To the Graduate Council:

I am submitting herewith a dissertation written by Karen Marie Davis entitled "Sociality, Cognition and Social Learning in Turtles (Emydidae)." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Psychology.

Gordon M. Burghardt, Major Professor

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SOCIALITY, COGNITION AND SOCIAL LEARNING IN TURTLES (EMYDIDAE)

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Karen Marie Davis
December 2009

DEDICATION

I dedicate this dissertation to my dear friend, Indie, for gracing me with her lovely spirit and constant companionship throughout the last 12 years of my career and life's journey. Each species and in particular each individual animal has much they can teach us about "Animal Behavior" if we truly observe them and learn to communicate with them on their terms. Indie has been a wonderful teacher to human and canine alike. My journey with Indie started with my naïve intention to help Indie with her "human" problem. She was extremely shy to the point of having almost 24 hour panic attacks about anything and everything related to the human world, with humans as the scariest things. Throughout our journey together she has taught me (along with many other animal teachers) something that can't be learned from a book; how to apply learning theory to communicate effectively and safely with animals while solving animal-human communication problems.

Indie Cindy Davis 2009

PREFACE

Giant Tortoise

I am related to stones
The slow accretion of moss where dirt is wedged
Long waxy hair that can split boulders.
Events are not important.

I live in my bone
Recalling the hour of my death.
It takes more toughness than most have got.
Or a saintliness.

Strength of a certain kind, anyway.
Bald toothless clumsy perhaps
With all the indignity of old age
But age is not important.

There is nothing worth remembering
But the sliver glint in the muck
The thickening of great trees
The hard crust getting harder.

Anthony Hecht

ACKNOWLEDGMENTS

Throughout my six years working on my dissertation at U.T., many people have helped me in a variety of ways both academically and personally. I am equally grateful to all who have helped me throughout this dissertation process, so the order of this list of acknowledgments does not represent a hierarchy of importance placed on differing types of guidance. I also realize that many more friends and colleges have touched my life in the past 6 years than I can mention here so to all those who are not otherwise mentioned here, thank you.

First, I want to thank my advisor Dr. Gordon M. Burghardt; and the rest of my committee: Dr. Todd Freeberg, Dr. Neil Greenberg, Dr. John Malone, and Dr. Rich Saudargas for all of their advice and mentorship during various stages of this process. Gordon has challenged me academically and scientifically in countless ways. Furthermore, I have learned more than I ever bargained for about managing an animal research lab and mentoring undergraduates while in Dr. Burghardt's lab. I am grateful to Dr. Freeberg for allowing me to attend his lab journal club. This exchange of ideas and feedback on various projects has been essential to my growth as a scientist. Furthermore, Dr. Freeberg has given me valuable feedback and constructive advice on earlier presentations and drafts of my dissertation work through the years, always with a patient, pleasant attitude mixed with his famous dry humor. Dr. Greenberg has continued to remind me to think outside the box while remembering to remain grounded in "DEEP" ethology in order to put my work in perspective. Dr. Saudargas and Dr. M. have been invaluable resources of learning theory, an important component of my project.

Next I would like to thank my lab mates Lauren Kirby, Kerry Hansknecht, Rita Mehta, and John Placyk for comments on earlier presentations of parts of this material. Rita, Lauren, Ellen Mahurin, and Jennifer Miller engaged me academically as well as making my first few years at U.T. more fun. My present lab mate, Kerry, has been a great help with encouragement, dissertation formatting, and SPSS graphing skills at the last minute.

Furthermore, the Freeberg lab students: Julia Bartmess-LeVasseur, Carrie Branch, Sheri Browning, Jessica Owens, Ami Padget, Ellen Mahurin, and Ellen Harvey Williams have reviewed earlier presentations and drafts of this work. I also wish to thank the undergraduate students I have mentored over the years who specifically helped care for the turtles, digitize Chattanooga tapes, and helped me run my intensive learning trials: Carrie Branch, Leaha Burke, Meghan McCall, Kathryn McCullough, Ben Cohen, Ramsey Cox, Rachel Edwards, Derek Goff, Julie Haskew, Jordan Hensley, Erick Jenkins, Emily Long, Jessica Lovely, Ruben Luna, Jessica Mayfield, Jeff Orgain, Lacy Sams, Jennifer Southerland, and Rhonda Williams. I would also like to thank Kaihla Dailey, Lacey Hubbs, Catherine Smith, and Natalie Wyszynski, all of whom helped me with supervising the other undergraduates and keeping the lab running over the last few years. The expertise of the Psychology department staff members: Alecia Davis, Kelly Dailey, Louise Murr, Connie Ogle, and Sandy Thomas helped me run the Burghardt Lab and fulfill my GTA duties.

My adventure into the world of turtles through observations of turtles at the aquarium would not have been possible without the gracious hospitality and help of the staff at the Tennessee Aquarium in Chattanooga, especially Dave Collins and Tim Schmiedenhausen. I also need to thank Mike O'Neil for his statistical and SPSS consultation on part of my project and, Tim Hermin at Toledo Zoo for his technical advice on the lighting of my turtle enclosure. The Chicago Herpetological Society, the Department of Psychology, and Science Alliance at the University of Tennessee Knoxville funded parts of this research. Individuals listed above are individually acknowledged later in this dissertation in specific sections of my project.

Now, I would like to thank my many friends and mentors over the years who have helped me pursue my academic career from its foundations through to the present. It is therefore only fair to start with my family. My parents' Mark and Arlene Davis, and my brother Adam's love and support have made this journey possible. My parents' constant encouragement throughout my educational endeavors has been essential to my value of education and choice to pursue higher education.

During my undergraduate years at Purdue University, Dr. Erich Klinghammer, Wolf Park, and the four legged experts introduced me to ethology, and inspired me to pursue a PhD in animal behavior. During my years as a zookeeper at the Utica Zoo, my friends Beth, Mike, and Lloyd were great colleagues and friends with whom I had many adventures. Vitaly, the Siberian lynx we raised, Arctic, Lenny the sealion, and the many other animals we worked with and trained, taught me a lot about applying animal behavior to training and managing captive exotic animals.

I wish to thank the Huber lab my "B.G. family"; Robert, Moira, Sebastian, Jules, Adam, Katie, Angie, Karlo, and Anne for all the fun times, encouragement, and support, which has enriched my life. They came out with me at four in the morning to help me look for Indie when she escaped just prior to my M.S. defense, I am forever grateful for their love and support especially when my Indie was missing. Dr. Robert Huber’s mentorship throughout the years has been essential to my growth as a scientist and human.

My long time friend Marty Huth, all the volunteers at Wolf Timbers, and Nira, Keeley and Ingo have helped me recharge my batteries with much needed wolf time on my trips up North. Also all my friends throughout the years, especially Amy Sanderson, Betsy Mallory Simpson and Beth Ricci have continued to encourage and support me despite my being far from New York State and in school “forever.”

Sophia, Mandy, Melissa B., the people at Gypsy Hands, and all the people I have met at TVUUC over the last year have truly helped me survive a challenging year. I could not have finished this dissertation without all your love and support. Ellen Mahurin and family, and Clever Critters have helped me have fun with dogs and given me the opportunity to teach human-canine communication. I thank Christine at Happy Yap Doggie Day Camp for taking good care of my Indie and Lily so I could do my work without worrying.

Indie and Lily my canine companions have been a constant source of comfort and joy over the years. I must also mention “Smokey the Cat” my independent little friend. Last but certainly not least, all the non-human animal species I have raised, observed and worked with over the years have taught me things you can’t learn in a book, but instead need to learn from the “experts” themselves. In particular, I would like to acknowledge the Emydidae turtles I observed at the Chattanooga Aquarium and the nine Florida Red-bellied Cooters (*Pseudemys nelsoni)* I worked with in the lab over the last six years.

ABSTRACT

Turtles are little studied with respect to learning, cognition and social behavior in spite of being phylogenetically a central group. Populations of many species of these long-lived animals are declining due to commercial activities (pet trade and food), pollution, and habitat destruction. This integrative study of freshwater turtle (Emydidae) behavior investigated their sociality, individual learning and memory capabilities, and the ability of turtles to learn from others.

First, I studied turtle underwater social behavior which involved naturalistic observations and ethogram development of the underwater social behavior of (Family Emydidae) at the Chattanooga Aquarium. Turtle social behavioral repertoire and interaction sequencing while underwater were much more complex and varied than those recorded for turtle basking interactions. Turtles also formed stable dominance hierarchies.

Second, I trained and tested 9 Florida Red-bellied Cooters (*Pseudemys nelsoni*) in a discrimination choice task that I developed. Turtles were first trained to an instrumental response task (dislodging clear plastic bottles to obtain food pellets). These turtles not only showed rapid learning, but required minimal to no retraining after a period of 2 years. This study marks the first time that turtles have been shown to exhibit extensive long-term memory measured in years in a controlled experimental task. Olfactory and other controls were run to confirm that the turtles were responding only to visual cues.

Finally, I investigated whether turtles could learn about a visual object cue to obtain food reinforcement by observing other experienced turtles that had learned the task. All five *P. nelsoni* turtles tested showed evidence of social facilitation and stimulus enhancement learning i.e. they

learned not only to follow another turtle to a stimulus indicating food but also to approach the correct bottle that contained food reinforcement. This is the first experimental study of social learning in turtles.

This integrative study of social behavior, learning, and cognition of turtles will hopefully spark interest in turtle behavior and cognition, help advance the field of comparative animal cognition, and aid in the development of their management in the wild.

TABLE OF CONTENTS

LIST OF TABLES

Table **Page**

LIST OF FIGURES

Figure **Page**

PART 1: INTRODUCTION

Background and Goals

The study of behavioral plasticity and cognitive processes in diverse animals has been revitalized by the recent methods and concepts of comparative cognition (e.g., Shettleworth, 1998). Learning psychologists traditionally focus on general process learning approaches such as operant conditioning and classical conditioning in laboratory contexts, focusing on a few model species, and artificial problems (Burghardt, 1973, 1977; for review of learning approaches see Malone, 2002). Beginning in the 1960s, cognitive psychology studies arose which focused more on decision making and 'higher' level information processing with an emphasis on topics such as implicit and explicit memory, categorization, recollection, and representation. More recently, a melding of the two views has resulted in the growing field of comparative animal cognition (Balda, Pepperberg & Kamil, 1998; Shettleworth, 1998; Beckoff, Allen & Burghardt, 2002; Pearce, 2008). Here species differences and similarities are explicitly studied using more complex tasks that are often used in more ecologically relevant and species typical contexts. I will use here the more recent cognitive language, realizing that many of the phenomena described can be interpreted from different conceptual viewpoints. In this study I will use Shettleworth's definition of animal cognition as "the mechanisms by which animals acquire, process, store, and act on information from the environment…These include perception, learning, memory, and decision making" (p. 5, Shettleworth, 1998).

Turtles are either the most basal of living reptiles, the sister taxon to the highly social birds and crocodilians (Zardoya & Meyer, 2004), or a highly derived group most closely related to snakes, lizards, and tuatara (see reviews Rieppel, 2008; Ernst & Lovich, 2009). Turtle phylogeny is still controversial as they are traditionally considered the most basal of living reptiles, and the only living anapsids. More recent molecular evidence indicates they may be diapsids which includes birds, crocodilians, snakes, lizards and tuatara (Iwabe et al., 2004; Zardoya & Meyer, 2001, 2004). Recently a new turtle fossil *Odontochelys semitestacea,* was discovered in China which has been placed phylogenetically basal to all other known turtles both fossils and extant (Li et al., 2008). The inclusion of *Odontochelys* in the analysis of turtle phylogeny represents the first paleontological evidence supporting the placement of turtles within diapsid reptiles (Li et al., 2008). This important paleontological find leaves some controversy as to where turtles fit within diapsids, i.e. are they more closely related to crocodilians and birds or snakes, lizards and tuatara (Reisz & Head, 2008). Despite these recent findings, the topic of turtle phylogenic relationships is still under dispute (for recent reviews see Rieppel, 2008; Ernst & Lovich, 2009).

Regardless, turtles are an important group for studying the evolution of social behavior and cognitive abilities in vertebrates. Comparative studies of turtle social behavior with that of birds, crocodilians, snakes, lizards and tuatara may help determine the evolution of sociality in reptiles as well as provide more data which may help solve the controversy of turtle evolution. For example, if turtles exhibit social behavioral repertoires more similar to that of birds and crocodilians verses that of snakes, lizards and tuatara this could lend support for turtles being more closely related to crocodilians and birds. However, given the problem of separating out convergent and divergent evolution, comparative studies of reptiles focusing on cognitive abilities along with comparative studies of social behaviors will provide more data to help sort out phylogenetic relationships of turtles to other reptile groups.

Social behavior of turtles has been little studied. Although post-hatching parental care, ubiquitous in birds and crocodilians, is lacking in turtles, they do interact during feeding (Boice, 1970; Froese & Burghardt, 1974), courtship (Weaver, 1970; Jackson & Davis, 1972a; Kramer, 1989a), and basking (Bury & Wolfheim, 1973; Bury, Wolfheim, & Luckenbach, 1979; Lovich, 1988; Lindeman, 1999). Nevertheless, detailed studies of social dynamics (such as social behavioral repertoire, categories of behaviors, and dominance hierarchy) from a comparative perspective, especially of aquatic turtles, are rare. Land tortoises have been studied more than aquatic turtles with respect to social behavior. Auffenberg's classic studies (1965, 1966, and 1969) showed that tortoises exhibit a variety of interactive behaviors during courtship. Land tortoise social behavior, including agonistic interactions and courtship interaction has been quantified, including detailed ethograms (Weaver, 1970; Boice, Quanty, & Williams, 1974; Niblick, Rostal, & Classen, 1994; Ruby & Niblick, 1994) and they have even been recorded to form dominance hierarchies (rev. Harless, 1979). Moreover, box turtles have been shown to selectively associate and demonstrate individual discrimination ability (M. Davis, 1981).

Due to difficulties in viewing aquatic turtles, most studies of social behavior focus on basking behavior and competition for preferred basking sites (Bury & Wolfheim, 1973; Bury et al., 1979; Lovich, 1988; Lindeman, 1999). Descriptions of underwater behavior are mainly limited to brief observational descriptions of courtship displays (Taylor, 1933; Lagler, 1941; Wood, 1953; Cagle, 1955; Legler, 1955; Jackson, 1969; Ernst, 1967, 1974) with a few more recent quantitative studies of courtship (Jackson & Davis, 1972a, b; Kramer, 1989a, 1989b). However, Kaufman (1992) found that Wood Turtles (*Clemmys insculpta*) in the field exhibit most of their social behaviors under water and were observed to exhibit courtship, agonistic, and neutral social behaviors along with forming dominance hierarchies.

In addition, Kramer (1986, 1989b) performed a long-term field study of adult *Pseudemys nelsoni* and *P. concinna*, supplemented with laboratory studies, of the social behavior of juvenile *P. nelsoni,* with detailed behavioral descriptions of courtship, agonistic, social and non-social behaviors. He found that, although basking was social, it differed from aquatic social behavior. Furthermore, in the field adult *P. nelsoni* and *P. concinna* engaged in male-male agonistic behavior, male-female courtship and agonism, but aggression was not observed during female-female interactions (1986). Kramer also found turtles in mixed female-male groups or all male groups, independent of the distribution of nesting sites i.e. non-random distribution of wild turtles.

Captive studies on a variety of land turtles, Kramer's field studies and my own results from naturalistic observations at the Chattanooga Aquarium (see Part 2) all provide evidence that turtles interact socially and spend time in close proximity to others of their own species. Moreover, aquatic turtles, which live in an energy efficient media for locomotion, engage in object play (Burghardt, Ward, & Rosscoe, 1996) and even social play in the form of precocial courtship (Kramer & Burghardt, 1998; for review of turtle play see Burghardt, 2005). Social facilitation appears to be involved in the emergence of hatchling Green Sea Turtles (*Chelonia mydas*) and aids in their survival (Carr & Hirth, 1961). Furthermore, gregarious behavior of nesting Pig Nose Turtles (*Carettochelys insculpta*) may allow females to assess potential nesting sites through their interactions with others, thereby reducing the costs of nesting (Doody, Sims,

& Georges, 2003). Given all the evidence for sociality in turtles, they are good candidates for the study of social learning.

Among non-avian reptiles, turtles are tempting subjects for instrumental conditioning and discrimination tasks for several reasons. For example, turtles will train for small food rewards more readily than many other exothermic reptiles (Burghardt, 1977; Kramer 1989a). Secondly, turtles, particularly many emydid turtles, are readily available, adapt and perform well under captivity, and are long–lived (Burghardt, 1977). Finally, turtles are highly visual, and can discriminate shapes and colors in stationary stimuli (e.g., reviewed in Burghardt, 1977; Arnold & Neumeyer, 1987), which makes them a favored group among reptiles for visual discrimination learning tasks.

Non-avian reptile learning has been studied less than that of mammals, birds, and even fish (Shettleworth, 1998; Bshary, Wickler & Fricke, 2002; Laland, Brown, & Krause, 2003). Within the reptile learning literature, turtles have been the subject of more laboratory learning studies than any other major group (lizard, snakes, or crocodilians); most of these studies were conducted 30 or more years ago (review in Burghardt, 1977), with only several published more recently. Studies by experimental psychologists during the 1960's and 1970's focused on visual discrimination abilities of turtles and documented that they have sophisticated visual abilities and can be trained in a number of respondent and instrumental learning tasks including visual and spatial reversal learning (Kirk & Bitterman, 1963; Bitterman, 1964; reviews in Burghardt, 1977; Morlock, 1989). Recent studies by Lopez et al. (2000, 2001) found that turtles have spatial learning and memory capabilities that similar to those of mammals and birds.

Turtles are long-lived reptiles, with many having the ability to live at least 70 years and probably longer. Furthermore, although sea turtles are known for nest site homing, freshwater turtles also show nest site fidelity (Freedberg, Ewert, Ridenhour, Neiman, & Nelson, 2005; Rowe, Coval, & Dugan, 2005). For example, a long-term study of 7 European Pond Turtles, *Emys orbicularis*, showed some marked females exhibited nesting area fidelity for over 10 years and most exhibited nest site fidelity for 2-4 consecutive years (Mitrus, 2006). Turtles returning to nest sites across years, coupled with turtle longevity indicate the adaptive significance of turtle long-term memory. Long-term memory measured in weeks, months and years has rarely been studied in non-human animals (see Part 4 introduction for detailed review).

Cognitive studies of social learning, have been studied mainly in primates, birds and rats (reviewed in Zentall & Galef, 1988; Heyes & Galef, 1996; Pearce, 2008), and even studied in fish (reviewed in Brown & Laland, 2003), but have not been explored in turtles. Social learning can be defined as learning that involves socially provided information. Specifically it "refers to any incidence in which individuals acquire new behaviour or information about their environment via observation of, or interaction with, other animals or their products" (Brown & Laland, 2003, p. 281). Social learning, or learning from others may occur by a variety of processes ranging from simple non-imitative processes such as 'contagion' to more complex forms of learning such as 'true imitation' (Zentall, 1996; Brown & Laland, 2003).

Turtles belong to the order Testudines which is divided into two suborders, the hidden neck turtles (Cryptodira*)* and side neck turtles (Pleurodira) which compose 14 living families of turtles (Halliday & Adler, 2002; Ernst & Lovich, 2009). Pleurodirans are found only in the southern hemisphere in Australia, Africa, Madagascar and South America. The Cryptodira turtles occur on all continents and inhabit seas, freshwaters and land (Ernst & Lovich, 2009). North America and its surrounding seas contain turtles from seven Cryptodiran families. Emydidae which includes freshwater pond and marsh turtles is the most abundant family in North America (Ernst & Lovich, 2009). Eleven genera and 32 species of this family are found in North America, with the most diversity of species (31) in eastern North America and only 2 species occurring in western North America (Ernst & Lovich, 2009).

The main study species, *Pseudemys nelsoni*, (Florida Red-bellied Cooters), is a semi-aquatic pond turtle that is active year round and found throughout Florida and a small area in southeastern Georgia (Ernst & Lovich, 2009). *P. nelsoni* is only active during daylight and leaves the water daily to bask with terrestrial movements limited to nesting females, or occasional movements between ponds (Kramer, 1986; Ernst & Lovich, 2009). Agonistic behavior, courtship, and other kinds of behavior have been studied in this species in the field and in captivity (Kramer, 1986; Kramer, 1989 a, b; Kramer & Burghardt, 1998). This dissertation study aims therefore to: 1) Investigate the extent of turtle social behavioral and individual association, 2) investigate turtles' individual visual learning and memory abilities and 3) examine a turtle's abilities to learn from others.

Overview of Parts

Part 2 is primarily a descriptive account of the underwater social ethology of a mixed species group of emydid turtles in a naturalistic enclosure at the Tennessee Aquarium, in Chattanooga. This part includes an ethogram of the social behavioral sequences of the turtles and reports aspects of inter and intra specific social behavior. Part 3 investigates the ability of freshwater turtles, *Pseudemys nelsoni*, Florida Red-bellied Cooters, to learn a task to find food. This part describes the training of turtles to the tasks and reports their overall average success at the task and preliminary data on long-term memory. Part 4 is an extension of the experiment in part 3 in which the retention and savings of turtles for the discrimination task was measured for up to two years and individual data and olfactory controls are reported. The experiment reported in part 5 was inspired by observations made during the study of social behavior in part 2. Part 5 evaluated the social learning ability of the turtles used in parts 3 & 4 for a novel visual task to find food. Part 6 is an overall conclusion section for the entire dissertation.

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PART 2: SOCIALTIY OF EMYDID TURTLES IN A NATURALISTIC SETTING

Abstract

Turtle social behavior is little studied in spite of the controversy of their phylogenetic position. Although parental care, ubiquitous in birds and crocodilians, is lacking in turtles, they do interact during feeding, courtship, and basking. Nevertheless, detailed comparative studies of social dynamics (such as social behavioral repertoire, categories of behavior, and dominance hierarchies), especially of aquatic turtles, are rare. Social interactions of an established mixed species group of closely related freshwater turtles (Emydidae) were studied in a naturalistic enclosure. Video sequences of underwater turtle interactions were analyzed. Turtles were found to interact and spend time in close proximity, with individuals of their own or most closely related species. Social behaviors were documented and grouped into three categories: agonistic, courtship, and general social. Behavioral repertoire and frequency of social interactions varied seasonally. Social interactions were seen in all sexual pairings and frequency of social behavior category differed significantly with sexual pairing. Intense agonistic interactions were more prevalent with male-male pairs, courtship interactions were more common with female-male pairs, and generalized social interactions were seen in female-female pairs. Some agonistic interactions included intense harassment of a smaller, newly introduced male by coalitions of two or more larger males. Additionally, both male-male and female-female pairs exhibited social interactions that included behaviors normally categorized as courtship, such as titillation, in contexts that clearly did not involve courtship. These findings indicate that turtles are active social animals that interact preferentially with conspecifics. More studies into the social complexity of turtles of many species are needed and may be essential for their conservation.

Introduction

Turtles are an interesting group to study with respect to social behavior. Most studies that focus on mammalian social behavior note the importance of parental care in the initiation and learning of effective social behavior. Turtles are a group of reptiles in which no species is known to exhibit any post-hatching parental care (Zug, Vitt, & Caldwell, 2001; Wyneken, Godfrey & Bels, 2008; Ernst & Lovich, 2009). Nonetheless, they exhibit a variety of social behaviors (see part 1 for details). Turtles can not learn these behaviors from parents and so they must rely on innate mechanisms and maturation, individual learning, practice, play or interactions with peers. Since not much is yet known about the behavior of hatchling and young turtles it remains to be determined if they are learning how to effectively interact through interactions with other hatchlings - maybe through play (Kramer & Burghardt, 1998; for review of turtle play see Burghardt, 2005).

Turtle social behavioral studies, especially of aquatic turtles, are rare. Land tortoises and box turtles have been studied most, and a number of their social behaviors have been described and quantified (see Harless, 1979; Miller & Dinkelacker, 2008). Turtle social behavior studies, mainly on tortoises, have demonstrated that turtles exhibit social behavior (interact with their own species) in a large variety of contexts. Turtles' known social behavior includes: food competition (Boice, 1970; Froese & Burghardt, 1974), basking site competition (Bury, Wolfheim, & Luckenbach, 1979; Lindeman, 1999), courtship (Auffenberg, 1966, 1969; Weaver 1970; Niblick, Rostal, & Classen, 1994; Miller & Dinkelacker, 2008), a variety of agonistic interactions (Weaver, 1970; Ruby & Niblick, 1994), dominance hierarchy formation (Harless, 1979; Kaufman, 1992), play (Burghardt, 2005) and nesting aggregation (Doody, Sims, & Georges, 2003).

Due to difficulties in viewing aquatic turtles most studies of social behavior focus on basking behavior and competition for preferred basking sites (Lovich, 1988; Lindeman, 1999). These studies of basking competition suggested that turtles exhibit a very limited repertoire of agonistic interactions, such as snaps, bites and pushing, with the largest turtles outcompeting smaller turtles for basking sites. Descriptions of underwater behavior are mainly limited to courtship displays (Jackson & Davis, 1972; Kramer, 1989a, 1989b). The underwater courtship behaviors quantified by Jackson and Davis included a set of behaviors very different and more varied than basking site competition behaviors. Furthermore, Kramer's (1986, 1989b) study of *Pseudemys nelsoni* found that turtles performed courtship, agonistic and other social behaviors underwater and that these behaviors differed in complexity of sequencing and behavioral repertoire from basking behaviors. He also found turtles in the field distributed non-randomly in mixed female-male groups. Kramer's underwater turtle behavior observations indicate that aquatic turtles may have a more varied and complex social behavioral repertoire then formerly thought based on limiting turtle behavioral observations to basking interactions and courtship displays.

Variation of turtle social behavior within and across species may affect turtle survival in ways we don't yet understand. Therefore, understanding turtle social behavior and its diversity may be important for conservation efforts. Furthermore, to put turtle learning and cognition into the context of turtle social behavior will help researchers test turtles in a more ecologically relevant context as well as study aspects of turtles' learning that are relevant to turtles. Moreover, having knowledge of turtle social behavior and how it varies with respect to differing species, researchers will have more information with which to interpret a finding of differences in learning between turtle species.

The specific goals to this report were 1) to determine if turtles had a spatial affiliation preference for species or individuals and 2) to describe turtles' social behaviors underwater and the context in which they occur, focusing on agonistic, courtship and social relationships. The first part of goal 2 was to create a social behavioral ethogram with which specific underwater social behavioral hypotheses were tested (see hypotheses below).

Hypotheses

1. Turtles will prefer to associate with turtles of their own species (conspecifics) i.e. non-random spatial affiliation by species. *Null*: Turtle will show no preference for their own conspecifics (random spatial affiliation across species).
2. Turtle behavioral repertoire and category of interaction will vary with respect to sex pairing. *Null*: No variation in behavioral repertoire or category of interaction with respect to sex pairing.
3. Turtle behavioral repertoire and category of interaction will vary with respect to season. *Null*: No variation in behavioral repertoire with respect to season.
4. Aquatic turtles form dominance hierarchies. *Null:* Aquatic turtles do not form dominance hierarchies.

Method

Study Site

Social interactions of the study subjects were observed in a large mixed species naturalistic exhibit in the delta lake section of the Tennessee Aquarium in Chattanooga, Tennessee (Figure 2.1[1]). This exhibit included land and water areas with artificial trees with live vegetation, natural trees, and green vegetation close to the water level. It had a high clear greenhouse type ceiling which allowed natural sunlight in and allowed for air temperatures to match the outside environment. The water section of the exhibit (92,740 liters) included variation in depth and width, a pebble substrate, and a large glass viewing area accessible from the public walkway and ideal for filming underwater turtle behavior (Figure 2.1A). This exhibit included multiple basking areas for turtles made from drift wood which were arranged along the banks (Figure 2.1B) as well as a hollowed out underwater tree for shelter. The largest basking area included multiple logs crossing a section of the tank at differing angles with heat lights above them (covered by a piece of bark so they were not visible to the public). This enclosure contained songbirds, ducks, large carp fish, and a mixture of south eastern North American pond turtle species from the family Emydidae.

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[1] All tables and figures are in the appendix at the end of part 2.

The clear ceiling allowed natural sunlight to enter the exhibit which exposed the animals to natural photoperiod and air temperatures. The water temperature was cooled and heated seasonally by aquarium staff to match the natural environmental temperature annual fluctuations. The water temperatures were cooled down in the fall starting with a temperature drop to 26.7°C in September and ending at 18.9°C by December. During the spring, starting on the 1st of March, the water was heated to 20°C and was heated up to 27.8°C by July. The exhibit included mud filled areas along the shore under the water line and soil along the land areas in which turtles could hibernate over the winter. The turtles were studied initially in the fall of 2004 (September 22, 2004 – December 17, 2004) and the spring of 2005 (February 27, 2005 –June 24, 2005). Then two years later turtles in the same exhibit were observed from April 2007 through to November 2007.

Subjects

The animals observed during this study included 11 closely related species of freshwater turtles (Emydidae) (Table 2.1). Table 2.1 lists the total number of males and or females for each species found throughout the entire study period which spanned a 3 year period in the life of the turtles. During this three year period some turtles died and some turtles were added allowing for the species groups to change between the 2004-2005 study period and the 2007 study period.

