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Factors Influencing Movements and Foraging Ecology of American Alligators (*Alligator mississippiensis*) in a Dynamic Subtropical Coastal Ecosystem

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

FACTORS INFLUENCING MOVEMENTS AND FORAGING ECOLOGY OF
AMERICAN ALLIGATORS (*ALLIGATOR MISSISSIPPIENSIS*) IN A DYNAMIC
SUBTROPICAL COASTAL ECOSYSTEM

A dissertation submitted in partial fulfillment of

the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Adam E. Rosenblatt

2013

To: Dean Kenneth G. Furton
College of Arts and Sciences

This dissertation, written by Adam E. Rosenblatt, and entitled Factors Influencing Movements and Foraging Ecology of American Alligators (*Alligator mississippiensis*) in a Dynamic Subtropical Coastal Ecosystem, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

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The dissertation of Adam E. Rosenblatt is approved.

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Florida International University, 2013

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DEDICATION

To my mother and father, Ann Freedman and Rand Rosenblatt, for encouraging me to pursue my passions even when those passions scared the crap out of them.

To my brother, David Rosenblatt, for leading by example.

And to my wife, Rachel Decker, for her patience, kindness, insight, and love.

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ABSTRACT OF THE DISSERTATION

FACTORS INFLUENCING MOVEMENTS AND FORAGING ECOLOGY OF
AMERICAN ALLIGATORS (*ALLIGATOR MISSISSIPPIENSIS*) IN A DYNAMIC
SUBTROPICAL COASTAL ECOSYSTEM

by

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Florida International University, 2013

Miami, Florida

Professor Michael Heithaus, Major Professor

Top predators can have large effects on community and population dynamics but we still know relatively little about their roles in ecosystems and which biotic and abiotic factors potentially affect their behavioral patterns. Understanding the roles played by top predators is a pressing issue because many top predator populations around the world are declining rapidly yet we do not fully understand what the consequences of their potential extirpation could be for ecosystem structure and function. In addition, individual behavioral specialization is commonplace across many taxa, but studies of its prevalence, causes, and consequences in top predator populations are lacking. In this dissertation I investigated the movement, feeding patterns, and drivers and implications of individual specialization in an American alligator (*Alligator mississippiensis*) population inhabiting a dynamic subtropical estuary. I found that alligator movement and feeding behaviors in this population were largely regulated by a combination of biotic and abiotic factors that varied seasonally. I also found that the population consisted of individuals that displayed an extremely wide range of movement and feeding behaviors, indicating that individual

specialization is potentially an important determinant of the varied roles of alligators in ecosystems. Ultimately, I found that assuming top predator populations consist of individuals that all behave in similar ways in terms of their feeding, movements, and potential roles in ecosystems is likely incorrect. As climate change and ecosystem restoration and conservation activities continue to affect top predator populations worldwide, individuals will likely respond in different and possibly unexpected ways.

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PREFACE

The following chapters have been published and have been formatted for those publications.

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CHAPTER III

Rosenblatt A, MR Heithaus (2011) Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? *Journal of Animal Ecology* 80:786-798

CHAPTER I

GENERAL INTRODUCTION

Top predators can affect ecosystem structure and function through a variety of mechanisms, most of which involve their interactions with and impacts on prey. Predators can affect prey populations through direct consumption and indirectly because they pose a predation risk, i.e. prey alter their behaviors to avoid predators (“risk effects”; Preisser et al. 2005; Creel and Christianson 2008). In some situations top predators can initiate trophic cascades in which their effects on prey density or behaviors indirectly affect the density or behaviors of organisms at lower trophic levels (Schmitz et al. 2004; Terborgh and Estes 2010). Furthermore, the strength, scale, and spatiotemporal patterns of the effects that top predators have on ecosystems often are structured by their movement behaviors because these determine both the range of habitats and the types of prey communities that top predators regularly encounter (Turchin 1998). Understanding movement patterns is also important because it allows for the investigation of the potential for consumer-mediated nutrient flow between disparate habitats (e.g., Rosenblatt and Heithaus 2011).

Studying the movement and feeding behaviors of top predators and elucidating their roles in ecosystem structure and function has historically been difficult because of their low population densities relative to prey (Heithaus et al. 2002) and because of their cryptic behaviors (Williams et al. 2004). However, technological innovations in recent decades have produced relatively small and long-lasting tracking devices that allow researchers to passively monitor top predator movements and behaviors (e.g., Heupel et al. 2006; Schofield et al. 2007), and new minimally-invasive techniques for assessing the trophic interactions of top predators have become commonplace (e.g., stable isotope analysis; Fry 2006). Despite these advances, long-term movement and foraging behaviors

are still unknown for many top predator species, limiting our understanding of their potentially complex effects on ecosystem structure and function. The knowledge gap needs to be urgently addressed because many top predator populations worldwide are disappearing (Estes et al. 2011). Also, the rapid pace of climate change and other anthropogenic impacts on ecosystems will have myriad effects on ecosystem and community dynamics partially through their effects on top predators (Estes et al. 2011).

In addition, individuals within a population can exhibit considerable variation in behaviors that are not attributable to age, size, sex, or morphology (Bolnick et al. 2003). Individual niche specialization (INS) has important implications for evolutionary processes and community and population dynamics (e.g., speciation, competition; Bolnick et al. 2003; Dall et al. 2012). Although “generalist” species are known to exhibit INS (Bolnick et al. 2003), there remain important questions about the prevalence and drivers of INS within populations (Araujo et al. 2011), especially for top predators.

In my dissertation I investigate the factors affecting movements, feeding behaviors, and patterns of INS in the last native, large-bodied, and abundant top predator in the southeastern United States, the American alligator (*Alligator mississippiensis*; Mazzotti and Brandt 1994). Alligators are one of the best-studied crocodylians on the planet, yet we understand relatively little about their roles in ecosystems, particularly in coastal estuaries. In my dissertation I investigate the behavior, movements, and trophic interactions of adult alligators with a focus on those inhabiting the Shark River Estuary (SRE) in southwest Florida. Alligators are dominant apex predators in mangrove estuaries of southern Florida, including the SRE, and could play an important role in these ecosystems. However, the dynamics and scales of alligator trophic interactions have

never been investigated in such habitats. My research is timely and important because the SRE is predicted to change significantly as Everglades restoration activities and climate change-driven sea level rise will likely alter the hydrological patterns and ecosystem structure that currently characterize the SRE (Davis et al. 2005). Thus, by studying the movement and feeding behaviors of the alligators in the SRE as they currently exist, my ultimate goal is to be able to predict how alligators, and their potential roles in the coastal Everglades, will change.

I begin, in Chapter 2, with an experimental study of the dynamics of stable isotope values in the tissues of alligators. Stable isotope analysis is a widely used, minimally-invasive technique for assessing trophic interactions. Used appropriately, stable isotope analysis can provide insights into the sources of production consumed by a species and its relative trophic level. However, to properly interpret stable isotope data from wild animals one must understand rates of isotopic turnover and magnitudes of change in isotope values between consumer and resource which are somewhat unique to different species (Dalerum and Angerbjorn 2005). My study represents the first investigation of stable isotope dynamics in any crocodylian and therefore will be valuable to future studies of other crocodylians and ectothermic top predators in general.

In Chapter 3, I use a novel movement tracking technology, passive acoustic telemetry (Heupel et al. 2006), in conjunction with stable isotope analysis to study the habitat use patterns of alligators in the SRE, the potential for alligators to act as biological vectors of connectivity between disparate habitats, and how these habitat use patterns and potential ecological roles are affected by variation in both biotic and abiotic factors.

In Chapter 4, I continue my investigations of alligator movement patterns by examining their activity ranges and rates of movement in the SRE, focusing on individual specialization in these behaviors and the potential implications of such variability for ecosystem structure and function.

In Chapter 5, I synthesize data on alligator stomach contents and stable isotope values across a large range of habitats to investigate patterns and drivers of feeding specialization within populations.

Finally, in Chapter 6, I discuss the implications of my research for understanding the roles of alligators in ecosystems specifically and large top predators more generally. I also discuss how alligators may respond to future environmental change in both the coastal Everglades ecosystem and other coastal ecosystems in the context of environmental restoration activities and sea level rise.

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CHAPTER II

SLOW ISOTOPE TURNOVER RATES AND LOW DISCRIMINATION VALUES IN THE AMERICAN ALLIGATOR: IMPLICATIONS FOR INTERPRETATION OF ECTOTHERM STABLE ISOTOPE DATA

Rosenblatt A, MR Heithaus (2013) Slow isotope turnover rates and low discrimination values in the American alligator: implications for interpretation of ectotherm stable isotope data. *Physiological and Biochemical Zoology* 86:137-148

Abstract

Stable isotope analysis has become a standard ecological tool for elucidating feeding relationships of organisms and determining food web structure and connectivity.

There remain important questions concerning rates at which stable isotope values are incorporated into tissues (turnover rates) and the change in isotope value between a tissue and food source (discrimination values). These gaps in our understanding necessitate experimental studies to adequately interpret field data. Tissue turnover rates and discrimination values vary among species and have been investigated in a broad array of taxa. However, little attention has been paid to these parameters in ectothermic top predators. I quantified the turnover rates and discrimination values for three tissues (scutes, red blood cells, and plasma) in American alligators (*Alligator mississippiensis*). Plasma turned over faster than scutes or red blood cells, but turnover rates of all three tissues were very slow in comparison to endothermic species. Alligator $\delta^{15}\text{N}$ discrimination values were surprisingly low in comparison to other top predators and varied between experimental and control alligators. The variability of $\delta^{15}\text{N}$ discrimination values highlights the difficulties in using $\delta^{15}\text{N}$ to assign absolute, and possibly even relative, trophic levels in field studies. My results suggest that interpreting stable isotope data inferred from parameter estimates from other species can be problematic and suggest that large ectothermic tetrapod tissues may be characterized by unique stable isotope dynamics relative to species occupying lower trophic levels and endothermic tetrapods.

Introduction

Over the last 30 years, stable isotope analysis (SIA) has become a common tool for elucidating trophic interactions and food web structure. Stable isotope analysis has been used to study temporal and spatial variation in food web structure (e.g., Fry 1991; Hobson and Welch 1992), interspecific niche partitioning (e.g., Stewart et al. 2003), habitat connectivity (e.g., Anderson and Polis 1998; Rosenblatt and Heithaus 2011), and individual specialization (e.g., Bearhop et al. 2006; Newsome et al. 2009; Matich et al. 2011) among other applications. The most commonly used elements in ecological SIA are carbon (C) and nitrogen (N; Fry 2006). The ratio of ^{13}C to ^{12}C (expressed in standard delta notation as $\delta^{13}\text{C}$) is only altered slightly as C moves up the food chain (typically between -1‰ and +1‰), while the ratio of ^{15}N to ^{14}N ($\delta^{15}\text{N}$) typically increases as the amount of ^{15}N in consumer tissues increases (between +2‰ and +6‰ per trophic level) as N moves up the food chain (DeNiro and Epstein 1978, 1981; Minigawa and Wada 1984; Peterson and Fry 1987; Post 2002; Caut et al. 2009). Thus $\delta^{13}\text{C}$ can be used to track the original source(s) of a consumer's nutrients, and $\delta^{15}\text{N}$ can be used to estimate a consumer's relative trophic position (i.e., higher $\delta^{15}\text{N}$ indicates higher trophic position; Fry 2006). Despite its prevalence in ecological studies, however, there remain important questions concerning the dynamics of isotopes as they move through the food web that necessitate controlled studies to adequately interpret field data.

Of particular importance are the changes in δ ratios with each trophic transfer ("discrimination" or Δ values) and the time required for tissues, especially metabolically active ones, to incorporate the δ values of their diets ("turnover rates"). It is well known that discrimination values and turnover rates can vary considerably among species and

tissue types because of variable metabolic rates and pathways (Gannes et al. 1997; Post 2002; Caut et al. 2009). Selection of appropriate discrimination values and turnover rates, therefore, is critical for assessing trophic interactions, trophic positions, and patterns of specialization of consumers (e.g., Caut et al. 2009; Hussey et al. 2010; Bond and Diamond 2011).

Discrimination values and turnover rates have been experimentally determined for many tissue types in many species of animals, but there is a high degree of variation among taxa. For example, a literature search using Web of Science and combinations of the search terms “isotope,” “turnover,” “discrimination,” and “fractionation” returns C or N isotope discrimination values or turnover rates for at least one tissue from 62 fishes, 41 invertebrates, 30 birds, and 25 mammals. In contrast, isotope parameters are available for only one species of amphibian (McIntyre and Flecker 2006) and eight species of reptile (Seminoff et al. 2006, 2007, 2009; Reich et al. 2008; Fisk et al. 2009; Warne et al. 2010; Murray and Wolf 2012). The lack of stable isotope parameters for ectothermic tetrapods limits our overall understanding of stable isotope dynamics, in particular possible differences between large ectothermic and endothermic top predators. Elucidating these differences is important because large ectothermic top predators, particularly crocodylians, have been dominant predators in tropical aquatic systems for millions of years and likely exert variable degrees of control over aquatic and terrestrial ecosystem dynamics. Currently, many of the extant crocodylian species are endangered or threatened (Martin 2008) yet their functional roles in tropical ecosystems are still largely unknown. Accurate application of SIA to these animals could lead to greater understanding of their roles in food webs and improved management and conservation strategies.

In this study I quantified discrimination values and turnover rates for the American alligator (*Alligator mississippiensis* Daudin), an ectothermic top predator that inhabits the southeastern United States (Mazzotti and Brandt 1994). I hypothesized that isotopic turnover rates for alligators would be slower than most other vertebrates previously studied because of their slow metabolism, but had no *a priori* predictions about how $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ discrimination values might compare to other vertebrates. My overarching goal was to elucidate the isotope parameters of a large reptilian top predator and investigate how stable isotope dynamics might vary between ectotherms and endotherms in general, among large carnivores, and among species of reptiles.

Material and methods

Experimental design

All procedures were carried out under a permit from Florida International University's Institutional Animal Care and Use Committee (#09-015). The study was conducted between May 2010 and May 2011 at the St. Augustine Alligator Farm (SAAF) in St. Augustine, FL, USA using 14 captive born and raised juvenile American alligators. Each individual was identified using previously implanted passive integrated transponder tags (Avid Identification Systems Inc., Norco, CA, USA). Each alligator was measured for total length, snout-vent length, head length, and tail girth to the nearest 0.1 cm, and mass to the nearest 0.5 kg before the study began. Body condition was calculated using Fulton's condition factor formula, $(M/SVL^3) \cdot 10^5$, where M = body mass and SVL = snout-vent length (Fujisaki et al. 2009). At the beginning of the experiment the alligators ranged in age from 3.3-8.4 years (mean = 5.7 ± 1.2 SD) and 78.6-114.8 cm total length

(mean = 93.4 ± 13.4 SD). All individuals were immature males (size at maturity = 1.5–1.8 m; Abercrombie 1989; Dalrymple 1996), which minimized the possible confounding effect of variation in metabolism between sexes and life stages. Also, because juvenile alligators grow at similar rates until maturity (i.e., growth rates vary little across ages and sizes of juvenile alligators; Jacobsen and Kushlan 1989) it is unlikely that variation in growth rates would confound results.

To assess isotope turnover rates of three tissues easily collected during field studies (scutes, red blood cells (RBCs), blood plasma) I carried out a diet-switch experiment in which the alligators were split into two groups. The control group ($n = 7$) was housed in a fenced-in outdoor un-roofed pen (6 m x 6 m with a 0.5 m deep pool) and the experimental group ($n = 7$) was housed in a concrete enclosed roofed pen (4 m x 4 m with a 0.5 m deep pool) to limit the possibility of small birds and mammals from accidentally becoming prey for the experimental group and shifting the isotope values of their tissues. Both groups were composed of randomly selected individuals. The two groups did not differ in length, weight, or body condition at the beginning of the experiment (t-test: respectively, $t_{12} = -0.37$, $p = 0.72$; $t_{12} = -0.66$, $p = 0.52$; $t_{12} = -1.65$, $p = 0.13$). For approximately three years before the study began all of the alligators were predominantly fed a diet of homogenized pork-based food pellets (protein = 45.0%, fat = 9.5%; Mazuri, Richmond, IN, USA), manufactured specifically for captive crocodilians. Rarely, their diet was supplemented with mice and rats. When the experiment began, the alligators in the control group continued to be fed the pellet diet, while the alligators in the experimental group were switched to a diet of channel catfish (*Ictalurus punctatus*; protein = 16.4-17.5%, fat = 10.3-13.2%; Grant and Robinette 1992; Silva and

Ammerman 1993). All of the catfish were farm-raised (Carolina Classics Catfish Inc., Ayden, NC, USA) on a diet that consisted mainly of soy, corn, and wheat. The catfish were all harvested in one batch to minimize isotopic variability and were frozen whole and shipped to SAAF where they were stored in a normal freezer. Before being fed to the alligators in the experimental group the catfish were thawed and cut into small chunks. Each group was fed equal amounts of food approximately two times per week and efforts were made to ensure that each of the study animals was fed equally during each feeding, though occasionally during feedings some individuals consumed slightly more than others. Isotopes from 14 random samples each of the catfish and pellet diet were analyzed at the beginning of the study to determine the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the two diets and to assess their consistency. I only performed SIA on diet samples at the beginning of the study because stable isotope ratios are unaffected by storing tissues in normal freezers (Bosley and Wainright 1999; Barrow et al. 2008; Bugoni et al. 2008). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the pellet diet were $-17.55\text{‰} \pm 0.14\text{‰}$ SE and $5.97\text{‰} \pm 0.03\text{‰}$ SE, respectively, while $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the catfish diet were $-23.19\text{‰} \pm 0.58\text{‰}$ SE and $9.69\text{‰} \pm 0.70\text{‰}$ SE, respectively. The differences in δ values between the two diets (5.64‰ for $\delta^{13}\text{C}$ and 3.72‰ for $\delta^{15}\text{N}$) are similar in magnitude to the spread of isotope values found in wild alligator populations (e.g., Rosenblatt and Heithaus 2011) and thus represent real isotopic shifts that could naturally occur. Other candidate foods for the experimental diet (*Rattus rattus*, *Oncorhynchus mykiss*, *Gallus gallus domesticus*, *Mugilidae* sp.) were tested but isotopic values were not sufficiently different from the control diet to provide insights into discrimination values and turnover rates.

Before the diet switch, small samples (~1 cm²) of scutes (raised scales on the back and tail) were collected from the terminal tail scutes of each alligator using surgical scissors. Also, a small amount of blood (3-4 ml) was collected from the dorsal cervical sinus using an 18 gauge, 3.8 cm needle and a 5 ml syringe (Owens and Ruiz 1980). Blood samples were immediately separated into their RBC and plasma components using a centrifuge spun at 3000 rpm for 30 seconds. All samples were frozen and transported to the laboratory where they were stored at -4°C. These initial samples served as baseline isotope measurements for each group. After the diet switch, blood samples were collected from each alligator in both groups after two weeks, four weeks, eight weeks, 16 weeks, 32 weeks, and one year. Because I predicted slower isotope turnover rates in scute tissue, I only collected scute samples after eight weeks, 32 weeks, and one year. During each sampling period, all alligators were weighed and measured. The experiment had to be terminated after one year because of space limitations at the SAAF facility.

Once in the lab, scute samples were washed with deionized water and then transferred, along with the plasma and RBC samples, to an oven and dried at 60°C for at least 72 hours. All samples were then powdered using a mortar and pestle and between 0.4 and 0.7 mg of sample was placed in individual 3 x 5 mm tin cups for analysis. Crocodilian scutes are not homogenous tissues but instead are composed of a keratin surface layer and a collagen core (Radloff et al. 2012). I analyzed them whole instead of separating them into their constituent parts because when the two tissues are sampled from wild alligators they do not significantly differ in their isotope values (J. Nifong, unpublished data), though they may differ in their isotope turnover rates and discrimination values. Isotopic analyses were performed at Florida International

University's Stable Isotope Laboratory using standard elemental analyzer isotope ratio mass spectrometer procedures (Fry 2006). Seven scute samples, 10 plasma samples, and 20 RBC samples were analyzed in duplicate, and the mean error attributable to the equipment was $0.05\text{‰} \pm 0.006\text{‰}$ SE for $\delta^{15}\text{N}$ and $0.09\text{‰} \pm 0.01\text{‰}$ SE for $\delta^{13}\text{C}$. The standard deviations of an internal standard (glycine), based on 12 within-run samples during each of eight runs, were 0.06‰ for $\delta^{15}\text{N}$ and 0.08‰ for $\delta^{13}\text{C}$.

Lipid content of isotope samples is a potential confounding factor in SIA because lipids generally are depleted in ^{13}C in comparison to carbohydrates and proteins and therefore exhibit more negative $\delta^{13}\text{C}$ values (DeNiro and Epstein 1977; Post et al. 2007). Therefore, tissue samples characterized by high lipid content could appear to have lower $\delta^{13}\text{C}$ values than low-lipid tissues when in fact they may just contain different fractions of biochemical components. As a result, lipid-influenced $\delta^{13}\text{C}$ values could alter estimates of discrimination values. Furthermore, the different biochemical components of the diet can be subject to "isotopic routing," meaning ingested nutrients may not be used equally to build and maintain different consumer tissues (Gannes et al. 1997). For animals that consume high protein diets, such as the alligators fed the pellet diet in my study, dietary protein is most likely exclusively used for tissue synthesis while carbohydrates and lipids are catabolized (Gannes et al. 1997). Therefore, in my study alligator tissues and diets that exhibited high lipid content needed to be normalized through lipid extraction for proper analysis of the $\delta^{13}\text{C}$ discrimination values.

First I analyzed all of the samples without extracting any lipids because lipid extraction procedures carry the possibility of altering the $\delta^{15}\text{N}$ value of the tissues (Logan et al. 2008). Then, I identified if tissues from either group of alligators or the pellet diet

exhibited C:N ratios > 3.5 because this threshold indicates the potential presence of a large fraction of lipids that could affect $\delta^{13}\text{C}$ analyses (Post et al. 2007). A subset of tissue and diet samples characterized by high C:N ratios then were re-analyzed after lipids had been extracted using the following procedure: approximately 50 mg of each sample was weighed on filter paper (Whatman, Buckinghamshire, UK), then folded up inside the filter paper, secured with a sterile paper clip, and placed in a vial. Each vial was then filled with 4 ml of 2:1 dichloromethane:methanol solvent, which is as effective at removing lipids as chloroform but does not remove as much protein (Erickson 1993; Cequier-Sanchez et al. 2008). Vials were then capped and placed in a refrigerator for 15 hours. The solvent was then drained and 3 ml of fresh solvent added for 3 hours, followed by 2 ml of fresh solvent for another 3 hours. Samples were then removed from the vials, re-dried for at least 72 hours, weighed into tin cups, and analyzed using the previously described procedure.

Analyses

To determine the isotope turnover rates for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for all three tissues, I fit exponential decay curves to the isotope data gathered from the experimental group. I used the exponential decay equation $y = a + be^{ct}$, where y is the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ value at time t (days since diet switch), a is the value of the asymptote being approached by the curve, b is the total change in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ value after the diet switch, and c , the parameter that was solved for, is the fractional turnover value (Hobson and Clark 1992a; Seminoff et al. 2007). I then used the fractional turnover value (c) to calculate the isotopic half life ($t_{1/2}$) using the equation $t_{1/2} = \ln(0.5)/c$, where $t_{1/2}$ represents the amount

of time (in days) it takes for half of the isotopes to be exchanged in a tissue, and 0.5 indicates that 50% of the isotopes were exchanged (Seminoff et al. 2007). Complete isotopic turnover is reached in roughly four half lives, so I multiplied each $t_{1/2}$ value by four to estimate the complete turnover rate for each isotope for each tissue (Seminoff et al. 2007; Vander Zanden et al. 2010).

Diet-tissue discrimination values (Δ) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each tissue were calculated using the equation $\Delta = \delta_{\text{tissue}} - \delta_{\text{diet}}$, where δ_{tissue} represents the mean δ values of each tissue sampled from the control group for the duration of the study and δ_{diet} represents the mean δ value of the pellet diet (Hobson and Clark 1992b). I averaged the δ values of each tissue over the duration of the study for control group individuals because the control group had been fed on the same diet for at least four years (three years prior to study plus one year during study) thus I assumed that all three tissues had reached isotopic equilibrium with the diet. If the C:N ratio of a tissue or the pellet diet was > 3.5 then I calculated Δ for $\delta^{13}\text{C}$ using the $\delta^{13}\text{C}$ values from the lipid extracted samples. All analyses were carried out using SigmaPlot 11 (Systat Software Inc., Chicago, IL, USA).

Results

Growth

Alligators in both control and experimental groups grew during the experiment (average SVL growth = 3.2 cm \pm 2.4 SD [6.6% of initial SVL \pm 4.5 SD], average weight gain = 1.0 kg \pm 0.9 SD [28.7% of initial body mass \pm 20.4 SD]), but there were no significant differences in growth between treatments (t-test: $t_{11} = 0.7$, $p = 0.5$; $t_{11} = 1.3$, $p = 0.2$, respectively). There was no difference in body condition of individuals between

groups at the start (see methods) or conclusion of the experiment (control group $\bar{x} = 2.9 \pm 0.4$ SD; experimental group $\bar{x} = 2.8 \pm 0.2$ SD; Mann-Whitney Rank Sum Test: $T = 43.0$, $p = 0.9$).

Turnover rates

I did not detect any significant differences in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ between different sampling events for the control group tissues (ANOVA: all $p > 0.27$ except scutes $\delta^{13}\text{C}$ where $p = 0.06$) suggesting that isotope values for all tissues in the control group were at isotopic equilibrium (Figure 1). In contrast, in the experimental group all three tissues showed clear shifts away from the control diet and towards the experimental diet for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Figure 2). However, for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ only plasma appeared to equilibrate with the experimental diet after one year (Figure 2). Despite this result, the exponential decay functions applied to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values significantly fit the data for plasma and RBCs (all $p < 0.001$), and the fits for the scute $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were marginally non-significant ($p = 0.06$ and $p = 0.05$, respectively), most likely because of the use of only four data points (Figure 2). For plasma, RBCs, and scutes the $\delta^{13}\text{C}$ half-lives were 63.0 days, 141.5 days, and 147.5 days, respectively, and the $\delta^{15}\text{N}$ half-lives were 62.4 days, 277.3 days, and 103.5 days, respectively. The estimated $\delta^{13}\text{C}$ complete turnover times (i.e. four half-lives) for plasma, RBCs, and scutes were 252.0 days, 566.0 days, and 590.0 days, respectively, and the estimated $\delta^{15}\text{N}$ complete turnover times were 249.6 days, 1109.2 days, and 414.0 days, respectively.

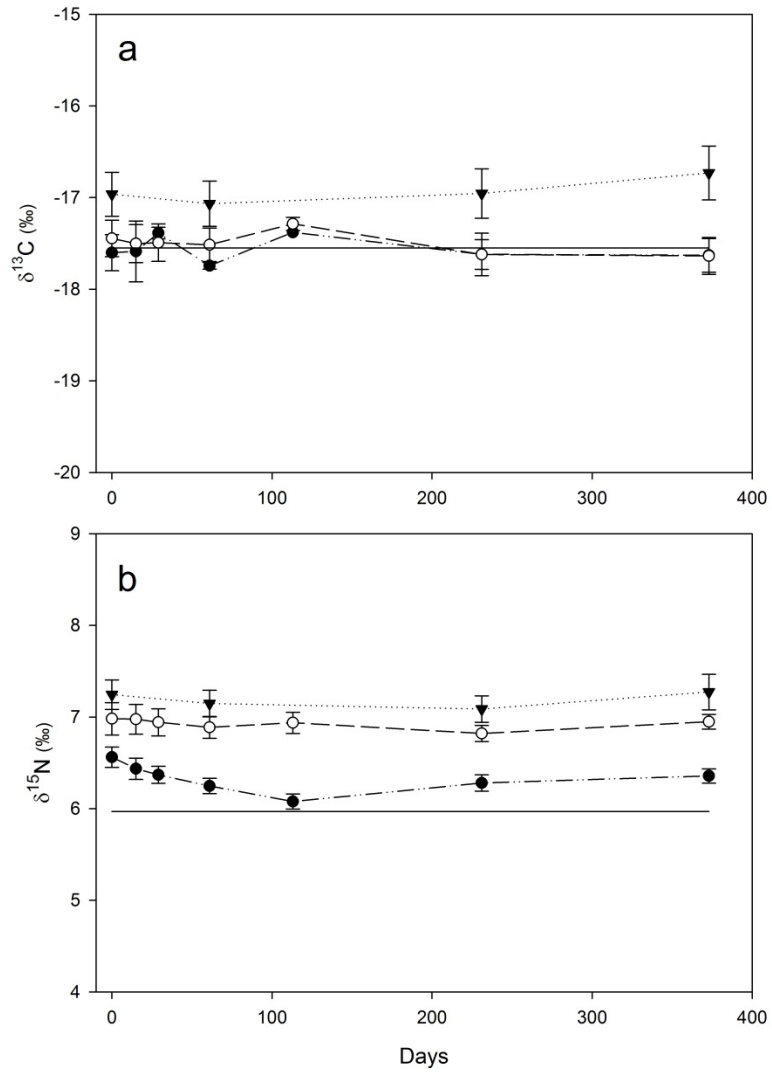


Figure 1: a) $\delta^{13}\text{C}$ stable isotope values and b) $\delta^{15}\text{N}$ stable isotope values from three American alligator tissues sampled from the control group over one year. The control group did not undergo a diet-switch prior to tissue collection. Closed circles and the dash-dot line represent blood plasma, open circles and the dashed line represent red blood cells, and triangles and the dotted line represent scutes. Solid lines represent the mean isotope value of the control diet. Error bars are \pm SE.

