Spatial ecology and population estimation of the American alligator (*Alligator mississippiensis*) in inland systems of Mississippi

By

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Wildlife management and conservation frequently rely on understanding mechanisms that influence distribution and abundance of animals. I quantified space use for a population of inland riverine adult male alligators in Mississippi. Results indicated habitat selection is a scale-dependent process and aquatic vegetation, water depth, and water temperature may be important factors influencing alligator foraging and thermoregulation. Apparent habitat suitability and low alligator density did not manifest in an observed body size-based dominance hierarchy. I also analyzed long-term Mississippi alligator spotlight survey data for trends and effects of environmental covariates on counts. Model results indicated alligator counts have increased over time. This response likely reflects benefits accrued from decades of protection and wetland conservation. Distance sampling does not appear to be a feasible monitoring technique for riverine alligator populations. Nevertheless, it is important that survey protocols and monitoring programs account for imperfect detection and model important covariates.

DEDICATION

I dedicate this thesis to my wonderful family (Mom, Dad, Carrie, and Alex) and my lovely girl (Katherine). Without each of you, my studies would have been a near impossible endeavor. Your support, encouragement, and love were beacons in the dark.

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CHAPTER I

INTRODUCTION

The American alligator (*Alligator mississippiensis*), herein “alligator,” is a generalist top predator that potentially has top-down effects, mobile vector of nutrients between terrestrial and aquatic systems, and ecosystem engineer that manipulates water flow and influences plant communities (Mazzotti et al., 2009; Rosenblatt & Heithaus, 2011). The alligator is a well-studied species of crocodilian with a considerable body of literature available on most aspects of its biology, physiology, and behavior. Despite considerable research in coastal estuarine systems on habitat use, movement patterns, and population dynamics, few studies have examined inland alligator populations. Consequently, ecological information of alligators has been generalized from coastal studies to populations in the larger inland portion of the alligator’s range. This information may rely on untested assumptions about similarities of habitat, resource use, and biological interactions in these two different systems (Webb, Zuur, Calkins, & Duguay, 2009). No apparent differences in genetic structure exist between coastal and inland alligator populations; however, subdivisions among populations (coastal and riverine) have been argued given potential reduced gene flow in the more fragmented and isolated landscapes of inland systems (Ryberg, Fitzgerald, Honeycutt, & Cathey, 2002). Alligator populations in coastal areas use relatively homogeneous shallow marshes and wet prairies with occasional open water and canals, whereas inland alligators occupy a more spatially and structurally heterogeneous environment (Subalusky, Fitzgerald, & Smith, 2009). Inland alligators inhabit wetlands, river and creek drainages, and natural and manmade ponds and reservoirs with areas of shallow vegetated and deep open water (Webb et al., 2009). Differences in resource availability, seasonality, and other environmental parameters may result in varying life history patterns, habitat selection, and demographics. Increased ecological knowledge of the alligator throughout its distribution, especially when harvest and management strategies have been generalized to inland populations, is needed. Plausibility of genetic and behavioral differences suggests uniform management strategies may not be appropriate for all alligator populations (Webb et al., 2009).

Several studies represent alligator populations in different states and regions of the United States (e.g., South Carolina (Brandt, 1991); Louisiana (Joanen & McNease, 1972); Texas (Altrichter & Sherman, 1999); Florida (Rosenblatt & Heithaus, 2011); and Georgia (Subalusky et al., 2009)). Nevertheless, there has been virtually no research conducted in Mississippi on alligators. More importantly, research at the northern most limit of the species distribution is lacking. My studied population is at or near the northern limit of the species' range. Ecological processes may be more variable at boundaries of geographic distributions due to increasing gradients in biological and environmental parameters (Sexton, McIntyre, Angert, & Rice, 2009). Information on alligator population ecology and resource selection will contribute to knowledge of this important predator in the state.

Using radio-telemetry and population estimation methods, my research will contribute to ecological knowledge gaps of inland riverine populations in Mississippi by:

1) quantifying home range and resource selection at multiple spatial scales, 2) addressing potential exhibition of a size-dependent dominance hierarchy, 3) evaluating trends and effects of covariates in long-term state alligator surveys, and 4) recommending improvements to a state alligator monitoring program. Providing this information will contribute to the conservation and management of alligator habitat and populations across the species' entire range. Particularly as alligators have recently been listed as a game species in Mississippi, science-based management must rely on ecological knowledge for decision-making.

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CHAPTER II

SCALE-DEPENDENT HABITAT SELECTION AND SIZE-BASED DOMINANCE IN ADULT MALE AMERICAN ALLIGATORS

Introduction

Wildlife management and conservation frequently rely on understanding mechanisms that influence spatial distribution of organisms (Kennedy & Gray, 1993). Animals distribute themselves in the environment by searching for the most suitable areas that provide adequate food, access to mates, and resources for other behaviors (e.g., denning and thermoregulation) to optimize reproduction and survivorship, and consequently, fitness (Oro, 2008). Habitat selection is a hierarchical process varying across spatial and temporal scales (Johnson, 1980; Krausman, 1999). From habitat selection theory, one assumes that an animal chooses a home range and then makes decisions about what resources and patches to use (Johnson, 1980). The most important limiting factors are suspected to drive behavior and influence selection at the coarsest scales (e.g., population, home range), maximizing individual fitness (Rettie & Messier, 2000). Therefore, habitat selection at a single scale may not reflect patterns at other scales. Also, habitat selection is an active behavioral process involving innate and learned behaviors (Krausman, 1999). This makes the selection process complex and influenced by more than just resource availability, including factors such as predation and competition (McLoughlin, Morris, Fortin, Wal, & Contasti, 2010).

Behavioral mechanisms such as dominance may affect the spatial distribution of conspecifics (Fretwell, 1972). Despotism, through dominance hierarchies or territoriality, arises when competitive asymmetry constrains the ability for any individual to occupy all areas within the habitat (Calsbeek & Sinervo, 2002). The result is spatial segregation and exclusion of subordinates from the most suitable resources (Belant, Griffith, Zhang, Follmann, & Adams, 2010; May et al., 2008). Therefore, dominance serves to manage intraspecific risk where an aggressive contest may result in injury or death and results in the despot securing an unequal stake of resources to improve fitness. Dominance in animal social structures is manifested through traits including age, gender, body size, and aggression (French & Smith, 2005). Further, dominance rank can purportedly influence an individual's reproductive success, survivorship, foraging efficiency, and may also influence movements and resource selection (Beacham, 2003; French & Smith, 2005).

Crocodilian social behavior has been largely characterized by size-dependent absolute hierarchies (independent of time and location), where large, aggressive males control access to mates and food (Drews, 1990; Kaufmann, 1983; Kay, 2004; Lang, 1987). This social structure has been observed in captive American alligators (Garrick, Lang, & Herzog, 1978; Vliet, 1989), but evidence is lacking for wild populations. Social dominance in crocodilians appears to be asserted by species-specific, complex social signals (e.g., exposing body length and inflating posture) (Lang, 1987). Social signals such as headslapping and bellowing are observed frequently in adult male alligators during the breeding season and may serve to define territory, claim mates, and establish dominance (Vliet, 1989). In contrast, submission is demonstrated by retreating underwater on approach or by lifting the head and submerging the body (Lang, 1987).

Understanding the mechanisms that drive habitat selection of crocodilians is valuable given that their role as top predators in aquatic ecosystems can influence lower trophic levels through top-down effects (Rosenblatt, Heithaus, Mazzotti, Cherkiss, & Jeffery, 2013; Subalusky, Fitzgerald, & Smith, 2009). My objective was to examine the social structure and space use of a wild population of male American alligators in an inland riverine system. My intention was to adequately address both selection and dominance; thus due to logistic and monetary limitations I only studied one population segment. I studied habitat selection at a coarse scale (home range) and a fine scale (patch) to determine if congruency in selection existed and what habitat variables are important for selection. Overall, I did not expect congruency in resource selection between scales because one general habitat selected at the coarse scale is unlikely to satisfy the multiple needs (e.g., thermoregulation, foraging) that are more important in finer scale selection. If a dominance hierarchy is present, I would expect larger, dominant alligators to control access to more suitable resources and that individual resource selectivity would be a function of conspecific body size at both scales, but particularly for the selection of home range. I predicted that selection of, and proximity to, areas of deep, open water (suitable habitat) (Joanen & McNease, 1972; Webb, Zuur, Calkins, & Duguay, 2009) within home ranges will increase with increasing body size. Also, I predicted dominant individuals will have smaller home ranges (despite larger energetic needs) because they occupy more suitable habitat.

