THE ROLE OF SEASONAL WETLANDS IN THE ECOLOGY OF THE

AMERICAN ALLIGATOR

A Thesis

by

AMANDA LEE SUBALUSKY

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ABSTRACT

The Role of Seasonal Wetlands in the Ecology of the American Alligator.

(August 2007)

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Dr. Lora L. Smith

The American alligator (*Alligator mississippiensis*) has been frequently studied in large reservoirs and coastal marshes. Large ontogenetic shifts in their diet and morphology have been linked with changes in habitat use, with adult males using deep, open water and juveniles and nesting females relying on vegetated marsh. In certain regions of the inland portion of the alligator's range, these different aquatic habitats are represented by seasonal wetlands and riverine systems that are separated by a terrestrial matrix. Ontogenetic habitat shifts, therefore, would require overland movements between systems, which has important implications for conservation of the species.

I tested several commonly used methods of surveying alligator populations to determine the most effective method of studying alligators in seasonal wetlands. I then used systematic trapping, nest surveys and radio telemetry to determine habitat use and overland movement rates by different sex and size classes. I found that seasonal wetlands provided nesting and nursery sites for these inland alligator populations, but that both juveniles undergoing an ontogenetic shift and nesting females move between

the wetlands and riverine systems. Overland movements by alligators between the wetland and riverine habitats establish a level of functional connectivity between these aquatic ecosystems. I constructed a habitat suitability index of both the wetlands and the surrounding landscape to determine which patch and landscape characteristics were important to wetland use by alligators. I found that both descriptive wetland characteristics and the spatial relationships between wetlands were important predictors of alligator use. Overland movement was related to upland landuse as well as distance between aquatic habitats. Conserving a variety of wetland sizes and types within an intact upland matrix is critical to maintaining connectivity across the landscape. Furthermore, understanding how species may act as mobile links between ecosystems, particularly those with ontogenetic niche shifts, illustrates the importance of approaching conservation from a landscape perspective.

DEDICATION

This thesis is dedicated to the alligators of Ichauway, whose lives spent within the dark, tannic waters of cypress wetlands have driven my intrigue and curiosity for a number of years now, and who have tolerated my scientific pursuits with a great deal of patience.

ACKNOWLEDGEMENTS

I began studying alligators on Ichauway in 2002, and there are a phenomenal number of people who have contributed to this work over the years. Jonathan Stober and Bobby Bass laid the foundation for everything I did with years of survey data and observations they graciously shared. The beginning of my project is due largely in part to the scientific curiosity and enthusiasm of Anna Liner, and many of the possibilities I can now explore with it are due to her foresight at the time. The development of the project over the years is also largely thanks to the untiring assistance in both field and academic components of Shannon Hoss. Myriad other scientists, research technicians, graduate students and friends contributed to this project through their volunteer efforts. Robert Horan, in particular, contributed greatly to the final season. Several folks helped me learn how to safely and properly handle large alligators, including folks from the Florida-Caribbean Science Center, Amanda Rice, Travis Glenn, Liberty Moore, and Cris Hagan. However, Benny West has truly been my mentor in alligator work, from handling large adults, to building trip-snare traps, to understanding the general ecology of these inland populations. Benny provided countless hours of service, pieces of parachute cord, and words of advice, in addition to being a reliable friend.

The ability to safely and securely carry out this research was also due to the many efforts of the members of the administration and security of the Joseph W. Jones Ecological Research Center, including Lindsay Boring, Bill Walton and Lee Tribble, who trusted my abilities and judgment, and David Green, Jack Mulliford and Larry

patience. Dave Laurencio, Mike Hill, Toby Hibbitts and KJ Lodrigue greatly broadened my knowledge of the reptiles and amphibians of the southwest and of herpetology in general. Michael Parkes and Brandon Bowers came all the way out to Georgia to see the system in which I worked and to volunteer their time. Bret Collier was generous with his time and his statistical knowledge. It has been an honor to have both Kirk Winemiller, whose scientific work will continue to inspire me throughout my career, and X. Ben Wu, whose approaches to landscape ecology have continually challenged me to think more deeply, serve as committee members, and I am grateful to these incredibly busy fellows for their time and encouragement. In addition, Chris Romanek and Travis Glenn, of the Savannah River Ecology Lab, opened my eyes to the mysteries of nature you could unlock from inside of a lab and taught me new ways to think about the questions I was asking.

With all the folks to whom I owe my thanks for the last several years, there are several without whom none of this most amazing experience would have ever happened. First, I have deep gratitude to my parents, who have always encouraged me to follow my passions, and have enabled me to do so in every way possible. Not only did they patiently accept my desire to study alligators, they scheduled several visits to Ichauway to help me carry and place traps, wrangle alligators and prepare trap parts. They have enabled and inspired every part of me that is worthwhile.

I cannot speak highly enough of the two scientists with whom I have been privileged to work for a number of years now. Lora Smith first encouraged me to follow my curiosity about alligators five years ago, and she has been an unflagging supporter

and friend every step along the way since that time. Regardless of how many challenges and stumbling blocks I encountered, her enthusiasm for the project, her love of science and field biology, and her willingness to get her hands dirty as she helped me with all the hardest elements of this project inspired and encouraged me, and made it a whole lot of fun! Lee Fitzgerald has been a kindred spirit to me, both in matters of life and science in general as well as in the specifics of this project. He placed very fruitful seeds at crucial steps along the way that developed into my understanding of the ecological theories evident at work within this system. His ability to both guide and foster my scientific understanding while allowing me to follow my own path has been truly invaluable in my development as a scientist.

And finally, the study's very existence is due to the alligators that live in this system. Our work as ecologists often carries a price for the system and the organisms we study. I hope that the product of my efforts does some justice to the unique system in which this study took place, and that its contribution to our understanding and ability to conserve it outweighs any harm done along the way.

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CHAPTER I

INTRODUCTION

Isolated seasonal wetlands constitute a unique and important habitat in the southeastern United States coastal plain (Sharitz and Gibbons 1982; Kirkman et al. 1999; Sharitz 2003). Fluctuating hydrologic conditions support a high diversity of plant and animal species, including a number of rare and endemic species. Because these wetlands dry up nearly every year, they have a paucity of predatory fishes, which makes them a low-predator environment for aquatic invertebrates and larval amphibians. Many frogs, toads and salamanders use these wetlands as breeding sites, returning to the surrounding upland matrix as adults (Gibbons 2003; Semlitsch and Bodie 2003). Freshwater turtles and semi-aquatic snakes also rely on these wetlands for foraging and habitat, regularly making use of the surrounding terrestrial matrix for nesting, aestivation, foraging or movement to other wetlands (Burke and Gibbons 1995; Buhlmann 1998; Roe et al. 2004). Seasonal wetlands are also important to a suite of birds and some mammals (Naugle et al. 2001).

Many amphibian species that inhabit seasonal wetlands occur as metapopulations, with each wetland having a sub-population involved in the extinction and colonization dynamics for a regional population (Semlitsch and Bodie 1998; Babbitt 2005; Herrmann et al. 2005). Other species that are larger or more mobile, such as water snakes or turtles, use multiple wetlands throughout their lifetime, moving between them

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This thesis follows the style of Conservation Biology.

in response to resource fluctuation, seasonal changes or breeding periods (Joyal et al. 2001; Roe et al. 2004; Glaudas et al. 2007). For species with either of these population structures, their conservation has been linked to protection of a variety of wetland types and sizes within a matrix of intact upland habitats (Semlitsch and Bodie 1998; Joyal et al. 2001; Liner 2006).

Due to their small size and temporal variability, seasonal wetlands receive little legal protection (Whigham 1999; Gibbons 2003; Sharitz 2003). The minimal protection they received under the Clean Water Act was recently compromised by the 2001 Supreme Court decision, *Solid Waste Agency of Northern Cook County v. U.S. Army Corps of Engineers, 531 U.S. 159* (SWANCC). SWANCC limited U.S. jurisdiction to navigable waterways, their tributaries and adjacent wetlands (Gibbons 2003; Sharitz 2003; Zedler 2003). As most seasonal wetlands in the southeastern coastal plain fill primarily from precipitation and are not hydrologically connected to navigable waterways, this decision affords little to no federal protection for this important component of the ecosystem. Isolated wetlands also are not legally protected at the state level in most of the coastal plain. However, as many researchers have shown, these wetlands show high levels of functional connectivity, both to other aquatic habitats as well as to surrounding terrestrial habitat, through movement patterns of species that inhabit them (Burke and Gibbons 1995; Gibbons 2003; Semlitsch and Bodie 1998; Zedler 2003).

Organisms that actively move across the landscape between distinct ecosystems act as mobile links (Lundberg and Moberg 2003). They may transfer energy or nutrients

(resource linkers), move genetic material (genetic linkers) or affect the trophic structure or physiochemical environments (process linkers) of the ecosystems they inhabit. Mobile link species affect ecosystem structure, function and resilience, and when these species also act as "keystone species," they exert a disproportionate influence on the ecosystems they occupy (Lundberg and Moberg 2003; Helfield and Naiman 2006).

Animals may use multiple ecosystems throughout their lives to accommodate shifting habitat needs as they grow. Species with complex life histories that undergo ontogenetic shifts often experience shifting ratios in growth rate and mortality risk, often selecting for use of different habitats as juveniles versus as adults (Wilbur 1988). Movement between juvenile and adult habitat can result in the transfer of production and resources between systems (Deegan 1993; Beck et al. 2001; Gillanders et al. 2003). These species depend on and affect multiple habitats within the ecosystem, and their conservation depends on the protection of multiple habitats as well as the interconnecting matrix.

American alligators (*Alligator mississippiensis*) are a model for studying how a species can function as a mobile link between ecosystems through ontogenetic niche shifts. Large ontogenetic shifts have been documented in their morphology (Dodson 1975; Erickson et al. 2003), diet (Delaney and Abercrombie1986; Delaney 1990; Platt et al. 1990) and habitat use (Joanen and McNease 1970, 1972; McNease and Joanen 1974). Juvenile alligators eat invertebrate prey and may travel longer distances over land; however, they are highly susceptible to predation and cannibalism by larger alligators (Rootes and Chabreck 1993). Adult alligators, which have no natural predators other

than humans, can consume much larger prey items than juveniles; however, their movements tend to be more restricted to aquatic systems. The resulting ontogenetic niche shift results in different habitat use by different size classes of alligators.

Alligators have been studied frequently; however, most research has been conducted in large reservoirs and contiguous coastal marshes (Ryberg et al. 2002). In those habitats, adult males stay in deep, open water, while females move from open water where they breed to dense, vegetated marshes where they nest (Joanen and McNease 1970, 1972). Juveniles spend the first few years of life near the natal den and disperse subsequently (McNease and Joanen 1974; Dietz 1979). In inland portions of the alligator's range, however, available aquatic habitats vary in their occurrence and spatial arrangement. For instance, in some parts of the southeastern coastal plain, the deep water used by adult males primarily consists of creeks and rivers, whereas the vegetated marshes used by nesting females and juveniles are primarily composed of seasonal wetlands distributed in an upland matrix. Alligator movement patterns have not been studied in these habitats, where ontogenetic shifts in habitat use require use of disjunct aquatic ecosystems and overland travel between them (Ryberg et al. 2002).

In this study, which took place at the Joseph W. Jones Ecological Research Center on Ichauway in Baker County, Georgia, I investigated habitat use of alligators in the inland portion of their range. I studied the use of seasonal wetlands by alligators and their movements between ecosystems. My primary objectives were threefold:

1)   Compare eyeshine surveys with systematic trapping to establish the

most effective method for studying alligators in seasonal wetlands.

2)   Use equal trapping effort, nesting surveys and radio telemetry in the seasonal wetlands and in the riverine system to determine variations in habitat use and overland movement by sex and size class.

3)   Construct a habitat suitability index for the wetlands on site and the overall landscape to determine the wetland variables that are important to alligator use and those landscape components that are important to movement between the aquatic ecosystems.

Evidence that densities of juveniles are higher in seasonal wetlands and that regular dispersal occurs from the wetlands to the riverine system as alligators undergo an ontogenetic niche shift would support the hypothesis that seasonal wetlands serve as nursery habitats for alligators in this portion of their range (Beck et al. 2001). Establishing regular movements between the wetland and riverine systems by nesting females and juveniles also would establish alligators as resource and process linkers between these aquatic ecosystems. Furthermore, alligators are known as both ecosystem engineers and keystone species (McIlhenny 1935; Craighead 1968; Mazzotti and Brandt 1994) because they manipulate their environment through the construction of burrows, wallows and nest mounds. Their presence in both the wetland and the riverine systems likely has important implications for the structure and function of both. For example, during periods of drought, alligator burrows in seasonal wetlands provide the only available aquatic refuge for a number of species, including turtles, snakes and amphibians (A.L.S., pers. obs.).

   Understanding the role that seasonal wetlands play in the ecology of the

American alligator is critical to understanding and conserving inland populations of

alligators. Because management guidelines for alligators are typically based on studies

of higher density populations in coastal marshes (Ryberg et al. 2002), this research is an

important contribution to the literature on alligators. It also has important implications

for the conservation of seasonal wetlands within an intact upland matrix. Demonstration

that terrestrial corridors are being used by the American alligator, a commercially

valuable species, to connect isolated wetlands to navigable waterways could potentially

be used to redefine jurisdictional wetlands (Gibbons 2003). Finally, understanding the

contribution of alligators as a mobile link species to the structure and function of

multiple aquatic ecosystems illustrates the necessity of landscape scale approaches to

conservation that extend beyond ecosystem boundaries.

CHAPTER II

USE OF DOUBLE-OBSERVER SURVEYS AND SYSTEMATIC TRAPPING TO

DETECT ALLIGATORS IN ISOLATED, SEASONAL WETLANDS IN

SOUTHWEST GEORGIA

SYNOPSIS

Whereas the American alligator has been well-studied in coastal marshes and

large reservoirs, few studies have taken place in inland systems. Understanding alligator

populations in these systems is important because, although they are subject to the same

management strategies and regulations as their more well-studied counterparts, they may

have markedly different population dynamics and densities. Additionally, understanding

patterns of alligator presence in these small, inland wetlands is important for

understanding how alligators may affect those critical habitats by acting as ecosystem

engineers. However, survey methods designed for large, open water systems may not

work in small, inland wetlands, and their efficacy in the latter habitat has yet to be

documented. I used a double observer method to determine the detection probability of

eyeshine surveys in isolated, seasonal wetlands in southwest Georgia, and to model the

effect of wetland type on that parameter. I found that detection probability for eyeshine

surveys under the most well-supported model was 57%. I then compared eyeshine

surveys with systematic trapping to ascertain which method was most effective and

which components of the population were more likely to be detected by each method. I

determined that both methods were effective in detecting a range of size classes;

however, there were contradictory trends in which method worked best in each wetland

type. In small wetland systems with low population densities, use of multiple methods will likely provide the most thorough data on the presence of alligators and the demography of the population.

INTRODUCTION

The American alligator (*Alligator mississippiensis*) is among the most well-studied vertebrates in North America. However, these studies have been conducted almost exclusively in coastal marshes (McNease and Joanen 1974; Mazzotti and Brandt 1994; Wilkinson and Rhodes 1997) and large reservoirs (Ruckel and Steele 1984; Brandt 1991). Although these habitats contain relatively dense populations of alligators, they constitute a small fraction of the alligator's total native range, which extends from central Texas to coastal North Carolina, and as far inland as central Arkansas (Figure 2.1, Conant and Collins 1998). There is evidence that inland populations of alligators differ from coastal populations in their ecology and population dynamics (Hayesodum et al. 1993; Ryberg et al. 2002; Lutterschmidt and Wasko 2006), but these populations are not well studied.

