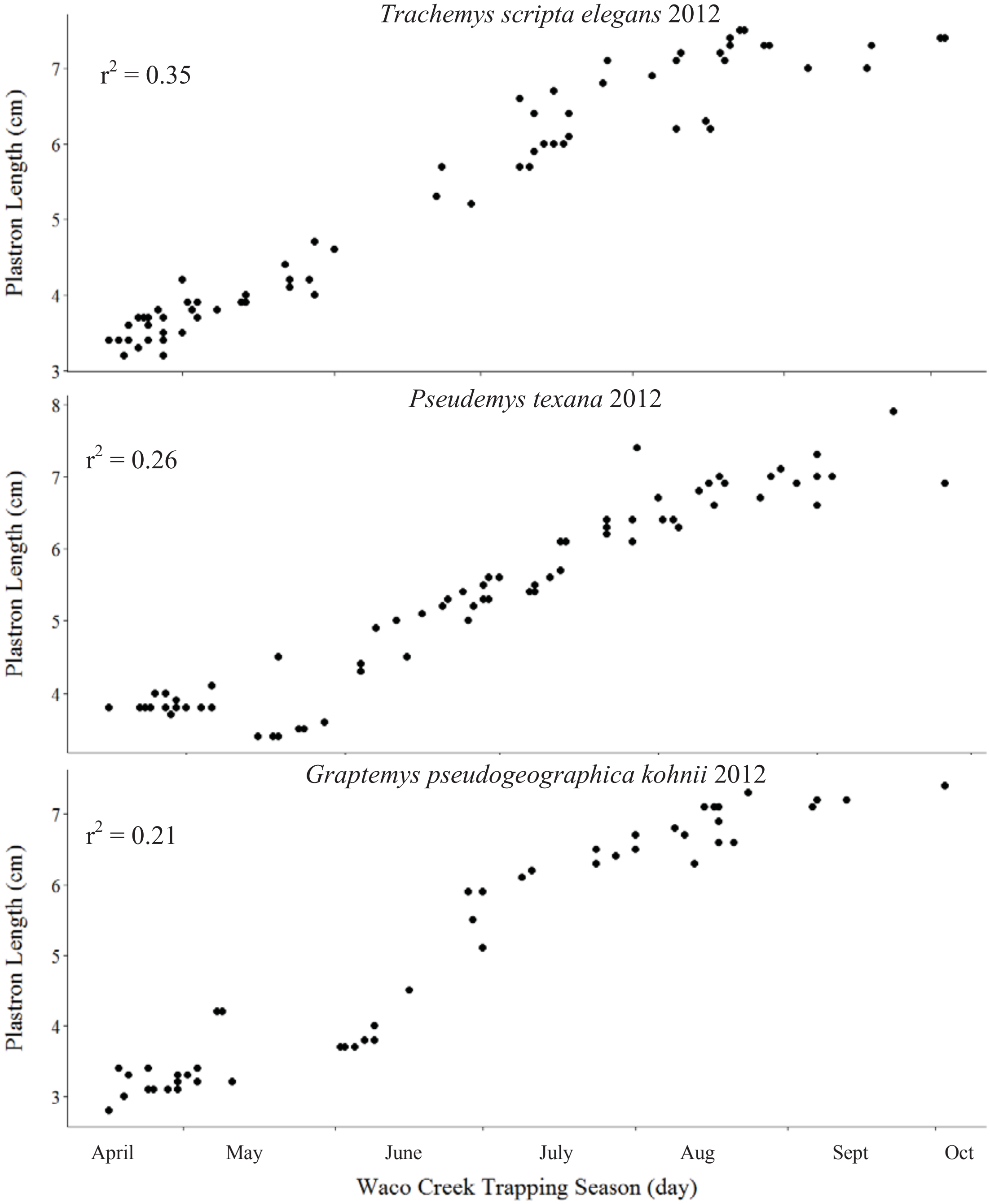


Figure 5.2 – Second season juvenile growth records for Waco Creek, 2012 with adjusted r-square values using third order orthogonal polynomial mixed models with individual identification as a random variable

Table 5.2 – Comparing seasonal turtle plastron length prediction among a Polynomial overlay, von Bertalanffy growth, and Fabens growth mixed models using ANOVA ($\alpha = 0.05$) among a recaptures dataset (k-growth) with turtle individual as a random variable

Trachemys scripta elegans 2011

	df	AIC	BIC	logLik	χ^2	χ df	p-value
Polynomial	6	67.02	80.33	-27.509			
von Bertalanffy	30	180.92	247.50	-60.459	0.00	24	1.000
Fabens	37	-416.72	-344.60	245.358	611.64	7	< 0.000

Trachemys scripta elegans 2012

	df	AIC	BIC	logLik	χ^2	χ df	p-value
Polynomial	6	5.66	18.97	3.17			
von Bertalanffy	31	142.88	211.68	-40.44	0.00	25	1.000
Fabens	35	239.06	316.74	-84.53	0.00	4	1.000

Pseudemys texana 2011

	df	AIC	BIC	logLik	χ^2	χ df	p-value
Polynomial	6	14.30	23.28	-1.149			
von Bertalanffy	16	55.312	79.26	-11.656	0.00	10	1.000
Fabens	18	-231.57	-204.63	133.79	290.88	2	< 0.000

Pseudemys texana 2012

	df	AIC	BIC	logLik	χ^2	χ df	p-value
Polynomial	6	-35.98	-22.57	24.00			
von Bertalanffy	36	191.73	272.15	-59.86	0.00	30	1.000
Fabens	44	-12.38	85.92	50.19	220.11	8	< 0.000

Graptemys pseudogeographica kohnii 2011

	df	AIC	BIC	logLik	χ^2	χ df	p-value
Polynomial	6	19.93	26.90	-3.92			
von Bertalanffy	13	73.06	88.38	-23.53	0.00	7	1.000
Fabens	16	-209.28	-190.43	120.64	288.34	3	< 0.000

Graptemys pseudogeographica kohnii 2012

	df	AIC	BIC	logLik	χ^2	χ df	p-value
Polynomial	6	-23.70	-12.35	17.85			
von Bertalanffy	25	109.14	156.44	-29.57	0.00	19	1.000
Fabens	33	72.84	135.27	-3.42	52.30	8	<0.000

Criterion (BIC) values, species data best fit by the Polynomial Model include *T. scripta* 2012, *P. texana* 2012, and *G. pseudogeographica* 2012. Data best fit by the von Bertalanffy Model include *T. scripta* 2011 and by the Fabens Model, *P. texana* 2011.

Discussion

During the course of this study, growth model parameters estimates for various sampled species using the capture-last recapture technique (Table 5.1A) ranged for *T. scripta*: b (0.5887-0.5970), k (0.0013-0.0021), and PL_A (7.2800-7.4200 cm); *P. texana*: b (0.5716-0.5786), k (0.0017), and PL_A (7.2200-7.3400 cm); and *G. pseudogeographica*: b (0.6143-0.6592), k (0.0010-0.0017), and PL_A (7.2400-8.200 cm). Estimates or the capture-subsequent recapture technique (Table 5.1B) ranged for *T. scripta*: b (0.5886-0.5968) and k (0.0011-0.0020), *P. texana*: b (0.5714-0.5786) and k (0.0015-0.0016), and *G. pseudogeographica*: b (0.6143-0.6590) and k (0.0007-0.0016), with PL_A not differing between Table 5.1A and 5.1B. This compares to other studies examining *Trachemys* *scripta elegans*: b (0.98-1.10) and k (0.130-0.284) (Frazer et al., 1990), *Pseudemys texana*: b (0.780-0.898) and k (0.191-0.129) (Lindeman, 2007), *Graptemys* spp.: b (0.672-0.866) and k (0.110-0.498) (Lindeman, 1999c). This disparagement is likely due to the smaller sample sizes (n = 15-49) and juvenile demographics of the turtles within this study compared to the larger (n = 30-70) and mature demographic samples reported in the literature. Within the confines of this study, b and k estimate are similar across annual sampled demographics and further study of other second season juvenile populations may shed more light on the subject.

In theory, a third order orthogonal linear mixed Polynomial Model should act as a baseline null model for any collection of predictive growth model comparisons. The polynomial model approximates the shape of a logistic curve without the constraining effects of logistic model parameters—the perfect empirical data-selected model fit describing changing plastron length over time. In the literature, Fabens Growth Model is shown to be a better fit for logistic growth data among freshwater turtles than the von Bertalanffy Growth Model upon which it is based (Fabens, 1965; Frazer et al., 1990; Lindeman, 1997). Expected demographic model fit should settle from best to worst: Polynomial null model, Fabens Growth Model, and von Bertalanffy Growth Model. This would allow the polynomial model to be used as a basis for comparison for the logistic growth models. This expected pattern holds true for the 2012 data (Table 5.2), but not the 2011 data (Table 5.1), due most likely to the low sample sizes and relative scarcity of recaptures in 2011 (Fig. 5.2) compared to 2012 (Fig. 5.3), which results in large holes within the data over the sampling season.