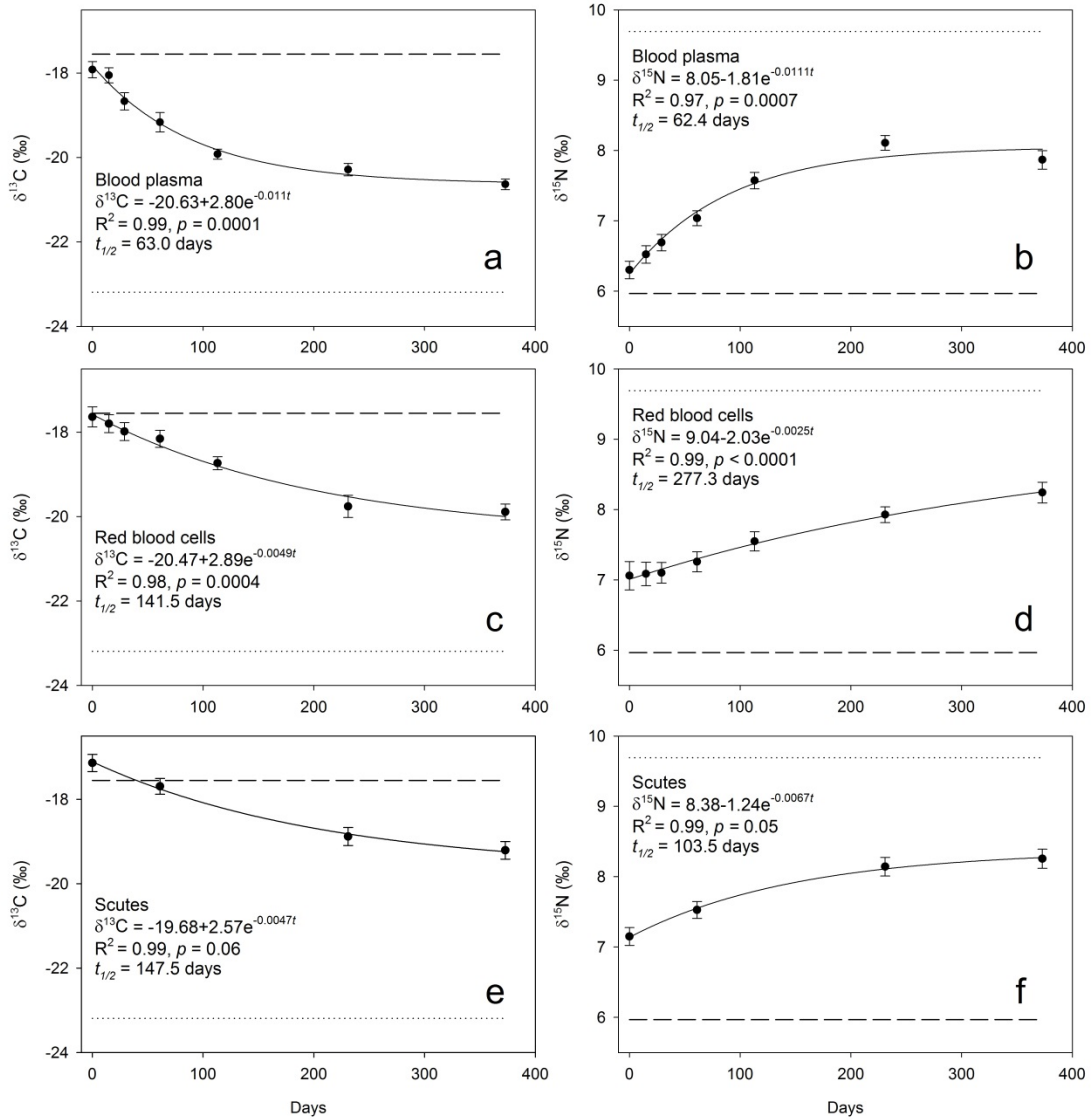


Figure 2: Stable $\delta^{13}\text{C}$ isotope values from a) blood plasma, c) red blood cells, and e) scutes and stable $\delta^{15}\text{N}$ isotope values from b) blood plasma, d) red blood cells, and f) scutes from American alligators (*Alligator mississippiensis*) in the experimental group collected over one year following a diet-switch. The curved line on each graph represents the exponential decay curve ($y = a + be^{ct}$, see text for definitions of each parameter) used to model each set of isotope turnover parameters. The parameter $t_{1/2}$ represents the time it takes (in days) for 50% of the isotopes in each tissue to turnover and was determined using the equation $t_{1/2} = \ln(0.5)/c$. Dashed lines represent the mean isotope value of the control diet and dotted lines represent the mean isotope value of the experimental diet. Error bars are \pm SE.

Discrimination values

The mean C:N ratios of the plasma, RBC, and scute samples from the control group were 3.65 ± 0.02 SE, 3.17 ± 0.009 SE, and 3.09 ± 0.02 SE, respectively, and the C:N ratio of the pellet diet was 5.92 ± 0.07 SE. The mean C:N ratios of the plasma, RBC, and scute samples from the experimental group were 3.66 ± 0.03 SE, 3.19 ± 0.01 SE, and 3.08 ± 0.01 SE, respectively. Therefore, I extracted lipids only from the pellet diet and plasma samples from each group because their C:N ratios were > 3.5 (Post et al. 2007). The mean C:N ratios of the pellet diet and plasma samples from the control and experimental groups after lipid extraction were 5.00 ± 0.06 SE, 3.43 ± 0.02 SE, and 3.61 ± 0.02 SE, respectively. The $\delta^{13}\text{C}$ values of the pellet diet and plasma samples from the control and experimental groups before lipid extraction were $-17.52\text{‰} \pm 0.15$ SE, $-17.60\text{‰} \pm 0.07$ SE, and -19.42 ± 0.23 SE, respectively, and after lipid extraction the values were $-17.30\text{‰} \pm 0.17$ SE, $-17.54\text{‰} \pm 0.07$ SE, and -19.23 ± 0.24 SE, respectively. These shifts in δ ratios were not statistically significant (Mann-Whitney Rank Sum Test: $T = 208.0$, $p = 0.1$ for diet; $T = 922.0$, $p = 0.3$ for control plasma; $T = 740.0$, $p = 0.4$ for experimental plasma), therefore I used the non-lipid extracted $\delta^{13}\text{C}$ values for all subsequent analyses. I also compared the lipid extracted plasma $\delta^{13}\text{C}$ values to the expected plasma $\delta^{13}\text{C}$ values generated by Post et al.'s (2007) lipid correction equation for aquatic animals (see below). I found that the $\delta^{13}\text{C}$ values produced by the lipid correction equation (mean = -17.29 ± 0.07 SE) were significantly higher than the lipid extracted $\delta^{13}\text{C}$ values (Mann-Whitney Rank Sum Test: $T = 642.0$, $p < 0.001$), but only by 0.25‰ which is not a large enough difference to be ecologically meaningful.

The mean $\Delta\delta^{15}\text{N}$ values for all control alligators were positive, but of lesser magnitude than traditionally assumed for all tissues (plasma = $+0.35\text{‰} \pm 0.04$ SE; RBCs = $+0.95\text{‰} \pm 0.05$ SE; scute = $+1.22\text{‰} \pm 0.08$ SE) (Figure 2). The $\Delta\delta^{13}\text{C}$ values were relatively small for each tissue (plasma = $-0.04\text{‰} \pm 0.07$ SE; RBCs = $+0.03\text{‰} \pm 0.07$ SE; scutes = $+0.61\text{‰} \pm 0.12$ SE). For comparison, I also calculated the approximate Δ values for each tissue from the individuals in the experimental group by using the estimated complete turnover times as the t parameters in the exponential decay equations and solving for $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$. I then subtracted these estimated tissue isotope equilibrium values from the isotope values of the catfish diet. The C:N ratio of the catfish diet was 6.77 ± 0.51 SE so I used a lipid correction equation for aquatic animals ($\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + (0.99 * \text{C:N})$) to normalize the catfish $\delta^{13}\text{C}$ values (Post et al. 2007). The $\Delta\delta^{13}\text{C}$ values calculated from the alligators in the experimental group were different from those of the control group, but were still relatively small (Table 1). In contrast, there was an important difference between the two groups concerning the $\Delta\delta^{15}\text{N}$ values. All $\Delta\delta^{15}\text{N}$ values were negative for the experimental group (Table 1).

Discussion

Quantifying species- and tissue-specific stable isotope discrimination values and turnover rates is essential for proper analysis and interpretation of field data. Using a diet-switch experiment, I provide the first data on isotope turnover rates and discrimination values of a crocodilian. I found that isotope turnover rates of American alligators were considerably slower than most other taxa studied, especially for RBCs, and that $\Delta\delta^{15}\text{N}$ values were much smaller than often is assumed. These results underscore important

Table 1: Approximate discrimination values (Δ) calculated from estimated isotope values at tissue equilibrium from alligators in the experimental group.

Isotope	Tissue	Estimated isotope value at tissue equilibrium	Isotope value of catfish diet	Approximate Δ value at equilibrium	Δ value from control group
$\delta^{13}\text{C}$	Plasma	-20.45‰	-19.80‰	-0.65‰	-0.04
	Red blood cells	-20.29‰	-19.80‰	-0.49‰	+0.03
	Scutes	-19.52‰	-19.80‰	+0.28‰	+0.61
$\delta^{15}\text{N}$	Plasma	7.94‰	9.69‰	-1.75‰	+0.35
	Red blood cells	8.91‰	9.69‰	-0.78‰	+0.95
	Scutes	8.30‰	9.69‰	-1.39‰	+1.22

Note: The Δ values were calculated using the equation $\Delta = \delta_{\text{issue}} - \delta_{\text{diet}}$, and the $\delta^{13}\text{C}$ value of the catfish diet was corrected for lipid content using the equation $\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + (0.99 * \text{C:N})$ (Post et al. 2007). Δ values from the control group are provided for comparison.

differences in isotope dynamics between different reptilian species and between endothermic and ectothermic taxa.

Across taxa, there is relatively predictable variation in relative turnover times across tissue types. Plasma tends to turn over most rapidly, skin the slowest, and RBCs are intermediate (reviewed by Dalerum and Angerbjorn 2005). While alligators exhibited this pattern of tissue turnover rates for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ turnover rates deviated from this pattern. The $\delta^{15}\text{N}$ turnover rate for RBCs was by far the slowest rate of all three tissues and almost twice as slow as the $\delta^{13}\text{C}$ rate for RBCs. This result can partially be explained by the fact that reptilian RBCs are nucleated (Dessauer 1970) and therefore have longer lifespans than the same cells in species which have non-nucleated RBCs (e.g., mammals). Indeed, alligator RBCs display exceptionally long lifespans, reaching 1320 days under some conditions (Cline and Waldmann 1962), while mammalian RBCs can only survive 36-120 days (reviewed by Rodnan et al. 1957). Also, the $\delta^{15}\text{N}$ turnover rate may be much slower than the $\delta^{13}\text{C}$ rate in RBCs because N is a crucial component of the hemoglobin molecule that makes up much of the mass of long-lived alligator RBCs, whereas metabolically generated C is transported into and out of alligator RBCs in the form of CO_2 as the RBCs carry the molecule to the lungs to be exhaled (Jensen et al. 1998). Therefore, hemoglobin-linked N may remain in an RBC for the entire lifespan of the cell while C may turn over relatively more quickly as part of respiration.

Ectotherms generally exhibit slower metabolic rates than endotherms (Hulbert and Else 2004), thus I would expect ectotherm tissues to be characterized by slower isotope turnover rates than endotherms. Dalerum and Angerbjorn (2005), in a review of mammal and bird isotope studies, reported no estimated complete turnover rates ($t_{1/2} * 4$)

for plasma or RBCs greater than 160 days, with all but two rates less than 20 days. More recent studies have also found relatively short estimated complete turnover rates for plasma and RBCs in Pallas's long-tounged bat (*Glossophaga soricina*; estimated complete turnover = 97-158 days; Mirón et al. 2006) and the arctic fox (*Vulpes lagopus*; estimated complete turnover = 16-172 days; Lecomte et al. 2011). In contrast, reptile plasma and RBC tissues can display short estimated complete turnover rates (e.g., 19 days for *Caretta caretta*; Table 2), but also much longer rates (e.g., 1109 days for *Alligator mississippiensis*; Table 2) that have never been found in endotherms. Other ectotherms display similar patterns to reptiles in terms of estimated complete isotope turnover rates for RBCs and plasma, with fishes (including sharks) displaying widely varying rates that range from 11-432 days (Buchheister and Latour 2010; German and Miles 2010; Logan and Lutcavage 2010; Kim et al. 2012). These trends suggest that isotope turnover rates in ectotherms can be relatively fast in some species and even comparable to rates observed in endotherms (possibly because some ectotherms metabolically resemble homeotherms (Goldman et al. 2004), but that isotope turnover rates in other ectotherm species can also be orders of magnitude slower than in endotherms. The mechanisms responsible for differences in turnover rates amongst ectotherms are not clear, but potential factors include variation in body size, activity levels, diet type and quality, growth rates, and species specific physiology.

The estimated complete turnover rates found for juvenile alligators in this study – which ranged from 250 days to 1109 days – are among the slowest recorded for any animal, despite their growth during the study (mean increase in body mass = 41% ± 21

Table 2: Known discrimination values and turnover rates for reptile plasma, red blood cells, and scutes.

Species	Tissue	Discrimination value (‰)		Half-life (days)		Estimated complete turnover rate (days)		Source
		$\Delta \delta^{13}\text{C}$	$\Delta \delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	
<i>Chelonia mydas</i>	Plasma	-0.12	+2.92					Seminoff et al. 2006
	Red blood cells	-1.11	+0.22					
<i>Trachemys scripta</i>	Plasma		+3.80		35.6		142.4*	Seminoff et al. 2007
	Red blood cells		+1.90					
<i>Caretta caretta</i> (hatchling)	Plasma	+0.29	+0.32			20.0	18.5	Reich et al. 2008
	Red blood cells	-0.64	-0.25			76.9	71.4	
<i>Caretta caretta</i> (juvenile)	Plasma	-0.38	+1.50			20.0	18.5	Reich et al. 2008
	Red blood cells	+1.53	+0.16			76.9	71.4	
<i>Dermochelys coriacea</i>	Plasma	-0.58	+2.86					Seminoff et al. 2009
	Red blood cells	+0.46	+1.49					
<i>Crotaphytus collaris</i>	Plasma	+0.20				44.4		Warne et al. 2010
	Red blood cells	+1.20				311.4		
<i>Sceloporus undulatus</i> <i>consobrinus</i>	Plasma	-0.50				25.0		Warne et al. 2010
	Red blood cells	-1.10				60.7		
<i>Gopherus agassizii</i>	Plasma	+1.00-1.60				32.9		Murray and Wolf 2012
	Red blood cells	+0.20-0.80				126.7		
<i>Alligator</i> <i>mississippiensis</i>	Plasma	-0.04	+0.35	63.0	62.4	252.0*	249.6*	
	Red blood cells	+0.03	+0.95	141.5	277.3	566.0*	1109.2*	This study
	Whole scutes	+0.61	+1.22	147.5	103.5	590.0*	414.0*	

Note: Δ values for alligators were taken from the calculations using the control group. * indicates estimated complete turnover rate values calculated by multiplying $t_{1/2}$ values by four. Calculation methods for the other turnover rates can be found within the given source material.

SD). Fisk et al. (2009) reported slower estimated complete $\delta^{15}\text{N}$ turnover rates for whole blood and muscle (1664 and 2496 days, respectively) in corn snakes (*Elaphe guttata guttata*) but only for those individuals fed an “uptake” diet, i.e., a diet that was enriched in ^{15}N isotopes in relation to the previous diet. In contrast, snakes fed on an “elimination” diet (i.e., the diet was depleted in ^{15}N isotopes relative to the initial control diet) exhibited much faster estimated complete turnover rates of only 300 days and 454 days for whole blood and muscle, respectively. In my study, the experimental group of alligators was also fed an uptake diet in terms of $\delta^{15}\text{N}$ values, but an elimination diet in terms of $\delta^{13}\text{C}$ values. Boecklen et al. (2011) conducted a meta-analysis on the effects of diet-switch directionality on isotope turnover rates and did not find support across taxa for the pattern reported by Fisk et al. (2009), but because of small sample size they concluded that the effects of diet-switch directionality on isotope turnover rates remains an open question.

Isotope turnover rates are composed of two components: turnover as a consequence of growth and turnover as a consequence of normal tissue maintenance (catabolic turnover; Hesslein et al. 1993; Reich et al. 2008). I used juvenile alligators that are capable of relatively rapid growth in comparison to adult alligators (Chabreck and Joanen 1979). Thus the turnover rates quantified in my study are some combination of growth turnover and catabolic turnover and may be faster than the turnover rates of adult alligators that, though they grow indeterminately (Jacobsen and Kushlan 1989), grow more slowly than juveniles. Both Reich et al. (2008) and Murray and Wolf (2012) were able to partition isotope turnover rates into their growth and catabolic turnover components using exponential growth models based on changes in body mass. Unfortunately, in my study I was unable to accurately partition isotope turnover rates into

their growth and catabolic turnover components because of the low number of sampling events ($n = 7$), the slow growth of the alligators in terms of body mass (mean = 0.95 kg/year), and the lack of accuracy in my body mass measurements (0.5 kg increments). For loggerhead turtles (*Caretta caretta*) Reich et al. (2008) found that, depending on the tissue type, growth was responsible for 15 to 52% of the turnover rates. Murray and Wolf (2012) reported that growth was responsible for 13 to 50% of carbon turnover in multiple tissues of juvenile desert tortoises (*Gopherus agassizii*). I would expect turnover rates in juvenile alligators to follow a similar pattern, and thus it is very likely that adult alligators actually display slower turnover rates than the ones I found in the present study (e.g., Sun et al. 2012).

Consistent with the general trend across taxa (reviewed by Caut et al. 2009), the $\Delta\delta^{13}\text{C}$ values of alligators (range = -0.65‰ to +0.61‰) were small and, therefore, should closely reflect dietary sources in the wild. Alligator $\Delta\delta^{15}\text{N}$ values (range = -1.75‰ to +1.22‰; Table 2) were less than the values found for the same tissues in every non-reptilian species studied to date (+1.23‰ to +6.30‰; reviewed by Caut et al. 2009) and considerably below the +3.40‰ value often applied to calculations of isotopic trophic levels (Post 2002). Indeed, the approximate $\Delta\delta^{15}\text{N}$ values from the experimental group were actually negative, suggesting that even the assumption that $\delta^{15}\text{N}$ values increase with each trophic step may not hold for all species and all diet types. Previous studies of $\Delta\delta^{15}\text{N}$ values for three different reptile species using the same tissues that I used found $\Delta\delta^{15}\text{N}$ values ranged from +0.16‰ (juvenile *Caretta caretta*) to +2.92‰ (juvenile *Chelonia mydas*) despite using comparably sized growing juveniles and with similarly carnivorous diets (Seminoff et al. 2006, 2009; Reich et al. 2008). This broad range of

$\Delta\delta^{15}\text{N}$ values highlights the difficulties in using $\delta^{15}\text{N}$ to assign absolute, and possibly even relative, trophic levels in field studies. Observed differences among species could have been caused by a number of factors, including differing activity levels, species specific physiology, and diet quality (Caut et al. 2009). Given the broad similarities between the studies, I hypothesize that the variation in $\Delta\delta^{15}\text{N}$ values between the reptile species is caused by some combination of different species specific growth patterns, isotopic routing pathways, and patterns of protein synthesis. Identifying the specific causes of these differences is difficult because of the lack of understanding about isotope dynamics at the molecular level.

Additionally, when my alligator data are compared with data currently available for large endothermic carnivores, the results suggest that $\Delta\delta^{15}\text{N}$ values are not conserved within broadly similar trophic guilds (i.e. mobile large-bodied top predators). For example, alligator plasma $\Delta\delta^{15}\text{N}$ values are much smaller than those of endothermic large top predators like seals (e.g., harbor seal, *Phoca vitulina* = +2.7‰ to +3.2‰, gray seal, *Halichoerus grypus* = +2.9‰ to +3.3‰, harp seal, *P. groenlandica* = +3.6‰; northern fur seal, *Callorhinus ursinus* = +5.2‰; Kurle 2002; Lesage et al. 2002). Though extensive data on $\Delta\delta^{15}\text{N}$ values across tissues of both large carnivorous endotherms and ectotherms are lacking, these initial studies may indicate that in general large carnivorous ectotherms are characterized by lower $\Delta\delta^{15}\text{N}$ values than large carnivorous endotherms, and thus generalized isotope parameters should not be applied across such varied groups because it could lead to the assignment of incorrect trophic levels.

Both $\Delta\delta^{15}\text{N}$ and $\Delta\delta^{13}\text{C}$ values vary with diet type and quality (Robbins et al. 2005, 2010; Mirón et al. 2006; Caut et al. 2009, 2010; Hill and McQuaid 2009; Dennis et

al. 2010). A review of isotope data from 82 different species from many disparate groups revealed a pattern wherein $\Delta\delta^{15}\text{N}$ and $\Delta\delta^{13}\text{C}$ values tend to decrease as the isotope values of the diet increase (i.e., discrimination values are lower at higher $\delta^{15}\text{N}$ and less negative $\delta^{13}\text{C}$; Caut et al. 2009). Despite some disagreement in the literature (Auerswald et al. 2010; Perga and Grey 2010), the isotope-diet inverse relationship has been further supported by recent laboratory experiments (Caut et al. 2008; Dennis et al. 2010) and data re-analysis (Caut et al. 2010). Although my results for $\Delta\delta^{15}\text{N}$ values were consistent with this pattern, my results for $\Delta\delta^{13}\text{C}$ values were not. Although I only used two different diets during the experiment and the Δ values derived from the experimental group are somewhat rough estimates, my results still imply that alligator Δ values can vary considerably depending on the type of diet being consumed.

Lastly, my findings concerning tissue-specific turnover rates in alligators have implications for the use of stable isotopes from ectotherms for the reconstruction of diet histories and measures of individual specialization. Over the past decade SIA has been promoted as an important tool for answering questions of individual specialization (e.g., Bolnick et al. 2002; Matthews and Mazumder 2004; Urton and Hobson 2005; Newsome et al. 2009). One way SIA can be used to elucidate patterns of individual specialization is to compare isotope values between multiple tissues that turn over at different rates (e.g., Bearhop et al. 2006; Matich et al. 2011). For example, if three tissues with different turnover rates (e.g., 10, 30, and 90 days) all displayed similar isotope values (allowing for differential discrimination values) for one individual then that individual could be considered a specialist since its isotope values were constant across different temporal scales. However, the applicability of this method may be limited in species like alligators

because tissues that turn over quickly in other species (e.g., plasma) turn over comparatively slowly in alligators. Thus, isotope information gathered from alligator plasma would be unable to resolve questions concerning daily, weekly, or even monthly diet variability, and therefore some specialization metrics (e.g., Bearhop et al. 2006; Matich et al. 2011) could over-estimate specialization in alligators since any short-term diet variability would be obscured by the turnover rate of the tissue. Other metrics for understanding specialization, however, may be facilitated by long turnover rates in tissues. For example, the spread between individual isotope values within a population (Layman et al. 2007) can be an indicator of long-term differences in diets among individuals on the time scale reflected by the tissue being used. Therefore, although alligator tissues may not be amenable for understanding stability of diets over relatively short time periods, even a single tissue type may provide information on within-population variation in trophic interactions (e.g., Burkholder et al. 2011).

In conclusion, the observed variation in the quantified isotope parameters from my study along with studies of other reptiles and non-reptiles underscores the need for species- and tissue-specific values to be used in the interpretation and analysis of any field-based isotope study. The values derived in my study are the first isotope parameters described for any crocodylian species and should be useful for elucidating the roles of alligators and closely related crocodylians in food web and community dynamics. Yet, many important questions regarding discrimination values and turnover rates remain. For example, how do diet quality, body size, and variation in growth and metabolic rates between individuals of the same age class and/or gender influence discrimination values and turnover rates? Answering these questions and elucidating isotope dynamics in a

wider array of species will more fully enable an understanding of the complexities of SIA, including its proper applications and limitations.

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CHAPTER III

DOES VARIATION IN MOVEMENT TACTICS AND TROPHIC INTERACTIONS AMONG AMERICAN ALLIGATORS CREATE HABITAT LINKAGES?

Rosenblatt A, MR Heithaus (2011) Does variation in movement tactics and trophic interactions among American alligators create habitat linkages? *Journal of Animal Ecology* 80:786-798

Abstract

Highly mobile top predators are hypothesized to spatially and/or temporally link disparate habitats through the combination of their movement and feeding patterns, but recent studies suggest that individual specialization in habitat use and feeding could keep habitats compartmentalized. I used passive acoustic telemetry and stable isotope analysis to investigate whether specialization in movement and feeding patterns of American alligators (*Alligator mississippiensis*) in an oligotrophic subtropical estuary created habitat linkages between marine and estuarine/freshwater food webs. Individual alligators adopted one of three relatively distinct movement tactics that were linked to variation in diets. Fifty-six percent of alligators regularly traveled from the upstream (freshwater/mid-estuary) areas into the downstream (marine-influenced) areas where salinities exceed those typically tolerated by alligators. Thirty-one percent of the alligators made regular trips from the mid-estuarine habitat into the upstream habitat; thirteen percent remained in the mid-estuary zone year-round. Stable isotopic analysis indicated that, unlike individuals remaining in the mid-estuary and upstream zones, alligators that used the downstream zone fed at least partially from marine food webs, and likely moved to access higher prey abundance at the expense of salt stress. Therefore, “commuting” alligators may link marine food webs with those of the estuary and marshes in the coastal Everglades and create an upstream vector for allochthonous nutrient inputs into the estuary. The present study lends further support to the hypothesis that large-bodied highly mobile predators faced with trade-offs are likely to exhibit individual specialization leading to habitat linkages, rather than compartmentalization. However, the conditions under which this scenario occurs require further investigation.

Introduction

Top predators can play important roles in the dynamics of their communities and ecosystems by coupling spatially and/or temporally segregated food webs (Polis, Anderson & Holt 1997; McCann, Rasmussen & Umbanhowar 2005; Rooney *et al.* 2006). Coupling may occur because diet breadth increases at higher trophic levels and top predators are more likely to feed from multiple resource pools (Pimm, Lawton & Cohen 1991). When top predators are highly mobile, and capable of using a wide variety of distinct resource pools, then they act as a stabilizing force in community and ecosystem dynamics (McCann *et al.* 2005; Rooney *et al.* 2006; Rooney, McCann & Moore 2008). The majority of studies investigating trophic coupling by predators, however, assume that all of the individuals in a population exhibit similar behaviours (e.g., Helfield & Naiman 2006). Recent tracking and stable isotopic studies, however, have revealed that even individuals from the same population can display quite different behaviours (e.g., Eichhorn *et al.* 2009; Fossette *et al.* 2010). Assumptions of population homogeneity in trophic studies, therefore, may overlook important temporally stable variation among individuals in their movements, foraging tactics and diets (“individual specialization”; see Bolnick *et al.* 2003). For example, Eurasian perch (*Perca fluviatilis*) captured within the same lake were hypothesized to couple littoral and pelagic food webs, but in fact individuals displayed individual specialization in both diets and habitat use and therefore perch did not couple these food webs (Quevedo, Svanback & Eklov 2009). Whether specialization in highly mobile top predators outside of lake systems might lead to compartmentalization of food webs is poorly known and is perhaps less likely because the scale of their movements allows them to access food resources at a distance from

locations that might be used for other behaviours. In such situations, individual variation in behaviours might actually enhance trophic coupling or lead to unexpected directions of predator-mediated nutrient flow (e.g., Matich, Heithaus & Layman 2011).

Estuaries are critical habitats for many species of recreational, commercial, and ecological importance because they are characterized by high primary and secondary productivity and serve as “nurseries” for many fish and invertebrate species (Beck *et al.* 2001). Species with broad salinity tolerances are generally thought to connect estuaries with other coastal ecosystems whereby they feed in productive estuaries and then move into coastal waters where they deposit nutrients. For example, female blue crabs (*Callinectes sapidus*) feed in estuaries and then move to the mouth of the estuary after mating to release their eggs during spawning (Kennedy & Cronin 2007). Despite the large amount of effort devoted to studying the dynamics of estuaries and their connections to the surrounding terrestrial and aquatic ecosystems, the role of large predators in these systems has largely been overlooked (possibly because they are relatively rare or difficult to study) as has the possibility that they may exhibit specialization in their behaviours that could influence ecosystem dynamics.

American alligators (*Alligator mississippiensis* Daudin) are the most abundant large-bodied predators in the southeastern United States (Mazzotti & Brandt 1994). Although they are generally thought of as a freshwater species, they are also found in brackish waters of estuaries (Mazzotti & Brandt 1994). Alligators require frequent access to low salinity waters throughout their lives because, unlike some crocodylians, they lack functioning salt glands that can excrete excess salt (Taplin 1988). Thus, although the American alligator may inhabit diverse habitats within a broad geographic range, the

species is limited by its osmoregulatory capabilities in coastal areas (Dunson & Mazzotti 1989). Indeed, studies of juvenile alligators suggest that they cannot survive for long periods in salinities over 10ppt (Lauren 1985). Alligators are opportunistic generalist predators (Wolfe, Bradshaw & Chabreck 1987) that are capable of long-range movements over short time periods (Joanen & McNease 1972), but are somewhat constrained in their habitat choices by their physiological limitations. Because of their large bodies, however, adult alligators could tolerate short-term exposure to salt-stress and, therefore, have the capacity to be a vector of nutrient flow within and among estuaries and adjacent habitats.