Understanding alligator populations in inland wetlands is critical for two main reasons. First, state-wide management plans for alligators are based on monitoring and research conducted in areas where alligator densities are highest (i.e. coastal marshes and large reservoirs). If alligator populations in inland wetlands have distinctly different abundance levels and population dynamics, then applying such broad-scale management strategies may lead to an over-harvesting of these populations (Ryberg et al. 2002). Second, the seasonal wetlands of the coastal plain constitute unique communities that
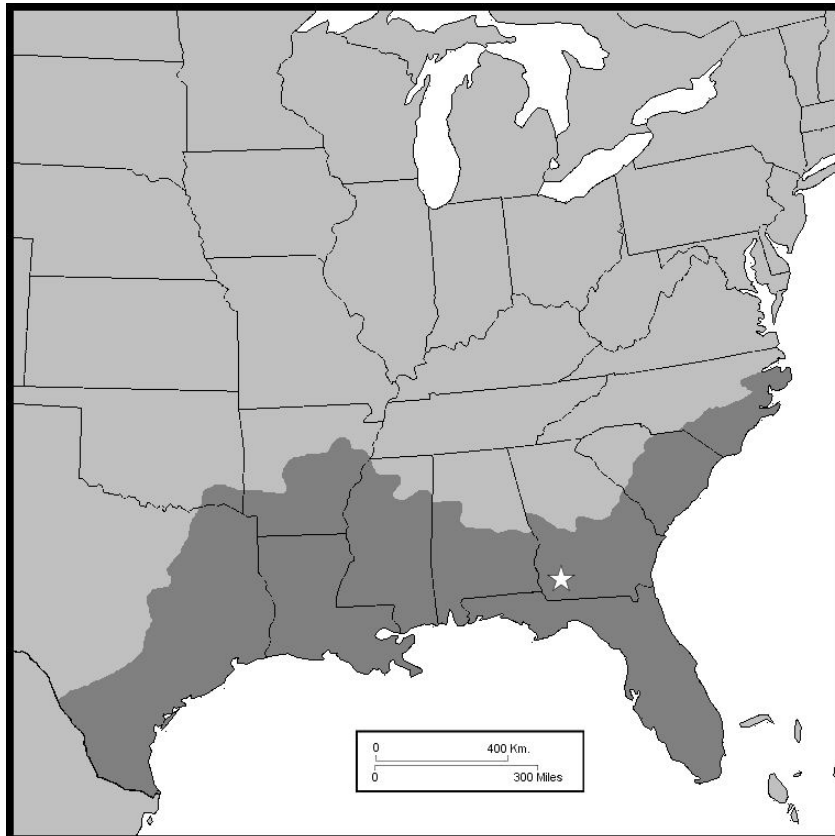
Figure 2.1: The known historical range of *Alligator mississippiensis*, with the location of

the study site at the Joseph W. Jones Ecological Research Center in Baker County,

Georgia marked with a star.

provide critical habitat for a variety of threatened and endangered plants and animals (Gibbons 2003; Semlitsch and Bodie 2003; Sharitz 2003). Because these wetlands dry nearly every year, they provide a low-predator environment for aquatic invertebrates and larval amphibians and are often important breeding sites for frogs, toads, and salamanders. They are also used by a number of reptiles, as well as a suite of birds and some mammals, for foraging and habitat (Burke and Gibbons 1995; Naugle et al. 2001; Roe et al. 2004). As alligators are large, aquatic predators that are known to heavily manipulate their environment through the construction of nest mounds and burrows (McIlhenny 1935; Jones et al. 1994; Palmer and Mazzotti 2004), it is likely their presence may play an important role in the dynamics of these small communities.

To obtain data on the presence and abundance of alligators in these systems, appropriate survey methods are required. However, the methods traditionally used for surveying and sampling alligator populations are specifically designed for the large, open-water systems in which most historic studies have been conducted. Eyeshine surveys, the most common method used for obtaining an index of alligator population size, are generally conducted in open water from a boat, which gives the observer the advantage of height, for increased visibility, and speed, to cover more ground. This method has been shown to vary in effectiveness based on a number of environmental factors (Woodward and Marion 1978; Wood et al. 1985; Woodward et al. 1996). The primary sources of variation in counts were water temperature, which was positively correlated with alligator activity, and water level, as increasing water levels allowed alligators to access adjacent wetland areas and subsequently decreased their

detectability. Eyeshine studies that have used mark-recapture or population modeling to estimate the average proportion of alligators detected have placed the detection probability between 9-25% (Taylor and Neal 1984; Woodward et al. 1996). However, the effectiveness of this method in inland wetlands, which are typically too shallow and vegetated to allow use of watercraft, has not yet been documented.

Double-observer methods allow the estimation of detection probability and abundance for surveys (Nichols et al. 2000; Bart et al. 2004). This approach is advantageous in small, inland systems because low population densities are likely to make parameter verification with mark-recapture methods unlikely. Additionally, the analysis of double-observer data within a Huggins' closed-capture model framework allows the use of grouping variables to test for habitat and observer effects on variation in the parameter estimates (Huggins 1989). This method has been used to estimate detection probabilities for bat species (Duchamp et al. 2006) and whitetail deer (Collier et al. 2007), and it may provide a rigorous way to test the efficacy of eyeshine surveys for alligators as well.

Many capture methods that are traditionally used to sample alligator populations are similarly designed for open water systems (Chabreck 1966). Researchers may use boats to get close enough to an animal to snare it, or large gill nets may be used to drag an area. However, the vegetative structure of these inland systems makes the application of these methods impossible. To sample alligators in forested wetlands in east Texas, Ryberg and Cathey (2004) used box traps to capture alligators and had reasonably high trap success (12.5-21.5%).

In order to evaluate the occurrence, abundance, and subsequent ecological role of alligators in inland systems, appropriate survey methods first must be established. The objectives of this study were to 1) evaluate the use of eyeshine surveys in two different types of seasonal wetlands in southwest Georgia (grassy marshes and cypress/gum swamps) using double observer surveys, and 2) compare eyeshine surveys and systematic trapping in their utility for estimating alligator population size and demography in this system.

METHODS

Study Site

This study was conducted at Ichauway, the outdoor laboratory of the Joseph W. Jones Ecological Research Center, located in Baker County, Georgia. The 11,600 ha reserve is predominantly composed of longleaf pine (*Pinus palustris*) and wiregrass (*Aristida beyrichiana*) uplands interspersed with more than 100 shallow, ephemeral limesink wetlands. There are three main types of wetlands on site (Kirkman et al. 2000): 1) cypress savannas, 2) grass-sedge marshes and 3) cypress-gum forests (*Taxodium ascendens* and *Nyssa biflora*, respectively). Cypress savannas are the smallest of the wetland types and also have the shortest hydroperiods (Kirkman et al. 2000; Liner 2006), making them less conducive to use by alligators. Cypress-gum forests generally have the longest hydroperiod, and grass-sedge marshes are generally the largest of the wetland types with an intermediate hydroperiod, making these two wetland types most conducive to use by alligators (Kirkman et al. 2000; Liner 2006; A.L.S. pers. obs.). I focused my study in 4 cypress-gum wetlands (4.69-12.18 ha) and 3 grass-sedge marshes (3.15-19.56

ha) which were known to have had alligators present within the two previous years. The site is also bisected by 25 km of the Ichawaynochaway Creek, and bordered by 20 km of the Flint River and a small section of the seasonally dry Big Cypress Creek.

Eyeshine Surveys

I conducted eyeshine surveys during three consecutive nights in each of seven isolated wetlands. I placed transects 100 m apart to maximize coverage of each wetland while minimizing the probability of observing the same individual on multiple transects. The number of transects used in each wetland varied between three and six, depending on the size of the wetland. During daylight hours, I marked all transects with reflective flagging. I returned at night and used a 200,000 candlepower spotlight to walk transects and search for alligator eyeshine.

All eyeshine surveys were conducted between June 10 and June 26, 2003. For each survey, the start and end time, weather condition (a categorical value where 0 = clear, 1 = <50% cloud cover, 2 = >50 % cloud cover, 3 = rain), moon phase, and water and air temperatures were recorded. A double-observer method was used for three consecutive nights at each wetland to allow me to calculate detection probability (Nichols et al. 2000; Thompson 2002; Moore et al. 2004). The two observers were drawn from a pool of 6 people, all of whom had some experience surveying for alligator eyeshine. To maintain independence of observations, each observer recorded their own data, and the secondary observer followed approximately 10 m behind the primary observer. Observers noted transect number, approximate distance from the transect centerline to the alligator, and the animal's approximate size. The size of alligators was

recorded as one of five size class categories: 1 = 0-2 total length in feet, 2 = 2-4 feet, 3 = 4-6 feet, 4 = 6-8 feet, and 5 = > 8 feet (Chabreck 1966). Using location and size information, I was able to determine which individuals were observed by both observers and which were only observed by either the first or second observer.

Eyeshine Survey Data Analysis

I used a Huggins' closed-capture model to calculate detection probability using Program MARK (Huggins 1989; White and Burnham 1999; Collier et al. 2007). Huggins' closed-capture models treat the observations of primary and secondary observers as capture and recapture data and use maximum likelihood theory to estimate detection probability and abundance. These models also allow data to be grouped according to environmental or sampling variables, such as wetland type and observer in this case, in order to determine the effect of those variables on the derived parameters.

I developed a set of four candidate models to test the effect of wetland type and observer on detectability of alligators. Due to limited sample size, I was constrained in the number of variables that I was able to include in the models. The models ranged from a constant model, p(.), in which capture probabilities were equal across habitat types and observers (# of parameters = 1) to a model p(t*g) in which detection varied across both observers (t) and wetland types (g) (# of parameters = 4). I evaluated the fit of each model using Akaike's Information Criterion, adjusted for small sample size (AIC$_c$; Burnham and Anderson 2002), as computed by MARK (White and Burnham 1999).

Trapping

Three weeks after eyeshine surveys were completed, six of the seven wetlands were sampled using baited trip-snare traps (Murphy and Fendley 1974) and Tomahawk cage traps to trap alligators. Three wetlands were trapped at a time over the course of 2 weeks, between July 15 and July 28. Five traps of each type were used for four consecutive nights for a total of 40 trap-nights per wetland. The traps were checked each morning and all captured animals were measured and marked. Morphometric measurements were taken including snout-vent length and tail length, sex was noted, and animals were marked using both a tail scute notching scheme (Mazzotti 1983) and PIT tags (Passive Integrated Transponders, Biomark, Inc.).

In characterizing the sizes of animals detected by eyeshine surveys and comparing the eyeshine survey results to trapping, I used data from the one night out of the three eyeshine surveys in which the maximum number of individuals was observed for each wetland. Using the maximum number observed on a single night allowed use of the greatest amount of observations for a given wetland without risk of biasing the data with repeated observations of the same individual. For trapping data, I used the sum total of individuals for each wetland, excluding recaptured animals.

RESULTS

Detection Probability

Double-observer eyeshine surveys resulted in 18 encounter histories of alligators. Observations in forested (cypress-gum) wetlands accounted for 44.44% of observations and marsh (grass-sedge) wetland observations accounted for the remaining 55.56%. Each observer detected 72.22% of the alligators, but only 44.44% of individuals were

detected by both observers. The most parsimonious model in this study was the model in which detection probability was held constant between both wetland types and both observers (Table 2.1). This single-parameter model had the lowest AIC_c value (0.000) and an AIC_c weight of 0.459. The estimated detection probability of alligators in seasonal wetlands, according to this model, was 0.570 ± 0.048 SE with 95% confidence intervals of 0.474-0.660 (Table 2.2).

The next most likely model was one which accounted for different detection probabilities between the first and second observer, with an AIC_c weight of 0.310. The detection probability for the first observer was 0.606 ± 0.058 SE and the detection probability for the second observer was 0.538 ± 0.056 SE. Although the second observer had a lower detection probability, the confidence intervals for these estimates overlapped, indicating the difference was not significant (Table 2.2). The model that accounted for different detection probabilities between the two wetland types had a fairly low AIC_c weight of 0.182. Although this model indicated detection probability was higher in marsh wetlands, it was not well supported by the data.

Table 2.1: Evaluation of 4 models of detection probability of alligators in inland

wetland systems using eyeshine surveys, with observer and wetland type as

grouping variables. ΔQAICc = 0.000 for the model most appropriate for the data

set, and these values increase as parsimony decreases.

Model	Model Description	Parameters	AIC_c	$\Delta QAIC_c$	QAICc weight
p(.)	Constant	1	237.335	0.000	0.459
p(t)	Obs. 1 ≠ Obs. 2	2	238.122	0.788	0.310
p(g)	Marsh ≠ Forested	2	239.181	1.846	0.182
p(t*g)	Obs. 1≠ Obs. 2,	4	241.835	4.500	0.048
	Marsh ≠ Forest				

Table 2.2: Estimates of detection probability of alligators in inland wetlands using

eyeshine surveys for the two most likely models according to AIC model

selection, p(.), the constant model, and p(t), which accounts for differences

between observers.

Model	Observer	Detection Probability	Std. Error	Lower 95% CI	Upper 95% CI
p(.)	NA	0.570	0.048	0.474	0.660
p(t)	1	0.606	0.058	0.488	0.712
	2	0.538	0.056	0.428	0.643

Huggins' closed-capture models estimate abundance as a derived parameter that is calculated separately for each observer (Huggins 1989). Because model p(t), which allowed for different detection probabilities for each observer, was fairly well supported by the data, I present only the abundance estimates calculated for that model (Table 2.3). The derived abundance estimate for alligators in the 7 wetlands surveyed was 110.078 ± 7.449 SE for observer 1, and the data from observer 2 increased that estimate by 22.017 ± 2.480 SE.

Eyeshine Surveys

To compare detection between eyeshine surveys and trapping, the following results were limited to the six wetlands (three forested and three marsh) where trapping also took place. There were 8 observations in forested wetlands over three nights of surveys and 10 observations in the marsh wetlands. The maximum number of alligators observed in a single wetland on one night ranged from 0 to 3, with a median value of 1. Four individuals in size classes 1 to 3 were observed in the three forested wetlands, and five individuals in size classes 1 to 4 were observed in the three marsh wetlands (Table 2.4).

Table 2.3: Derived estimate of abundance of alligators in the 7 inland wetlands surveyed, according to model p(t), which allows for observer effect. Because abundance estimates are given separately for each observer, I used the model which allowed for different detection probabilities between the two observers.

Observer	Abundance Estimate	Standard Error	Lower 95% CI	Upper 95% CI
1	110.078	7.449	99.932	130.588
2	22.017	2.480	19.319	30.236

Table 2.4: Comparison of size classes of alligators detected by eyeshine surveys and trapping in inland wetlands.

		Forest		Marsh	
Sizes (feet)	Size Class	Eyeshine	Trapping	Eyeshine	Trapping
<2	1	1	0	1	0
2-4	2	1	5	0	2
4-6	3	2	1	1	1
6-8	4	0	2	3	0
>8	5	0	1	0	0

Trapping

Twelve alligators were captured, ranging in size from 43.0 to 147.5 cm snout-vent length, with an average of 72.1 cm SVL. Six (43 to 66.5 cm SVL) were captured in Tomahawk cage traps, and six (53.4 to 147.5 cm SVL) were captured in Murphy-Fendley trip-snare traps. Only one alligator was recaptured during the sampling period, and it was caught in a trip-snare trap, at the same wetland, both times.

Alligators were captured at each of the three forested wetlands where they were trapped and only one of the marsh wetlands. A total of 9 individuals were trapped in forested wetlands, ranging from 43.0 to 147.5 cm SVL with a mean of 77.71 cm. Three individuals were captured in marsh wetlands, ranging from 44.0 to 66.5 cm SVL, with a mean of 55.4 cm (Table 2.5).

To compare the size classes of animals trapped to those of animals observed during eyeshine surveys, I converted the total length of the trapped animals to feet and grouped them according to the 5 size class categories. In the forested wetlands, trapping efforts detected animals in size class categories 2 through 5, while in marshes, trapping detected animals in categories 2 and 3 (Table 2.4).

Table 2.5: Average size of alligators trapped in forested and marsh wetlands, given as snout-vent length (cm).

Wetland Type	Sample Size	Average SVL (cm)	Std. Dev.	Lower 95% CI	Upper 95% CI
Forested	9	77.7	40.5	46.6	108.9
Marsh	3	55.4	11.3	27.4	83.3

DISCUSSION

Both eyeshine surveys and systematic trapping detected alligators in this inland wetland system. Eyeshine surveys were more effective than expected, with a detection probability of 57%. This estimate was between 2 and 5 times higher than previously reported from studies in open-water systems (Taylor and Neal 1984; Woodward et al. 1996). This result suggests eyeshine surveys are more effective in seasonal wetland systems than in open water systems, which is counter-intuitive given the dense vegetation structure of the wetlands. However, the small size of the wetlands in this study (3.15-19.56 ha) allowed fairly thorough coverage, which may have offset the effect of dense vegetation.

The constant model, which modeled equal capture probabilities across observers and wetland type, was best supported by the data; however, this was likely a consequence of having only 18 encounter histories. The model that accounted for

different detection probabilities between the first and second observer also was relatively well-supported by the data. This could be because alligators on Ichauway appear particularly wary, and quickly submerge when disturbed (A.L.S., pers. obs.); thus, the second observer is less likely to observe the same individual as the first observer. The model which accounted for different detection probabilities by wetland type was not very well-supported by the data, suggesting that dense emergent grasses had roughly the same effect on detection of eyeshine as dense stands of cypress and gum trees. I obtained an estimate of ca.130 alligators among all seven wetlands surveyed by adding together the derived abundance parameter for the first and second observer under model p(t). In order to have greater power to model the effect of group factors and to obtain a more precise abundance estimate, more surveys and more encounter histories are needed.

Thirteen alligators were captured over 240 trap-nights, for a total trap success of 5.4%. This success rate was much lower than Ryberg and Cathey (2004) achieved with box traps (12.5-21.5%). However, box traps large enough for adult alligators are expensive to build and difficult to carry through dense vegetation (Elsey and Trosclair 2004). These factors limit their use on a large scale, and resulted in my selection of the trip-snare design (Murphy and Fendley 1974). The trip snares and Tomahawk cage traps did catch animals of overlapping size classes, indicating that these trapping methods were sufficient to detect a wide and continuous range of sizes. Additionally, the smallest alligator I captured using a Tomahawk trap was 89.1 cm total length (TL), which was over 10 cm smaller than the smallest alligators captured in box traps (Ryberg and Cathey

2004), indicating that I may have been more likely to detect smaller individuals with my trapping methods.

Eyeshine surveys and systematic trapping detected different size classes, although the trend was not consistent across wetland types. In forested wetlands, smaller individuals were detected by eyeshine surveys and larger ones by trapping. In marshes, the opposite trend occurred. My data were not robust enough to draw definitive conclusions about how these survey methods vary by habitat type. They do indicate, however, that in inland wetland systems, use of multiple methods might be the best way to survey a broad cross section of the population, which may be especially important due to low population numbers and subsequent low sample size.