Recording Methods

Underwater and basking behaviors of turtles were observed and filmed in the fall of 2004 (September to December) and again in the spring of 2005 (February to the end of June). Then Two years later turtles were observed and filmed during the spring, summer and fall of 2007 (April to December). Throughout the study periods the researcher (KD) collected data usually one to two times a week when possible. Turtles were studied between 0800 and 1600 hours with the majority of filming and observation occurring between 0900 and 1300 hours. All video was filmed with a Sony Hi8 digital camcorder (model DCR-TRV3120).

Throughout the study periods KD took notes by hand in a notebook, during breaks, to go along with the video collected on a certain day. While filming turtles' behaviors underwater KD moved the camera along the viewing area and zoomed in an out depending on how far back turtles were from the glass in order to catch as much of an interaction as possible. Furthermore, KD left the camera away from her face, using the video panel to be sure the turtles were in the camera view field, which allowed her to scan the rest of the exhibit and vocally noted into the camera any additional important contextual cues or interactions not visible in the view area. She also placed the camera on a monopod when possible to get better video while still being able to move the camera up and down or left to right quickly. Turtles were observed and filmed through the large glass underwater viewing area accessible from the public walkway (Figure 2.1). These multiple recording methods resulted in more complete data collection with a richer context. Additionally, on each study day starting in spring of 2005, the following information was recorded in the notebook: date, tape number, time of filming, air temperature, water temperature, weather conditions, and any other important notes. This page was then filmed onto the tape as an additional code. All tapes were then copied to DVDs, catalogued, and subsequently used for quantifying spatial and behavioral data.

The study turtles were all individually identified by differences in their species, sex characteristics, carapace coloration, and shape. Pictures were taken of individual turtles for identification purposes. Undergraduates helped copy and catalogue the 110 hours of video tapes to DVDs in summer 2007 to spring 2009, during which time they practiced identifying turtle species, individuals and interaction types. They were tested on their ability to identify turtle species, individual turtles and the type of interaction they were observing. Additionally, all interactions could be repeatedly played, paused, and advanced frame by frame since they were copied onto DVD. This data collection technique combined with live observations, field notes, and vocal commentary recorded onto the video, allowed the researcher to catch rare behaviors, analyze behavioral sequences in detail, and assure for more reliable observations across observers. Furthermore, in addition to describing behaviors, still pictures of behaviors were made by freezing the film and using I-movie HD software.

Data Analysis

Association data

A sample of 12 hrs of tape (6 fall, 6 spring), which comprised a span of 20 hrs of real time (10 fall, 10 spring), was analyzed for the hours of 0900 – 1300. Proximity data samples were taken every 10 minutes of tape across all 12 hours of tape. At each sample a freeze frame of the video was used to collect data on how close each animal was to every other animal within view on screen. Species affiliations were described by total counts of each species' associations (within 60 cm) within and across species (Figure 2.2). The large number of study subjects resulted in low sample sizes for individual turtle's associations with other individuals within and across species; thus, formal statistical tests were not applicable. Therefore, individual association counts were organized into tables of association within and across species (Table 2.2).

Behavioral data

Every turtle interaction and the behaviors performed by each turtle during these interactions were collected. An ethogram of observed behaviors was constructed (Table 2.3). The behavior patterns performed were categorized into three categories; agonistic (Table 2.4A), courtship, (Table 2.4B) and other social (Table 2.4C).

The underwater social behaviors exhibited by turtles during the two observation years (2004-2005 and 2007) are listed and defined in Table 2.3. The terms used in Table 2.3 were the same as those already used in the literature, when applicable, for consistency and ease of comparing behaviors observed with those noted in other studies. Most terms were adapted from Kramer's (1989) dissertation on the ethology of *Pseudemys nelsoni*. The three categories of behavior describe the context under which certain behaviors were observed by males and female turtles. Some behaviors are found in multiple categories since turtles used them in multiple contexts. Often the turtles exhibited more than one of the behaviors in varying sequences during an agonistic encounter or courtship interaction. The term "other social" is used for behaviors that are social but are not obviously associated with aggression or courtship and may include behaviors in contexts in which the function of the behavior is uncertain, such as during new turtle introductions to the enclosure.

Table 2.4 (A, B, C) provides qualitative occurrence data indicating those behaviors observed in each category for each species for observations from year 1 (2004-2005) and year 2 (year 2007). Table 2.5 (A, B, C) reports all occurrences of each behavior within agonistic, courtship or other social categories for a subset of species (Florida Red-bellied Cooters (*P. nelsoni)*, River Cooters,(*P. concinna)*, and Yellow-bellied / Red-eared Slider,(*Trachemys scripta)* groups) collected from the main data set of 12 hours of tape from year 1 (2004-2005).

Dominance Hierarchies - Male dominance hierarchies were determined for *P. nelson*i, *P. concinna*, and *Trachemys scripta* turtles by the number of agonistic encounters won and lost between each individual within each group and dominance matrices were constructed (Table 2.6 A, B, C). Not all individual turtles within a group engaged in agonistic interactions due to long established hierarchies in which the status of some individuals was not challenged. Rank could still be determined by observing the postures of these individuals when they were in close proximity even if no fighting occurred, and taking their interactions with other turtles in the group into account. Established status for turtles with rank differences was easy to determine. Dominant (higher ranking) turtles exhibited extended tails and approached lower ranking turtles with head and neck extended, whereas lower ranking turtles consistently tucked their tails and retracted head and limbs in the presence of a higher ranking individual even when no agonism occurred. Alternatively they simply avoided a higher ranking individual. These dominant /submissive posture displays are comparable to the dominant/submissive postures seen in social mammal interactions for groups with established hierarchies (for classic wolf dominant/ submissive postures see Zimen, 1981/1978).

Offensive Behavior - The total number of male agonistic interactions for each of the three species were collected from 16 hours of video tape from 2004-2005. Comparison of offensive agonistic behavioral repertoires and intensity of aggression for each species was done by creating levels of aggressive/offensive intensity (0-5). These levels were coded based on the inclusions of patterns of agonistic behaviors of the aggressor (Figure 2.6). Each of the aggression levels (0-5) represent combinations of agonistic behaviors defined in Table 2.3. Level 0 = approach, level 1 = approach and stare, level 2 = inclusion of gapes and/or snaps, level 3 = inclusion of bites and/or chases. Level 4 = both turtles engage in a face-off, that includes some or all of the behaviors in levels 0-3. Level 5 = one turtle grips, drags, or yanks another turtle by its limbs, incorporating some or all of level 0-4 behaviors. Additionally, intense face offs can reach level 5 with or without grips and yanks.

Defensive Behavior - Comparison of defensive agonistic behavioral repertoires and intensity of defensive behaviors for each species was similarly accomplished by creating levels of defensive intensity (0-$^{-}5$). These levels were coded based on the inclusions of patterns of agonistic behaviors reached by the lower ranking turtles that lost fights (Figure 2.7). Negative levels (0-$^{-}5$) were created by coding defensive behavior combinations into increasingly more defensive/submissive behaviors with negative numbers. Level $^{-}1$ = loser looks away from winner, Level $^{-}2$ = turtle moves away, Level $^{-}3$ = turtle retracts head & limbs prior to moving away, level $^{-}4$ = loser retreats from winner, and level $^{-}5$ = loser flees from winner (see Table 2.3 for definitions of submissive behaviors).

Statistical Analysis

Although this is primarily a comparative descriptive study, proximity data and behavioral variation with species, sex, and season were analyzed using Pearson's Chi-Square tests. The variation between species (*Pseudemys nelsoni* (FRBs), *P. concinna* (RCs), *Trachemys scripta* (YBSs)) in frequency of M-M agonistic interactions was analyzed using Pearson's Chi-Square test. Winner aggression levels and Loser defensive levels reached for M-M agonistic encounters between species (*P. nelsoni* (FRBs), *P. concinna* (RCs), *T. scripta* (YBSs)) were analyzed using One-way Analysis of Variance tests to determine if the means differed. To determine which species' pairs were contributing the significant results for winner aggression and loser defensive levels, Tukey post-hoc multiple comparison tests were run with Holm's procedure for alpha adjustments (Aickin & Gensler, 1996). All Statistics and graphs were produced using SPSS 17.0.

Results

Ethogram

A variety of underwater interactive behaviors were observed for the mixed species group of turtles. An ethogram of turtle social behavior was created from these observed behaviors (Table 2.3) and used for further qualitative and quantitative analysis described in the sections below. Behaviors listed in bold have never been described before for underwater turtles. Many of the behaviors observed and described in this ethogram of adult emydid turtles (Table 2.3) match that of Kramer's observations of social behaviors in juvenile *P. nelsoni* turtles (1989). Specific results will be described later in this section.

Proximity

Turtles were found to interact significantly more frequently with individuals of their own species or the most closely related species (Pearson's Chi-Square test, $\chi^2_{36,\,180} = 347.71$, $P <$ 0.0001, Figure 2.2). The only times turtles interacted across species were if that turtle species lacked the presence of others of the same species or subspecies, during basking interactions, or during feeding interactions. During feeding interactions the large turtles would often obtain the food by snapping at or pushing any other turtle regardless of species (kleptoparasitism); similar types of interactions were seen during basking competitions. However, although turtles would take food away from others regardless of species, within species the dominant turtles (see agonistic behavior section below for more details on turtle rank orders and Table 2.6 A,B,C) would sometimes prevent lower ranking individuals of their species from even coming near the food source, something they would not direct toward turtles of any of the other species. The *Trachemys scripta* (YBS) and the *Pseudemys concinna* (RC) male groups were the two where the highest ranking male exhibited agonistic behaviors and attempted to chase off the lower ranking male.

Additionally, throughout many hours of observations within and across species certain individuals were repeatedly associating and or interacting with specific individuals (Table 2.2). For example the two large female map turtles (*Graptemys barbouri*) were found together consistently and interacted often, but mainly ignored the small *G. barbouri* and other species of maps when they tried to interact (Table 2.2G). The River Cooter (*P. concinna*) males RC1 and RC2 were often interacting with titillation displays, but rarely interacted with RC3 except to snap at him when he approached them (Table 2.2H). Also, the large Florida Red-bellied Cooter (*P. nelsoni*) male (FRB3), who was ignored by the other two male FRBs, often interacted with RC3. More details on the nature of these interaction types will be discussed in the section on other social behaviors.

Basking Behavior

Basking interactions were rarely seen in this study since plenty of basking areas were available. Out of 23 basking sessions recorded in 2004-2005 only 9 interactions were observed of which only 3 involved turtle-turtle competition. The remaining 5 interactions occurred between a male duck, who was in a favored log position under the heat lamps in November, and a RC (*P. concinna)*, RES (*Trachemys s. elegans*), YBS (*Trachemys s. scripta)*, and a SP

(*Chrysemys dorsalis*). The interactions all occurred while competing for the limited basking space under the heat lamps, which was only an important limitation during colder months. Behaviors exhibited included a turtle pushing with it head or body on either a duck or other turtle, a larger turtle climbing over a smaller turtle, or face on face gapes, snaps or head withdrawals during turtle-turtle or turtle-duck competition. Other behaviors included sliding, falling or diving into the water by the losing turtle.

In turtle-turtle competitions, the larger turtle always won the spot with a smaller turtle jumping into the water or being pushed into the water. Smaller turtles were often seen in basking areas further way from the heat lamps at a distance from the larger turtles. Since paints were the smallest species, they often were seen in different basking sites than the larger turtle species. Turtles not only exhibited competition for basking spots with any other turtle regardless of species, 5 turtles directed these behaviors toward a duck. Interestingly, the duck pecked back at the turtles and so they went back and forth snapping and pecking, with the turtle lunging and snapping then retracting its head when the duck pecked at it. This went on for a few minutes before one animal gave in and left the log, which usually ended up being the duck.

In addition to the non-species specific direction of agonistic interactions during basking interactions, unlike that of underwater turtle interactions, basking interactions were rare, and very limited in behavioral repertoire. The basking behavioral repertoire differed from the turtle's underwater behavioral repertoire (Table 2.3, 2.4, 2.5). The purpose for turtle behavior here appeared to be very different from underwater interactions. For example, sometimes pairs of turtles of the same species would be observed basking together away from the heat lamps (especially in the summer) and during these times, presumably, basking areas were not a limited resource. A few times during the summer of 2007, YBS1 and YBS3 were observed basking together off by themselves and exhibiting no agonistic behaviors, which was odd given that these two turtles continually exhibited intense agonistic interactions underwater (see below). For example, a few times these same turtles were observed diving back into the water, at which time the higher ranking male immediately began chasing the lower ranking male.

Agonistic Behaviors

Agonistic social interactions included, but were not limited to, gapes, snaps, bites, chases, and retreats (Table 2.3, 2.4, 2.5) with most aggression directed at conspecific individuals. Social interactions were seen in all sexual pairings. Behavior types, which were analyzed in *P. nelsoni*, significantly differed with sex category (Pearson's Chi-Square test, $\chi^2_{2, 227} = 346.57$, $P < 0.0001$, Figure 2.3). Thus, intense aggressive interactions were significantly more prevalent with male-male pairs and courtship interactions were more common with female-male pairs (Table 2.4 A, B, 2.5 A, B; Figure 2.3). The behavioral repertoire used and frequency of social interactions varied seasonally in *P. nelsoni* (Pearson's Chi-Square test, $\chi^2_{2, 227} = 38.27$, $P < 0.0001$, Figure 2.4).

P. nelsoni, P. concinna, and *Trachemys scripta* males significantly differed in number of total agonistic encounters over 16 hours of tape with *P. nelsoni* males fighting the least and *T. scripta* males fighting the most (Pearson's Chi-Square test, $\chi^2_{4, 54} = 108.0$, $P < 0.0001$, Figure 2.5). The highest offensive aggressive level reached by winners of fights for each of these three species significantly differed (One-Way ANOVA, F = 15.31 (2, 51), $P < 0.0001$, Figure 2.6).

Tukey post-hoc multiple comparison tests with Holm's procedure for alpha adjustments (Aickin & Gensler, 1996) showed the average aggression level of *P. nelsoni* fights was higher than that of both *P. concinna* ($t = 2.8$, $P < 0.0001$) and *T. scripta* fights ($t = 1.50$, $P < 0.003$) and *T. scripta* fight aggression levels were higher than *P. concinna* ($t = 1.31$, $P < 0.004$). The highest defensive level reached by losers of fights also significantly differed across species (One-Way ANOVA, $F = 11.81$ (2, 52), $P < 0.0001$, Figure 2.7). Tukey post-hoc multiple comparison tests with Holm's procedure for alpha adjustments (Aickin & Gensler, 1996) showed the average defensive level of *T. scripta* fights was higher than both *P. nelsoni* ($t = 2.04$, $P < 0.001$) and *P. concinna* ($t = 1.62$, $P < 0.003$) fights. The defensive level of *P. nelsoni* and *P. concinna* did not differ ($t = 0.42$, $P < 0.790$). Furthermore, the behavioral repertoire and type of offensive behaviors differed for each of the species (Figure 2.6) whereas variation in defensive behavioral repertoire did not vary as much across species (Figure 2.7). *P. nelsoni* fights consisted almost entirely of long lasting face-off contests. *P. concinna* offensive agonistic behaviors were very brief and consisted mainly of gapes, snaps, bites and chases and face offs were never observed.

Social Rank Order

As noted in an earlier section, turtle groups within a species formed stable relationships in which there was a stable rank (Table 2.6) with the dominant or highest ranking turtle often chasing the lower ranking turtles away from resources such as food or potential mates. These relationships were stable over years with fluctuation in groups occurring mainly when new turtles of their species were introduced into the enclosure and or turtles in the group were removed or died. The same set of turtle subjects in 2004-2005 and again two years later in 2007 were studied in the delta lake exhibit, but there were some changes in the groups that occurred between years. Furthermore, in summer of 2007 KD observed the introduction of two *Chrysemys dorsalis*, Southern Painted (SP) turtles (1 male and 1 female) into the enclosure as well as 2 FRBs (1 male and 1 female – these *P. nelsoni* were ID 4 and ID6 from parts 3 & 4 and were intentionally added by KD).

Rank order was separate for female turtles from that of male turtles. The rank of male turtle groups was much easier to determine since they more frequently showed agonistic interactions and these were very obvious (Table 2.4A, 2.5A). Female turtles rarely interacted agonistically. Only *P. nelsoni* females had a sufficient number of turtles interact for the full rank order to be determined. The largest female *P. nelsoni* (F-FRB1) was clearly the dominant / alpha female as she was repeatedly seen snapping at any and all other female FRB's that came in contact with her, especially after the introduction of a new F-FRB in the summer of 2007.

Detailed rank explanations below and all quantitative statistics run on aspect of agonistic interactions focused on M-M interactions. Dominant male turtles would repeatedly direct gapes, snaps, bites and chases toward other turtles (Table 2.3, 2.4A, 2.5A). These behaviors can be considered offensive behaviors. The lower ranking turtles exhibited more defensive behaviors such as defensive gapes, snaps, circling, tilting, limb retraction, and most often, retreats or fleeing behaviors (Table 2.3, 2.4A, 2.5A). The aggressor was consistently the higher ranking turtle and the lower ranking turtle consistently lost fights and was chased away. Therefore, a turtle's rank order was determined based on which turtle consistently initiated and won agonistic encounters and which turtle repeatedly exhibited defensive behaviors and or retreated from the encounters (Table 2.6).

YBS & RES (Trachemys scripta) Group Ranks - During the first observation year (2004-2005) this group consisted of 5 male turtles from September - November 12th. A 6th male turtle (YBS5) was introduced into the delta lake exhibit between November 12th and November 17th of 2004. The highest ranking male in this group was an older melanistic male with scars (YBS1). Another old melanistic male (YBS2) was second in rank. The Red-eared Slider (RES1), although a different subspecies, was 3rd in rank. YBS3 was also a melanistic male and was about the same rank as RES, at 4th. Then came YBS4, the lowest ranking turtle (prior to the introduction of YBS5), who was often chased completely way from the feeding area by YBS1 with the help of YBS2, RES, and YBS3 (See Table 2.6C).

YBS4 had hard, crusted looking, white scar tissue on its' neck area (an area often bitten during agonistic encounters) indicating it had been harassed over a long period of time. Due to its low rank YBS4 was rarely seen. When it was seen out of hiding, it was often fleeing from the other YBS turtles. He generally only came out from hiding, occasionally, during feeding times. During November of 2004 another YBS male called YBS5 was introduced into the exhibit. This male was half the size of the rest, who were all about the same size and full grown. YBS5 was harassed heavily in the spring of 2005 by YBS1 and the rest of the group (see coalition section below for more details).

When observations resumed in spring of 2007, YBS2, YBS4, and YBS5 had died or been removed and a female F-RES turtle had been added to the enclosure. YBS1 was still dominant, followed by the male M-RES and YBS3. However YBS3 was initiating aggressive encounters with YBS1. The following week (April 8, 07) YBS1 was still winning interactions with YBS3, but YBS3 was winning against the RES1 male who had formerly been dominant over YBS3. The next time KD observed the turtle enclosure (April 13, 07) YBS1 was almost always hiding out of sight; when he was finally seen he had an injury on his carapace. He also was actively avoiding YBS3. When they interacted, YBS1 was showing defensive behaviors – and YBS3 exhibited offensive behaviors toward YBS1 and won any encounters, clearly demonstrating a change in rank between YBS1 and YBS3, with YBS3 as the new dominant male. After years of seeing YBS1 being dominant, this sudden reversal was very impressive. The RES male was also showing agonistic offensive behaviors toward YBS1 so the rank had changed from YBS1 > RES > YBS3 to YBS3 > RES > YBS1 (Table 2.6C).

Male RC (Pseudemys concinna) Group Ranks - This group was stable, with RC1 as highest ranking followed by RC2, then the lowest was RC3 (both of these turtles were almost twice the size of RC3) (Table 2.6B). RC1 was often interacting with RC2 and agonistic interactions between RC1 and RC2 were not intense. RC1 and RC2 would gape, snap and chase RC3 when he was in close proximity to either of them, but these were generally very brief and not intense interactions like those of the YBS group (Table 2.4A, Figure 2.6). For example, the higher ranking RC's did not chase RC3 all over the tank and consistently gape, snap, bite, and chased him like the YBS1 would do to lower ranking YBS turtles.

Male FRB (P. nelsoni) Group Ranks - The FRB males did not exhibit as many or as diverse agonistic interactions as the YBS group (Table 2.4A, 2.5A; Figure 2.5, 2.6). They also did not consistently show gape, snap, and chase behaviors at the lower ranking individuals. The only times that intense interactions occurred were during male-male contests (see section below and Figure 2.5). There were 3 male FRB's and their rank ordering was only obvious when these turtles exhibited agonistic interactions, which occurred in the spring and mainly during contests.

FRB1 and FRB2 were about the same size and these were the two that competed in the contests (Table 2.6A; Figure 2.5, 2.6, 2.7 and Figure 2.8 picture illustrations) with FRB1 exhibiting more offensive gapes, more snaps and chasing FRB2 away during agonistic interactions. FRB3 was an older melanistic male about twice the size of FRB1 and 2, yet he did not interact with them often and was never directly involved in the contests. The rank order was FRB1 > FRB2 > FRB3 (Table 2.6A). When FRB3 attempted to interrupt one of FRB1-2's contests, it was FRB2 that gaped, snapped and chased him away. There were more agonistic interactions between FRB2 and FRB3 then FRB1 and FRB3, perhaps because FRB2 was attempting to maintain rank above FRB3.

Male-Male

Agonistic interactions- The behaviors patterns gapes, snaps, bites, grips, yanks, drags, face-offs and extended heads and tails were seen in offensive aggression by higher ranking males as noted above (see Table 2.3, 2.4A, 2.5A and Figures 2.8, 2.9 for illustrations of some behaviors). Defensive behaviors included, for example, gapes with head tucked instead of extended, snaps, limb and head retractions, circling, tilting, tucked tail, moving way, and retreating or fleeing from the aggressor depending on the level of threat (see Figures 2.8, 2.9 for illustrations). Low ranking turtles consistently tucked their tails (Figure 2.8B) when interacting or even passing higher ranking turtles of their group. Furthermore, during contests the turtle's tail positions would go from extended when they aggressed to tucked when the other turtle snapped at or bit at them.

Contests – M-M combat was only seen in the spring between male FRBs (*P. nelsoni*), but was observed in both spring and fall in YBSs (*Trachemys s. scripta*), and was never seen in RC

(*P. concinna)* males. Contests only occurred in the spring for FRB males and in the spring and fall for YBS males. These contests included many of the agonistic behaviors within their bouts, but had a more complex and stereotyped sequence (Table 2.3; Figure 2.8). They always started with two males facing each other with their back ends up off the substrate or up at an angle in the water column- this behavior is called a face-off (Table 2.3; Figure 2.8 A, B). During these contests both males stay in a face-off stance, but can perform a variety of offensive behaviors while facing the other turtle, such as offensive gapes, snaps, bites, and pushes. The males usually went back and forth between offensive behaviors just mentioned and defensive behaviors such as defensive gapes, retract limbs, tail tuck, circle, and tilt (see illustrations of offensive & defensive contest behaviors Figure 2.8 A-E). The winner of the contest was the turtle who finally got the other to retreat.

Coalitions- Some aggressive interactions included intense harassment of a newly introduced, smaller, male *Trachemys s. scripta* (YBS), in the spring by coalitions of two larger high ranking male *T. s. scripta* (YBS1, YBS2) and the *T. s. elegans*, M-RES, (Figure 2.9 C, D). The intense harassment of this smaller lower ranking male included YBS1 and YBS2 grabbing his limbs. YBS1 grabbed his right back foot and dragged him to another area of the enclosure (Figure 2.9D). YBS2 was on top of YBS5 so it could not get away and M-RES was right around as well. These types of harassment, with lower ranking animals being dragged across the enclosure, were never observed in the FRBs or the *Chyrsemys dorsalis* (SP) even when new males and females were introduced. Grabbing of limbs was seen occasionally by males towards females also – in the case of the female RES, YBS grabbed her limbs and yanked her once.

When the new female SP turtle was introduced in 2007, she got into a contest with another SP and her limb was grabbed and yanked- this may have been courtship related.

The male FRBs did show some intense interactive behavior when a new male (M-FRB4) was introduced into the tank. This behavior involved snaps, bites, and very brief limb grab by M-FRB3 but the intensity of the limb grab and duration was in seconds *vs*. the M-YBS harassment, which lasted for more than 5 minutes. The other behaviors exhibited by the M-FRBs toward the newly introduced M-FRB were very different from the M-YBS behaviors so they are described in the section on “other social” behaviors.

Male-Female

Agonistic behaviors were usually performed by males and directed at females. The most intense agonistic encounters occurred in the YBS-RES group in which males chased, snapped at, bit, and grabbed the limbs of the female F-RES and, in a few cases, yanked and dragged her (Table 2.4). These behaviors could also be considered aggressive courtship behaviors and will be noted in the courtship section. There were a few agonistic interactions between the male Florida Chicken Turtle (FCK), *Deirochelys r. chrysea*, and the female F-FCK turtles. In one instance the male was attempting to court one of the females and she kept circling way from him and he eventually snapped and bit her. The less receptive of the two F-FCK turtles usually snapped at the male when he approached her. The male in these cases appeared to be attempting to start courtship, but very quickly retreated when she snapped at him. There were no instances of agonistic behavior between male and female FRBs during the fall or spring courtship seasons (Table 2.4A, 2.5A). During the summer of 2007, I did observe that male FRBs avoided the female FRBs especially the highest ranking female who would snap at them and other females during this time. Southern Painted turtle aggression was rare and only seen in the last year when a new female and male were added to the tank. The aggression included a male grabbing the new female and the two circling as the female attempted to bite the male who yanked on the female. This may have been courtship related aggression.

Female-Female

Very few instances of aggression were seen between females of any of the species (Table 2.4A, 2.5A). When aggression did occur it was often a snap and seemed to occur the most between FRBs during the summer of 2007 when a new female was introduced into the enclosure. Gapes and snaps were seen between the two female B-MAPs during there frequent interactions which were considered part of the “other social” (Table 2.4C, 2.5C) category, Female-Female interactions will be discussed more thoroughly in the “other social” section.

Courtship

Male-Female

Male-female courtship in *P. nelsoni*, the focal species for courtship displays, was observed in both the fall and spring but was much more common in the spring (Figure 2.4). FRB males were often seen exhibiting stages of courtship such as follow, swim above, limb wave and titillation (Figure 2.10). No aggression was ever seen from a FRB male towards any FRB female during courtship (Table 2.4B, 2.5B).

The male Florida Chicken Turtle (*Deirochelys r. chrysea*) was often seen courting female conspecifics. He seemed to have a preference for the larger female and /or the other female would not let him court her. The FCK male would follow the female and nose-tail touch prior to swimming in front of the female. The female and male FCK turtles would often nose-nose touch, once he was swimming in front of her, by extending their extra long necks. Then, if the female did not swim away, the male would limb wave while staying in front of the female and staying afloat. (Table 2.4B, 2.5B and see Figure 2.7 for illustrations). Once or twice when the male chicken turtle was trying to court the female, she kept circling so that he had to circle and after a number of turns he snapped at her, however, agonistic behavior was rarely seen by him toward either female. In fact, the female FCK2 (who he did not court often) would usually lung and snap at him if he approached.

The YBS group only had a female RES in 2007. The YBS 1 & 3 in early spring showed considerable agonism toward the female RES, such as snaps, limb grab, yank, and chasing her around the enclosure. The males, later in the spring, showed less aggression and more courtship displays. The *Chrysemys dorsalis* (SP) turtles did not exhibit courtship in 2004-2005, since there were no males, but with the addition of a few males and some females, titillation was seen by the small male towards the females in 2007.

Other Social

There were a number of behaviors that were normally associated with agonisitic or courtship categories, but that were observed being used in other contexts or very low intensity levels. In these instances the behaviors were categorized as other social since the function of the behaviors were in question (see Table 2.4C and Figure 2.11). Most female-female interactions included approach, stare, nose, look away, move away and or a snap (Table 2.3). Usually

Female-Female encounters were very brief. On very rare occasions the above behaviors were seen in Male-Male encounters, but only by FRB males and then not during the courtship season.

When new turtles were introduced into the enclosure, new behaviors as well as behaviors normally found in courtship were exhibited (Table 2.4C, Figure 2.11). For example, when two FRBs, one male and one female, were introduced on the same day new behaviors were seen from the resident male FRBs, but only toward the new male, whereas the female resident FRB only interacted with the newly introduced female FRB6. The male FRB3 was the first to interact with and harass the new male. He nosed, snapped at, bit, gripped a limb, pinned and cornered the new male. He also titillated from above at the new male. When he had the new male pinned, the new male performed lots of throat vibrations – where the throat goes in and out. This may be a behavior associated with a sound that travels through water; this behavior has never been documented in aquatic turtles. The other two FRBs joined in by investigating this new male with titillation displays, and FRB2 mounted him.

The dominant female FRB1 approached the new female, nosed her, titillated at her in a face to face position, and snapped at her once. F-FRB1 continued this over days and then started titillating at other FRB females that were residents. After the new female SP was introduced she exhibited another new behavior, which had not been observed previously. She performed a behavior only seen in one bout. She flicked her tail up and down and left and right when she was approached by a male. (Southern Painted turtles have harder and less fleshy tails then other emydid turtles, which makes tail flicking possible for them and perhaps less available for the other species being observed). She continued this behavior for some time.