Turtle growth models have been cited to start breaking down at smaller sample sizes (Lindeman,1999c) and a minimum demographic recapture event frequency of 15 is recommended based on these results when using k-growth based models. Another factor is the relative dispersal of captures over their comparable sampling seasons. Despite the n = 18 parameter (Table 5.1), *T. scripta* 2011 did not follow model comparison expectations likely due to the May-July sparse distribution. Similarly, *P. texana* 2011 recaptures were sparse from May-June and *G. pseudogeographica* from April-June. In short, uniform data dispersal is just as important as data frequency.

In conclusion, the use of mixed models offers a promising venue for growth model comparisons among juvenile turtles. The fixed and random variable designations allow for incorporation of repeated recapture measurements without incurring major statistical violations, which in turn increases sample size. Third order polynomial mixed models also offer a reliable best fit standard control by which logistic growth models may be compared rather than comparing the growth models to each other. When examined in tandem with high basking frequency among second season juvenile turtles, biological significance of these logistic growth patterns show that relative metabolic demands influence daily time and resource allocation among immature individuals.

Acknowledgments

I wish to thank the Baylor University Biology department and Graduate School for their support during this project. This study was funded in part by the Jack G. and Norma Jean Folmar grant. Turtles were sampled under Texas Parks and Wildlife Scientific Permit #SPR-0609-127. This project was reviewed and approved by Baylor University's Institutional Animal Care and Use Committee.

CHAPTER SIX

Conclusion

Four main conclusions may be drawn from studying the basking turtle community within the mouth of Waco Creek from 2010-2012. The lack of lotic/lentic species bias compared to prior studied ponds, rivers, and canals and multiannual individual site fidelity lead to the first conclusion: the mouth of Waco Creek offers intermediate conditions which allow for unbias sympatric basking among pond and riverine species. Biological relevance of this finding: these unique habitat conditions foster species diversity and weaken sympatric competition.

Evidence of geographic demographic scattering among other emydid turtle populations, severely male skewed, sexually non demographic Waco Creek populations among typically male-skewed sexually demographic species, stable sex ratios over time, and the dominant abundance of juveniles lead to the second conclusion: the mouth of Waco Creek offers conditions which lead to a skewed immature-dominated basking turtle community in the absence of larger females. Therefore, this unique habitat is attractive to juvenile congregation among multiple species or resource limited for larger individuals.

Basking intra trap configurations had little effect on community demographic sample response compared to inter trap-type configurations examined in prior studies, species showed varied conspecific trap capture affinity, and both species and sex ratios varied between sample and Lincoln-Perterson estimates at least one month during a single sampling season. For the third conclusion, accounting for both demographic trends and trap-based sources of sampling bias are required to yield accurate estimates of basking species density and activity. Thus with individual selection as the root of all sampling bias, demographic behavior partially explains individual behavior.

The juvenile/immature male demographic are the most frequent baskers; among one, two, and three plus seasons, only the second showed a logistic growth trend; and second season growth conformed to pre-existing logistic growth models among both sparse and evenly distributed datasets. The fourth conclusion: basking frequency and growth rate are demographically linked with evidence of high metabolic rates among juvenile turtles across species. Of biological significance, relative metabolic demands influence daily time and resource allocation among mature versus immature individuals.

APPENDIX

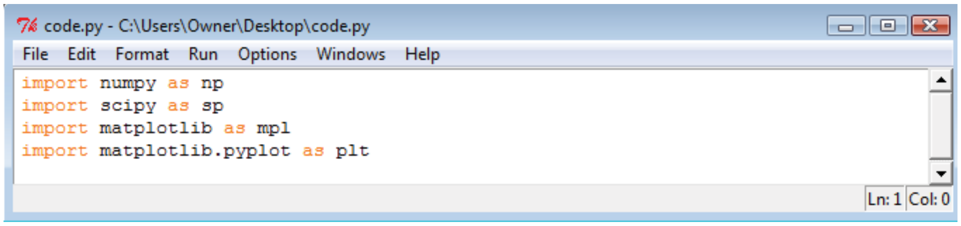
APPENDIX A

Statistical analytical programs come in two varieties—graphical user (GUI) or command line interfaces (CLI)—the first allowing the user to select from a menu of predetermined analyses at the expense of constrained test selection and the latter allowing the user freedom to tailor their analyses at the expense of the effort required to learn the appropriate language and program it. Despite the initial steep learning curve, I believe the advantages of CLI statistical languages outweigh any disadvantages (which are ephemeral depending on programming hurdles).

Several such languages are available, including but not limited to SAS, python, and R, each of which runs basic statistical analyses and possesses their own strengths and weaknesses. One may take advantage of GUI versions of classic CLI statistical programs, such as JMP in lieu of SAS and RStudio in lieu of R command line. However, these GUI versions are usually not as versatile or efficient as their original CLI counterparts. JMP in particular likes to recommend particular analyses for you, following the recent modern trend in computer software to be excessively helpful to the user. Part of running an analysis involves graphically interpreting your data first, evaluating the worth of various statistics towards your analytical goals and requirements mandated by your data second, and then cheerfully ticking off all the assumptions you will have violated before backpedaling to step two. Repeat ad nauseum.

A comparative analysis of the freeware multiplatform python and R programs will be discussed later; SAS will not be included as it is proprietary software and as a matter of personal preference. Before proceeding, download python 2.7, supplemental packages SCIPY, NUMPY, RPY (or RPY2) and MATPLOTLIB as well as IDLE or another python language interface. If you encounter problems writing python or r code, consult the helpful forums at stackoverflow or cross validated, respectively. The url addresses are subject to change, but using a search engine for those terms will get you there. Please make sure your question has not been already asked and answered before posting it.

Open python 2.7 IDLE. Delete everything and write the following code:



```
import numpy as np
import scipy as sp
import matplotlib as mpl
import matplotlib.pyplot as plt
```

Save this file as code.py, then open code.py; modify as required. When you are ready to analyze the data, execute the “Run” command or hit the hotkey shortcut “F5.” This will open a second command line window. Enter the appropriate command(s). Hit enter.

Example 1: How to compare sample gender proportions to expected 1:1 proportions?

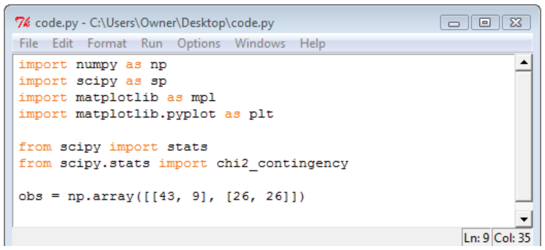
Raw Frequency Data

	Male	Female
Sample 1	43.0	9.0
Sample 2	26.0	26.0

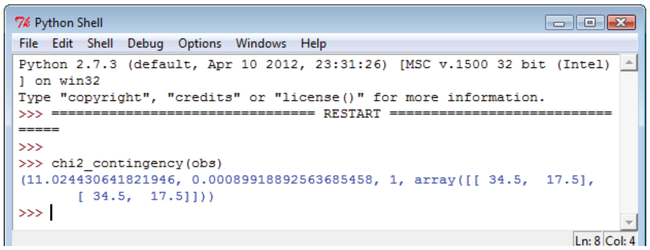
Proportions

	Male	Female
Sample 1	0.827	0.173
Sample 2	0.500	0.500

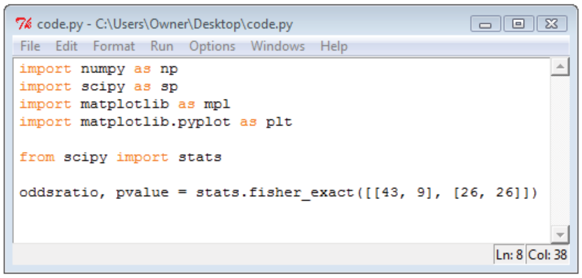
Answer 1: Chi-squared contingency analysis (use when all frequencies >5)
Fisher’s Exact test (use when one frequency (< 5)