In conclusion, I found that eyeshine surveys were effective in these small, inland wetland systems. Use of double-observer methods and Huggins' closed-capture model analysis enabled me to calculate detection probabilities and to obtain an estimate of abundance, as well as to quantify the effect of grouping variables on those parameters of interest. While some traditional methods of alligator capture such as snaring from boats are unusable in this habitat, systematic trapping was effective in surveying a wide range of size classes in both wetland types. Depending on the available resources and the goals of the study, either box traps or trip-snare traps are effective methods of trapping alligators. The use of both eyeshine surveys and systematic trapping provided a more complete picture of the alligator populations of these small, inland wetland systems. Understanding the patterns of alligator presence and abundance in these systems is critical to developing appropriate management strategies for inland populations of

alligators as well as to understanding the ecological role of alligators in these systems. However, the first step towards these goals is developing appropriate survey methods and evaluating their effectiveness.

CHAPTER III

ONTOGENETIC NICHE SHIFTS IN AMERICAN ALLIGATORS ESTABLISH

FUNCTIONAL CONNECTIVITY BETWEEN AQUATIC SYSTEMS IN

INLAND HABITATS

SYNOPSIS

Functional connectivity between ecosystems can be established by animals that act as mobile links, moving energy, nutrients, and matter between otherwise isolated food webs. Animals that demonstrate ontogenetic shifts in habitat use and use distinct ecosystems during their development may provide a mobile link between those ecosystems. The American alligator (*Alligator mississippiensis*) is a model species for studying the ecological implications of ontogenetic habitat shifts, because they grow in size by several orders of magnitude from hatchling to adult, with accompanying changes in body plan and resource use. Studying alligators in the inland portion of their range, in which different aquatic habitats are distributed across an upland matrix, permitted the examination of ontogenetic habitat shifts within a landscape ecological context. I used equal trapping effort, radio telemetry and nest surveys to document shifts in habitat use between isolated, seasonal wetlands and riverine systems by alligators of different sex and size classes. Isolated, seasonal wetlands appear to provide nesting and nursery sites for adult females and juveniles; however, as the juveniles grow, they disperse through the terrestrial matrix into nearby riverine systems. Overland travel between these two aquatic systems by individuals undergoing niche shifts and by females moving to nesting

areas establishes functional connectivity between the systems. Understanding these movement patterns has implications for the conservation of both the species and the landscape it occupies.

INTRODUCTION

Energy and nutrient flow can occur across ecosystem boundaries through animal movement patterns (Gibbons 2003; Gillanders et al. 2003; Helfield and Naiman 2006). This type of functional connectivity, in which units in a mosaic interact through fluxes of energy, matter or organisms, may in turn alter the structure and dynamics of the mosaic, thus resulting in a high level of ecosystem complexity (Cadenasso et al. 2006). Such horizontal transfers of biomass, energy and nutrients have been demonstrated in studies of "mobile link" species that migrate across ecosystem boundaries, connecting otherwise separate food webs (Helfield and Naiman 2006; Kremen et al. 2007).

There are three functional groups of mobile link organisms (Lundberg and Moburg 2003). Resource linkers transport organic material, nutrients and minerals across habitats, often leading to fluxes of resources from areas of high productivity to areas of low productivity (Polis et al. 1997; Stapp et al. 1999). Genetic linkers carry genetic information across habitats through seed dispersal and pollination (Sekercioglu 2006). And trophic and non-trophic process linkers significantly influence the food web (Helfield and Naiman 2006) or the physiochemical environment (Naiman et al. 1988), respectively, across habitats.

Animals that exhibit ontogenetic shifts in habitat use throughout their lives may constitute a mobile link between discrete systems. Ontogenetic shifts in habitat occur

due to changing ratios in mortality risk to growth rate (Wilbur 1980; Gillanders et al. 2003). The movement of organisms from juvenile to adult habitat can result in substantial transfer of biomass, nutrients and energy between the systems (Deegan 1993; Gibbons et al. 2006; Regester et al. 2006). Nursery areas, for example, are habitats with high potential for export of biomass through recruitment of individuals into the adult population (Beck et al. 2001; Gillanders et al. 2003). To identify mobile links due to ontogenetic niche shifts, information would be needed on differential use of habitats by distinct size classes of a population, and animal movements among habitats or landscape components (Beck et al. 2001).

As a species that has continuous growth, increases in size by 4-5 orders of magnitude over its lifetime, and exhibits allometric scaling in its morphology, the American alligator provides an excellent model for studying ecological implications of ontogenetic shifts in habitat use (Polis 1984; Werner and Gilliam 1984). Allometric growth in American alligators is consistent with the theory that morphology, diet and habitat use shift in concert. Positive allometry in snout length, jaw musculature and bite force in alligators (Dodson 1975; Erikson et al. 2003), is associated with increasing prey size as they grow. Hatchling alligators primarily subsist on insects, whereas juveniles between 61 and 122 cm total length (TL) begin to include crustaceans and fish in their diet (Delaney 1990; Platt et al. 1990). Around 122 cm TL, sub-adults undergo a second dietary shift and include larger vertebrate prey in their diet (Delaney and Abercrombie 1986; Delaney et al. 1999). Negative allometry in limb lengths and mechanical

properties of the femoral retractor muscles in alligators indicates a higher propensity for terrestrial locomotion in juveniles over adults (Dodson 1975).

These ontogenetic morphological and trophic shifts in alligators are reflected in differential habitat use among size classes. Studies of alligators in coastal marshes have shown that adult males, which are typically the largest individuals in a population, rely on deep, open water, likely in part because of the availability of more abundant large prey. Adult females typically use deep water only for breeding, and then return to more vegetated marsh (Joanen and McNease 1970, 1972; Taylor 1984). Juveniles spend the first few years of their lives with their mothers near the natal site, and then begin to utilize a wide range of habitats (McNease and Joanen 1974; Dietz 1979). The tendency of juveniles to remain near their mother in vegetated marsh may be related to higher densities of invertebrate prey in that habitat as well as decreased exposure to predation and cannibalism (Rootes et al. 1991; Rootes and Chabreck 1993; Lance et al. 2000).

Although these patterns of habitat use have been documented in contiguous coastal marshes, alligators in inland wetland systems remain relatively unstudied, and the range and connectivity of available habitats may be markedly different in these systems (Ryberg et al. 2002). For example, in some upland systems in the southeastern coastal plain, deep, permanent bodies of water like those typically used by adult males are primarily found in creeks and rivers, whereas the vegetated marsh habitat favored by nesting females and juveniles primarily exists in isolated, seasonal wetlands surrounded by a terrestrial habitat matrix. If ontogenetic habitat shifts are occurring in this inland portion of the alligator's range, the alligators may be acting as mobile links between the

two aquatic ecosystems. Seasonal wetlands, with relatively high invertebrate diversity and vegetative cover, provide preferred habitat for hatchling and juvenile alligators and preferred nesting sites for reproductive females. However, wetlands lack larger prey items because they dry down periodically, and as alligators grow, large individuals need permanent water with larger, more abundant prey. At approximately 120 cm TL, the size at which ontogenetic shifts occur in many crocodilians (Fitzgerald 1978; A.L.S. and L.A.F., unpublished data), sub-adult alligators begin to disperse across the landscape and into riverine systems.

Herein, I test the hypothesis that ontogenetic niche shifts in alligators within a landscape context result in functional connectivity between two disjunct aquatic systems. Specifically, alligator movement patterns that accompany ontogenetic shifts in habitat use should result in alligators serving as mobile links between isolated wetlands and riverine systems. I used equal trapping efforts in the two aquatic systems to test the prediction that wetlands were primarily inhabited by juveniles and adult females and the creek by sub-adults of both sexes and adult males. I conducted nest surveys in the two systems to test my prediction that the wetlands provided preferred nesting habitat over the creek. I used radio telemetry to quantify animal movements between landscape components (wetlands, terrestrial matrix, and riverine systems). I predicted that sub-adults undergoing an ontogenetic niche shift would move from the wetland to the riverine system, and adult females would migrate to nesting sites associated with wetlands. Taken together, support for these predictions should establish the extent to

which the ontogenetic niche shift in alligators may result in functional connectivity between these distinct aquatic ecosystems.

METHODS

Study Site

I conducted my study within the inland portion of the range of *A. mississippiensis*, on Ichauway, the outdoor laboratory of the Joseph W. Jones Ecological Research Center, in Baker County, Georgia (Fig. 3.1). The study site is located within the Dougherty Plain physiographic region of the Lower Coastal Plain and Flatwoods ecoregion of the southeastern United States (McNab and Avers 1994). This region has a karst landscape, and it is characterized by predominantly sandy and clayey soils over a limestone base (Kirkman et al. 2000). In this region of the coastal plain, large lakes and expansive marshes are rare, and within my study site, bodies of water consisted of creeks and rivers incised in limestone, and depressional limesink wetlands with a hydroperiod driven by precipitation and evapotranspiration.
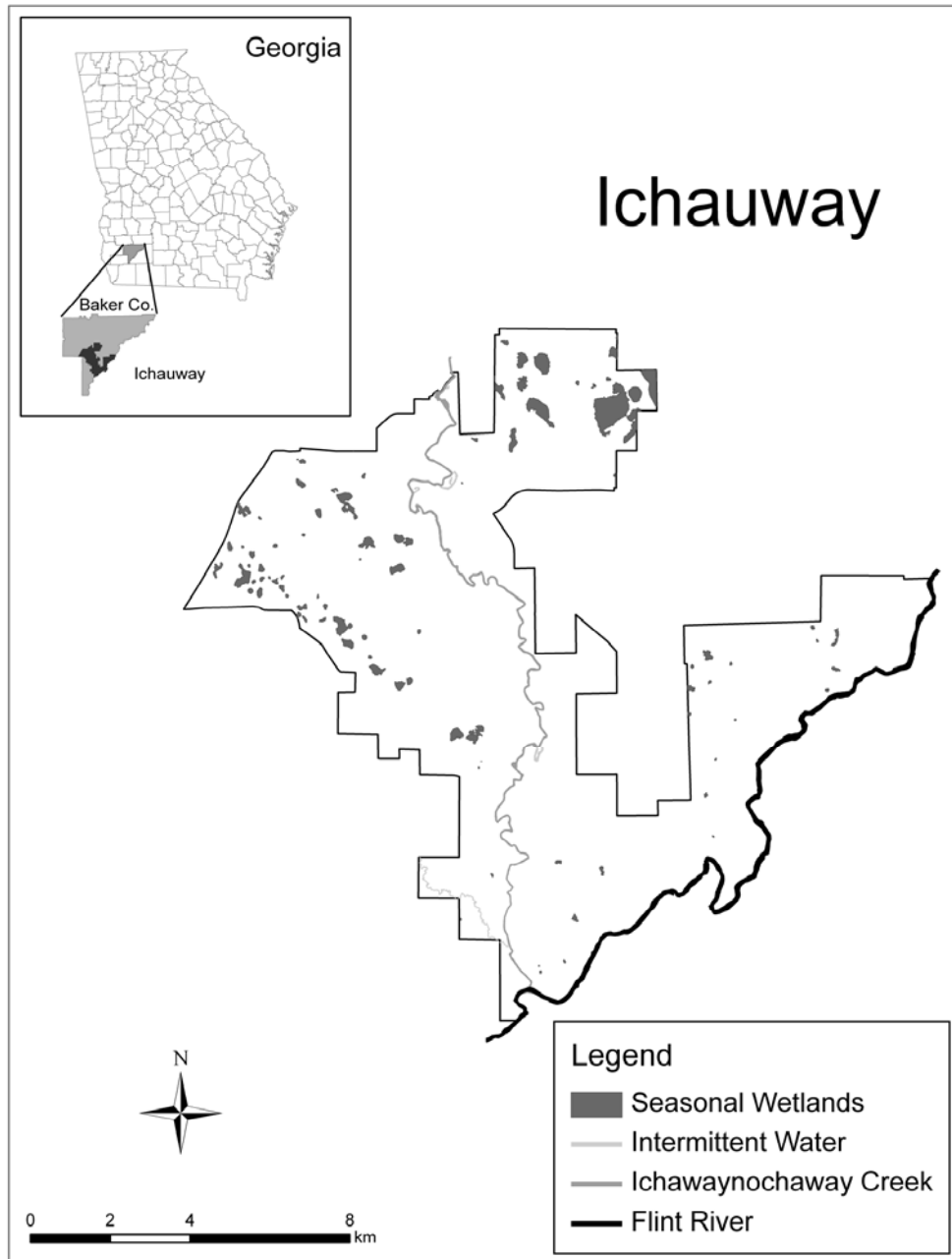
Figure 3.1: Map of the study area showing Ichauway's location in Baker County,

Georgia, and the configuration of isolated wetlands, creeks, and rivers in the Ichauway

landscape.

Ichauway is an 11,600 ha reserve predominantly composed of longleaf pine (*Pinus palustris*) and wiregrass (*Aristida beyrichiana*) uplands interspersed with over 100 shallow, ephemeral limesink wetlands. The site is bisected by 25 km of the Ichawaynochaway Creek, and bordered by 20 km of the Flint River on the eastern side and a small section of the seasonally dry Big Cypress Creek on the western side (Figure 3-1). I focused my sampling on the 25 km of the Ichawaynochaway Creek contained within Ichauway's borders and a subset of 13 seasonal wetlands in which I had consistently seen alligators over several years of survey. There are three main types of wetlands on site (Kirkman et al. 2000): 1) cypress-gum forests (*Taxodium ascendens* and *Nyssa biflora*, respectively), 2) grass-sedge marshes and 3) cypress savannas. My focal wetlands were primarily cypress-gum forests, although two were emergent marshes. The sites ranged in size from 1.07-14.37 ha.

Trapping Effort

In order to capture a wide size range of alligators, I used two different kinds of traps. Tomahawk cage traps, when used in an earlier study, captured animals between 89.1 and 134.9 cm TL, and Murphy-Fendley trip-snare traps, used in the same study, captured animals from 105.5 to 275.2 cm TL (Murphy and Fendley 1974; A.L.S. Ch. 2). Used together, these traps allowed me to sample the juvenile, sub-adult and adult components of the population.

To ensure equal trapping effort between riverine and wetland habitats, I divided the creek into four segments of approximately equal length and placed the wetlands in four groups of three based on geographic proximity. I treated each segment of creek as

being essentially "equal" to one group of three wetlands for the purpose of trapping the two systems with equal effort. It is difficult to make size comparisons between these two systems, because perimeter and area have an inherently different relationship in linear as opposed to circular bodies of water. However, this approach gave thorough trap coverage to both systems while being logistically manageable. I randomly selected the trapping order for the 8 different groups.

I used five trip-snare traps and five Tomahawk cage traps in each seasonal wetland for a total of fifteen of each trap type for a group of 3 wetlands. In order to achieve an equal number of trap types between the 2 systems, I also used fifteen of each trap type along a segment of creek. I trapped each group of sites for 10 nights, resulting in a total of 300 total trap nights per grouping, and 1200 total trap nights per system (wetlands vs. riverine).

In 2005 I trapped from the end of June to the middle of October. I tried to equalize temporal effects (time within season, moon phase, temperature, etc.) on trapping results by trapping one creek segment and one group of wetlands simultaneously. However, in 2006, in order to reduce unnecessary stress on animals in traps, I alternated trapping effort between the two systems. In 2006 I began trapping in May, but due to a drought, the wetlands were almost completely dry by July, so I abbreviated my trapping effort at the midpoint. I trapped two of the four sections of creek and 7 of the 13 wetlands, for a total of 600 trap nights per system. Water levels in some of the wetlands were too low by late June to use 10 total traps without overly

saturating the area, so I included an additional wetland to spread out traps while maintaining the same overall numbers in the system.

I took morphometric measurements on all captured animals, including snout-vent and tail length, determined sex (Chabreck 1963; Joanen and McNease 1978), and marked animals using a tail scute notching scheme (Mazzotti 1983) for quick visual identification, and a PIT tag (Passive Integrated Transponder, Biomark, Boise, Idaho) underneath the skin on the ventral side of the tail for permanent unique identification. I considered alligators less than 120 cm TL to be juveniles, alligators between 120 and 180 cm TL as sub-adults, and alligators longer than 180 cm TL reproductive adults (Joanen and McNease 1980, 1989). I used SPSS 12.0 (SPSS, Chicago, Illinois) to test the data for normality using the Shapiro-Wilks test ($p = 0.586$), and I used t-tests and analyses of variance to compare size class distributions between the two systems. An alpha value of 0.05 was used for all significance testing.

Radio Telemetry

When animals captured during the equal trapping effort or captured incidentally on site were greater than 120 cm TL, I attached a radio transmitter to their nuchal scutes (Blackburn Transmitters, Nacogdoches, Texas). Transmitters weighed < 200 g, which was 3.6% of the body mass of the smallest alligator in my study. I used a local anesthesia (2% Lidocaine Hydrochloride) prior to transmitter attachment, and then drilled holes with a sterilized drill bit through the two pairs of nuchal scutes. Transmitters were attached with surgical-grade steel wire (2005) or braided Spectra line (2006) threaded through the transmitter and through the holes in the nuchal scutes

(McNease and Joanen 1974; Kay 2004). The transmitter and wire/line attachments were then covered with waterproof epoxy to improve hydrodynamic qualities as well as increase longevity of attachment.