Alligator mediated nutrient flow may be particularly likely where marine waters are more productive than estuarine or freshwater habitats. Such ecosystems include the “upside-down” (Childers *et al.* 2006) coastal estuaries of southwest Florida, including the Shark River Estuary (SRE). Alligators are present throughout the SRE from upstream marshes to its mouth. Alligators in this area are almost always detected alone and appear to primarily be engaged in foraging, traveling, and resting behaviours (personal observation). Previous work in the SRE suggests that sex ratios are highly male-biased (Rice, Hart & Mazzotti 2009), which probably is the consequence of a preference for deep open water habitats in adult males that typify the SRE whereas females generally prefer shallower ponds in marsh landscapes (Joanen & McNease 1970, 1972; Goodwin & Marion 1979) that occur upstream of the estuary. Alligator mating occurs during April-June in south Florida (Mazzotti & Brandt 1994), but only a third of females tend to breed in any year (Thorbjarnarson & Wang 2010). Therefore, the low number of females captured historically in the SRE likely is not a result of seasonal breeding movements.

I used American alligators moving throughout the SRE as a model system for investigating whether top predators might link spatially disparate food webs and if individual specialization in movements might be an important feature of estuarine top predator behaviour. Specifically, I used a combination of acoustic tracking and stable isotope analysis to quantify movement tactics of individual alligators and to determine whether variation in movement tactics was related to differences in trophic interactions (e.g., foraging locations) and their possible role in nutrient transport.

Materials and Methods

Study system

The study was conducted from Nov 2007 – Dec 2009 in the Shark River Estuary (SRE) of Everglades National Park (ENP), Florida, USA (approximately 25°25' N, 81°00' W, Fig. 1). The waters that flow through the SRE originate in the Shark River Slough, the main source of freshwater flow through ENP (Dalrymple 1996). The SRE is a mangrove dominated tidal river with tidal mean amplitude of 0.5-1.0m (Romigh *et al.* 2006) and depths that range from 0.5-4.0m. In downstream areas the mangrove forests are well-developed with a dense canopy, while mid-estuary areas support smaller mangrove trees that form a thin buffer between the marsh and open waters (Simard *et al.* 2006). Upstream marshes are dominated by sawgrass (*Cladium jamaicense*). Salinity varies spatially and temporally throughout the estuary as the system alternates between high precipitation “wet” seasons and low precipitation “dry” seasons (Romigh *et al.*

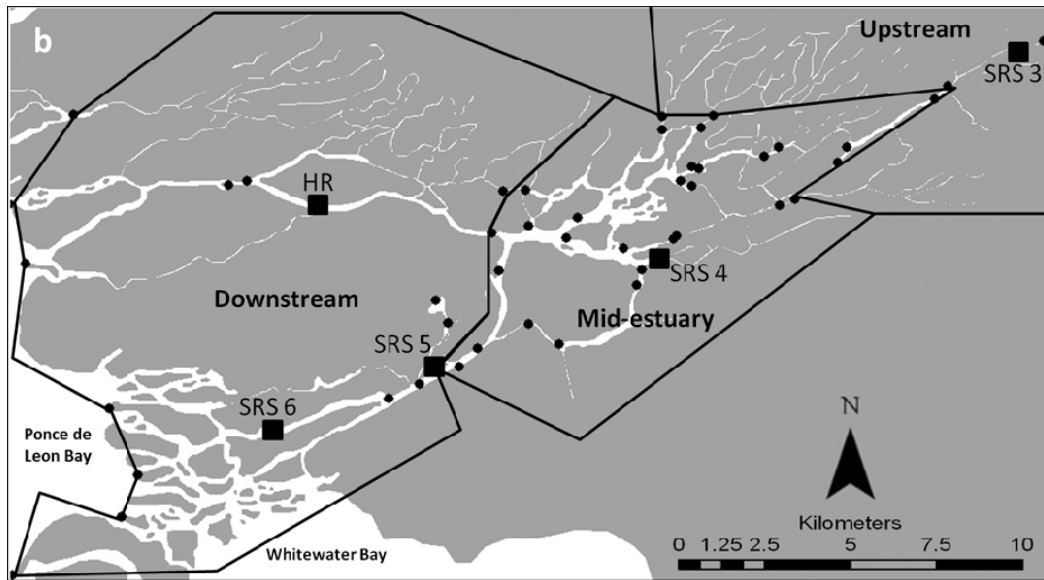
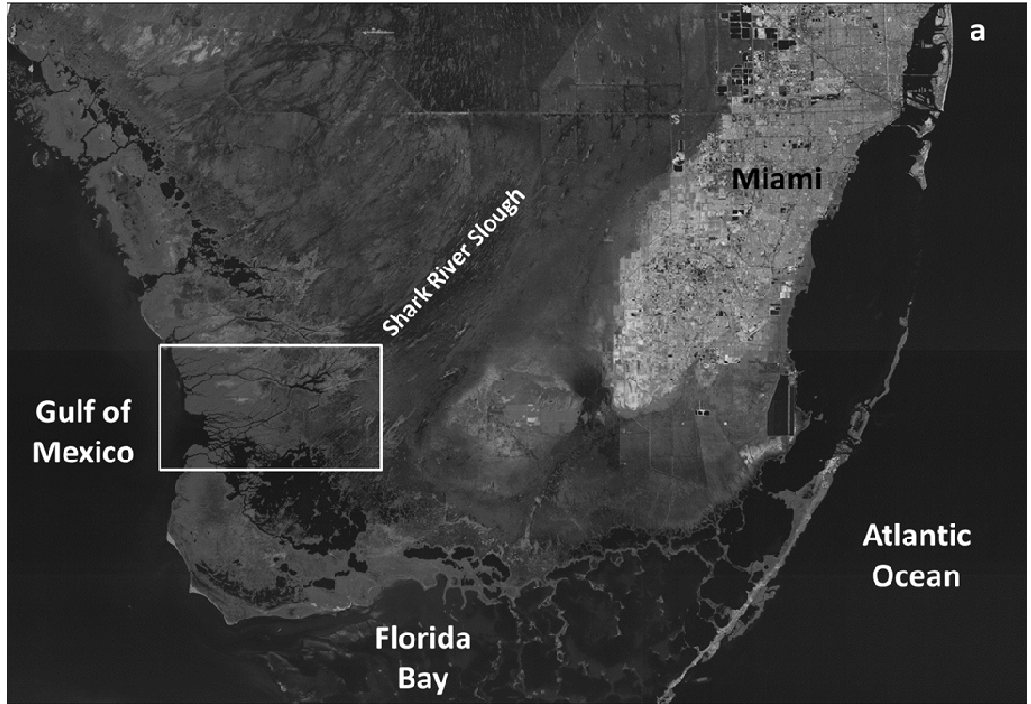


Figure 1: a) The study site (white box) is located in the Shark River Estuary of southwestern Florida. b) Acoustic monitoring stations (circles) and salinity monitoring stations (squares) were located throughout the study site and were used to delineate sampling zones (delineated by black lines). Salinity monitors in the Shark River Slough (“SRS”) are operated by FCE LTER, and “the monitor in the Harney River (“HR”) is operated by Everglades National Park ENP.

2006). During the dry season (Jan.-Jun.) salinities measuring >20ppt may occur up to 17km from the mouth of the estuary (AE Rosenblatt, unpublished data), while salinities at the mouth, where oceanic waters dominate, can fall in the wet season (Jul.-Dec.) to <15ppt (Childers *et al.* 2006).

I divided the SRE into three broad habitats for the purposes of understanding how alligator use of the estuary might vary in response to shifts in physical conditions and whether individuals might show consistent differences in their movement patterns: 1) the “downstream” marine influenced zone, 2) the “mid-estuary” mixing zone, and 3) the “upstream” freshwater zone. The boundary lines for each zone were delineated by the placement of four permanent salinity monitoring stations operated by the Florida Coastal Everglades Long Term Ecological Research (FCE LTER) program (SRS 3, 4, 5, and 6; data available at <http://fcelter.fiu.edu/>) and one by Everglades National Park (HR), and the movement monitoring stations nearest to each of them (Fig. 1). While these zones do not represent distinct habitats, this division of the estuary is appropriate for investigating broad-scale changes in space use of alligators, spatiotemporal variation in the environmental conditions that they may encounter, and their potential access to marine-derived food webs.

Field Methods

Alligators were captured in the downstream and mid-estuary zones of the SRE during both seasons using standard techniques (Chabreck 1963). Briefly, I searched for alligators at night from a 6m boat using high-powered spotlights. Searches were made from near the mouth of the river into the upper reaches of the mid-estuary zone. Narrow

channels and/or shallow water depths made it impossible to capture alligators in the upstream zone. Search effort was not equal across the two zones (~75% mid-estuary, ~25% downstream) because of higher encounter rates with alligators mid-estuary, but the spatial distribution of effort was similar across seasons. Potential biases introduced by capture distributions were further minimized by deploying relatively few transmitters on a particular night and searching widely every night. When an individual was located, I approached and slipped a metal snare around the neck using a long pole and tightened the snare. Before bringing an alligator onboard, I secured the mouth with a second snare and then with electrical tape. I measured total length, snout-vent length, head length, and tail girth to the nearest 0.2cm. Sex was determined by cloacal examination (Chabreck 1963). All captured individuals were over 1.8m total length and, therefore, adults (size at maturity in south Florida is 1.5-1.8m for both sexes; Abercrombie 1989; Dalrymple 1996). For stable isotope analysis, I collected small skin samples (~1cm²) from the terminal tail scutes of each captured alligator using sterile surgical scissors. The samples were placed on ice and transported to the lab where they were stored at -20°C.

Alligator movement patterns were quantified with passive acoustic telemetry. Passive acoustic telemetry provides a relatively low-cost means to determine movements of aquatic organisms within restricted areas or across broad spatial scales and has been used previously for crocodylians (e.g., Franklin *et al.* 2009, Campbell *et al.* 2010). Individually-coded V16-4H (Vemco, Halifax, NS) acoustic transmitters (6.8cm long x 1.6cm diameter, 24g in air, random transmission interval every 60-120 sec, lifespan *ca.* 1250 days) were attached using stainless steel wire (encased in nylon tubing to prevent abrasion) threaded through holes made in four tail scutes. The transmitter and wire were

then encased in a cool-setting marine-grade epoxy (West Marine, Watsonville, CA) to streamline the attachment and eliminate tangling.

In order to determine the position of tagged alligators I deployed an array of 46 Vemco VR2W monitors, each recording the time and identity of tags detected, from downstream exits of the SRE to upstream meshes (Fig. 1). On the basis of range testing in the array, transmitters were detectable at up to 1149m (Table S1). To determine the general location of alligators when they were not within detection range of a monitor and to assess the direction of travel, most monitors were set in pairs – on opposite sides of the bank and displaced ~400 m along the channel – to form “gates.” Because of the large detection ranges of the monitors relative to channel width (Table S1) and the density of mangroves along the shore making over-land movement difficult, alligators rarely escaped detection. During this study there were no cases in which an alligator was detected by one set of monitors and then was detected on a second set without being detected on monitors between them (i.e., a gate was never “missed” as a result of an animal moving around it overland or missed detections during transit). Monitors were partially housed in PVC pipes embedded in 15kg concrete blocks attached by chain to a Danforth anchor on one end and a subsurface float on the other. Data were downloaded from the monitors every 2-3 months during the course of the study.

Permanent monitoring sites collected composite water samples consisting of four 250ml subsamples drawn every 18 hours over three days using ISCO autosamplers (Teledyne ISCO Inc., Lincoln, NE), thereby averaging daily salinities across dawn, noon, dusk, and midnight. Water temperature was measured at the five monitors closest to each of the five salinity sampling stations using HOBO Pro v2 data loggers (Onset, Cape Cod,

MA). Water temperature (accuracy $\pm 0.2^{\circ}\text{C}$) was automatically recorded every 10 minutes throughout the study and daily means were used for all analyses.

I used salinity variation among sites as an indicator of the physiological stress that would be experienced by alligators residing in each zone. Experimental studies show that salinities above 10 ppt have negative effects on juvenile alligators (e.g., starvation, death; Lauren 1985). Although the animals tracked in this study were all adults and may have higher salinity tolerances than juveniles, there are no data on salinity tolerances for adults. I therefore used the proportion of days that salinity at the most seaward salinity monitoring station in each zone (SRS 6 for downstream, SRS 5 for mid-estuary, and SRS 3 for upstream) exceeded 10ppt as an estimate of the relative physiological stress alligators would experience there. I also used the 10ppt threshold for my definitions of the wet and dry seasons: the wet season started when salinity at SRS 5 (the boundary between the downstream and mid-estuary zones) first dropped below 10ppt (July) and the dry season began when salinity first went above 10ppt at this site (January).

Laboratory methods

Stable isotopes provide a time-integrated view of the diet of an individual and can be used to track the ultimate source(s) of the consumer's assimilated nutrients, relative trophic position in food webs (Fry 2006), and patterns of individual specialization (e.g. Hatase et al. 2002, Vander Zanden *et al.* 2010). Nutrient sources are tracked using the $^{13}\text{C}:^{12}\text{C}$ ratio ($\delta^{13}\text{C}$) and relative trophic position is tracked using the ratio of $^{15}\text{N}:^{14}\text{N}$ ($\delta^{15}\text{N}$). I used $\delta^{13}\text{C}$ to differentiate the relative importance of marine-based and freshwater/estuary-based food webs. Within the Shark River estuary, primary producers

and low mobility consumers resident in the freshwater/estuarine food web exhibit $\delta^{13}\text{C}$ values always less than -25‰ and usually less than -28‰ while residents in the marine food web exhibit $\delta^{13}\text{C}$ values between -11‰ and -19‰ (Chasar *et al.* 2005; Williams & Trexler 2006; Matich *et al.* 2011). I used the combination of stable carbon isotope values of individuals and their patterns of movements to estimate the relative degree of habitat coupling.

Tissue samples from the field were washed with deionized water and then dried at 60°C for at least 72 hours before being powdered using a mortar and pestle. Between 0.4-0.7mg of sample was placed in a 5 x 3mm tin cup for analysis. I did not extract lipids or make mathematical lipid corrections because C:N ratios (max. = 3.2) were all below the recommended threshold for extraction or correction (3.5; Post *et al.* 2007). Isotopic analyses were performed at Florida International University's Stable Isotope Laboratory using standard elemental analyzer isotope ratio mass spectrometer (EA-IRMS) procedures. One fifth of the samples were analysed in duplicate, and the mean error attributable to the equipment was 0.25‰ (\pm 0.11‰ SE) for $\delta^{15}\text{N}$ and 0.15‰ (\pm 0.06‰ SE) for $\delta^{13}\text{C}$. The standard deviations of an internal standard (glycine) used by the isotope lab were 0.18‰ for $\delta^{15}\text{N}$ and 0.17‰ for $\delta^{13}\text{C}$.

Data analysis

Because of the large number of individual detections (up to 180,000 for one individual), I used a custom computer program (Gated Acoustic Telemetry Optimization Routine, "GATOR"; Andrew Fritz, FritzTech, Houston, TX) that used the last known location and direction of travel for each alligator (determined from the order of detection

and disappearance from monitors) to collapse raw data into dates and times of entry into and exit out of specific “zones” of the study area. I considered any individual alligator that was detected by the same monitor at least twice in one hour as being in the vicinity for the entire hour. When an alligator traveled from one zone (zone A) to another (zone B) I calculated the maximum displacement as the Euclidean distance between the monitor marking the boundary between the two zones and the furthest monitor in zone B that detected the alligator on that trip. My estimates of distance traveled per trip are conservative since the density of monitoring stations was relatively low and distances between gates were long, especially in the downstream zone (Fig. 1).

To determine the factors that influenced the probability of alligator movement between zones I used multiple logistic regressions (MLR). Multiple logistic regressions can be used to identify the factors which contribute to the probability of occurrence of a binary response variable (Hosmer & Lemeshow 1989), in this case whether an alligator occupies a certain zone or not. I used MLR to determine the effects of body length, salinity, temperature (daily mean), and length*salinity on alligator use of zones. Independent MLRs were used for different groups of alligators depending on their zone-use characteristics and were run in the program R 2.1 (R Development Core Team 2009) as generalized linear models with binomial distributions and logit link functions. The model’s goodness-of-fit was determined using the Pearson chi-square test.

I calculated Layman *et al.*’s (2007) total area (TA) metric in isotope bi-plot ($\delta^{13}\text{C}$ - $\delta^{15}\text{N}$) space for groups of alligators with similar movement tactics. The TA metric is a quantitative measure of the isotopic niche space occupied by each group, and by measuring the amount of overlap between the different polygons I could elucidate

possible differences in trophic interactions of the groups. Because isotopic signatures of alligator skin turns over relatively slowly (Chapter II), differentiation of isotopic niche spaces reflect long-term differences in average trophic interactions of individuals. I used a jackknife randomization protocol to test whether observed overlaps of TAs of groups of alligators that varied in movement patterns were less than expected by chance. For each iteration, I randomly reassigned observed isotopic values to individuals with known movement tactics and calculated the resulting overlap in convex hulls of the isotope space occupied by each group of alligators. I completed 1000 iterations of the protocol and considered groups to show significant differentiation if more than 95% of iterations produced greater overlap of convex hulls than were observed (i.e. $p < 0.05$ for a one-tailed test). I used a one-tailed test because my *a priori* expectation was for there to be differentiation (rather than significant overlap) on the basis of movement tactics. I further explored the relationships between stable isotopes and body length, capture season, capture location, distance traveled, average trip duration, and “pause time” using multiple linear regression. I was unable to assess the influence of alligator body condition on stable isotope values because mass measurements were not collected for all individuals.

Results

Interzone variation in abiotic conditions

There was significant variation in daily average salinities among sites (Kruskal-Wallis test, $H_4 = 780.9$, $p < 0.001$) and between seasons (Mann-Whitney rank sum test, $T = 885475.5$, $p = < 0.001$) with salinity decreasing as distance from the Gulf of Mexico increased and remaining higher in the dry season than in the wet (Fig. 2). Post hoc

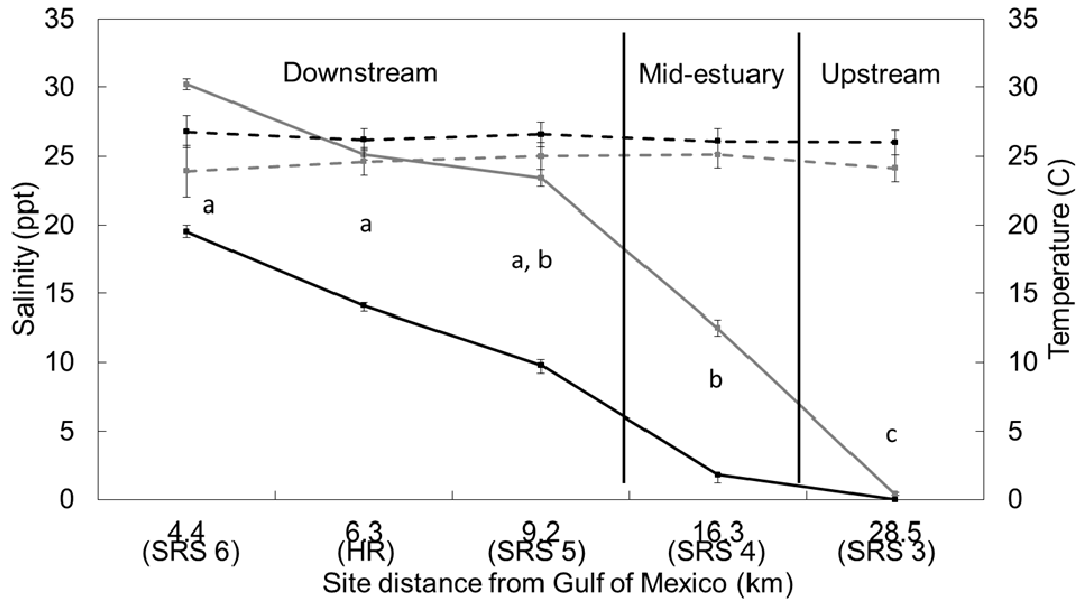


Figure 2: Spatial variation in temperature (dashed lines) and salinity (solid lines) during the wet (black lines) and dry (gray lines) seasons. Vertical black lines indicate boundaries between zones. Sites with different letters exhibited significant differences in average monthly salinity within a season. Error bars are \pm SE.

pairwise Dunn's tests revealed significant variation (all $p = < 0.01$) in salinities among all the sites. During the wet season, salinities were never above 10ppt in the upstream zone, above 10ppt 40% of the time in the mid-estuary zone and 94% of the time in the downstream zone. During the dry season, salinities were >10 ppt 0% of the time in the upstream zone, 92% of the time in the mid-estuary zone, and 100% of the time in the downstream zone. Daily mean water temperature was significantly higher in the wet season ($26.2^{\circ}\text{C} \pm 0.08$ SE) than the dry season ($24.6^{\circ}\text{C} \pm 0.09$ SE; $T = 2579521.0$, $p = < 0.001$) across all sites, and water temperature varied across sites ($H_4 = 22.2$, $p = < 0.001$; Fig. 2) with water temperature increasing slightly (*ca.* 0.7° between upstream monitors and the mouth of the Shark River) as distance from the Gulf of Mexico decreased. Post hoc pairwise Dunn's tests showed that water temperatures varied significantly only between SRS 6 and SRS 3 and between SRS 5 and SRS 3. Therefore, spatial variation in water temperatures existed within the tracking array and alligators could access slightly higher water temperatures in the downstream zone. Daily average salinity and temperature were not temporally correlated at any site (linear regression, all $R^2 = < 0.01$, $p = > 0.6$ for all sites).

Movement tactics

From Nov 2007 – Dec 2009 I captured and tracked 35 alligators ranging from 184.0-280.6cm total length (mean = $229.3\text{cm} \pm 3.2$ SE). The sex ratio was heavily skewed towards males (32:3). Interestingly, the three females were captured at different times of the year (January and July). Seven individuals were captured downstream and 28 mid-estuary. Twenty were captured during the dry season and 15 during the wet

season. Four of the alligators were never detected within my monitoring array, suggesting their transmitters malfunctioned or they left the array immediately after release.

Sixteen alligators (all males) were detected within the tracking array for at least six continuous months that included part of one wet and one dry season (Table 1). These 16 individuals had average times between first and last detection on my array of 418.6 days (± 56.6 SE). Because the other 19 individuals spent much shorter amounts of time on my array (mean = 41.7 days ± 8.8 SE) and were only present during a single season, they were not included in further analyses. During the wet season the 16 alligators collectively spent 48% of their time in the downstream zone, 44% in the mid-estuarine zone, and 8% in the upstream zone. During the dry season they spent 16% of their time in the downstream zone, 73% in the mid-estuary zone, and 11% in the upstream zone. These trends in zone use were generally consistent throughout the study except for the 2009 wet season when downstream zone use was almost triple that of mid-estuary zone use (Fig. 3), though this result was most likely caused by small sample size near the end of the study.

Despite the appearance of general population habitat use patterns, three different broad classes of alligator movements were identified amongst these 16 individuals (Table 1). The first group (“residents,” $n = 2$) remained within the mid-estuary zone for the entire detection period. The second group (“downstream commuters,” $n = 9$) regularly moved between the mid-estuary and downstream zones and occasionally entered the upstream zone. The third group (“upstream commuters,” $n = 5$) regularly moved between the mid-estuary and upstream zones and never used the downstream zone. No alligators remained resident in the downstream zone and the spatial pattern of my captures and

Table 1: Summary of acoustic monitoring data for the 16 American alligators (all male) tracked in the Shark River Estuary that yielded sufficient data for comparisons of movements among seasons. “UC” = upstream commuter, “DC” = downstream commuter. A “trip” is defined as the period of time after an alligator moves from the mid-estuary zone into the downstream zone or from the mid-estuary zone into the upstream zone.

Date deployed	Xmitter code	Movement tactic	Capture zone	Total length (cm)	Total detection period (days)	Total number of trips	Mean trip duration (days (\pm SE))	Min./max. trip duration (days)	Min./max. displacement downstream (km)
4-Oct-2007	6825	UC	Mid-estuary	221.8	193	4	13.2 (\pm 9.8)	0.1/42.3	NA
4-Oct-2007	6827	DC	Downstream	254.6	483	43	5.5 (\pm 1.5)	0.1/64.3	1.0/13.4
19-Oct-2007	6822	DC	Mid-estuary	255.4	796	28	6.0 (\pm 3.1)	0.02/81.5	1.0/1.0
19-Oct-2007	6824	DC	Mid-estuary	218.6	750	52	2.9 (\pm 0.4)	0.1/11.2	1.0/2.4
19-Oct-2007	6826	DC	Mid-estuary	243.6	598	24	6.2 (\pm 1.8)	0.5/39.2	1.0/11.6
19-Oct-2007	6828	DC	Mid-estuary	249.0	288	17	0.7 (\pm 0.3)	0.1/4.2	1.0/2.2
20-Nov-2007	6821	DC	Mid-estuary	234.0	771	20	15.6 (\pm 3.6)	0.6/60.8	2.4/2.4
20-Nov-2007	6823	DC	Downstream	213.8	261	25	5.1 (\pm 3.0)	0.3/74.1	1.0/2.4
20-Nov-2007	6829	Resident	Mid-estuary	234.0	268	0	NA	NA	NA
31-Jan-2008	9636	DC	Mid-estuary	230.2	697	13	22.2 (\pm 20.1)	0.5/263.6	1.0/11.6
20-Feb-2008	9635	Resident	Mid-estuary	244.2	169	0	NA	NA	NA
9-Apr-2008	2162	UC	Mid-estuary	280.6	314	526	0.4 (\pm 0.02)	0.04/3.0	NA
9-Apr-2008	2169	UC	Mid-estuary	239.2	298	12	8.4 (\pm 1.7)	0.05/21.6	NA
28-Apr-2008	2165	UC	Mid-estuary	252.4	346	247	0.3 (\pm 0.02)	0.01/2.0	NA
18-Jul-2008	2167	UC	Mid-estuary	226.4	241	6	15.8 (\pm 6.2)	0.2/36.4	NA
25-Jul-2008	2163	DC	Downstream	261.2	224	22	7.2 (\pm 2.0)	0.1/31.2	1.0/11.6

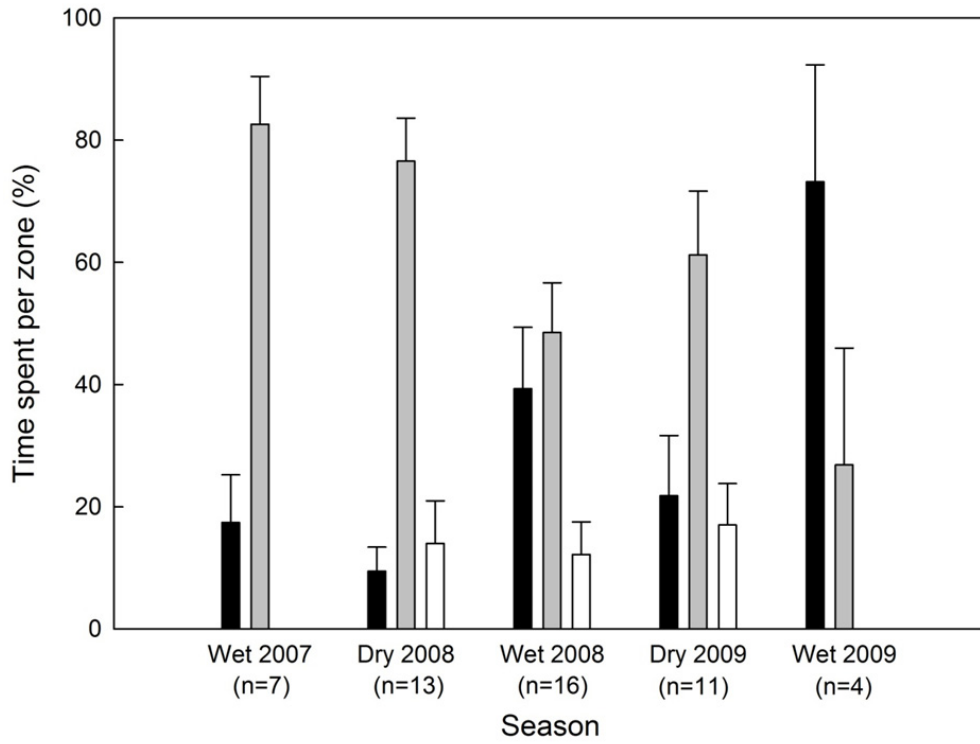


Figure 3: Mean variation in the use of the downstream (black bars), mid-estuary (grey bars), and upstream (white bars) zones during wet and dry seasons by 16 American alligators. Not all 16 alligators produced data during every season. Error bars are \pm SE.

array layout made it impossible to document upstream residents. I did not detect any difference in body length between alligators that used downstream zones and those that did not (t-test, $t_{14} = -0.3$, $p = 0.8$)

Commuting alligators made frequent trips between multiple zones and varied widely in the amount of time spent in the downstream or upstream zones (Table 1). Downstream commuters (DCs) traveled between the mid-estuary and downstream zones between 13 and 52 times each during the course of the study (mean = 27.1 ± 4.2 SE) and spent significantly more time downstream during the wet season than during the dry (paired t-test, $t_8 = 4.4$, $p = 0.002$; Fig. 4), though one individual displayed the opposite trend. Downstream commuters generally did not spend much time downstream per trip, averaging 6.6 days (± 1.3 SE). However, four of the DCs remained within the downstream zone for more than 60 consecutive days, indicating a high degree of variation in trip duration. “Pause” times between downstream trips were consistent, averaging 3.0 days (± 0.4 SE) in the mid-estuary zone. Only two individuals paused for more than 40 days at a time. Interestingly, trip duration and pause time were not correlated ($R^2 = 0.002$, $p = 0.5$). Distance traveled per trip was relatively short for the DCs, averaging 2.6km (± 0.2 SE), but because of the spacing of monitors in this zone DCs may have actually moved considerably further. Indeed, four alligators traveled to the coastal waters of the Gulf of Mexico (22-26km roundtrip) during some trips (Table 1). Movements into the downstream zone occurred mostly during the wet season ($74\% \pm 10$ SE). Eight of the nine DCs were tracked during portions of two wet seasons, and all of these individuals displayed downstream commuting behavior in both seasons. Therefore, movement tactics appear to be stable across years. Indeed, for the six individuals that

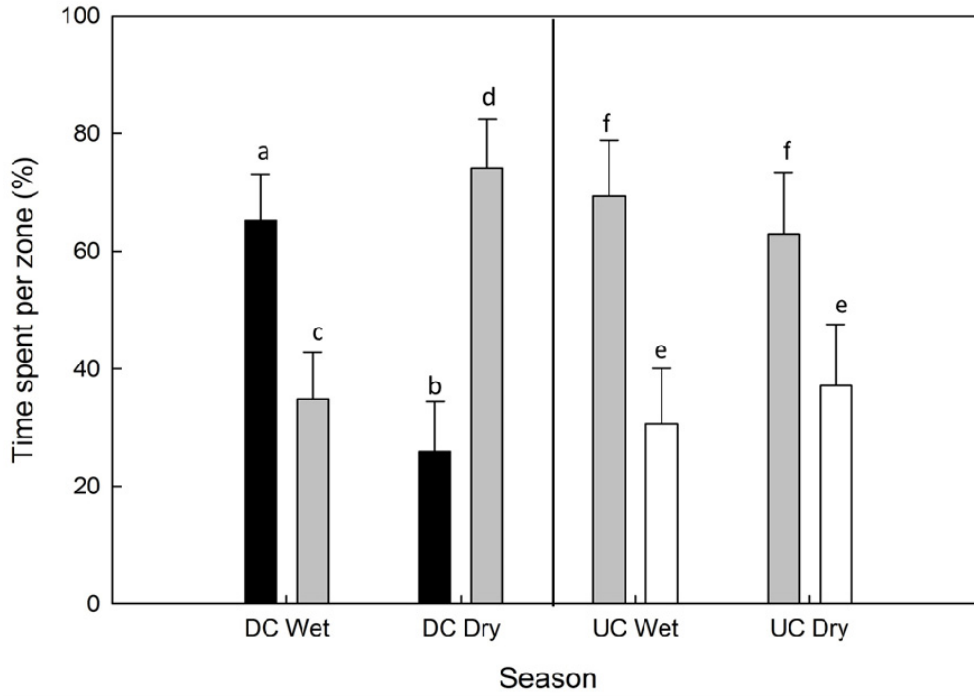


Figure 4: Seasonal variation in mean zone use among downstream commuters (DC, n = 9) and upstream commuters (UC, n = 5). Downstream = black bars, mid-estuary = grey bars, and upstream = white bars. Bars of the same color with different letters above them are significantly different. Error bars are \pm SE.

were tracked for two consecutive full length wet seasons (none were detected in the array for more than two) there was no evidence of interannual variation in the number of trips made per wet season ($t_5 = -0.1, p = 0.9$). Three DCs made trips into the upstream zone; all of these trips ($n = 5$) occurred during the dry season.