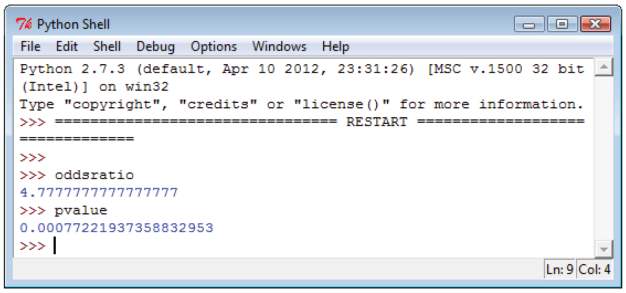
```
import numpy as np
import scipy as sp
import matplotlib as mpl
import matplotlib.pyplot as plt

from scipy import stats
from scipy.stats import chi2_contingency

obs = np.array([[43, 9], [26, 26]])
```



```
Python 2.7.3 (default, Apr 10 2012, 23:31:26) [MSC v.1500 32 bit (Intel)
] on win32
Type "copyright", "credits" or "license()" for more information.
>>> ================================ RESTART ================================
=====
>>> 
>>> chi2_contingency(obs)
(11.024430641821946, 0.00089918892563685458, 1, array([[ 34.5,  17.5],
       [ 34.5,  17.5]]))
>>> 
```



```
import numpy as np
import scipy as sp
import matplotlib as mpl
import matplotlib.pyplot as plt

from scipy import stats

oddsratio, pvalue = stats.fisher_exact([[43, 9], [26, 26]])
```



```
Python 2.7.3 (default, Apr 10 2012, 23:31:26) [MSC v.1500 32 bit
(Intel)] on win32
Type "copyright", "credits" or "license()" for more information.
>>> ================================ RESTART ====================
=============
>>> 
>>> oddsratio
4.7777777777777777
>>> pvalue
0.00077221937358832953
>>> 
```

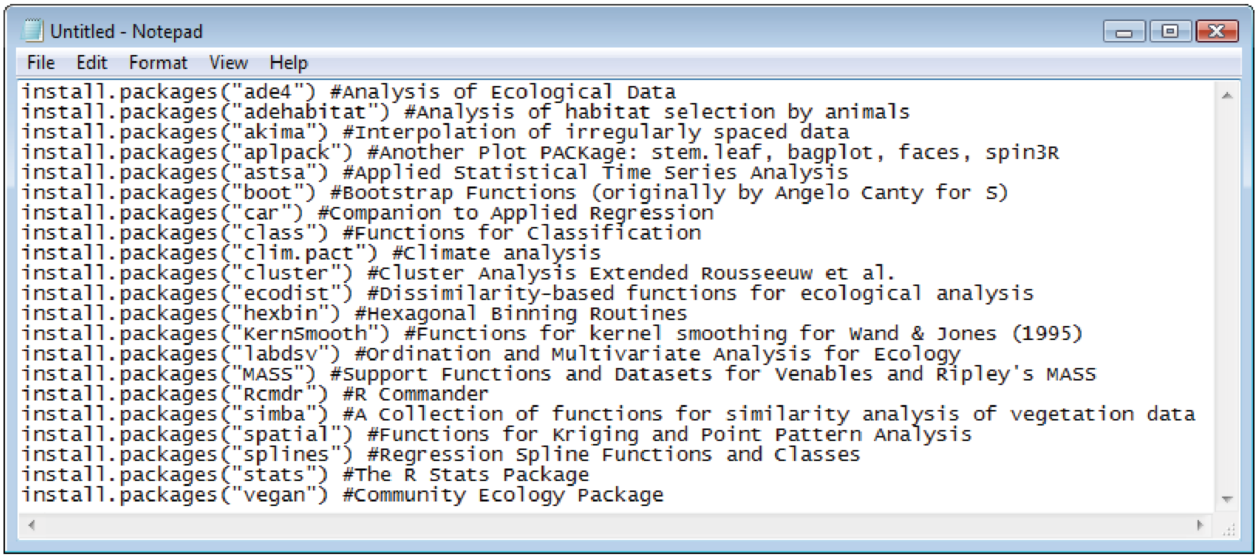
Interpretation: p-value < 0.05, therefore sampled (or sample 1) proportions significantly differ from expected (or sample 2) proportions

Before proceeding, download R 2.15.1—as of 2013, python does not have any ecological tests (i.e., population analyses, overlap indices, ordination, bray-curtis distance matrices, polynomial regression, or time series analysis), but R has several library packages to make up this lack. Both programs are freeware, operating with a GNU public license, and updated with contributions from the scientific community. One might question if R is such a superior analysis tool compared to python (it is, in spades), why not ditch python altogether?

The answer lies in the limits and utility of each program. R is an excellent program, but has no broader utility beyond data manipulation, statistical analysis, and graphical presentation. Within this scope, R excels. However, R exhibits awful performance handing large, complicated datasets and very small or very large floating variables: i.e., x = 0.0000000000000000000000001. Python is not only capable of handling large databases (and significant figures), but also able to interface directly with most data recording equipment (not to mention your computer), apply data mining techniques, use a basic statistical suite, and allows the user to create an interactive graphical user interface for generating programs or models. However, python lacks R's higher end statistical analytical capabilities. Beyond indentation, python also lacks any major syntax such as the arrows, parentheses, and brackets which clutter so many other computer languages such as C+, Pearl, or Tcl, yet bridges between these languages simultaneously. You may of course expand or integrate the capabilities of either r or python by writing your own functions and programming libraries.

Make sure you install R directly in the C:\ drive (or someplace else you have read/write access), **not** in C:\Programs. Then make a new folder on your desktop named "R.home," right click on your R desktop icon to access R program properties; change the Start in: pathway to C:\Users\Owner\Desktop\R.home. Henceforth, place all your working data in this folder as tab-delimited txt files so R knows where to find them.

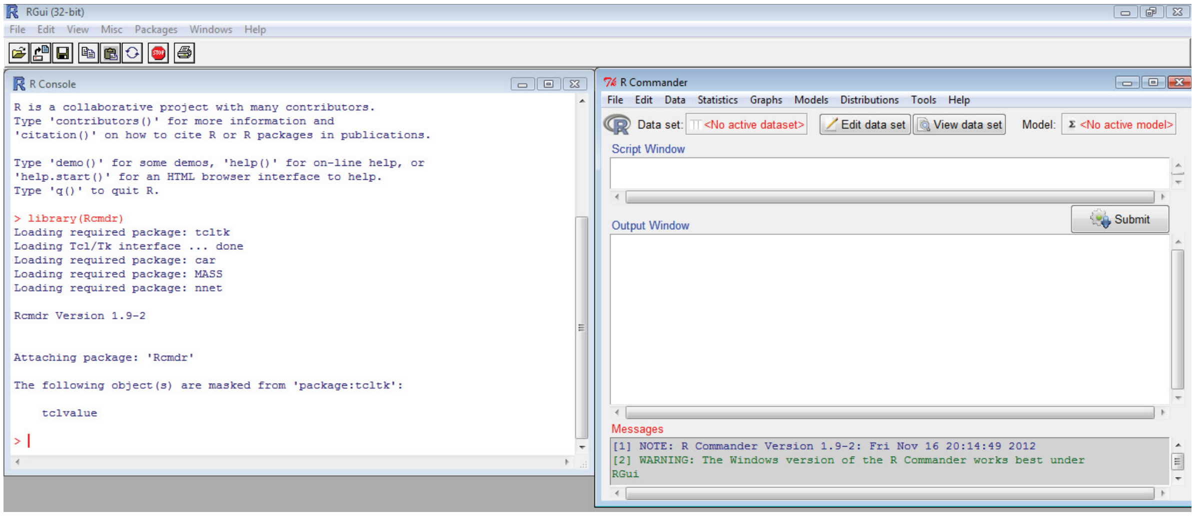
Open R. Open Notepad or some other text-based program. Write the following code in the text program, then cut (CTRL + X) and paste (CTRL + V) into R as one massive bloc of code. Hit enter to execute. You should be given a list of online server locations. Select one and start downloading supplemental R library packages. Peruse the CRAN project website for additional packages as your needs warrant.



```
install.packages("ade4") #Analysis of Ecological Data
install.packages("adehabitat") #Analysis of habitat selection by animals
install.packages("akima") #Interpolation of irregularly spaced data
install.packages("aplpack") #Another Plot PACKage: stem.leaf, bagplot, faces, spin3R
install.packages("astsa") #Applied Statistical Time Series Analysis
install.packages("boot") #Bootstrap Functions (originally by Angelo Canty for S)
install.packages("car") #Companion to Applied Regression
install.packages("class") #Functions for Classification
install.packages("clim.pact") #Climate analysis
install.packages("cluster") #Cluster Analysis Extended Rousseeuw et al.
install.packages("ecodist") #Dissimilarity-based functions for ecological analysis
install.packages("hexbin") #Hexagonal Binning Routines
install.packages("KernSmooth") #Functions for kernel smoothing for Wand & Jones (1995)
install.packages("labdsv") #Ordination and Multivariate Analysis for Ecology
install.packages("MASS") #Support Functions and Datasets for Venables and Ripley's MASS
install.packages("Rcmdr") #R Commander
install.packages("simba") #A Collection of functions for similarity analysis of vegetation data
install.packages("spatial") #Functions for Kriging and Point Pattern Analysis
install.packages("splines") #Regression Spline Functions and Classes
install.packages("stats") #The R Stats Package
install.packages("vegan") #Community Ecology Package
```