Titillation

Titillation, as mentioned above, was observed in the FRB M-M introduction as well as the F-F introduction of a new animal. For the Female-Female FRB interaction it needs to be noted that prior to that introduction no titillation was ever seen between female FRB's. This is a new context in which titillation has been observed, except for juvenile turtles (e.g., Kramer and Burghardt, 1998). Titillation is classified in the literature as only a courtship behavior. M-M titillation was also seen repeatedly between RC1 and RC2, with the dominant RC1 always on top titillating at RC2. Male RC3 was often seen titillating at male M-FRB3 (Figure 2.10). The two female B-MAPS, who had no males, always associated together and interacted displaying front on (face to face) titillation and nose-nose interactions often.

Discussion

Turtles were found to preferentially affiliate and interact with individuals of their own or most closely related species. Repeated observations of the same individuals associating indicate a possible preference not just for their own species, but for certain individuals. Social interactions were seen in all sexual pairings and frequency of social behavior category differed significantly with sexual pairing and season in *Pseudemys nelsoni*. Intense agonistic interactions were more prevalent with M-M pairs, courtship interactions were more common with F-M pairs, and generalized social interactions were seen in F-F, and M-M pairs. The M-M agonistic behavioral repertoire and intensity differed across the species, with the *Trachemys scripta* group exhibiting the most complex and intensive agonistic repertoire.

Male turtles formed stable dominance hierarchies with instability of rank mainly occurring when group members changed. Basking behavioral repertoire, frequency of interactions, and apparent function of interactions differed from underwater turtle interactions. Some agonistic *T. scripta* interactions included intense harassment of a smaller, newly introduced, male by ‘coalitions’ of two or more larger males. Additionally, both M-M and F-F pairs exhibited social interactions that included behaviors normally categorized as courtship, such as titillation, in contexts that clearly did not involve courtship.

These findings indicate that turtles are active social animals with complex underwater social behavioral repertoires. Although the captive setting included higher turtle densities and more species diversity than would be found in natural environments, the findings are congruent with the frequent reports of turtle aggregations by herpetologists in nature (personal communication with multiple herpetologists). Unfortunately, research on turtle underwater social behavior and aggregation in the wild are lacking with one exception, Kramer's field observations of *P. nelsoni* and *P. concinna* (1986), which supports the validity of my captive findings. Kramer found that in the field adult *P. nelsoni* and *P. concinna* engaged in M-M agonistic behavior, M-F courtship and agonism, but aggression was not observed during F-F interactions (1986). Kramer also found turtles in mixed F-M groups or all male groups, independent of the distribution of nesting sites i.e. non-random distribution of wild turtles. Clearly many more detailed studies of turtle underwater behavior in both the field and captivity are needed.

Since Carpenter and Ferguson's (1977) description of reptile social behavior as stereotyped and context specific, behavioral patterning of reptilian social behavior has rarely been studied without this bias. For example they described only the courtship related behaviors of turtles, focused on land tortoises. This bias of just focusing on turtle courtship, which is often the most striking behavior sequencing noted during brief observations, has perpetuated the view that turtle social behavior consists primarily of courtship related behaviors. The majority of social behavior descriptions of turtles, in particular aquatic turtles, continue to focus on courtship behavior (Jackson & Davis, 1972; Harless, 1979; Miller & Dinkelacker, 2008).

More specifically, use of terms such as "titillation," implying functional courtship behaviors, are biased as they assume that whenever a male titillates it involves a courtship context. A more objective term would be "foreclaw display behavior" as used by (Thomas & Altig, 2006). Thomas and Altig's study also concluded that the "titillation" behavior observed between wild caught females (likely strangers) put together in staged interactions was inconsistent with the assumption by other researchers that titillation is always associated with courtship. Their findings support my findings that when a female was newly introduced other females exhibited titillation. Moreover, my observations of F-F map turtle titillation does not fit with a courtship function.

Despite observing this phenomenon of “titillation” in contexts other than the traditional M-F courtship situation, earlier studies did not investigate them further or consider if they may serve another function - communicate different information than courtship. Unfortunately M-M titillation has been labeled “homo-sexual mounting” and essentially been ignored (e.g. Kramer, 1989b). The findings of this study indicate that “titillation” (so termed so that the behavior can be easily identified by readers as it is so widely used and expected) occurs in M-M and F-F interactions under differing contexts, and thus titillation is not limited to M-F courtship, where only males exhibit the behavior. The observation of ‘titillation” in both male and female same sex pairings, between individuals who prefer to associate together, and with either both turtles or the more dominant turtle titillating consistently, all indicate that this behavior pattern may serve as a lower level social interaction and perhaps to maintain status.

Furthermore, same-sexed titillation and mounting occurred with the introduction of new turtles and was directed at newly-introduced animals of both sexes (M-M and F-F), which lends more credence to the idea that this behavior can be involved in investigating new animals, establishing rank, and maintaining rank. Another possible interpretation of titillation may be that it is a form of social play. Juvenile males and females have been demonstrated to exhibit these repeated titillation bouts, often not in normal sequence or directed at typical stimuli (see Burghardt, 2005). Courtship play in same sex parings may be an important way for turtles who do not have parental care to practice a behavioral sequence (other parts of the courtship behaviors were seen in these same sex groups) important for reproductive success. It is also possible that titillation my have different functions depending on the context and sex pairs involved.

My study showed that in a stable captive environment emydid turtles formed stable underwater dominance hierarchies that lasted for years. The changes in groups created in this study by turtles dying, being removed and or added to the enclosure always resulted in more agonistic interactions while the group ranks were being challenged and may mimic what would happen in the wild when turtles join or leave a group. All of the 3 species of males studied formed linear dominance hierarchies in this naturalistic captive setting. Despite arguments that animals commonly form more transitive hierarchies in the wild (Mech & Luigi Boitani, 2003; Van Doorn, Hengeveld, Weissing, 2003), Kaufmann (1992) found in his field study of marked Wood Turtles (*Clemmys insculpta*) that they formed linear hierarchies. This finding is very interesting since Wood Turtles live in a much more transitive environment (living partially on land and partially in streams) than the basking turtles in my study. Therefore, one would at least expect to find stable dominance hierarchies in the more stable lake environments with turtles that live in social groups. Factors such as the stability of the environment (i.e. stream vs lake or pond), the life history of the turtle species (do they live on both land and water like the Wood turtle, or are they semi-aquatic, aquatic, or land turtles), and their level of sociality (social, semi-social or solitary species), will all affect the social structure of turtle species and populations and may determine whether turtles form dominance hierarchies and whether they are stable or transitive. More captive and field studies (with marked individuals) are needed of all of the many turtle species to determine the role these factors have on turtles' social structure.

Regardless, Turtles in this study exhibited complex social repertoires with plasticity across contexts, and courtship behaviors were seen in play-like contexts. These findings, as well as some of the specific behaviors, are very similar to those found in mammals and birds (Dugatkin, 2004). Specifically, many social behaviors correlate to contest behavioral sequences related to access to mates and/or behaviors related to obtaining food. These same behavioral sequences may be involved in mate competition, social status and group dynamics, and play (Burghardt, 2005). Like wolves (Zimen, 1981; Mech & Boitani, 2003), turtles formed dominance structures that were separate for males and females in a stable naturalistic setting. However, agonistic interactions and fluctuations in rank occurred when groups changed due to additions or subtractions of turtles to the enclosure. Turtles also exhibited sets of offensive behaviors, primarily in the dominant or aggressor turtles, and defensive behavior seen especially in the lower ranking turtles. Most notable, and yet surprisingly not mentioned in other turtle social behavior studies, is that dominant turtles extended their tails during interactions with lower ranking turtles and the lower ranking turtles consistently tucked their tails when in the presence of higher ranking turtles, even if they were not being attacked. Since turtles have a rigid body structure they cannot move the rest of their body as easily as mammals, but tail positions have been commonly noted in mammals as related to aggression level and rank. For example, high ranking or status challenging wolves will raise their tails high where as lower ranking wolves tuck their tails in the presence of higher ranking wolves (Zimen, 1981; see Wolf Park's ethogram, Goodmann & Klinghammer, 1985).

The findings reported here illustrate that turtle underwater social behavior is much more complex then their basking behavioral interactions and that different rules of sociality apply for interactions underwater vs. those on land, consistent with Kramer's finding for *P. nelsoni* in the wild (Kramer, 1986, 1989b). These findings also provide evidence that turtles have more plasticity in behavioral repertoires across contexts. Furthermore, this extensive long term study illustrates that the behaviors, sequences, and contexts of these behaviors are similar to those of mammals and birds, supporting the view that turtles are an excellent group to study social behavior and its evolution in the absence of parental care.

Acknowledgments

I would like to start by thanking the staff at the Tennessee Aquarium in Chattanooga for their gracious hospitality for with out their help and access to the aquarium this project would not have been possible. Dave Collins and Tim Schmeidehausen were especially helpful. Tim in particular was the herpetologist whom I interacted with the most since he takes care of the Delta lake section. He allowed me to take up his valuable time to capture, weigh and measure the turtles which was important for getting size estimates used during proximity data analysis. Thanks also to Mike O'Neil for his statistical and SPSS consultation on part of my project. The Department of Psychology, and Science Alliance at the University of Tennessee Knoxville funded of parts of this research. Many undergraduate research students in the Burghardt lab helped me with the long process of converting the Hi8 turtle video to DVDs so that it could be analyzed more readily. Furthermore, some of them spent hours learning to identify turtles' species and behaviors so they could help with the tape logs. Thanks to the following undergraduates: Leaha Burke, Meghan McCall, Ben Cohen, Ramsey Cox, Derek Goff, Jordan Hensley, Emily Long, Jessica Lovely, Ruben Luna, Jessica Mayfield, Jeff Orgain, Lacy Sams, Jennifer Southerland, and Rhonda Williams.

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Appendix

Table 2.1. Study Subjects at the Chattanooga Aquarium Delta Lake Exhibit During Fall 2004 - Spring 2005 and Spring, Summer and Fall of 2007.

Genus Species	**Common Name**	**Abv.**	**Female**	**Male**	**Total**	**Carapace (cm)**
Chrysemys dorsalis	Southern Painted	SP	7	2	9	14-15
Deirochelys reticularia chrysea	Florida Chicken	FCK	2	1	3	13-23
Graptemys barbouri	Barbour's Map	BMAP	3	0	3	18-26
G. ernsti	Escampia Map	EMAP	2	0	2	15
G. ouachitensis sabinensis	Sabine Map	SMAP	1	0	1	14
Pseudemys alabamaensis	Alabama Red-bellied	ARB	2	0	2	23-27
P. nelsoni	Florida Red-bellied	FRB	6	4	10	17-30
P. concinna	River Cooter	RC	0	4	4	21-28
Trachemys scripta elegans	Red-eared Slider	RES	1	1	2	20
T. scripta scripta	Yellow-bellied Slider	YBS	0	5	5	15-19
	Total count		**24**	**17**	**41**	

Table 2.2. A-K Individual Turtle Associations Within and Across Species. These tables (A-K) show the number of times each individual turtle of each species was found on screen within 60cm of the other turtles both within and between species. The letter infront of each species abbreviation, for each individual, indicates sex, F = Female and M = Male. The number after the species name is the individual's identification number. Proximity data samples came from freeze frame samples taken every 10 minutes from 12 hours of video tape spanning a 20 hour time period. See Figure 2.2 for a collapse of individual turtle data into number of times each species of turtle was found on screen with in 60cm of the other species of turtles.

(A) Florida Chicken Turtle vs. Florida Chicken Turtle

		Individual 2		
		F-FCK1	M-FCK1	Total
Individual 1	F-FCK1	0	11	11
	M-FCK1	11	0	11
	Total	11	11	22

(B) Florida Chicken Turtle vs. Florida Red-bellied Cooter

		Individual 2	
		F-FRB3	Total
Individual 1	F-FCK1	1	1
	M-FCK1	1	1
	Total	2	2

(C) Florida Red-bellied Cooter vs. Florida Red-bellied Cooter

		Individual 2								Total
		F-FRB1	F-FRB2	F-FRB3	F-FRB4	F-FRB5	M-FRB1	M-FRB2	M-FRB3	
Individual 1	F-FRB1	-	1	1		1	3	2	1	9
	F-FRB2	1	-							1
	F-FRB3	1		-			2		3	6
	F-FRB4				-		3			3
	F-FRB5	1				-	1		2	4
	M-FRB1	3		2	3	1	-	1	1	11
	M-FRB2	2					1	-		3
	M-FRB3	1		3		2	1		-	7
	Total	9	1	6	3	4	11	3	7	45

(D) Florida Red-bellied Cooters vs. Alabama Red-bellied Cooters

		Individual 2		
		F-FARB1	F-FARB2	Total
Individual 1	F-FRB3	1	1	2
	Total	1	1	2

(E) Florida Red-bellied Cooter vs. River Cooter

		Individual 2		
		M-RC2	M-RC3	Total
Individual 1	F-FRB1	1	1	2
	F-FRB2		1	1
	F-FRB3		1	1
	F-FRB5	1		1
	M-FRB1	1	1	2
	M-FRB3	1	2	3
	Total	4	6	10

(F) Florida Red-bellied Cooter vs. Yellow-bellied Slider

		Individual 2	
		M-YBS1	Total
Individual 1	F-FRB2	1	1
	M-FRB1	1	1
	Total	2	2

(G) Map Turtle vs. Map Turtles (B = Barbouri, E = Escampi**a**)

		Individual 2			
		F-BMAP1	F-BMAP2	F-EMAP3	Total
Individual 1	F-BMAP1	-	13	5	18
	F-BMAP2	13	-	3	16
	F-EMAP3	5	3	-	8
	Total	18	16	8	42

(H) River Cooter vs. River Cooter

		Individual 2			
		M-RC1	M-RC2	M-RC3	Total
Individual 1	M-RC1	-	3	1	4
	M-RC2	3	-		3
	M-RC3	1		-	1
	Total	4	3	1	8

(I) River Cooter vs. Yellow-bellied Slider

		Individual 2	
		M-YBS1	Total
Individual 1	M-RC2	1	1
	Total	1	1

(J) Yellow-bellied Slider vs. Yellow-bellied Slider

		Individual 2				
		MYBS1	MYBS2	MYBS3	MYBS5	Total
Individual 1	MYBS1	-	1	4	1	6
	MYBS2	1	-			1
	MYBS3	4		-	1	5
	MYBS5	1		1	-	2
	Total	6	1	5	2	14

(K) Yellow-bellied Slider vs. Red-eared Slider

		Individual 2	
		MRES	Total
Individual 1	MYBS1	2	2
	MYBS2	1	1
	MYBS3	2	2
	MYBS5	1	1
	Total	6	6

Table 2.3. Ethogram of Turtle Social Behaviors Recorded in this Study. The behavior patterns observed in each category are listed alphabetically (see also Table 4.3). Behaviors in bold are described for the first time in this report. Many of the behaviors defined here have also been described for juvenile *P. nelsoni* (Kramer 1989 a, b).

Behavior	**Definition**
Approach	An animal moves toward another turtle, body focused on said animal.
Bite	Animal extends head forward quickly with jaws open and closes jaws, making contact with skin (back of neck, or feet) of another turtle. It then releases the other animal within a second.
Chase	Animal swims after another turtle that is in the process of retreating or fleeing from it.
Circle	Moves around another in a circular motion, usually while tilting body so carapace faces other turtle, and often will retract limbs and or tail. In response to agonistic behavior from other turtle
Close eyes	Animal shuts eyelids, in response to other turtle's titillation
Complete retraction	All limbs are withdrawn under carapace, defensive response to offensive agonistic behavior from another turtle.
Face-off	Two animals face one another with necks retracted so only their heads are visible, either while staying afloat in water column or on substrate. If the animals are on substrate both turtle's back ends are arched up off the substrate.
Flee	Turtle swims rapidly away from another which is often chasing it, with its tail tucked.
Follow	Approaching an animal that is moving away slowly via swimming or walking. Generally occurs when recipient is facing away from approaching animal.
Gape	This occurs when an animal partially retracts its head and rapidly opens its mouth.

Table 2.3. Continued

Behavior	**Definition**
Limb wave	Turtle moves front and back limbs back and forth in a figure eight pattern. This behavior was usually seen to keep a male swimming above or in front of a female. It was also seen in slider males when on the substrate and in front of a female.
Look away	Animal avoids looking directly at other turtle's face, by turning its head slightly away from other turtle. Occur when another animal stares at it.
Mount	A turtle slides back and upward so its back end and tail are pointed down and inward toward the bottom turtle's tail. This is often the next step in the courtship process just prior to copulation, but was also seen in other social contexts with male-male turtle pairings.
Move away	Animal slowly walks or swims away or turns their body around.
Neck Extension	One turtle stretches its neck out from carapace toward another turtle or object. This behavior is often followed by a nose or gape or snap.
Nose	Occurs in two different contexts: 1) *nose-tail* -male extends neck forward at female facing the same directions and places it nostrils within a mm of the tail or carapace of the turtle (female) in front (courtship) 2) *nose- nose* - Two turtles in close proximity slowly extend their necks until their noses touch or almost touch not necessarily directly facing each other.
Pin	One turtle lies on top of another turtle while cornering the turtle underneath it on the substrate or a side of the tank so the turtle below can not escape.
Push	Two male turtles involved in a face off retract their heads, touch fronts of their shells together, and push each other back and further with their back limbs.
Retract head	Withdrawal of head under carapace
Retract head and forelimbs	Withdrawal of head and front limbs under carapace

Table 2.3. Continued

Behavior	**Definition**
Retreat	Turtle moves backward away from another animal for about one to four body lengths by crawling or swimming. Then it stops or turns and swims away. Head is partially withdrawn.
Sink	Animal allows itself to drift to the bottom
Snap	Individual thrusts head forward with jaws open, and jaws close short of the other animal
Stare	An animal faces another within a few body lengths and looks directly at its face.
Swim above	Pre-titillation mode in which one turtle swims above another orienting to its head and attempting to position itself for titillation. Also included in this phase is (Rotate- forelimbs) – the forefeet are brought forward roughly parallel to the head.
Tail extension	The tail is fully extended out from the body in an arch, upward so that the tail is raised further up so that is straight out and parallel to the carapace so it looks longer then in the normal state where the tail is angled downward at a 45° angle from the carapace.
Tail flick	Turtle moves tail either up and down or left to right rapidly. This behavior was only observed in a female painted turtle.
Tail tuck	Turtle moves the tail sideways either to the left or right so it is up against the body, perpendicular to the carapace and is not protruding out from the carapace
Throat vibrate	The throat moves in and out and the mouth slightly opens and closes. This is usually done when two turtles are facing each other or when one turtle is on top of another.
Tilt	Turtle moves carapace so it is body is at a 45°angle to the other turtle with the carapace facing the other turtle’s head.

Table 2.3. Continued

Behavior	**Definition**
Titillation	The digits of the forelimbs are vibrated rapidly, with the claws placed just above or in front of another turtle's head. This only occurred when a male was already in swim above mode. As the limb movements become more rapid the claws touch the other turtle's face. Usually only one animal titillates
Yank	An animal pulls on the foot or neck of another animal with jaw clenched to body part and swims backward resulting in sometimes dragging the recipient. male- male

Table 2.4. Social Behaviors Exhibited by Each Species for Each of the Three Behavioral Categories: (A) Agonistic Behavior, (B) Courtship Behavior, and (C) Other Social Behavior. Behaviors were observed and collected from128 hours of video tape during 2004-2005 & 2007 at the Tennessee Aquarium in Chattanooga (for full description of behaviors see Table 2.3).

(A) Agonistic Behavior

Behavior	**PT**		**CHK**		**BMAP**	**EMAP**	**SMAP**	**ARB**	**FRB**		**RC**	**RES**		**YBS**
	M	**F**	**M**	**F**	**F**	**F**	**F**	**F**	**M**	**F**	**M**	**M**	**F**	**M**
Approach	x	x	x	x	x				x	x	x	x		x
Bite									x		x	x		x
Chase			x						x		x	x		x
Circle	x	x		x					x	x	x	x		x
Face-off									x			x		x
Flee									x		x	x	x	x
Gape	x				x				x	x	x	x	x	x
Grip	x											x		x
Look Away	x	x			x			x	x	x				
Move Away	x	x	x	x	x	x		x	x	x		x	x	
Retreat	x	x							x		x	x	x	x
Retract Head & Limbs	x				x				x	x	x	x	x	x
Retract Complete									x			x	x	x
Snap	x	x	x	x	x				x	x	x			
Stare					x				x	x	x	x	x	x
Tail extension	x								x	x	x	x		x
Tail Tuck	x								x	x	x	x	x	x
Tilt	x				x				x		x	x	x	x
Yank														x

(B**)** Courtship

Behavior	**SP**		**FCK**		**BMAP**	**EMAP**	**SMAP**	**ARB**	**FRB**		**RC**	**RES**		**YBS**
	M	**F**	**M**	**F**	**F**	**F**	**F**	**F**	**M**	**F**	**M**	**M**	**F**	**M**
Approach	x		x						x		x	x		x
Bite	x											x		x
Chase			x									x		x
Circle	x	x		x									x	
Close Eyes										x				
Flee													x	
Follow	x		x						x			x		x
Gape	x	x	x	x								x	x	x
Grip	x											x		x
Kick				x				x		x				
Limb wave	x		x						x		x	x		x
Move Away		x		x				x		x			x	
Neck Extension			x	x					x		x			
Nose			x						x		x	x		x
Retreat	x	x	x							x			x	
Retract Head				x						x			x	
Retract Complete													x	
Snap	x	x	x	x						x		x	x	x
Sink										x				
Swim Above									x		x			
Swim in Front	x		x											
Tail Extension									x			x		x
Tail Tuck										x			x	
Tilt		x											x	
Titillation	x								x		x	x		x
Yank														x

(C) Other Social

Behavior	SP		FCK		BMAP	EMAP	SMAP	ARB	FRB		RC	RES		YBS
	M	F	M	F	F	F	F	F	M	F	M	M	F	M
Approach	x	x	x	x	x	x	x	x	x	x	x			
Circle		x			x									
Follow		x		x	x	x	x	x		x	x			
Gape					x				x					
Limb wave									x	x	x			
Look Away		x			x			x	x	x	x			
Move Away		x		x	x	x		x	x	x	x			
Mount	x								x					
Neck extension				x					x	x				
Nose				x	x	x			x	x				
Pin	x				x				x					
Retract Head & Limbs					x				x	x				
Snap		x		x	x				x	x				
Stare		x			x				x	x				
Swim Above										x	x			
Swim in front		x			x									
Tail Extension					x				x	x	x			
Tail Flick		x												
Tail Tuck					x	x			x	x	x			
Throat Vibration									x	x				
Tilt					x									
Titillation		x			x				x	x	x			

Table 2.5. Frequency of Social Behaviors Exhibited by a Subset of Species Described in Table 2.3 for Each of the Three Behavioral Categories: (A) Agonistic Behavior, (B) Courtship Behavior, and (C) Other Social Behavior. Behaviors were observed and collected from 12 hours of video tape during 2004-2005 at the Chattanooga Aquarium (for full description of behaviors see Table 2.3).

(A) Agonistic Behavior

Behavior	**FRB**		**RES**	**YBS**
	M	**F**	**M**	**M**
Approach	16		5	4
Bite	3	1	1	2
Chase	2		4	2
Circle			3	9
Face-off	14			8
Flee	1		4	13
Follow	5		1	1
Gape	25		4	4
Grip		1*		3
Kick	1	2		
Look Away	6		2	2
Move Away	3	1	3	4
Neck Extension	4		4	4
Push	2		4	2
Retreat	13	1	3	2
Retract Head & Front Limbs	25		14	2
Retract Complete	1			1
Snap	12	1	4	3
Stare	27	10		
Tail Extension	4		4	4
Tail Tuck	1		16	21
Tilt	12		6	13
Yank	2	1*		2

***** Female-Female aggression occurred during food competition

(B) Courtship

Behavior	FRB		RES	YBS
	M	F	M	M
Approach	3			
Bite				
Chase				
Circle				
Close Eyes		8		
Flee				
Follow	28			
Gape				
Grip				
Kick		2		
Limb Wave		32		
Look Away		1		
Mount	4			
Move Away		62		
Neck Extension				
Nose	2			
Retreat		1		
Retract Head				
Retract Complete				
Snap				
Sink		18		
Swim Above	28			
Swim in front				
Tail Extension				
Tail Tuck				
Tilt				
Titillation	38			
Yank				

(C) Other Social

Behavior	FRB		RES	YBS
	M	F	M	M
Approach		7	1	1
Circle				
Follow			1	
Gape				
Kick		2		
Limb wave				
Look Away	1	5		
Move Away		8	1	1
Mount				
Neck Extension		3	1	
Nose	2	2		
Pin				
Retract Head & front Limbs		2		
Retract Complete		1		
Snap				
Stare				
Swim Above				
Swim in Front				
Tail Extension		3		
Tail Tuck		1		
Tail Flick				
Throat Vibration				
Tilt				
Titillation				

Table 2.6. Male Turtle Underwater Dominance Hierarchy Matrices of the Three Species with Multiple Males, (A) Florida Red-bellied Cooters (FRB), *Pseudemys nelsoni*, (B) River Cooters (RC), *P. concinna*, and (C) Yellow-bellied Sliders (YBS), *Trachemys scripta scripta*. Since the Male Red-eared Slider (RES), *Trachemys s. elegans*, was part of the YBS social group he was included in the YBS dominance matrix.

(A) Florida Red-bellied Cooter Matrix

	Loser		
Winner	M-FRB1	M-FRB2	M-FRB3
M-FRB1	-	6	
M-FRB2		-	3
M-FRB3			-

(B) Male River Cooter Matrix

	Loser		
Winner	M-RC1	M-RC2	M-RC3
M-RC1	-	3	4
M-RC2	1	-	4
M-RC3			-

(C) Male Yellow-bellied Slider Matrix

	Loser					
Winner	M-YBS1	M-YBS2	M-RES1	M-YBS3	M-YBS4	M-YBS5
M-YBS1	-			8	2	3
M-YBS2		-				
M-RES1			-	8	2	5
M-YBS3				-	2	3
M-YBS4					-	
M-YBS5						-

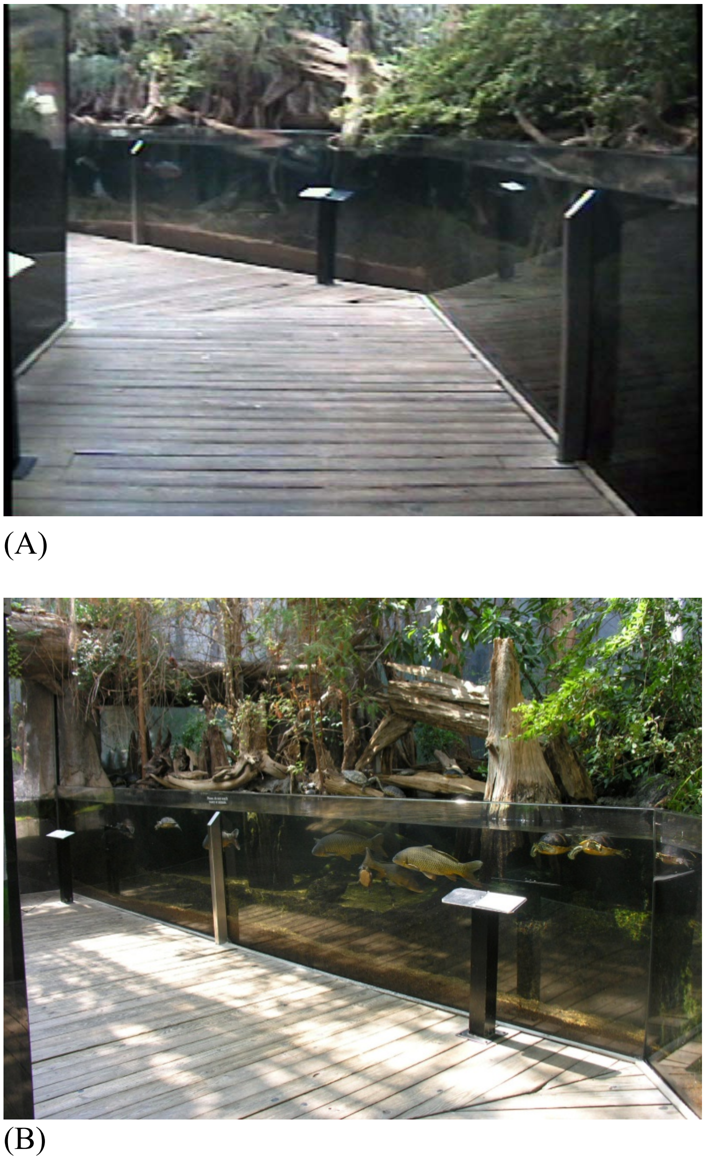


Figure 2.1. Pictures (A) and (B) of the Tennessee Aquarium in Chattanooga Mixed Species Enclosure Illustrating Glass Viewing Sections. (A) The overall glass viewing area the front and side section of the exhibit. (B) Close up of the front (larger) section with the underwater glass viewing area and the basking area above.