Upstream commuters (UCs) did not differ significantly in the amount of time spent upstream or in the mid-estuarine zone across seasons ($t_4 = -0.9, p = 0.4$; Fig. 4). Also, UCs did not vary seasonally in the number of trips made per individual (Wilcoxon signed rank test, $z = -0.7, p = 0.6$) or average trip duration ($t_4 = -0.2, p = 0.9$). There were two distinct patterns of alligator movements into upstream habitats. Two individuals (2162 and 2165) made hundreds of short trips, with each trip averaging only 8.5 hours (± 0.3 SE) spent upstream. In contrast, the other three UCs (2167, 2169, and 6825) made infrequent, but longer, trips that averaged 10.2 days (± 2.8 SE) per trip. The distribution of trips between wet and dry seasons followed the opposite pattern as that for DCs, with 44% (± 13 SE) of trips occurring during the wet season and 56% (± 13 SE) during the dry. I was unable to gather data on distance traveled per trip into the upstream zone because it lacked distinct channels and, therefore, I only placed one monitoring station 2.6 km upstream from my furthest upstream “gate.” The upstream monitor detected two alligators (one UC (2165) and one DC (6822)) over four days and one day, respectively, during the 2009 dry season.

Salinity, temperature, body length, and length*salinity were significant predictors of downstream habitat use for DCs (Table 2). The DCs were more likely to be present in the downstream zone when salinity was low and water temperature was high, and smaller DCs were more likely to be found downstream than larger DCs, with the smallest DCs

Table 2: Multiple logistic regression analysis of the effects of salinity, temperature, and body length on presence/absence of downstream commuter alligators in downstream zone and upstream commuter alligators in upstream zone.

Movement type	Ind. Variable	Estimate	Standard error	z value	p value
Downstream commuter use of downstream zone	Intercept	-3.97	1.41	-2.81	0.005
	Length	0.01	0.006	2.24	0.025
	Salinity	0.24	0.07	3.21	0.001
	Temperature	0.12	0.01	12.15	<0.001
	Length*salinity	-0.002	0.0003	-5.04	<0.001
Residual deviance = 4004.3 on 3956 degrees of freedom Pearson chi-square <i>p</i> value = 0.71					
Upstream commuter use of upstream zone	Intercept	-15.19	0.95	-15.99	<0.001
	Length	0.06	0.004	15.83	<0.001
	Salinity	14.70	8.81	1.67	0.10
	Temperature	0.05	0.01	3.05	0.002
	Length*salinity	-0.06	0.04	-1.60	0.11
Residual deviance = 1497.0 on 1340 degrees of freedom Pearson chi-square <i>p</i> value = 0.99					

reducing their use of the downstream zone during higher salinities less than larger DCs (Fig. 5). Body length and temperature were significant predictors of upstream habitat use by UCs but salinity was not (Table 2). The UCs were more likely to be found upstream when temperatures were higher and larger UCs were more likely to be found upstream than smaller UCs.

Trophic interactions

The mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for all 35 alligators were -24.8‰ (± 0.3 SE) and 8.1‰ (± 0.2 SE), respectively. Values of $\delta^{13}\text{C}$ ranged from -27.61‰ to -21.41‰ and $\delta^{15}\text{N}$ ranged from 6.3‰ to 10.3‰ . Although there was no significant difference in $\delta^{15}\text{N}$ values between DC alligators and individuals that did not use downstream areas ($t_{14} = -1.7$, $p = 0.1$), the average $\delta^{13}\text{C}$ of DC alligators ($-24.1\text{‰} \pm 0.5$ SE) was significantly greater than that of mid-estuary residents and UC alligators combined ($-26.7\text{‰} \pm 0.3$ SE, $t_{14} = 3.9$, $p = 0.002$). Furthermore, only 1.9% of the TA of alligators that used downstream areas overlapped with that of individuals that never used downstream areas, and this overlap was driven by a single alligator (Fig. 6). The amount of overlap was significantly less than expected by chance. Only three of the 1000 jackknife randomizations of isotopic values of alligators resulted in equal or less overlap than was observed ($p = 0.003$). The isotopic values of the 19 alligators for which movement tactic was unknown fell largely within the TAs of those with known movement tactics (Fig. 6).

I used multiple linear regression to test for effects of body length, maximum distance traveled downstream, total time in the downstream zone, total pause time between trips downstream, average trip duration, and average pause duration on $\delta^{13}\text{C}$ and

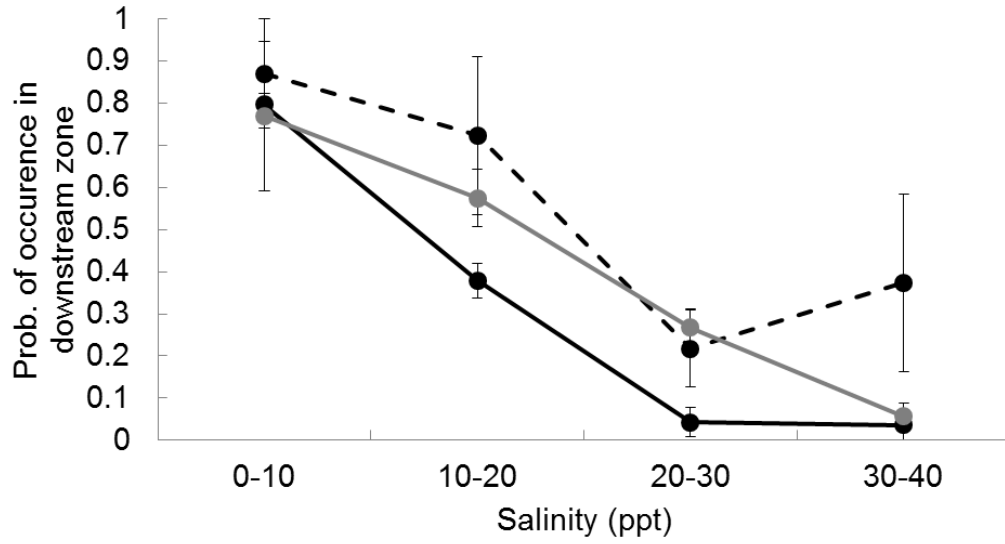


Figure 5: Probability of occurrence in the downstream zone for the largest third of the DC alligators (grey line), medium third (black line), and smallest third (dashed black line) at varying levels of salinity. Error bars are \pm SE.

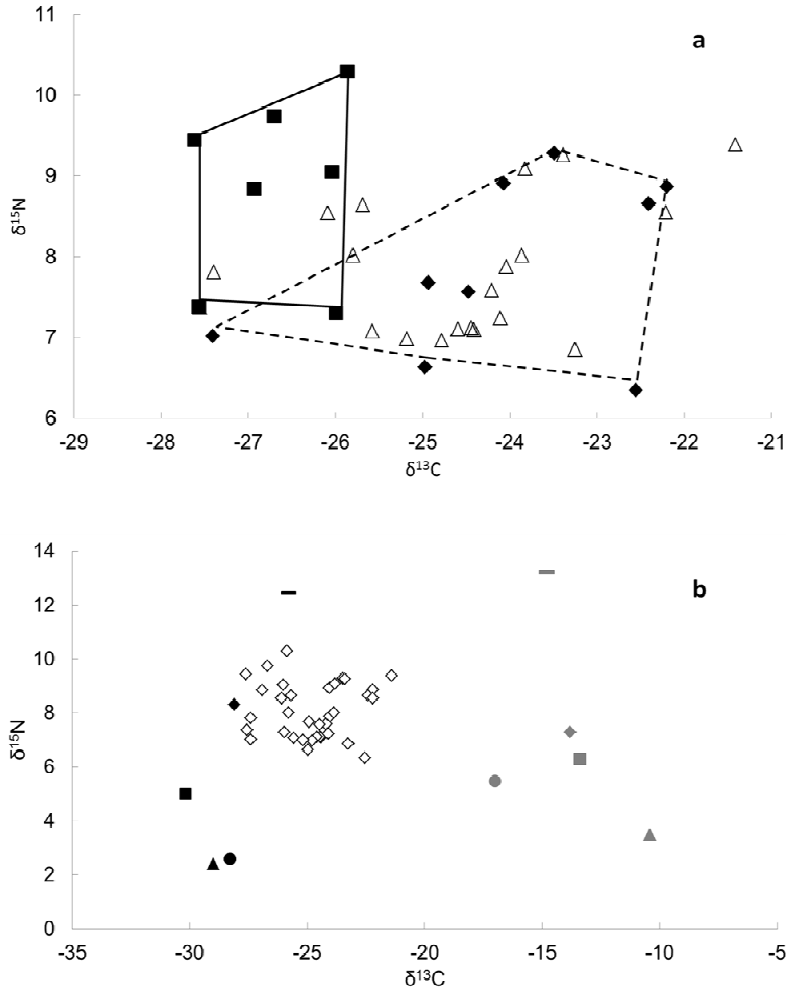


Figure 6: a) Stable isotopic values of skin from residents/upstream commuters (black squares) and downstream commuters (black diamonds). White triangles represent alligators for which movement tactic is unknown. Boundaries representing convex hull polygons are shown for residents/upstream commuters (solid line) and downstream commuters (dashed line). b) Mean isotope values of representative primary producers and consumers in the Shark River Estuary relative to the signatures of all alligators captured during this study (white diamonds). Black shapes represent species that reside in the freshwater/estuarine food web and gray shapes represent species that reside in the marine food web. The freshwater/estuarine food web consists of floc (\blacktriangle), periphyton (\bullet), ramshorn snail (\blacksquare , Planorbidae), blue crab (\blacklozenge , *Callinectes sapidus*), and Florida gar ($-$, *Lepisosteus platyrhincus*). The marine food web consists of turtle grass (\blacktriangle , *Thalassia testudinum*), seston (\bullet), bay scallop (\blacksquare , *Argopecten irradians*), shrimp (\blacklozenge , Penaeidae), and tarpon ($-$, *Megalops atlanticus*). Error bars are omitted for simplicity. Data from species other than alligators are from Chasar et al. (2005), Williams and Trexler (2006), and MR Heithaus (unpublished data).

$\delta^{15}\text{N}$ values for DCs, and body length, total time upstream, and average trip duration on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for UCs (Table 3). The only significant relationship was between $\delta^{15}\text{N}$ and maximum distance traveled downstream for DCs, with $\delta^{15}\text{N}$ increasing as distance traveled increased. When all of the alligators were grouped together there was a significant increase in $\delta^{15}\text{N}$ ($R^2 = 0.4, p = 0.03$) with body size, but there was no relationship with $\delta^{13}\text{C}$ ($R^2 = 0.001, p = 0.9$). Lastly, there was no significant difference in $\delta^{13}\text{C}$ between individuals with known movement tactics captured in the dry (mean = -26.1‰, ± 0.6 SE) or wet (mean = -24.8‰, ± 0.6 SE) seasons ($t_{14} = -1.7, p = 0.1$) or between individuals captured in the downstream (mean = -23.6‰, ± 0.7 SE) or mid-estuary (-25.6‰, ± 0.5 SE) zones ($t_{14} = 1.3, p = 0.2$).

Table 3: Results of multiple linear regression analysis of the effects of multiple variables on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of downstream commuter alligators (top) and upstream commuter alligators (bottom). For the definition of “trip” see Table 3. “Pause time” is the amount of time spent in the mid-estuary zone between trips into the downstream zone.

Ind. Variable	$\delta^{13}\text{C}$				$\delta^{15}\text{N}$			
	Estimate	Standard Error	t value	p value	Estimate	Standard Error	t value	p value
Intercept	-12.8	10.2	-1.3	0.3	2.4	1.8	1.4	0.3
Avg. pause time	-0.01	0.3	-0.05	0.9	0.09	0.05	1.7	0.2
Avg. trip duration	-0.2	0.3	-0.6	0.6	0.03	0.05	0.7	0.6
Body length	-0.5	0.04	-1.2	0.3	0.02	0.007	2.6	0.1
Max. distance traveled downstream	0.3	0.2	2.0	0.2	0.2	0.03	5.6	0.03
Total pause time	0.0005	0.01	0.04	0.9	-0.004	0.002	-1.6	0.2
Total time downstream	0.003	0.02	0.2	0.9	-0.001	0.003	-0.4	0.7
Residual SE = 1.64 on 2 degrees of freedom F-statistic = 1.02 on 6 and 2 DF, $p = 0.6$					Residual SE = 0.28 on 2 degrees of freedom F-statistic = 19.38 on 6 and 2 DF, $p = 0.05$			
Intercept	-18.6	28.9	-0.6	0.6	-19.2	23.7	-0.8	0.6
Total time upstream	0.005	0.02	0.2	0.9	-0.02	0.02	-1.3	0.4
Avg. trip duration	-0.1	0.3	-0.5	0.7	0.1	0.2	0.6	0.6
Body length	-0.03	0.1	-0.3	0.8	0.1	0.1	1.2	0.4
Residual SE = 1.03 on 1 degree of freedom F-statistic = 0.31 on 3 and 1 DF, $p = 0.8$					Residual SE = 0.85 on 1 degree of freedom F-statistic = 1.97 on 3 and 1 DF, $p = 0.5$			

Discussion

Highly mobile predators faced with spatial and temporal heterogeneity in resource availability or abiotic stresses often adopt flexible behaviours (e.g., Estes *et al.* 1998). In some cases, however, individuals specialize on consuming a particular suite of resources, foraging in particular habitats, or using different feeding tactics (e.g., Hatase *et al.* 2002; Urton & Hobson 2005; Caut *et al.* 2008; Woo *et al.* 2008; Darimont, Paquet & Reimchen 2009). Although the majority of food web studies tend to ignore consistent differences among individuals in their trophic interactions, a growing literature suggests that individual specialization is widespread (Bolnick *et al.* 2003) and can have important implications for evolutionary (Baird, Abrams & Dill 1992; Bolnick *et al.* 2003) and ecological (e.g. Quevedo *et al.* 2009) dynamics. I found that American alligators in the Shark River Estuary exhibit individual specialization in movement tactics that is linked to long-term variation in trophic interactions and the coupling of habitats in the coastal Everglades. I identified three broad classes of alligator movements that were linked to differences in trophic interactions. The first two movement tactics – individuals that remained in the mid-estuarine brackish zone year-round (residents) and individuals that made periodic trips from the brackish zone into the upstream freshwater zone (UCs) – were associated with feeding primarily in estuarine and freshwater food webs, while individuals using the third tactic – making frequent trips into the downstream zone of the estuary (DCs), including coastal waters – exhibited increased foraging in marine food webs despite spending a large proportion of time in mid-estuary habitats.

For the present study, I used passive acoustic telemetry to determine broad-scale movements by alligators. One obvious limitation of this approach in a system as large

and complex as the Shark River Estuary is the relatively low spatial resolution of movements. The low resolution is especially evident for alligators moving into the upstream or marsh habitats, which cannot be tracked within this zone using my methods, and those moving downstream where the nature of the habitat makes it impossible to accurately determine how far downstream alligators have moved in many cases. For the latter, isotopic data helped to resolve the movements. The greater contribution of marine-based food webs to the diets of downstream commuters (see below) suggests they move reasonable distances downstream where prey from marine-based food webs are available. The use of GPS-tracking, especially Fastloc technology, could provide much more accurate descriptions of movements than I obtained using passive acoustic tags (Rutz & Hays 2009). Indeed, an alligator equipped with a GPS tag moved into coastal waters and hauled out on islands at the mouth of the SRE (AE Rosenblatt, unpublished data). The drawback to GPS technology, however, is its high cost that can limit sample sizes. For example, in my system, where recapturing alligators to remove tags is likely to be unsuccessful in many cases (personal observation), my sample sizes using GPS transmitters would have been limited to only a few individuals and, therefore, I would have been unable to answer questions about tactical variation in movements and its links to variation in alligator trophic interactions. Despite its high cost, GPS technology would be useful in gaining further insights into alligator movements both within my study area and across broader spatial scales.

Although I attached acoustic transmitters to 35 alligators, I only obtained sufficient data to elucidate movements of 16 across both wet and dry seasons. Some of the transmitters on the “lost” alligators may have failed (four tags released within the

array never produced data), which is a common aspect of tracking studies (Hays *et al.* 2007). Other individuals (n = 2) had transmitters attached relatively late in the study and had not been active in the system for a long enough time to be included in analyses. On the basis of their movement patterns before they disappeared I suspect that the majority of “lost” individuals (n = 13) left the study area by permanently relocating to marsh habitats or adjacent estuarine waters outside of my tracking array. Another possibility is that some of these individuals took up residence in areas between monitors that were not within detection range of any monitors. Although three transmitters were deployed on females, none of them produced enough data to be included in my analyses. One exited the system at the mouth of the estuary (Ponce de Leon Bay), one exited into the marsh, and one transmitter was never detected. Interestingly, even though a large number of alligators left the system, isotopic values of these alligators mostly fell within the isotopic niches of the well-defined movement tactics. In fact, 14 (74%) of the individuals with unresolved feeding tactics fell within the TA of downstream commuters and two (13%) within the TA of alligators remaining mid-estuary and upstream. Therefore, individuals for which I could not identify movement tactics likely do not represent a distinct group with different movement tactics and trophic interactions.

Alligators that used different movement tactics likely were exposed to different degrees of physiological stresses on a broad scale and likely also experienced different abundances of potential prey. Seasonal changes in movement patterns of alligators suggest that the relative costs and benefits of particular movement tactics vary seasonally. Indeed, DCs made the large majority of their trips into the downstream zone during the wet season when salinities were low (i.e. lower physiological costs) and spent almost

triple the amount of time in the downstream zone during the wet season versus the dry, indicating that this zone may be too stressful physiologically during the dry season for most alligators or potential foraging benefits do not outweigh physiological costs. Two individuals, however, used this zone during the dry season. Although changes in salinity likely are the primary physical driver of alligator use of the downstream zone, I also found that DCs were more likely to be found downstream when temperatures were higher (generally during the wet season). High temperatures in the Everglades have been hypothesized to negatively affect alligators through increased metabolic costs associated with thermoregulatory behaviours (Jacobsen & Kushlan 1989). Therefore, it is likely that the temperature effect is driven by alligators responding to the generally lower salinities in the downstream zone during the warmest times of the year rather than selecting warmer habitats.

Alligators likely use downstream areas in spite of salt-stress to access greater prey resources. The SRE is an “upside-down” phosphorus-limited estuary (Childers *et al.* 2006). It receives the majority of its phosphorous from the Gulf of Mexico and exhibits decreasing P and productivity as distance from the river mouth increases (Childers *et al.* 2006, Simard *et al.* 2006). Unlike most estuaries, there is no productivity peak where marine and freshwaters meet (Childers 2006). As a result of increased precipitation during the wet season, P inputs from the ocean are compressed towards the downstream portion of the estuary (Childers *et al.* 2006). These trends in P supply and productivity, combined with relatively lower prey availability in mangrove-lined channels of the mid-estuary and upstream zone (Rehage and Loftus 2007), suggest that downstream and coastal areas likely have higher prey availability for alligators during the wet season

when most downstream commuting is occurring. In the dry season, patterns of prey availability may be more complicated than during the wet season. Freshwater fishes move into mangrove channels of the upstream and mid-estuary zones in response to marsh dry-down (Rehage & Loftus 2007) and DC alligators may reduce movements downstream because of greater prey availability in mid-estuary areas as well as increased salt-stress downstream. Because most mating and nesting activities occur in freshwater marsh habitats (Mazzotti & Brandt 1994) and adult alligators are not subject to predation, reproductive and anti-predator explanations for movements downstream are unlikely. Furthermore, movements downstream would not be expected if similar or greater prey resources were available in the mid-estuary and upstream areas and carbon isotopic values of DC alligators suggest that they forage at least partially in downstream areas (see below). Finally, alligators using the DC tactic were not smaller than those in upstream and mid-estuary zones suggesting that dominance interactions are not likely forcing DCs to adopt a “best of a bad job” tactic whereby individuals must move into high-stress and low-prey habitats.

The UCs did not change their habitat-use patterns seasonally in the same ways as the DCs. Though the UCs made more trips into the upstream zone during the dry season than during the wet, the overall amount of time they spent upstream was consistent across seasons. Salinity in the upstream zone was at or near 0 ppt for the duration of the study, and use of the upstream zone was not affected by salinity. Larger individuals were more likely to be found upstream than smaller individuals, and individuals were more likely to move upstream when water temperatures were high. It is likely that these movement

patterns are associated with the onset of the mating season, which occurs in freshwater habitats of the Everglades in April-June (Mazzotti & Brandt 1994).

Stable isotope analyses revealed that alligators with different movement tactics were feeding partially in different food webs. The freshwater/estuarine areas that the residents and UCs occupied support consumers with relatively low $\delta^{13}\text{C}$ values ($<-25\text{‰}$) while the coastal waters of the downstream zone support a food web characterized by higher $\delta^{13}\text{C}$ values ($>-19\text{‰}$; Matich *et al.* 2011). Upstream commuter and resident alligators had $\delta^{13}\text{C}$ values similar to those of the freshwater/estuarine food webs while the $\delta^{13}\text{C}$ values of most DC alligators, and many individuals for which movement tactic was unknown, fell above this range and suggest that they feed at least partially from marine food webs (Fig. 6). None of the $\delta^{13}\text{C}$ values for DC alligators suggested feeding exclusively from marine food webs and were below the most extreme values found for other highly mobile upper trophic level predators in the Shark River estuary that may commute to marine waters to feed (e.g., juvenile bull sharks; Matich *et al.* 2011). Isotopic values between marine and freshwater/estuarine food webs are not unexpected even if DC alligators feed largely in marine food webs during the wet season because alligator skin exhibits slow isotopic turnover rates (Chapter II). Thus isotopic values of skin likely reflect diets over multiple seasons. Therefore, because DC individuals spend at least half of each year in the mid-estuarine/freshwater zones, a large portion of their diets reflected in the isotopic values of skin will be from the freshwater and mid-estuarine zones.

Although stable isotope data in this study represent feeding that occurred before I quantified individual movements, they still are useful in understanding links between movement and trophic interactions and patterns of individual specialization. First, there

was remarkable temporal consistency in individual movement tactics across years. No alligator that was tracked across multiple years switched movement tactics, suggesting that movement tactics that were used during the time period that isotopic values developed were similar to those recorded during my study. If this was not the case, I would not have expected isotopic niches of the movement tactic groups to be as highly differentiated as I found, especially for a tissue that turns over slowly. Incorporating data on stomach contents and isotopic values of tissues with shorter turnover rates (e.g., blood plasma) would provide greater resolution on temporal variation in the relative contributions of marine and freshwater/estuarine prey to alligator diets.

Although the average diets or behaviours of predators often leads to the appearance that they couple food webs, recent studies have suggested that individual specialization may result in the separation of food webs through niche partitioning. For example, Eurasian perch separate into littoral and pelagic specialists that do not move between habitats, thereby keeping these food webs separate (Quevedo *et al.* 2009). However, when individuals can easily traverse habitats that contain separate food webs, individual specialists may actually enhance connectivity (e.g., Matich *et al.* 2011). My results suggest that, like juvenile bull sharks (Matich *et al.* 2011), alligators inhabiting an oligotrophic estuary likely link separate habitats, but only some individuals fulfill this ecological role. In the case of alligators, different suites of individuals appear to link different portions of the Everglades landscape. UC alligators may link marsh and estuarine areas while a different subset of the population, DCs, link coastal marine food webs with estuaries and even the marsh.

Long-distance, potentially habitat-coupling, movements are not unique to American alligators within the crocodylian family. Using acoustic tracking, Campbell *et al.* (2010) documented estuarine crocodiles (*Crocodylus porosus*) in northern Australia using river tidal currents to sometimes travel more than 50km between freshwater rivers and coastal marine waters where they may remain for up to 64 days at a time, possibly to feed. Although the movements of alligators in the SRE are also likely for foraging, the duration of their trips is more constrained than those of estuarine crocodiles because of their lack of functional salt glands and resulting susceptibility to salt-induced physiological stress (Taplin 1988).

The presence of trade-offs appears to be an important driver of individual specialization (e.g., orcas, *Orcinus orca*, Baird *et al.* 1992; black-tailed deer, *Odocoileus hemionus*, Darimont, Paquet & Reimchen 2007), which may be enhanced by resource scarcity (e.g., Svanback & Bolnick 2007; Tinker, Bentall & Estes 2008; Darimont *et al.* 2009). Trade-offs appear to be important both in driving individual specialization in alligators and bull sharks in the Shark River Estuary as well as their coupling of marine and estuarine/freshwater systems. Juvenile bull sharks experience enhanced foraging opportunities downstream where the risk of predation from larger sharks is higher (Matich *et al.* 2011) while alligators appear to face the trade-off between foraging opportunities and increased salt-stress. Like bull sharks, only some alligators accept higher costs to access marine-based food webs and do so primarily during the least stressful times of year. It might be expected that larger individuals that would be less susceptible to salt-stress would be more likely to use downstream areas. However, alligator habitat use did not follow such a pattern, and in fact within the DC group

smaller individuals had higher probabilities of using the downstream zone during the highest salinity periods. Such a counterintuitive result could have been caused by smaller individuals seeking out areas with higher prey abundances necessary for growth (though even the small alligators had already reached sexual maturity), smaller individuals actively avoiding the territories of larger males, or larger males preferring to stay closer to upstream areas so that they would not have to travel as far during the mating season to find mates. Clearly further studies are needed to understand the factors driving the use of particular movement and feeding tactics by alligators within the Shark River estuary.