Animals were tracked 1-3 times per week. Locations were obtained by taking compass bearings from 2-3 known locations (GPS stations) and using program Locate (Pacer Computing, Tatamagouche, Nova Scotia, Canada) to obtain the coordinates of their intersection. Notes were made as to the signal strength of the animal and the time between bearings to allow determination of the quality of the location coordinates. In general, bearings were taken within 15 minutes of one another and within several hundred meters of the animal.

I examined the number and distance of overland movements and the number of water bodies used as a function of sex and size class of the individual. Locations within a water body were grouped into one point at the centroid of the wetland (to accommodate drastic changes in the perimeters of these wetlands during wet and dry seasons), and overland movement distances were calculated in ArcMap (ESRI, Redlands, California) as the Euclidean distance from wetland centroid to centroid, or from wetland centroid to the nearest creek edge. Animals captured moving overland were assumed to be moving from a wetland, and the distance of the movement was calculated from their capture location.

Nest Surveys

Alligators often nest in June and July and eggs hatch in August and September (Ruckel and Steele 1984). Previous observations indicate that alligators on Ichauway

nest during the latter end of that timeframe, probably because the site is located north of where most nesting studies have been conducted, and eggs hatch in early to mid September (A.L.S., pers. obs.). I assumed a nesting event had taken place in a given year if I located a recently active nest with eggshell fragments still nearby or if I located a pod of hatchlings <15 cm SVL and with a mass < 100g during or after September. If I located a pod of young <20 m SVL and with a mass <100g before September, I assumed the nest hatched the previous year.

During 2005, I recorded locations of nests and pods of hatchlings incidentally encountered. In 2006 I conducted systematic nest surveys in both the wetland and the riverine systems. Using ArcGIS I calculated the average perimeter of one of the 13 wetlands I surveyed and used this as the length of 13 equal transects along the creek. I placed 13 random points along the creek in ArcGIS and created transects from those starting points, alternating between the east and west side of the creek. I used two observers to walk approximately 30 m wide transects along the ecotonal boundary of the wetlands and the creek searching for nests. Any potential nests were carefully approached and opened to determine whether eggs were present, and I searched for signs of egg shells or alligator paths in the near vicinity to include old or recently depredated nests.

RESULTS

Equal Trapping Effort

During 2005 and 2006, I captured 27 individuals in the two systems, ranging from 111.5 – 265.8 cm TL, with a mean TL of 188.2 cm (SD = 41.7) (Table 3.1).

Alligators captured in the creek were significantly larger than those in the seasonal

wetlands (F = 0.092, p = 0.764, Levene's test for equality of variances; t = 4.834, df =

25, and p = 0.000).

Because alligators are sexually dimorphic by size, differential habitat use by

males and females could explain the larger size of the captured individuals in the creek.

Of the 14 alligators captured in the creek, 50% were female, while 84.6% of the 13

alligators caught in wetlands were female (p = 0.066, one-sided Fisher's Exact Test;

Table 3.1). There was a significant effect of habitat type on size (F = 33.817, p = 0.000),

and a statistically significant interaction between habitat and sex (F = 9.443, p = 0.005)

(Table 3.2).

Table 3.1: Summary statistics for alligators captured in the Ichawaynochaway Creek

and within 13 seasonal wetlands on Ichauway using equal trapping efforts between the

two systems.

	Wetlands			Creek		
	Number	Mean TL (cm)	SD	Number	Mean TL (cm)	SD
Males	2	120.0	12.0	7	231.2	26.0
Females	11	165.7	27.6	7	200.0	27.8
Total	13	158.7	30.7	14	215.6	30.5

Table 3.2: A univariate analysis of variance examining the effect of habitat and sex on the total length (TL) of American alligators captured in the Ichawaynochaway Creek and within 13 seasonal wetlands on Ichauway.

Source	df	Mean Square	F	Sig.
Habitat	1	24,174.562	33.817	<0.0001
Sex	1	243.528	0.341	0.565
Habitat * Sex	1	6,750.340	9.443	0.005
Error	23	714.864		

Radio Telemetry

I radio-tracked 12 sub-adult females, 2 sub-adult males, 3 adult females and 4 adult males between 14 June 2005 and 31 October 2006. With the exception of two sub-adult males that left the site after 27-29 days, the subjects were monitored from 172 to 453 days, and the number of locations was between 19 and 102 (mean = 62 locations per individual). The number of movements recorded represents a known minimum (Table 3.3).

Table 3.3: A summary of the individual American alligators tracked, the number and type of water bodies used, and the number and distance of overland movements (calculated as Euclidean distance between wetland centroids or between wetland centroid and nearest creek edge in ArcMap). Animals captured moving overland were assumed to be moving from a wetland; the distance for that movement was calculated from the capture location.

Sex	Size Class	No. of Indiv.	No. of Water Bodies Used (wetl., crk., river)	Mvts. from Wetl. to Crk. Total (Range)	Mvts. from Crk. to Wetl. Total (Range)	Mvts. between Wetl. Total (Range)	Overland Mvts. Min (Mean) Max	Dist. of Overland Mvts. (m) Min (Mean) Max
F	Sub-Adult	12	0-5, 1, 0	4 (0-1)	1	15 (0-5)	0 (1.6) 5	218 (749) 1588
M	Sub-Adult	2	1-2, 0, 0	0	0	5 (2-3)	2 (2.5) 3	216 (588) 835
F	Adult	3	1, 1, 0	2 (0-1)	2 (0-1)	7 (2-5)	0 (3.7) 7	257 (436) 756
M	Adult	4	0, 1, 1	0	0	0	0	0

Five of the 14 sub-adult animals spent the duration of the study at the location where captured. Another 5 sub-adults used more than one wetland and made multiple overland movements. The remaining 4 moved overland between multiple wetlands and the creek. Out of the group of 14, 4 individuals moved through 2-3 wetlands in a short period of time, staying <10 d at each one before staying in the creek or a wetland for a substantial amount of time. The movements of 2 other individuals were seasonal, starting and ending in one wetland, but moving into a separate wetland to over-winter.

Of the 3 adult females, one spent the duration of the study in the wetland in which she was captured. The other two were captured in the creek, moved into a complex of 2 wetlands for a period of 1-3 months, and then moved back into the creek. For one female, the movement to a wetland appeared to be for the purpose of nesting (see below).

All of the adult males spent the duration of the study either on the Ichawaynochaway Creek in which they were captured or in the Flint River. No movement overland or use of seasonal wetlands was recorded for this group at any point in the study.

Nesting Surveys

I documented 8 nesting events in seasonal wetlands in 2005. Four observations were made during the fall of 2005, two during early spring of 2006, which were presumed to be 2005 nests, one nest was under construction in 2005 but never used, and one nesting attempt was assumed due to a gravid female alligator who was radio tracked

to a seasonal wetland. In contrast, there were no observations of active or recently active nests or of pods of hatchlings on the creek.

In 2006, systematic nest surveys were conducted between 19 July and 8 August 2006. The one active nest located through systematic survey methods was at the edge of a seasonal wetland. The low overall nesting activity in 2006 was likely due to drought (Georgia Automated Environmental Monitoring Network 2007). Almost all of the wetlands were completely dry, except for the water remaining in the alligator burrows and wallows. I monitored the nest weekly throughout the remainder of the incubation period; however, it was eventually depredated. Other observations in the region suggested widespread alligator nest failure in 2006 (A.L.S., pers. obs.; West, pers. com.).

DISCUSSION

The results converged on the conclusion that alligators do represent a form of functional connectivity between the isolated wetland and creek-river systems in this region. This functional connectivity is a consequence of the ontogenetic niche shift in habitat as alligators grow. Functional connectivity was not only demonstrated by movements of sub-adult alligators across the landscape among wetlands and eventually to the creek and river, but also by females that migrated from the creek, presumably to nest in wetlands.

The use of seasonal wetlands as nursery sites was supported by the different densities of juveniles and adults in the two aquatic habitats. The significant interaction between sex and habitat on body size reflected the fact that sub-adult males were only caught in wetlands and adult males were only caught in the creek, whereas females of

both size classes were caught in both systems. Furthermore, since I began working in this system in 2002, 78.6% of 159 alligators caught in seasonal wetlands were juveniles, 15.1% were sub-adults, and only 6.3% were adults (A.L.S., pers. obs.). Of 10 adults, only 2 were adult males. These findings corroborate the pattern elucidated by equal-trapping efforts in both systems.

Nesting surveys further supported the hypothesis that seasonal wetlands provide suitable nursery sites for juveniles. All nesting attempts documented on Ichauway in this study were located in seasonal wetlands, whereas none were located in the riverine environment. Beck et al. (2001) defined a nursery as any habitat that contributes a greater number of individuals to the adult population per unit area than other habitats in which juveniles occur. This may happen through any combination of four factors: higher density of juveniles, increased growth or increased survival of juveniles, and direct movement to adult habitats. In this study, I documented the first and fourth factors occurring in seasonal wetlands, indicating they operated as a nursery for alligators in this system (Beck et al. 2001; Gillanders et al. 2003). It is reasonable to predict that juvenile growth and survival would be higher in the wetlands than in the riverine system because the ephemeral nature of the wetlands results in a different predator guild than that present in the creek. Periodic drying prevents the establishment of large fish and precludes their use by many large alligators, both of which are potential predators of juveniles. However, the wetlands are rich in invertebrates, which constitute the primary prey of juveniles.

Overland movements were typically observed among sub-adults undergoing an ontogenetic niche shift from wetland to riverine system, and by females moving into the wetlands in search of nesting sites. Sub-adults made the majority of their movements either among wetlands or from the wetlands to the creek, while adult females made equal movements between the creek and wetlands. In contrast, adult males made no overland movements during the course of this study and were never documented using seasonal wetland habitat. This suggests that breeding occurs in the riverine system, with adult females migrating overland between breeding and nesting sites.

In animals with complex life histories, shifts in the ratio of growth rate to mortality risk may occur in concert with ontogenetic shifts in morphology and diet. (Wilbur 1980). As a result, animals may optimize their fitness by using different habitats as juveniles and adults (Wilbur 1980; Gillanders et al. 2003). The hatching and growth of juveniles in a nursery habitat, dispersal into and growth within adult habitat, and the subsequent return of adult females to the nursery habitat to nest, may result in the substantial movement of energy and nutrients across ecosystem boundaries (Deegan 1993; Gibbons et al. 2006; Regester et al. 2006). Alligators use multiple aquatic ecosystems at different stages of their lives, and they are large predators as well as ecosystem engineers due to the burrows and wallows they create in systems in which they occur (McIlhenny 1935; Craighead 1968; Mazzotti and Brandt 1994). In this way, alligators act as mobile trophic and nontrophic process linkers between the multiple systems they use (Naiman et al. 1988; Lundberg and Moberg 2003; Helfield and Naiman

2006), thereby establishing a level of functional connectivity between those systems (Gibbons 2003).

When individuals within a population rely on multiple habitat types throughout their lifetime, there are conservation implications for both the species and the habitat. In order to protect the population, both the discrete habitat types and their interconnecting matrix must be conserved in order to allow the individuals to disperse as needed. Protection of the species and maintenance of these pathways has reciprocal effects on the habitat. The net flux of productivity (energy, nutrients and biomass) may be critical for ecosystem resilience in some systems. Mobile link species also may trigger disturbance events which may help to promote and maintain species diversity in the systems in question (Lundberg and Moberg 2003).

Consideration of mobile link species and their contribution to the functioning and dynamics of ecosystems is increasing, but conservation at the landscape level has lagged behind. For instance, alligators are not the only species to rely on and move between multiple aquatic habitats that include seasonal wetlands. Similar phenomena have been documented for turtles (Burke et al. 1995; Tuberville et al. 1996; Joyal et al. 2001), salamanders (Scott 1994; Gibbons 2003), snakes (Siegel et al. 1995; Roe et al. 2004) and birds (Naugle et al. 2001; Amat et al. 2005). A recent U.S. Supreme Court decision, Solid Waste Agency of Northern Cook County v. U.S. Army Corps of Engineers (No. 99-1178; SWANCC) removed seasonal wetlands from federal protection under the Clean Water Act based on their lack of hydrological connectivity to navigable waterways. However, as demonstrated by alligators in this study, seasonal wetlands are

functionally connected to riverine waterways via the movement patterns of species, some of which are of conservation or commercial interest. Understanding ecosystem functioning and conservation at the landscape scale requires an approach that extends past ecosystem boundaries. The requisite movements of mobile link species driven by ontogenetic shifts epitomize that concept.

CHAPTER IV

USE OF SEASONAL WETLANDS BY AMERICAN ALLIGATORS:

FLUCTUATIONS IN THE IMPORTANCE OF PATCH AND LANDSCAPE

CHARACTERISTICS

SYNOPSIS

Species that utilize patchily distributed habitat require landscape scale approaches to conservation. Characteristics of both the patch and the landscape are important to habitat suitability as well as overall landscape connectivity. However, the relative importance of certain variables can depend on what component of the population is being modeled. I studied the changing importance of descriptive versus spatially-explicit patch characteristics for different components of an alligator population that inhabits seasonal wetlands, because alligators are known to undergo large ontogenetic niche shifts with corresponding changes in habitat use and overland dispersal capability. I created a series of suitability models to test the importance of descriptive and spatially-explicit patch characteristics on wetland use by alligators, and I tested those models with datasets representing different components of the population. My findings reveal that both descriptive wetland characteristics and variables related to the spatial relation of multiple water bodies were important for predicting wetland suitability. I also constructed a landscape-level habitat suitability model to identify components of the landscape as a whole that were important to overland dispersal. This habitat suitability model was tested using radio telemetry data, and illustrated that overland movements

were highly related to the landuse surrounding wetlands as well as the distance between

bodies of water.

INTRODUCTION

To understand the distribution of a species across a landscape, the size and

quality of habitat patches, their spatial relationships to one another, and the dispersal

capabilities of the species of interest must all be taken into account (Fahrig and Merriam

1994). Habitat use on the landscape scale can also be affected by variation within a

species. For example, an individual's sex, age/size, or reproductive condition may be

linked to differences in habitat requirements or vagility (Weaver et al. 1996; Amat 2005;

Belisle 2005). For species that use multiple patches throughout their lifetime and make

frequent movements between them, the spatial relationships of patches to one another

are particularly important (Roe et al. 2004).

Isolated seasonal wetlands are excellent systems for study of ecological

implications of patchily distributed habitat because they are discrete aquatic habitats

imbedded in a terrestrial matrix. Many species have been documented using both the

wetland and the surrounding matrix (Burke and Gibbons 1995). Habitat models

constructed for such species have shown that descriptive patch characteristics such as

wetland size and hydroperiod, and variables related to the spatial relation of multiple

wetlands, such as nearest neighbor distance, are generally important in determining

wetland use (Snodgrass et al. 1999; Snodgrass et al. 2000; Attum et al. 2007). However,

species more dependent on water primarily use the terrestrial matrix to travel between

wetlands. For these species, spatially-explicit characteristics reflecting the relationships

between multiple habitat patches are expected to be more important to understanding wetland use by that species (Roe et al. 2004).

Inland populations of American alligators provide a model system for addressing the relative importance of spatially-explicit and descriptive patch characteristics on wetland occupancy by different components of the population. In southwest Georgia, permanent bodies of water generally consist of man-made reservoirs and creeks and rivers that are excised in limestone. Extensive marshes and high-water floodplains, the habitats in which most alligator studies have occurred, are not available for alligator use in this region. Ontogenetic habitat shifts (Joanen and McNease 1970, 1972; McNease and Joanen 1974), in which juvenile and nesting female alligators use densely vegetated marsh and adult males use deep, permanent water bodies, necessitate the use of two aquatic habitats that are separated by a terrestrial matrix in this region. Previous studies in this system have shown that seasonal wetlands are primarily used as nesting and nursery sites by adult female alligators and juveniles, sub-adults and nesting females disperse overland between the wetland and the riverine system, and adult males primarily stay in the creek or river (A.L.S. Ch. 3). Due to these shifts in habitat use by different components of the population, I would expect to see variation in which wetland characteristics are important to alligators in general and to nesting females in particular.

Habitat modeling is increasingly used to characterize and predict suitable habitat for species. However, rarely are multiple hypotheses involving both descriptive and spatially-explicit patch characteristics tested for their applicability to distinct components of a population. In this study, I constructed a series of models of wetland

suitability for alligators using both descriptive and spatially-explicit patch characteristics in one particular system. I tested the models with independent data sets that represented differing use of wetlands by different components of the population, including records of alligator presence, existence of alligator burrows indicating long-term habitation, and use by nesting females.

I predicted that hydroperiod, which is related to wetland size and type, would be an important variable in modeling wetland use. However, due to the overland movements associated with an ontogenetic niche shift in subadults and those of adult nesting females, variables related to the overall connectivity of aquatic habitats (e.g., distance to nearest wetland, area-weighted proximity of nearby wetlands, and distance to the riverine system) would also be important. These landscape variables should be particularly important in wetlands used consistently by alligators over time, as indicated by the presence of burrows, or in wetlands used for nesting and as nurseries. Specifically, I predicted that a measure of wetland proximity (Program Fragstats proximity index; Gustafson and Parker 1992; McGarigal and Marks 1995) would provide a better fit than Euclidean nearest neighbor distance because it provides a more comprehensive picture of the spatial configuration of multiple wetlands across the landscape. Furthermore, I predicted that distance to the creek or river would be most important in wetlands used as nesting sites because adult females move between the riverine and wetland systems for breeding and nesting.