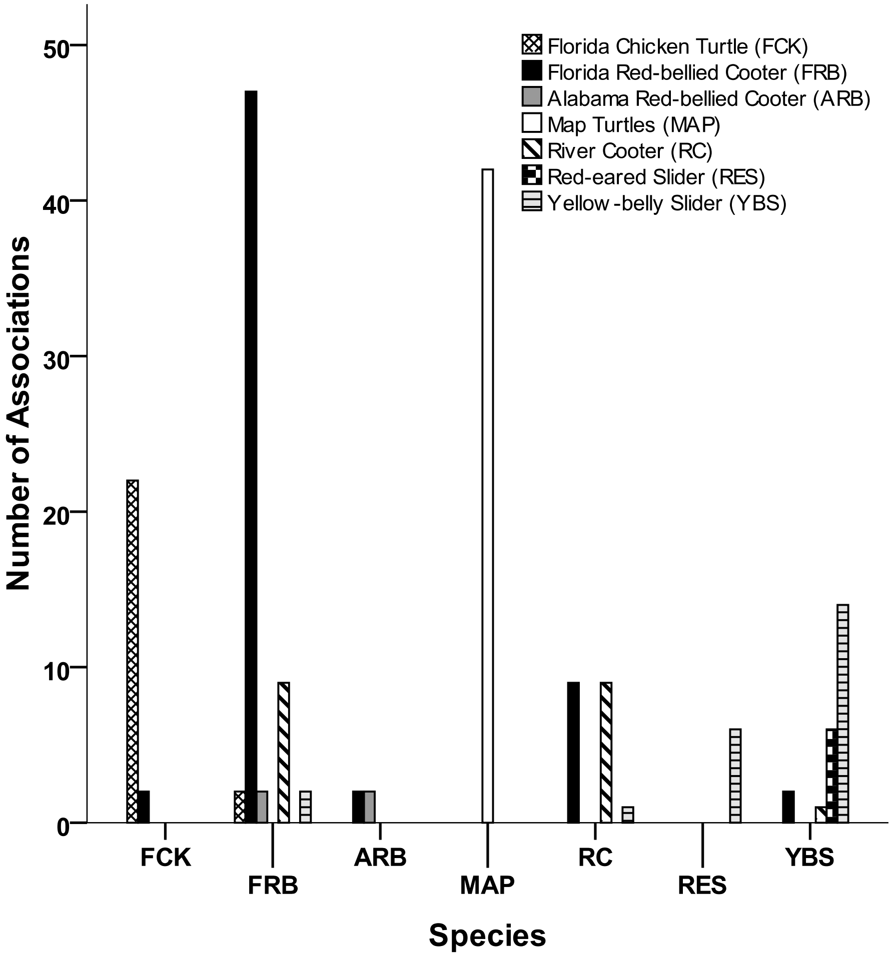


Figure 2.2. Turtles Prefer to Affiliate with Their Own Species. This figure shows the number of times each species of turtle was found on screen within 60cm of the other species of turtles. Proximity data samples came from freeze frame samples taken every 10 minutes from 12 hours of video tape spanning a 20 hour time period. Turtles preferred associating in close proximity to members of their own species. See Table 2.2 for individual turtle affiliation data.

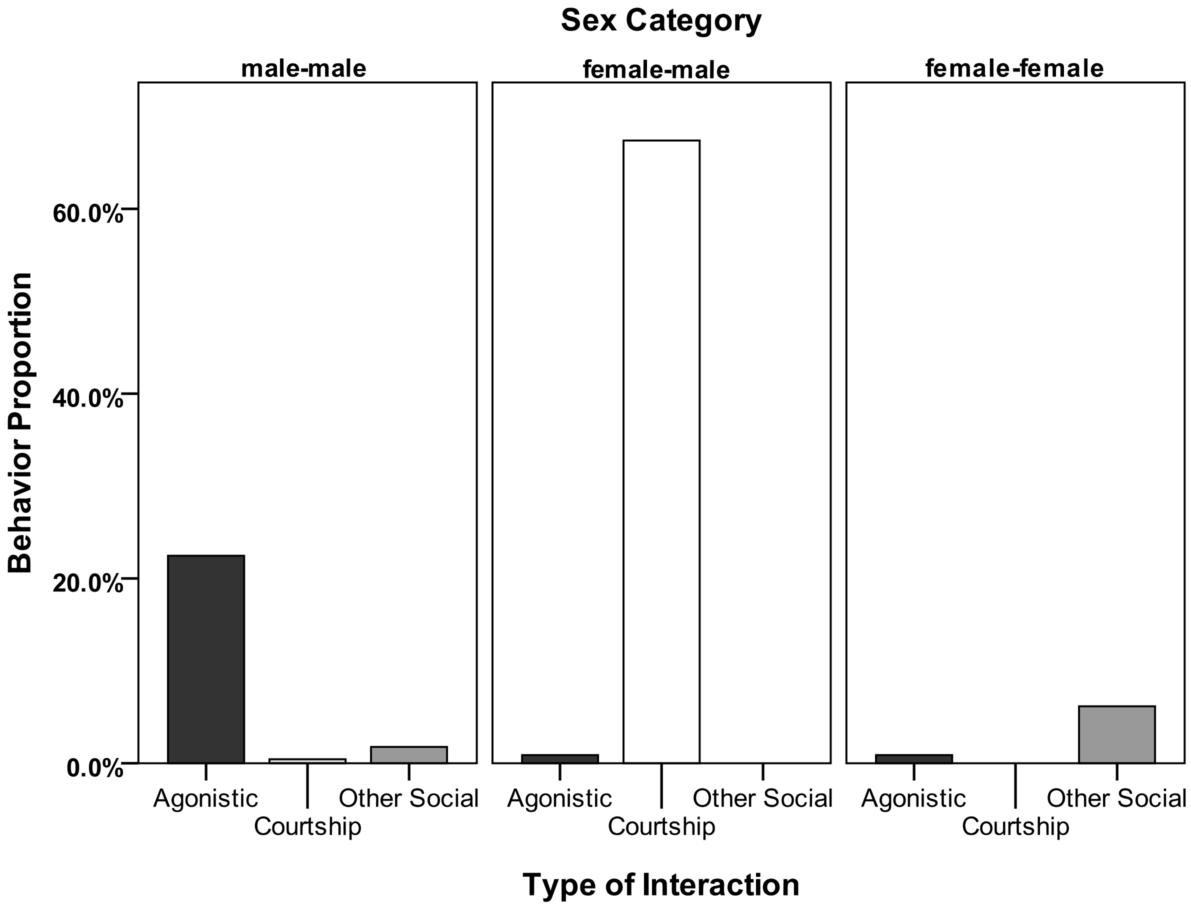


Figure 2.3. Behavioral Types Differs with Sex Category in Florida Red-bellied Cooters (*Pseudemys nelsoni*). This figure shows that behavior types significantly differ with sex category. Agonistic interactions occurred mainly between males, and courtship was seen between Males-Female pairs.

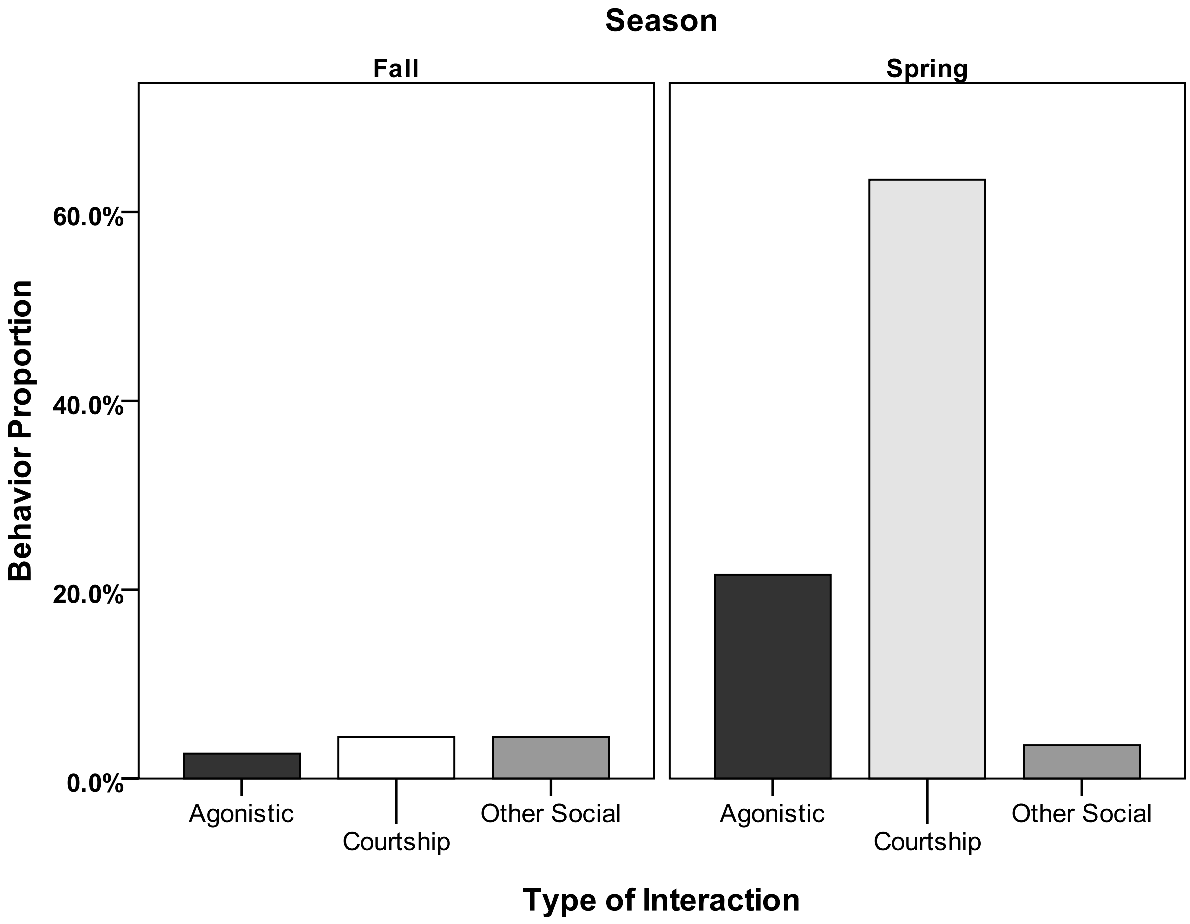


Figure 2.4. Seasonal Differences in Proportions of Behavioral Interaction Categories for Florida Red-bellied Coopters(*Pseudemys nelsoni*). Proportions of behavioral categories changed seasonally, with more courtship and agonistic behavior in the spring.

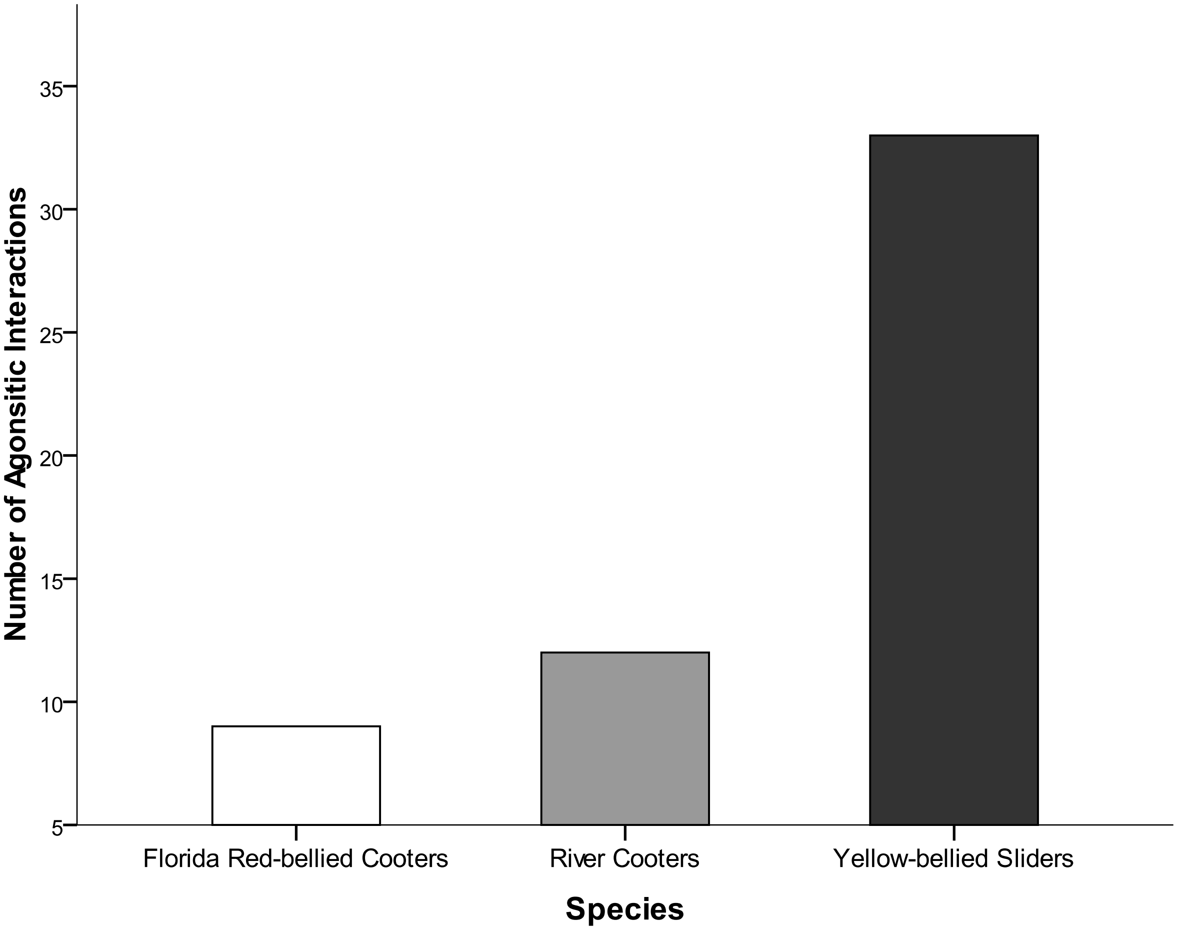


Figure 2.5. Number of Male Agonistic Interactions Differed Across Florida Red-bellied Cooters (*Pseudemys nelsoni*), River Cooters (*P. concinna*) and Yellow-bellied Slider Turtles (*Trachemys scripta*). Florida Red-bellied Cooters exhibited the least agonistic interactions while Yellow-bellied Sliders interacted agonistically the most. The total number of male agonistic interactions for each of the three species were collected from16 hours of video tape from 2004-2005.

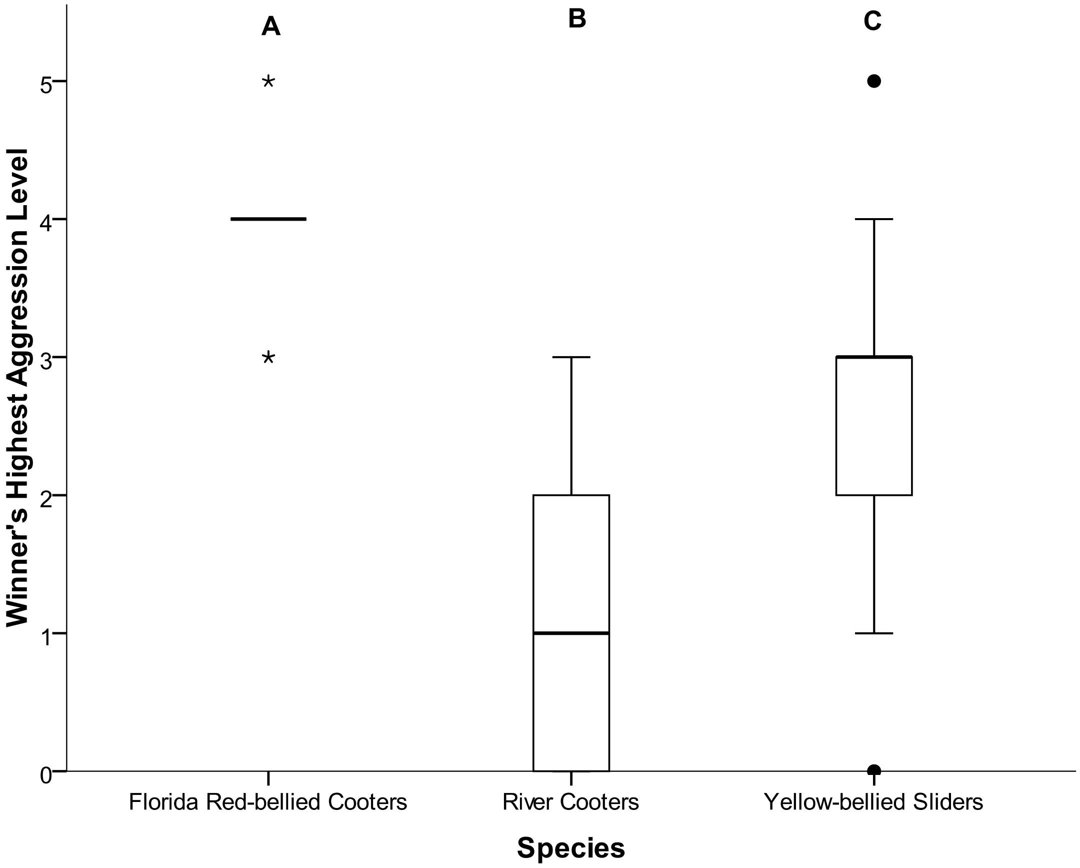


Figure 2.6. The Highest Aggression Level Reached by Winners of M–M Fights for Florida Red-bellied Cooter (*Pseudemys nelsoni*), River Cooter (*P. concinna*), and Yellow-bellied Slider (*Trachemys scripta*) groups. Each of the aggression levels (0-5) represent combinations of agonistic behaviors listed in Table 2.3. Level 0 = approach, level 1 = approach and stare, level 2 = inclusion of gapes and/or snaps, level 3 = inclusion of bites and/or chases. Level 4 = both turtles engage in a face-off, that includes some or all of the behaviors in levels 0-3. Level 5 = one turtle grips, drags, or yanks other turtle by its limbs and includes some or all of level 0-4 behaviors. Additionally, intense face-offs can reach level 5 with or without grips and yanks. This figure shows that the higest aggression level differed between each species, represented by the letters (A-C) above each box plot. The range and types of agonistic behaviors performed differed between species as illustrated by the levels reached.

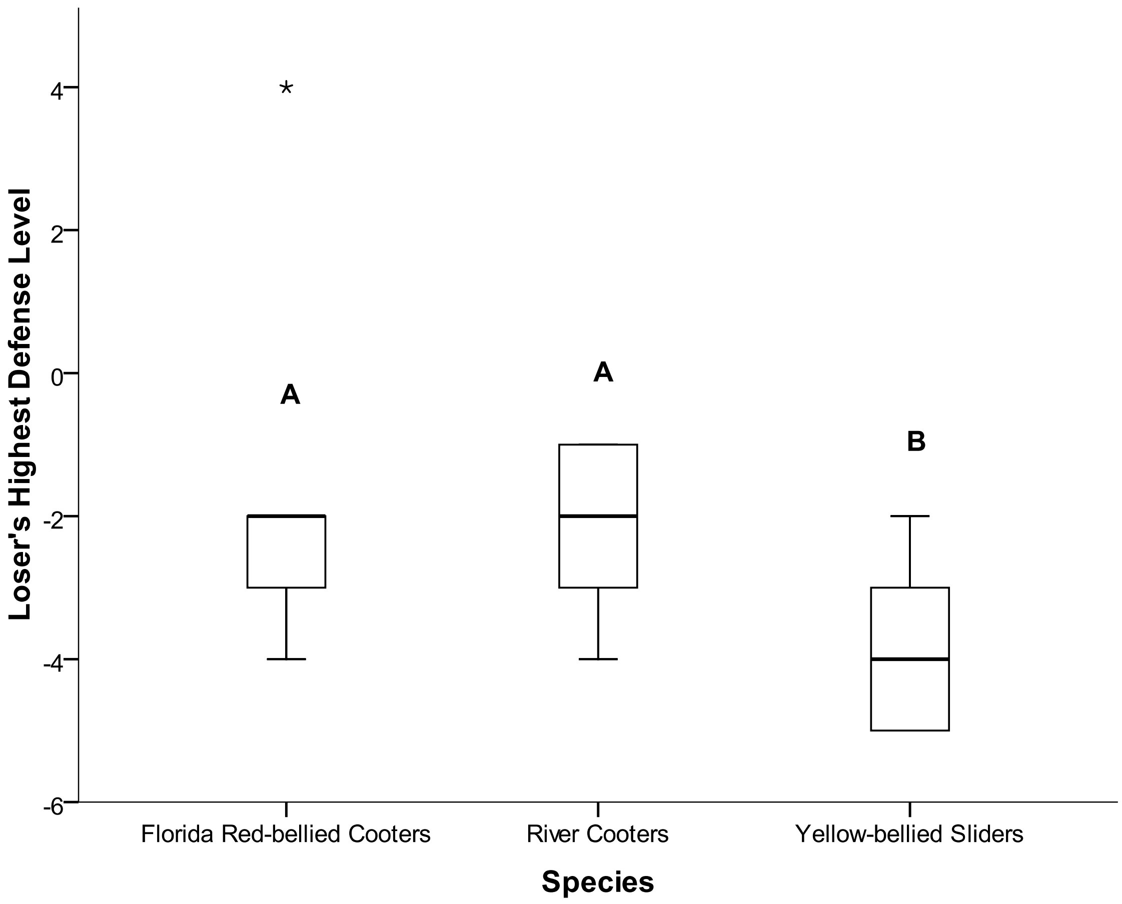


Figure 2.7. The Highest Defensive Level Reached by Losers of M–M Fights for Florida Red-bellied Cooter (*Pseudemys nelsoni*), River Cooter (*P. concinna*), and Yellow-bellied Slider (*Trachemys scripta*) groups. Each of the Aggression levels (0-¯5) represent combinations of agonistic behaviors listed in Table 2.3. This figure shows that FRBs and RCs significantly differ in the highest level of defensive behaviors reached compared to YBSs, with YBSs reaching the most intense defensive behaviors. Level ¯1 = loser looks away from winner, level ¯2 = turtles moves away, level ¯3 = turtle retracts head & limbs prior to moving away, level ¯4 = loser retreats from winner, and level ¯5 = loser flees from winner.

Figure 2.8. (A-E) Male-Male Agonistic Behaviors Exhibited During Contests are Illustrated with Florida Red-bellied Cooters (*Pseudemys nelsoni*). (A) FRB face-off in the water column, (B) Face-off on substrate illustrates that the back end of the turtles are up at an angle, with M-FRB1 demonstrating (left) tail tucked and M-FRB2 (right) snap. (C) M-FRB1 (Right) snap and tail extension, at M-FRB2 (left) who is tilting. (D) Double Gape: FRB1 (Left) offensive gape with neck extension, FRB2 (right) defensive gape - head retraction.

(A) FRB Face-off

(B) Tail Tucked (Male Left), Snap (Male Right)


(C) M-FRB1 (Right) Snap and tail extension, at M-FRB2 (left) Tilting

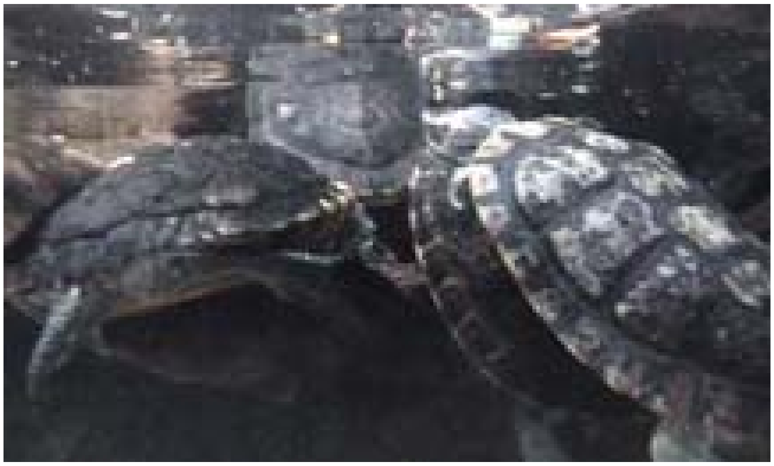

(D) Double Gape - M-FRB1 (Left) Offensive gape, M-FRB2 (right) Defensive Gape


(E) Face off interrupted - M-FRB1 (left), M-FRB2 (Center) Gape, M-FRB3 (Right)

Figure 2.9. (A-D). Male-Male Agonistic Behaviors Illustrated by *Pseudemys concinna* (RC), and Slider turtles - *Trachemys scripta scripta* (YBS) and *T. s. elegans* (RES). (A) Gape & Snap Offensive - RC2 (left) Gapes and snaps at RC3 (right) who half-gapes defensively. (B) Chase and Retreat - YBS (left) retreats from RES (Right) who is chasing him. (C) Harassment of smaller newly introduced YBS (top center), By YBS1 (left), YBS2 (right - under RES), and RES (far right). (D) Grip and Drag - YBS1 (top right) is gripping the back limb of new YBS turtle, YBS5 (bottom right).

(A) Gape & Snap Offensive (RC2 Left), Half-Gape Defensive (RC3 Right)

(B) Chase and Retreat - YBS (Left) Retreats from RES (Right)


(C) Harassment of Smaller Newly Introduced M-YBS5 (Top Center), By YBS1 (Left), YBS3 (Right- under RES), and RES (Far Right)


(D) Grip and Drag - YBS1 (Top Right) Gripping and Dragging new YBS5 (Bottom Right)

Figure. 2.10. (A-F) Male-Female Courtship Behaviors Illustrated with Florida Chicken Turtles (CHK), *Deirochelys r. chrysea*, and *Pseudemys nelsoni* (FRB) Turtles. (A) Follow - male CHK turtle (left), female CHK (right). (B) Nose-tail Touch - male CHK (left) noses females tail, female CHK (right). (C) Neck Extension & Nose-Nose - female CHK (left), male CHK (right). (D) Limb Waving - female CHK (left), male CHK (right) limb wave at female. (E) Swim Above - male FRB (top) swimming above the female FRB (bottom). (F) Titillation - male FRB (top), female FRB (bottom).

(A) Follow - Male CHK Turtle (Left), Female CHK (Right)

(B) Nose-Tail Touch - Male CHK (Left) Noses Females Tail, Female CHK (Right)

(C) Neck Extension & Nose-Nose - Female CHK (Left), Male CHK (Right)


(D) Limb Waving - Female CHK (Left), Male CHK (Right) - Limb Wave


(E) Swim Above - Male FRB (Top), Female FRB (Bottom)


(F) Titillation - Male FRB (Top), Female FRB (Bottom)

Figure. 2.11. (A - J). Other Social Behaviors Exhibited by Male-Male and Female-Female Sex Pairings Illustrated by Florida Red-bellied Cooters (FRB), *Pseudemys nelsoni*, River Cooters (RC), *P. concinna,* female Barbour Maps (B-MAP), *Graptemys Barbouri* and Southern Painted turtles (SP), *Chrysemys dorsalis*. (A) Nose-nose - FRB males. (B) Mounting- female SP (top), mounting newly introduced female SP (bottom). (C) Pin - newly introduced female SP (bottom) pinned by SP Female (D) Pinned in corner- newly introduced male FRB (far left) cornered by male FRB3 (top) who is also biting him while male FRB2 noses his tail (bottom). (E) Introduction - male-male multi-male mounting male FRB (bottom left) mounted by FRB male 2 (center) and FRB male 3 (top) & RC3 (far right top). (F) Female- Female Titillation- newly introduced female FRB (left) titillated at by the dominant female FRB1 (Right). (G) Female-Female Stare - BMAP2 (left) and BMap1 (right). (H) Female- Female Titillation - BMAP1 (left) and BMAP2 (right) titillating at each other. (I) Male-Male titillation - RC1 (top) is titillating at RC2 (bottom). (J) Male-Male Interspecies Titillation - RC3 (top) and FRB3 (bottom).

(A) FRB Males Nose-Nose Touching

(B) Mounting - Female SP (Top), Newly Introduced Female SP (Bottom)

(C) Pin - Newly Introduced Female SP (Bottom) SP Female resident (Top)

(D) Pinned in Corner - New Male FRB (Far Left), Male FRB3 (Top) Male FRB2 (Bottom)

(E) Introduction - Multi-Male Mounting- New Male FRB4 (Bottom Left), FRB2 (Center) and FRB3 (Top) & RC3 (Far Right Top)

(F) Female-Female Titillation - newly introduced female FRB (Left), female FRB1 (Right)

(G) Female-Female Stare – B-MAP2 (Left) and B-MAP1 (Right)

(H) Female- Female Titillation – B-MAP1 (Left), B-MAP2 (Right)

(I) Male-Male Titillation - RC1 (Top) and RC2 (Bottom)

(J) Male-Male Interspecies Titillation - RC3 (Top) and FRB3 (Bottom)

PART 3: TRAINING AND LONG-TERM MEMORY OF A NOVEL FOOD ACQUISITION TASK IN A TURTLE (*PSEUDEMYS NELSONI*)

Part 3 is a version of a paper with the same name published in the journal Behavioural Processes in 2007 by Karen M. Davis and Gordon M. Burghardt:

Davis, K. M. & Burghardt, G. M. 2007. Training and long-term memory of a novel food acquisition task in a turtle (*Pseudemys nelsoni*). *Behavioural Processes*, *27*, 225-230.

My use of "we" in this section refers to my co-author and myself. My primary contributions to this paper include: selection of the topic and development of goals, data design, collection, analysis and most of the writing.

Abstract

We developed a shaping procedure for training Florida Red-bellied Cooters, *Pseudemys nelsoni*, to dislodge clear plastic bottles to obtain food pellets. The animals were then trained in a 2-choice problem to choose only the bottle containing pellets. All nine turtles learned the task of knocking over bottles for food. For the discrimination task, turtles chose the correct bottle 71% on average. After two months (82-84 days), and again after another 7.5 months (228 days) of no interaction with the bottles, turtles were retested and many retained both the response and the discrimination (mean success rates 77-81%), with significant savings in retraining all turtles. The turtles showed two basic response strategies, which changed across time for some individuals. This study demonstrates that in a laboratory context turtles can learn and retain a novel skill.