Useful R Code

citation("car") #get a reference citation for the car library
dir() # show files in current directory
getwd() # get working directory (where R scans for txt data files)
help.search("topic") # search the help system
library() # see your current library packages
library(help = "stats") # details how to use the stats package
library(Rcmdr) # call up a graphic user interface
ls() # shows objects in the search path
setwd() # change working directory (don't bother, it'll revert every time you reboot)
str(a) # display internal structure of R object



```
R is a collaborative project with many contributors.
Type 'contributors()' for more information and
'citation()' on how to cite R or R packages in publications.

Type 'demo()' for some demos, 'help()' for on-line help, or
'help.start()' for an HTML browser interface to help.
Type 'q()' to quit R.

> library(Rcmdr)
Loading required package: tcltk
Loading Tcl/Tk interface ... done
Loading required package: car
Loading required package: MASS
Loading required package: nnet

Rcmdr Version 1.9-2


Attaching package: 'Rcmdr'

The following object(s) are masked from 'package:tcltk':

    tclvalue

> 
```

```
[1] NOTE: R Commander Version 1.9-2: Fri Nov 16 20:14:49 2012
[2] WARNING: The Windows version of the R Commander works best under
RGui
```

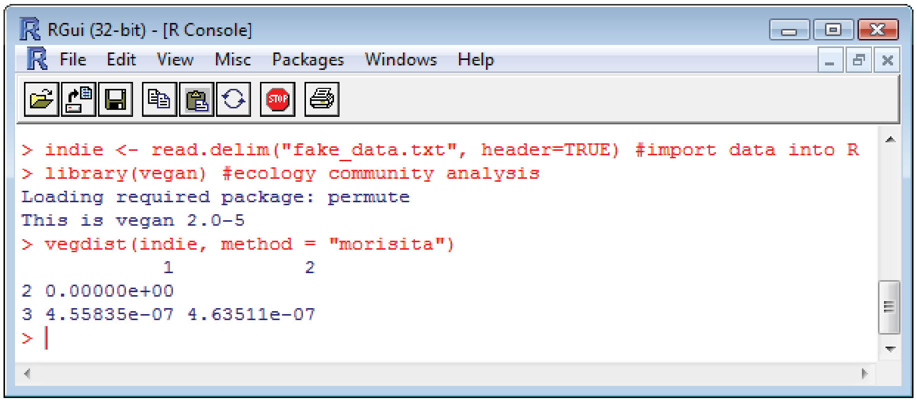
Example 2: How to compare a sample's changing individual composition year to year?

	T1001	T1002	T1003	T1004	T1005	T1006	T1007	T1008	T1009	T1010
2010	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.0
2011	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.0
2012	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	5.0

Using Excel, save your data shown above as a tab-delimited txt file, fake_data.txt, and place it in your R.home folder. Note the lack of spaces in the filename. R can't handle those: fake data.txt would crash. Don't use numerics in your heading labels. The program also won't work if you transpose your table. For most dissimilarity, diversity, or overlap indices, sites or samples = (rows) and sample species or individuals = (columns).

Open R. Input the following command lines of code (red). Hit enter for results (blue).

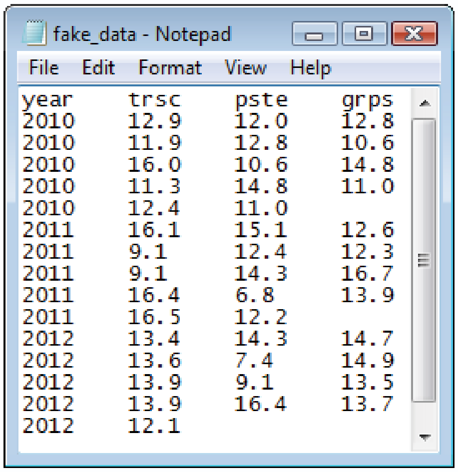
Answer 2: Morisita's Overlap Index (use for frequency data and unequal sample sizes)



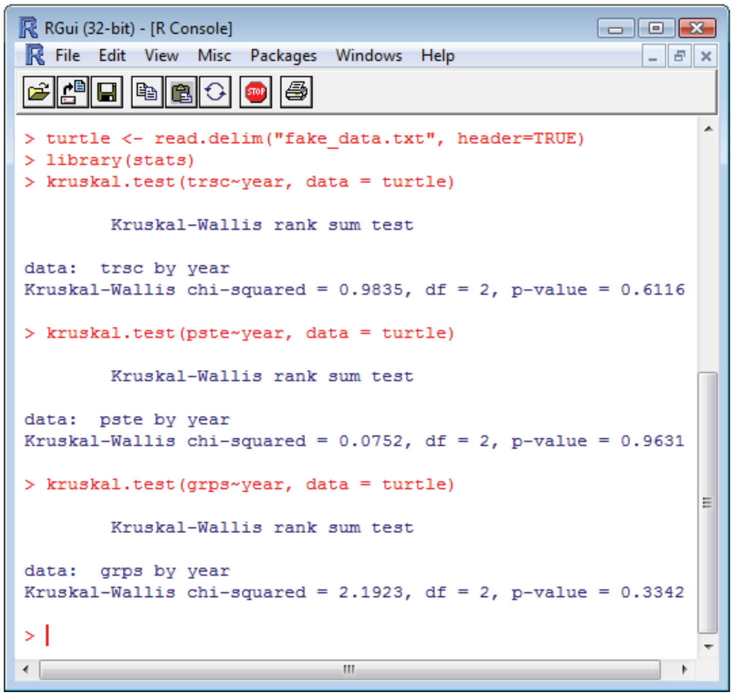
```
> indie <- read.delim("fake_data.txt", header=TRUE) #import data into R
> library(vegan) #ecology community analysis
Loading required package: permute
This is vegan 2.0-5
> vegdist(indie, method = "morisita")
            1           2
2 0.00000e+00            
3 4.55835e-07 4.63511e-07
> 
```

Interpretation: Overlap ranges from 0 (full overlap) to 1 (no overlap). The two years with exactly the same individual composition, 2010 (1) and 2011(2), have an overlap score $C_{\lambda} = 0.0 \times 10^{0}$ whereas the two sets of years whose compositions deviate, 2010 (1) and 2012 (3) as well as 2011 (2) and 2012 (3), both score $C_{\lambda} = 4.6 \times 10^{-7}$.

Example 3: How to compare annual nonparametric male turtle plastron length samples?
Anwer 3: Use a Kruskall-Wallis test with years as the grouping factors.



```
year    trsc    pste    grps
2010    12.9    12.0    12.8
2010    11.9    12.8    10.6
2010    16.0    10.6    14.8
2010    11.3    14.8    11.0
2010    12.4    11.0
2011    16.1    15.1    12.6
2011    9.1     12.4    12.3
2011    9.1     14.3    16.7
2011    16.4    6.8     13.9
2011    16.5    12.2
2012    13.4    14.3    14.7
2012    13.6    7.4     14.9
2012    13.9    9.1     13.5
2012    13.9    16.4    13.7
2012    12.1
```

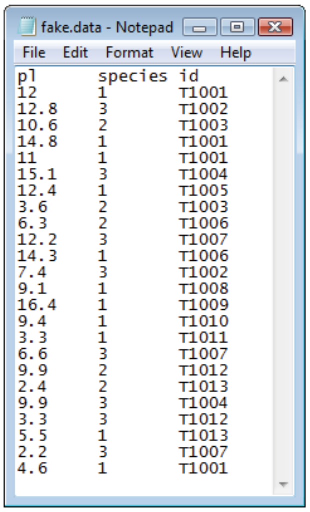


```
> turtle <- read.delim("fake_data.txt", header=TRUE)
> library(stats)
> kruskal.test(trsc~year, data = turtle)

        Kruskal-Wallis rank sum test

data:  trsc by year
Kruskal-Wallis chi-squared = 0.9835, df = 2, p-value = 0.6116

> kruskal.test(pste~year, data = turtle)

        Kruskal-Wallis rank sum test

data:  pste by year
Kruskal-Wallis chi-squared = 0.0752, df = 2, p-value = 0.9631

> kruskal.test(grps~year, data = turtle)

        Kruskal-Wallis rank sum test

data:  grps by year
Kruskal-Wallis chi-squared = 2.1923, df = 2, p-value = 0.3342

> |
```