Study Area

I conducted the study on the Pearl River and the upper portion of the Ross Barnett Reservoir (RBR) in central Mississippi (32°31’12.3”N 89°55’28.1”W; Figure 2.1A, 2.1B). The Pearl River is a sand- and gravel-bottomed river that originates in northern Mississippi and flows southwest to the Mississippi Sound draining 23,000 km^2 of bottomland forest and agricultural lands (Piller, Bart, & Tipton, 2004). The RBR is a 133.5 km^2 monomictic, mesotrophic reservoir created from an impoundment of the Pearl River in 1964 to meet the water supply needs and provide recreational opportunities for the residents of Jackson, Mississippi and surrounding counties (Cooper & Knight, 1985; Piller et al., 2004). The reservoir has a 3.66 m mean depth (10.67 m maximum) where annual water level fluctuations average less than 1 m and few littoral areas become dewatered at any point during the year (Cooper & Knight, 1985).

Methods

Capture and tagging

In spring and summer 2012 assisted by Mississippi Department of Wildlife, Fisheries, and Parks agent trappers, I captured adult male alligators using a rod and reel. I attached a weighted (57 g lead) 10/0 treble hook to 68 kg test braided, hi-vis yellow line via a Palomar knot and casted with a heavy duty baitcast reel and a 2.4 m medium-heavy action rod to snag alligators from a distance. I used a 3.2 mm restraining line, 1.5 m locking cable snare, and 12.7 mm cotton rope (4.5 m in length) to hoist and restrain animals. Also, I used electrical tape and 6.4 mm nylon rope to secure the mouth and tie the legs. For each captured alligator, I recorded gender from cloaca examination (Chabreck, 1963) and measured total length (TL) from the tip of the snout to the end of the tail following the dorsal contour (Table 2.1). I attached a numbered livestock tag (Duflex #6341 and #6321; Destron Fearing; South St. Paul, Minnesota, USA) visible from either side of the tail in the second posterior scute after the scutes merged into a single row and a small metal clip tag (1005-3 or 1005-681 (size 3); National Band & Tag Co.; Newport, Kentucky, USA) in the webbing of each hind foot between the second and third toe.

I fitted each adult male alligator (TL > 1.83 m; Chabreck, 1963) with a radio-transmitter (Ultimate V5H 227A; Sirtrack; North Liberty, Iowa, USA). First, I cleaned scutes with a disinfectant solution and drilled a 3.2 mm hole into each of the last 4 tail scutes before the scutes merge into a single row. I then threaded stainless steel wire (0.14 mm diameter) encased in nylon tubing (3.175 mm diameter) through the transmitter and into the holes made in the 4 scutes (A.E. Rosenblatt, Yale University, personal communication). Once the transmitter was fitted between the rows of scutes, I inserted the wire through one scute, the holes of the transmitter, then the hole of the paired scute. I continued threading the same wire through the other paired scutes and tied the ends of the single wire. To reduce potential loss of the transmitter, I covered exposed wire and transmitter with marine-grade epoxy (PC-11; PC-Products; Allentown, Pennsylvania, USA). Finally, I released all animals at the capture site after handling. Animal capture and handling procedures were conducted under Mississippi State University Institutional Animal Care and Use Committee protocol 12–016.

Radio-telemetry

I tracked adult male alligators from 1 March to 15 October 2012–2013 from sunrise to sunset; tracking dates correspond with the period of greatest alligator activity at this latitude (Chabreck, 1965; Joanen & McNease, 1972; McIlhenny, 1935). A tracking route with each animal's expected location was generated using each individual's capture site or recent locations. I started tracking each day at random start times (between 0600 to

1300 hours) allowing enough time to locate all individuals. I selected the first tracked individual using a random number generator. If I did not observe a radio-marked alligator at its expected location, I searched for it in the vicinity and along the tracking route, while continuing to locate other animals. Typically (about 90% of tracking days), all animals were searched for in one daily effort. I randomly selected the direction of tracking along the route daily and order of animals on the tracking route every three months.

I performed radio-telemetry from a boat by homing to a specific transmitter using a VHF digital receiver (TR-5; Telonics; Mesa, Arizona, USA) and a 3-element Yagi antenna (Sirtrack; North Liberty, Iowa, USA). It was frequently impractical or impossible to pinpoint an animal's exact location due to thick emergent aquatic vegetation or shallow water. In these cases, I approached the radio-marked alligator and homed on the direction of the "strongest signal" (Springer, 1979), taking a directional bearing using a magnetic compass (KB-14; Suunto; Vantaa, Finland), while attempting to minimize disturbing the animal.

I conducted an evaluation to estimate distance of radio-transmitters at a specific receiver gain using signal strength (White and Garrott 1990). First, I attached transmitters to channel markers in open water (*n* = 6) about 5–10 cm below the surface and within representative vegetation (*n* = 5) to assess signal attenuation and reflection. I oriented the antenna toward the transmitter and recorded receiver signal strength at each gain level (215 to 235 units in 5-unit increments) from 600 to 25 m at increments of 100, 50, or 25 m. I measured distances using a laser range finder (Elite 4200; Bushnell; Overland Park, Kansas, USA) and verified these distances using a hand-held GPS. Using this data, I conducted generalized linear models to predict distance at a given signal strength and gain. I ran a null model and then global models including all combinations of signal strength and gain as well as interaction and quadratic terms. I used Akaike's Information Criterion corrected for small sample sizes (AICc) for model selection (Burnham & Anderson, 2002).

I conducted additional trials to estimate telemetry angular and location error, and determine bias and sampling error (Springer, 1979; White & Garrott, 1990). A technician hid transmitters (*n* = 10; 4–7 locations each) in open water or locations representing the range of vegetation conditions about 5–10 cm under the surface of the water. A technician, without knowledge of transmitter location, estimated direction to the transmitter using the strongest signal. Bearing, signal strength, gain, and location were recorded at about 2-minute intervals from the time the signal was heard until it was found. I used this information to generate an estimated distance from the transmitter predicted by the best linear model from the previous trial. I compared these distances and bearings to distances and directions verified using GPS to yield location and angular errors. Finally, I used Student's t tests to compare mean errors to 0 to estimate bias.

Spatial database development and resource variables

I obtained aerial imagery flown in August 2012 from the United States Department of Agriculture's National Agriculture Imagery Program (Figure 2.1B; 1-m resolution, natural color spectral resolution) (United States Department of Agriculture, 2012). I clipped the raster dataset to the study area using a minimum convex polygon (MCP) of all relocations plus a 30 m buffer to account for radio-telemetry error. I also obtained a water depth grid of RBR with 8-m resolution collected by the Mississippi Department of Wildlife, Fisheries, and Parks (1505 Eastover Drive, Jackson, Mississippi) in August 2005 (Figure 2.1D). I performed all geospatial analyses and resource variables map development using ArcMap 10.2 (Environmental Systems Research Institute; Redlands, California, USA).