Introduction

The study of behavioral plasticity and cognitive processes in diverse animals has been revitalized by the recent methods and concepts of comparative cognition (e.g., Shettleworth, 1998). Although reptiles as a group have been studied less than mammals, birds and even fish (Shettleworth, 1998; Laland, Brown, & Krause, 2003), turtles have been used in more learning studies than other reptile groups (review in Burghardt, 1977); most of these studies were conducted 30 or more years ago and focused on visual discrimination abilities, documenting that turtles have acute visual abilities and can be trained in a number of respondent and instrumental learning tasks including visual and spatial reversal learning (Kirk & Bitterman, 1963; Bitterman, 1964; reviews in Burghardt, 1977; Morlock, 1989). More recently, López, Rodríguez, Gómez, Vargas, Broglio, and Salas (2000, 2001) found that turtles' spatial learning and memory capabilities similar to those of mammals and birds. Turtles share a common ancestor with birds and mammals and are an important group for studying the evolution of cognitive abilities in vertebrates.

Turtles are ideal subjects for instrumental conditioning and discrimination tasks for several reasons. For example, turtles will train for small food rewards more readily than many other exothermic reptiles (Burghardt, 1977; Kramer 1989a). Furthermore, turtles (particularly many emydid turtles) are readily available, adapt and perform well under captivity, and are long-lived (Burghardt, 1977). Finally, turtles are highly visual, with the ability to discriminate shapes and colors in stationary stimuli (e.g., Burghardt, 1977; Arnold & Neumeyer, 1987), which makes them a favored group among reptiles for visual discrimination learning tasks.

The study species, Florida Red-bellied Cooters, *Pseudemys nelsoni,* is a semi-aquatic emydid pond turtle found only in Florida. They leave the water primarily to bask and, if female, to lay eggs (Kramer, 1986). Agonistic behavior, courtship, foraging, and other kinds of behavior have been studied in this species in the field and captivity (Kramer, 1986; Kramer, 1989 a, b; Kramer & Burghardt, 1998).

The goals of this report were to test whether turtles 1) would learn to dislodge a clear barrier (a bottle) set outside the water to obtain food, 2) solve a discrimination task (food vs. no food) by dislodging the correct bottle, the one with food in it, and 3) retain the task of dislodging the transparent plastic bottles for food reinforcement for periods measured in months.

Method

Study Subjects and Test Dates

Subjects consisted of nine Florida Red-bellied Cooters (*Pseudemys nelsoni*) raised in captivity from eggs collected and hatched in 2000 from three lakes (Lakes Apopka, Griffin & Woodruff) in North Central Florida. All nine turtles (six females, three males) were three years old at the beginning of the study and became sexually dimorphic by July 2004. At the beginning of training, the female turtles' carapace lengths ranged from 87-150mm and masses ranged from 111-385g; the male turtles' carapace lengths ranged from 120-139mm and masses ranged from 228-339g. At the start of the final tests, about a year later, females' carapaces ranged in length from 160-225mm and mass ranged from 523-1033g, while males' carapaces ranged from 70-178 mm and mass ranged from 498-634 grams. The later size dimorphism was primarily due to the fact that females grow to be larger than males. All nine turtles were individually identified by a number painted on their carapace with colored nail polish (males: nos. 2, 6, 7; females: nos. 1, 3, 4, 5, 8, 9).

The experiments, including training and discrimination trials, were split into three phases, with phase 1 (initial training) starting on November 5, 2003 (Table 3.1)[1]. Phase 1 included both training and discrimination trials and ended between November 21-24, 2003. Long–term memory trials constituted retraining and discrimination trials for both phase 2 and 3. Phase 2 started, after turtles had 2 months (82-84 days) of no interaction with the bottles and were fed

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[1] All tables and figures are in the appendix at the end of part 3.

only in the water, with test discrimination trials on February 11, 2004. Seven days later (February 18, 2004) turtles started retraining or continuation of discrimination trials as needed with phase 2 ending between April 4 and June 2, 2004. Phase 3 started on April 3, 2005, about 12 months (306-364 days) after the end of phase 2 and after 7.5 months (228 days) of no interaction with the bottles (another bottle task was run during the summer of 2004 and ended August 18, 2004).

Housing

Turtles were housed in two tanks during phase 1, with the three larger turtles in one tank and the other six turtles in the second tank. As the turtles grew the group of six turtles was separated into two tanks of three turtles. All tanks were constantly filtered (Fluval 4) clear plastic aquaria (70 x 34 x 44 cm). Each aquarium had two rows of stacked bricks for basking (20 x 20.5 x 44 cm), the top of which was just above the water level, where a suspended 150W UV sunlamp was located. The room temperatures ranged from 26-29 ^{0}C air and 25-30 ^{0}C water for phases 1 and 2. Phase 3 testing was conducted in a different room (with a one-way window) with temperatures ranging from 24-29 ^{0}C air and 23-28 ^{0}C for water. The temperature on the bricks containing the bottles and food was at least 30 ^{0}C.

Turtles were kept on a 12L:12D cycle (0830-2030) with training and discrimination trials run mostly from 1230-2030 hrs, but ranged between 1000-2115 hrs due to scheduling problems that led to lights remaining on later during one test session. Since testing of all nine turtles in phases 2 and 3 on the same day took 6 hrs or more, time of day effects were controlled by randomizing the order turtles were tested each test day. During normal maintenance and throughout the experiments, the turtles were typically fed three times a week. As the turtles were usually tested three times a week, they received their normal diet exclusively during the training and testing phases. Each turtle was given the same number of their standard diet food pellets (Turtle Brittle, Nasco International, Inc, Atkinson, Wisconsin) during the training and trial stages. Turtles were trained and tested individually in their home aquaria at the standard room temperature for all three phases. During training and test trials, all turtles from the particular tank being tested were placed in the holding tank (identical to each of the home aquaria, see above), then the turtle being tested would be placed from the holding into the test tank (home tank), and replaced in the holding tank after each trial. The order of tanks chosen and individual turtles tested within each tank was randomized daily.

Training

The instrumental task involved the turtle leaving the water to climb onto a brick and knocking over one of two clear plastic bottle (5.3 x 3.5 x10 cm high with a 1.1 cm high x 2.4 diameter circular base) to obtain a food-pellet reward. The end goal/task for the training trials was for turtles to knock over either of two transparent plastic bottles which only contained food inside for food reinforcement. Thus, to complete the training task, turtles had to climb up out of the water, and knock over either of the plastic bottles. The training task was challenging for these semi-aquatic turtles, since they normally find food and eat in the water, and must return to the water to swallow their food.

Training involved 5 stages of shaping (Figure 3.1) where animals moved on to the next stage after they could perform the stage task for 6 consecutive trials within a test day. *Stage 1:*

approach involved shaping animals with food pellet reinforcement to approach the bricks. Shaping procedure varied depending on the initial behavior of individual animals and was modified for each individual turtle. For example, during stage 1, reinforcement for turtle behaviors involved dropping food pellets in front of the turtle when it stuck its head out of the water, then when it stuck its head out of the water and faced the bricks, until ultimately it was only fed for approaching and touching the bottom brick. *Stage 2: climb* involved shaping turtles to climb up the lower brick and emerge completely out of the water to grab pellets out of the water on top of the upper brick. *Stage 3: topple one bottle* involved shaping turtles to topple one plastic bottle with 2 pellets under it and 2 pellets in front of and directly against the bottle. To ensure that the bottle tipped over easily, the bricks were elevated during training to a slight angle so that, if the turtle touched the bottle, it would topple over. Turtles typically knocked the bottle over (seemingly by accident), when biting at the pellets in front of the bottle, facilitating learning that food could also be obtained from inside the bottle. Turtles moved onto the next stage once they reliably and deliberately knocked the bottle over by using their head or foot. Once an animal no longer accidentally knocked the bottle over, toppling the bottle consisted of an animal looking at the bottle and using its head or foot to knock it over. *Stage 4: topple two bottles* involved the introduction of a second bottle with food in front of and underneath the bottles as in stage 3. During stage 4, the turtles were allowed to go to either bottle and then were also allowed to knock over the second bottle before being removed from the tank (non-correction method) so that the turtle would learn that food could be found in either bottle. As they progressed at this stage, the number of pellets that were put in front of the bottles was decreased from two to one. *Stage 5: only topple bottles containing food* involved exposing turtles only to bottles with food only inside, not outside, the bottles. Initially some animals were shuttled back and forth between stages 4 and 5 to keep them interested in the task as they learned to topple the bottles over with food only inside of them. Stage 5 was the final training stage with the goal to topple plastic bottles for food reinforcement in which food was visible under both bottles. When turtles reached criterion they moved on to the discrimination trials.

The training trials for phase 1 were run every day for 9 consecutive days, 6-8 trials a day, for 8 of 9 animals despite some of the 8 reaching criterion by the end of day 7. One turtle took 16 consecutive days to reach criterion during phase 1. When the first 8 turtles had reached criterion, they began discrimination trials.

At the start of all trials, the turtles were gently released at the end of the tank opposite the bricks. A stop watch recorded times from release to when they obtained reinforcement or knocked over a bottle. The platform brick and bottles were rinsed between trials and bottles replaced when severely scratched.

Discrimination Trials

Discrimination tests consisted of testing the subject's success rate for choosing (and toppling) a bottle containing a piece of food vs. an identical bottle that did not contain food. To avoid confounding side preferences, we used the L-R ordering sequences published by Fellows (1967). A non-correction technique was used in that turtles were removed from the test tank after their first choice, whether correct or not. However, all turtles regardless of willingness to perform or success rate received their full diet, with the remaining food pellets fed after the completion of a particular test day.

Latencies (sec) to reach the lower submerged brick, to knock the bottle over, and to begin eating were recorded with a stopwatch, along with the method of knocking the bottle over, side the bottle was on, and instances of bottle biting. Due to a strong relationship among the latency measures, only data for the most relevant latency, to knock over the bottle, are presented here.

Turtles had three different methods for knocking the bottles over: one, the turtle bit the bottle until it fell over, either head sideways or straight forward; two, the turtle bumped the bottle with his or her nose, either by retracting its head then darting it forward while stationary on the bricks, or by pushing forward with the head extended with moving momentum; or three, the turtle swiped sideways at the bottle, pushing it with either their right or left foot, which involved extending the foot out and sideways. During phase 1 discrimination task trials, each animal was run every other day, 12 trials a day across 4 test days for a total of 48 trials (Table 3.1).

Retention/ Memory Trials

After the completion of phase 1, turtles were fed in the water with no exposure to bottles for 10 weeks prior to the start of phase 2, which started on February 11, 2004. After the completion of phase 2, turtles had another extended period without exposure to the bottles, with phase 3 beginning on April 3, 2005 (Table 3.1).

Prior to retraining in phases 2 and 3, all turtles were first tested with a discrimination trial to determine their retention of the discrimination task. For phases 2 and 3, both retraining and discrimination trials were run every other day 3 times a week, for 3-6 trials a day for a total of 28-48 trials for phase 2, and 6 trials a day for a total of 42-54 trials for phase 3 (Table 3.1). Retraining was similar to training in phase 1, with turtles being retrained for each of the 5 stages until they reached criterion prior to starting discrimination trials. If turtles performed the discrimination task on the first day for 6 consecutive times, they skipped retraining and continued with the discrimination trials.

The researcher was in the room with the turtles during phases 1 and 2 throughout the entire tests, but was always behind the turtles (with turtle facing the opposite direction toward the bottles) during testing. Inter-observer reliability control tests were run on a subset of the data in phase 3 to determine if a naïve observer would record the same events similarly. Furthermore, in phase 3 the animals were tested in a nearby room containing a one-way glass observation window; a subset of phase 3 tests was run with the observer outside the room and behind the one way glass to control for observer effects or researcher cueing. No obvious observer effects were found. The turtles seemed to be under minimal stress as they had been handled and in contact with humans in the laboratory from the time of hatching and behaviorally anticipated feeding opportunities.

Statistical Analysis

Friedman Two-way Analysis of Variance by Ranks and non-parametric Nemenyi multiple comparisons were run to compare training day data across phases with adjusted alpha values according to Zar (1999). Latency to completion of the task was compared across sessions using a Repeated Measures ANOVA and Tukey’s post-hoc test for multiple pair-wise comparisons. Pearson’s Chi-square tests were used to compare individual success rates across phases for each turtle.

Results

Training

All nine turtles learned the training task, completing all 5 phases of training and meeting the criterion for inclusion in the discrimination trials (6-8 consecutive successful trials) for all 5 stages.

Individual animals varied in how quickly they learned the training task stages. Some animals became inactive or swam at the opposite end of the enclosure from the bricks at various times throughout training. If turtles did not show any interest in the task they were taken out after 4 min. and put back into the holding tank between training trials. These animals varied in their reactivity, but tended to be slower at learning the task than the turtles that showed only food motivated behavior.

Discrimination Trials and Retention

All nine turtles learned the training task in phase 1 (Table 3.1) with an average success rate for discrimination trials of 71.4%. After 10 weeks of no interaction with the bottles, 6 turtles still performed the original task without any retraining and discrimination success was high (Table 3.1). When subsequently tested again after 7.5 months of no interaction with the bottles, 8 of 9 performed the task with no retraining, indicating long-term memory for this task. All nine turtles performed the discrimination task by day two and the average success for phase 3 was

76.9% (Table 3.1). Average success rates were thus above chance levels, ranging from 71-81% for all 3 phases, but did not differ significantly across phases (Friedman test, $\chi^2_{2,9} = 2.80$, $P = 0.247$). Inter-observer agreement for latency to topple bottle and bottle choice taken on a subset of 36 trials across 3 animals in phase 3 were both 100% (Pearson correlation: $r = 1.00$, N=36, $P = 0.0001$).

Despite the fact that the average success rate did not differ across phases, individual animals did differ over phases, with some animals increasing in success rate from phase 1 to phase 2, whereas some animals developed side preferences resulting in decrease in success rate across sessions (Figure 3.2). Success rate differed significantly across phases for turtles no. 2 ($\chi^2_{2,100} = 13.13$, $P < 0.002$) , 7 ($\chi^2_{,100} = 13.13$, $P < 0.002$) , 8 ($\chi^2_{2,149} = 13.32$, $P < 0.002$), and 9 ($\chi^2_{2,145} = 8.35$, $P < 0.02$). Turtles 7, 8 and 9 increased their success rate from phase 1 to phases 2 and 3, whereas turtle 2 developed a side preference and his success rate decreased from phase 1 to 2 and 3.

In contrast with the discrimination trials, the number of training days for phases 1, 2 and 3 differed significantly (Friedman test, $\chi^2_{2,9} = 16.8$, $P < 0.0001$) (Figure 3.3). Nemenyi, non-parametric multiple comparisons tests (Zar, 1999) showed that phase 2 training took significantly fewer days than phase 1 ($q_{2,9} = 11.11$, $P < 0.005$). Phase 3 training took significantly fewer days than phase 1 ($q_{2,9} = 13.89$, $P < 0.001$) and phase 2 ($q_{2,9} = 6.0$, $P < 0.049$) (Figure 3.3A).

The latency to task completion (knocking the bottle over) significantly differed across phases (Repeated Measures ANOVA, $F_{2,9} = 6.318$, $P = 0.01$) with a significant increase between phase 1 and phase 3 (Tukey's test, $q_{2,9} = 18.78$, $P = 0.02$) (Figure 3.3B). Phase 2 was intermediate and did not significantly differ from phase 1 (Tukey's test, $q_{2,9} = 9.444$, $P > 0.05$) or phase 3 (Tukey's test, $q_{2,9} = 9.333$, $P > 0.05$) (Figure 3.3B).

There were also individual strategy differences across animals and phases. Most notably, turtle 5 was the first to use a slow (mean 39.1 s latency) to task completion. This 'deliberate' strategy during phase 1, involved pausing at the various task stages and looking in both directions, whereas turtles 4 (mean 6.8 s) and 8 (mean 8.4 s) exclusively used a faster, 'impulsive' strategy with little evidence of assessing the two stimuli. Using the impulsive strategy resulted in lower success rates (especially noticeable in phase1).

Discussion

All turtles completed the 5 stages of training, solved the discrimination task, and exhibited long term retention for the task across phases. Since the turtles might smell the food as well as see it, future experiments are needed to isolate the specific cues used. Although food motivation can change with season and age, our results suggest this training and testing method was effective regardless of these possible factors.

The increase in time to task completion, coupled with observations of animals during tasks, suggests that the turtles' strategies changed across phases. Specifically, there was a change from most animals swimming quickly to the bottles, often without looking at both ('impulsive'), to turtles pausing and looking at both bottles ('deliberate') at various stages of the task (i.e., when first put in the tank, touching the lower brick, and or when directly next to the first choice bottle). The increase in latency to task completion seen in Figure 3.3B was mirrored by a switch in strategy from 'impulsive' to 'deliberate' for most turtles during phases 2 and 3. This switch in strategies may be a result of turtles learning the rules of the new task, i.e. only one bottle contains food and only one choice is allowed. Inspection of individual differences indicated that the strategies used may have been influenced by how quickly turtles reached training stage 5 in phase 1. However, differences in turtle strategies could be a result of behavioral syndromes (i.e. a set of correlated behaviors expressed within a particular behavioral context or across contexts: Sih, Bell, Johnson, & Ziemba, 2004). Interestingly, a study on responses to handling by wild caught slider turtles resulted in two behavioral responses that parallel the two strategies found in the turtles in this study: handling led to turtles becoming either hyperactive or passive and still

(Cash & Holberton, 1999). Although some turtles shifted to a deliberate from an impulsive strategy, others using the more impulsive approach developed side preferences, resulting in a decreased success rate across phases (see Figure 3.2). Further studies will explore this phenomenon.

Previous studies of turtle discrimination focused on discrimination only, but this study shows, in a laboratory context, that turtles can retain information about a food task for as long as 7.5 months (228 days). This finding of long-term memory in *Pseudemys nelsoni* parallels in length the long-term memory abilities in birds (7-9 months) for caching location (Balda & Kamil, 1992).

Turtles are long lived reptiles, with many having the ability to live at least 20-60 years and probably longer. Furthermore, although sea turtles are known for nest site homing, freshwater turtles also show nest site fidelity (Freedberg, Ewert, Ridenhour, Neiman, & Nelson, 2005; Rowe, Coval, & Dugan, 2005). For example, a long-term study of 7 European Pond Turtles, *Emys orbicularis*, showed some marked females exhibited nesting area fidelity for over 10 years and most exhibited nest site fidelity for 2-4 consecutive years (Mitrus, 2006). Turtles returning to nest sites across years, coupled with turtle longevity indicate the adaptive significance of turtle long-term memory found in this laboratory study.

Acknowledgments

We would like to thank the Reptile Ethology lab**;** Lauren Kirby, Kerry Hansknecht, Rita Mehta, and John Placyk for comments on earlier presentations of parts of this material. The Florida Cooperative Fish and Wildlife Research Unit for provided the *Pseudemys nelsoni* eggs, which Drew Crain incubated and hatched at Maryville College. The Chicago Herpetology Society, the UT Department of Psychology, and the UT Reptile Ethology Research fund helped with funding of this project. This research was conducted under approved protocol #222 of the University of Tennessee Animal Care and Use Committee.

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Appendix

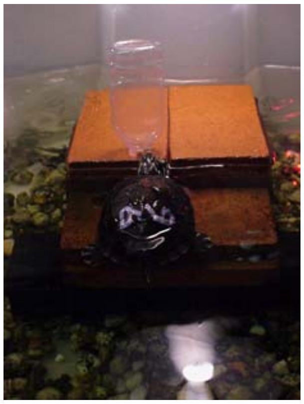
Table 3.1. Summary of Phase Details. The start month and number of training days, test days and discrimination trials as well as mean success rate (+/- 95% confidence intervals) for each of the three phases.

	Phase 1	**Phase 2**	**Phase 3**
Start month	November 2003	February 2004	April 2005
Number of training days	9 days for 8 Ss, 16 days for 1 S	6 Ss performed start of day 1; 3 Ss 8 days retraining	8 performed day1; by end of day 2 last animal retrained
Number of test days	4 days for 8 Ss, 1 day for 1 S	8-11 days	8 days
Number of discrimination trials	48 for 8 Ss 7 for 1 S	28-48 depending on amount of retraining	42-54 depending on amount of retraining
Average success rate (% correct choices)	71.4% ± 9.3%	80.6% ± 7.9%	76.9% ± 8.7%

Figure 3.1. The Five Stages of Training. Turtles had to reach criterion (6-8 consecutive successful trials) for each stage task before they moved onto the next stage. *Stage 1:* approach lower brick for food; *Stage 2:* approach and eat off top brick; *Stage 3:* topple bottle when there was food inside and outside; *Stage 4:* topple bottles when there are two bottles with food inside and out; *Stage 5:* topple bottles when there was food only inside, not outside the bottles.

Stage 1= Approach

Stage 2= Climb



Stage 3 = Topple one bottle

Stage 4 = Topple two bottles

Stage 5 = Only topple bottles containing food

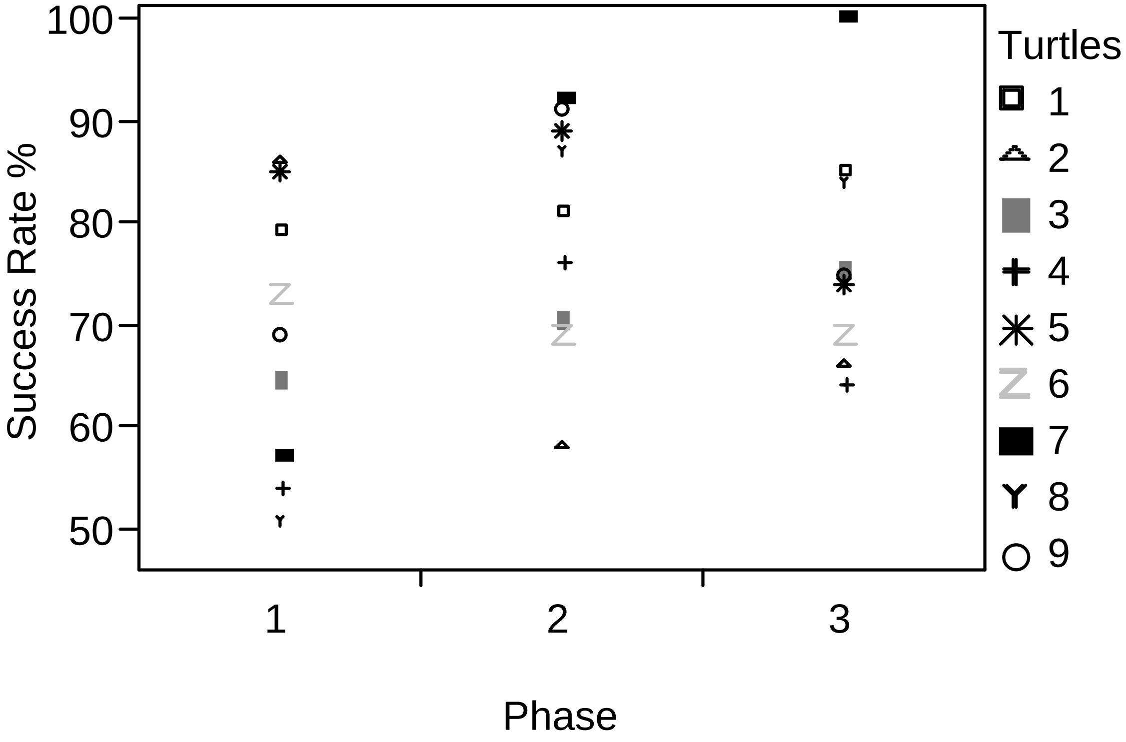
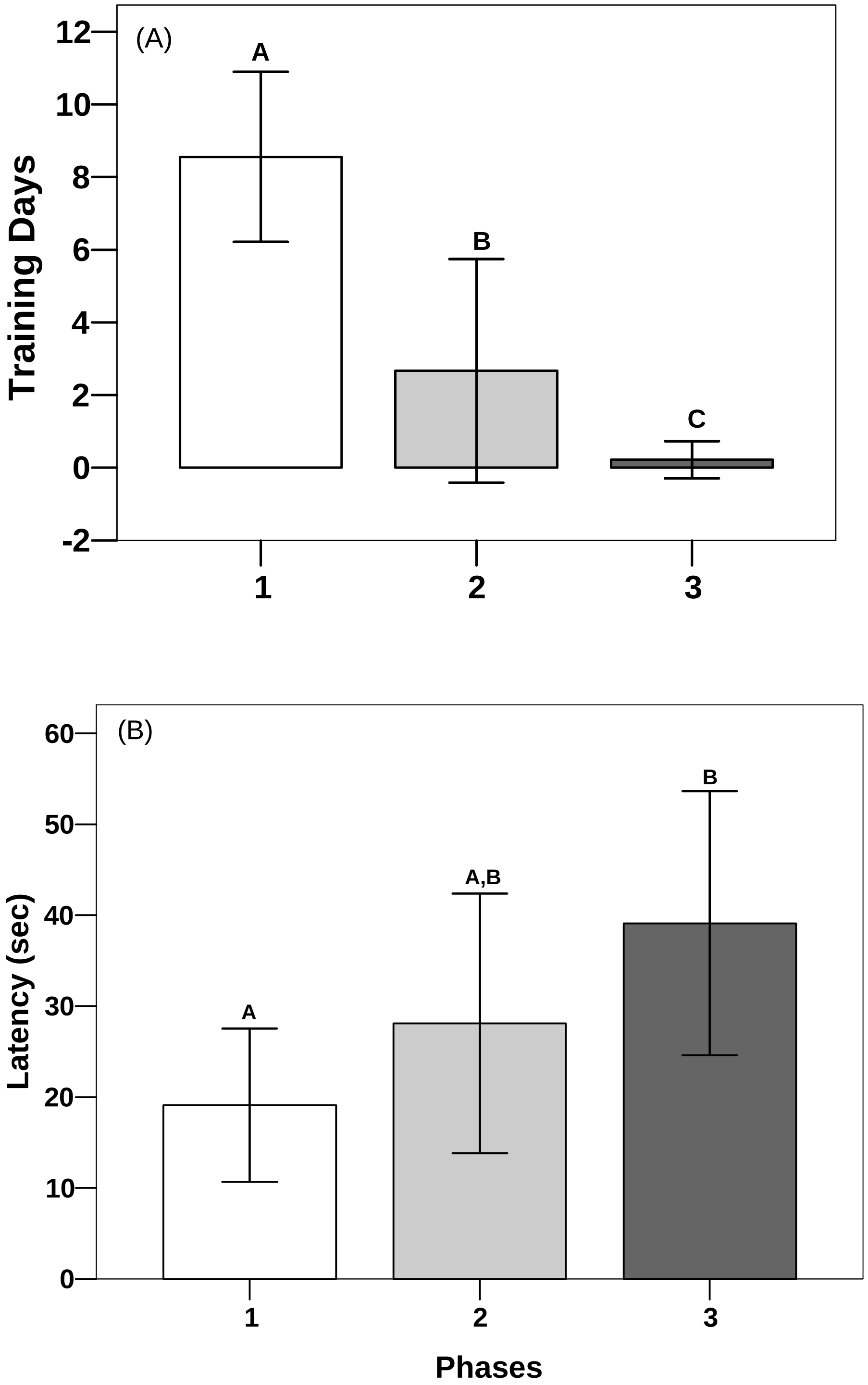


Figure 3.2. Each of the 9 Turtle's Average Success Rates for Each of the Three Phases. There was individual variation in turtle success rate after the first phase, with some improving across phases while others did worse, primarily due to developing side preference.

Figure 3.3. (A) The Mean Number of Training Days and (B) Mean Latency to Task Completion for Each Phase. (A) The mean number of training days for each phase. Lines represent 95 % Confidence Intervals. Letters above the bars indicate the results of the Nemenyi non-parametric multiple comparisons tests. Different letters reflect significant differences between the phases. (B) The mean latency to task completion (knocking the bottle over) with 95% Confidence Intervals. Duplicate letters above the bars show that not all phases significantly differed from each other.


(A)
Training Days
12
10
8
6
4
2
0
-2
A
B
C
1
2
3
(B)
Latency (sec)
60
50
40
30
20
10
0
A
A,B
B
1
2
3
Phases

PART 4: EVIDENCE OF LONG-TERM RETENTION OF A VISUAL TASK BY FLORIDA RED-BELLIED COOTERS (*PSEUDEMYS NELSONI*)

Part 4 is a version of a paper by the same name which will be submitted to the Journal of Comparative Psychology by Karen M. Davis and Gordon M. Burghardt:

Davis, K. M. & Burghardt, G. M. (in prep). Further evidence of long-term retention of a visual task by Florida Red-bellied Cooters (*Pseudemys nelsoni*). To be submitted to the J*ournal of Comparative Psychology*.

My use of "we" in this section refers to my co-author and myself. My primary contributions to this paper include: selection of the topic and development of goals, data design, collection, analysis and most of the writing.

Abstract

We tested the long-term memory capability of turtles for a novel foraging task involving visual discrimination. Freshwater pond turtles (Family Emydidae) are long-lived, can be easily conditioned with small food rewards, and are adept at visual discrimination. In this study we tested nine Florida Red-bellied Cooters, *Pseudemys nelsoni*, on their retention and savings for both a procedural food acquisition task and visual discrimination task learned in a previous experiment (Part 3). The turtles were tested and retrained after two months, after another 7.5 months, and finally after two additional years of no interaction with the test apparatus. Turtles retained memory for the choice task and needed little retraining throughout. Furthermore, in another visual discrimination task, turtles showed 100% retention after 3.5 months of no testing. Odor-controlled tests were performed to eliminate non-visual cues. Turtles showed no difference in correct choices between normal and odor-controlled tests. The latter tests confirmed that turtles were using visual cues to solve the task. Thus, in a laboratory context, turtles demonstrate long-term memory of visual discrimination tasks.