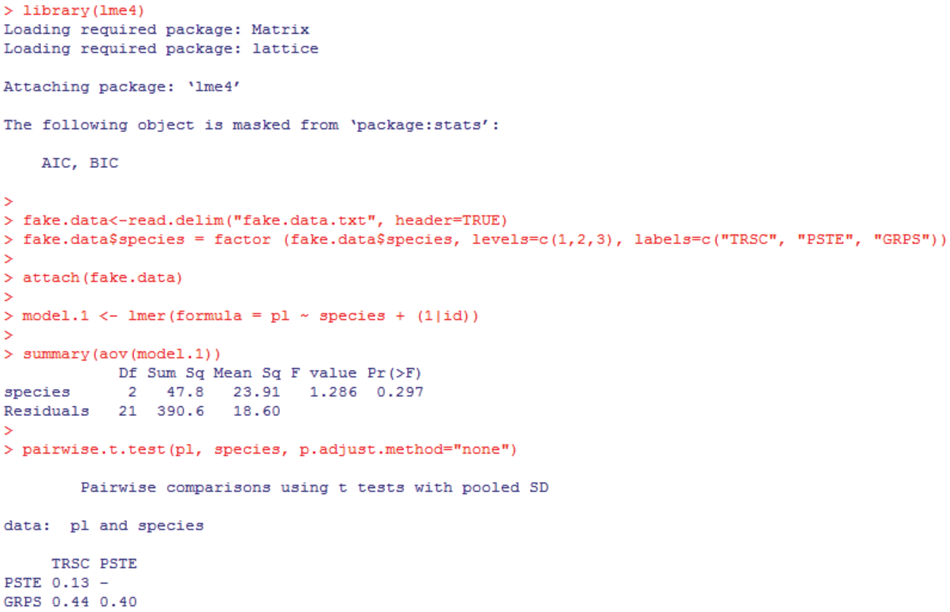
Interpretation:
P-value > 0.05 for all species, so none of the annual groups | species were significantly different from the others

Example 4: How to compare plastron length among species on longitudinal, uneven group repeated measures data which violates most ANOVA assumptions?

Answer 4: Run a mixed model regression on it first, then run the ANOVA and posthoc



```
pl      species id
12      1       T1001
12.8    3       T1002
10.6    2       T1003
14.8    1       T1001
11      1       T1001
15.1    3       T1004
12.4    1       T1005
3.6     2       T1003
6.3     2       T1006
12.2    3       T1007
14.3    1       T1006
7.4     3       T1002
9.1     1       T1008
16.4    1       T1009
9.4     1       T1010
3.3     1       T1011
6.6     3       T1007
9.9     2       T1012
2.4     2       T1013
9.9     3       T1004
3.3     3       T1012
5.5     1       T1013
2.2     3       T1007
4.6     1       T1001
```

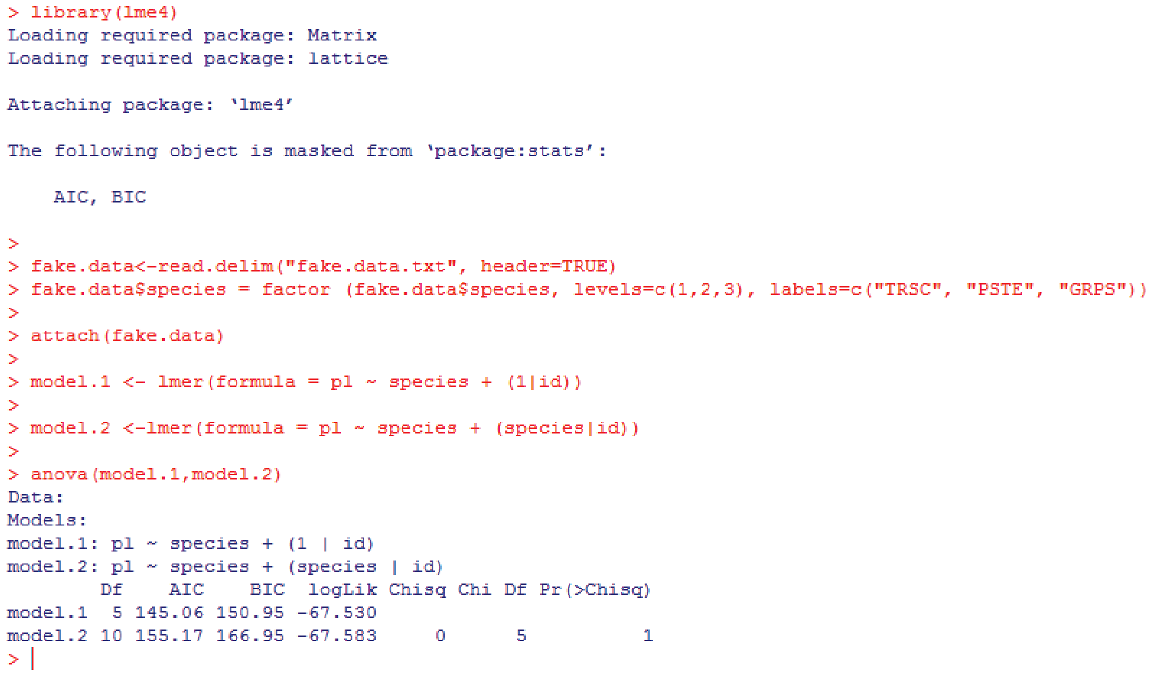


```
> library(lme4)
Loading required package: Matrix
Loading required package: lattice

Attaching package: ‘lme4’

The following object is masked from ‘package:stats’:

    AIC, BIC

>
> fake.data<-read.delim("fake.data.txt", header=TRUE)
> fake.data$species = factor (fake.data$species, levels=c(1,2,3), labels=c("TRSC", "PSTE", "GRPS"))
>
> attach(fake.data)
>
> model.1 <- lmer(formula = pl ~ species + (1|id))
>
> summary(aov(model.1))
            Df Sum Sq Mean Sq F value Pr(>F)
species      2   47.8   23.91   1.286  0.297
Residuals   21  390.6   18.60
>
> pairwise.t.test(pl, species, p.adjust.method="none")

        Pairwise comparisons using t tests with pooled SD

data:  pl and species

     TRSC PSTE
PSTE 0.13 -
GRPS 0.44 0.40
```

Interpretation: ANOVA p > 0.05, so none of the species mean plastron lengths is statistically different from the others as verified by the Tukey pairwise comparison.

Example 5: Using the data from Example 4, how would you generate various different regression models and then compare them to see which best fit the data?

Answer 5: Use ANOVA to compare among multiple models rather than groups within a single model. (Note: The response data should be from the same sample for each model)



```
> library(lme4)
Loading required package: Matrix
Loading required package: lattice

Attaching package: 'lme4'

The following object is masked from 'package:stats':

    AIC, BIC

>
> fake.data<-read.delim("fake.data.txt", header=TRUE)
> fake.data$species = factor (fake.data$species, levels=c(1,2,3), labels=c("TRSC", "PSTE", "GRPS"))
>
> attach(fake.data)
>
> model.1 <- lmer(formula = pl ~ species + (1|id))
>
> model.2 <-lmer(formula = pl ~ species + (species|id))
>
> anova(model.1,model.2)
Data:
Models:
model.1: pl ~ species + (1 | id)
model.2: pl ~ species + (species | id)
        Df    AIC    BIC  logLik Chisq Chi Df Pr(>Chisq)
model.1  5 145.06 150.95 -67.530
model.2 10 155.17 166.95 -67.583     0      5          1
> |
```

Interpretation: According the both the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) values, model.1 better fits the data than model.2 as the scores are lower

BIBLIOGRAPHY

Allen, J. F. and R. A. Littleford. 1955. Observations on the feeding habits and growth of immature Diamondback Terrapins. Herpetologica 11:77-80.

Anderson, R. V., Gutierrez, M. L., and M. A. Romano. 2002. Turtle habitat use in a reach of the upper Mississippi River. Journal of Freshwater Ecology 17:171-177.

Angilletta, M. J. 2001. Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). Ecology 82:3044-3056.

Avery, H. W., Spotila, J. R., Congdon, J. D., Fischer, R. U. Jr., Standora, E. A., and S. B. Avery. 1993. Roles of diet protein and temperature in the growth and nutritional energetic of juvenile slider turtles, *Trachemys scripta*. Physiological Zoology 66:902-925.