Point intercept survey data collected by Sartain et al. (2013) in June 2012 provided detailed accounts of littoral zone (depths < 3 m) plant species at RBR. I overlaid the 300 m grid point intercept survey on the aerial imagery to identify, group, and validate pixel classification. Map pixels were categorized using maximum likelihood classification techniques based on visual color and reflectance signatures of the image (Figure 2.1C). I classified the map into 6 ecologically relevant habitats using the visual color and reflectance guidelines of Cox and Madsen (2011). Habitat categories included:

1) Main channel and reservoir open water (MC) – Boat and watercraft traffic was common through most areas of the main channel and reservoir.
2) Open water in backwater areas and oxbow lakes (OX) – Backwaters and oxbow lakes were dominated by different plant and animal assemblages than the main channel and are considered important habitats for fish reproduction and recruitment (Lehtinen, Mundahl, & Madejczyk, 1997; Sartain & Madsen, 2013).
3) Forests and swamps (SW) – This habitat included forested riparian areas along the main river channel, forested islands, backwater swamps, and surrounding oxbow lakes. Black willow (*Salix nigra*) and oak (*Quercus* spp.) dominated these areas and were interspersed with stands of pine (*Pinus* spp.). Alluvial swamps were characterized by bottomland hardwood trees including: bald cypress (*Taxodium distichum*), water tupelo (*Nyssa aquatica*), tupelo gum (*Nyssa sylvatica*), sugarberry (*Celtis laevigata*), elm (*Ulmus* spp.), and hickory (*Carya* spp.) (Conner

& Sharitz, 2005).

4) Shallow water wetlands (WT) – This habitat contained sediment and submersed vegetation dominated by native coontail (*Cerotophyllum demersum*) and exotic hydrilla (*Hydrilla verticillata*). Shallow wetlands were typically along the reservoir perimeter.
5) Floating, emergent vegetation (DV) – This habitat included dense mats of exotic alligator weed (*Alternanthera philoxeroides*) and water hyacinth (*Eichhornia crassipes*), native floating plants such as water primrose (*Ludwigia peploides*) and white waterlily (*Nymphatea odorata*), and thick concentrations of native grasses including giant cutgrass (*Zizaniopsis miliacea*) and cattail (*Typha* spp.).
6) Lotus (LO) – This habitat contained highly monotypic populations of American lotus (*Nelumbo lutea*), the most common littoral plant in RBR (Sartain et al., 2013).

To accommodate location error, I resampled the classified raster to 30-m resolution containing the dominant habitat in each 30 m by 30 m pixel. I also calculated Euclidean distances from the center of each cell to the main channel and nearest floating, emergent vegetation. I created a 30 m by 30 m point grid (points as centroids of 30 m by 30 m pixel) over the study site and assigned each grid point a habitat (binary output), distance-to-habitat, water depth, and geographic coordinates. Ground-truthed data using 25 samples from each habitat yielded a 94% accuracy rate.

Resource selection analysis

I used K-select analysis to estimate individual selection strategies on radio-marked individuals that had greater than 15 relocations per year (Calenge, Dufour, &

Maillard, 2005). This method allows evaluation of potentially correlated environmental variables that contribute most to habitat selection. In K-select analysis, a supplied habitat variable denotes one dimension in ecological space (sum of these variables is representative of multidimensional ecological space or niche). For each animal, a marginality vector points from the centroid of available resource space to the centroid of used resource space; vector direction indicates which variables are selected and vector length (squared distance) represents strength of selection by an animal (Calenge et al., 2005). Thus, differences in marginality vectors represent individual variation in selectivity of habitat. K-select analysis uses a non-centered principal component analysis (PCA) of a table of marginality vectors of each animal (row) on the habitat variables (column) to reduce the multidimensional resource space to principle components (factorial axes), each representing a linear combination of the original habitat variables, while maximizing marginality on the first axis (Calenge et al., 2005; Calenge, 2007). Biological significance of the factorial axes can be inferred from loadings of each environmental variable (Calenge et al., 2005).

K-select analysis is hierarchical and allows for multi-scale evaluation of resource selection. I analyzed second-order (home range level) habitat selection (Johnson, 1980) where available habitat was defined by the MCP encompassing all locations in the study area and used habitat was represented by relocations within individual 95% MCP home ranges. I also analyzed third-order (patch level) selection of adult male alligators with available resource space characterized as the 95% MCP home range and used resource space determined from relocations of each animal. Analyses at both scales included a multiannual home range and pooled locations from both years due to a limited sample size of locations for each individual in each year. I performed randomization tests (n = 10,000 steps) using the first eigenvalues to determine influence of each habitat variable on marginality of each animal and if observed use differed significantly than what is expected under the random habitat use hypothesis. For these tests, I expected the explanatory variables to vary greatly so I set $\alpha = 0.10$ using Bonferroni correction. I also extracted the distances of the marginality vectors (measure of selectivity) for each animal and modeled them with body size and home range size as dependent variables using linear regression.

I performed statistical analyses using R (Mac version 3.0.2; R Foundation for Statistical Computing; Vienna, Austria), including the adehabitat package (Calenge, 2007), to estimate home ranges and habitat selection. I reported means with ± 1 standard deviation (SD) and outliers were determined using interquartile range (Zuur, Ieno, & Elphick, 2010).

Results

Radio-telemetry data

I captured 20 adult male alligators and used 17 animals with sufficient numbers of relocations for resource selection analyses. I collected on average 34 ± 8 (SD) locations for each animal per active period totaling 1,145 relocations (Table 2.1, Figure 2.1B). Estimated animal locations were best explained by the equation: distance = -1,765 + 3.523*signal + 9.138*gain - 0.0201*signal*gain (adjusted $R^2 = 0.684$, $F_{[3, 224]} = 35.71$, $P < 0.001$). Mean angular error (-2.4 ± 13.3 degrees) did not differ from zero and directional bearings were unbiased ($t_{50} = -1.304$, $P = 0.198$; 95% CI = -6.155–1.310).

Similarly, location error ($t_{21} = 1.126$, $P = 0.2731$; 95% CI -5.216–17.523) was unbiased and averaged 6 ± 14 m.

Forests and swamps accounted for 48% of the study area, followed by shallow wetlands (15%), main channel (12%), floating, emergent vegetation (9%), backwaters and oxbow lakes (8%), and lotus (8%). However, percentage of animal relocations was disproportionate to percentages of available habitat: 24% of relocations were in forests and swamps, shallow wetlands (19%), main channel (2%), floating, emergent vegetation (29%), backwaters and oxbow lakes (14%), and lotus (12%).

Home range selection

The first axis explained 58% of the variation in the data and was related positively to water depth and related negatively to distance to main channel (Figure 2.2A, 2.2B, 2.2C). Including the second axis accounted for an additional 20% of the variation and corresponded negatively to swamp and forest habitat (Figure 2.2A, 2.2B, 2.2C). The first eigenvalue λ_1 was greater than expected ($\lambda_1 = 1.477$, $P < 0.001$) meaning habitat use patterns are informative. Marginality was nonrandom for four animals (Table 2.2; Figure 2.2D). Three individuals avoided swamp habitat, one selected for lotus habitat, and one selected for wetlands. Also, two animals selected home ranges near the main channel and reservoir.

Patch selection

The first axis explained 40% of the variation in the data and was related negatively to water depth, main channel, and oxbow habitats (Figure 2.3A, 2.3B, 2.3C). Including the second axis accounted for an additional 15% of the variation and corresponded negatively to wetland habitats (Figure 2.3A, 2.3B, 2.3C). The first eigenvalue λ_1 was greater than expected ($\lambda_1 = 0.460$, $P < 0.001$). Marginality was nonrandom for nine animals (Table 2.3; Figure 2.3D). Six animals selected for areas with floating, emergent vegetation and two animals selected areas near this habitat. Two animals avoided oxbow and backwater areas and two other animals avoided the main channel and reservoir habitat.

Marginality, home range, and body size models

Alligator TL averaged 2.8 m and ranged from 1.8 to 3.7 m (Table 2.1). Multiannual 95% MCP home ranges of radio-marked alligators (mean = 33.0 ± 59.6 ha, range = 0.5–254.8 ha, (Table 2.1) were not associated with TL ($F_{[1,15]} = 0.028$, $P = 0.870$, adjusted $R^2 = -0.065$), even after removing one animal (x2715) that was an outlier regarding home range size. I therefore retained all animals for further analyses.