To determine which components of the landscape facilitate overland movements of alligators, I constructed a GIS-based landscape model to predict areas of high

suitability for dispersal of alligators between the seasonal wetlands and the riverine system. I tested this model using data on alligator movements obtained with radio telemetry. I predicted overland movements would decrease with increasing distance from water bodies and that overland movements would be more likely to occur in intact upland habitat.

An understanding of habitat suitability in terms of patch types that are necessary for distinct life stages of a population can provide critical information for developing holistic conservation plans for a species. In this case, analyses of wetland suitability and landscape connectivity for different life stages of American alligators can be applied to management of inland alligator populations. Moreover, information on how relationships between isolated wetlands, the terrestrial habitat matrix, and riverine systems can affect habitat suitability highlights the need for a landscape-scale approach to conservation of isolated seasonal wetlands.

METHODS

Study Site

This study was conducted at Ichauway, the outdoor laboratory of the Joseph W. Jones Ecological Research Center, in Baker County, Georgia (31º14'30.2"N, 84º27'58.6"W). Ichauway is located within the Dougherty Plain physiographic province of the southeastern coastal plain and within the Apalachicola-Chattahoochee-Flint River drainage. The site is an 11,600 ha reserve predominantly composed of longleaf pine (*Pinus palustris*) and wiregrass (*Aristida beyrichiana*) uplands interspersed with over 100 seasonal limesink wetlands and hardwood depressions. There are three main types

of wetlands on site (Kirkman et al. 2000): 1) cypress savannas, 2) grass-sedge marshes, and 3) cypress-gum forests (*Taxodium ascendens* and *Nyssa biflora*, respectively). While all wetland types are host to a large assemblage of macroinvertebrates (Battle and Golladay, 2001), they vary greatly by average size and hydroperiod. Cypress savannas, which tend to be the smallest wetlands on site, also have the shortest hydroperiod. Emergent marshes, although typically the largest wetlands on site, have an intermediate hydroperiod. Cypress-gum forests are intermediate in size but have the longest hydroperiod (Kirkman et al. 2000; Liner 2006). The site is bisected by 25 km of the Ichawaynochaway Creek, and bordered by 20 km of the Flint River and a small section of the seasonally dry Big Cypress Creek.

The property is managed using prescription burning on a two-year rotation. Fire maintains the open overstory crucial to the species diversity of the longleaf-wiregrass ecosystem. It also helps prevent hardwood encroachment into the emergent marshes and cypress-savannas. As a result of these land-management practices, Ichauway provides a unique opportunity to study the ecological processes of the once-dominant forest type of the southeastern coastal plain.

Approach

I used a landuse classification map of Ichauway that was developed by photointerpretation from 1:12,000 color infrared photography in 1995 (Brock, pers. com.). The mylar overlay was transferred via vertical sketchmaster to 1:12,000 quadrangle enlargements. The lines were digitized using ArcInfo (Ecological Systems Research Institute (ESRI), Redlands, California), edgematched and attributed with the

Anderson level land cover code. Landuse was classified as one of eight types: wetlands, open water, forested, scrub/shrub, inert/barren land, wildlife food plots, agriculture, or urban. Updates to the GIS coverages take into account land use changes that have taken place over the last twelve years. I worked within ArcGIS 9.0 and 9.1 (ESRI 2004-05) to confirm the wetland type classification using 2002 aerial photography, a 1986 Natural Features Inventory conducted on Ichauway by The Nature Conservancy, and the U.S. Fish and Wildlife Service National Wetlands Inventory.

To model descriptive characteristics of the wetlands, I compiled data on the size and type (marsh, cypress savanna, or cypress-gum forest) of each wetland on site. I then calculated three spatially-explicit wetland variables. Because streams and creeks are the only permanent water within the study area, I calculated the distance from wetland centroid (to account for changes in the perimeters of the wetlands during wet and dry periods) to nearest creek or river edge. I then used Program Fragstats (McGarigal and Marks 1995) to calculate two other spatially-explicit wetland variables: Euclidian Nearest Neigbor (ENN) and PROXIMITY. The ENN is the distance from one wetland edge to the edge of the nearest wetland. The proximity index for a focal patch is the sum of the area of each patch of similar type (i.e. wetland) divided by the square of the edge to edge distance to that patch for a given neighborhood around the patch of interest (Gustafson and Parker 1992; McGarigal and Marks 1995). I used a neighborhood distance of 300 m to accommodate the 300 m buffer of GIS coverage surrounding the study site. Three wetlands crossed the site boundary and were therefore excluded from any model using PROXIMITY as one of the variables.

I grouped all wetland variables into categories from 1 (lowest suitability) to 5 (highest suitability) (Table 4.1). I ranked wetland types according to hydroperiod, with savannas having the shortest hydroperiod and forested wetlands having the longest (Kirkman et al. 2000; Liner 2006). I ranked larger wetlands as more suitable, not only because of increased habitat and prey resources (Attum et al. 2007), but also because of the positive effect of size on length of hydroperiod (Snodgrass et al. 2000). For the distance from the wetland to the creek or river ("distance"), I based my classification on average distance of overland movements, ca. 450-750 m, documented in the radio-telemetry portion of the study (A.L.S. Ch. 3). I used a combination of natural breaks and visual determination to distribute the nearest neighbor and proximity values into categories.

Table 4.1: Coding of descriptive (wetland size and type) and spatially-explicit wetland variables (distance to the creek or river, Euclidean nearest neighbor, and proximity) for suitability of seasonal wetlands on Ichauway for alligator use and number of wetlands with each code.

Habitat Suitability	Wetland Type	No. of Wetlands	Size (ha)	No. of Wetlands	Dist. to the Creek or River (m)	No. of Wetlands	ENN	No. of Wetlands	PROXIMITY	No. of Wetlands
1	Savanna	13	<1	69	>3500	43	>1000	9	0	72
2		-	1-5	38	2500-3500	20	500-999	20	1-9	33
3	Marsh	79	5-10	10	1500-2500	22	250-499	30	10-19	9
4		-	10-15	4	750-1500	23	100-249	28	20-99	8
5	Forested	34	>15	5	<750	18	<100	45	100-1028	9

To test which wetland characteristics were most important to wetland suitability for alligators, I created 7 models using different combinations of the variables (Appendix 1 (a-g)). The models were constructed by summing the variables for each layer, then re-classifying them according to 5 habitat suitability categories: very low; low; medium; high; and very high. I tested these models using 4 different data sets. "Presence" was a cumulative list of all wetlands in which alligators or alligator sign (including burrows or nests) had been observed in four different years of survey, 1986, 1994, 2000 and 2002 (n = 29). The second data set ("Burrow") consisted of wetlands in which alligator burrows had been documented, indicating repeated and long-term use by the animals (n = 18). The third data set ("Nest") included all wetlands in which a nest or pod of hatchling alligators had been documented between 2002 and 2006 (n = 10). The fourth data set ("Dispersal") was constructed to estimate wetlands used as "stepping stones" for dispersal, and was limited to wetlands in which alligators had been observed but which did not contain burrows (n = 11). I used a chi-square goodness of fit test to determine which models showed a significantly different distribution of observations than would be expected due to chance. Expected frequencies were calculated by weighting the number of wetlands in a given dataset by the proportion of total wetlands in each suitability category. Because models were not independent of one another, I used the Bonferroni method for limiting overall experiment-wise error rate by dividing $\alpha = 0.05$ by the number of tests run. For all models that had a p value <0.007143, I graphed the deviations of observed to expected frequencies, standardized to a scale of -1.0 to 1.0, for each suitability category (Fitzgerald et al. 1999) (Figures 4.1 (a-d)).
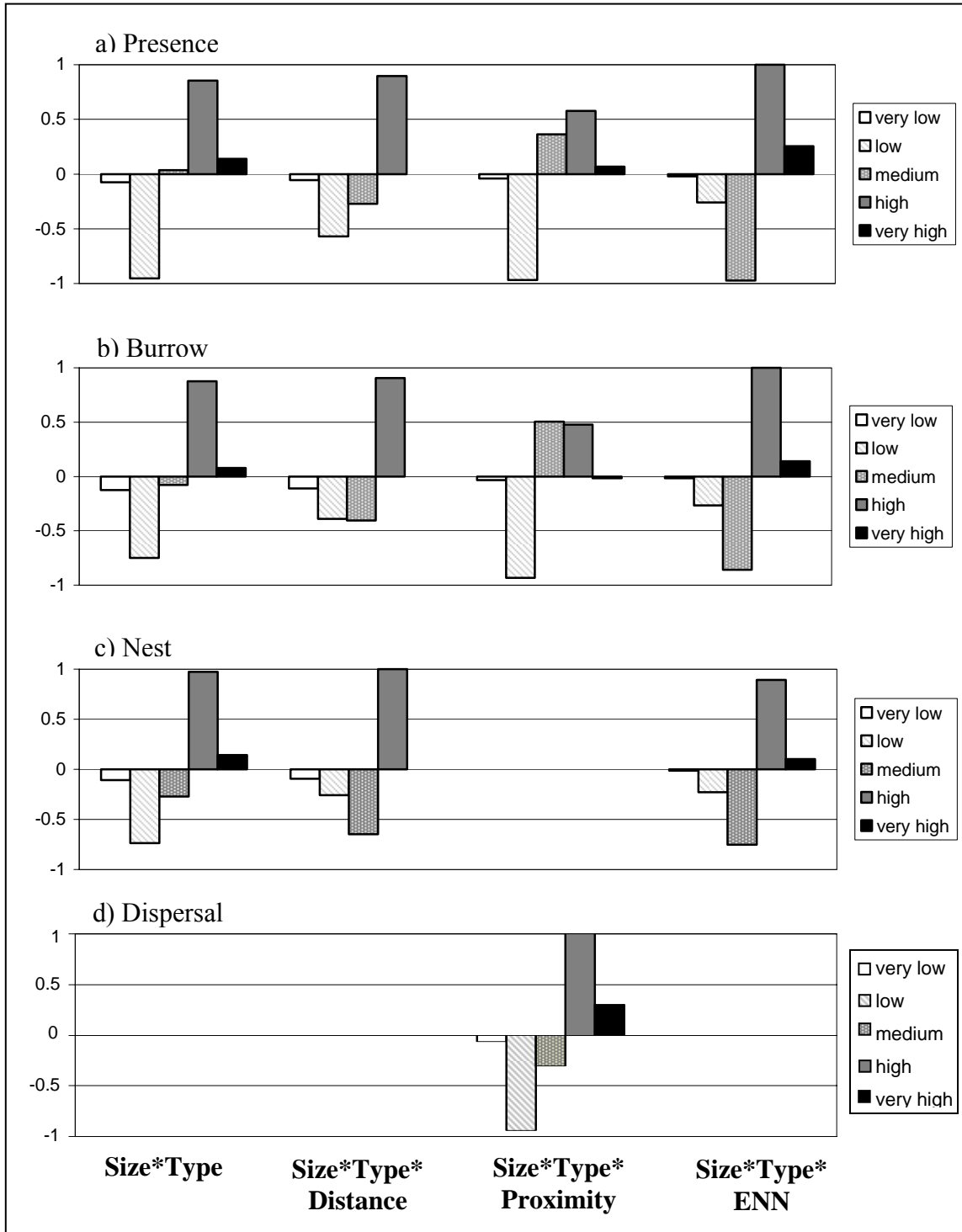
Figure 4.1 (a-d): Significant wetland models (p < 0.007) showing the deviation of

observed from expected values, standardized from -1 to 1, for each suitability category.

I used a cost-distance analysis at 1-m resolution to create a habitat suitability model that would illustrate areas of connectivity between the wetlands and riverine system. I used all bodies of water as the source grid and created a cost grid by coding land-use types on a scale from 1 (easiest to traverse) to 5 (most difficult to traverse), from least to most altered by human disturbance (Table 4.2). I tested the predictions of this model by overlaying radio-telemetry locations for 9 animals on the connectivity map. Animals were tracked 1-3 times per week, and exact overland paths were unknown, therefore, I used straight-line distance between the water bodies they used to simulate paths.

Table 4.2: Land-use classifications for the cost-distance analysis, classified from 1 (least cost for travel) to 5 (highest cost for travel).

	Water	Forested	Scrub/ Shrub	Wildlife Food Plot	Built Up/ Agriculture
Code	1	2	3	4	5

RESULTS

For each wetland suitability model that had a significantly different distribution of observations than expected due to chance, there were fewer wetlands in the lower ranked categories and more wetlands in the higher ranked categories than expected (Fig. 4-1 (a-d)). The Presence, Burrow and Nest datasets all had observations that were distributed differently than expected ($p<0.003$) for the following models: size*type, size*type*distance, and size*type*nearest neighbor. The Presence and Burrow datasets also had a significantly different distribution than expected due to chance for the size*type*proximity model ($p<0.001$). The Dispersal dataset was the only one which did not show a significant relationship with the solely patch-based model, size*type. The only model for which the Dispersal observations were significantly different than expected was size*type*proximity ($p<0.001$).

Based upon the landscape-level suitability model calculated using cost-distance analysis, of the nine animals tracked with radio telemetry that made overland movements, straight-line distances between used water bodies never crossed the very low or low habitat suitability categories. One individual's movements crossed suitability categories medium, high and very high, six crossed only categories high and very high, and two individuals only crossed the very high suitability category. Five of the six individuals who made overland movements between the wetland and riverine systems only used the high and very high suitability categories (movements of three individuals are depicted in Fig. 4.2).
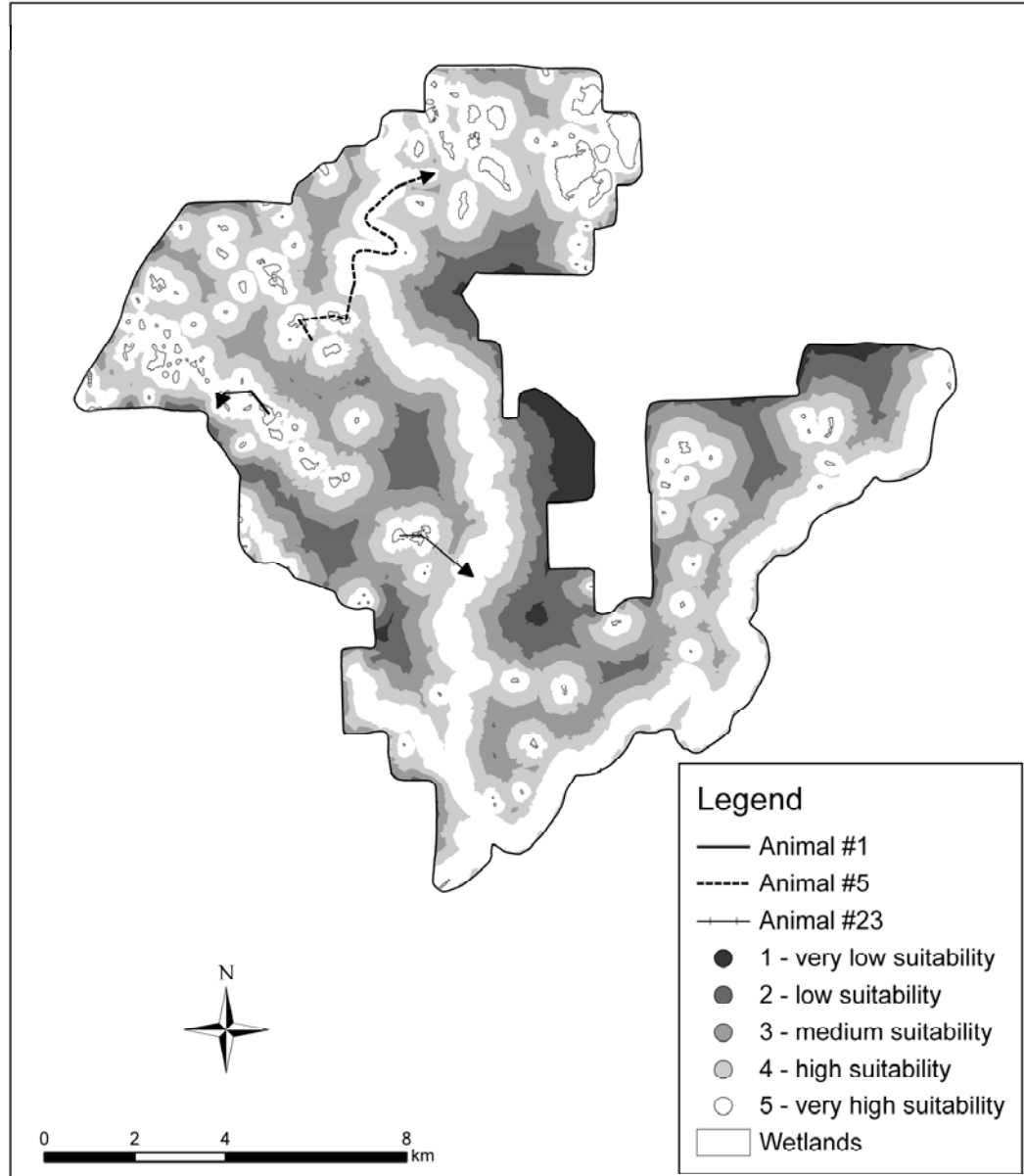
Figure 4.2: Landscape suitability model of Ichauway showing connectivity between the wetlands and riverine system as a function of landuse type and distance between aquatic habitat. Movements of individuals #1 (June 14-June 26, 2005), #5 (July 26-October 8, 2005) and #23 (May 1-June 11, 2006), all sub-adult females, are shown overlaid on the model.