Barko, V. A., Briggler, J. T., and D. E. Ostendorf. 2004. Passive fishing techniques: A cause of turtle mortality in the Mississippi River. Journal of Wildlife Management 64:1145-1150.

Bates, D., Maechler, M. and B. Bolker. 2013. lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2.

Bider, J. R. and W. Hoek. 1971. An efficient and apparently unbias sampling technique for population studies of painted turtles. Herpetologica 27:481-484.

Bjorndal K.A. and A.B. Bolten. 1990. Digestive processing in a herbivorous fresh-water turtle: consequences of small intestine fermentation. Physiological and Biochemical Zoology 63:1232–1247.

Bjorndal, K. A. and A. B. Bolten. 1993. Digestive efficiencies in herbivorous and omnivorous freshwater turtles on plant diets: Do herbivores have a nutritional advantage? Physiological Zoology 66:384-395.

Bodie, R. J. and R. D. Semlitsch. 2000. Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. Oecologia 122:138-146.

Bouchard, S. S. and K. A. Bjorndal. 2006. Ontogenetic diet shifts and digestive constraints in the omnivorous freshwater turtle *Trachemys scripta*. Physiological and Biochemical Zoology 79:150-158.

Boyer, D. R. 1965. Ecology of the basking habit of turtles. Ecology 46:99-118.

Braid, M. R. 1974. A bal-chatri trap for basking turtles. Copeia 2: 539-540.

Brody, S. 1945. Bioenergetics and Growth. Reinhold, New York, New York.

Bull, J. J. and R. C. Vogt. 1979. Temperature-dependent sex determination in turtles. Science 206: 1186-1188.

Bulté, G. and G. Blouin-Demers. 2009. Implications of extreme sexual size dimorphism for thermoregulation in a freshwater turtle. Oecologia 162:313-322.

Burke, V. T., Greene, J. L., and J. W. Gibbons. 1995. The effect of sample size and study duration on metapopulation estimates for Slider Turtles (*Trachemys scripta*). Herpetologica 51:451-456.

Cadi, A. and P. Joly. 2003. Competition for basking places between the endangered European pond turtle (*Emys orbicularis galloitalica*) and the introduced red eared slider (*Trachemys scripta elegans*). Canadian Journal of Zoology 81:1392-1398.

Cagle, F. R. 1939. A system of marking turtles for future identification. Copeia 1939:170-173.

Cagle, F. R. 1942. Turtle populations in southern Illinois. Copeia 1942:155-162.

Cagle, F. R. 1946. The growth of the slider turtle, *Pseudemys scripta elegans*. American Midland Naturalist 36: 685-729.

Cagle, F. R. 1950. The life history of the Slider Turtle, *Pseudemys scripta troostii* (Holbrook). Ecological Monographs 20:31-54.

Cagle, F. R., and A. H. Chaney. 1950. Turtle populations in Louisiana. American Midland Naturalist 43: 383-389.

Carriere, M. A., Rollinson, N., Suley, A. N., and R. J. Brooks. 2008. Thermoregulation when the growing season is short: Sex-based basking patterns in a northern population of Painted Turtles (*Chrysemys picta*). Journal of Herpetology 42:206-209.

Chao, A., Chiu, C. H., and L. Jost. 2010. Phylogenetic measures based on Hill Numbers. Philosophical transactions of the Royal Society Bulletin 365:3599-3609.

Clark, D. B. and J. W. Gibbons. 1969. Dietary shift in the turtle *Pseudemys scripta* (Schoepff) from youth to maturity. Copeia 1969:704-706.

Coleman, J. L. and R. L. Gutberlet, Jr. 2008. Seasonal variation in basking in two syntopic species of map turtles (Emydidae: *Graptemys*). Chelonian Conservation and Biology 7:276-281.

Congdon, J. D., Dunham, A. E., and D. W. Tinkle. 1982. Energy budget and life histories of reptiles. In: Gans, C. and F. H. Pough (ed). Biology of the Reptilia, Vol 13. Academic Press, New York. pp. 233-271.

Congdon, J. D. and J. W. Gibbons. 1983. Relationships of reproductive characteristics to body size in *Pseudemys scripta*. Herpetologica 39:147-151.

Congdon, J. D. and J. W. Gibbons. 1996. Structure and dynamics of a turtle community over two decades. In: Cody, M. L. and J. A. Smallwood. (ed). Long-term studies of vertebrate communities. Academic Press. New York, N. Y., 1996. p.137-159.

Conner, C. A., Douthitt, B. A., and T. A. Ryan. 2005. Descriptive ecology of a turtle assemblage in an urban landscape. American Midland Naturalist 153:428-435.

Corn, P. S., and R. B. Bury. 1990. Sampling methods for terrestrial amphibians and reptiles. USDA Forest Service, Gen. Tech. Rept. PNW-GTR-256, Portland, OR.

Craig, M. J. 1992. Radio-telemetry and tagging study of movement patterns, activity cycles, and habitat utilization in Cagle's map turtle, *Graptemys caglei*. M.S. thesis, West Texas State University, Canyon.

Crawford, K. M., Spotila, J. R., and E. A. Standora. 1983. Operative environmental temperatures and basking behavior of the turtle *Pseudemys scripta*. Ecology 64:989-999.

Davis, A. K., and A. M. Grosse. 2008. Measuring fluctuating asymmetry in plastron scutes of Yellow-Bellied Sliders: The importance of gender, size, and body location. American Midland Naturalist 159:340-348.

DonnerWright, D. M., Bozek, M. A., Probst, J. R., and E. M. Anderson. 1999. Responses of turtle assemblage to environmental gradients in the St. Croix River in Minnesota and Wisconsin, USA. Canadian Journal of Zoology 77:989-1000.

Dreslik, M. J. 1999. Dietary notes on the Red-eared Slider (*Trachemys scripta*) and River Cooter (*Pseudemys concinna*) from southern Illinois. Transactions of the Illinois State Academy of Science 92:233-241.

Dreslik, M. J., Kuhns, A. R., and C. A. Phillips. 2005. Structure and composition of a southern Illinois freshwater turtle assemblage. Northeastern Naturalist 12:173-186.

Dunham, A. E., Morin, P. J., and H. M. Wilbur. 1988. Methods for the study of reptile populations, p. 331-386. In: Biology of the Reptilia, vol. 16, Ecology b: defense and life history. C. Gans and R. B. Huey (eds.), Alan R. Liss, New York, New York.

Enge, K. M. 2001. The pitfalls of pitfall traps. Journal of Herpetology 35: 467-478.

Enge, K. M. 2012. What the world needs is a better Gopher Tortoise trap. Herpetological Review 43: 574-578.

Ernst, C. H. 1971. Growth of the Painted Turtle, *Chrysemys picta*, in southeastern Pennsylvania. Herpetologica 27:135-141.

Ernst, C. H. 1972. Temperature-activity relationship in the Painted Turtle, *Chrysemys picta*. Copeia 1972:217-222.

Ernst, C. H., and J. E. Lovich. 2009. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D.C., USA.

Ewert, M.A. and C. E. Nelson. 1991. Sex determination in turtles: diverse patterns and some possible adaptive values. Copeia 1991:50-69.

Fabens, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29:265-289.

Foley, R. E. and J. R. Spotila. 1978. Effect of wind speed, air temperature, body size, and vapor density difference on evaporative water loss from the turtle *Chrysemys scripta*. Copeia 1978:627-634.

Fox, J. and S. Weisberg. 2011. An {R} companion to applied regression, Second Edition. Thousand Oaks CA: Sage.

Frazer, N. B., Gibbons, J. W., and J. L. Greene. 1990a. Exploring Fabens' Growth Model with data on a long-lived vertebrate, *Trachemys scripta* (Reptilia: Testudinata). Copeia 1990:112-118.

Frazer, N. B., Gibbons, J. W., and J. L. Greene. 1990b. Life tables of a slider turtle population. In: Gibbons, J. W. (ed). Life history and ecology of the slider turtle. Smithsonian Institution Press. Washington, D.C., 1990, p.182-200.

Frazer, N. B., Gibbons, J. W., and T. J. Owens. 1990c. Turtle trapping: Preliminary tests of conventional wisdom. Copeia 4: 1150-1152.

Frazer, N. B., Greene, J. L., and J. W. Gibbons. 1993. Temporal variation in growth rate and age at maturity of male Painted Turtles, *Chrysemys picta*. American Midland Naturalist 130:314-324.

Gamble, T. and A. M. Simons. 2004. Comparison of harvested and nonharvested Painted Turtle populations. Wildlife Society Bulletin 32:1269-1277.