Home range level marginality was not related to body size ($F_{[1,15]} = 0.208$, $P = 0.655$, adjusted $R^2 = -0.052$). Patch level marginality was also not related to body size ($F_{[1,15]} = 1.543$, $P = 0.233$, adjusted $R^2 = 0.033$). Finally, mean selection values for each habitat variable were not correlated with body size, except for patch level selection of oxbow habitat ($F_{[1,15]} = 4.718$, $P = 0.046$, adjusted $R^2 = 0.189$).

Discussion

Alligators overall demonstrated greater selection for habitat variables at the patch level and were less selective at the home range level. As expected, I did not find congruency among selection at the two spatial scales. This suggests there are fewer limiting factors when selecting a home range at RBR and resources are likely plentiful.

At large scales, animals may not select for a particular habitat even if important for a specific behavior (e.g., thermoregulation, foraging) because that habitat may not satisfy other needs. This would explain the observed high patch level selection for floating, dense vegetation, possibly for thermoregulation, whereas no alligators selected for this habitat at the home range level. It follows that a strategy could be to select a home range with several habitats in close proximity to meet multiple needs. Selection at the home range level should reflect avoidance of the most limiting factors (Rettie & Messier, 2000). Alligators in this study at the home range level avoided swamps and forests, which comprised almost half of the study area. In contrast, some individuals maintained close proximity to the main river channel and reservoir potentially as foraging sites (Joanen & McNease, 1972), to improve mobility afforded by the channel (Kay, 2004), and to reduce costs of traversing densely wooded swamps and forested islands.

Larger alligators did not select deep, open water. In fact, no animals selected the open water categories (main channel and oxbow) and only two alligators selected home ranges near the main channel and reservoir. Four individuals avoided these two habitats at the patch level and no animal selected water depth. Previous research suggests that adult male alligators prefer deep, open water because of availability of large prey and capacity of deep water to buffer extreme temperature fluctuations (Joanen & McNease, 1972; Subalusky et al., 2009; Webb et al., 2009). The relatively shallow depth of RBR may restrict thermal buffering, limiting selection for areas with deeper water. Alternatively, higher levels of observed recreation and boating activity in open water habitats (pers. obs.) could constrain alligator selection for this habitat. Alligators at RBR were wary when approached, possibly due to hunting pressure, previous capture, and potential risk from recreational boaters, anglers, and hunters. Crocodilians are injured by boats and generally avoid boats (Grant & Lewis, 2010; Lewis, Cain, & Denkhaus, 2014). In addition, wave action (from wind and boat traffic) may impair visual prey location and limit foraging (Murphy, 1977).

Unexpectedly, floating, emergent vegetation was the most selected habitat within the home range. This habitat contains dense, abundant invasive plant species (e.g., water hyacinth and alligator weed) that shade out native aquatic plants and may reduce fish habitat quality (Sartain & Madsen, 2013; Wersal, Madsen, & Tagert, 2006). In addition, dense vegetation can reduce foraging success of aquatic predators due to increased structural complexity (Savino & Stein, 1982). As lesser prey abundance and increased difficulty of prey capture would be expected to reduce foraging suitability of this habitat, I suggest that alligators may use this dense vegetation as a thermal refuge (Giles & Childs, 1949; Joanen & McNease, 1972). The water underneath dense, mat forming vegetation is likely cooler and provides alligators with a buffer from direct solar radiation. Behavioral thermoregulation strongly influences alligator daytime movements (Lang, 1987; Nifong et al., 2014; Watanabe, Reyier, Lowers, Imhoff, & Papastamatiou, 2013).

I found no relationship between resource selection or home range size with body size, suggesting size-dependent dominance hierarchies did not influence alligator resource selection or space use. Other factors, including density dependence, may have a stronger effect on alligator resource selection. Information on alligator social behavior has been primarily from higher-density coastal and captive populations in habitat more homogenous than riverine systems (Ryberg, Fitzgerald, Honeycutt, & Cathey, 2002;

Subalusky et al., 2009; Webb et al., 2009). Population density can influence the occupation rate of habitat and degree of resource competition (Tucker, Limpus, McCallum, & McDonald, 1997), in turn affecting social dominance structure (Estevez, Andersen, & Naevdal, 2007) and habitat selection (Boyce, Vernier, Nielsen, & Schmiegelow, 2002; Rosenzweig, 1991). Size-dependent social hierarchies may also be responsible for regulating population density in some crocodilian populations (Staton & Dixon, 1975). Exclusive territories are common in low-density populations (Lang, 1987). As density increases, defending exclusive territories becomes increasingly difficult and behavioral responses may favor establishment of a strict social system for access to resources, limiting risk of injury or death (Lang, 1987). Consequently, dominance interactions may be strongest in more crowded coastal habitats and captive situations due to increased social interactions and greater pressures on available resources (density dependent effects). The RBR population may be below the density dependent threshold required to saturate available resources where competition would become manifested in the form of social dominance. Selection of habitat variables was weak at the home range level suggesting resources are abundant. High resource availability could lead all or most adult males to occupy suitable home ranges, thus limiting differences in resource selection.

I assumed that dominance rank was directly proportional to body size based on other studies of crocodilian social behavior (Drews, 1990; Kay, 2004; Lang, 1987). However, dominance rank could also be determined by variable behaviors among individuals, including temperament (Reale, Reader, Sol, McDougall, & Dingemanse, 2007) and personality (Dall, Bell, Bolnick, & Ratnieks, 2012; Rosenblatt et al., 2013;

Watanabe et al., 2013). In addition, more than visual displays of size may influence dominance rank, especially during the breeding season. The role of other behaviors including bellowing and headslapping in establishing and maintaining dominance is unknown (Garrick et al., 1978).

Dominance hierarchies in adult male alligators were not manifested through space use at two spatial scales, but there could be temporal elements to behavior. Alligators may have similar movements and habitat use between day and night (Hutton, 1989); however, at least movements may differ during these periods (Nifong et al., 2014; Rosenblatt et al., 2013; Watanabe et al., 2013). Thus, effects of space use from dominance rank may be more detectable at night when interactions among males and foraging are more common. Also, I was unable to compare alligator breeding season (April–May) to non-breeding period relocations when courtship behaviors may facilitate competition over mates and dominance interactions among competitors.

Habitat selection of adult male alligators is a scale-dependent process and reveals the importance of each habitat to overall fitness (Rettie and Messier 2000) that could be used to improve species management and conservation. Aquatic vegetation, water depth, and water temperature may be important factors influencing alligator foraging and thermoregulation (Goodwin & Marion, 1979; Joanen & McNease, 1972; Webb et al., 2009). State water management plans and programs for the local control of aquatic pests could consider: 1) allowing parts of the natural flood plain to flood seasonally for sub-adult dispersal and 2) maintaining patches of thick vegetation to help alligators mitigate their heat budgets. Though apparent habitat suitability and low alligator density did not manifest in an observed dominance hierarchy, a change in either could increase intraspecific interactions, facilitating a dominance hierarchy. The mechanisms by which social hierarchies form is an interesting area of behavioral evolutionary ecology that allows for improved understanding of animal distribution theory (Beacham, 2003; Estevez et al., 2007). Alligators are generalist top predators that potentially have top-down effects, mobile vectors of nutrients between terrestrial and aquatic systems, and ecosystem engineers that manipulate water flow and influence plant communities (Mazzotti et al., 2009; Rosenblatt & Heithaus, 2011). Due to the broad and diverse ecological roles of alligators, understanding the factors that influence their social dominance and space use can provide great insight into their functional role in the ecosystem.

Table 2.1 Total length, number of relocations, and home range size for radio-tracked adult male alligators at Ross Barnett Reservoir and Pearl River, Mississippi, USA, 2012–2013.

Animal	Total length (m)	Number of locations			95% MCP (ha)
		2012	2013	Combined	
x0507	2.39	43	35	78	16.3
x0910	2.47	34	40	74	3.7
x1308	2.83	25	38	63	9.8
x1912	3.57	43	40	83	18.3
x2310	2.54	26	31	57	25.4
x2509	2.86	35	33	68	46.4
x2715	2.73	21	23	44	254.8
x2910	2.72	24	34	58	11.0
x3090	2.72	16	25	41	5.1
x3312	2.61	36	41	77	5.7
x3522	3.35	44	41	85	0.5
x3915	3.72	40	39	79	36.9
x5123	2.43	43	40	83	7.9
x5327	1.80	36	39	75	3.8
x5516	2.44	36	35	71	60.0
x5926	2.69	25	41	66	19.3
x6122	3.19	17	26	43	37.0
Mean	2.77	32	35	67	33.0

Table 2.2 Marginality of home range selection of radio-tracked adult male alligators at Ross Barnett Reservoir and Pearl River, Mississippi, USA, 2012–2013.