Introduction

The field of comparative cognition has re-emphasized the need to study the behavioral plasticity and cognitive processes of a variety of animals (e.g., Shettleworth, 1998). Although an increasingly diverse group of mammals, birds, and even fish is being studied (Shettleworth, 1998; Laland, Brown, & Krause, 2003), non-avian reptiles continue to be under-represented in comparative cognition research (López et al., 2000, 2001; Davis & Burghardt, 2007; Wilkinson, Chan & Hall, 2007).

In addition to being a phylogenetically interesting group (Rieppel, 2008) that needs to be included in comparative cognitive studies, turtles are particularly advantageous subjects for investigations of long-term retention. First, turtles have sophisticated visual abilities and can be trained in many respondent, instrumental tasks and especially visual discrimination tasks (Burghardt, 1977; Morlock, 1989; Davis & Burghardt, 2007). Second, turtles are known for their longevity (Gibbons, 1987; Lizgus, 2006), and many return to the same nest sites annually and some show nest site fidelity for up to 10 years (Bowen et al., 1992; Freedberg, Ewert, Ridenhour, Neiman, & Nelson, 2005; Rowe, Coval, & Dugan, 2005; Mitrus, 2006). Thus, it is surprising that turtle long-term memory has rarely been studied.

Animal retention studies have focused mainly on short "long-term" memory (which includes anything from 30 seconds to 24 hours); these have demonstrated retention in rats, primates, birds, fish, and honeybees (review in Pearce, 2008). Turtle retention ability for up to 5 minute inter-trial intervals has been recently noted by Wilkinson et al. (2007).

Long-term retention measured in weeks, months, and years in all non-human animals has been studied considerably less often than that of shorter term (within 24hrs) memory. The type of memory, length of retention interval, and number of studies varies considerably between species. Experimental studies of learning and memory have demonstrated that rats (life span 2-3 years) remember conditioned shock stimuli for 90 days (Gleitman, 1971) and spatial stimuli for 21 days (Broadbent, Squire & Clark, 2007). Longer lived Corvids remember cache sites for up to 9 months (Balda & Kamil, 1992), and pigeons can retain visual discrimination of pictures for 2-5 years (see Pearce, 2008). A sea lion remembered how to solve visual match-to-sample discriminations after as long as 10 years (Reichmuth-Kastak & Schusterman, 2002). Elephants have a life span of 70 years, but their memory has rarely been studied experimentally, with one study demonstrating visual discrimination retention for 8 years (reviewed in Pearce, 2008). The experimental studies on long-term memory for the animals listed above demonstrate the extent of long-term memory that has been demonstrated based on the few experiments and limited time periods measured. It is likely therefore, that these studies' results may represent retention intervals far shorter than these species long-term memory capacity.

Turtles, like elephants, have a 70- plus year lifespan, but long-term retention studies involving this group are also rare. Although a number of learning studies have focused on turtles (review in Burghardt, 1977; Morlock, 1989), most of these did not concern memory. A few studies have briefly looked at turtle memory. Studies of the dorsal and medial cortex lesions to investigate brain areas involved in turtle learning and memory involved only a 5 day retention period (López, Gómez, Varagas, & Salas, 2003a; López, Varagas, Gómez, & Salas, 2003b). Furthermore, there is one study of aversive conditioning in turtles over a 60 day retention period

(Spigel, 1964), and a study of chemical-sense memory demonstrated retention by turtles for a 6 month study period (Grassman, 1993).

In a prior paper we demonstrated that turtles could be trained in both a procedural food acquisition task and a visual discrimination task and they could retain considerable information about the tasks for at least 10 months (Part 3[1], Davis & Burghardt, 2007). This evidence of long-term retention for a visual discrimination task in our turtles prompted the present study, which focuses on long-term memory of turtles measured in years. Experiment 1 of the present study, including training and discrimination trials, was split into four phases. More detail of the methods for phases 1-3 (fall 2003 - spring 2005) are described in Davis and Burghardt (2007). This earlier paper focused on the 5 stages of the initial training to the procedural task in phase 1. Davis and Burghardt (2007) also focused on the procedure of retraining the turtles prior to the discrimination tests for phases 2 and 3 (for review of phase details see Table 4.1[2]). Phase 1 involved the initial training to the procedural task and discrimination task. Phase 2 started after turtles had 2 months of no interaction with the bottles and were fed only in the water, with test discrimination trials. Phase 3 started on April 3, 2005, about 12 months after the end of phase 2 and after 7.5 months of no interaction with the bottles (for more detail see Davis and Burghardt, 2007). Although this previous experiment noted retention intervals for the turtles, the focus was on average success rates for turtles' retention and savings data were not analyzed. Therefore in experiment 1 of this study, phases 1-3 were analyzed to test for retention and savings of both the procedural and discrimination tasks. Phases 1-3 retention and savings data were then compared

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[1] Part 3 of this dissertation is a version of the Davis and Burghardt, 2007.

[2] All tables and figures are in the appendix at the end of part 4

to additional memory tests (phase 4) which were run during this study. In phase 4 an additional odor control was run to be sure turtles were only using visual cues to solve the discrimination task.

The goals of experiment 1 of this study were 1) to determine if turtles had the ability to remember both a procedural and a visual discrimination task for an additional longer period measured in years; 2) to analyze more thoroughly the retention data for the already noted periods of 2 months, 7.5 months, and 10 months (Davis & Burghardt, 2007) and compare the details of these with a longer interval measured in years; and 3) to conduct odor-controlled tests to determine if the turtles were solving the task using vision.

Experiment 2 involved testing the turtles' ability to learn and retain visual information for a different visual task with black/white bottles where food pellets were not visible. The goals were 1) to determine if turtles could learn and retain information about a different visual discrimination task not directly associated with food and 2) to confirm that turtles were able to solve the task using only visual cues by implementing an additional odor control.

Experiment 1: Opaque Bottle Tasks

Experiment 1 (phase 4) started on March 2007, approximately 2 years after the completion of phases 1-3 (Table 4.1), which are reported in more detail in Davis and Burghardt (2007). Between phases 3 and 4, turtles had no interaction with the bottles. Phase 4 started on March 23, 2007 and ended on April 13, 2007. The specific goals of this experiment were 1) to determine if turtles had the ability to remember both a procedural and a visual discrimination task for a longer period measured in years; 2) to analyze the retention data for the already noted periods of 2 months, 7.5 months, and 10 months and compare the details of these with a longer interval measured in years; 3) evaluate individual differences in learning and retention, and 4) to conduct more stringent odor-controlled tests to determine whether the turtles were solving the task using visual cues alone.

Method

Subjects

Subjects were the same nine captive-raised Florida Red-bellied Cooters (*Pseudemys nelsoni*) used in an earlier study (Davis & Burghardt, 2007). All nine turtles (six females, three males) were sexually dimorphic and seven years old during this experiment. Females' carapaces ranged in length from 160-225 mm, and their masses ranged from 527-1526 g. Males' carapaces ranged from 152-178 mm, and their masses ranged from 498-735 g. All nine turtles were individually identified by a number painted on their carapace with colored nail polish.

Housing

After the completion of phases 1-3, turtles continued to grow larger so that by December of 2006, prior to the current study, all 9 turtles were moved to a larger enclosure. Turtles were housed in a circular enclosure (60 cm deep x 146 cm diameter) ¾ full of water (800 l, see part 5, Figure 5.1). Full spectrum lights were programmed to come on for 6 hours (1100-1700 h) to mimic when sunlight would be at its height. The room's overhead florescent lights were kept on a 12L:12D (0830-2030) cycle.

Turtles were normally fed NASCO turtle pellets and beetles *(Tenebrio molitor)* individually every other day by being taken out of their home enclosure and placed in their feeding aquarium, which was also the testing apparatus as in phases 1-3. The turtle pellets were also their reward during testing. Air temperature in the housing and testing room ranged from 25-26 ^{0}C. Water temperature ranged from 24-25 ^{0}C in the social housing tank and 26-28 ^{0}C in the testing tank.

Procedure

Turtle retention trials for phase 4 were run between 1240-1630 hours with time of day effects controlled by randomizing the order turtles were tested each test day. During normal maintenance and through the trials turtles were fed the same diet three times a week as in phases 1-3. Furthermore, turtles were tested in the same feeding and testing aquaria (Figure 4.1) as in phases 1-3 (see part 3) with the only difference being that in phase 4 turtles were housed in a different social enclosure described above (see also part 5, Figure5.1).

Instrumental Procedural Task

The instrumental procedural task (stage 5 of the training task) involved the turtle leaving the water to climb onto a brick and knock over either of two clear plastic bottles for food reinforcement (for more detail see part 3, Davis & Burghardt, 2007). The training task was challenging for these semi-aquatic turtles, since they normally find food and eat in the water, and they must return to the water to swallow their food. Turtles were given 3 training sessions per week with 6 trials per session.

Prior to retraining in the earlier phases 2 & 3 and the present experiment, phase 4, all turtles were first tested with a discrimination trial (see *Discrimination trials* below) to determine their retention of the discrimination task. As with phases 2 and 3, both retraining and discrimination trials were run every other day three times per week (typically MWF), six trials per day, for a total of 24-60 trials for phase 4. Retraining was similar to training in phase 1, with turtles being retrained for each of the five stages of training (Davis & Burghardt, 2007) until they reached criterion (dislodging the bottle six out of six times) prior to starting discrimination retention trials. If turtles performed the discrimination task on the first day six consecutive times, retraining was skipped and discrimination trials were run.

At the start of all trials, the turtles were gently released at the end of the tank opposite the bricks. Latency from the time of release to the acquisition of food or toppling of a bottle was recorded with the aid of a stopwatch. The platform brick and bottles were rinsed between trials, and bottles were replaced when severely scratched.

Discrimination Trials

Discrimination trials consisted of testing the subject's success rate for choosing (and toppling) a bottle containing a piece of food vs. an identical bottle that did not contain food (Davis & Burghardt, 2007).

Odor Controls

To control for any possible food odor emanating from under the bottle, an odor control was implemented by using a pellet sealed inside one of the two bottles. Both bottles during odor control trials had a clear plastic cover glued to the base of the bottle (the bottle opening which was face down on the brick) with epoxy. The bottle that contained the food pellet had the pellet inside the bottle glued to the inside of the clear plastic cover. Odor-control trials were otherwise identical to normal-bottle trials and were alternated with the latter to determine if there was a difference in success rate between the two. Furthermore, to ensure that turtles were choosing the bottle containing the pellet as only a visual cue, turtles' responses were reinforced with food from outside the enclosure in both the control and normal trials. Rewards were delivered by dropping food (beetles, *Tenebrio molitor*, or turtle pellets) in front of the turtle with forceps when an animal made the correct bottle choice.

Data Analysis

We used retention and savings as our two measures of the turtles' long-term memory ability for the procedural and discrimination tasks. ***Retention*** is measured as the percent of trials in which turtles responded correctly on the first day or two of testing. If turtles reached criterion on the first day, they were rated as having reached full retention. Criterion for the procedural (training) task was 6 out of 6 trials correct and the criterion for the discrimination task was 5 out of 6 trials correct. The discrimination task was much more difficult than the procedural task so criterion for the discrimination task was set at 5 out of 6 correct. ***Savings*** is measured as the difference between the number of trials to reach criterion for either the procedural or the discrimination tasks in phases 2-4 vs. the number of trials in phase 1 (the initial task training phase).

Statistical Analysis

Friedman Two-way Analysis of Variance by Ranks was run to compare number of trials to criterion across all 4 phases for both the procedural and discrimination tasks. To determine which phases were contributing to the significant results, Wilcoxon matched- pairs signed-rank tests were run with Holm's procedure for alpha adjustments (Aickin & Gensler, 1996). Finally, binomial tests were run for each turtle by combining two of their best consecutive sessions at each phase to determine each turtles' individual success rate for each phase. Pearson's Chi-Square tests were run to compare the normal and odor control trials for the odor control procedure.

Results

Procedural Task

The number of training trials to reach criterion for the procedural task differed significantly across the 4 phases (Friedman test, $\chi^2_{3,9} = 22.88$, $P < 0.001$; Figure 4.2).A one-tailed Wilcoxon matched-pairs signed-rank tests with Holm's procedure for alpha adjustments

(Aickin & Gensler, 1996) showed that turtles required significantly fewer trials to reach criterion during retraining in phase 2 ($Z_9 = -2.67$, $P = 0.004$), phase 3 ($Z_9 = -2.68$, $P = 0.0035$), and phase 4 ($Z_9 = -2.68$, $P = 0.0035$) than during initial training in phase 1 (Figure 4.2). These results demonstrate savings by the turtles for the procedural task. Furthermore, 6 out of 9 turtles during phase 3 and 8 out of 9 turtles during phase 4 showed full retention for the task on day one.

Visual Discrimination Task

The number of trials to reach criterion (5 out of 6 correct) in the visual discrimination task differed significantly across the 4 phases (Friedman test, $\chi^2_{3,8} = 10.57$, $P = 0.014$; Figure 4.3). All but turtle ID 9 were included as 9 did not complete the criterion within the 48 trial time frame, like the other turtles in phase 4, due to a side preference, which it picked up in phase 3 and retained into phases 4. Since this animal had to be retrained, it was an outlier, adding noise to the visual discrimination data and was excluded only from the visual discrimination task analysis. Wilcoxon one-tailed signed-rank tests with Holm's procedure for alpha adjustments (Aickin & Gensler, 1996) showed that during memory trials in phase 3 ($Z_8 = -2.12$, $P = 0.017$) and phase 4 ($Z_8 = -2.38$, $P = 0.009$), turtles took significantly fewer trials to reach criterion with the discrimination task than during phase 1. This demonstrates savings by the turtles for the discrimination task. During phase 3, retention for the visual discrimination task was demonstrated by 2 out of 9 subjects reaching criterion (5 out of 6 correct) on the first day. During phase 4, even more turtles exhibited full retention on the first day (4 out of 9 reached criterion), and by day two, 3 more turtles reached criterion. There was no significant difference between the normal trials (pellet not sealed inside the bottle) and the control trials with the extra odor control.

These results provide evidence that turtles are using visual cues without odor cues to solve the task (see Table 4.2).

Individual Turtle Success Rate Across Phases

All turtles showed greater-than-chance success rates (67-100%) during all phases. Most turtles chose the correct bottle significantly above chance (binomial test) in which the criterion was set at minimum of 10 out of 12 trials correct over two consecutive test days (Table 4.3).

Discussion

In experiment 1, turtles took significantly fewer trials to reach criterion for the procedural task in Phases 2, 3, and 4, which demonstrated that the turtles had savings for the task over a period as long as 2 years. Furthermore, for phases 3 and 4 many turtles showed full retention for the procedural task. What is even more impressive is that turtles also showed savings and retention for the discrimination task for as long as 2 years. In addition to having savings for up to two years, the turtles showed improved savings and retention during Phase 3 and 4, the longest memory periods. This indicates that more practice with long periods of time in between may enhance turtle memory for stimuli. Odor control tests were negative, meaning turtles could just use visual cues to solve this task. The studies on turtle memory measured in months by other scientists were testing odor memory. This experiment demonstrates the first evidence of long-term visual discrimination measured in periods of years.

The visual cue for experiment 1 of a food pellet behind an opaque plastic bottle, was a small visual cue and therefore a challenging learning and memory task for the turtles. Some might however, argue that even though it is a challenging task for turtles, if turtles were recognizing the pellet behind the bottle as a pellet and not just a visual cue indicating a food source, this may be a stimulus that once learned would be very salient and therefore more likely to be remembered. As with any learning experiment, it is important to determine if an animal can learn different tasks that test the same ability. Therefore we ran experiment 2 using a different non-food pellet visual cue to determine if turtles could learn this task and remember it. We also wanted to determine how well the turtles could learn and remember this new task with a larger more obvious visual cue.

Experiment 2: Black-White Bottle Discrimination Task

The goals of experiment 2 were 1) to investigate an additional visual task in which a visual cue other than food was used in order to gain more evidence for long-term visual memory and 2) to incorporate yet another odor control test to further eliminate any possible odor cues for solving the task.

Method

Subjects and Housing

Two of the female subjects (ID 5 and 1) from experiment 1 were trained to the new discrimination task. Turtle no. 1 was trained to dislodge a black bottle while turtle no. 5 was trained to dislodge a white bottle for food reinforcement. The instrumental task involved the turtle leaving the water to climb onto a brick and knock over either a black-tape covered bottle or a white-tape covered bottle (5.3 x 3.5 x 10 cm high with a 1.1 cm high x 2.4 diameter circular base) to obtain a food-pellet reward (Figure 3.4). Housing was the same as in experiment 1, with the only difference being that turtles were fed and tested in a different apparatus, described below. These turtles were trained to this task in October of 2007 for another experiment which stopped in December 2007. Turtle testing and retraining to determine memory occurred in spring 2008.

Testing Apparatus

Tests were conducted in an opaque fiberglass tank (124 cm x 46 cm x 43.5 cm, see Figure 5.2 in Part 5) that had a mirror above it. A JVC digital mini DV video camera (model no. GR-DV500U) recorded the trials via the mirror. On one end of the aquarium were two rows of stacked bricks on which the bottles were placed during testing. The water level was up to the top brick (15cm), and above and to the sides of each set of bricks were suspended two 150W sunlamps. Prior to the start of tests, the tank contained two plastic dividers, one or both of which were removed during testing (turtles were allowed to acclimate to the dividers and to their removal during maintenance feeding in the summer of 2007). One divider was clear and was placed half way between the bricks and the opposite end of the tank, and the turtles started out behind the clear divider. The other divider was opaque black and was placed close to and in front of the bottles prior to the start of testing. This created a visual barrier so the turtles could not see on which side the bottles where placed or under which bottle the food was placed.

Temperatures during training of the turtles to the correct bottle choice in fall 2007 were as follows: air 22-27^{0}C, social tank water 22-25^{0}C, and test tank water 27-30^{0}C. For the memory tests in spring 2008, temperatures were as follows: air 23-26^{0}C, social tank 22-25^{0}C, and test tank water 28-30^{0}C. Turtles were given 10 minutes to acclimate to tank temperature changes.

Turtles were kept on a 12L:12D cycle (0830-2030), with training and test trials run between 1145 and 1630 hrs. Because testing of all turtles on a test day took a few hours to complete, time of day effects were controlled by randomizing the order turtles were tested each test day. The feeding and testing schedule was the same as noted in experiment 1 of this study.

Procedure

The end goal/task for the training trials was for turtles to knock over the correct bottle (black for no. 1 and white for no. 5) when two choices were presented with food inside only the correct bottle. Training the two turtles to the tasks involved 3 stages of training similar to training stages 3-5 in the previous experiment (Davis & Burghardt, 2007).

Stage 1: topple one bottle involved shaping turtles to topple the correct taped (black/white plastic bottle with a pellet under it and a pellet in front of and directly against the bottle, with only one bottle present. To ensure that the bottle tipped over easily, the bricks were elevated during training to a slight angle so that, if the turtle touched the bottle, it would topple over.

*Stage 2**:** topple one of two bottles* involved the introduction of the second and incorrect bottle which contained no food, while the correct bottle had food inside and outside.

Stage 3: topple only the correct bottle containing food involved exposing turtles to both bottles, while food was inside of (but not outside of) only the correct taped (black/white) bottle. The turtles were shuttled back and forth between stages 2 and 3 as needed to keep them interested in the task as they learned to topple the bottles over with food only inside of them. Tests consisted of testing the subject's success rate for choosing (and toppling) the correct bottle containing a piece of food. A number of trials were run with food under both bottles as a control to determine if the turtles were attending to food-related chemical cues. Turtles reached a 100% success rate in training to the task in fall 2007 and were given a number of trials to practice the task (136 trials) as part of another experiment. The initial training as well as the re-training and testing for savings were run every other day 3 times a week for 6-8 trials per session. The retention tests occurred after 3.5 months of no bottle interaction. At the start of each trial, both plastic dividers were removed, and the turtle being tested was given visual and physical access to the task. The platform brick and bottles were rinsed between trials, and bottles were washed with Alconox soap between subjects. An additional odor control similar to the one in experiment 1 of this study (part 4) was performed in this experiment. During normal trials the correct bottle contained food, but during control trials there was no food in either bottle.

To avoid confounding side preferences, we used the L-R ordering sequences published by Fellows (1967) when the turtles were tested. A non-correction technique was used, meaning that turtles were separated from the bottles after their first choice by the black and clear dividers, whether correct or not. However, both turtles, regardless of willingness to perform or success rate, received the remainder of their full diet at the end of each test day.

The researcher was in the room with the turtles during all phases of the experiment for logistical reasons, but was looking down from above or through the mirror to control for observer effects or cueing. The test aquarium was high off the floor and opaque, so turtles could not look over at the experimenter during the tests.

Data Analysis

The same measures for retention and savings were used in this experiment as were used in experiment 1 of this study (part 4).

Statistical Analysis

Pearson’s Chi- Square tests were run to compare the normal and odor control trials for the odor control procedure.

Results

Learning the Visual Discrimination

Turtle 1 was trained to the black taped bottle stimulus as the correct choice. By the end of training day 4 (with 8 trials a day or 32 trials), turtle 1 reached criterion of dislodging the correct stimulus 6 out of 6 times. Turtle 5 was trained to the white taped bottle as the correct choice. Likewise, by the end of day 5 or after 40 trials Turtle 5 reached criterion of dislodging the correct stimulus 6 out of 6 times. After reaching criterion, both turtles continued to dislodge their correct stimulus on 100% of the trials. These two turtles became demonstrator turtles for naïve turtles in another study (see Part 5) so they repeated the task with 100% success for 136 trials after training.

Retention of Visual Discrimination

After 3.5 months of no interaction with the bottle, the two turtles tested on their savings and retention for the black and white bottle discrimination showed 100% correct choices. They needed zero retraining and therefore had 100% retention and savings for this task. There were no significant differences between the number of correct choices of normal trials where there was food under the correct bottle vs. control trials with no food under either bottle (Pearson's Chi-Square test, ID5; $\chi^2_{1, 35} = 0.972$ and ID1; $\chi^2_{1, 51} = 0.000$).

Discussion

Both turtles were able to learn to dislodge the correct colored stimulus with 100% success within 40 training trials. Furthermore, both turtles had 100% retention for the task and retained a success rate of 100% after 3.5 months of no interaction with the stimuli. Turtles therefore had a higher success rate and retention for this more obvious visual task then they did for the visual task described in part 3 and experiment 1 (part 4) of this study. These results provide further evidence that turtles can learn and remember visual tasks and that the complexity of the visual task will affect their learning and memory abilities. These experiments also included additional odor controls, which eliminated all odor cues from the visual stimuli and the turtles were able to solve the task with 100% success without any odor cues. Therefore this experiment confirms that turtles were only using visual cues to solve the task.

General Discussion

Turtles exhibited savings and retention for both the procedural and discrimination tasks during all retention phases (2-4), indicating substantial long-term memory. Turtles also, surprisingly, showed the best retention and savings after the 1 and 2-year memory time periods. This may indicate that turtle visual discrimination learning and memory is similar in retention duration to that of elephants (review in Pearson, 2008), given that both animal groups take a number of repetitions to learn something but retain it for periods of years. It would be interesting to compare turtle and elephant memory capabilities, but because neither elephants nor turtles have been adequately studied with respect to long-term retention, further research is needed to make such comparisons. Both elephants and turtles are long-lived species that could potentially be studied for many years to test the extent of their long-term memory capacity and duration.

The turtle brain, like that of the avian brain, has structures associated with learning and memory and these structures appear parallel in function to those of birds and mammals (Grisham & Powers, 1989; López et al. 2003a, b). These studies by López et al. (2003a, b) and Grisham & Powers, (1989) involved training turtles to spatial and visual tasks, lesioning the either the dorsal or medial cortex of turtles, and then comparing their learning and retention abilities to that of controls. They found that the medial cortex was associated with spatial retention, hence similar in function to the mammalian hippocampus. However, the medial cortex was not involved in learning. The dorsal cortex was important for learning and may parallel the visual cortex in mammals.

The turtles' ability to retain visual information for two years in this experiment is relevant to turtle memory of nesting sites, although apparently there are no field experiments documenting the role of specific visual cues in the wild. What is known is that many turtles return to the same nest sites year after year (Bowen et al., 1992; Freedberg et al., 2005; Rowe et al., 2005; Mitrus, 2006). Spatial cues may be used for long distance homing, but as turtles get in close range to nest sites they would likely need to use visual cues. For example, Green sea turtle hatchlings have been shown to have trouble homing to the sea with their eyes covered, indicating that visual cues are also important (Ehrenfeld & Carr, 1967), which may explain from an evolutionary and ecological perspective the long-term memory for visual cues the turtles demonstrate in this study. Visual cues could be relevant in the wild for close range memory of nesting sites, as well as foraging sites.

This study demonstrates for the first time that turtles possess long-term retention abilities sufficient to remember a visual discrimination task for at least two years. Additionally, this study demonstrates turtles are able to learn and remember different types of visual tasks. This study also illustrates that turtles are a good group to study long-term memory for visual discrimination tasks. These exciting findings illustrate the importance of further cognitive studies of turtles to gain a broader understanding of comparative vertebrate cognition.

Acknowledgments

We want to thank Todd Freeberg, Julia Bartmess-LeVasseur, Carrie Branch, Sheri Browning, Jessica Owens, Ami Padget, Ellen Mahurin, and Ellen Harvey Williams, for constructive comments on earlier presentations and drafts of this manuscript. Thanks also to undergraduates; Rachel Edwards, Julie Haskew, Erick Jenkins, Ruben Luna, Jeff Orgain in the Burghardt lab for helping to care for the turtles. This research was conducted under approved protocol numbers 222 & 1597 of the University of Tennessee Animal Care and Use Committee

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Appendix

Table 4.1. Overview of Phases 1 to 4 Described in Experiment 1**.** This table describes the start months of each phase, the training task (includes 5 stages to reach criterion of procedural task) and retraining. After subjects reach criterion on the training (procedural task) they start discrimination trials. Also the inter-phase interval is described.

Phases	**Start Month**	**Training Task**	**Discrimination**	**Task Details**	**Inter-Phase Duration**
Phase 1	November 2003	5 Stages of training; 9-16 days, 6-8 trials per day	48 trials	Phase 1 initial training of tasks	
					2.5 months
Phase 2	February 2004	Retraining of stages: 1-8 days	28- 48 trials	Phase 1 to 2: 10 weeks subsequent to no bottle interaction	
					10 months
Phase 3	April 2005	Retraining of stages: 0-2 days	42-54 trials	Phase 2 to 3: 12 months after phase 1 with 7.5 months no bottle interaction	
					24 months
Phase 4	April 2007	Retraining of stages:0-1day		Phase 3 to 4: 2 years no bottle interaction	

Table 4.2. Odor Control Test Results for Turtles in Experiment 1. This table shows the number of trials each turtle (ID 1-9) choose correctly and the number of trials run for normal and odor control trials over five days of testing. Trials were divided as evenly as logistically possible between normal and control trials.

Animal ID	Normal	Control	Chi-Square test	P-value
1	11/12	9/12	$\chi^2_{1,24} = 1.2$	NS
2	10/15	13/16	$\chi^2_{1,31} = 0.86$	NS
3	11/15	9/10	$\chi^2_{1,25} = 1.04$	NS
4	11/17	10/16	$\chi^2_{1,33} = 0.017$	NS
5	12/13	11/13	$\chi^2_{1,26} = 0.377$	NS
6	12/15	13/15	$\chi^2_{1,30} = 0.34$	NS
7	12/12	12/12	$\chi^2_{1,24} = 0.000$	NS
8	11/12	11/12	$\chi^2_{1,24} = 0.000$	NS
9	10/15	9/15	$\chi^2_{1,30} = 0.144$	NS

Table 4.3. Individual Success Rates Across All 4 Phases Analyzed in Experiment 1. This table shows the number of correct trials for each turtle subject (ID 1-9) for the discrimination task at each of 4 phases. The task criterion was that a turtle reached binomial significance out of 12 trials (in two consecutive test days). In order to reach criterion turtles had to get a minimum of 10/12 correct. Number of correct choices of 10-12 (in bold below) were significant with the binomial test $P < 0.05$:12 ($p < 0.001$), 11 ($p < 0.006$), 10 ($p < 0.038$) were as 9 ($p = 0.146$) and 8 ($p = 0.388$) were not significant.

Subject	**Phase 1**	**Phase 2**	**Phase 3**	**Phase 4**
1	**10**	**11**	**10**	**11**
2	**12**	**10**	**10**	**11**
3	**10**	**11**	**11**	**10**
4	**10**	9	8	8
5	**10**	**11**	**11**	**11**
6	**10**	9	9	**12**
7	**12**	**11**	**11**	**12**
8	9	**10**	**11**	**11**
9	9	**10**	**11**	**12**

Figure 4.1. Learning Apparatus for Experiment 1. This apparatus is the same one used in part 3. Turtles were released from the end opposite the bricks at the start of each trial and the stimuli were located on the top front brick on each end as noted in part 3.