In addition to linking the population dynamics of predators and prey across habitat boundaries (e.g., Polis *et al.* 1997), movements by alligators into downstream areas could play a role in nutrient dynamics of the oligotrophic estuary, specifically by transporting P derived from prey inhabiting the marine-dominated parts of the estuary to the freshwater-dominated areas of the SRE. Unfortunately, data on feeding and gastric evacuation rates are lacking for alligators in the SRE, making it impossible to estimate the potential role of alligators in nutrient dynamics at this time. However, alligators are large-bodied and relatively abundant in the system and the downstream commuting tactic, which involves short-duration trips into downstream waters, appears to be somewhat common. Therefore, it is possible that if downstream commuters consistently haul out or bask at particular locations, they could create nutrient “hotspots” in the mid-estuary zone derived from marine resources that are somewhat akin to the nutrient hotspots created by fish movements and habitat use in tropical rivers (e.g. McIntyre *et al.* 2008). A similar role has been suggested for other species of crocodylians. Fittkau (1973) hypothesized that caiman populations (*Melanosuchus niger* and *Caiman crocodilus*) in the Amazon

were key nutrient recyclers and thereby contributed to increasing primary production and the size of fish populations. Further studies will be needed to assess whether alligators could likewise play an important role in nutrient dynamics in the coastal Everglades.

My study suggests that highly mobile predators could play an important role in linking coastal habitats including marine, estuarine, and freshwater zones. Unlike species with lower mobility or smaller body sizes individual specialization by mobile large-bodied species that are buffered against short-term abiotic stress may lead to habitat connections that are maintained only by a subset of the population. While tradeoffs appear to be an important driver of specialization and habitat linkages in the Shark River Estuary, further studies investigating the generality of these results within other estuaries, the factors that lead to the adoption of particular movement tactics, and the overall importance of nutrient translocation by highly mobile predators, like alligators, to the dynamics of the coastal Everglades ecosystem are still required.

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CHAPTER IV

INTRAPOPULATION VARIATION IN ACTIVITY RANGES, MOVEMENT RATES, AND HABITAT USE OF AN AMERICAN ALLIGATOR POPULATION IN A SUBTROPICAL ESTUARY

Abstract

Movement and habitat use patterns are fundamental components of the behaviors of mobile animals and determine the scale and types of interactions they have with their environments. Movement behaviors are especially important to quantify for top predators because these animals can have strong effects on lower trophic levels and the wider ecosystem. Most top predator movement and habitat use studies focus on general population level trends, but recent research suggests that intrapopulation variation in animal behaviors is commonplace and can affect ecological and evolutionary dynamics as well as ecosystem management and conservation efforts. In an effort to better understand the prevalence of intrapopulation variation in top predator movement behaviors and the potential effects of such variation on ecosystem structure and function, I examined the movement and habitat use patterns of a population of adult American alligators (*Alligator mississippiensis*) in a subtropical estuary for four years. I found that alligators exhibited extremely wide-ranging behavioral variation in terms of activity ranges, movement rates, and habitat use, and that these individualized behaviors were stable over the years of my study. I also found that the variations across the three types of behaviors were correlated such that consistent behavioral types emerged, with an exploratory type on one end of the continuum and a sedentary type at the other end. The results of my research show that top predator populations can exhibit high levels of intrapopulation variation in terms of movement and habitat use, and that the individual variation could potentially lead to individuals filling different ecological roles in the same ecosystem. My research also suggests that one-size-fits-all conservation and management

strategies that do not account for potential intrapopulation variation in top predator behaviors may not produce the expected conservation outcomes.

Introduction

Activity ranges and movement rates are fundamental components of the interactions which mobile animals have with their environments and provide insight into habitat use patterns (Turchin 1998). Understanding these behaviors for large, highly mobile top predators is especially important because they can structure lower trophic levels through top-down effects and are key drivers of community and ecosystem dynamics (Pace et al. 1999; Terborgh et al. 2001; Estes et al. 2011). Recent advances in tracking technology (Rutz and Hays 2009) have enabled researchers to collect detailed data on individual top predator movements at multiple spatial scales, yet most studies focus on activity ranges, movement rates, and habitat use at the population level.

Individual specialization, i.e., when individuals in a population use a narrower subset of a given resource than the population as a whole, is behavioral specialization that occurs independently of variation caused by sex, morphology, and age/size (Bolnick et al. 2003). Individual specialization has received much attention from ecologists over the past decade because of its implications for ecological and evolutionary dynamics as well as conservation efforts (Bolnick et al. 2003; Dall et al. 2012). Much of the individual specialization literature focuses on dietary variation (Dall et al. 2012), yet for highly mobile top predators dietary specialization is often inherently linked with movement and habitat use specialization (e.g., Menard et al. 2007; Woo et al. 2008; Rosenblatt and Heithaus 2011). Intrapopulation variation in activity ranges, movements, and habitat use

has been reported for some large top predators, such as sixgill sharks (*Hexanchus griseus*; Andrews et al. 2007), tiger sharks (*Galeocerdo cuvier*; Heithaus et al. 2002), and estuarine crocodiles (*Crocodylus porosus*; Kay 2004a; Brien et al. 2008), but most often the variation can be attributed to age, size, and/or sex, and therefore is not considered true individual specialization, or the behaviors have been investigated over short time periods. Thus, the prevalence of individual specialization in large top predator movements and habitat use and the potential implications of such specialized behaviors have rarely been examined.

Crocodylians are hypothesized to exert important top-down effects in a variety of ecosystems (e.g., Craighead 1968; Bondavalli and Ulanowicz 1999; Nifong and Silliman 2013). However, many crocodylian populations have been drastically reduced over the past century, and currently seven species (30% of all crocodylian species) are considered endangered or critically endangered by the International Union for the Conservation of Nature (Martin 2008). Low abundances relative to those present historically make understanding crocodylian ecology a pressing challenge. Understanding individual specialization in relation to crocodylian activity ranges, habitat use, and their rates of movement is particularly important because these behavioral attributes will determine the size and scope of future crocodylian conservation strategies. Previous studies have examined activity ranges, movement rates, and habitat use in American alligators (*Alligator mississippiensis*; Chabreck 1965; Joanen and McNease 1970, 1972; McNease and Joanen 1974; Goodwin and Marion 1979; Rodda 1984; Morea et al. 2000), caimans (*Caiman crocodilus*; Ouboter and Nanhoe 1988; Campos et al. 2006), estuarine crocodiles (Kay 2004a; Read et al. 2007; Brien et al. 2008; Campbell et al. 2010),

freshwater crocodiles (*Crocodylus johnstoni*; Tucker et al. 1997), gharials (*Gavialis gangeticus*; Bustard and Singh 1983), and Nile crocodiles (*Crocodylus niloticus*; Hutton 1989; Hocutt et al. 1992). However, most were only able to collect location estimates for animals infrequently and for less than one year, meaning we know very little about the stability of crocodilian activity ranges, movement rates, and habitat use over the long-term given the relatively long lifespan of adults. Furthermore, individual specialization has never been considered as a component of crocodilian movements (but see Rosenblatt and Heithaus 2011).

In this study, I used Global Positioning System (GPS) transmitters and passive acoustic telemetry (hereafter “acoustic tracking”) to quantify activity ranges, movement rates, and habitat use of a population of American alligators inhabiting a subtropical estuary for multiple years and to investigate individual specialization. Alligators are the most abundant native large-bodied predators in the southeast United States and, though they are commonly thought of as a freshwater species and lack functional salt glands (Taplin 1988), inhabit many estuarine systems (Mazzotti and Brandt 1994). Alligators in marshes differ in their activity ranges and movement rates in terms of sex and age, with adult males typically occupying large ranges, adult females occupying much smaller ranges, and juvenile alligators falling somewhere in between (Joanen and McNease 1970, 1972; McNease and Joanen 1974). Alligators inhabiting subtropical estuaries of southwest Florida can roam widely and may exhibit some specialized movement tactics in relation to estuarine salinity gradients (Rosenblatt and Heithaus 2011), but the spatial extent of behaviors have not been investigated fully. Accurate knowledge of alligator activity ranges, movement rates, and habitat use will enable ecosystem managers to more

appropriately plan for conservation of the species by identifying key habitats and movement strategies, and knowledge of the prevalence of alligator individual specialization will reveal whether one or multiple conservation strategies are necessary for effective protection of the species.

Materials and methods

Field methods

The study was conducted from October 2007 to April 2011 in the Shark River Estuary (SRE) of Everglades National Park, Florida, USA (c. 25°25' N, 81°00' W, Fig. 1). The SRE is dominated by red mangroves (*Rhizophora mangle*) and is the main conduit for freshwater from the Everglades to drain into the Gulf of Mexico (Rosenblatt and Heithaus 2011). The SRE is characterized by high salinities during the dry season (January-June) when rainfall is light, and lower salinities during the wet season (July-December) when rainfall is much heavier (Romigh et al. 2006).

Alligators were captured from a 6 m boat using standard trapping techniques (Chabreck 1963; Rosenblatt and Heithaus 2011). After their mouth was taped shut, each alligator was brought on board the boat and an acoustic tracking device (model V-16H; Vemco, Halifax, NS, Canada) was attached to the tail using stainless steel wire and marine-grade epoxy prior to release (Rosenblatt and Heithaus 2011). Each acoustic tracking unit produced a unique coded signal randomly every 60-120 s and had an estimated battery life of 1250 days. All acoustic signals were monitored by an array of 46 Vemco VR2W monitors strategically placed throughout the SRE (Fig. 1) that recorded the date, time, and ID of each animal that passed by. The array of monitors was arranged

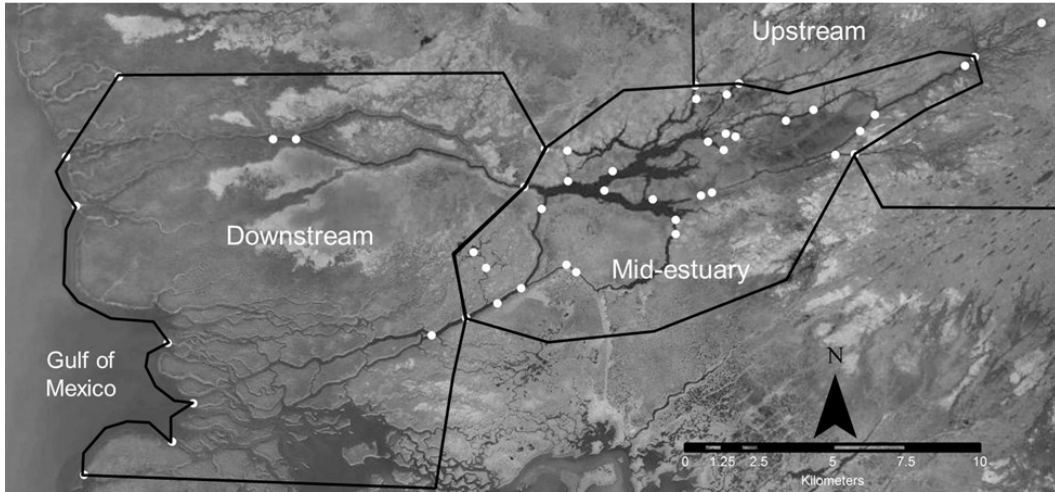


Figure 1: The Shark River Estuary located in southwest Florida (c. 25°25' N, 81°00' W). Forty-six acoustic monitoring stations (circles) were located throughout the study site and were used to define sampling zones (delineated by black lines).

such that the rough positions of each alligator and their direction of travel were known at all times while the alligators were inside the array (Rosenblatt and Heithaus 2011).

To supplement data from acoustic tracking, I deployed GPS-VHF dual tracking units (H.A.B.I.T. Research Ltd., Victoria, BC, Canada) on the nuchal scutes of two alligators (also equipped with acoustic transmitters) following a protocol similar to that used by Kay (2004b). First I immobilized each alligator by strapping their body to a 2.5 m wooden plank. Then, local anesthetic was administered to the scutes, the area was sterilized with alcohol, and a drill (Dremel, Racine, WI, USA) was used to make four holes through the scutes. Saline solution was sprayed on the drill during this process to prevent overheating. The transmitters were positioned on the nuchal plate and held in place by surgical grade stainless steel wire threaded through PVC tubing placed in the scute holes and the transmitter. Lastly, the scute holes and the sides of transmitters were covered in cool-setting marine-grade epoxy to streamline the entire unit and prevent it from becoming snagged during regular movements of the animals, while not interfering with the ability of the units to communicate with satellites. Each alligator was also measured for head length, snout-vent length, total length, tail girth, and body mass. Body condition was calculated using Fulton's condition factor formula, $(M/SVL^3)*10^5$, where M = body mass and SVL = snout-vent length (Fujisaki et al. 2009). Sex was determined by cloacal examination (Chabreck 1963). The entire capture, measurement, and attachment process took approximately 90 minutes per animal for GPS/acoustic tag attachment and 20 minutes for acoustic tag attachment only.

The GPS units were packaged in an epoxy resin with the VHF antenna exiting at 45° from the posterior end of the unit. The units were approximately 12 cm x 3 cm x 3

cm, weighed 350 g, and had battery lives of approximately 120 days. Pre-deployment, the GPS units were programmed to acquire satellite fixes once hourly. The units were unable to acquire satellite fixes when submerged and were not equipped with a “switch” that would turn the unit off while submerged to save battery life. Data from the GPS units were downloaded at predetermined fixed-time intervals every three weeks until the batteries expired. During download trips, alligators were located using a Yagi directional antenna attached to an Osprey receiver (H.A.B.I.T. Research Ltd., Victoria, BC, Canada). Once an alligator was located, the antenna was aimed at the GPS unit from a distance of <100 m and data from the GPS unit were transmitted to the receiver over a 5-10 minute period. Data were then transferred to a laptop computer on the boat. Data collected by the GPS units for each successfully recorded location included latitude and longitude, time of fix, number of satellites used per fix, and accuracy information in the form of position dilution of precision values (PDOP (unit-less); El-Rabbany 2002). During download trips I occasionally observed the movements of the alligators. There was no apparent fouling of either the GPS or acoustic tracking units or impacts on the alligators (e.g., irritation near tag).

Movement analyses

The activity ranges of the alligators were quantified using acoustic tracking data recorded between January 2008 and April 2011 and GPS data recorded between October 2007 and February 2008. Acoustic tracking data acquired prior to January 2008 were not used because the monitor array was not yet fully deployed and after April 2011 few individuals with active transmitters were still within the array. For each alligator, I

assessed activity ranges using the metric minimum mid-stream linear range (MMSLR; modified from Kay 2004a). Minimum mid-stream linear range was measured for each individual alligator using the acoustic tracking data by drawing a line between the most distantly spaced monitors that had detected an alligator using the middle of the portion of river/estuary traveled between the monitors instead of the banks. The path that was measured was always the shortest between the points. If an alligator was detected by a certain monitor then it was assumed to have traveled to the exact location of the monitor for simplicity, though the actual detection range of each monitor was between 58 and 1149 m (mean = 336 m \pm 225 SD; Rosenblatt and Heithaus 2011). For the GPS data, MMSLR was measured using the same technique but with GPS location fixes in place of monitor locations. This metric provided a measure of the total river range across which an alligator moved, not the total distance moved during the monitoring period. Minimum mid-stream linear range is an appropriate method for range calculations if the animals under study are geographically restricted (Kay 2004a), and the alligators in my study were restricted to the aquatic portions of the SRE except when they basked on the banks (Rosenblatt and Heithaus 2011). In spite of the fact that in the upper portions of the SRE individual alligators could exit the tracking array as they entered the freshwater marsh, this method still provides a robust measure of estuarine activity ranges. I was unable to use kernel utilization distribution methods for calculating home ranges (Worton 1989) using acoustic tracking data because the structure of my acoustic tracking array did not allow me to pinpoint exact locations for individual alligators at any time, and my GPS data were temporally limited (see Results). Therefore I do not present my results as home ranges but instead as minimum activity ranges (*sensu* Goodwin and Marion 1979) that

incorporate all the locations collected for each animal. MMSLRs were calculated separately for each individual alligator in both the wet and dry seasons.

Movement rates were quantified for the GPS data by measuring river distance (as opposed to straight-line distance) between consecutively recorded points. For the acoustic tracking data, river distance was measured between monitors that consecutively recorded the presence of an individual. Rate of movement (ROM) was calculated as the distance covered divided by the time it took to travel that distance, and ROMs were compared both between seasons and day/night. These distance measurements were also made using the minimum mid-stream linear method, therefore my distance measurements and movement rates are conservative estimates.

Habitat use was measured according to the SRE habitat divisions employed by Rosenblatt and Heithaus (2011). Briefly, the SRE was divided into three zones: upstream (freshwater year-round), mid-estuary (freshwater/estuarine year-round), and downstream (estuarine/marine year-round; Fig. 1). I calculated the percent time spent in each zone during each season using acoustic tracking data. Activity range, ROM, and habitat use data were compared between seasons and years for individuals that were active for both seasons and more than one year. All mapping and spatial calculations were performed using ArcGIS 9 (Esri, Redlands, CA, USA) and all statistical analyses were carried out using SigmaPlot 11 (Systat Software Inc., Chicago, IL, USA).

Results

From October 2007 to April 2011 I captured and tracked 52 adult alligators ranging from 176.8 to 280.6 cm total length (mean = 226.8 cm \pm 23.8 SD). The sex ratio

of tracked alligators was male-biased (5.5:1). Thirty-three of the individuals were captured during the dry season and 19 during the wet season. Ten animals were caught during 2007, 14 during 2008, 16 during 2009, and 12 during 2010. Eight of the alligators were never detected on the monitor array, which may have been caused by tag failure or individuals never moving within range of a monitor. Of the remaining 44 alligators, only 23 individuals (all male) were detected on the array for at least half of one season (90 days). These individuals had total detection times on the array between 106 and 1151 days (mean = 391 days \pm 308 SD). Because the other 21 individuals were detected for relatively short periods of time (range = 1-57 days, mean = 35 days \pm 14 SD) and were each only present on the array for less than half of one season, they were excluded from further analyses. Two of the 23 individuals (Alligator 6825 and 6827) were fitted with GPS units during the night of 4 October 2007, but 6.7 km apart (Fig. 2). Though 6827 was 33cm larger than 6825, both animals were in similar body condition. Alligator 6825 produced 63 GPS locations over 58 days, while Alligator 6827 produced 304 locations over 146 days. The “fix-rates” (number of successful fixes divided by total number of attempted fixes; Frair et al. 2010) were 4.6% and 8.7% for Alligator 6825 and Alligator 6827, respectively. The mean PDOP accuracy for the location fixes was 6.35 (\pm 0.31 SE; range 1.72-13.99) for Alligator 6825 and 4.69 (\pm 0.36 SE; range 1.75-9.99) for Alligator 6827. The number of satellites used per fix was 14.24 (\pm 0.47 SE; range 5-20) for Alligator 6825 and 17.60 (\pm 0.26 SE; range 9-20) for Alligator 6827.

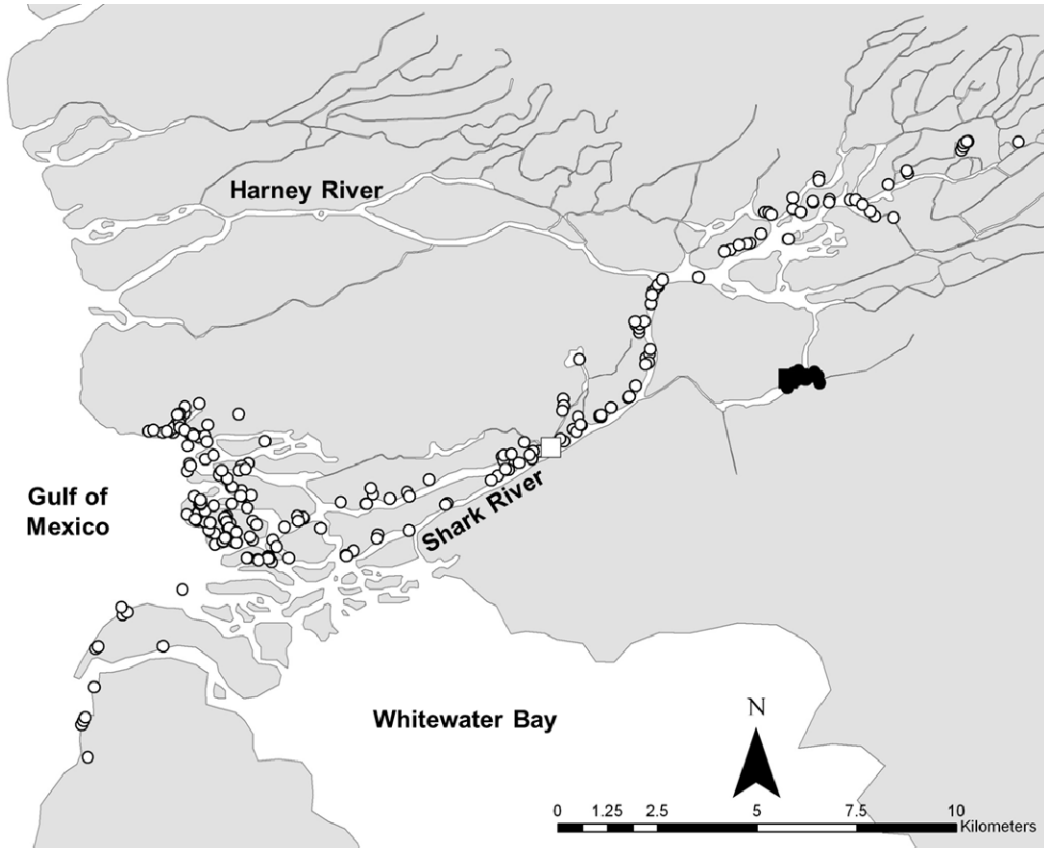


Figure 2: Alligator 6825 (capture site = black square) and Alligator 6827 (capture site = white square) were tracked using GPS telemetry from Oct 2007 – Feb 2008. Location fixes for Alligator 6825 are indicated by black circles and location fixes for Alligator 6827 are indicated by white circles.

Activity ranges

Acoustic MMSLRs of the 23 alligators ranged from 0.5 to 62.4 km river distance (mean = 17.2 km \pm 15.6 SD). Six (23%) of the alligators had MMSLRs <5 km while 12 (52%) had ranges over 15 km (Fig. 3). Of the two alligators equipped with GPS units, one had an activity range of 66.2 km (62.4 km acoustic) and the other a range of 1.2 km (12.3 km acoustic; Fig. 2). When examined using linear regression, acoustic MMSLR did not significantly vary with total tracking time ($R^2 = 0.05$, $p = 0.3$) or alligator size ($R^2 = 0.01$, $p = 0.6$). There were, however, large differences between alligator activity ranges in the wet and dry seasons (Fig. 4), with the mean wet season MMSLR (8.4 km \pm 10.7 SD) about half that of the mean dry season MMSLR (15.6 km \pm 10.7 SD; Mann-Whitney rank sum test, $T = 187$, $p = 0.02$). The mean distance between the ocean and the centroid of MMSLRs during the dry season (22.2 km \pm 6.3 SD) were approximately 1.5 times farther upstream than during the wet season (18.4 km \pm 9.4 SD; signed rank test, $Z = -3.1$, $p < 0.001$). For the only four individuals active for three wet or three dry seasons, there were no significant differences between MMSLRs across years for particular seasons (ANOVA, all $p > 0.4$).

Movement rates

The total distances traveled by the acoustically tagged alligators ranged from 9.1 to 1134.5 km (mean = 354 km \pm 355.9 SD). The average ROMs of the acoustically tagged alligators were quite variable, ranging from 0.05 km/day to 3.2 km/day (mean = 0.9 km/day \pm 0.8 SD). There was a significant positive relationship between average ROM and total activity range (linear regression, $R^2 = 0.25$, $p = 0.02$; Fig. 5).

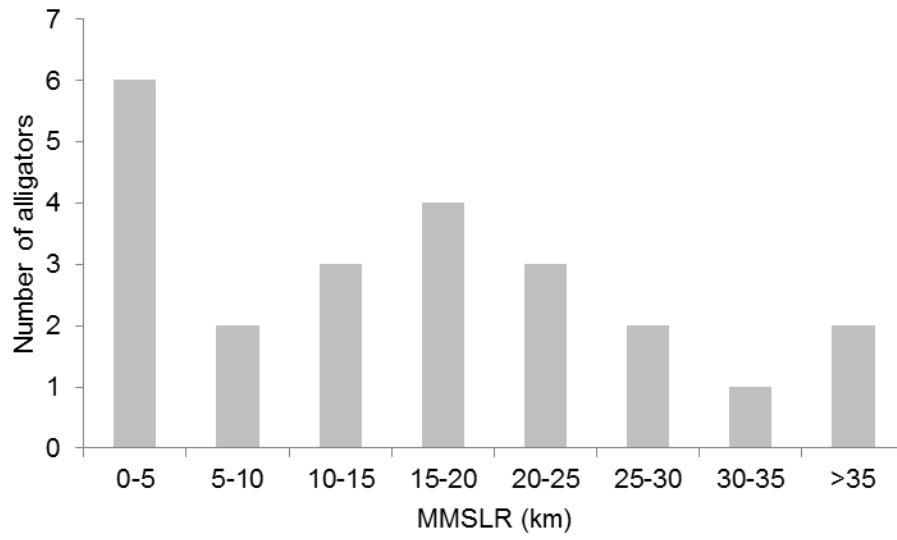


Figure 3: Distribution of 23 alligator minimum mid-stream linear ranges (MMSLR) recorded between 2008 and 2011 in the Shark River Estuary.

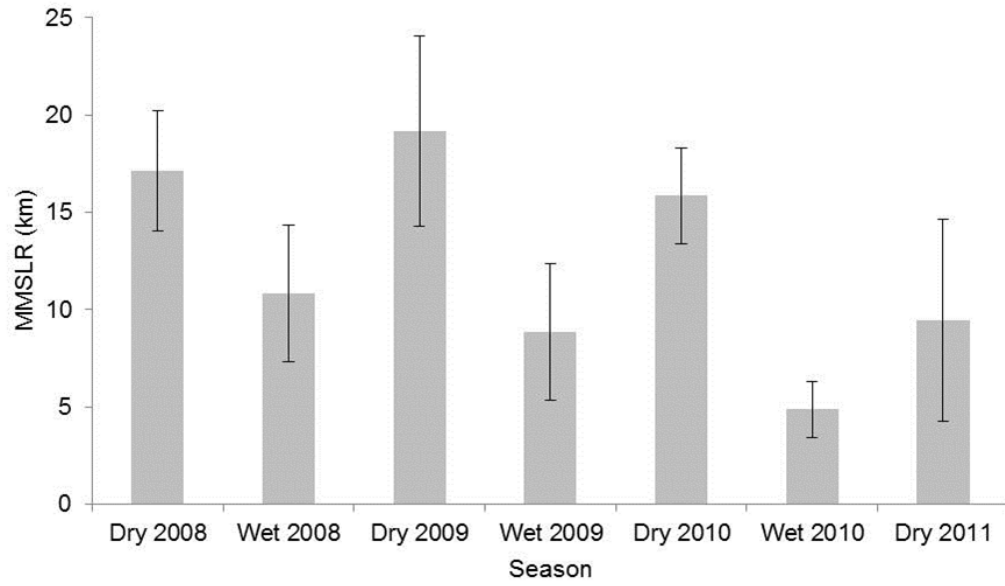


Figure 4: Average size of 23 alligator minimum mid-stream linear ranges (MMSLR) during the wet and dry seasons between 2008 and 2011 in the Shark River Estuary. Vertical bars represent standard error.

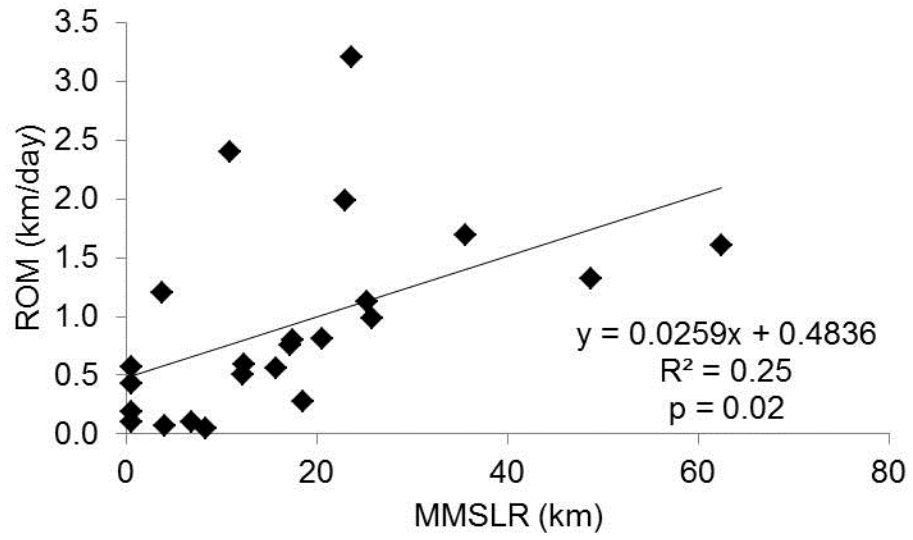


Figure 5: The relationship between alligator total average rate of movement (ROM) and total minimum mid-stream linear range (MMSLR) for 23 adult male alligators tracked in the Shark River Estuary between 2008 and 2011. Trend line represents linear regression.