Animal	Marginality	Selection of habitat variables								
		LO	MC	WT	DV	SW	OX	MCdi	DVdi	Wdep
x0507	2.28	0.89	-0.36	-0.26	0.24	0.49	0.54	-0.57	-0.59	0.21
x0910	2.30	-0.12	-0.36	0.19	0.65	-0.33	0.24	-0.76	-0.78	0.59
x1308	1.54	0.38	-0.36	0.06	0.35	-0.33	0.21	-0.66	-0.72	0.17
x1912	2.12	0.72	-0.15	0.23	0.39	-0.70	0.03	-0.65	-0.69	0.05
x2310	2.46	-0.30	0.30	-0.24	0.33	-0.12	0.13	-0.93	-0.64	0.90
x2509	2.26	0.94	-0.36	-0.10	0.05	-0.60	0.68	-0.42	-0.27	0.41
x2715	2.41	0.65	0.62	-0.12	-0.08	-0.86	0.43	-0.48	0.36	0.54
x2910	1.20	-0.27	-0.36	-0.06	0.39	0.32	-0.21	-0.52	-0.64	0.13
x3090	5.00[a]	-0.30	-0.36	1.77[b]	0.07	-0.96[a]	0.09	0.07	-0.67	-0.50
x3312	3.46[a]	0.05	-0.12	0.02	0.88	-0.61	0.28	-0.92[b]	-0.80	0.86
x3522	7.62[a]	-0.30	-0.36	-0.42	1.47	-0.96[b]	1.53	-0.56	-0.85	0.88
x3915	1.38	0.31	-0.15	0.12	0.51	-0.55	0.18	-0.54	-0.60	-0.05
x5123	3.10	0.98	-0.36	0.17	0.61	-0.83	0.11	-0.57	-0.75	-0.12
x5327	2.38	-0.21	-0.36	-0.36	0.20	-0.11	1.09	-0.51	-0.63	-0.41
x5516	4.19[a]	-0.25	-0.36	1.53	0.24	-0.80	-0.12	0.82	-0.12	-0.50
x5926	1.47	-0.09	0.18	0.02	0.30	-0.27	0.03	-0.78[b]	-0.68	0.43
x6122	3.67	1.30[a]	-0.36	0.01	-0.07	-0.95[a]	0.92	-0.29	0.03	0.10

Results of randomization tests with n = 10,000 steps on the marginality of each animal. Significant levels reflect Bonferroni corrections.

[a] Significant at the 5% level

[b] Significant at the 10% level

Abbreviations of habitat variables: main channel (MC), backwaters and oxbow lakes (OX), floating, emergent vegetation (DV), lotus (LO), forest and swamps (SW), very shallow wetlands (WT), water depth (Wdep), distance to main channel (MCdi), and distance to floating, emergent vegetation (DVdi).

Table 2.3 Marginality of patch selection of radio-tracked adult male alligators at Ross Barnett Reservoir and Pearl River, Mississippi, USA, 2012–2013.

Animal	Marginality	Selection of habitat variables								
		LO	MC	WT	DV	SW	OX	MCdi	DVdi	Wdep
x0507	1.28[a]	-0.36	0.00	0.25	0.83[a]	-0.01	-0.56[b]	0.00	-0.25	0.10
x0910	0.86[a]	-0.04	0.00	0.02	-0.41	0.73[b]	-0.26	0.08	0.00	0.28
x1308	0.42	-0.22	0.00	-0.10	0.08	-0.02	0.29	0.01	-0.03	0.52
x1912	0.20	-0.23	-0.15	0.04	0.22	0.02	0.14	0.09	-0.05	-0.23
x2310	1.82[a]	0.00	-0.57[b]	0.04	0.61[a]	0.23	-0.20	0.03	-0.18	-1.00[a]
x2509	0.83[a]	0.03	0.00	0.10	0.46	-0.22	-0.33	0.48	-0.29	-0.37
x2715	4.10[a]	-0.17	-0.85[a]	0.61[b]	0.64[a]	0.01	-0.17	0.67[b]	-1.12[a]	-0.91[a]
x2910	2.22[a]	0.03	0.00	0.38	0.58[b]	-1.14[a]	0.09	-0.13	-0.17	0.62[b]
x3090	0.10	0.00	0.00	0.22	-0.13	0.00	-0.11	-0.14	0.06	-0.02
x3312	0.54	-0.23	0.35	-0.10	0.31	0.15	-0.38	-0.15	-0.04	-0.27
x3522	0.13	0.00	0.00	0.00	0.12	0.00	-0.10	-0.05	-0.02	-0.31
x3915	0.51	-0.11	-0.18	-0.31	0.43	0.34	-0.04	-0.19	-0.15	-0.05
x5123	0.15	0.22	0.00	0.05	-0.21	0.00	-0.11	-0.08	0.02	-0.18
x5327	1.43[a]	-0.06	0.00	-0.06	0.10	0.90[a]	-0.75[a]	0.16	-0.09	-0.11
x5516	4.57[a]	0.01	0.00	-1.14[a]	1.45[a]	-0.15	0.08	-0.76[a]	-0.75[b]	0.03
x5926	0.38	-0.05	-0.28	0.26	0.12	-0.09	0.04	-0.18	-0.06	-0.41
x6122	1.42[a]	-0.45	0.00	0.16	0.86[a]	-0.02	-0.38	0.23	-0.41	-0.28

Results of randomization tests with n = 10,000 steps on the marginality of each animal. Significant levels reflect Bonferroni corrections.

[a] Significant at the 5% level

[b] Significant at the 10% level

Abbreviations of habitat variables: main channel (MC), backwaters and oxbow lakes (OX), floating, emergent vegetation (DV), lotus (LO), forest and swamps (SW), very shallow wetlands (WT), water depth (Wdep), distance to main channel (MCdi), and distance to floating, emergent vegetation (DVdi).

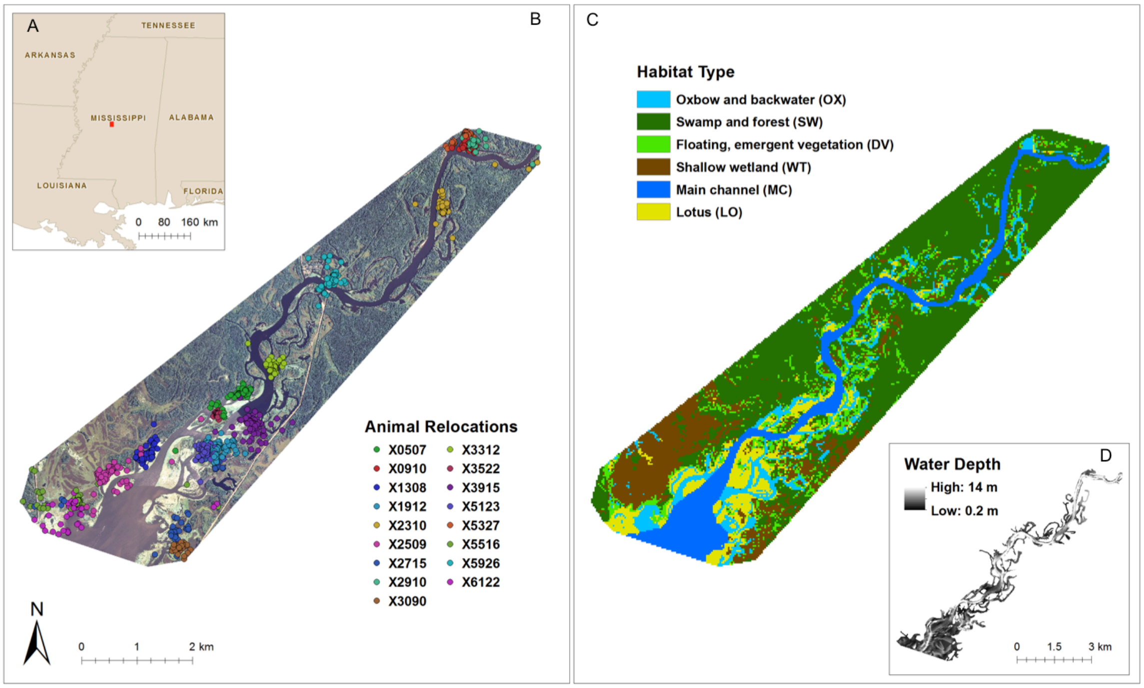

Figure 2.1 Map of the study area and radio-tracked adult male alligator relocations at Ross Barnett Reservoir and the Pearl River, Mississippi, USA, 2012–2013.