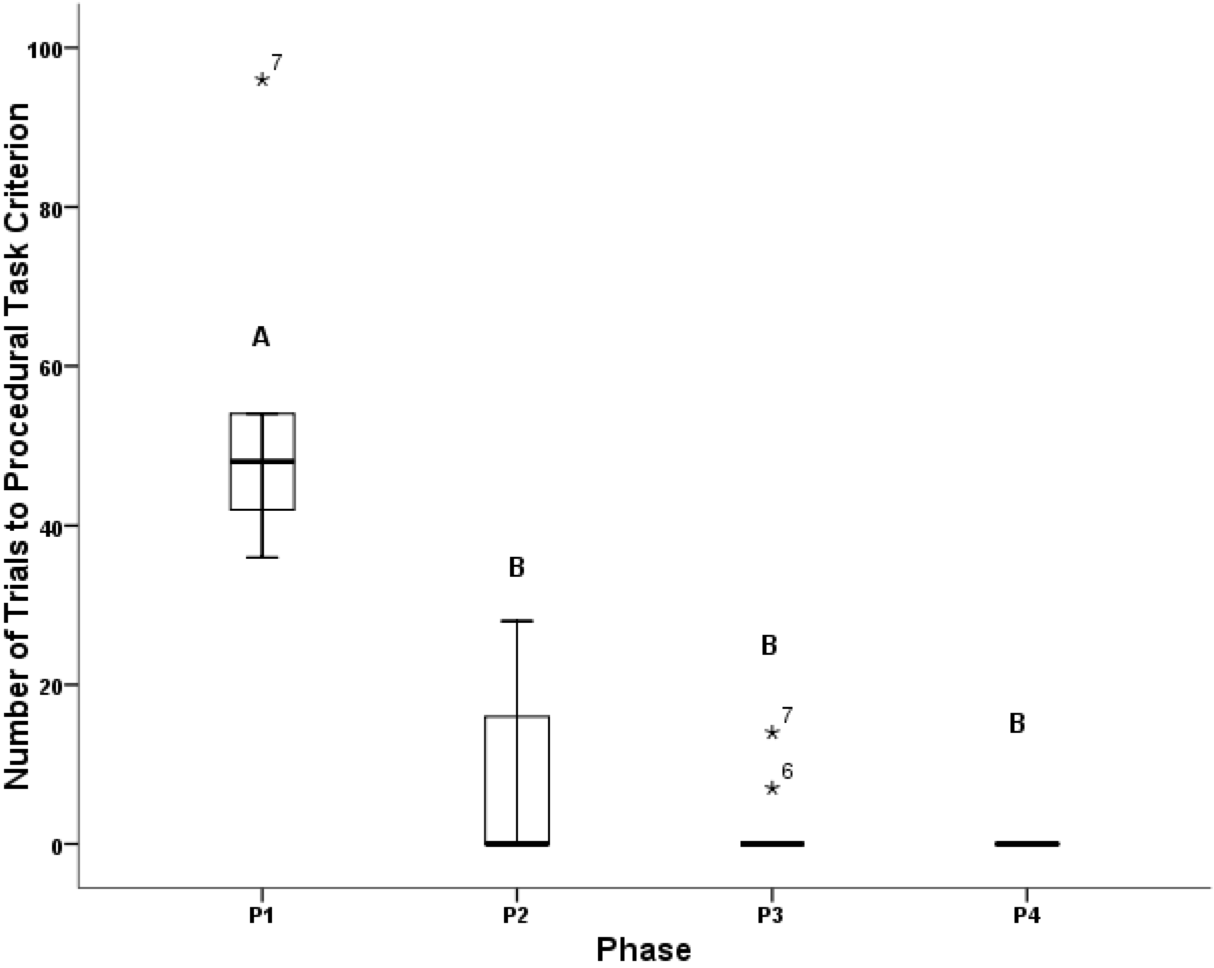

Figure 4.2. The Experiment 1 Trials to Procedural Task Criterion Decreased Across Phases. The number of trials significantly differed across phases. Letters above the box plots indicate the results of multiple comparison tests. Differing letters indicate significant differences between phases. During phases 2, 3, and 4 turtles took significantly fewer training trials to re-learn the task of dislodging the bottles. Box plot red stars indicate extreme cases.

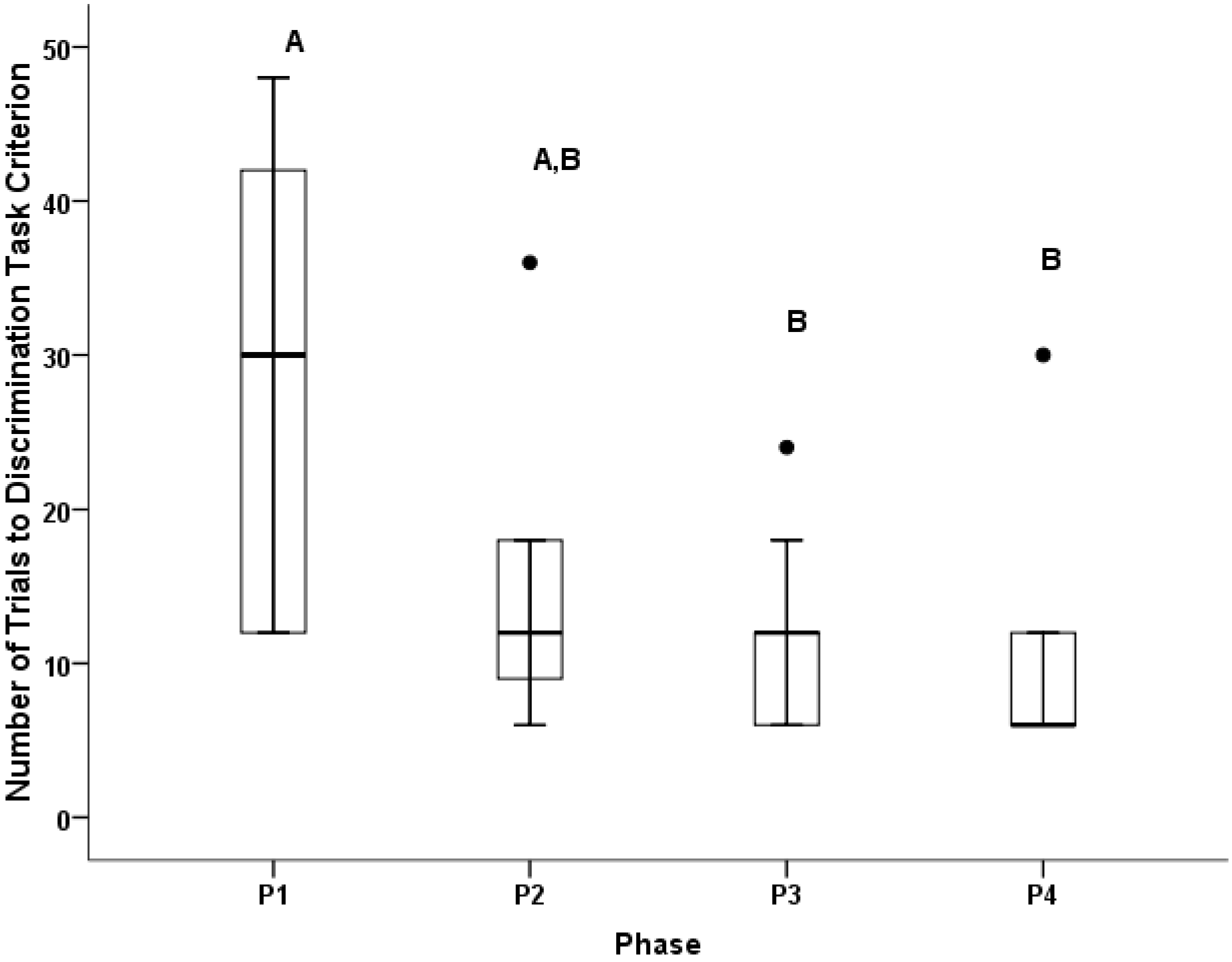

Figure 4.3. The Number of Discrimination Trials to Criterion in Experiment 1 Decreased Across Phases. The number of trials to reach criterion were significantly fewer than phase 1 for phases 2, 3, and 4. Letters above the box plots indicate the results of multiple comparison tests.

Figure 4.4. The Visual Stimuli for Experiment 2. This picture illustrates the set-up of the visual stimuli used during experiment two. The black and white bottles locations switched from left to right each trial according the ordering sequence. The bottles were always placed in the front center of the top brick and were just above the water level.

PART 5: SOCIAL LEARNING IN TURTLES (*PSEUDEMYS NELSONI*): TURTLES LEARN ABOUT VISUAL CUES INDICATING FOOD FROM EXPERIENCED TURTLES.

Abstract

Social learning has become a popular area of study in non-human primates, many other mammals, birds, and even fish, but has not been studied experimentally in any reptile. This study investigated whether turtles could learn about a visual object cue to obtain food reinforcement by observing other experienced turtles that had learned the task. All five *P. nelsoni* turtles tested showed evidence of social facilitation and stimulus enhancement learning: i.e., they learned not only to follow another turtle to a stimulus indicating food, but also to approach the correct bottle that contained food. Turtles were able to learn to focus on just the visual cue and ignore spatial cues associated with the task. This is the first experimental study of social learning in turtles and it demonstrates that turtles have the ability to learn from other turtles through both social facilitation and stimulus enhancement.

Introduction

Learning studies by comparative psychologists during the 1960s and 1970s focused on visual discrimination abilities of turtles and documented that they have sophisticated visual abilities and can be trained in a number of respondent and instrumental learning tasks including visual and spatial reversal learning (Kirk & Bitterman, 1963; Bitterman, 1964; Burghardt, 1977; Morlock, 1989). Recent studies by Lopez et al. (2000, 2001) found that turtles have spatial learning and memory capabilities similar to those of mammals and birds. Furthermore, Davis and Burghardt (2007) found turtles had long-term memory for visual cues. However, social learning (learning from others) has been studied mainly in primates, birds and rats (reviewed in Zentall & Galef, 1988; Heyes & Galef, 1996), although also studied in fish (reviewed in Brown & Laland, 2003), it has not yet been explored in turtles. Social learning, "refers to any incidence in which individuals acquire new behaviour or information about their environment via observation of, or interaction with, other animals or their products" (Brown & Laland, 2003, p. 281). Social learning may occur by a variety of processes ranging from simple non-imitative processes such as 'contagion' to more complex forms of learning such as 'true imitation' (Zentall, 1996; Brown & Laland, 2003) (see Table 5.1[1] for definitions).

My observations of a group of mixed species fresh water emydid turtles' underwater behavior in a naturalistic setting at the Tennessee Aquarium in Chattanooga documented that turtles interact socially outside of courtship contexts (part 2; K. M. Davis, unpublished data). Furthermore, my incidental observations of turtles in this naturalistic setting suggested that

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[1] All tables and figures are in the appendix at the end of part 5.

turtles may learn about food sources from others. One example is the following description of an observation that occurred October 9, 2007 around 12 pm (most of which was also filmed) of the turtles in the Delta lake exhibit in the Tennessee Aquarium (see part 2): A solitary female Florida Red-bellied Cooter (*Pseudemys nelsoni*) started to jump out of the water to reach a leaf of a tree hanging into the enclosure. When she succeeded, she chewed on the leaf and then repeated the behavioral sequence a few times. Other turtles, when they looked in the direction of this turtle, swam over to her and either attempted to jump out of the water and obtain a leaf themselves or if they could not reach it, attempted to take the food from the larger more successful turtles. This observation, along with others, indicates that turtles may be socially attracted to another turtle's behavior that indicates the location of a food source. This naturalistic observation inspired me to look at the ability of turtles to learn about a visual object indicating food from others.

Possible Outcomes and Expectations

Since this is the first experiment, I am aware of, that looks at social learning in turtles, each of the three goals listed below represent different aspects of a task that a naïve (observer) turtle could learn from a model (demonstrator) turtle. The goals of this experiment were to investigate whether: 1) naive turtles can learn to go to the correct colored bottle (visual cue) from an experienced model turtle while ignoring spatial cues, 2) naïve turtles can learn to dislodge the correct bottle to access food by observing an experienced model, and 3) naïve turtles learn the particular method used to dislodge the bottle from the experienced model.

The testing design controlled for alternatives to imitation (Caldwell & Whiten, 2002; Zentall, 2003) and allows for testing the possibility that turtles can learn socially by the complex process of true imitation if they perform all three parts of the task. It was designed with three distinct parts to the task so that if the turtles demonstrate evidence of learning any part of the task they will be demonstrating some process of social learning (see Table 5.1). Each stage, if learned by the observer from the model, will indicate turtles' abilities to learn socially using increasingly complex processes.

In order to control for the occurrence of contagion and social facilitation, after turtles had observed the novel task with the model, they were tested without the model present. If they learned none of the three tasks from the demonstrator turtle, but merely learned to follow the demonstrator when it was present, and showed an interest in the stimuli and/or that end of the tank when tested alone, but did not choose the correct visual stimulus, they exhibited social facilitation.

To distinguish local enhancement from stimulus enhancement, the location of the correct colored stimulus was varied between two sides across the modeled trials as well as the test trials. Therefore, if the naïve turtle learned to approach the correct stimulus every time (goal 1), regardless of location, while the demonstrator turtle was not present, they were exhibiting stimulus enhancement. If the naïve turtles learned to dislodge the bottle for food reinforcement they may be exhibiting goal emulation (goal 2) or behavior imitation. Since the two model turtles used different methods to dislodge the bottles, if each observer used the same method as their model to dislodge the bottle (goal 3) then they would exhibit evidence of turtle's ability to imitate due to the two-action procedure control (Zentall, 2003). Since this is the first such experiment in turtles I was testing my experimental design, making modifications as needed. Nonetheless, by using this broad experimental approach I hoped to find evidence of turtles' ability to learn from other turtles if present, as well as develop insights as to more efficient or effective types of experiments to perform in future studies.

Method

Study Subjects and Test Dates

Subjects consisted of 6 Florida Red-bellied Cooters (*Pseudemys nelsoni*) raised in captivity from eggs collected and hatched in 2000 from three lakes (Lakes Apopka, Griffin & Woodruff) in north central Florida. All 6 turtles (5 females, 1 male) had previous experience with a different visual task from an earlier learning experiment (Davis and Burghardt, 2007) and were 7 years old and sexually dimorphic at the beginning of the study. The female turtles' carapace lengths ranged from 162 -214 mm and masses ranged from 561-1463 g; the male turtle's carapace length was 169 mm and mass 713 g. All 6 turtles were individually identified by a number painted on their carapace with colored nail polish, and the same number was used for each turtle as in an earlier experiment (Davis and Burghardt, 2007) (male: no. 7; females: nos. 1, 3, 5, 8, 9).

Housing and Maintenance

Turtles were housed in a large social tank which consisted of a circular cattle tank (60 cm deep x 146 cm diameter) ¾ full of water for about (803 liters). The enclosure was placed 39 cm off the ground on two layers of cinder blocks so the water level inside the enclosure was higher then the filtration system, which was held in a large (208 liters) plastic drum (83.5 cm tall x 66 cm diameter), so that the water will flow out of a hole in the bottom of the enclosure, and through pvc pipes up into the top of the filtration system drums via gravity (Figure 5.1). The inside of the cattle tank was painted with a non-toxic white paint (Aquata poxy, A-6 parts A & B made by Raven lining systems, Tulsa, OK) to protect the metal tank from rust and the turtles from toxins in the rust.

The filtration system within the plastic drum was composed of three layers of filter media to allow mechanical and biological filtration. The three layers the water flowed through are as follows: first the corse mechanical filtration media (aquatic ecosystem's green rolled Matala, RM 24G), second the finer biological filter (aquatic ecosystem's blue rolled Matala, RM 24 B) and third the 3ft^3 of bio-fill which is the home of nitrogen fixing bacteria. After running through the filtration layers at the bottom of the can there was a hole connected to a magnetic drive pump (Pond master, model 12B, 12000 GPH) which pumped the clean water back into the enclosure on the opposite end from where it left to go to the filtration system.

The turtles were kept under special full spectrum lights (Eiko supreme, EXT/Su 12v 50W, MR 16) with the glass taken out to assure they gave off UVA and UVB radiation. These lights have been tested and give off more UVA and UVB if the glass is taken out than other marketed reptile lights (Tim Hermin, Toledo Zoo). Four of these Eiko lights were plugged into 4 MR 16 Pinhole cylinders on a Hampton Bay expandable halogen track lighting kit (x2) with two 75 watt bulbs plugged into par-30s for extra heat. The Hampton Bay lighting system converts the DC Eiko lamps to AC and these two sets of Hampton Bay track lighting were mounted, one on each side of the enclosure, to two portable telescoping display stands (USA light and Electric) on the cross bar between the poles. The lighting for each track was then plugged into its own separate digital timer. These lights were also both connected to a high temperature cut off device that would cut both sets of lights off if the room temperature ever went above a critical value. This insured the room could never become too hot and injure the turtles. These lights were programmed to come on at 1100 hrs and off at 1700 hrs (6 hours total), to mimic when sunlight would be at its height. The room overhead lights were kept on a 12L:12D cycle. Turtles were normally fed every other day by being taken out of their home enclosure into the feeding tank which was also the test apparatus.

Testing Apparatus

The opaque test tank (124cm x 46 cm x 43.5cm) had a mirror above it into which a JVC digital video camera (model no. GR-DV500U) recorded the trials (Figure 5.2). On one end of the aquarium were two rows of stacked bricks on which turtles were normally fed during maintenance and on which the bottles were placed during testing. The water level was up to the top brick (15cm) and to the sides of each set of bricks were suspended two 150W sunlamps. The test tank prior to the start of a test had two plastic dividers, one or both of which were moved away during testing, so turtles were allowed to acclimate to the dividers and their removal during maintenance feeding in the summer of 2007. The clear divider was placed half way between the bricks and the opposite end of the tank, and the demonstrator and/or observers started out behind this divider at the beginning of each trial (Figure 5.2). A black divider was placed close to and in front of the bottles prior to the start of testing which created a barrier so the turtles could not see on which side the bottles where placed or under which bottle the food was placed.

The room temperatures where as follows for each phase; air 22-27^{0}C, social tank water 22-25^{0}C, and test tank 27-30^{0}C for set 1, for set 2 air 23-26^{0}C, social tank 22-25^{0}C, and test tank

28-30^{0}C, and for set 3 air 22-25 ^{0}C, social tank 21-25 ^{0}C, and test tank 30 ^{0}C. The temperature on the bricks containing the bottles and food was at least 30^{0}C. Turtles were given time prior to testing to warm up, and given extra time on days when the housing tank was colder due to building heating problems.

Turtles were kept on a 12L:12D cycle (0830-2030) with training and test trials run between 1145 and 1630 hrs. Since testing of all turtles on a test day took a few hours to complete and time of testing spanned a length of 4 hrs., time of day effects were controlled by randomizing the order turtles were tested each test day. During normal maintenance and throughout the experiments, the turtles were typically fed three times a week. As the turtles were usually tested three times a week, they received their normal diet exclusively during the training and testing phases. Each turtle was given the same number of their standard diet food pellets (Turtle Brittle, Nasco International, Inc, Atkinson, Wisconsin) during the training and trial stages. Turtles were trained and tested individually in the test aquaria.

Training and Procedure

The experiment included first training the demonstrators to perform the task consistently and then exposing one pair of observers per training/testing set to each to a designated demonstrator. After the demonstrators were trained to respond to the correct side 100% of the time, the observers were allowed to watch them and were periodically probed to assess whether they had learned anything about the visual task by observing the demonstrator solve the task. Finally, the observers were then individually trained and tested on how long it took them to complete the final task (dislodging the correct bottle) which was compared to the demonstrator training time to criterion.

The experiment included three sets of observer pairs with each set run after the completion of the previous set, since the same demonstrators were used throughout, so not all observers could be logistically trained and tested simultaneously. Set 1 included the initial training of demonstrator D1 to dislodge the black bottle for food and demonstrator D5 to dislodge the white bottle. Then observer O8 observed D1 knock the black bottle and observer O3 observed D5 knock over the white bottle and complete the task under differing conditions. Set 1 started in October 2007, by training the demonstrators individually by stages of shaping. The observers started to watch demonstrators on the ninth test day. Set 1 of the experiment ran through December 2007.

Long–term memory trials constituted retraining and discrimination trials for the demonstrator turtles in set 2 (see part 4, experiment 2 for details). Set 2 started in March 2008, after demonstrator turtles had had no interaction with the bottles for 3.5 months. Both demonstrators showed 100% correct memory for dislodging their correct bottles. Therefore they were only run for 4 test days (24 trials) to make sure they maintained the skill as demonstrators for the set 2 observers. In April 2008 observer training began with two new turtles. O7 observed D1 knock the black bottle while O9 observed D5 knock the white bottle.

Set 3 started in June 2008. In this set, two of the former observers were trained as demonstrators, each to either a yellow or a green colored taped bottle. During set 3 the former demonstrators 1 and 5 became the observers and former observer 3 and 7 became demonstrators. However, since O5 stopped eating, only D3, trained to the yellow bottle, demonstrated for O1.

This is a slightly different task for O1 as previously she was trained to the black (darker) bottle. This animal now had to learn to go to the yellow-taped bottle, a much lighter stimulus than previously, by watching O3.

Demonstrator Training

The instrumental task involved the turtle leaving the water to climb onto a brick and knocking over either a black-tape covered bottle or a white-tape covered bottle (5.3 x 3.5 x10 cm high with a 1.1 cm high x 2.4 diameter circular base) to obtain a food-pellet reward. The end goal/task for the training trials was for turtles to knock over the correct bottle when two choices were presented with food only inside the correct colored bottle for each demonstrator.

Demonstrator training involved training the demonstrator turtles with 3 stages of training similar to training stages 3-5 in the previous experiment (Davis & Burghardt, 2007). *Stage 1: topple one bottle* involved shaping turtles to topple the correctly colored plastic bottle with a pellet under it and a pellet in front of and directly against the bottle. To ensure that the bottle tipped over easily, the bricks were elevated during training to a slight angle so that, if the turtle touched the bottle, it would topple over. *Stage 2**:** topple one of two bottles* involved the introduction of the second and incorrect bottle which contained no food. *Stage 3: only topple the correct bottle containing food* involved exposing turtles to both bottles but food was only inside of and not outside of the correctly colored bottle. The turtles were shuttled back and forth between stages 2 and 3 as needed to keep them interested in the task as they learned to topple the bottles over with food only inside of them. When both demonstrators would reliable dislodge the correct bottle for 100% of the trials for multiple days in a row the training of observers started. Demonstrator tests consisted of testing the subject's success rate for choosing (and toppling) the correct colored bottle containing a piece of food. A number of trials were run with food under both bottles as a control to determine if the demonstrators were following only the visual cue. Demonstrators reached a 100% rate in set 1 and maintained this success rate throughout the observer training trials. Demonstrator turtles were retrained prior to starting observer training in set 2 and had 100% correct choices at the beginning of the observer training trials. During the last observer training days D5 stopped being food motivated (this happens to turtles sometimes during season changes even when they are kept under constant light cycle). This did not seem to affect O9's success.

Observer Training Days

During set 1 both observers watched their respective demonstrator from behind the clear glass divider. This meant that the demonstrator had to be up against the divider until the black divider was removed and the demonstration trial started. A total of 18 observer training days with, 8 demonstrator trials each day, were run with the demonstrator and observer present after which time the observers were tested individually for a total of 22 test days.

Observers were given tests in which they were allowed to approach the black or white bottle on days 3-8 after watching the demonstrator 6x each day. During the observer tests days, three through six, the bottles were mounted on stoppers so that the observers were not able to knock the bottles over. After a while the observers started to lose interest in watching the demonstrators from behind the clear divider so for training days 9-18 observers were allowed to have access to the demonstrators and the bottles while the demonstrator was running each observer training trial. During days 9-12 the demonstrator was held back by hand and released on one side of the plastic divider followed by the clear divider being removed so the observer had access to the demonstrator during the trial. This did not work so well logistically so for days 13-18 both the demonstrator and observer started behind the clear divider and were released simultaneously. Observers were again tested on days 13-18 after first observing their demonstrator on each of these days. During the individual tests, after having watched their demonstrator on days 15-18, observers were individual trained starting at stage 1; food was placed in front of the correct bottle to start to teach the turtles to knock the bottles. To this point they had only approached the correct bottles but would not knock them over on their own. The individual training of the observers continued on days 19-22, but for these last 4 days the observer turtles did not watch demonstrations of the task prior to the 6 observer tests. Observers in this set observed their demonstrator perform the task for a total of 136 trials and 72 of these were with the demonstrator and observer together during the demonstration trials.

Set 2 observer training was slightly modified from set 1 to take into account the methods which had worked the most effectively for the observers. During set 2 observers were given 19 days of training trials, 13 of which were with their demonstrator performing the task. All of the first 13 days with the demonstrator present involved the observer and demonstrator starting together behind the clear divider and being allowed access to the bottles at the same time (same method as days 13-18 for set 1). Demonstrators ran 6 trials each training day for a total of 78 observation trials. Observers were tested after observing their demonstrator from days 6-13. During the testing on days 9-13 the observers were given a pellet in front of, as well as inside, the bottles. Observers no longer watched the demonstrators for 6 trials before their 6 tests on days 14-19 instead they were tested on individual learning.

Set 3 observer training was different in that the former demonstrator 1 was now the observer for a different colored set of bottles (green and yellow). Former observer 3 was trained to go to the yellow bottles. Then O1 had to learn to follow D3 to the yellow bottle which meant learning a reversal of color shade (form dark to light), by watching the demonstrator.

Procedure

The training and testing of demonstrators and observers were run every other day 3 times a week throughout the three experimental phases. Demonstrators were run 8 trials a day in set 1 and 6 trials a day for sets 2 & 3. At the start of each trial the black divider was removed and the clear plastic divider was removed or the demonstrator was released. The platform brick and bottles were rinsed between trials and bottles were washed with Alconox soap between animals.

To avoid confounding side preferences, we used the L-R ordering sequences published by Fellows (1967) when demonstrators or observers ran trials or were tested. A non-correction technique was used, meaning that turtles were separated from the bottles after their first choice by the black and clear dividers whether correct or not. However, all turtles regardless of willingness to perform or success rate received their full diet, with the remaining food pellets fed after the completion of a particular test day in the test tank which was also their feeding tank.

The turtles used three different methods for dislodging the bottles, as in the previous experiment (part 3; Davis & Burghardt, 2007): 1) biting the bottle, 2) pushing the bottle with nose or, 3) swiping sideways at the bottle and pushing it with either their right or left foot. The method of knocking for the demonstrators and observers, whether an observer touched a bottle without knocking it, and the choice of the bottle to knock over was recorded on paper in addition to the whole experiment being video recorded from the mirror since some details in the video could not be clearly seen due to distance. Therefore the researcher was in the room with the turtles during all phases of the experiment for logistical reasons but was looking down from above or through the mirror to control for observer effects or cueing and the test aquarium was high and solid so turtles could not look over at the experimenter throughout the tests. Inter-observer reliability control tests were run on data in part 3 with 100% inter-observer agreement on correct stimulus choices.

Statistical Analysis

Binomial tests were run on the number of correct stimuli choices during test trials for each of 4 observer turtles.

Results

Demonstrators

Both demonstrators learned to dislodge the correct visual stimulus (see part 4, experiment 2 for more details) and then performed the task with 100% accuracy for their perspective observers. D1 consistently used its front limbs to dislodge the bottle whereas D5 consistently bit the bottle to dislodge it. However, D5 stopped reliably performing during the last few days she was demonstrating for O9 in set two. Thus, O9 did not receive as complete a training experience as did the other 3 observers.

Observer Tests After Observing Demonstrators

Set 1

The two observers first observed their demonstrators from a distance while separated physically from the demonstrators. When they were tested these turtles both preferred the same colored bottle as their observer (Table 5.2) but lost interest in the task very quickly and would not move when tested. This is likely due to not being close enough to see and smell the food the demonstrators received when they completed the task. In order to keep testing these observers on their social learning ability we needed to keep them motivated to complete the task throughout the testing. Therefore the methods were modified so that the demonstrator and observer were together while the demonstrator performed the task.

At first the naïve turtles did not follow the demonstrator turtles, but soon they started following the demonstrators and were near them when the demonstrators completed the task. The fact that these turtles followed their demonstrator to the stimulus indicates social facilitation (Table 5.1) one of the two simplest processes by which turtles can learn from others. When the observers were tested (demonstrators were absent) both observers continued to choose the correct stimulus by either approaching the correct stimulus or approaching and touching this stimulus. Both of the turtles chose the same stimulus as their demonstrators significantly better than chance (Binomial tests, see Table 5.3). Since they significantly chose the correct stimuli (approached and or touched it) during tests in which the demonstrator was no longer present, these two observers were exhibiting stimulus enhancement. However, neither turtle would dislodge the bottle when alone, so neither demonstrated a completion of the task, and therefore did not demonstrate goal emulation (dislodging the bottle), or imitation of the method used by the demonstrator for dislodging the bottle.

Set 2

Since the observers in set 1 lost interest in the task when separated from their demonstrators, but showed more interest when allowed to be with the demonstrators during demonstrations, we chose to start this set with demonstrators and observers together during demonstrations of the task. Just like the observers in set 1, the observers at first hung back and did not follow the demonstrators, but as they saw the demonstrators complete the task and eat food they started to follow the demonstrators to their location and hence exhibited social facilitation. Turtle O7 also learned to scrounge when its demonstrator performed the task – he would get right next to the demonstrator and try to get the food once the bottle was dislodged, yet he never attempted to dislodge the bottle himself. He was sometimes able to get the pellet before the demonstrator ate it. Both of these observers also approached the correct stimulus when tested significantly more often than chance (Table 5.3) therefore these two observers also exhibited stimulus enhancement from watching another turtle.