Gatten, R. E. 1974. Effects of temperature and activity on aerobic and anaerobic metabolism and heart rate in the turtles *Pseudemys scripta* and *Terrapene ornata*. Comparative Biochemistry and Physiology 48A:619-648.

Gatten, R. F. 1980. Metabolic rates of fasting and recently fed Speckled Caimans (*Caiman crocodilus*). Herpetologica 36:361-364.

Getz, W. M. 1993. Metaphysiological and evolutionary dynamics of populations exploiting constant and interactive resources—r-K selection revisited. Evolutionary Ecology 7:287-305.

Gibbons, J. W. 1990. Sex ratios and their significance among turtle populations. In: Gibbons, J. W. (ed). Life history and ecology of the slider turtle. Smithsonian Institution Press. Washington, D.C., 1990, p.171-182.

Gibbons, J. W. and J. E. Lovich. 1990. Sexual dimorphism in turtles with emphasis on the Slider Turtle (*Trachemys scripta*). Herpetological Monographs 4:1-29.

Gibbons, J. W. and J. L. Greene. 1979. X-ray photography: A technique to determine reproductive patterns of freshwater turtles. Herpetologica 35:86-89.

Gibbons, J. W., Semlitsch, R. D., Greene, J. L., and J. P. Schubauer. 1981. Variation in age and size at maturity of Slider Turtle (*Pseudemys scripta*). The American Naturalist 117:841-845.

Gibbs, J. P. and D. A. Steen. 2005. Trends in sex ratios of turtles in the United States: Implications of road mortality. Conservation Biology 19: 552-556.

Gordon, D. M. and R. D. MacCulloch 1980. An investigation of the ecology of the map turtle, *Graptemys geographica* (LeSueur), in the northern part of its range. Canadian Journal of Zoology 58:2210-2219.

Greenberg, C. H., Neary, D. G., and L. D. Harris. 1994. A comparison of herpetofaunal sampling effectiveness of pitfall, single-ended, and double-ended funnel traps used with drift fences. Journal of Herpetology 28:319-324.

Hammond, K. A., Spotila, J. R., and E. A. Standora. 1988. Basking behavior of the turtle *Pseudemys scripta*: Effects of digestive state, acclimation, temperature, sex, and season. Physiological Zoology 61: 69-77.

Harding, J. H. 2006. What, if anything, is a reptile? Bulletin of the Chicago Herpetological Society 41:141-146.

Hart, D. R. 1983. Dietary and habitat shift with size of red-eared turtles (*Pseudemys scripta*) in a southern Louisiana population. Herpetologica 39:285-290.

Hays, K. A. and K. McBee. 2010. Population demographics of Red-eared Slider turtles (*Trachemys scripta*) from Tar Creek Superfund Site. Journal of Herpetology 44: 441-446.

Hennemann, W. W. 1979. The influence of environmental cues and nutritional status on frequency of basking in juvenile Suwanee terrapins (*Chrysemys cocinna*). Herpetologica 35:129-131.

Hill, S. K. 2008. The influence of urbanization on the basking behavior of a central Texas freshwater turtle community. Ph.D. Dissertation, Baylor University, USA.

Hothorn, T., Bretz, F, and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal 50:346-363.

Hutchison, V. H. 1979. Thermoregulation. In: Turtles: Perspectives and research. Edited by M. Harless and H. Morlock John Wiley and Sons, New York. pp. 207-228.

Jackson, C. G., Jr. 1970. A biometrical study of growth in *Pseudemys concinna suwanniensis*, I. Copeia 1970:528-534.

Janzen, F. J. 1994. Vegetational cover predicts the sex ratio of hatchling turtles in natural nests. Ecology **75:**1593–1599.

Janzen, F. J., Paukstis, G. L., and E. D. Brodie III. 1992. Observations on basking behavior of hatchling turtles in the wild. Journal of Herpetology 26:217-219.

Kass, R. E., Ullrey, D. E., and A. L. Trapp. A study of calcium requirements of the Red-eared Slider turtle (*Pseudemys scripta elegans*). The Journal of Zoo and Animal Medicine 13: 62-65.

Kennett, R. 1996. Growth models for two species of freshwater turtle, *Chelonia rugosa* and *Elseya dentata*, from the wet-dry tropics of northern Australia. Herpetologica 52:383-395.

Knight, T. W., Layfield, J. A., and R. J. Brooks. 1990. Nutritional status and mean selected temperature of hatchling Snapping Turtles (*Chelydra serpentina*): Is there a thermophilic response to feeding? Copeia 1990:1067-1072.

Koper, N. and R. J. Brooks. 2000. Environmental constraints on growth of Painted turtles (*Chrysemys picta*) in northern climates. Herpetologica 56:421-432.

Kornilev, Y. V., Dodd, C. K. Jr., and G. R. Johnson. 2012. Retention of paint markings for individual identification of free-ranging basking aquatic turtles (Suwannee Cooters, *Pseudemys concinna suwanniensis*). Herpetological Review 43:61-63.

Krawchuk, M. A. and R. J. Brooks. 1998. Basking behavior as a measure of reproductive cost and energy allocation in the Painted turtle, *Chrysemys picta*. Herpetologica 54:112-121.

Kuno, E. 1991. Some strange properties of the logistic equation defined with r and K – inherent defects and artifacts. Researches on Population Ecology 33:33-39.

Lagler, K. F. 1943. Methods of collecting freshwater turtles. Copeia 1: 21-25.

Lefevre, K. and R. J. Brooks. 1995. Effects of sex and body size on basking behavior in a Northern population of the Painted Turtle, *Chrysemys picta*. Herpetologica 51:217-224.

Lindeman, P. V. 1990. Closed and open model estimates of abundance and tests of model assumptions for two populations of the turtle, *Chrysemys picta*. Journal of Herpetology 24:78-81.

Lindeman, P. V. 1997. Contributions toward improvement of model fit in nonlinear regression modeling of turtle growth. Herpetologica 53:179–191.

Lindeman, P. V. 1999a. Aggressive interactions during basking among four species of emydid turtles. Journal of Herpetology 33:214-219.

Lindeman, P. V. 1999b. Surveys of basking map turtles Graptemys spp. in three river drainages and the importance of deadwood abundance. Biological Conservation 88:33-42.

Lindeman, P. V. 1999c. Growth curves for *Graptemys*, with a comparison to other emydid turtles. American Midland Naturalist 142:141–151.

Lindeman, P. V. 2001. Investigations of the ecology of *Graptemys versa* and *Pseudemys texana* in southcentral Texas. Chelonian Conservation and Biology 4:223-224.

Lindeman, P. V. 2003. Sexual difference in habitat use of Texas map turtle (Emydidae: *Graptemys versa*) and its relationship to size dimorphism and diet. Canadian Journal of Zoology 81:1185-1191.

Lindeman, P. V. 2005. Aspects of the life history of the Texas Map Turtle (*Graptemys versa*). American Midland Naturalist 153:378–388.

Lindeman, P. V. 2007. Diet, growth, body size, and reproductive potential of the Texas River Cooter (*Pseudemys texana*) in the southern Llano River, Texas. The Southwestern Naturalist 52:586-594.

Litzgus, J. D. and T. A. Mousseau. 2004. Demography of a southern population of the Spotted Turtle (*Clemmys guttata*). Southeastern Naturalist 3:391-400.

Loncke, D. J. and M. E. Obbard. 1977. Tag success, dimensions, clutch size, and nesting site fidelity for the snapping turtle, *Chelydra serpentina*, (Reptilia, Testudines, Chelydridae) in Algonquin Park, Ontario, Canada. Journal of Herpetology 11:243-244.

Lovich. J. 1988. Aggressive basking behavior in Eastern Painted Turtles (*Chrysemys picta picta*). Herpetologica 44:197-202.

Lucey, E. C. 1974. Heart rate and physiological thermoregulation in a basking turtle, *Pseudemys scripta elegans*. Comparative Biochemistry and Physiology 39A:471-482.

Magwene, P. M. 2001. Comparing ontogenetic trajectories using growth process data. Systematic Biology 50:640-656

Manning, B. and G. C. Grigg. 1997. Basking is not of thermoregulatory significance in the "basking" of freshwater turtle *Emydura signata*. Copeia 1997:579-584.

Modesto, S. P. and J. S. Anderson. 2004. The phylogenetic definition of reptilia. Systematic Biology 53:815-821

Moore, M. J. C. and R. A. Seigel. 2006. No place to nest or bask: Effects of human disturbance on the nesting and basking habits of yellow-blotched map turtles (*Graptemys flavimaculata*). Biological Conservation 130:386-393.