(A) Inset shows study area as a solid red square. (B) Aerial imagery with animal relocations for 2012 and 2013 combined. (C) Categorical map of the six habitat types classified from aerial imagery. (D) Bathometric display of study area. Outside the main channel and reservoir white represents no data and inside it represents the deepest water.

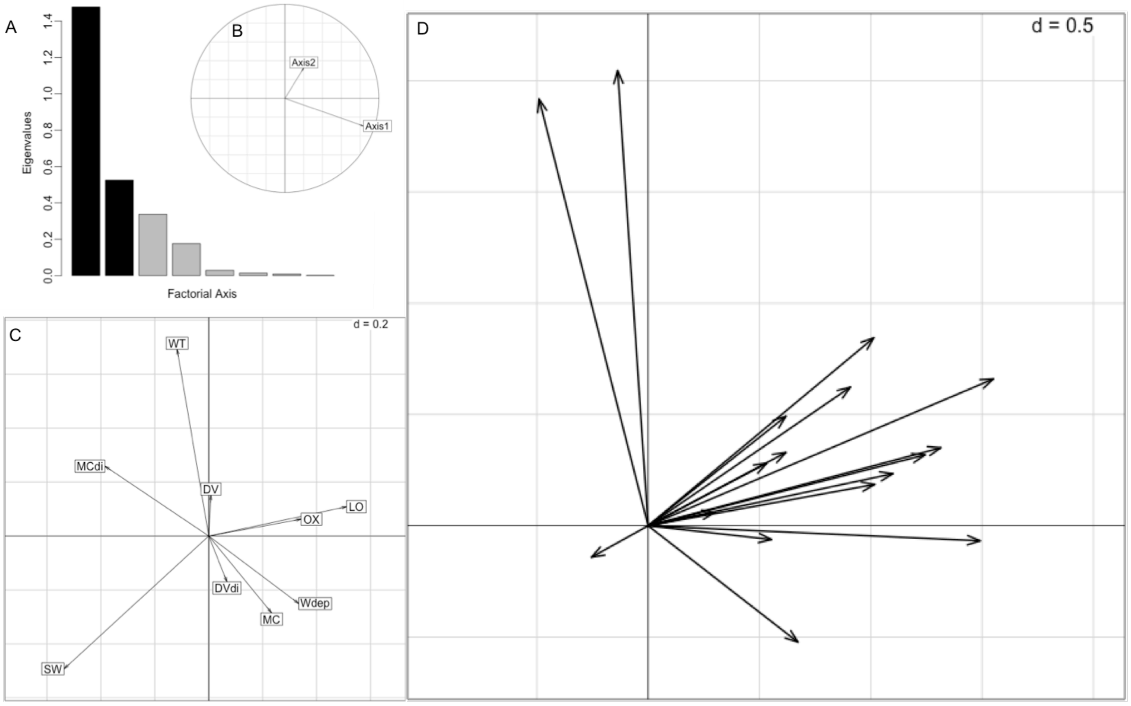

Figure 2.2 Home range level resource selection plots from the K-select analysis for radio-tracked adult male alligators at Ross Barnett Reservoir and the Pearl River, Mississippi, USA, 2012–2013.

(A) Scree plot of eigenvalues where Axis 1 and 2 are shown as black bars and other axes are represented as gray bars. (B) Orthogonality plot for Axis 1 and 2. (C) Habitat variable loadings. Abbreviations of habitat variables: main channel (MC), backwaters and oxbow lakes (OX), floating, emergent vegetation (DV), lotus (LO), forest and swamps (SW), very shallow wetlands (WT), water depth (Wdep), distance to main channel (MCdi), and distance to floating, emergent vegetation (DVdi). (D) Marginality vectors of each animal.

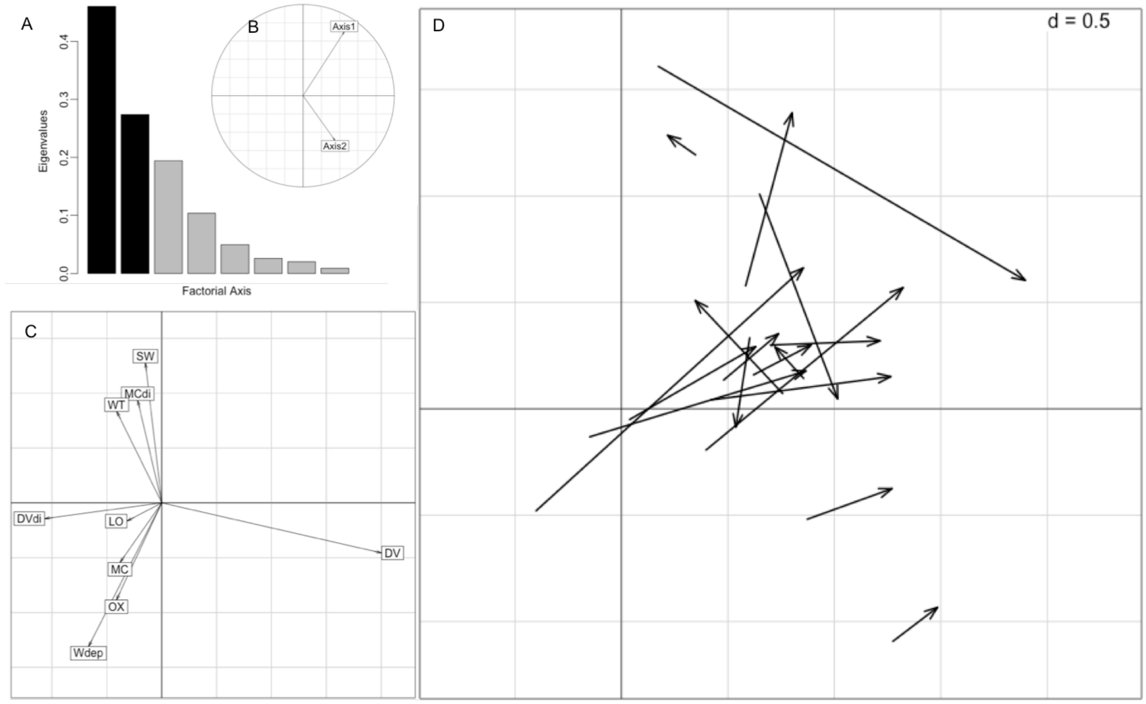

Figure 2.3 Patch level resource selection plots from the K-select analysis for radio-tracked alligators at Ross Barnett Reservoir and the Pearl River, Mississippi, USA, 2012–2013.

(A) Scree plot of eigenvalues where Axis 1 and 2 are shown as black bars and other axes are represented as gray bars. (B) Orthogonality plot for Axis 1 and 2. (C) Habitat variable loadings. Abbreviations of habitat variables: main channel (MC), backwaters and oxbow lakes (OX), floating, emergent vegetation (DV), lotus (LO), forest and swamps (SW), very shallow wetlands (WT), water depth (Wdep), distance to main channel (MCdi), and distance to floating, emergent vegetation (DVdi). (D) Marginality vectors of each animal.