DISCUSSION

For each significant model, alligators were more likely to occur in high ranked wetlands and less likely to occur in low ranked wetlands than would be expected due to chance, indicating that the variables used in these models were accurate predictors of alligator habitat use. All significant models included descriptive variables, and most also included variables related to spatial relationships of wetlands, but no significant models were composed solely of the latter variables.

Alligators of different size and sex use habitats for distinct purposes, for example refuge, nesting, and dispersal. As such, I found variation in the predictive capability of the models for each of the four datasets according to different wetland characteristics that corresponded to use of wetlands by alligators of different life stages. For the Presence and Burrow datasets (Fig. 4-1(a,b)), the size*type*nearest neighbor model had the largest deviation from expected values for both the low and high ranked wetlands, suggesting that this model may be the best predictor of both wetland use, in general, as well as long-term habitation by alligators. For the Nest dataset (Fig. 4-1 (c)), the size*type model had the largest deviation from the lowest ranked wetlands, but the size*type*distance model had the largest deviation from the highest ranked wetlands, suggesting these three variables were most important in predicting nesting site wetlands. The importance of distance from the riverine system in predicting nesting site wetlands fit my predictions, given the frequent movement between the two systems by nesting females. For the Dispersal datatset (Fig. 4-1 (d)), only the size*type*proximity dataset

was significant, indicating that these three variables were most important to predicting

wetlands used as "stepping stones" during dispersal events.

Nearest neighbor appeared to be a more effective predictor than proximity for

Presence, Burrow, and Nest datasets, but the proximity metric performed better for the

dispersal wetlands dataset. Because the proximity metric is weighted by the area of each

wetland around the target wetland, it produced a higher suitability rank for small

wetlands with large wetlands nearby. Although small wetlands may not be suitable for

long-term use alone, it is likely they contribute to the overall connectivity of the

wetlands. The proximity metric may thus be a suitable addition to models designed to

capture the relative importance of these "stepping stone" wetlands.

The importance of stepping stone wetlands and intact upland matrix to landscape

scale connectivity is illustrated by the landscape-scale habitat suitability model I

constructed (Figure 4-2). By maintaining a range of different sized wetlands in a well-

protected upland matrix, larger, more suitable wetlands are accessible to alligators

through regions of high suitability that connect the riverine and wetland systems. These

corridors may allow alligators to travel longer distances overland to reach suitable

wetlands than they would be able to do otherwise. Radio telemetry data supported my

prediction that alligators move overland between bodies of water that were in proximity

to other bodies of water or connected by intact upland habitat. Almost all overland

movements by alligators documented using radio telemetry likely occurred in the two

highest habitat suitability categories. Furthermore, movement between the wetland and

riverine systems occurred in all but one instance at locations predicted as high suitability by the cost grid model.

My findings are consistent with other habitat models for seasonal wetland systems showing that patch characteristics, such as size and hydroperiod, and connectivity characteristics, such as distance to the nearest wetland, are important variables in predicting wetland suitability for an organism of interest (Snodgrass et al. 1999; Snodgrass et al. 2000; Attum et al. 2007). However, additional spatially-explicit variables, such as distance to permanent water and a neighborhood-based metric of wetland proximity, also contributed significantly to the alligator models, especially for nesting females and dispersing juveniles, respectively. This demonstrates the importance of considering different components of the population (e.g., sexes and life stages), which may differ in habitat use or vagility, when constructing habitat suitability models (Weaver et al. 1996; Amat 2005; Belisle 2005). When considering how elements of the matrix affect connectivity between aquatic systems, both overland distance and upland landuse appear to be important for alligators. My suitability map clearly demonstrates the importance of conserving a range of wetland types and sizes, regardless of their individual level of suitability, in order to promote overall connectivity across the landscape.

Current conservation approaches for isolated, seasonal wetlands focus on protecting large wetlands and buffer zones around them (Snodgrass et al. 2000; Roe et al. 2003; Babbitt 2005). However, for species which use multiple habitat types and have high dispersal rates between them, small wetlands and intact upland habitat can be

crucial to maintaining connectivity and suitability of larger wetlands (Joyal et al. 2001; Naugle et al. 2001). In conclusion, seasonal wetlands are not isolated at all; they are connected to one another, to their upland surroundings and to nearby riverine systems through the movement patterns of species that inhabit them. As a result, the protection of a single species may be dependent on the conservation of multiple interconnected habitat types. Conservation efforts to protect both the species and the habitat must consider the landscape-scale connectivity of the system as well as the changing needs of different components of the population.

CHAPTER V

CONCLUSIONS

There have been many studies on American alligators, almost all of which have taken place in contiguous coastal marshes and large reservoirs. Consequently, survey methods are designed to work within those systems, and knowledge of the ecology and habitat use patterns of alligators are similarly system-specific. In certain portions of their inland range, alligators have been found to use seasonal wetlands and riverine systems. To study these populations, appropriate survey methods are needed.

I used a double-observer approach to study the effectiveness of eyeshine surveys in seasonal wetlands. I analyzed my data using a Huggins' closed capture analysis in MARK and found that eyeshine surveys detected 56% of the alligators present in the most general model. There was some evidence for different detection probabilities by observer, but there was no evidence for difference by wetland type, which in this case ranged from forested wetlands to grassy marshes. With this model, I derived an abundance estimate of ~130 alligators in the 7 seasonal wetlands I surveyed; however, more observations are needed to produce a more reliable abundance estimate.

I compared eyeshine surveys to the use of both Tomahawk cage traps and trip-snare traps to determine which method most effectively surveyed a range of size classes. I found that the use of both trap types allowed the detection of a wide and continuous range of size classes, from juveniles to adults. Eyeshine surveys and trapping efforts differed in their ability to detect alligators in different types of seasonal wetlands, but the

trends were not consistent. In low density populations such as these, multiple methods are probably needed to thoroughly survey all components of the population.

In order to determine habitat use by different size classes in the wetlands versus the riverine system, I used equal trapping efforts across both systems using both trap types. Alligators captured in the wetlands were significantly smaller than alligators captured in the riverine system, and there was a significant interaction between sex and habitat. Only juvenile males were captured in the wetlands while only adult males were captured in the creek, whereas females of both size classes were captured in both systems. This variation in sex and size classes in the different habitats may indicate the wetlands are serving as nursery sites. All nesting events documented during the course of the study were located in the wetland system. The use of radio telemetry also showed differences in overland movement rates by sex and size class. All overland movements were made by sub-adults undergoing an ontogenetic shift or by adult females moving into nesting habitat in the wetlands. No adult males were documented using the seasonal wetlands or making any overland movements during the course of this study, although previous observations suggest they may use wetlands during wet years (A.L.S., pers. obs.).

The difference in size classes between the two systems and the movement of juveniles into adult habitat implies that the wetlands serve as nursery sites for alligators in this portion of their range. Their movement from the wetland into the riverine system as they grow, and subsequently back into the wetlands for nesting, establishes them as a mobile link between these two systems. Mobile links, especially those that also act as

keystone species, can have substantial impacts on the structure and function of the ecosystems they use. Their conservation relies on the protection of the multiple habitats they use as well as the interconnecting matrix.

To understand what variables were important to wetland use by alligators, I constructed a habitat suitability index of the wetlands on site using descriptive characteristics, such as wetland size and type, and spatially explicit characteristics, such as distance to the nearest wetland, proximity of multiple wetlands within a specified neighborhood and distance to the creek or river. Because different components of the population may have different habitat needs or levels of vagility, I tested a variety of models with several datasets representing all alligator use, long-term use as indicated by burrows, use by nesting females and use by dispersers. I found that both descriptive and spatially explicit characteristics were important in predicting alligator use, but that the importance of different variables depended on which component of the population was being modeled.

I constructed a habitat suitability model for the Ichauway landscape to determine what variables were important to overland dispersal between the aquatic ecosystems. I developed my model as a function of both upland landuse and distance between aquatic habitats. I tested this model using locality data of alligators obtained with radio telemetry and simulated movement paths. Alligator movements were positively associated with intact upland habitats and negatively associated with increasing distance between bodies of water. The landscape scale habitat suitability model illustrated the importance of

conserving a variety of wetland sizes and types within an intact matrix to facilitate overland dispersal.

The use of seasonal wetlands as nursery sites by American alligators in this portion of their range, and the subsequent overland dispersal into riverine systems as they undergo ontogenetic shifts, establishes alligators as mobile links between these disjunct ecosystems. Although seasonal wetlands are traditionally considered to be isolated, and the removal of federal protection of this critical habitat was based on their lack of hydrological connectivity to navigable waterways, animal movement patterns clearly can establish a degree of functional connectivity between the systems. In order to protect species which use multiple habitat types throughout their lives, as well as to protect the multiple ecosystems that those species impact, conservation must be undertaken on a landscape scale.

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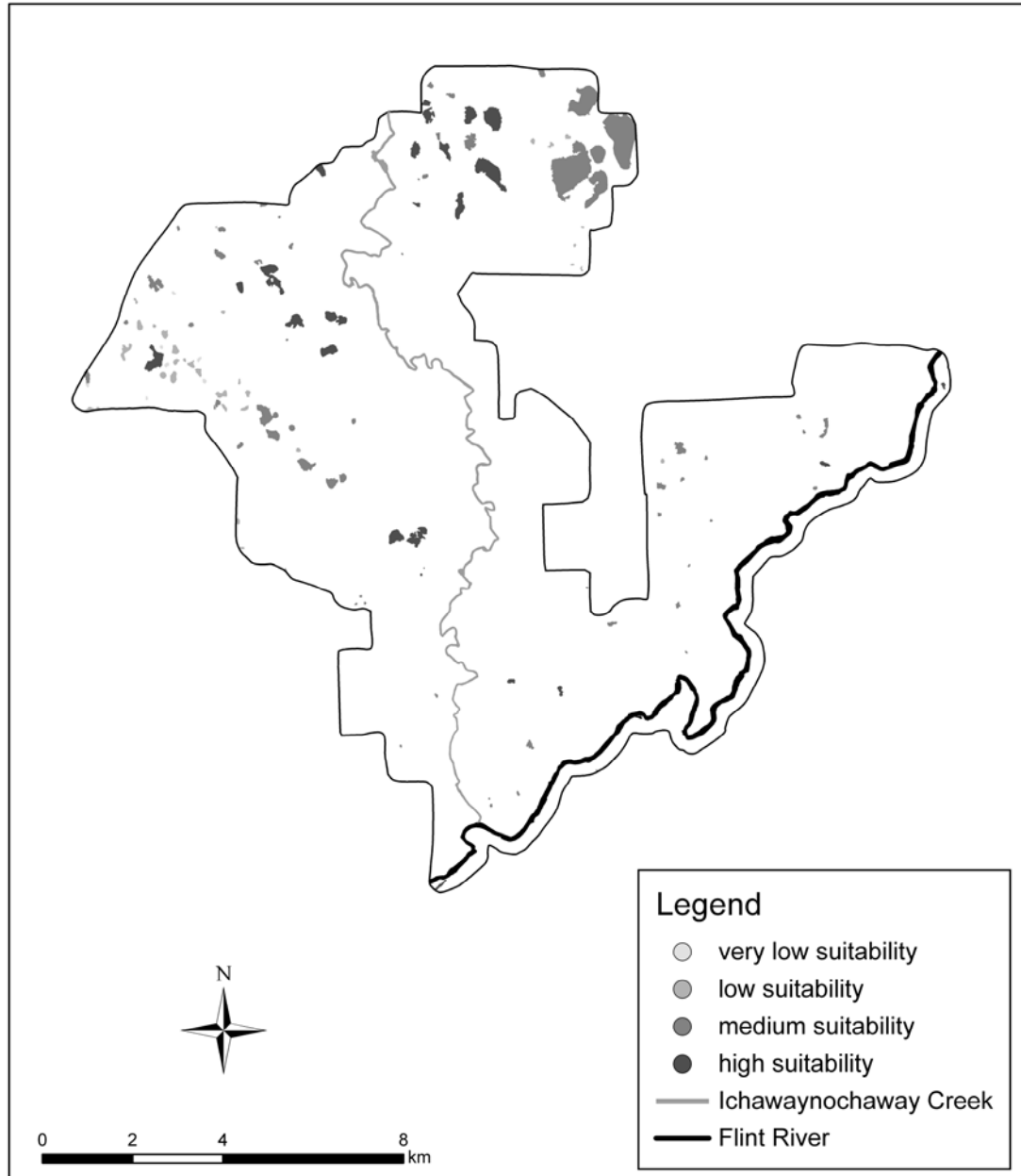
APPENDIX I