O7 never dislodged the bottle during observer testing or during the times when the demonstrator was present and never touched the bottle either, so it showed no evidence of goal emulation or imitation. Turtle O9 both approached and touched the bottle a number of times when the demonstrator was absent (Table 5.2). Even though touching the bottle is not evidence of imitation, it can be considered an indication of goal emulation. Furthermore, O9 knocked the correct stimulus over when tested by itself a few times, although not consistently. Turtle O9 held back a bit further than O7 while observing the demonstrator and did not learn to scrounge, but dislodged the bottle a few times during observer training. What makes this even more interesting is that O9's demonstrator, D5, stopped being food motivated and did not complete the task towards the end. So, despite having a demonstrator that was not as good at O7's, O9 still showed stimulus enhancement (Table 5.3) and even dislodged the bottle when D5 was absent, during observer testing, prior to being individually trained.

Set 3

In set 3 the former demonstrator D1, a now experienced turtle with the former task, became an observer in a different color contrasting visual choice task. Former O3 became the demonstrator for this new task after turtle 3 had learned the new discrimination. Since the new color discrimination still had a dark colored green bottle with similar hue to the black bottle, and turtle 1 had formerly been trained to dislodge the black bottle, the yellow colored bottle (lighter colored stimulus) was chosen as the correct bottle. Prior to letting O1 observe D3 perform the task, O1 was tested to see if it had a preference for one of the colored bottles (something we did not find in the naïve turtles in set 1 and 2, since the hue difference would be similar to those tested with the black and white bottle.

O1 had a strong preference for the green (dark stimulus) bottle – this turtle approached and dislodged this bottle when given the opportunity. Therefore in this task O1 had to learn a task reversal from the observer turtle, which added a layer of complexity to the task. During demonstrator trials O1 was together with D3, but unlike the naïve turtles who hung back then later followed slowly enough for the demonstrator to dislodge the bottle in front of them, O1 continuously ignored D3 and instead swam quickly directly to the green bottle and dislodged it. Therefore, we tried running the demonstrator trials with O1 separated from D3 by the divider, but in this case O1 showed no interest in D3, and did not even look in D3's direction. The experimenter then decided to continue with the observer training with O1 together with D3 during the demonstration of the task. O1 continued to ignore D3 during demonstrations and dislodged the green bottle continuously. When O1 was tested separately from D3 this turtle also continued to make the wrong stimulus choice and dislodged the green bottle (Table 5.2). There was never any food under the green bottle so O1's choice was never reinforced for dislodging the green bottle. Throughout the majority of the demonstrator trials and observer tests O1 kept the pattern of ignoring D3 and dislodging the incorrect bottle. Toward the end of the training process however, O1 did start to observe D3 dislodge the correct bottle. However, due to spending most of the training testing choosing the incorrect bottle the results of O1's correct bottle choices were not significant (see Table 5.2).

Individual Testing of Observers

All observer turtles were individually trained to the task after the completion of the demonstrator training period. Turtle O8 during training would not dislodge the bottle during the last stage for a long time; it took 66 individual trials to dislodge the bottle on its own for the first time. It then reached criterion of 6 out of 6 correct by trial 73. This is longer than the number of trials for either of the demonstrators to be trained to the task (D1 32 trials, D5 39 trials). O3 dislodged the bottle on its 21st individual trial and reached criterion in fewer trials (29 trials) than either demonstrator. Turtle O7 never did dislodge the bottle on his own but continued to approach and even nose the correct bottle. For a few of O7's test periods after observing D1, (toward the middle of set 2) D1 was on the other side of the clear divider separated from and behind O7. In these cases O7 approached the correct bottle as usual and stayed on the lower brick with his nose very close to the bottle, but instead of staring at the bottle he turned his head and looked at D1. It did this behavior then turned and looked at the bottle and back at D1. This was very interesting since it indicates that while learning to scrounge from D1 during demonstrator trials, and learning the correct stimulus to approach, it had learned to associate D1 with the completion of the task dislodging the bottle. After this we never left D1 on the other side of the enclosure while running O7, as it distracted O7.

Discussion

This study provides the first evidence that turtles can learn socially from other turtles. It also demonstrates that turtles can learn by both social facilitation and stimulus enhancement. It provides some evidence that turtles may even be capable of goal emulation. The results of set three also indicate that turtles may only be receptive to learning from other turtles about food stimuli if they are naïve. This study also provided evidence that turtles have different strategies for their use of socially provided information. This first study indicates that in order to truly test if turtles can learn socially by other processes more specific experimental designs are needed, with multiple experiments in order to answer these questions.

Turtles have no post-hatching parental care, and yet they associate and interact extensively as adults (part 2). This study shows adult turtles also exhibit social learning abilities. Most studies of social learning ability are focused on mammals and birds that exhibit post-hatching parental care (Rogers & Kaplan, 2004; Pearson, 2008). Most fish, however, that school, do not exhibit post-hatching parental care, yet these animals live in groups and forage together. Fish social learning, unlike turtles, has been studied (Brown & Laland, 2003). Fish exhibit social facilitation and mate choice copying and have similar social life histories to that of turtles. Turtles whom have not been considered for social learning studies prior to this present experiment, exhibited both social facilitation and stimulus enhancement with the possibility of more complex social learning processes. Therefore, turtles are an excellent group to study social learning from a comparative cognition perspective.

Turtles are also very food motivated, have visual discrimination abilities, learning and memory capabilities similar to birds and mammals (part 3 & 4; López et al., 2000, 2001).

Furthermore, turtles have learning and memory brain structures comparable to that of birds and mammals (López et al., 2003a, b). Moreover, turtles exhibit complex social behavior that is comparable to birds and mammals (part 2). For all these reasons future turtle social learning experiments testing for differing social learning processes as well as species differences in social learning abilities are needed to gain a broader comparative cognition perspective.

Turtles are exothermic, so energy expenditure needs to be considered when designing learning experiments. Turtles cannot run 1000 trials in a day, but still many more than other reptiles studied to date. Also, if they are not kept at optimum temperatures turtles brains will slow down and so testing their full capabilities will not be possible. Energy expenditure costs and the affects of temperature on turtle behavior and cognition are not issues most learning psychologists are used to considering and adjusting their experimental design accordingly. Turtles cannot run 1000 trials in a day, but still many more than other reptiles studied to date. Additionally, in the past researchers pulled wild turtles from ponds and streams to study their behavior in rather small captive aquaria. Turtles generally exhibit stress behavior such as becoming inactive or hyperactive, at which times they not likely to perform learning tasks or perform them at their full ability level (Burghardt, 1977; Cash & Holberton, 1999). Since turtles are long-lived if raised in captivity and socialized to people they can be great social-learning study subjects.

The likelihood of social learning occurring and what type of information may be learned from others in a group will depend on the social dynamics of the group (Coussi-Korbel & Fragaszy, 1995). Species that live in stable groups and interact in multiple contexts are likely to have more opportunities for social learning than solitary species. Furthermore, aspects such as dominance hierarchies and a particular animal's rank in a group may determine what an observer learns from a demonstrator. For example, Nicol and Pope (1994) found in a study of adult laying hens (*Gallus gullus domesticus*) observers learned more quickly when exposed to dominant demonstrators vs. subordinate demonstrators. Another example is the concept of producers vs scroungers - an observer may learn to follow an experienced demonstrator and instead of learning to perform a specific behavior similar to that of the demonstrator to obtain food it may learn to scrounge in the presence of the producer (Giraldeau & Lefebvre, 1986). These things must be taken into consideration when designing social learning experiments and in determining if an observer did learn something from a demonstrator, as they may learn something and respond with a complementary behavior instead of a similar behavior to that of the demonstrator, depending on which is more effective and efficient.

This first experimental study of social learning in turtles indicates first that turtles are capable of social facilitation and stimulus enhancement. It also illustrates that many more specifically designed experiments are needed to test if turtles in order to truly test if turtles can learn socially by other more complex processes. Furthermore, future social learning experiments in any species must consider the importance of really evaluating the behaviors observers' exhibit and individual differences in what is learned or how quickly it may be learned. These findings must be considered within the context of the social dynamics of the group. Additionally, when looking at social learning in turtles or other exothermic reptiles experimental design must take in to consideration the effects of energy expenditure and temperature on retile learning and cognitive abilities. For all these reasons future turtle social learning experiments need to compare turtle species for differences in social learning abilities. Comparisons of how turtle leaning abilities and the processes used relate to those of birds, mammals, fish and other reptiles, are needed to gain a broader comparative cognition perspective. Furthermore, in order to really compare social learning across taxon differences in biology and perception most be controlled for in experimental designs and conclusion about a taxon’s cognitive abilities based on experiments.

Acknowledgments

We would like to thank the Freeberg lab (Julia Bartmess-LeVasseur, Carrie Branch Sheri Browning, Todd Freeberg, Jessica Owens, Ami Padget and Ellen Harvey Williams) for comments and on earlier drafts of this manuscript. The Department of Psychology at University of Tennessee Knoxville Departmental grant helped fund part of this experiment. We would also like to thank the following undergraduates for helping care for the turtles and help run the experiment: Carrie Branch, Leah Burke, Ben Cohen, Emily Long, Lacey Sams & Jennifer Southerland. This research was conducted under approved protocol number 1597 of the University of Tennessee Animal Care and Use Committee.

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Appendix

Table 5.1. Definitions of Social Learning Processes. These definitions were adapted from a synthesis of current definitions in the social learning literature (Heyes & Galef, 1996; Brown & Laland, 2003; Pearce, 2008). When authors differed defining a word a consensus of the literature was taken into account, and the present author used her knowledge of animal behavior to adjust or choose the best definition.

Term	**Definition**
Contagion	Also called contagious behavior is behavior that is automatically triggered or released by a similar behavior in other animals. It is reflexive behavior that occurs in the presence of a performing model and does not need to be learned. Ex. yawning in humans
Social facilitation	Occurs when exposure to the presence of a model (another animal) engaging in a specific behavior (e.g. eating, courting) increases the observer's (naïve animal) arousal and activity. This increased activity level will cause the observer to be more likely to come in contact with the stimulus. (called social enhancement by Pearce, 2008)
Local enhancement	The behavior or merely the presence of the demonstrator attracts the attention of the observer to a particular location.
Stimulus enhancement	The behavior or presence of the demonstrator draws the observer's attention to a particular stimulus. In order to distinguish stimulus enhancement from local enhancement the experiment must control for position of the stimulus.
Observational conditioning	The observer learns the relationship between a stimulus and the following reinforcement. The demonstrator's behavior draws the observer's attention to both the stimulus and the reinforcement of the demonstrator. It is thought that these observations which involve association of the stimulus and demonstrator being reinforced with food may lead to a Pavlovian association in the observer.
Goal emulation	The observer learns the goal to pursue from observing the demonstrator's behavior. However, the observer does not mimic the exact movements and method the demonstrator uses to solve the task.
True imitation	The observer exactly reproduces the behavior or behavior sequence of the demonstrator attaining the goal. Additionally, the behavior that is imitated must be novel to the observer to be true imitation

Table 5.2. Summary of Tests of Observer Learning for Sets 1(S1), 2 (S2) and 3 (S3) During the Observer Training period. S1 refers to the first set of observers trained in fall 2007, and S2 the second set of observers trained spring 2008. S3 refers to the last phase where former D1 became an observer to ID3 for a different visual task. Separated means the observer was watching the demonstrator from behind the divider during the demonstrations (see Figure 5.2). Together means that while observer watched the demonstrator perform the task, the observer had access to the demonstrator. During sets 2 and 3 observer turtles were not separated from the demonstrator turtles, so the cells below for sets 2 and 3 that are related to "separated" have a dash in them.

ID	**CB**	**Separated**		**Separated**		**Together**		**Together**		**Total**	
		AW	**AB**	**ATW**	**ATB**	**AW**	**AB**	**ATW**	**ATB**	**W**	**B**
8 S1	B	1	3	1	3	0	5	0	0	2	11
3 S1	W	6	2	2	0	2	1	1	0	11	2
7 S2	B	-	-	-	-	0	9	0	0	0	9
9 S2	W	-	-	-	-	6	1	4	0	11	0
ID	**CB**	**AY**	**AG**	**ATY**	**ATG**	**AY**	**AG**	**KY**	**KG**	**Y**	**G**
1S3	Y	-	-	-	-	4	9	11	14	15	21

CB = correct bottle color, AW = approach white bottle, AB = Approach black bottle, ATW = approach and touch white bottle, ATB = approach and touch black bottle. AY = approach yellow, AG = approach green, ATY = approach and touch yellow, ATG = approach and touch green, KY = knock yellow, KG = knock green

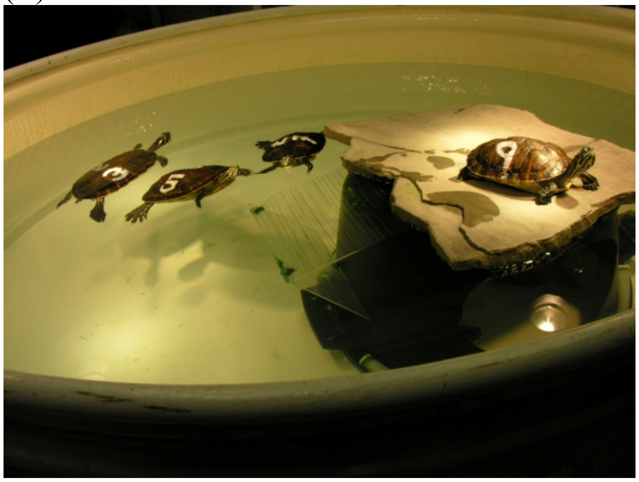
Table 5.3. Observer Turtles' Visual Stimuli Choices Match the Demonstrator Turtles' Choices. This table shows the overall number of choices each observer made toward each of its two visual stimuli throughout testing (as noted in Table 5.2). These numbers correspond to the numbers under the "total" section for sets 1 and 2 of Table 5.2. Observers chose the correct stimulus significantly above chance levels (One-tailed binomial test).

Subject	**Demonstrator**	**Correct Stimulus**	**Black**	**White**	**Binomial Test P-Value**
O8	D1	Black Bottle	**11**	2	0.011
O3	D5	White Bottle	2	**11**	0.011
O7	D1	Black Bottle	**9**	0	0.002
O9	D5	White Bottle	0	**11**	0.0001

Figure 5.1. The Social Housing Enclosure with Views of the Side (A), Overhead (B), and an Overhead Close-up (C). This diagram shows that the circular tank is off the ground supported by 2 layers of cinderblocks. The 2 lighting racks can be seen above the enclosure. Also the plastic drum filtration system can be seen, attached to the enclosure through piping.

(A)

(B)



(C)

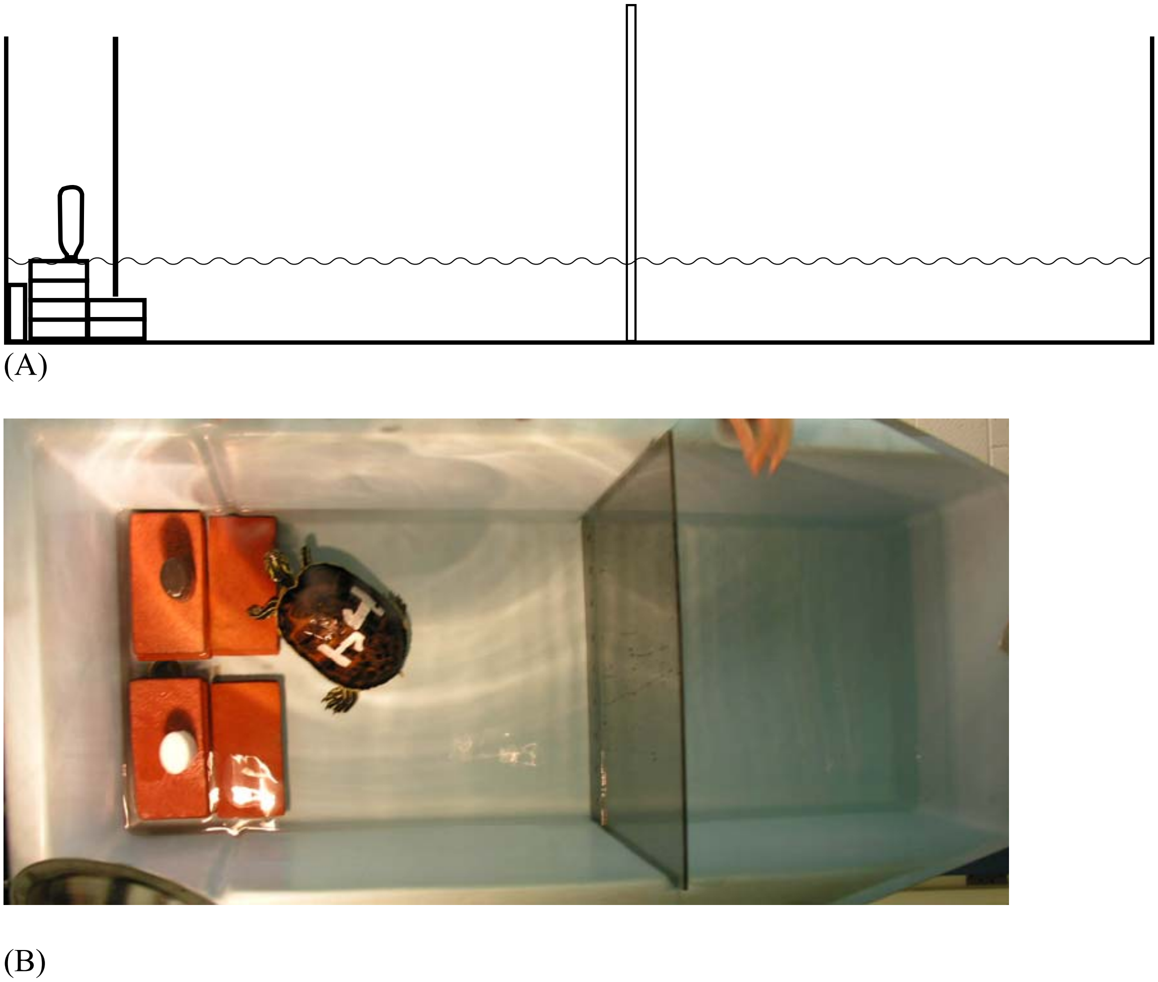


Figure 5.2. The Diagram and Picture Illustrations of the Side (A) and Top (B) of the Testing Apparatus. One of the bottles the turtles would knock over is seen placed on top layers of bricks. The black line in front of the bottle represents the black divider which was removed during testing. The hollow double line in the middle of this figure represents the clear plastic divider which separated the observer turtle and demonstrator turtle from the test part of the apparatus until time for the trial. The observer either stayed behind the clear divider separated physically, but not visually from the demonstrator or both dividers were removed and the observer had access to the demonstrator during observations.

PART 6: CONCLUSIONS

Overall Summary of Results of this Study (Parts 2, 3, 4 and 5)

Part 2 of this dissertation investigated the underwater social behavior of emydid turtles. This is the first extensive long-term study of aquatic turtle underwater social behavior in a naturalistic setting. Turtles were found to preferentially affiliate and interact with individuals of their own or most closely related species. The M-M agonistic behavioral repertoire and intensity differed across the species, with the YBS group exhibiting the most extensive and intensive agonistic repertoire. All 3 species of males studied formed linear dominance hierarchies in this naturalistic captive setting. Furthermore, they formed stable underwater dominance hierarchies that lasted for years. The marked Wood Turtles (*Clemmys insculpta*) that Kaufmanns (1992) observed in the field formed linear hierarchies thus supporting the validity of my finding stable linear turtle hierarchies in captivity. Since factors such as turtle ecology, environmental stability, habitat choice and social structure may affect turtle social structure and dominance hierarchy formation, it is essential the behavioral studies in the field as well as captivity are performed. Furthermore, these studies will be most useful if a comparative approach is used across turtle species that studies the role of phylogenetic vs. ecological factors on turtle social structure.

Some agonistic *Trachemys scripta* interactions included intense harassment of a smaller, newly introduced male, by ‘coalitions’ of two or more larger males. This ‘coalition’ formation has never been reported in turtles before. Additionally, both M-M and F-F pairs exhibited social interactions that included behaviors normally categorized as courtship, such as titillation, in contexts that clearly did not involve courtship. These findings indicate that turtles are active social animals with complex underwater social behavioral repertoires.

Although the captive setting included higher turtle densities and more species diversity than would be found in natural environments, the findings are congruent with Kramer's field observations of *P. nelsoni* and *P. concinna* (1986). More detailed comparative studies of turtle social behavior within and between turtle families and comparison of turtles' social behavior to that of birds, mammals, snakes, lizards and tuatara are essential for phylogenetic comparisons. As noted in part 1 turtle phylogeny is controversial. Turtles are either the most basal of living reptiles, the sister taxon to the highly social birds and crocodilians (Zardoya & Meyer, 2004), or a highly derived group either most closely related to snakes, lizards, and tuatara, (see reviews Rieppel, 2008; Ernst & Lovich, 2009). Therefore, comparisons of their social behavior are relevant in determining turtle phylogenetic origins as well as for a complete understanding of the evolution of vertebrate social behavior.

Furthermore, future studies of social behavior for aquatic as well as land turtles need to include a perceptual modality for communication which until recently has been ignored; the use of sound by both underwater and on land turtles during social interactions. Turtle behavioral studies have focused almost entirely on the use of visual displays in communication (rev, Harless, 1979; Miller & Dinkalacker, 2008; Ernst & Lovich, 2009) and the function and importance of turtle vocalizations, which have been noted to occur during courtship and copulatory behavior of land tortoises, have been ignored until recently (Galeotti, Sacchi, Fasola, & Ballasina, 2005). Galeotti and colleges (2005) reviewed the occurrence of vocalizations in tortoises during courtship and found that mounting vocalizations are an ancestral trait, show harmonic structure and may function as a signal of reproductive outcome.

Aquatic turtle vocalizations have been assumed not to occur and have not been studied prior to a very, recent study by Giles, Davis, McCauley, & Kuchling (2009). Giles and college's study of *Chelodina oblonga,* a long-necked freshwater turtle in a captive setting, found that this turtle exhibited a vocal repertoire of 17 categories. Their finding of this extensive vocal repertoire in a turtle species living in turbid water where visibility is low indicates the possible importance of vocalization for turtles for communication over distances greater than that of their visual display distances. During observations at the introduction of new turtles (part 2) I observed throat vibrations which indicated that these turtles may also be communicating through vocalizations. These findings suggest the importance of future turtle aquatic behavior studies which investigate if vocalizations occur during social interactions for each species of turtle and how the existence and extent of vocalization in both aquatic and land turtles relates to phylogeny and ecology.

These findings illustrate that turtle underwater social behaviors are much more extensive and complex than their basking behavioral interactions and that different rules of sociality apply for interactions underwater vs. those during basking. These findings also provide evidence that turtles have more plasticity in behavioral repertoires across different contexts. Furthermore, this extensive long term study illustrates that the behaviors, sequences and the contexts of these behaviors are similar to those of mammals, which supports the view that turtles are an excellent group to study from a comparative psychological perspective.

Parts 3 and **4** demonstrate that turtles have the ability to learn visual tasks and retain information about these visual tasks for long-term periods measured in years. This is the first long-term memory study on turtle visual discrimination learning, and the only turtle long-term memory study testing reptile retention for as long as two years. These studies illustrate that turtles are a promising group with which to investigate long-term retention. Future studies comparing turtle long-term memory for visual cues, spatial cues, chemical cues and the context in which turtles learn, retain and use these cues are needed. Part 4 also documented that turtles can learn a new visual discrimination rapidly after having mastered a different one.

Turtles are long lived reptiles, with many having the ability to live 70-plus years. The turtles' ability to retain visual information for two years in this experiment is relevant to turtle memory of nesting sites, although apparently there are no field experiments documenting the role of specific visual cues in the wild. Many turtles return to the same nest sites year after year, and some show nest site fidelity for up to 10 years (Bowen et al., 1992; Freedberg, Ewert, Ridenhour, Neiman, & Nelson, 2005; Rowe, Coval, & Dugan, 2005; Mitrus, 2006). Visual cues could be relevant in the wild for close range memory of nesting sites, as well as foraging sites. Turtles returning to nest sites across years, coupled with turtle longevity indicate the adaptive significance of turtle long-term memory found in this laboratory study.

The turtle brain, like that of the avian brain, has structures associated with learning and memory and some of these structures appear parallel in function to those of birds and mammals (Grisham & Powers, 1989; López, Gómez, Varagas, & Salas**,** 2003a; López, Varagas, Gómez, & Salas, 2003b). These studies by López et al. (2003a, b) and Grisham & Powers, (1989) found that the medial cortex was associated with spatial retention, hence similar in function to the mammalian hippocampus. However, the medial cortex was not involved in learning. The dorsal cortex was important for learning and may parallel the visual cortex in mammals.

This study demonstrates for the first time that turtles possess long-term retention abilities sufficient to remember a visual discrimination task for at least two years. Additionally, this study demonstrates turtles are able to learn and remember different types of visual tasks. This study also illustrates that turtles are a good group to study long-term memory for visual discrimination tasks. These exciting findings illustrate the importance of further cognitive studies of turtles to gain a broader understanding of comparative vertebrate cognition. Further studies of long-term memory for retention periods measured in months and years along with research into the function of the turtles' lateral and medial cortex in the learning and memory process are necessary. Such studies are necessary in order to understand turtle learning and memory abilities as well as to compare turtle learning and memory to other vertebrates.

Part 5 was inspired by observations of turtle behavior in a naturalistic setting (part 2) along with knowledge of turtle's ability to learn and remember visual discrimination tasks (part 3 and 4). This is the first experimental study of social learning in turtles /reptiles. This experiment provides strong evidence that turtles can learn, not only through social facilitation, but through the process of stimulus enhancement. It also indicates that turtles may be able to use other learning processes such as goal emulation. This first study indicates that in order to truly test if turtles can learn socially by other processes more specific experimental designs are needed, with multiple experiments in order to answer these questions.

Turtles exhibit no parental care, and yet they associate and interact extensively as adults (part 2). Unfortunately, not much is known about turtle juvenile social behavior in nature. This study shows adult turtles also exhibit social learning abilities. Most studies of social learning ability are focused on mammals and birds that exhibit parental care (Rogers & Kaplan, 2004; Pearson, 2008). Most fish, however, that school, do not exhibit post-hatching parental care, yet these animals live in groups and forage together. Fish social learning, unlike turtles, has been studied (Brown & Laland, 2003). Fish exhibit social facilitation and mate choice copying and have similar social life histories to that of turtles, yet turtles in this present experiment exhibit both social facilitation and stimulus enhancement with the possibility of more complex social learning processes. Therefore, turtles are an excellent group to study social learning from a comparative cognition perspective. Future turtle social learning experiments testing for differing social learning processes as well as species differences are needed to gain a broader comparative cognition perspective.

Turtles are exothermic, so energy expenditure needs to be considered when designing experiments. Also, if they are not kept at optimum temperatures turtles brains will slow down and so testing their full capabilities will not be possible. Energy expenditure costs and the affects of temperature on turtle behavior and cognition are not issues most learning psychologists are need to account for, and may explain early views of turtles as “stupid” (Spigel, 1964). Another contributing factor to the underestimation of turtle cognitive abilities in the past was researchers failed to consider the effects of handling stress on turtle behavior and therefore the need to have turtles use to captivity and handling prior to testing. Turtles generally exhibit stress behaviors such as becoming inactive or hyperactive to new situations such as new aquaria and human handling (personal observations, K, Davis), at which times they are not likely to perform learning tasks or perform them at their full ability level (Burghardt, 1977; Cash & Holberton, 1999). Since turtles are long-lived, if raised in captivity and socialized to people they have the potential to be great study subjects for learning experiments.

In Conclusion, my dissertation should help advance the study of turtle behavior and embed it within the more general research areas of comparative social systems, behavioral ecology, and comparative cognition. Many turtles are in danger of extinction due to human influence. However, since little is known about the behavior of most turtles effective conservation efforts are hampered.

The results of my research will also hopefully open the minds of Zoological Staff to consider the enrichment needs of reptiles in captivity. The visual food acquisition tasks discussed in parts 3 and 4 can easily be used and/or modified to stimulate and enrich the lives of the many turtle species (both aquatic and terrestrial) in captivity and spark an interest in finding ways to enrich other reptile groups by taking each species' *Umwelt* (Uexküll, 1934/1957) into account.

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VITA

Karen Marie Davis was born in Buffalo, New York, in 1974. She grew up in East Aurora, New York with her family and dog Otto. She graduated from Purdue University in 1997 with a B.S. in Ecology and Population Biology. During her time at Purdue University in West Lafayette, Indiana, she spent 4 years at Wolf Park in Battle Ground, Indiana were she learned about ethology, wolf behavior, and raised 13 wolves. In 1998 she became a zoo keeper at the Utica Zoo in Utica, New York. During her time at the Utica Zoo, Karen trained many exotic animals including; a sea lion, bears, raptors, and she raised a Siberian lynx. Karen started her Masters of Science degree at Bowling Green State University of Ohio in 2000 with Robert Huber, PhD. She received her M.S. in Biology with a focus on animal behavior studying crayfish behavior in the field in December, 2002. Karen started her PhD. in Experimental Psychology at the University of Tennessee, Knoxville Tennessee in August of 2003 with Gordon M. Burghardt, PhD.