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CHAPTER III

AMERICAN ALLIGATOR POPULATION ESTIMATION IN INLAND WATERS OF MISSISSIPPI USING SPOTLIGHT SURVEY COUNTS

Introduction

Estimating animal abundance is often necessary to implement conservation and management actions. Similarly, bias and robustness are important considerations in animal population estimation (Dawson, Wade, Slooten, & Barlow, 2008). Index counts are a function of abundance relying on assumptions concerning variables associated with the observer, species characteristics, environment, and temporal issues that are difficult to meet in most field situations (Anderson, 2001). Consequently, index counts may provide an imprecise measure of the number of individuals in a population and the relationship to actual population size is unknown (Hutton & Woolhouse, 1989). Trend analysis of index data may assign any apparent change, given constant survey methods, to population processes (Caughley, 1977).

Spotlight surveys, also known as eyeshine and nightlight surveys, are a widely used method to monitor abundance and size class structure of crocodilian populations (Da Silveira, Magnusson, & Thorbjarnarson, 2008; Fujisaki et al., 2011; Hutton & Woolhouse, 1989). Like other index counts, spotlight surveys rely on the assumption that animal detectability is constant across time and space (Subalusky, Fitzgerald, & Smith, 2009; Thompson, 2002). Several studies have attempted to standardize spotlight counts and account for the relationship of environmental and observer effects that can influence detectability (Chabreck, 1966; Hutton & Woolhouse, 1989; Woodward & Marion, 1978).

Crocodilian detection may be influenced by environmental conditions including water and air temperature (Hutton & Woolhouse, 1989), presence and density of vegetation (Cherkiss, Mazzotti, & Rice, 2006), observer variables such as spotlight intensity (Woodward & Marion, 1978), and animal behavior (Pacheco, 1996). However, traditional spotlight surveys are limited in their ability to quantify environmental and observer effects on detection probabilities and encounter rates. Other studies have used mark-recapture or mark-resight techniques, but these methods have not been widely used with crocodilians likely due to effort involved and availability of individuals for recapture (Bayliss, Webb, Whitehead, Dempsey, & Smith, 1986; Hutton & Woolhouse, 1989; Murphy, 1977). Available methods for estimating populations with accuracy and precision (e.g., distance sampling and double observer methods) have rarely been applied to crocodilians (Shirley et al., 2012; Subalusky et al., 2009). In general, spotlight survey protocols and encounter rate indices have been improved using distance sampling; however, distance sampling has not been used to estimate density of any crocodilian species (Ruette, Stahl, & Albaret, 2003).

The Mississippi Department of Wildlife, Fisheries, and Parks (MDWFP) has conducted alligator spotlight surveys since 1972. However, surveys were not standardized until the year 2000 with respect to survey locations nor were surveys replicated temporally, precluding population trend analysis and modeling. Current alligator surveys use a spotlight to detect eyeshine while traveling on a boat in the center of the channel or on the perimeter of rivers, creeks, reservoirs, and bayous at 14 sites across the state. My goals in this chapter were to analyze MDWFP alligator survey data, evaluate environmental and observer covariates that influenced counts, and assess current methods for potential improvements. Also, I present several alternative survey methodologies and a case study on the logistics of performing distance sampling on crocodilians.

Study Area

I selected 8 survey routes throughout the state of Mississippi (Figure 3.1). Route lengths were constant in length each year at a site, but variable among sites. Route locations included:

1. Big Black River (west-central Mississippi) – Major river (50–150 m wide) is densely forested with large woody debris in the main channel. Route starts 13.52 km upstream from Highway 61 South then ends downstream of Highway 61 South at the Old Ferry Bridge Crossing. Total length = 17.37 km.
2. Little Sunflower River (south-central Mississippi) – Major river (40–150 m wide) in the Mississippi Alluvial Valley includes a dredged flood control canal and naturally forested river drainage. Starts at the Greasy Lake Cutoff and continues upstream along the Yazoo Diversion Canal into the Little Sunflower River and ends at the Dummyline Road boat ramp at Delta National Forest. Total length = 18.62 km.
3. Okatibbee Lake (east-central Mississippi) – Entire shoreline is surveyed (33.09 km) of the 16.59 km^2 manmade flood control reservoir with hard banks and sparse herbaceous and woody vegetation.

4. Pelahatchie Bay - (central Mississippi) – Pelahatchie Creek (5 m wide) is surveyed before opening up half the distance of the route into Pelahatchie Bay, a large open water bay with patches of lotus located in the southeastern portion of Ross Barnett Reservoir. Total length = 7.19 km.
5. Percy Quinn State Park (south-west Mississippi) – Entire shoreline (6.373 km) is surveyed of Lake Tangipahoa, a 2.24 km^2 manmade recreational state lake with 30–40% characterized by 1–2 m deep water and dense lotus coverage.
6. Pearl River - Ratliff Ferry to Highway 43 (central Mississippi) – Slow moving river (80–400 m wide) empties half the distance of the route into the northeastern most portion of Ross Barnett Reservoir, a large open water reservoir with patches of lotus and some grasses. Total length = 17.20 km.
7. Pearl River - Ratliff Ferry to Lowhead Dam (central Mississippi) – Slow moving river (60 to 200 m wide) has forested banks and sparse aquatic vegetation. Total length = 11.53 km.
8. Steele Bayou (south-central Mississippi) – Major dredged and channelized flood control bayou (40–140 m wide) in the Mississippi Alluvial Valley has hard clean banks and areas of dense herbaceous cover. Begins at the flood control structure at Black Creek near Woodsaw Mill Road and continues to the weir crossing south of Highway 1. Total length = 19.80 km.

Methods

MDWFP alligator spotlight surveys

MDWFP personnel conducted alligator surveys yearly from 1999 to 2013 during summer (May–August). However, several routes were not surveyed during some years due to personnel issues and unpredictable water levels. Surveys were typically not conducted during new or full moon, following major weather events (i.e., thunderstorm or heavy rainfall), or on nights with high winds (> 10 km/h). Water temperature, wind velocity, cloud coverage, and precipitation during the last 24 hours (hereafter, rainfall) were obtained from local weather sources before each survey. Water level was visually estimated or water gage height obtained from the nearest U.S. Geological Survey station and categorized into a numeric variable as: very low (1), low (2), average (3), high (4), and very high (5) (United States Geological Survey, 2015). I obtained data on the fraction of the moon illuminated at midnight (Astronomy Applications Department of the United States Naval Observatory, 2015).

Surveys began at the start point of the established MDWFP route and started between 1930 and 2230 h and ended between 2125 and 0225 h. Average survey time across all routes was 148 minutes (range = 40–325 minutes). Survey team recorded start time and total time elapse and used a boat-mounted GPS unit (GPSMAP 76CSx; Garmin; Oalthe, Kansas) to track survey route and length (km), store starting and ending coordinates, and record location of each perpendicular observation.

Survey teams usually consisted of a driver/navigator, data recorder, and 1–3 trained observers. Spotlights used by observers varied by type, lumen intensity, and number per survey. Approximately 78% of the surveys used two 1-million candle power handheld lights. Boat and motor type varied among surveys; however, most surveys used a 75 horsepower motor (61%) and a 5 m boat (55%). The driver maintained a constant speed of around 10 km/h and monitored the speed using the GPS unit. Observers recorded individual alligators and placed each detection into size classes based on visual estimation of snout length as an index for total length (Chabreck, 1966). The driver diverted from the survey route to confirm size estimations when needed before returning to the survey route. With each observation, the team recorded size class, time, and location coordinates on the route.

I analyzed data from routes that had > 5 surveys. I did not use size class as an observation level covariate due to amount of missing data and high number of unknown size estimations (32% of detections). Further, MDWFP crews would repeat a survey the next night or later in the week if they deemed a nightly count was “unexpected” (typically too low). As repeated visits of select sites could introduce bias, I used only the first survey for analysis unless equipment failure was noted.