Furthermore, average ROMs were unrelated to total tracking time or alligator size (both $R^2 < 0.02$, both $p > 0.5$) but were significantly positively correlated with total distance traveled ($R^2 = 0.24$, $p = 0.02$). Wet season ROMs (mean = 0.9 km/day \pm 0.7 SD) were not significantly different from dry season ROMs (mean = 0.8 km/day \pm 0.7 SD; Mann-Whitney rank sum test, $T = 405$, $p = 0.9$). I compared the behaviors of the two GPS-tagged animals over the 58 day period (5 Oct – 1 Dec 2007) during which both alligators produced locations (63 for Alligator 6825 and 110 for alligator 6827). The activity patterns of the two alligators during this period were strikingly different. Alligator 6825 remained in one general location in the brackish area of the estuary and moved a total of 8.7 km over the 58 days, whereas Alligator 6827 ranged widely and traveled 325.5 km during the same time period (Fig. 2). Alligator 6825 displayed a ROM of 0.2 km/day and Alligator 6827 exhibited a ROM of 5.6 km/day, a greater than 28-fold difference. Furthermore, the maximum distance traveled by Alligator 6827 in one 24-hour period was 22.4 km, while the maximum distance traveled by Alligator 6825 over a 24-hour period was only 1.2 km. Lastly, the fastest ROM measured during the study period for each animal was 0.07 km/hr for Alligator 6825 and 2.6 km/hr for Alligator 6827 (though Alligator 6827 did record a ROM of 2.9 km/hr after 1 Dec 2007). For Alligator 6825, its GPS-derived ROM was less than its acoustically derived ROM over the remainder of the study (0.9 km/day), while for Alligator 6827 the opposite was true (acoustically derived ROM = 2.2 km/day).

As a group, the alligators exhibited significantly different ROMs between day and night (paired t-test: $t_{19} = -4.4$, $p < 0.001$), with nighttime ROMs (mean = 503 m/h \pm 313 SD) greater than daytime ROMs (mean = 319 m/h \pm 225 SD). However, there were large

differences between individual ROMs during both day and night: daytime ROMs ranged from 40 to 928 m/h and nighttime ROMs ranged from 30 to 990 m/h (Fig. 6). I did not detect a significant difference between wet and dry season daytime ROMs ($t_{11} = -2.0$, $p = 0.07$) or nighttime ROMs (Wilcoxon signed rank test: $Z = 1.8$, $p = 0.07$). There was a significant positive relationship between day and night ROMs ($R^2 = 0.66$, $p < 0.001$).

Habitat use patterns

Collectively, the 23 acoustically tagged alligators spent 9% of their time in the upstream zone, 74% in the mid-estuary zone, and 17% in the downstream zone. There were clear seasonal differences in habitat use, with alligators on average spending twice as much of their time in the downstream zone during the wet season ($25.5\% \pm 7.6$ SE) than during the dry season ($12.6\% \pm 4.8$ SE), twice as much of their time in the upstream zone during the dry season ($11.2\% \pm 5.4$ SE) than during the wet season ($5.5\% \pm 7.4$ SE; Fig. 7). The proportion of time individual alligators spent in the downstream zone during the wet season was positively correlated with wet season activity range size (linear regression: $R^2 = 0.36$, $p = 0.02$) but there was no similar relationship during the dry season ($R^2 = 0.02$, $p = 0.58$). The four individuals active for three wet or three dry seasons did not display significant differences in seasonal habitat use patterns across years (ANOVA, all $p > 0.2$). There were also clear differences in habitat use patterns among individuals. For example, 11 alligators never entered the downstream zone and 13 never entered the upstream zone. Furthermore, the alligators displayed wide ranges of use of each zone: the proportion of time each alligator spent in the downstream zone ranged from 0 to 75%, in the mid-estuary zone from 25 to 100%, and in the upstream zone from

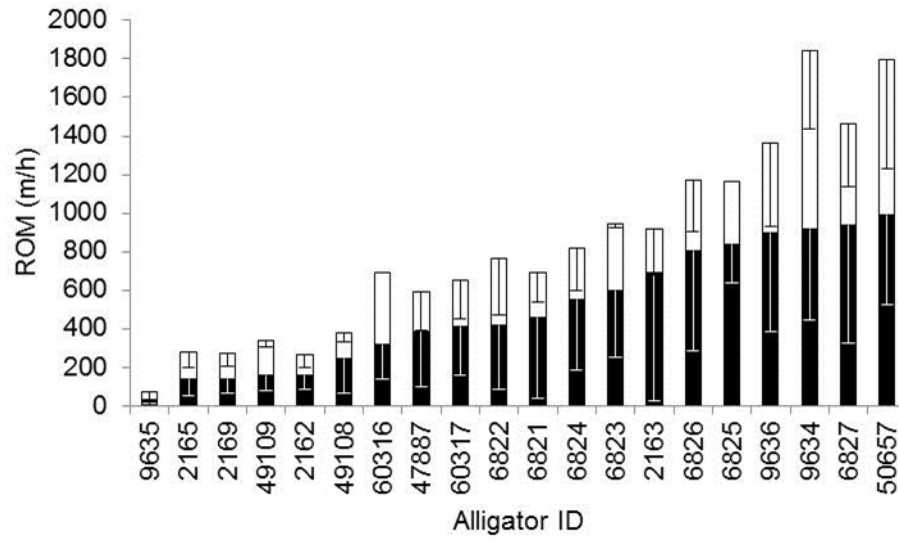


Figure 6: Mean nighttime and daytime rates of movement (ROM) for 20 individual alligators in the Shark River Estuary recorded between 2008 and 2011. Black bars = night, white bars = day. Vertical bars represent standard deviation.

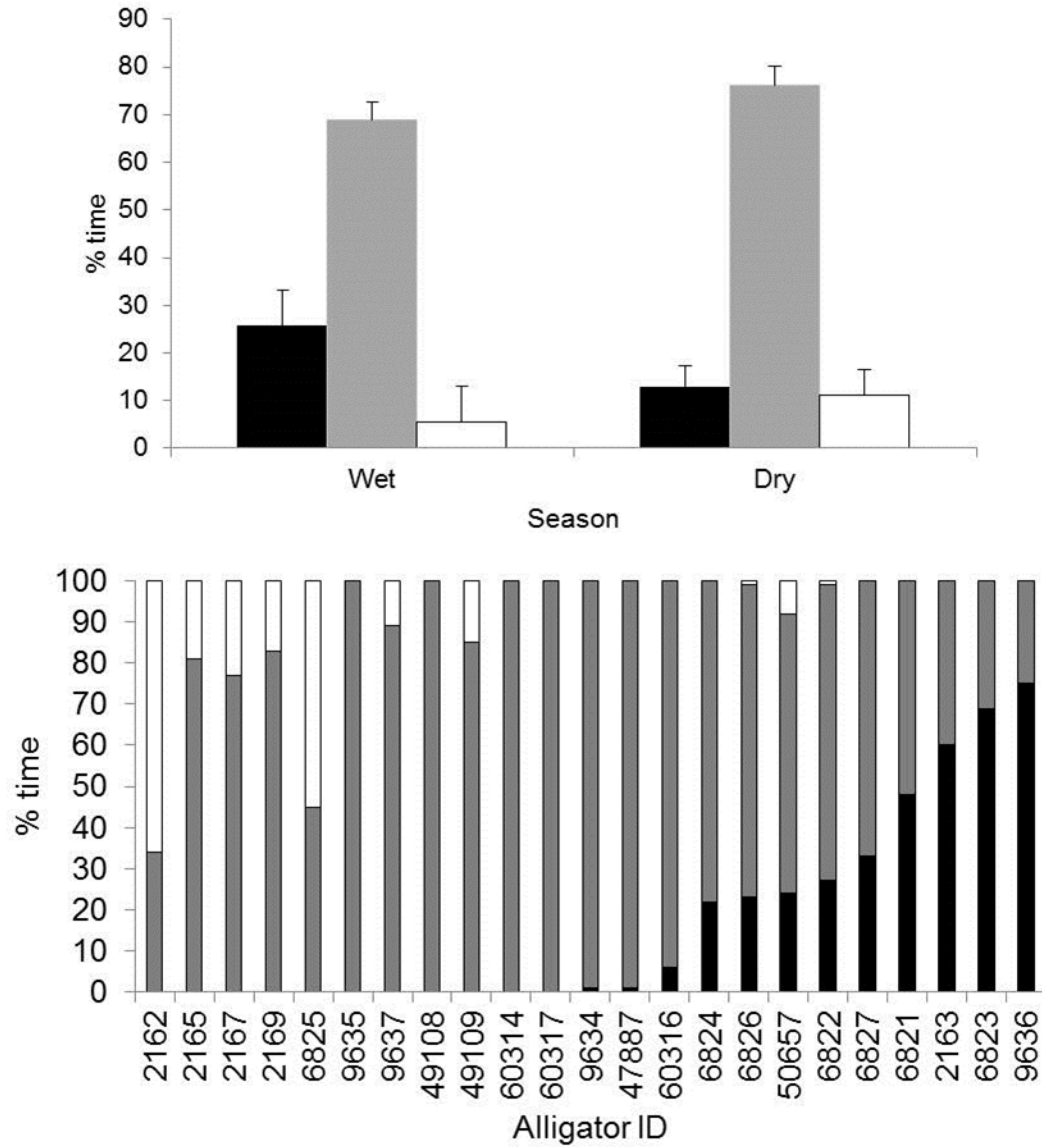


Figure 7: Upper: collective mean percent time spent by 23 alligators in each of three zones of the Shark River Estuary during the wet and dry seasons between 2008 and 2011. Black bars = downstream zone, gray bars = mid-estuary zone, white bars = upstream zone. Vertical bars represent standard error. Lower: individual mean percent time spent by 23 alligators in each of three zones of the Shark River Estuary during the wet and dry seasons between 2008 and 2011. Black bars = downstream zone, gray bars = mid-estuary zone, white bars = upstream zone.

0 to 66% (Fig. 7). Variation between alligator habitat use patterns was not attributable to differences in size or year of tracking (Table 1).

Table 1: Results of ANOVAs investigating the effects of alligator size and year on alligator habitat use in the Shark River Estuary between 2008 and 2011.

Habitat	Variable	Sum of squares	df	Mean square	F	P
Downstream	Size	824.5	2	412.3	1.3	0.3
	Year	148.1	2	74.1	0.2	0.8
Mid-estuary	Size	595.9	2	298	1.1	0.4
	Year	203	2	101.5	0.4	0.7
Upstream	Size	29.7	2	14.8	0.3	0.7
	Year	80.1	2	40.0	0.8	0.5

Discussion

Activity ranges and movement rates of top predators are often studied at the population level while behavioral differences between individuals are generally overlooked. My results show that a population of adult male American alligators exhibited a high degree of intrapopulation variation in movement and habitat use patterns, and that these patterns were stable over multiple years. Also, the variation was not associated with sex, age, or size, and therefore suggests that the alligators are individual specialists in terms of movement patterns (*sensu* Bolnick et al. 2003). These findings further suggest that individuals may have specialized roles in ecosystems over the long-term and that effective ecosystem management and conservation may require the incorporation of such variability into future plans.

In general, the alligators in my study displayed larger activity ranges during the dry season than during the wet season. The difference likely exists because at the beginning of the dry season some of the alligators still used the downstream zone infrequently and then transitioned into only using the mid-estuary/upstream zones as the dry season progressed. I also found that alligator ROMs did not vary between seasons, suggesting that though the total area covered by alligators varies between seasons the alligators maintain similar ROMs regardless of the area covered. Furthermore, the results of my alligator habitat use analyses agree with previous results from the SRE (Rosenblatt and Heithaus 2011): alligators in general decrease their use of the downstream zone during the dry season because of rising salinity and increase their use of the upstream zone as a result. Indeed, the centroids of each alligator's activity range during the dry season on average shifted much further away from the Gulf of Mexico relative to the wet

season centroids. However, despite these general trends at the population level I found large amounts of behavioral variation between individuals across all of my movement and habitat use metrics.

The primary cause of the highly variable movement and habitat use patterns I observed is likely limited and patchily distributed food resources. The Shark River Estuary is an oligotrophic system that receives the majority of its limiting nutrient (phosphorous) from the Gulf of Mexico (Childers et al. 2006), creating a situation in which downstream areas are more productive than upstream areas (Simard et al. 2006). However, the downstream areas are also more saline than upstream areas, limiting the ability of alligators to occupy downstream habitats for extended periods of time because of their limited osmoregulatory capabilities (Lauren 1985). Thus, the tradeoff for alligators in the SRE in terms of habitat use and movement patterns is clear from the present and previous studies (Rosenblatt and Heithaus 2011). Alligators can either have relatively large wet season activity ranges, travel far and fast, and access marine food resources in the downstream zone during the wet season while potentially exposing themselves to increased physiological stress caused by salt and likely expending more energy, or they can have relatively smaller wet season activity ranges, move slower and less frequently, and remain in less saline environments with possibly less access to food but likely conserve more energy. As a result of these variable behavioral patterns different individual alligators in the SRE may serve different ecological roles: the former group of alligators may act as biological vectors of connectivity between disparate habitats (Rosenblatt and Heithaus 2011) and have weaker top-down effects on a wider

range of prey and habitat types, while the latter group may not link habitats but exert stronger top-down control on localized food webs in smaller core areas.

The likely relationship between the large activity ranges of some of the alligators and patterns of food availability in the SRE is consistent with studies of other large predators, which in general increase their activity ranges when prey are scarce (reviewed by Gittleman and Harvey 1982). However, alligators appear to be somewhat unique in that some of the individuals in the SRE displayed very small activity ranges and low ROMs despite the overall scarcity of prey. These individuals are likely able to survive because as ectothermic predators they can use less energy as a consequence of low metabolic rates than similarly sized endothermic carnivores (Coulson and Hernandez 1983). The question remains as to why some individuals have small activity ranges while others have large ranges, and in the absence of obvious demographic factors (sex, age, size), I hypothesize that this variation could be driven instead by “personality” differences. A rich body of research has developed recently that shows that many populations of animals from diverse groups contain individuals with different personalities, whether in terms of bold vs. shy, aggressive vs. passive, or exploration vs. avoidance (Reale et al. 2007). The ultimate causes of personality differences and their possible effects on ecology and evolution have not been widely explored in top predators, but studies in other taxa suggest that variation in personality types may be determined by morphological/physiological adaptive plasticity, cultural transmission and early life experience, and differential genetic and epigenetic expression (Dall et al. 2012).

Past research on alligator activity ranges in Florida broadly agrees with my results. Goodwin and Marion (1979) and Morea et al. (2000) found similar patterns in

terms of seasonal activity ranges, with dry season/spring activity ranges being larger than at other times of year. My results are also similar to those from studies of other species of crocodilians. Kay (2004a) studied male estuarine crocodiles in a river in northwest Australia and reported MMSLRs between 11 and 87 km (mean = 46.7 km). However, the maximum distances traveled and ROMs for alligators in my study were much greater than values reported by other studies of alligators. For example, Morea et al. (2000) reported ROMs for male alligators between 0.1 and 0.2 km/day (mean = 0.18 km/day) and Rodda (1984) found that individuals moved as much as 3.5 km per night and 11.8 km over 11 days, and reached maximum swimming speeds over open water of 1 km/hr. Also, Joanen and McNease (1972) found that males had a maximum average ROM of 1.7 km/day. In my study, I found alligators in the SRE had a mean ROM of 0.9 km/day but maximum ROMs that ranged as high as 22.4 km/day and a maximum swimming speed of 2.9 km/hr. The differences between my results and other alligator studies may be caused by habitat differences: the alligators in the previous studies inhabited lakes or semi-aquatic marsh landscapes with presumably much higher rugosity and/or restricted movement ability than the estuarine river system used in my study.

My ROM findings, however, are comparable to studies involving other species of crocodilians inhabiting rivers. For example, Kay (2004a) found a highest mean ROM of 4.0 km/day, with a maximum ROM of 23.3 km/day, and Campbell et al. (2010) reported that estuarine crocodiles regularly made trips of more than 50 km in the Kennedy River in northern Australia, with one crocodile undertaking an oceanic trip of 590 km over 25 days (ROM = 23.6 km/day). Read et al. (2007) documented similar movement capabilities in estuarine crocodiles in northern Australia when adults were purposefully

displaced from their home sites. One individual traveled >400 km in 20 days (ROM = >20 km/day) to return to its home site. Similarly, one of my GPS-tagged alligators (Alligator 6827) moved 801.5 km over 146 days with a maximum ROM of 22.4 km/day.

In contrast to previous studies, my results are unique in that I documented that adult male alligators are capable of occupying temporally stable activity ranges since the alligators in my study occupied similarly sized activity ranges in both multiple dry and multiple wet seasons for at least three years. I was able to gather movement data for almost three times as long as the next longest study of crocodylian movements (1151 days vs. 448 days; Morea et al. 2000) because I used passive acoustic telemetry technology. The technology uses small, low-cost transmitters that do not use much energy and therefore can remain active for up to four years. Researchers do have to make a significant upfront financial investment in the monitors used to detect the transmitters, but the monitor array can be used to track a large number of individuals from many different species simultaneously and therefore can be very cost-effective in the long-run. The main drawback of the technology is that if animals with transmitters leave the vicinity of the monitor array then the researchers get no additional data from them. For example, a total of 19 alligators I tracked for more than 90 days but less than one year likely moved out of my monitor array and never returned, indicating that parts of their total activity ranges existed outside of the SRE. The GPS tracking devices are superior in this regard because they are not spatially limited, but the tradeoffs are that GPS devices are more expensive and generally have shorter battery lives. For example, in my study the two animals tracked with both GPS and acoustic devices displayed larger GPS-derived activity ranges and different GPS-derived ROMs when compared with acoustically

derived ROMs, but the GPS devices were only active for a comparatively short time before their batteries ran out.

I also found significant differences between daytime and nighttime movements. Alligators typically exhibit diurnal behaviors and vary their activity levels seasonally to optimize their body temperature (Smith 1975). During cold winter months they are generally more active during the day than during the night whereas during warm summer months the opposite is true (e.g., Smith 1975; Watanabe et al. 2013). I found that in general alligators in the SRE are more active during the night than during the day, though a minority of individuals (20%) displayed the opposite pattern. The dominant diurnal pattern was consistent across seasons likely because of the relatively high year-round temperatures in south Florida. Interestingly, there was a strong positive relationship between the day and night ROMs of individuals such that individuals that were more active during the night were also more active during the day. The positive relationship between day and night ROMs further supports the idea that alligators in the SRE are consistent behavioral specialists with potentially distinct behavioral types: alligators exhibiting exploratory behaviors are more active, regardless of season or time of day, than individuals exhibiting more sedentary behaviors and generally remaining in small core areas.

My research has implications for ecosystem and species-specific management. For example, individual specialization in movement behaviors and habitat use indicate that one-size-fits-all management policies may not achieve their goals. In the context of Everglades restoration, over the next several decades coastal areas are likely to be heavily impacted by increased freshwater flow and resulting alteration of salinity regimes (Davis

et al. 2005). These changes may not uniformly impact alligators. Individuals that currently move into marine habitats to find food may be adversely affected by large influxes of freshwater because their marine prey may be forced out of the system, whereas alligators that stay in fresher habitats may see benefits from restoration because of increased ranges of freshwater and estuarine prey. Conversely, as a result of future freshwater influx alligators that currently use marine habitats may be able to remain downstream for longer periods of time, providing them with extended access to marine resources. Regardless of specific mechanisms, effectively incorporating potential responses to changing abiotic conditions of top predator populations exhibiting variable movement and habitat use patterns will be key for successful ecosystem conservation and management plans.

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CHAPTER V

CONTEXT DEPENDENCE OF INDIVIDUAL SPECIALIZATION IN A LARGE “GENERALIST” APEX PREDATOR

Abstract

Individual niche specialization (INS), i.e., behavioral specialization not attributable to variation in age, size, sex, or morphology, is increasingly being recognized as an important component of ecological and evolutionary dynamics. However, most studies that have investigated the prevalence, consequences, and causes of INS have been carried out in laboratory and semi-controlled natural settings and have focused on small-bodied species for relatively short periods of time. Therefore little is known about the possible context dependence of INS in wild populations or the prevalence of INS in top predator populations. Top predators are an important group in which to investigate INS because they can have strong effects on community and population dynamics, therefore any variation in their behavior could lead to changes in ecosystem structure and function. I investigated the prevalence, potential context dependence, causes, and possible consequences of INS in feeding behaviors across many different populations of American alligators (*Alligator mississippiensis*) across much of their range using stomach contents and stable isotope analysis. I found that over short time periods alligator populations may occupy a wide range of the INS spectrum, but general patterns were apparent. Alligator populations inhabiting lakes generally exhibited less individual specialization than non-lake coastal populations, and these differences appeared to be driven by variation in habitat heterogeneity, movement rates, and relative prey availability. Stable isotope analyses revealed that over longer time spans, regardless of habitat type or context, individual alligators within populations exhibited very stable use of particular food sources available to them, but there could be a wide range of feeding behaviors. Ultimately, my research shows that patterns of INS in top predators can be context

dependent, and it is clear that knowledge of INS needs to be thoughtfully incorporated into top predator and ecosystem management and conservation strategies.

Introduction

Intrapopulation specialization in foraging behavior can be attributed to differences between sexes (“ecological sexual dimorphism”; e.g., Temeles et al. 2000) morphological types (“resource polymorphisms”; reviewed in Dall et al. 2012), and age groups (“ontogenetic niche shifts”; Polis 1984). Increasingly, however, it is recognized that individuals within a population can exhibit considerable variation in trophic interactions that are not attributed to these factors. Individual niche specialization (INS) has important implications for evolutionary processes and community and population dynamics (e.g., speciation, competition; Bolnick et al. 2003; Dall et al. 2012). Although “generalist” species are known to exhibit INS (Bolnick et al. 2003), there remain important questions about the context dependence of INS within species and its potential drivers (Araujo et al. 2011), especially for upper trophic level predators. If there is variation in the prevalence of INS among populations of particular top predators, then the effects of top predators on lower trophic levels could be more variable than previously thought and could lead to variation in their ecological roles across seemingly similar systems.

The niche variation hypothesis (NVH; Van Valen 1965) predicts that if a population occupies a region with a large diversity of habitats or low interspecific competition, then INS will increase relative to a population in a region with lower habitat diversity or higher interspecific competition. In addition, intraspecific competition can theoretically lead to increased or decreased INS depending on the variation in rank-

preference of available prey: INS should increase if all the individuals in a population prefer the same top-ranked resource but because of high intraspecific competition are forced to use secondary resources, whereas INS should decrease if they prefer different resources but are forced to use shared secondary resources as intraspecific competition increases (Araujo et al. 2011). The relative roles of these three factors (habitat variation, interspecific competition, intraspecific competition) in determining the degree of INS in a population is a matter of debate, and recent empirical evidence has been somewhat contradictory. For example, interspecific competition has been shown to both increase and decrease INS (Araujo et al. 2011). Furthermore, most studies that have investigated INS have either focused on controlled laboratory populations or small-bodied species in the wild for short periods of time.

These questions are particularly important to answer for large apex predators because of their rapidly declining populations and their ability to affect community and population dynamics (Goldschmidt et al. 1993; Heithaus et al. 2008; Estes et al. 2011; Nifong and Silliman 2013) as well as nutrient flow and cycling (Schmitz et al. 2010). If “generalist” apex predator populations are in fact made up of individual specialists, then conservation and management strategies targeting these animals and their habitats may need to be revised to take into account a diversity of feeding patterns. A number of diet studies have documented the presence of INS in large apex predators (e.g., Darimont et al. 2009; Matich et al. 2011; Thiemann et al. 2011), but few have addressed INS across many habitats over large spatial scales for the same species. Understanding context dependence, therefore, is a critical next step in these investigations. Indeed, such studies

remain generally lacking so it is unclear whether previously reported INS results only apply to regional populations or over short time periods.

Here I investigate the prevalence, possible context-dependence, stability, and causes of INS in a well-studied large apex predator: the American alligator (*Alligator mississippiensis*). Using two complementary techniques, stomach contents analysis (SCA) and stable isotope analysis (SIA), I assess INS in this species across a large spatial range and a variety of different habitats. Alligators are an excellent model “generalist” apex predator for such a study because: 1) their diets (as assessed through SCA) have been examined across their range repeatedly, 2) they inhabit almost every type of fresh and brackish water habitat across the southeastern US (Mazzotti and Brandt 1994), and 3) density data for alligators are regularly collected by some state agencies for certain habitats, thus making it possible to test *a priori* hypotheses on the basis of competitive interactions. I hypothesized that alligator populations inhabiting lakes would display relatively low degrees of INS because of low habitat variability and high intraspecific competition. In contrast, I predicted that alligator populations in coastal non-lake habitats (estuaries, islands, marshes) that have access to multiple ecosystems that support different food webs (freshwater, estuarine, marine) and have lower population densities, thus lower intraspecific competition, would exhibit higher degrees of INS.

Methods

Stomach contents collection and analyses

I compiled alligator stomach contents data from seven published studies containing data collected from 1220 alligators between 1977 and 2004 and four new

datasets collected from 192 alligators between 2007 and 2011 (Table 1). The datasets included populations from a wide geographic range and a variety of habitats including lakes, estuaries, coastal marshes, and barrier islands (Fig. 1). In some of the studies, alligator stomachs were sampled as part of state regulated harvests and nuisance control programs, while in others data were collected non-lethally using the hose-Heimlich technique (Table 1; for full description of the technique see Fitzgerald 1989). In the studies that have examined the efficacy of this technique 100% of ingested prey items have been recovered from 91% of the alligators tested (Fitzgerald 1989; Rice et al. 2005; Nifong et al. 2012), therefore I assumed no sampling bias between studies that used either lethal or non-lethal methods. For each alligator, every prey item found in the stomach contents was classified to the lowest possible taxon either immediately after collection or after being preserved in formalin or alcohol for various lengths of time.

To assess the prevalence of INS in the alligator populations using stomach contents data I applied Roughgarden's (1972) concept of total niche width (TNW; the full range of food resources used by a population), which can be subdivided into a between-individual component (BIC; the variance in food resource use between individuals) and a within-individual component (WIC; the variance in food resource use within individuals), such that $TNW = BIC + WIC$. The Shannon index of diversity (Shannon 1948) can be used as a proxy for variance in BIC and WIC (Roughgarden 1979), with BIC becoming the variance in the diversity of prey consumed between individuals and WIC becoming the diversity of species consumed within individuals (Bolnick et al. 2002). If BIC is larger than WIC for a given population, then the diet of the population is more different between individuals than they are within individuals. I divided BIC by TNW to generate

Table 1: Summary information for the American alligator stomach contents and stable isotope studies used in specialization analyses.

Data source	Locations	Habitat type	Duration	Collection method	N
Stomach contents					
Delany & Abercrombie 1986	Orange, Lochloosa, & Newnans Lakes, FL	Lake	1981-1983	Hunter harvested alligators	349
Delany et al. 1988	Duval, St. Johns, Alachua, Marion, Citrus, & Lake counties, FL	Lake	1977	Sacrificed nuisance alligators	78
Delany 1990	Orange Lake, FL	Lake	1986	Sacrificed alligators	77
Elsey et al. 1992	Marsh Island, LA	Island	1991	Hunter harvested alligators	101
Delany et al. 1999	Rodman, George, Hancock, & Trafford Lakes, FL	Lake	1985	Hunter harvested alligators	231
Rice et al. 2007	Apopka, Griffin, & Woodruff Lakes, FL	Lake	2001-2003	Hose-Heimlich stomach flushing	172
Gabrey 2010	Lafourche, Terrebonne, Cameron, Vermilion, & St. Charles parishes, LA	Marsh	2002-2004	Hunter harvested alligators	212
This study	Apopka & Woodruff Lakes, FL	Lake	2010	Hose-Heimlich stomach flushing and necropsies	29
This study	Merritt Island, FL	Island	2010	Hose-Heimlich stomach flushing and necropsies	10
This study	Shark River, FL	Estuary	2009-2011	Hose-Heimlich stomach flushing	54
J. Nifong (unpub. data)	Sapelo Island, GA	Island	2007-2010	Hose-Heimlich stomach flushing	99
Stable isotopes					
This study	Apopka & Woodruff Lakes, FL	Lake	2010	NA	29
This study	Merritt Island, FL	Island	2010	NA	10
This study	Shark River, FL	Estuary	2008-2011	NA	79
J. Nifong (unpub. data)	Sapelo Island, GA	Island	2009-2010	NA	56

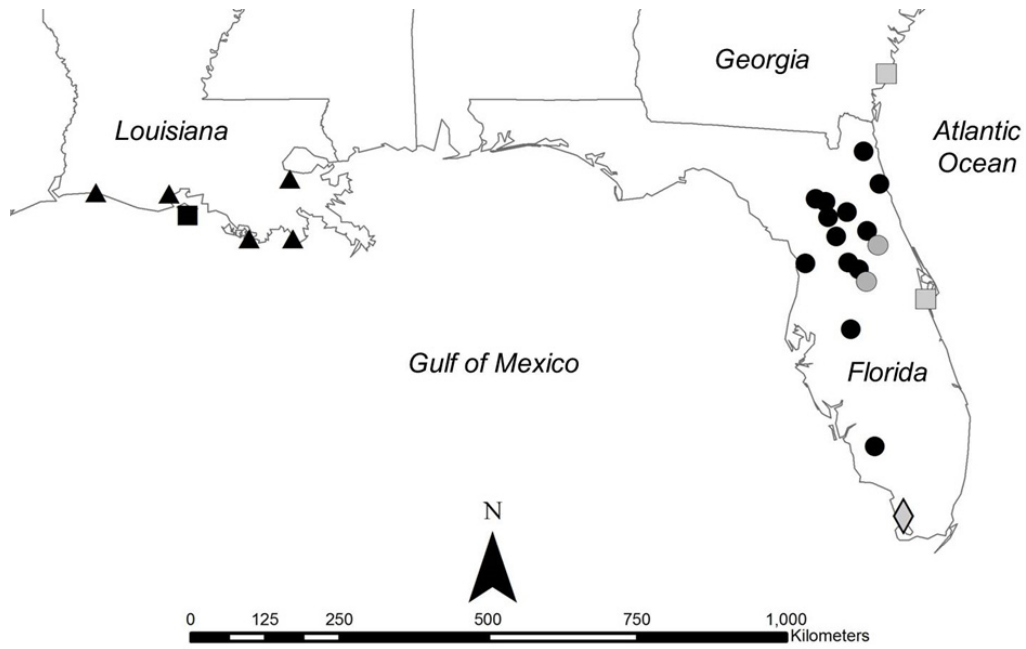


Figure 1: Map of alligator sampling locations used for diet specialization analyses. Circles = lakes, squares = islands, triangles = marshes, and diamonds = estuaries. Black shapes represent locations where only stomach contents were collected and gray shapes represent sites where both stomach contents and stable isotopes were collected.

an index of specialization that varied between 0 and 1, where 0 = pure generalist population (individuals completely overlap with population's resource use) and 1 = pure specialist population (individuals do not overlap with other individuals in the population at all). I chose to only focus on the BIC/TNW index because other individual specialization metrics generally produce similar results (Bolnick et al. 2002; Araujo et al. 2007). The BIC/TNW calculations are biased by the inclusion of individuals that only contain one prey item in their stomach (Bolnick et al. 2002), so I applied the following rules to each dataset to limit any bias in my INS results and produce conservative BIC/TNW values: 1) I removed all individuals with empty stomachs, 2) I removed all individuals with only one prey item in their stomach, and 3) I removed all individuals with only two prey items in their stomach, but only if both items were in the same prey category. I also applied another set of sorting rules to the prey data from each stomach: 1) all prey were grouped by family because many prey items could only be identified to the family level, 2) all gastropods were grouped together, 3) insects were grouped into terrestrial and aquatic categories, and 4) all plant material was grouped together.