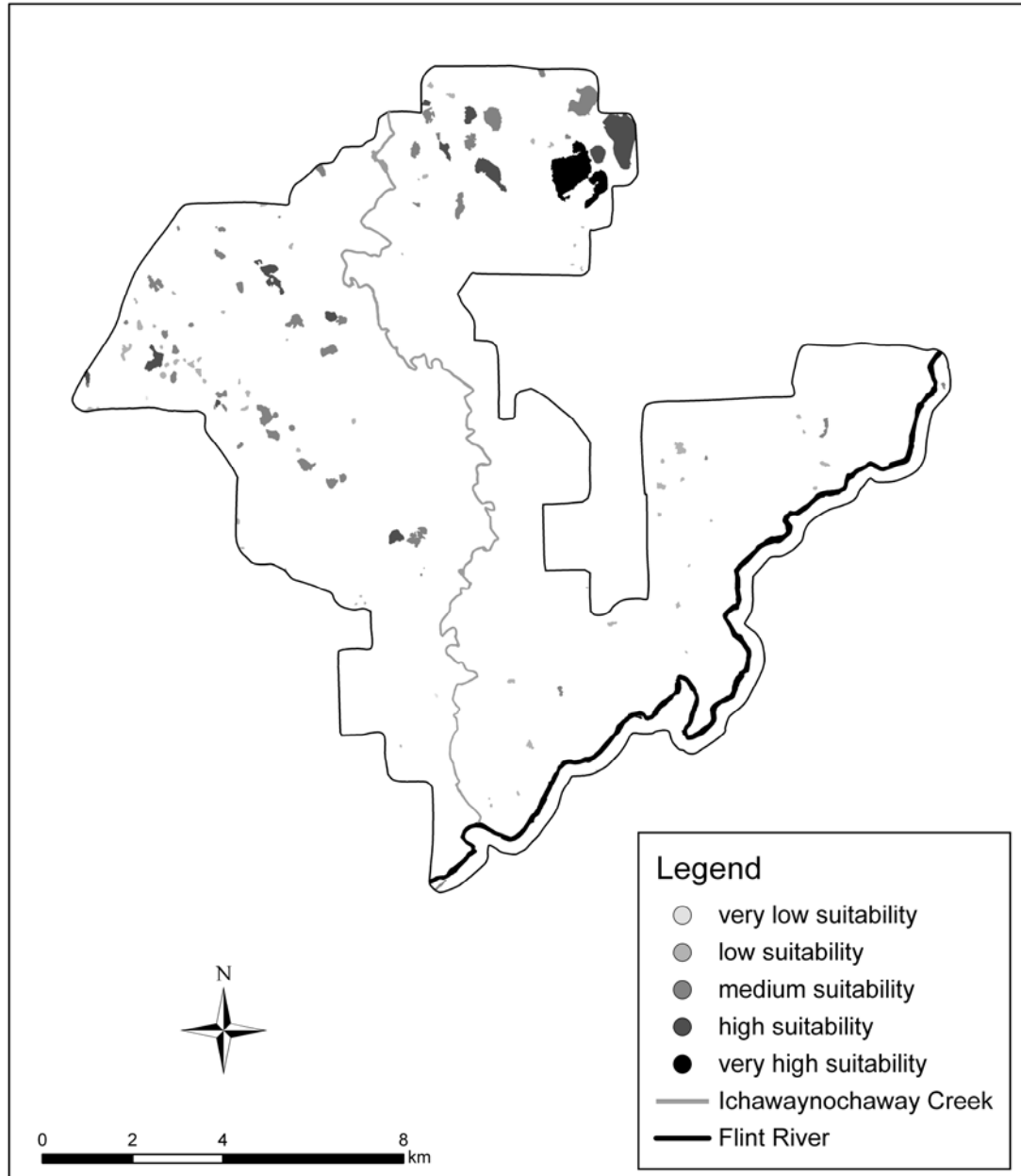**WETLAND SUITABILITY MAPS SHOWING THE**

7 MODELS AND 4 DATASETS USED
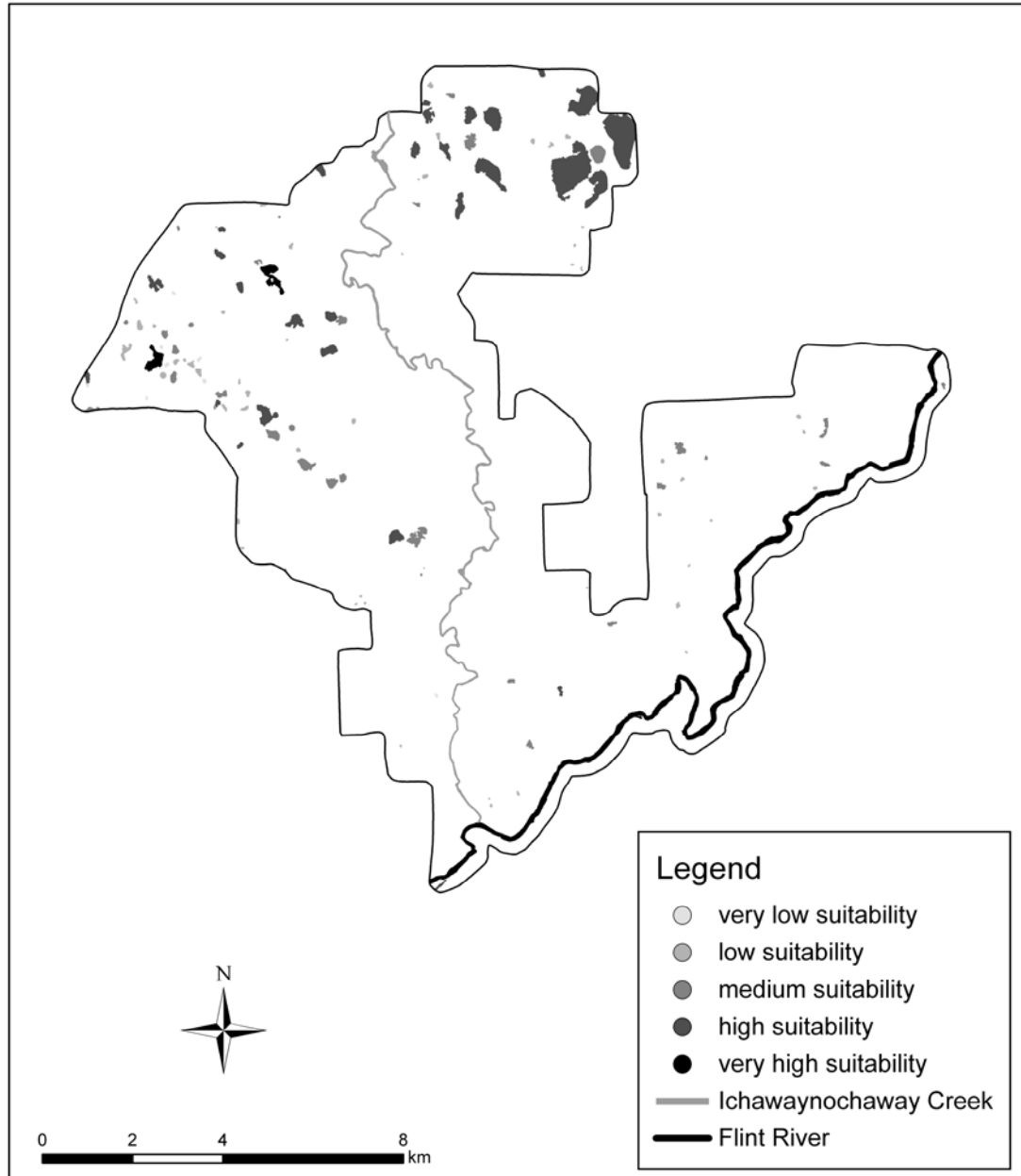
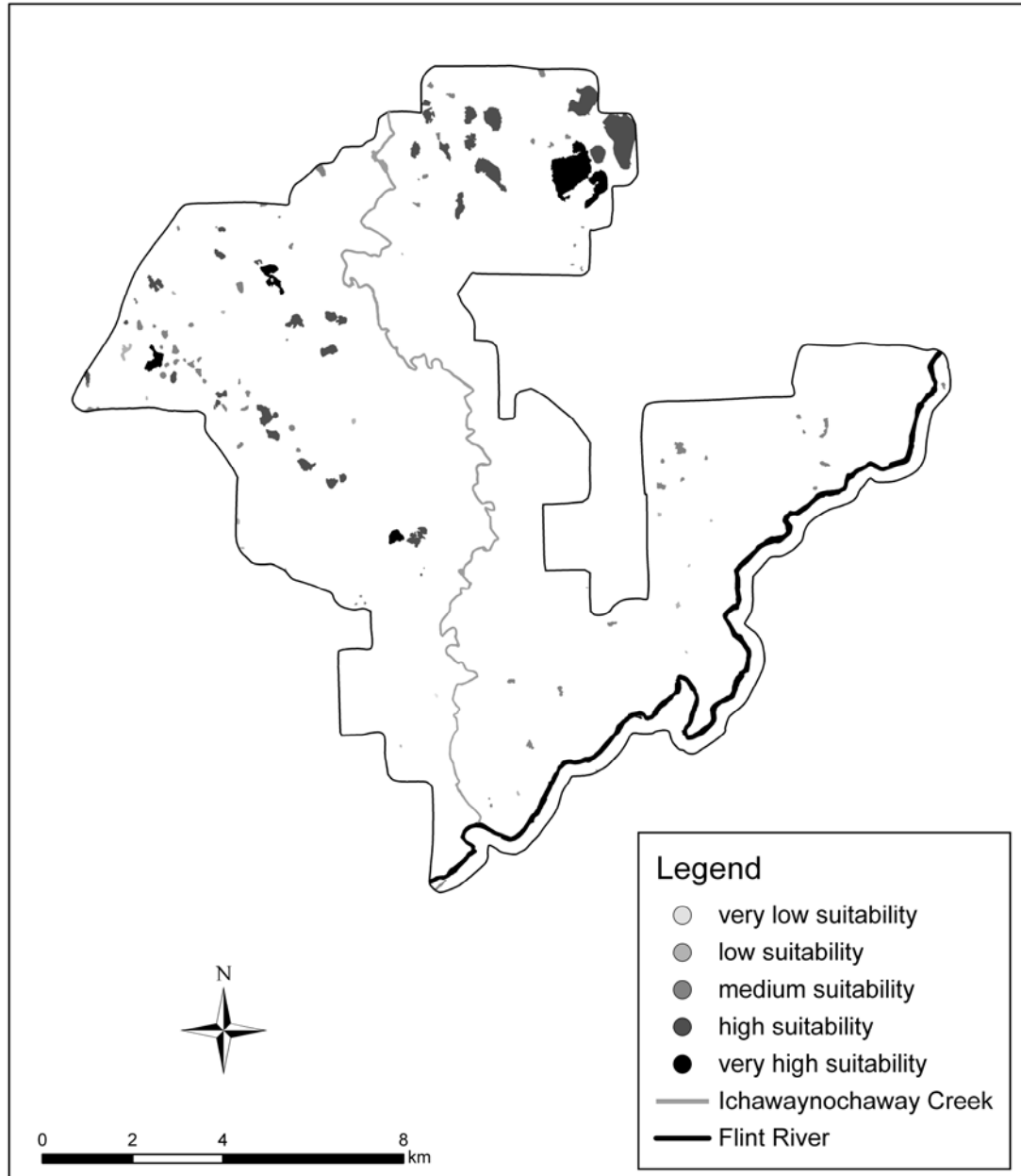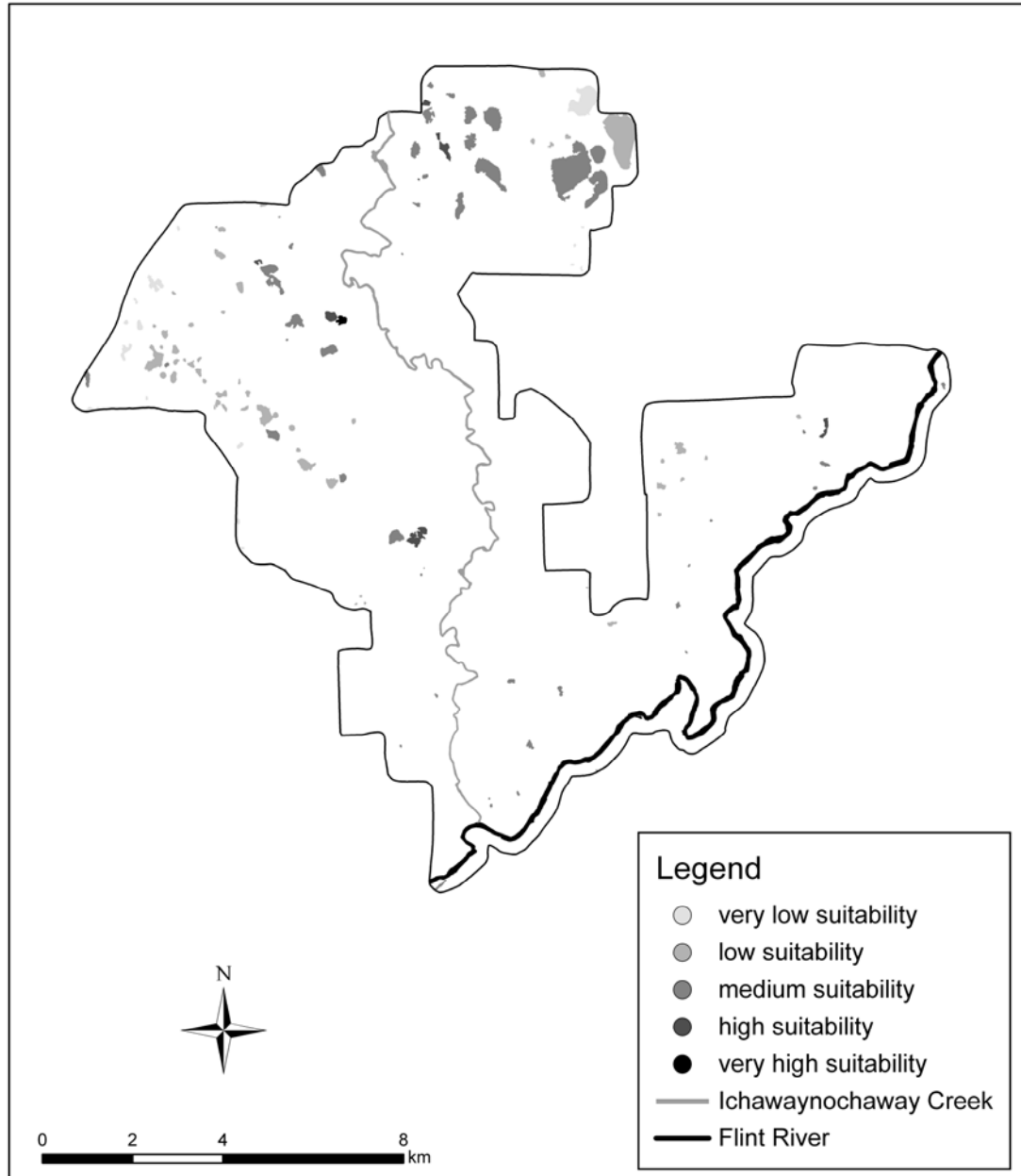Appendix 1(a): Size*type model for wetland suitability for alligators on Ichauway.

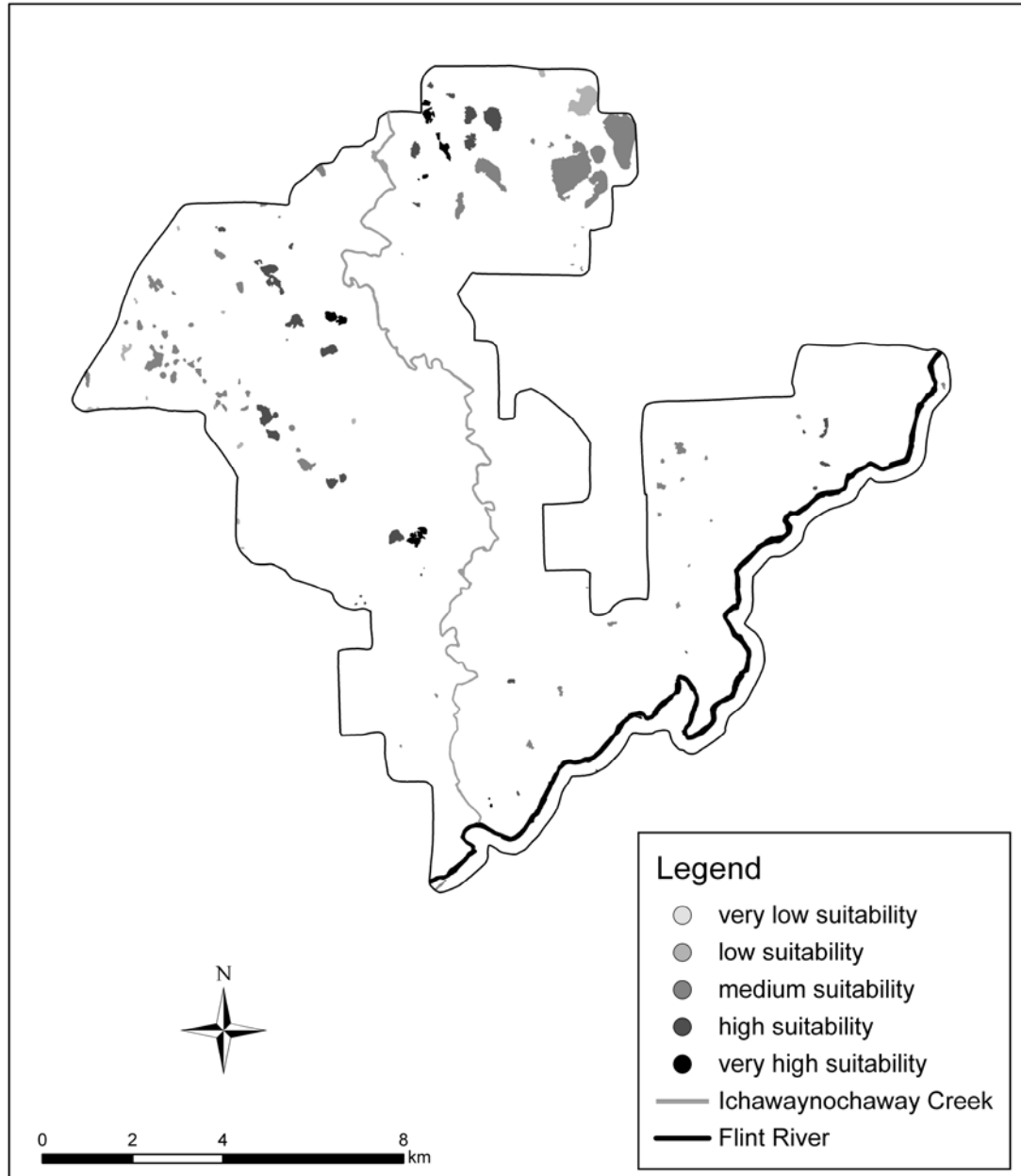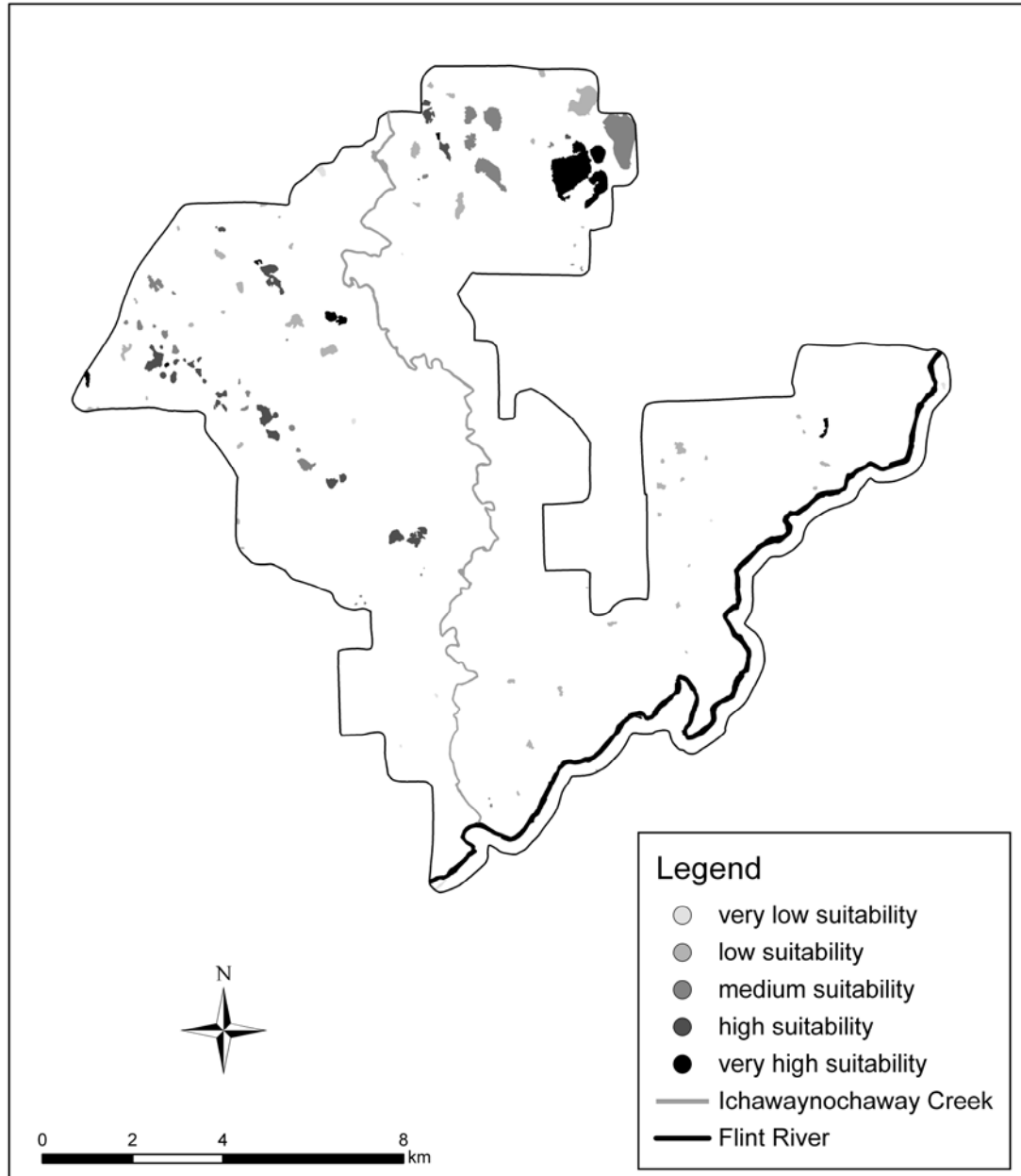Appendix 1(b): Size*type*distance model for wetland suitability for alligators on Ichauway.