Moreau, J. 1987. Mathematical and biological expression of growth in fishes: Recent trends and further developments. Pp. 81-113. In R. C. Summerfelt and G. E. Hall (Eds.), The Age and Growth of Fishes. Iowa State University Press, Ames, Iowa.

Morin, P.J. 1999. Community Ecology. Blackwell Sciences, Inc., Malden, MA.

Nietfeld, M. T., Barrett, M. W., and N. Silvy. Wildlife marking techniques. Pages 140-168. In Bookhout, T. A. (ed). 1996. Research and management techniques for wildlife and habitats. Fifth ed., rev. The Wildlife Society, Bethesda MD.

Nobre, J.S. and da Motta Singer. 2007. Residual analysis for linear mixed models. Biometrical Journal 49: 863-875.

Osborn, H. F. 1903. On the primary divison of the Reptilia into two sub- classes, Synapsida and Diapsida. Science 17:275-276.

Parker, W. S. 1984. Immigration and dispersal of slider turtles *Pseudemys scripta* in Mississippi farm ponds. American Midland Naturalist 112:280-293.

Parker, W. S. 1990. Colonization of a newly constructed farm pond in Mississippi by Slider Turtles and comparisons with established populations. In: Gibbons, J. W. (ed). Life history and ecology of the slider turtle. Smithsonian Institution Press. Washington, D.C., 1990, p.216-222.

Parmenter, R. P. 1980. Effects of food availability and water temperature on the feeding ecology of Pond Sliders (*Chrysemys s. scripta*). Copeia 1980:503-514.

Peterman, W. E. and T. J. Ryan. 2009. Basking behavior of Emydid turtles (*Chrysemys picta, Graptemys geographica,* and *Trachemys scripta*) in an urban landscape. Northeastern Naturalist 16:629-636.

Perez-Santigosa, N., Di'Az-Paniagua, C., and J. Hidalgo-vila. 2008. The reproductive ecology of exotic *Trachemys scripta elegans* in an invaded area of southern Europe. Aquatic Conservation: Marine and Freshwater Ecosystems 18:1302-1310.

Pianka, E. R. 1970. On r and K selection. American Naturalist 104:592-597.

Plummer, M. V. 1979. Collecting and marking, p. 45-60. In: Turtles: perspectives and research. M. Harless and H. Morlock (eds.). John Wiley & Sons, Inc., New York, New York.

Polo-Cavia, N., Lopez, P., and J. Martin. 2010. Competitive interactions during basking between native and invasive freshwater turtle species. Biological Invasions 12:2141–2152.

Price, P. W. 1980. Evolutionary Biology of Parasites. Princeton University Press, Princeton.

R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Readel, A., Warner, J. K., Holberton, R. L., and C. A. Phillips. 2008. Maturational changes in male slider turtles (*Trachemys scripta*) from Illinois. Herpetological Conservation and Biology 3:170-175.

Ream, C. and R. Ream. 1966. The influence of sampling methods on the estimation of population structure in painted turtles. American Midland Naturalist 75: 325-338.

Richards, F. J. 1959. A flexible growth function for empirical use. Journal of Experimental Botany 10:290-300.

Ricklefs, R. E. and M Lau. 1980. Bias and dispersion of overlap indices: results of some Monte Carlo simulations. Ecology 61: 1019-1025.

Robinson, K. M., and G. G. Murphy. 1975. A new method for trapping softshell turtes. Herpetological Review 6:111.

Roe, J. H., Hopkins, W. A., and L. G. Talent. 2005. Effects of body mass, feeding, and circadian cycles on metabolism in the lizard *Sceloporus*. Journal of Herpetology 39:595-603.

Schluter, D., and R.E. Ricklefs. 1993. Species diversity: An introduction to the problem. Pp 1–12, *In* R.E. Ricklefs and D. Schluter (Eds.). Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago, IL. 414 pp.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369-404.

Schoener, T. W., and A. Schoener. 1978. Estimating and interpreting body-size growth in some *Anolis* lizards. Copeia 1978:390-405.

Schubauer, J. P. and R. R. Parmenter. 1981. Winter feeding of aquatic turtles in a southeastern reservoir. Journal of Herpetology 15:444-447.

Schwarzkopf, L. and R. J. Brooks. 1985. Application of operative environmental temperatures to analysis of basking behavior in *Chrysemys picta*. Herpetologica 41: 206-212.

Seber, G.A.F. 1982. The Estimation of Animal Abundance and Related Parameters. Macmillan, New York, 2nd edition.

Secor, S. M. and A. C. Faulkner. 2002. Effects of meal size, meal type, body temperature, and body size on the specific dynamic action of the Marine Toad, *Bufo marinus*. Physiological and Biochemical Zoology 75:557-571.

Shine, R., and J. B. Iverson. 1995. Patterns of survivorship, growth and maturation in turtles. Oikos 72:343–348.

Shively, S. H. and J. F. Jackson. 1985. Factors limiting the upstream distribution of the Sabine map turtle. American Midland Naturalist 114:292-303.

Smith, G. R. and J. B. Iverson. 2004. Diel activity patterns of the turtle assemblage of a northern Indiana lake. American Midland Naturalist 152: 156-164.

Spotila, J. R. and E. A. Standora. 1985. Environmental constraints on the thermal energetics of sea turtles. Copeia 1985:694-702.

Spotila, J. R., Foley, R. E., Schubauer, J. P., Semlitsch, R. D., Crawford, K. M., Standora, E. A., and J. W. Gibbons. 1984. Opportunistic behavioral thermoregulation of turtles, *Pseudemys scripta*, in response to microclimatology of a nuclear reactor cooling reservoir. Herpetologica 40:299-308.

Spotila, J. R., Standora, E. A., Easton, D. P., and P. S. Rutledge. 1989. Bioenergetics, behavior, and resource partitioning in stressed habitats: Biophysical and molecular approaches. Physiological Zoology 62(2):253-285.

Stamps, J. A. 1995. Using growth-based models to study behavioral factors affecting sexual size dimorphism. Herpetological Monographs 9:75-87.

Timken, R. L. 1968. *Graptemys pseudogeographica* in the upper Missouri River of the northcentral United States. Journal of Herpetology 1:76-82.

Tinkle, D. W. 1958. Experiments with censusing of southern turtle populations. Herpetologica 14: 172-175.

Todd, B. D., Winne, C. T., Willson, J. D., and J. W. Gibbons. 2007. Getting the drift: Examining the effect of timing, trap type, and taxon on herpetofaunal drift fence surveys. American Midland Naturalist 158: 292-305.

Tracy, C. R. 1982. Biophysical modeling in reptilian physiology and ecology. In: Biology of the Reptilia Vol. 12, edited by C. Gans and F. H. Bough. Academic Press, New York. pp275-320.

Tucker, J. K., Maher, R. J., and C. H. Theiling. 1995. Year-to-year variation in growth in the Red-eared Turtle, *Trachemys scripta elegans*. Herpetologica 51:354-358.

Viosca, P. 1933. The *Pseudemys troostii-elegans* complex, a case of sexual dimorphism. Copeia 1933:208-210.

Vogt, R. C. 1980a. Natural history of the map turtles *Graptemys pseudogeographica* and *G. ouchitensis* in Wisconsin. Tulane Studies in Zoology and Botany 22:17-48.

Vogt, R. C. 1980b. New methods for trapping aquatic turtles. Copeia 1980:368-371.

Vogt, R. C. and J. J. Bull. 1982. Temperature-controlled sex determination in turtles: Ecological and behavioral aspects. Herpetologica 38:156-164.

Vogt, R. C. and J. J. Bull. 1984. Ecology of hatchling sex ratio in map turtles. Ecology 65:582-587.

Webb, R. G. 1961. Observations on the life histories of turtles (genus *Pseudemys* and *Graptemys*) in Lake Texoma, Oklahoma. American Midland Naturalist 65:193-214.

Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer, New York.

Wilbur, H. M. and J. M. Landwehr. 1974. The estimation of population size with equal and unequal risks of capture. Ecology 55: 1339-1348.

Willingham, E. 2005. Different incubation temperatures result in differences in mass in female Red-eared Slider turtle hatchlings. Journal of Thermal Biology 30:61-64.

Wilson, D. S., Tracy, C. R., and C. R. Tracy. 2003. Estimating age of turtles from growth rings: a critical evaluation of this technique. Herpetologica 59:178-194.

Zar, J.H. 1999. Biostatistical Analysis. 4th Edition. Prentice-Hall Inc., Upper Saddle River, NJ.

Zimmerman, L. C. and C. R. Tracy. 1989. Interactions between the environment and ectothermy and herbivory in reptiles. Physiological Zoology 62:374-409.