Since diet variation can be caused by sexual and ontogenetic differences, as well as inherent temporal and spatial resource variability, I needed to control for these potentially confounding factors before I could quantify the prevalence of INS. I accomplished this by testing each stomach contents dataset to see if they varied as a function of the independent variables capture season, capture year, capture location, size, and sex (Table 2; Araujo et al. 2007). First, I applied all the sorting rules to each dataset and then I did a principal component analysis (PCA) on the proportions of prey use by individuals that were transformed using an arcsine-square root function (Araujo et al.

Table 2: Results from alligator stomach contents PCA-MANOVA analyses and alligator isotope MANOVA analyses. TL = Total Length, SVL = Snout-Vent Length, Int = Intermediate.

Data source	Variable	Stomach contents				$\delta^{13}\text{C}$	
		MANOVA (90% PCA)		MANOVA (70% PCA)		MANOVA	
		Wilks' Λ	P	Wilks' Λ	P	Wilks' Λ	P
Delany & Abercrombie 1986	Capture year	0.606	<0.001	0.705	<0.001		
	Location (lakes)	0.494	<0.001	0.553	<0.001		
	Size (TL)	0.436	<0.001	0.536	<0.001	NA	
	Sex	0.895	0.571	0.907	0.288		
Delany et al. 1988	Location (lakes)	0.568	0.595	0.879	0.928		
	Size (TL)	0.106	0.634	0.268	0.611	NA	
	Sex	0.747	0.921	0.834	0.846		
Delany 1990	Size (TL)	0.334	<0.001	0.455	<0.001	NA	
Elsey et al. 1992	Size (TL)	0.863	0.810	0.908	0.806	NA	
	Sex	0.841	0.350	0.797	0.135		
Delany et al. 1999	Location (lakes)	0.027	<0.001	0.0505	<0.001		
	Size (TL)	0.274	0.013	0.409	0.018	NA	
	Sex	0.767	0.357	0.788	0.096		
Rice et al. 2007	Capture season (spring/summer/fall)	0.068	<0.001	0.305	.109		
	Location (lakes)	0.233	0.022	0.424	0.086	NA	
	Size (TL)	0.018	<0.001	0.319	0.003		
	Sex	0.501	0.109	0.620	0.089		
Gabrey 2010	Capture year	0.067	<0.001	0.174	<0.001		
	Location (fresh/int)	0.455	0.002	0.551	0.002	NA	
	Size (SVL)	0.056	<0.001	0.135	<0.001		
	Sex	0.326	<0.001	0.428	<0.001		
This study (Shark River)	Capture season (wet/dry)	0.001	<0.001	0.587	0.418	0.940	0.205
	Capture year	NA	NA	NA	NA	0.869	0.295
	Location (fresh/int/marine)	NA	NA	NA	NA	0.882	0.041
	Size (TL)	0.000	<0.001	0.502	0.745	0.967	0.783
	Sex	NA	NA	NA	NA	0.933	0.168
This study (Apopka & Woodruff Lakes)	Location (lakes)	0.116	0.168	0.673	NA	NA	NA
	Size (TL)	0.196	0.373	0.430	0.285	0.420	0.059
	Sex	0.079	0.087	0.484	0.390	0.518	0.037
This study (Merritt Island)	Size (TL)	0.086	0.476	0.086	0.476	0.797	0.451
J. Nifong (unpub. data, Sapelo Island)	Capture season (spring/summer)	0.000	<0.001	0.010	<0.001	0.917	0.668
	Location (fresh/int/marine)	0.000	<0.001	0.035	<0.001	0.541	0.002
	Size (TL)	0.000	<0.001	0.002	<0.001	0.337	<0.001
	Sex	0.001	<0.001	0.088	<0.001	0.915	0.301

2007). Then I ran two different MANOVAs, one using the scores of the major axes generated by the PCA that cumulatively accounted for 90% of the total variation as the dependent variables, and one using the scores of the major axes generated by the PCA that cumulatively accounted for 70% of the total variation as the dependent variables (Jolliffe 1986). I used varying combinations (depending on the context of each study) of capture date, capture year, capture location, size, and sex as the independent variables. I ran two different MANOVAs because many of the datasets generated large numbers of PCA axes and Jolliffe (1986) recommends using the 70% threshold in such situations, therefore I ran the MANOVAs using both 70% and 90% thresholds to see if they produced different results. For nine of the 11 datasets there were no differences between the analyses run using the PCA 90% threshold or the PCA 70% threshold in terms of which predictor variables significantly affected the diet variation. For the two studies that did exhibit different results between the two analyses, I used the more conservative PCA-MANOVA results for each study (90% threshold for Rice et al. 2007 and Shark River).

Capture seasons were divided into spring, summer, fall, and winter except for the Shark River study which was divided into wet and dry seasons. Capture locations refer to different lakes in the studies encompassing multiple lakes, while for studies conducted in marshes, on coastal barrier islands, and in estuaries, capture locations refer to fresh, intermediate, and marine habitats. Alligator size was divided into 50 cm increments of total length (TL) for all studies, except for the Gabrey (2010) study in which size was divided into 25 cm increments of snout-vent length because total length measurements were unavailable.

If any of the independent variables were revealed by the MANOVAs to be significant predictors of stomach contents variation in any given dataset, I divided the dataset into smaller subsets to remove the bias of those variables (e.g., splitting the dataset into male and female subsets to control for sexual differences). I then chose the subsets of each dataset with sample sizes of at least 10 individuals for BIC/TNW analysis using the program IndSpec 1.0 (Bolnick et al. 2002). Following Araujo et al. (2007), I used the program's built-in non-parametric Monte Carlo procedure to test the null hypothesis that any observed variation in diet was caused by individuals sampling randomly from a shared resource pool. For each dataset random diets were generated for each individual using multinomial sampling from the observed population diet distribution, and BIC/TNW values were recalculated from the new population resource distribution. The program generated 500 null populations and I rejected the null hypothesis if the observed BIC/TNW value was greater than 97.5% of the null BIC/TNW values. The Monte Carlo null hypothesis approach assumes that each prey item found in an individual's stomach represents an independent feeding event (Araujo et al. 2007) and I realize that this assumption may not hold for alligators in all instances (e.g., if alligators feed on schooling fish or dense aggregations of invertebrates; see Discussion).

I also measured the degree of INS in the different populations by subtracting the observed BIC/TNW values for each population from the mean expected BIC/TNW value for each population as generated by the iterative Monte Carlo procedure which assumed each individual in each population consumed prey randomly. The Monte Carlo null hypothesis approach assumes that each prey item found in an individual's stomach represents an

independent feeding event (Araujo et al. 2007). See the Discussion for a consideration of how this assumption may have impacted my results.

Finally, I assessed the impact of intraspecific competition on INS by examining the relationship between adult alligator densities and the BIC/TNW values I generated for adult alligator populations (TL > 1.5 m) from eight Florida lakes between 1981 and 2010. The Florida Fish and Wildlife Conservation Commission has conducted alligator surveys and generated adult population estimates for these lakes every year since 1988. In instances where the alligator stomach contents were sampled from the lakes prior to 1988 (i.e., between 1981 and 1986) I used the 1988 density values as estimates. I assumed that applying the 1988 densities to the lakes up to seven years in the past would not affect my results because the adult alligator populations of the same lakes did not significantly change during the following seven-year period (1988-1995; ANOVA on ranks: $H = 2.6$, $P = 0.9$).

Stable isotope collection and analyses

For the purposes of INS analyses SIA can be very useful because different tissues within the same consumer may incorporate new isotopes from the diet over different time periods (i.e., “turnover rates”; Dalerum and Angerbjorn 2005). Thus, multiple tissues collected from one individual can provide insight into the relative stability of dietary patterns over multiple timescales. Although SIA cannot be used to exactly identify specific prey taxa that have been consumed (except in very simple cases), values of $\delta^{13}\text{C}$ are indicative of the origin of a consumer’s nutrients and $\delta^{15}\text{N}$ is an indicator of trophic level (Fry 2006).

Tissue-specific turnover rates can vary widely between species (Dalerum and Angerbjorn 2005). An experimental diet-switch study of juvenile alligators (3-8 years old; Rosenblatt and Heithaus 2013) revealed that the approximate complete turnover time of alligator plasma for $\delta^{13}\text{C}$ (252 days) was roughly half that of red blood cells (RBCs; 566 days). Therefore, if $\delta^{13}\text{C}$ values for a given alligator were similar across tissue types it would suggest that the mixture of available carbon pools used across an eight month period is similar to that used across a 19 month period. Differing $\delta^{13}\text{C}$ values would indicate shifts in the relative contributions of different carbon pools across these timescales. For my analyses I used stable isotope data from plasma and red blood cell (RBC) samples from 174 alligators sampled between 2008 and 2011 from five sites where stable isotopes and stomach contents were available (Table 1; see Rosenblatt and Heithaus 2013 for a description of sample collection procedures). All samples were processed either at the Florida International University Stable Isotope Laboratory (FIU) or the University of Florida Geology Stable Isotope Laboratory (UF). The mean standard deviations of an internal standard (glycine) at FIU, measured by 14 within-run samples during each of five runs, were 0.09‰ for $\delta^{15}\text{N}$ and 0.09‰ for $\delta^{13}\text{C}$. The mean standard deviations of an internal standard (l-glutamic acid) at UF, derived from five within-run samples during each of seven runs, were 0.14 ‰ for $\delta^{15}\text{N}$ and 0.06‰ for $\delta^{13}\text{C}$. I did not extract lipids from any of the samples because $\delta^{13}\text{C}$ values of alligator plasma and RBCs do not significantly change with lipid extraction (Rosenblatt and Heithaus 2013).

Before assessing the prevalence of INS in the alligator populations using stable isotopes I needed to remove the possibility of my results being affected by variable discrimination factors between the two tissues (Dalerum and Angerbjorn 2005). To

account for this I subtracted experimentally determined discrimination values for each alligator tissue (Rosenblatt and Heithaus 2013) from the δ values for each tissue. Then, I used MANOVAs to determine if the stable isotope values of the datasets were significantly affected by the independent variables capture season, capture location, size, or sex. I only focused on the $\delta^{13}\text{C}$ values of the two tissues as the dependent variables because they contain information about nutrient origins. After controlling for possible confounding variables and the potential effects of discrimination factors, I employed four different yet complementary techniques for assessing INS. First, I used the program IndSpec 1.0 to generate BIC/TNW specialization index values derived from Roughgarden's (1972) equations, which were originally intended for use with continuous data like δ values. Second, for comparison I applied a two-tissue general linear model (GLM; Matich et al. 2011), in which the mean sum of squares of the model acts as a proxy for BIC and the mean sum of squares of the error acts as a proxy for WIC.

Third, I used linear regression to determine the relationship between the $\delta^{13}\text{C}$ values of plasma and RBCs. If individual alligators are indeed specialists over the long time periods represented by the two tissues, I would expect the $\delta^{13}\text{C}$ values of plasma and RBCs to be highly correlated, with a linear regression best-fit line characterized by a high R^2 value and a slope close to one. On the other hand, if alligators are true generalists I would expect the opposite to be true: linear regression best-fit lines characterized by low R^2 values and slopes farther away from one. Lastly, I used the variance between the $\delta^{13}\text{C}$ values of the two tissues as a proxy for WIC for each individual, then divided each WIC value by the appropriate TNW value from the GLMs, and then subtracted the resulting ratio from 1 to generate a BIC/TNW value for each individual alligator (modified from

Matich et al. 2011). The technique allowed me to assess INS at the individual level and determine which factors, if any, may influence INS. All statistical analyses were performed in SPSS 17.0 (IBM, Armonk, NY, USA) and SigmaPlot 11.0 (Systat, Chicago, IL).

Results

Stomach contents

As a group, the alligators in my study consumed a diverse array of prey. The number of different prey categories consumed per study ranged from 15 to 38 with a mean of 25.1 ± 8.6 SD (Table 3). Prey included crustaceans, mollusks, fishes, amphibians, reptiles, mammals, birds, aquatic and terrestrial insects, and seeds. Alligators with empty stomachs made up 6.2% (N = 87) of all the datasets put together (mean = $7.5\% \pm 7.0$ SD), with another 28.0% (N = 395) of the alligator stomachs only containing 1-2 prey items (mean = $26.9\% \pm 15.0$ SD). Therefore, according to my sorting rules, I removed 34.2% of the alligators from further analyses, leaving 930 individuals.

The PCA-MANOVA analyses revealed that for most of the datasets differences in diet existed separate from INS (Table 2). Capture location was a significant predictor of dietary patterns in 60% (N = 3) of lake studies and both studies done in other habitats (marshes, islands, estuaries). Capture season and year were both significant predictors of dietary patterns in the studies they were included in (N = 3 and N = 2, respectively). Furthermore, alligator size was a significant predictor of dietary patterns in 64% of the studies (N = 7) whereas sex was only a significant predictor in two of the eight (25%) studies in which it was included.

Table 3: Prey families consumed by American alligators across 11 studies. X = presence of prey in diet.

Species	Delany & Abercrombie 1986	Delany et al. 1988	Delany 1990	Elsy et al. 1992	Delany et al. 1999	Rice et al. 2007	Gabrey 2010	This study (Shark River)	This study (Apopka & Woodruff Lakes)	This study (Merritt Island)	Nifong (unpub data)
Amphibians											
Amphiumidae					X	X					
Anura				X		X					X
Sirenidae	X	X			X	X					
Annelids											
Clitellata											X
Arthropods (w/o crustaceans)											
Araneae				X			X				X
Belostomatidae	X				X				X		X
Blattodea			X		X	X					X
Carabidae											X
Chilopoda											X
Cicadidae					X						
Coleoptera	X	X	X	X	X	X	X				X
Corixidae											X
Diptera											X
Dytiscidae	X		X		X						X
Elmidae											X
Formicidae											X
Gryllidae					X						
Hemiptera	X										X
Hydrophilidae			X		X						X
Hymenoptera											X
Lepidoptera	X				X						
<i>Limulidae</i>										X	X
<i>Lygaeidae</i>											X
Miridae											X
Odonata	X	X	X	X	X	X	X				X

Orthoptera	X		X		X	X	X		X		X
Passalidae	X					X					
Scorpiones						X					
Tenebrionidae											X
Birds											
Anatidae	X										
Anhingidae					X	X		X			
Ardeidae	X										X
Icteridae			X								
Phalacrocoracidae						X					
Phasianidae			X								
Podicipedidae	X										
Rallidae	X				X			X			X
Strigidae								X			
Threskiornithidae						X					
Troglodytidae											X
Crustaceans											
Amphipoda											X
Astacidea	X	X	X	X	X	X	X				
Cambaridae								X	X	X	X
Menippidae											X
Ocypodidae											X
Palaemonidae	X		X	X	X	X		X			X
Panopeidae											X
Penaeidae				X							X
Portunidae		X		X		X		X			X
Sesarmidae											X
Fishes											
Amiidae		X			X	X	X				
Ariidae								X		X	
Atherinopsidae				X							
Belonidae						X					
Catostomidae					X						
Centrarchidae	X	X	X		X	X	X		X		

Cichlidae					X	X		X	
Clupeidae	X	X			X	X			
Cyprinidae						X			
Cyprinodontidae						X		X	X
Elassomatidae			X						
Engraulidae							X		
Esocidae	X				X				
Fundulidae			X	X	X				
Ictaluridae			X		X	X			
Lepisosteidae	X	X			X	X	X	X	
Mugilidae									X
Poeciliidae			X		X	X		X	X
Sciaenidae									X
Siluriformes	X	X			X	X	X		
<hr/>									
Mammals									
Canidae	X								
Cricetidae	X		X			X	X	X	X
Dasypodidae									X
Didelphidae				X			X		X
Leporidae			X						X
Muridae									X
Mustelidae			X				X		X
Myocastoridae			X				X		X
Procyonidae						X			X
Sciuridae	X	X							X
Suidae								X	
<hr/>									
Mollusks									
Ampullariidae	X		X		X	X		X	X
Gastropoda		X					X		
Mactridae				X					
Nassariinae									X
Planorbidae						X			X
Ostreidae	X								
Viviparidae						X			

Plant Seeds

Altingiaceae	X	X						
Annonaceae							X	
Chrysobalanaceae							X	
Fabaceae	X							
Fagaceae	X	X	X					
Juglandaceae	X	X	X					
Nymphaeaceae	X							
Pinaceae		X	X					
Platanaceae	X		X					
Rhizophoraceae							X	

Reptiles

Alligatoridae	X	X	X	X	X	X	X	X
Chelydridae		X	X		X	X	X	
Colubridae	X	X	X	X	X			X
Emydidae	X	X	X	X				X
Kinosternidae	X	X	X	X				X
Testudinidae				X				
Trionycchidae		X	X	X				
Viperidae		X		X				

After subdividing each dataset to control for significant predictor variables, the resulting BIC/TNW specialization values for SCA varied widely across all the populations, with a minimum of 0.24 and a maximum of 0.79 (mean = 0.54 ± 0.12 SD; Table 4). The Monte Carlo simulations revealed that despite the wide range of BIC/TNW values, all but one population exhibited greater specialization than predicted by random chance (Table 4). The BIC/TNW values were not affected by sample size or number of different prey categories consumed by each population (linear regression: both $R^2 < 0.02$, both $P > 0.5$), but BIC/TNW values were significantly different between habitat types (t-test: $t_{26} = 2.5$, $P = 0.02$), with populations from lakes exhibiting lower values (mean = 0.51 ± 0.11 SD) than populations from non-lake habitats (mean = 0.64 ± 0.11 SD). Also, the differences between the observed BIC/TNW values of lake populations and the expected BIC/TNW values generated by the Monte Carlo simulations (mean difference = 0.24 ± 0.14 ; Table 4) were significantly less ($t_{26} = -2.2$, $P = 0.03$) than the differences for non-lake populations (mean difference = 0.41 ± 0.21).

Interestingly, mollusks were one of the most frequently consumed prey groups across the populations and there was a significant negative relationship between BIC/TNW values of a population and the frequency of occurrence of mollusks in a population's diet ($R^2 = 0.28$, $P = 0.004$) and the absolute number of mollusks consumed by each population as a percentage of the whole diet ($R^2 = 0.39$, $P < 0.001$; Fig. 2). There was also a concomitant significant positive relationship between BIC/TNW values of a population and the absolute combined number of fishes and crustaceans (both of which were frequently consumed and are more highly mobile taxa) consumed by a population as a percentage of the whole diet ($R^2 = 0.25$, $P = 0.007$; Fig. 2). I did not detect a

Table 4: Results of American alligator stomach contents specialization analyses. BIC/TNW = Between Individual Component/Total Niche Width (observed), BIC/TNW MC = mean value generated by Monte Carlo simulations, TL = Total Length, SVL = Snout-Vent Length.

Data source	Location	Sample date	Sex	Size (TL; cm)	N	BIC/TNW	BIC/TNW MC
Gabrey 2010	Freshwater marsh, LA	Fall 2004	M	75-100 (SVL)	15	0.79**	0.57
Delany & Abercrombie 1986	Orange Lake, FL	Fall 1983	M, F	200-250	22	0.71**	0.20
Rice et al. 2007	Woodruff Lake, FL	Fall 2002	M, F	200-250	12	0.70**	0.10
This study	Merritt Island, FL	Spring 2010	M	250-350	7	0.69**	0.07
Delany & Abercrombie 1986	Lochloosa Lake, FL	Fall 1981	M, F	150-200	10	0.68**	0.20
This study	Shark River, FL	Fall 2009-2010	M	200-250	10	0.67**	0.02
Delany et al. 1988	Griffin & Tsala Apopka Lakes, FL	Summer 1977	M, F	100-350	27	0.58	0.57
Delany & Abercrombie 1986	Orange Lake, FL	Fall 1982	M, F	150-200	22	0.58**	0.38
Elsley et al. 1992	Marsh Island, LA	Summer 1991	M, F	100-200	81	0.57**	0.22
Delany 1990	Orange Lake, FL	Fall 1986	NA	50-100	27	0.56**	0.25
Delany & Abercrombie 1986	Orange Lake, FL	Fall 1981	M, F	250-300	10	0.55**	0.40
Delany et al. 1999	George Lake, FL	Summer 1985	M, F	200-250	10	0.55**	0.44
Delany 1990	Orange Lake, FL	Fall 1986	NA	0-50	27	0.54**	0.24
Delany & Abercrombie 1986	Orange Lake, FL	Fall 1983	M, F	100-150	12	0.52**	0.28
Delany & Abercrombie 1986	Orange Lake, FL	Fall 1982	M, F	200-250	19	0.52**	0.42
Delany & Abercrombie 1986	Orange Lake, FL	Fall 1982	M, F	100-150	13	0.52**	0.38
Delany & Abercrombie 1986	Orange Lake, FL	Fall 1983	M, F	250-300	13	0.51**	0.32
J. Nifong (unpub. data)	Sapelo Island, GA	Spring 2008	M	50-100	10	0.50**	0.29
Delany 1990	Orange Lake, FL	Fall 1986	NA	100-150	13	0.48**	0.18
Delany & Abercrombie 1986	Orange Lake, FL	Fall 1982	M, F	250-300	10	0.48**	0.35
Delany & Abercrombie 1986	Newnan's Lake, FL	Fall 1983	M	300-350	15	0.48**	0.32
This study	Apopka & Woodruff Lakes, FL	Spring 2010	M, F	200-350	20	0.47**	0.35
Delany et al. 1999	George Lake, FL	Summer 1985	M, F	150-200	18	0.46**	0.18
Delany et al. 1999	Rodman Lake, FL	Summer 1985	M	250-300	15	0.45**	0.11
Delany et al. 1999	George Lake, FL	Summer 1985	M, F	100-150	12	0.44**	0.16
Delany & Abercrombie 1986	Newnan's Lake, FL	Fall 1983	M, F	200-250	11	0.43**	0.22
Delany et al. 1999	Rodman Lake, FL	Summer 1985	M, F	200-250	11	0.33**	0.08
Delany et al. 1999	Rodman Lake, FL	Summer 1985	M	300-350	10	0.24**	0.14

** $P < 0.001$ (Monte Carlo bootstraps, 500 simulations).

All others, $P = 0.26$

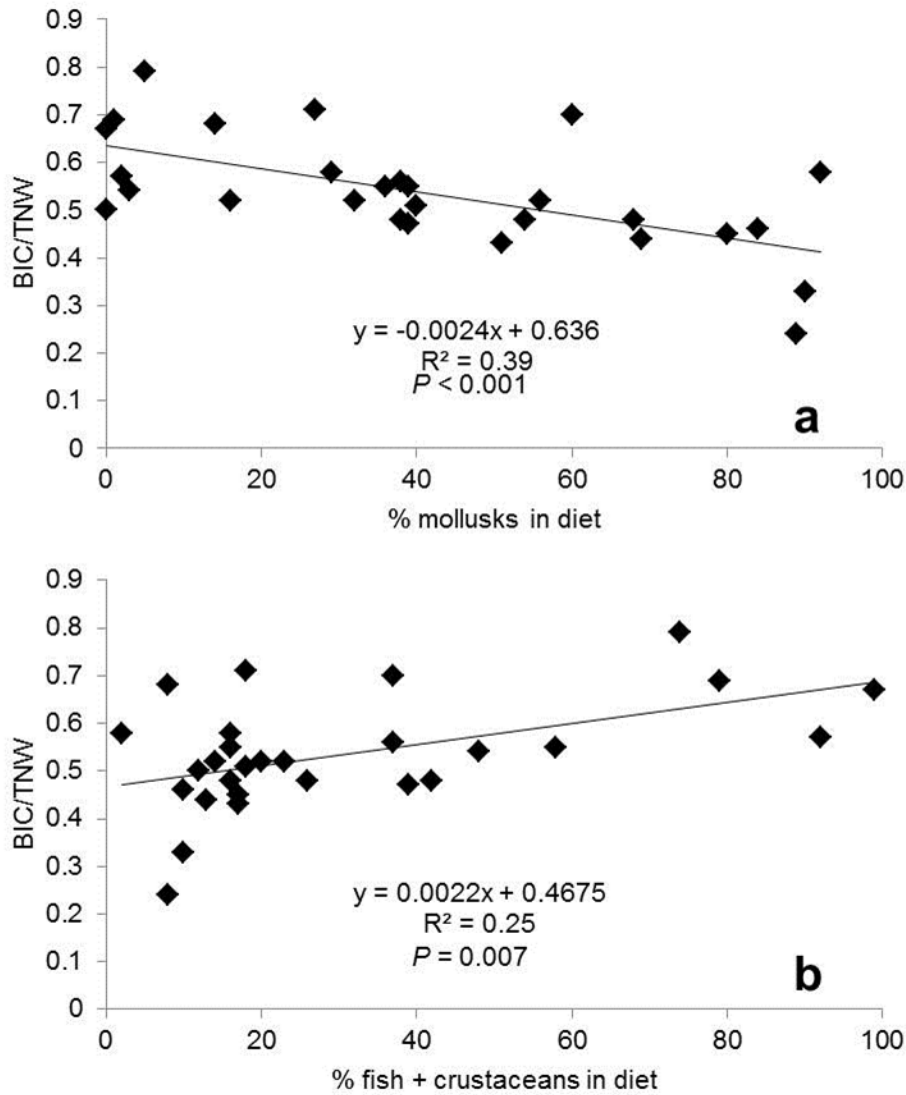


Figure 2: Specialization values (BIC/TNW) of different American alligator populations as predicted by two different types of prey found in alligator stomach contents samples: a) mollusks (total number of mollusks divided by total number of all prey items) and b) fishes and crustaceans combined (total number of fishes + crustaceans divided by total number of all prey items). Lines are linear regression trend lines.

significant relationship between adult alligator population densities in eight of the Florida lakes and BIC/TNW values ($R^2 = 0.08$, $P = 0.3$; Fig. 3).

Stable isotopes

The discrimination-corrected $\delta^{13}\text{C}$ values from both plasma and RBCs varied widely in most of the stable isotope datasets, with $\delta^{13}\text{C}$ ranges of 11.1‰ (plasma) and 7.6‰ (RBCs) for Shark River ($n = 79$); 14.1‰ (plasma) and 14.0‰ (RBCs) for Sapelo Island ($n = 56$); 14.0‰ (plasma) and 13.1‰ (RBCs) for Lake Apopka ($n = 15$); and 8.0‰ (plasma) and 6.0‰ (RBCs) for Merritt Island ($n = 10$). I did not use the Lake Woodruff isotopes in my analyses because the $\delta^{13}\text{C}$ range (2.0‰ and 2.7‰ for plasma and RBCs, respectively) was too small to produce ecologically meaningful results. The large $\delta^{13}\text{C}$ ranges in the other datasets are indicative of the large ranges (7.8‰ to 20‰) in $\delta^{13}\text{C}$ values of resource pools available to the alligator populations in each habitat (Peterson and Howarth 1987; Gu et al. 1997; Rosenblatt and Heithaus 2011; Adams and Paperno 2012).