Appendix 1(c): Size*type*proximity model for wetland suitability for alligators on Ichauway.

Appendix 1(d): Size*type*nearest neighbor model for wetland suitability for alligators on Ichauway.

Appendix 1(e): Proximity*distance model for wetland suitability for alligators on Ichauway.

Appendix 1(f): Nearest neighbor*distance model for wetland suitability for alligators on Ichauway.

Appendix 1(g): Proximity*nearest neighbor model for wetland suitability for alligators on Ichauway.
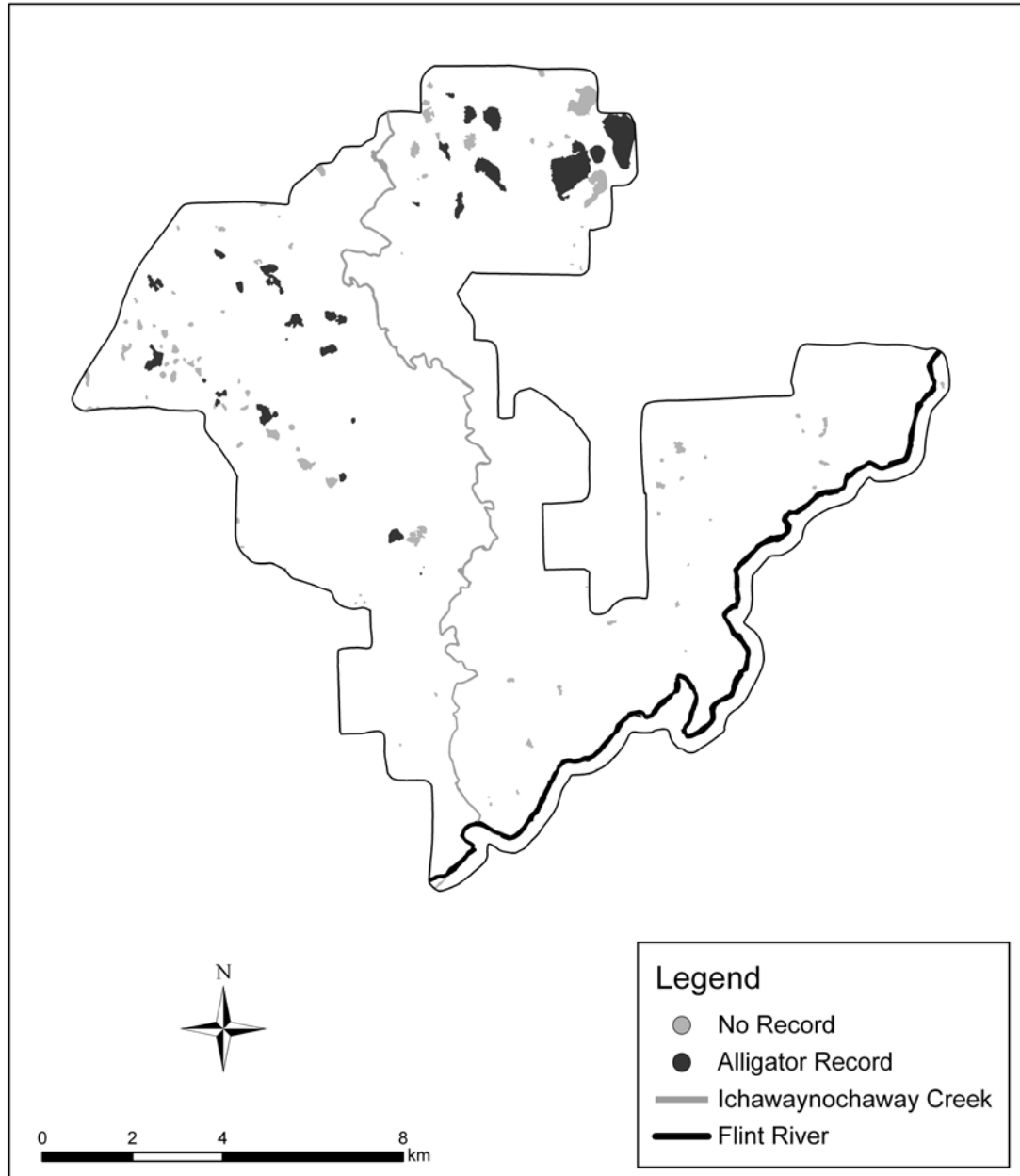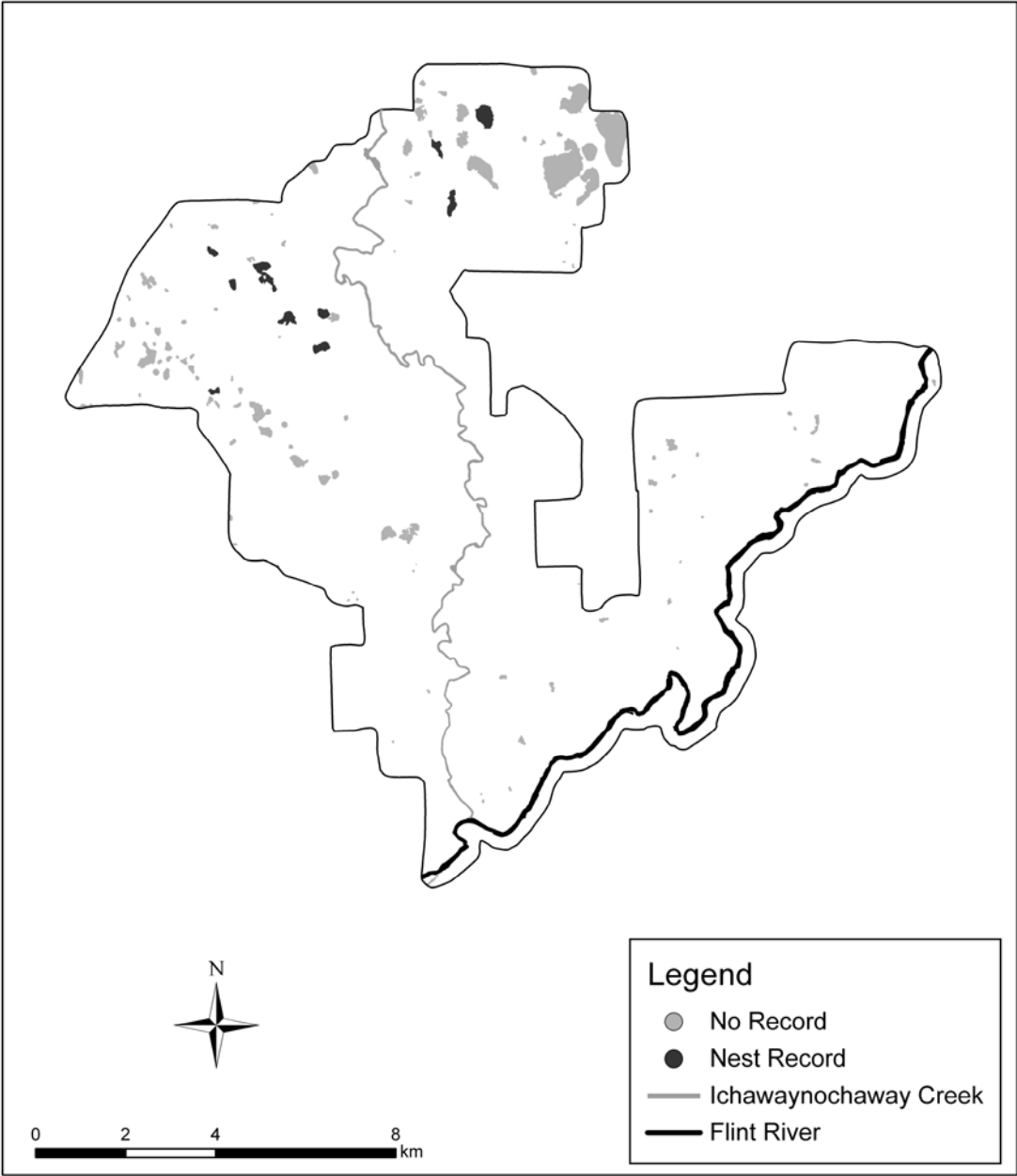
Appendix 1(h): Map showing all wetlands with any record of alligator presence.
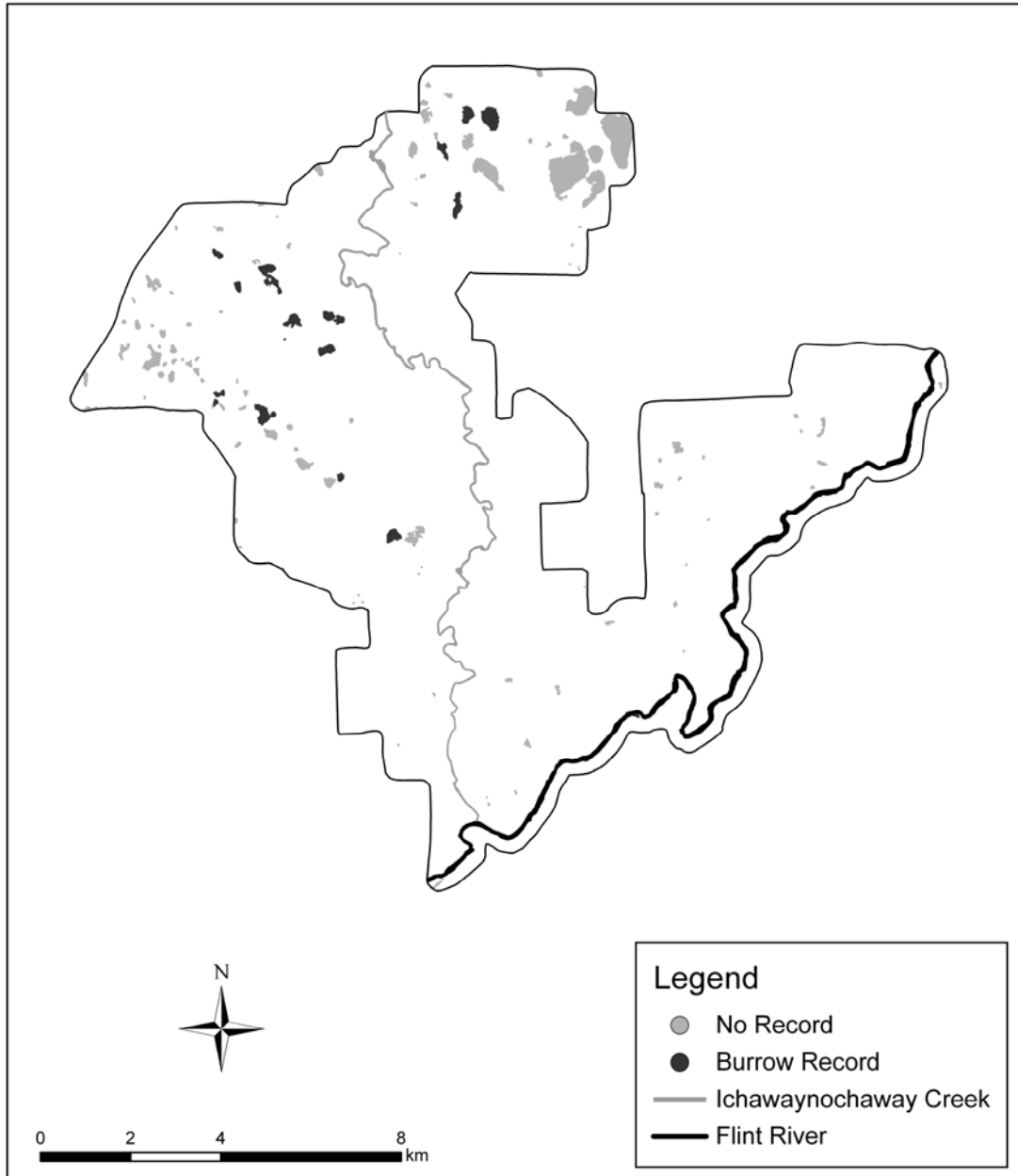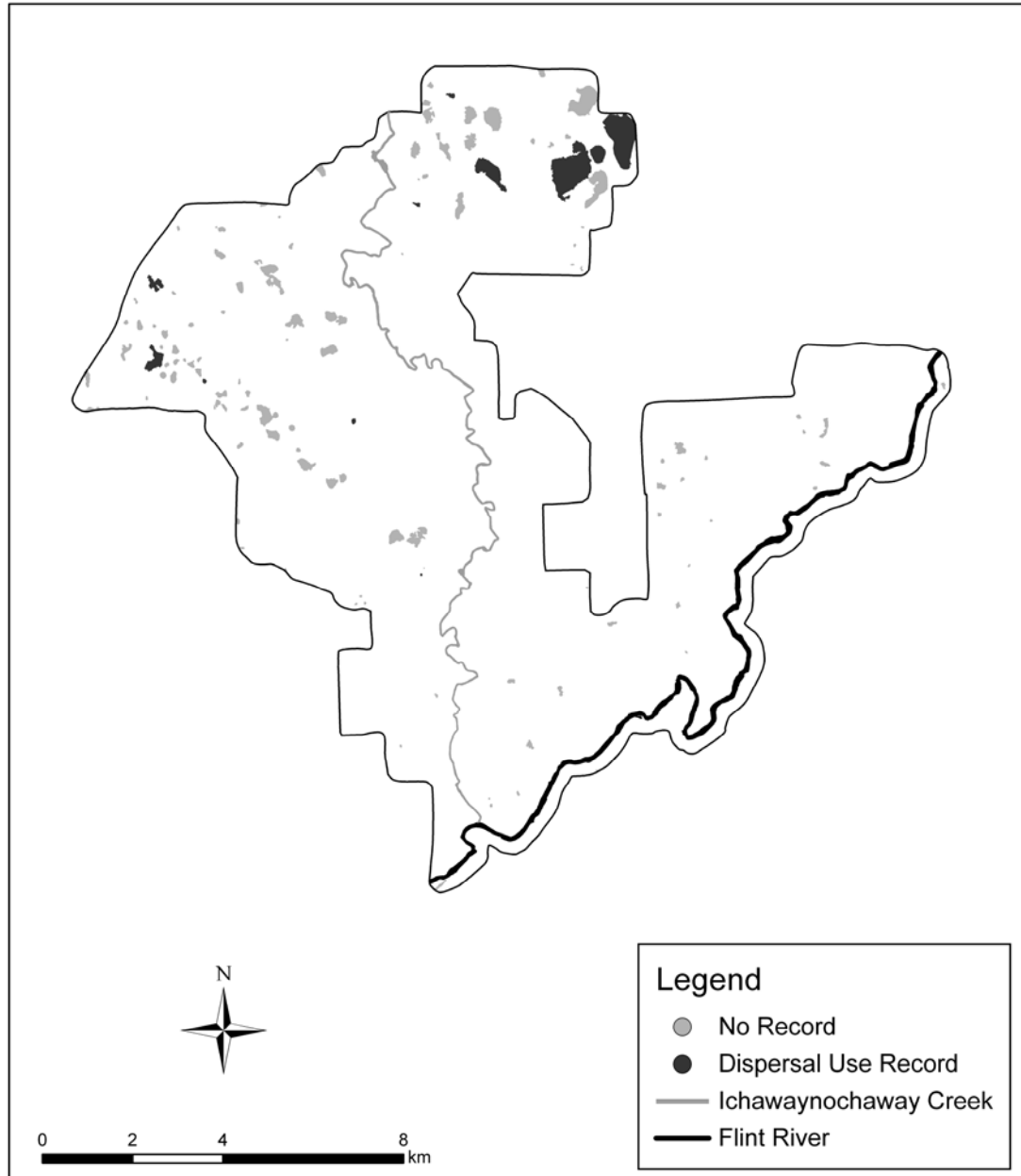
Appendix 1(i): Map showing all wetlands with any record of alligator burrows.

Appendix 1(j): Map showing all wetlands with any record of an alligator nesting event.

Appendix 1(k): Map showing all wetlands with any record of alligator presence but no record of alligator burrows.

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