Capture location (freshwater/intermediate/marine habitats) was a significant predictor of $\delta^{13}\text{C}$ values in the two estuarine studies (Table 2). Also, sex had a significant effect on $\delta^{13}\text{C}$ values in the Lake Apopka study and size had a significant effect on $\delta^{13}\text{C}$ values in the Sapelo Island study (Table 2), with the two smaller alligator size classes displaying much lower $\delta^{13}\text{C}$ values than the two larger size classes. After controlling for these confounding variables, I found that the BIC/TNW specialization values produced by IndSpec 1.0 did not vary as widely as those resulting from the stomach contents datasets and were all very high, ranging from 0.87 to 0.99 (mean = 0.96 ± 0.04 SD; Table

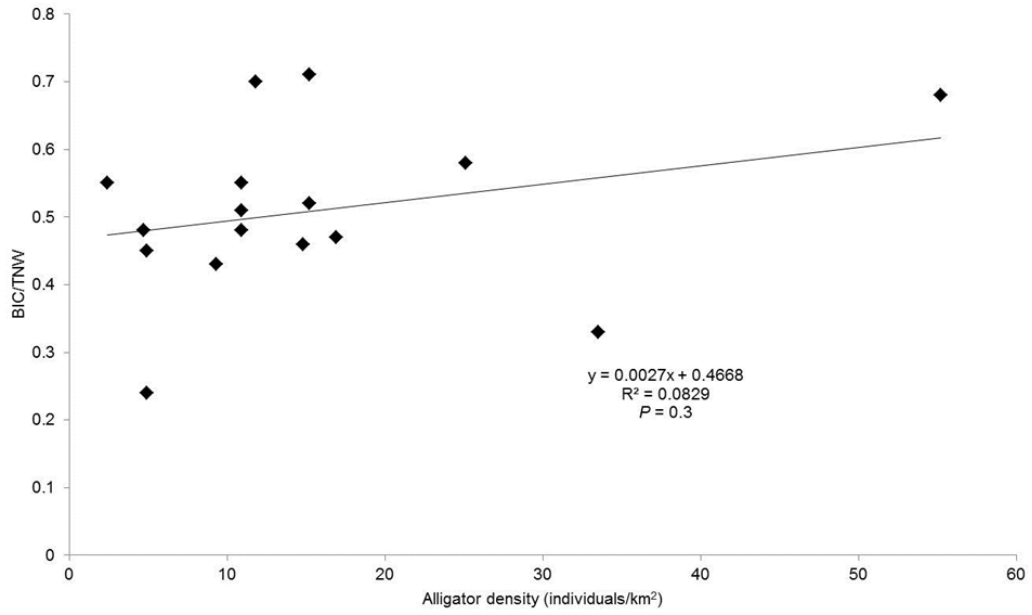


Figure 3: Relationship between adult alligator density across eight Florida lakes (George, Orange, Lochloosa, Rodman, Newnans, Woodruff, Apopka) between 1981 and 2010 and BIC/TNW values derived from stomach contents analyses for those populations.

5). All of the BIC/TNW values were highly significant as indicated by Monte Carlo simulations (Table 5). The GLM procedure (Matich et al. 2011) produced remarkably similar BIC/TNW results, with a range of 0.88 to 0.99 (mean = 0.97 ± 0.04 SD; Table 5). There were no relationships between BIC/TNW values and sample size for either method (linear regression: both $R^2 < 0.004$, both $P > 0.8$).

The results from the linear regression analyses agreed with the high levels of specialization indicated by the BIC/TNW analyses. For each subset of the four isotope datasets plasma and RBC $\delta^{13}\text{C}$ values were highly correlated, with R^2 values ranging from 0.77 to 0.99 (mean = 0.92 ± 0.07 SD, all $P < 0.001$) and with slopes very close to 1, ranging from 0.79 to 1.08 (mean = 0.96 ± 0.09 SD; Fig. 4). Indeed, seven of the eight slope values did not differ significantly from a slope of 1 (all $p > 0.1$). Also, the BIC/TNW values at the individual level were very narrowly distributed. Of the individuals included in GLM and IndSpec isotope analyses (Table 5), 91% ($N = 122$) exhibited individual BIC/TNW values greater than 0.9 (Fig. 5). There was no significant relationship between BIC/TNW values and alligator size ($R^2 = 0.01$, $p = 0.2$) and no difference between male and female values (Mann-Whitney Rank Sum Test; $T = 1443$, $p = 0.2$). There was, however, a difference in individual BIC/TNW values between some of the locations (ANOVA on ranks: $H_5 = 12.5$, $p = 0.03$), with Lake Apopka alligators displaying slightly higher BIC/TNW values (mean = 0.99 ± 0.01 SD) than either Merritt Island individuals (mean = 0.88 ± 0.16 SD) or Sapelo Island individuals captured in the marine zone (mean = 0.94 ± 0.13 SD).

Table 5: Results of American alligator stable isotope specialization analyses. BIC/TNW = Between Individual Component/Total Niche Width, GLM = General Linear Model, IndSpec = individual specialization program (Bolnick et al. 2002), TL = Total Length.

Data source	Location	Habitat type	Sex	Size (TL; cm)	N	GLM	IndSpec
						BIC/TNW	BIC/TNW
J. Nifong (unpub. data)	Sapelo Island, GA	Marine	M,F	100-150	10	0.99	0.99**
J. Nifong (unpub. data)	Sapelo Island, GA	Marine	M	50-100	8	0.99	0.99**
This study	Lake Apopka, FL	Lake	M	250-400	10	0.99	0.99**
J. Nifong (unpub. data)	Sapelo Island, GA	Marine	M, F	200-250	7	0.99	0.98*
This study	Shark River, FL	Estuarine	M, F	150-300	71	0.97	0.97**
This study	Shark River, FL	Marine	M, F	150-300	8	0.97	0.96**
J. Nifong (unpub. data)	Sapelo Island, GA	Estuarine	M, F	100-150	9	0.96	0.95*
This study	Merritt Island, FL	Island	M	250-350	10	0.88	0.87**

** $P < 0.001$ (Monte Carlo bootstraps, 500 simulations).

* $P < 0.01$ (Monte Carlo bootstraps, 500 simulations).

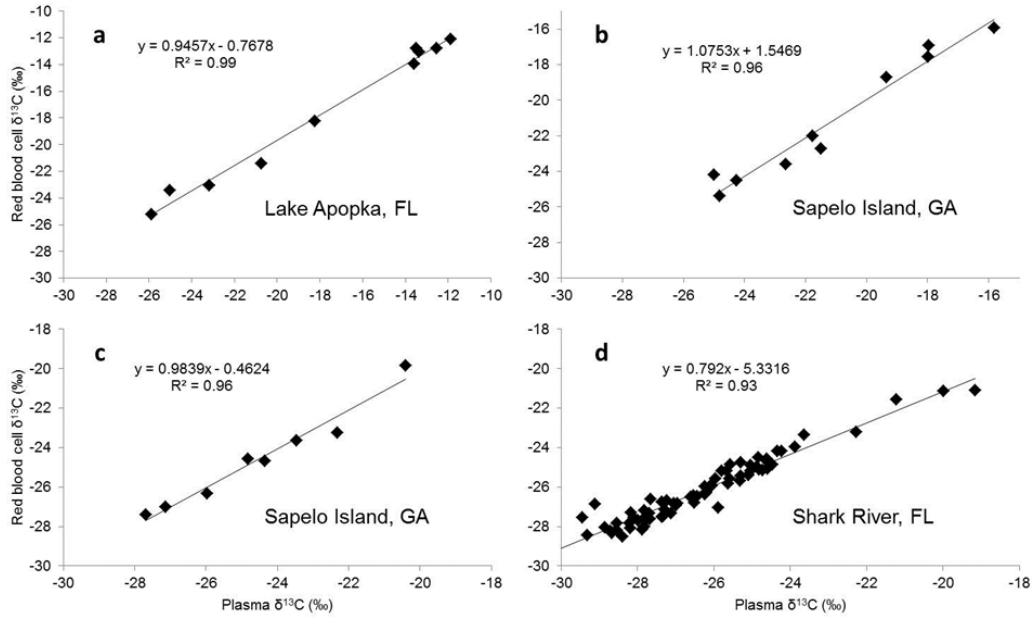


Figure 4: Linear regression plots depicting relationships between alligator plasma $\delta^{13}\text{C}$ values and red blood cell $\delta^{13}\text{C}$ values. a) Lake Apopka, FL (males, lake habitat, 250-400 cm total length(TL)), b) Sapelo Island, GA (males and females, marine habitat, 100-150 cm TL), c) Sapelo Island, GA (males, marine habitat, 50-100 cm TL), d) Shark River, FL (males and females, estuarine habitat, 150-300 cm TL). All $P < 0.001$. Note different scales on axes.

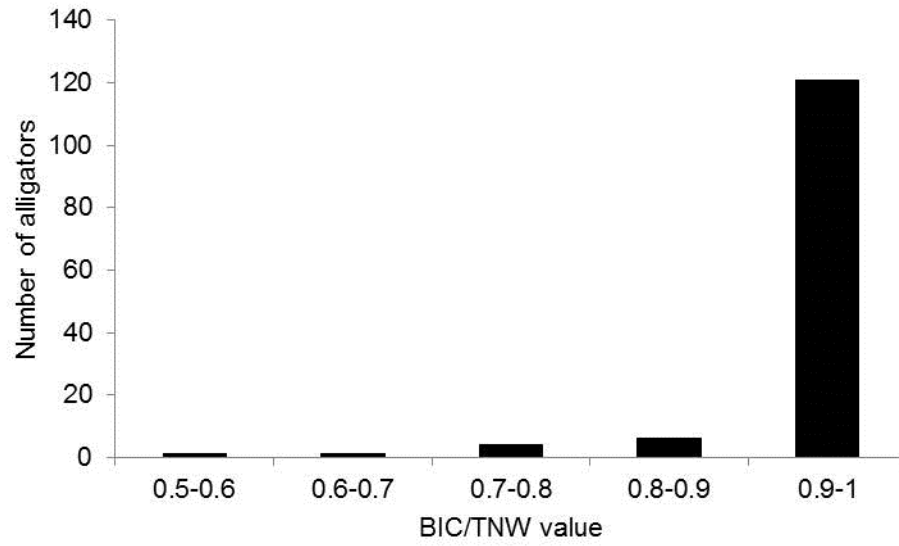


Figure 5: Number of alligators displaying different individual BIC/TNW specialization values on the basis of carbon stable isotopes. Values were calculated using the two-tissue variance method from Matich et al. (2011).

Discussion

My results show that even species widely thought to be dietary generalists and that exhibit broad diets at the population level may actually specialize at the individual level. Stomach contents analysis revealed that alligator populations exhibit highly variable short-term dietary patterns, ranging from generalized populations to more specialized populations. I also found that the strength of short-term INS was context dependent, with alligator populations from lakes exhibiting lower INS than populations from other habitats (marshes, islands, estuaries). Stable isotope analysis revealed long-term stability in the use of different carbon pools by individual alligators despite the wide ranging $\delta^{13}\text{C}$ values of those carbon pools: every population I studied exhibited individuals with very consistent $\delta^{13}\text{C}$ values over moderate to relatively long time spans, indicating that alligators generally maintain the same behavioral patterns through time. Importantly, the INS I documented existed in addition to dietary variation caused by differences between sexes, life stages, seasons, years, and locations.

Consistent with the NVH, my findings suggest that one of the main drivers of INS, at least in the short-term, may be habitat heterogeneity. Lower BIC/TNW values, and smaller differences between observed BIC/TNW values and expected values under random foraging scenarios, in alligator populations inhabiting some lakes may be a consequence of low habitat variation in lakes and their hard boundaries. For example, Lake Apopka in central Florida, which has an alligator population that was sampled several times across my datasets, has been a shallow, somewhat homogenous, turbid, algal-dominated lake supporting a poor fishery since 1947 (Bachmann et al. 1999). In contrast, the non-lake habitats sampled across my datasets (coastal marshes, estuaries,

barrier islands) contain a wide diversity of aquatic habitats (freshwater/estuarine/marine) and are unbounded, thus potentially allowing for greater movement of alligators. In fact, alligator movement studies indicate that alligators inhabiting lakes move shorter distances and occupy smaller activity ranges than alligators in non-lake habitats, and lake alligators almost entirely restrict themselves to littoral areas (Goodwin and Marion 1979; Rosenblatt and Heithaus 2011). Taken together, these results suggest that lake-bound alligators have access to less distinct habitat types than non-lake populations. Consistent with the hypothesis, in my analyses lake alligator populations exhibited lower use of potential prey categories present in their habitat ($48\% \pm 21$ SD) than non-lake populations ($64\% \pm 35$ SD).

My findings further suggest that another driver of short-term INS may be the abundance of particular prey types. The BIC/TNW values were negatively correlated with both the frequency of occurrence of mollusks, a common prey across most of the studies, and the absolute number of mollusks consumed as a percentage of the whole diet. In contrast, BIC/TNW values were positively correlated with the combined absolute number of fishes and crustaceans consumed as a percentage of the whole diet. I hypothesize that the presence of abundant low-mobility prey like mollusks in certain habitats may cause the majority of alligators in those habitats to take frequent advantage of such a resource that is easily found and captured. However, when these prey are not as abundant alligators must pursue more mobile prey which are presumably harder to capture and not as concentrated spatially. These contrasting contexts would make each individual's short-term diet in mollusk-dominated habitats more similar to conspecifics, thereby decreasing INS, but more different from conspecifics in habitats dominated by

more mobile prey, thereby increasing INS. In the latter context dietary variation between individuals could be caused by resource patchiness rather than behavioral specialization *per se*, but available evidence suggests that alligators do not move randomly through their environment and instead frequent the same areas over multiple years (Rosenblatt and Heithaus 2011). Thus, INS in habitats dominated by more mobile prey could be caused by fine-scale associations between individual alligators and specific areas.

Interestingly, BIC/TNW values were not correlated with adult alligator densities across eight Florida lakes, suggesting that intraspecific competition is not a major driver of alligator INS patterns. The finding runs counter to recent research demonstrating that INS increases as intraspecific competition increases (Svanback and Bolnick 2007; Araujo et al. 2011) and may be caused by low feeding rates in crocodylians. Wild juvenile estuarine crocodiles (*Crocodylus porosus*) only need to ingest food equivalent to 4% of their body weight per week to maintain average growth rates (Webb et al. 1991), and presumably adults would need to consume even less since their growth rates are much slower. Furthermore, when ambient temperatures drop below 20°C many crocodylians dramatically decrease their feeding rates or stop feeding altogether (Lang 1979). Low feeding rates may therefore reduce intraspecific competition amongst adult alligators in some cases and prevent such interactions from affecting the strength of INS in a given population. I did not have data on interannual fluctuations of prey availability in the Florida lakes and I recognize that adult alligator density relative to prey may be a more accurate measure of intraspecific competition than alligator density alone. Interspecific competition likely does not differ appreciably between lake and non-lake habitats, and therefore would not drive differences in INS either, because alligators are the last

remaining dominant aquatic apex predators across the entire southeastern US (Mazzotti and Brandt 1994). Also, though coastal habitats may support a larger diversity of large predators (e.g., sharks), alligators generally restrict themselves to shallow near-shore marine habitats, thus limiting their potential competition with large pelagic fishes.

Stomach contents analysis has specific drawbacks when it comes to investigating INS. For example, SCA can be biased by variable digestive rates of different prey items. In alligators specifically, certain prey with hard or indigestible parts (e.g., arthropods with chitinous exoskeletons, turtles, gastropods) may become over-represented in the diet because their hard parts are digested slowly in comparison to soft-bodied prey (Garnett 1985; Janes and Gutzke 2002; Nifong et al. 2012). The difference in digestive rates can cause some prey to appear more frequently and in higher numbers in stomachs which may bias dietary analyses. However, most of the prey groups consumed by alligators in my synthesis have at least one hard or indigestible body part (e.g., mammal hair, bird feathers, crustacean exoskeletons, snail shells) which means variable digestive rates likely did not have a large effect on my results, with the exception of a possible underestimation of amphibians in diets (Table 3).

Stomach contents analysis also can become biased by short-term resource patchiness. A stomach contents sample from an individual is only a snapshot of that individual's diet, meaning that recent prey encounters could artificially inflate INS analyses (Bolnick et al. 2002). For example, one of the alligator stomachs from the Shark River dataset contained 2332 anchovies (Engraulidae), suggesting that it had recently encountered a school of the fish and had eaten many individuals in a very short period of time. Therefore this one individual slightly inflated the population BIC/TNW value even

though it likely did not exclusively consume anchovies every day. However, this example of an extreme feeding event was quite rare: 92% of all the alligators contained less than 25 prey items, therefore I am confident that my stomach contents INS results are reasonable representations of short-term INS trends and are not overly biased by short-term resource patchiness, especially given that alligators return to the same foraging grounds repeatedly (Rosenblatt and Heithaus 2011). Repeated sampling of stomach contents from the same individuals over time could overcome this assumption (Bolnick et al. 2002), but for alligators this would be unfeasible in most cases because their high mobility and cryptic behaviors make recapture logistically difficult.

Stable isotope analysis revealed that all alligator groups studied exhibited highly consistent use of different carbon pools across moderate and longer time frames. The highly consistent $\delta^{13}\text{C}$ values I observed across tissues may have been caused by specialization on specific prey groups but could also be attributed to consistent use of specific habitats and movement patterns through time. I hypothesize that the latter explanation is more likely, i.e., that alligators specialize in certain behavioral patterns, like habitat choices, foraging tactics, or movement tactics, over long time periods. Although this was partially accounted for in my study by separating analyses for individuals captured in different habitats, because of their high mobility alligators captured in the same habitat still could move across the landscape in different ways. The hypothesis is supported by a previous study of alligator movement patterns in the Shark River where there was wide and temporally stable variation in movement patterns between individuals (Rosenblatt and Heithaus 2011): half of the alligators regularly commuted between freshwater/estuarine and marine habitats and the stable isotope values

of their skin indicated that they were consistently feeding in two different food webs, while the other half of the alligators limited their movements and feeding to strictly freshwater/estuarine habitats. Similar patterns appear to occur in sea turtles, although at a different time scale, in that individual turtles will use consistent “corridors” to move between nesting and foraging areas and will return to the same foraging areas repeatedly (Heithaus 2013). My study and others point to the difficulties in using SIA to infer INS behaviors as a stand-alone data source when turnover rates of even “fast” tissues are long, as in most reptiles (Rosenblatt and Heithaus 2013). Therefore I echo previous studies in suggesting that INS studies should combine isotope data with other behavioral data and stomach contents data where possible.

Many current ecosystem management and conservation strategies assume that all apex predators in a population will have similar effects on prey populations. However, if behaviors vary consistently across individuals, as my study and those of other taxa (Bolnick et al. 2003) suggest, then one-size-fits-all conservation and management strategies may have unintended consequences in many systems. For example, the Shark River is part of the Everglades which is an ecosystem currently undergoing large-scale restoration (Doren et al. 2009). Restoration activities are expected to bring more freshwater to the Shark River, thereby decreasing the overall salinity and potentially increasing the habitat quality for alligators which are dependent on freshwater for nesting and reproduction (Mazzotti and Brandt 1994). However, since many of the alligators in this system appear to specialize in exploiting the marine food web at least seasonally (Rosenblatt and Heithaus 2011), increased freshwater flow may negatively impact them by altering the distribution and abundance of their marine prey. Similarly, in northern

Kenya, African wild dog (*Lycaon pictus*) populations outside of protected areas exhibit specialized feeding on smaller prey than populations inside protected areas (Woodroffe et al. 2007). In this context, if wild dog conservation efforts were solely aimed at bolstering large prey populations some wild dog populations would see no benefit. Different restoration and conservation scenarios, therefore, must be weighed against potential benefits to subsets of apex predator populations.

Ultimately, my research shows that INS in large apex predators can vary substantially among populations but the degree of inter-individual variation can be affected by habitat type and patterns of available prey. Also, though competition may affect INS in small bodied species in controlled and natural environments my research suggests that competition may not affect INS in large ectothermic apex predators under certain natural conditions. It remains to be seen how apex predator species that exhibit INS will respond to specific ecosystem conservation and management scenarios, but it is clear that INS needs to be explicitly considered in such plans.

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CHAPTER VI

GENERAL CONCLUSIONS

Top predators can have strong effects on ecosystem structure and function, yet for many top predator species we still know relatively little about their complex roles in ecosystems and their potential impacts on the dynamics of prey populations and communities. The knowledge gap is a serious problem currently because many top predator populations around the globe are in rapid decline (Estes et al. 2011) or subjected to fast-paced environmental change. In most cases we do not yet fully understand the potential consequences of the extirpation of top predators or changes in their behaviors for ecosystem structure and function. To help fill this knowledge gap I examined the movement and feeding behaviors and potential roles of American alligators (*Alligator mississippiensis*), the dominant apex predator in the Shark River Estuary (SRE) of the coastal Everglades. The results of my research also helped to elucidate the prevalence and potential drivers of individual specialization in the SRE and other alligator populations. Together, my studies provide insights into the possible consequences for the structure and function of the coastal Everglades if alligator behaviors change as a result of ecosystem restoration activities and climate change.

My experimental study of alligator stable isotope dynamics (Chapter 2) generated the first species-specific stable isotope parameters (turnover rates and discrimination values) for any crocodylian which will make interpretations of future wild crocodylian stable isotope data more accurate and meaningful. The results of the study showed that alligator isotope dynamics are unique relative to other top predators in that alligator isotopes turnover very slowly and exhibit low discrimination values. These differences likely stem from alligator ectothermy. The results of my experiment were valuable for my studies of wild alligator feeding patterns.

My field studies demonstrated that alligators likely are important vectors of connectivity between disparate ecosystems, but the patterns of connectivity are driven by a combination of biotic and abiotic factors as well as intrinsic factors (i.e., individual specialization; Fig. 1). In Chapter 3 I showed that not all the individuals in the SRE population exhibited the same movement and feeding patterns. Some of the individuals regularly moved into the high salinity downstream zone of the SRE while other individuals never entered the area, and this behavioral variation was primarily regulated by the dynamic seasonal salinity patterns of the estuary. Also, using stable isotope analysis I determined that alligators that did use the downstream zone were doing so to access food resources in this more highly productive area (Childers et al. 2006). Since these results were unrelated to variation in sex, size, or age they suggested that the alligator population in the SRE consists of individuals with specialized behaviors and that those individuals that regularly moved between different zones of the SRE may act as biological vectors of connectivity between those habitats, either by transporting nutrients between habitats or affecting multiple unrelated prey groups simultaneously in the different zones. However, because the stable isotope data were based on a single tissue it was unclear to what degree specialization was present.

I then explored alligator movement and habitat use patterns and the intrapopulation variation in these behaviors using more detailed and temporally expansive movement analyses (Chapter 4). I examined alligator activity ranges, movement rates, and habitat use and found that the alligators displayed correlated suites of behavior that were again unrelated to sex, size, or age. Some individuals had large wet season activity ranges, moved far and fast throughout the SRE regardless of season,

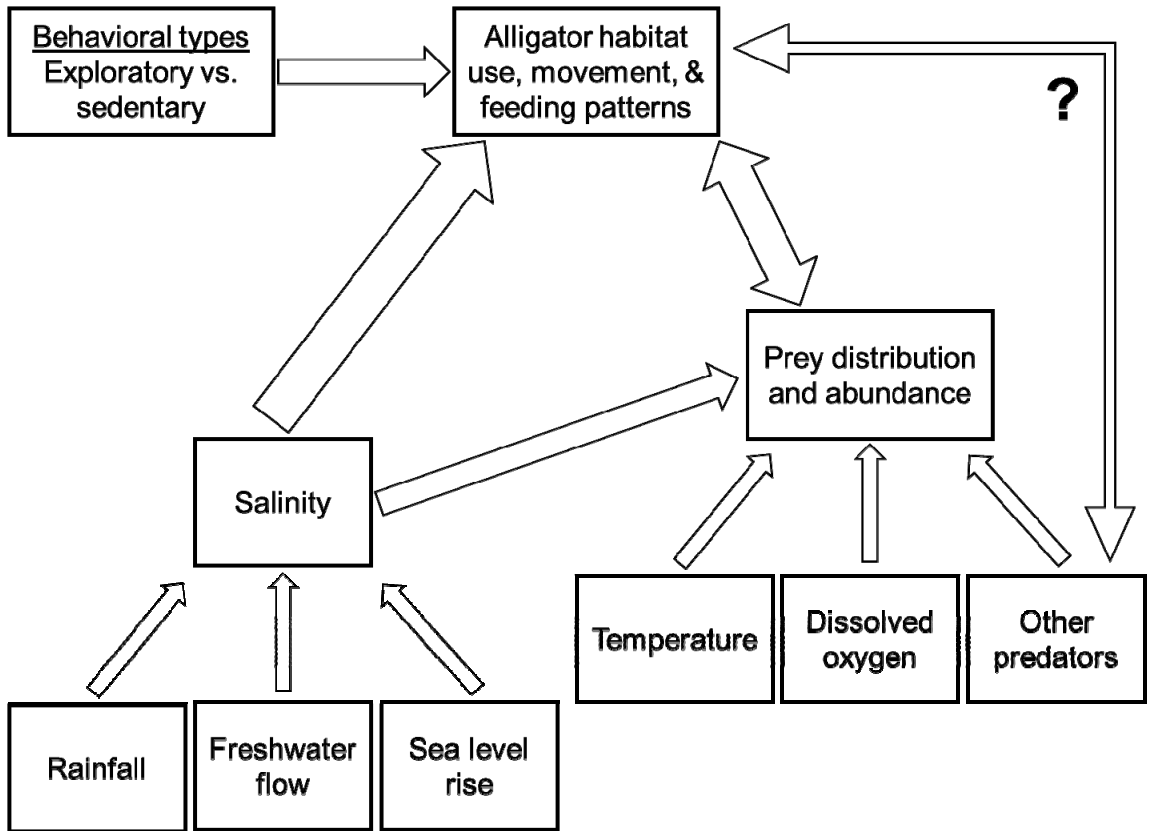


Figure 1: Conceptual model of the factors affecting the movement and feeding behaviors of adult American alligators inhabiting the Shark River Estuary. ? = potential, but empirically untested, connection.

likely experienced relatively high osmoregulatory stress, and likely expended relatively high amounts of energy. Other individuals exhibited exactly the opposite movement and habitat use patterns: they occupied small wet season activity ranges, moved slowly and infrequently in localized areas, likely experienced lower osmoregulatory stress, and likely conserved relatively more energy. In addition, day and night movement rates were strongly positively correlated, further suggesting that alligators in the SRE are consistent movement specialists. The causes of these divergent behavioral patterns were not immediately clear, but may be related to morphological or physiological adaptive plasticity, differences in learning or early life experiences, or variable genetic and epigenetic expression (Dall et al. 2012).

Finally, I examined the factors affecting individual specialization in feeding behaviors of alligators across much of their range using a combination of stomach contents and stable isotope data (Chapter 5). I found through stomach contents analysis that over short time periods populations varied greatly in the magnitude of individual specialization in feeding, but there were relatively consistent differences across habitat types. Alligator populations inhabiting lakes generally exhibited less individual specialization than non-lake coastal populations, and these differences appeared to be driven by variation in habitat heterogeneity (i.e. lake habitats are generally more homogenous than coastal habitats), differences in movement rates (i.e. lake alligators have smaller ranges than coastal alligators and therefore likely encounter fewer types of prey), and relative prey availability (i.e. lakes contained more abundant sessile prey like mollusks that alligators could easily capture and consume whereas non-lake habitats contained more abundant mobile prey like fishes and crustaceans). Stable isotope

analyses revealed that over longer time spans, regardless of habitat type or context, individual alligators within populations exhibited very stable use of particular food sources available to them, but there could be a wide range of feeding behaviors. This is not to say that all the individuals in the different populations were strict dietary specialists, but rather that they consumed nutrients from potentially different food webs in the same proportions from scales of months to a year or more.

My research has important implications for Everglades ecosystem management and our understanding of how coastal alligator populations in general may respond to climate change. The Everglades is currently undergoing one of the largest ecosystem restoration projects in the world, and over the next several decades coastal areas, including the SRE, are likely going to be heavily impacted by increased freshwater flow and resulting alteration of salinity regimes (Davis et al. 2005). At the same time, sea levels are predicted to rise between 1 and 2 m by the year 2100 (Allison et al. 2009), undoubtedly altering the low-lying coastal areas of the Everglades in the process (Saha et al. 2011). The outcome of the interaction between increased freshwater flow and sea level rise remain to be seen, but my research suggests that any changes that occur in the hydrological and salinity patterns of the coastal Everglades may not uniformly impact all alligators. In the event of increased freshwater flow, individuals that currently move into marine habitats to access food may be adversely affected because their marine prey may be forced out of the system, whereas alligators that reside solely in lower salinity habitats may see benefits from restoration because of increased ranges of freshwater and estuarine prey. If individuals that currently consume marine prey no longer have access to them, then their potential to link different ecosystems in the SRE may be compromised.

Conversely, as a result of future freshwater influx alligators that currently use marine habitats may be able to remain downstream for longer periods of time, providing them with extended access to marine resources and enhancing alligator-mediated connectivity between the different habitats. Increased freshwater will also likely expand viable alligator reproductive habitat since alligator nests are denser in low salinity habitats (Joanen and McNease 1989), possibly increasing the size of the alligator population in coastal areas.

In the event of significant sea level rise, coastal areas of the Everglades will become much more saline for longer amounts of time each year, potentially increasing the ranges of marine prey. Such an influx of prey deeper into the coastal Everglades would likely benefit those alligators that can better tolerate temporarily inhabiting more saline water, but would decrease feeding opportunities for alligators that prefer freshwater habitats. Higher salinity levels in coastal areas would also reduce available alligator nesting habitat, potentially decreasing the size of the alligator population in coastal areas. Unfortunately sea level rise will not solely affect the coastal Everglades, but will affect coastal habitats across the alligator's entire range, potentially having similar negative effects on alligator nesting and feeding opportunities of some individuals elsewhere.

Ultimately, the results of my research show that assuming that top predator populations consist of individuals that all behave in similar ways in terms of their feeding and movements and potential roles in ecosystems is likely incorrect. Top predator populations can consist of individuals that exhibit widely divergent behavioral patterns and may serve different ecological roles, with some individuals potentially acting as links

between habitats while other individuals may display more localized behaviors and have more concentrated effects on lower trophic levels. Further research is needed to elucidate the implications of individual specialization within top predator populations on ecosystem and community dynamics, but given the results from my research and those of other studies (e.g., Woo et al. 2008; Matich et al. 2011), ecosystem management, restoration, and conservation personnel should explicitly incorporate knowledge of top predator behavioral variation into their management strategies.

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