I aggregated all surveys among routes to examine effects of covariates on counts and assess the general count trend. I scaled all explanatory variables by subtracting the mean and dividing by the standard deviation of each variable for each observation. Following evidence of overdispersion in Poisson generalized linear mixed models (GLMMs) (function overdisp.glmer in package RVAideMemoire in Program R; Hervé, 2015), I used negative binomial GLMMs to estimate alligator counts (function glmer.nb in package lme4 in Program R; Bates et al., 2014). Further, I used route as random effect and year, Julian date, start time, route length, water temperature, rainfall, cloud coverage, wind velocity, moon phase, and water level as fixed effects. I estimated model overdispersion using the ratio of sum of squared Pearson residuals to the residual degrees of freedom (Ganio & Schafer, 1992). I included a null model with the random effect and a global model with all explanatory variables for model selection. I built 30 models based on combinations of variables and did not use any interaction terms. I used Akaike’s

Information Criterion corrected for small sample sizes (AIC_c) to rank models and selected competing models where AIC_c was within 2 units from the most supported model (Burnham & Anderson, 2002). In addition, I used Akaike weights (w_i) to perform model averaging and reported full model averaged coefficients and 95% confidence intervals with shrinkage (Burnham & Anderson, 2002). I used the MuMin package in Program R to perform multi-model inference and model averaging (Bartoń, 2014). Finally, I evaluated the significance of fixed effects at $\alpha = 0.05$.

Distance sampling surveys

Following a pilot season during summer 2012, I conducted distance sampling surveys in summer (July 1 through August 14) 2013 on the Pearl River - Ratliff Ferry to Highway 43 ($n = 6$) and Pelahatchie Bay ($n = 4$) MDWFP alligator survey routes. I performed the surveys independently (on different nights) of MDWFP's summer spotlight surveys. However, just as for MDWFP surveys, I did not conduct distance sampling during new or full moon, nights following major weather events, or nights with high wind.

During daylight before the first survey at each site, I recorded widths at systematic points along the two routes to calculate median width of the water body and establish distance interval cutoffs. I measured distances using a laser range finder (Elite 4200; Bushnell; Overland Park, Kansas) and used the same distance intervals at both sites. There were 4 distance intervals including a sub-interval at distance 0 m and 3 bins on each side of the centerline. The intervals increased in width with distance from the centerline, the boundary of the last interval on each side was the shoreline. Specifically, the center sub-interval was considered as the centerline at 0 m, the first bin was the centerline to 25 m, the second bin covered 25 to 50 m, and the last bin went from 50 m to the shore, which varied throughout the surveys.

I recorded the same environmental variables before each survey as MDWFP using the same sources. The team consisted of a driver/navigator, data recorder, and two trained observers who did not vary during trials. Before each survey, observers' sights were calibrated using a laser rangefinder and tested until distances intervals could be correctly visually estimated. Surveys began 15 minutes after dark. I recorded start time, total survey time, and used a boat-mounted GPS unit (GPSMAP 76CSx; Garmin; Oalthe, Kansas) to track the route and record coordinates of each perpendicular observation.

Observers used two 3.5 million candela spotlights (Cyclops Seeker; Grand Prairie, Texas) with 100-watt H3 halogen bulbs powered by fully charged 12-volt deep cycle marine batteries (EverStart Maxx; Walmart; Bentonville, Arkansas). Observers recorded and placed individual alligators or clusters into appropriate perpendicular distance intervals as the boat traveled along the center of the river channel. The driver kept the boat at a slow and constant speed (≈ 10 km/h). All surveys used the same 5 m aluminum boat (Duracraft; Monticello, Arkansas) and 75 horsepower motor (Mercury; Fond du Lac, Wisconsin). Further, the boat never left the center of the channel and observers did not estimate body size of detected animals.

Distribution of detections precluded estimation using distance sampling. However, raw counts from multiple controlled surveys in a single season did allow for a measure of variation. I used a one-sample t-test to compare mean of the distance sampling counts for both routes to the observed value in the MDWFP spotlight count for the same year.

I performed statistical analyses using R (Mac version 3.0.2; R Foundation for Statistical Computing; Vienna, Austria) and I reported means with ± 1 standard deviation (SD).

Results

MDWFP alligator spotlight surveys

The MDWFP recorded 3,185 alligators during 84 surveys at 8 sites across Mississippi during 1999–2013 (Table 3.1). Counts averaged 21.00 ± 7.21 for the Big Black River, 22.00 ± 10.80 for Little Sunflower River, 15.64 ± 6.19 for Okatibbee, 41.20 ± 9.33 for Pelahatchie Bay, 20.33 ± 9.73 for Percy Quinn State Park, 124.30 ± 34.46 for Pearl River Hwy 43, 35.80 ± 13.90 for Pearl River Lowhead Dam, and 23.91 ± 5.08 for Steele Bayou.

Average water temperature during surveys was 30 °C (range = 20–37.2 °C) and rainfall averaged 0.12 ± 0.79 cm (range = 0–5.08 cm). Wind speed maximum was 18.5 km/h, but averaged 4.5 ± 3.2 km/h. Cloud cover averaged 24 ± 28%, but attained 100%. Percentage of the moon illuminated on average was 53 ± 33%, but surveys were conducted on new ($n = 3$) and full moons ($n = 4$). Lastly, water levels were classified as average by biologists in 67% of the surveys and only 4% of surveys were conducted under “very” high or low levels according to the scale.

The Poisson GLMM with route as random effect exhibited overdispersion ($\hat{c} = 3.819$; $P < 0.001$), thus a negative binomial distribution was used for the additional dispersion parameter. Inclusion of route as a random effect in the models was supported by comparing marginal R^2 (0.09), concerned with the variance explained by fixed effects, and conditional R^2 (0.93), concerned with fixed and random effects, for the global model

(Nakagawa & Schielzeth, 2013). Predicted number of alligators per survey derived from the averaged model indicated mean count nearly doubled (20 to 39 alligators per survey) across all routes from 1999 to 2013 (Figure 3.2). Of 32 candidate models, 8 competing models exhibited ΔAIC_c less than 2 (Table 3.2). Year had a positive effect on count for all competing models, suggesting an increasing count at every route. Water temperature had a positive effect in the top 3 models and wind had a negative effect on all competing models. Other variables included in the competing models were rainfall and water level. After model averaging, year had a relative variable importance of 1.00, wind 1.00, water temperature 0.60, water level 0.39, and rainfall 0.38. The 95% confidence intervals for water temperature, water level, and rainfall all included 0, indicating these variables had no effect on alligator counts (Table 3.3).

Distance sampling surveys

Counts averaged 136.50 ± 30.99 alligators (7.93 ± 1.80 alligators/km) for the Pearl River and 52.75 ± 9.22 alligators (7.33 ± 1.28 alligators/km) for the Pelahatchie Bay routes. The 2013 MDWFP counts for these routes did not differ from my totals for Pearl River ($t_5 = 0.198$, $P = 0.851$; 95% CI = 103.979–169.021) and Pelahatchie Bay ($t_3 = 2.333$, $P = 0.102$; 95% CI = 38.087–67.413).

For all surveys at both routes combined, 2% of observations were on the centerline (0 m), 10% in bin 1 (centerline–25 m), 18% in bin 2 (25–50 m), and 70% in bin 3 (50 m–shore) (Figure 3.3). On the Pelahatchie Bay route 2% of detections were on the centerline, 28% in bin 1, 14% in bin 2, and 56% in bin 3 (Figure 3.3). For the Pearl River route, 3% were observed on the centerline, 5% in bin 1, 18% in bin 2, and 74% in bin 3 (Figure 3.3).

Discussion

The model results of MDWFP alligator surveys indicated counts have increased yearly across routes. Similar to other portions of the species' range (Altrichter & Sherman, 1999; Brandt, 1991), the observed positive response of alligator counts in Mississippi may reflect the benefit of listing the species under the Endangered Species Act, long-term wetland conservation practices, and species protection laws implemented in the state. Alligators were historically common and widely distributed throughout the southeastern United States, but pressures of unregulated harvest, water pollution, and wetland habitat degradation greatly reduced breeding populations from vast portions of their geographic range during the early 1900s (Altrichter & Sherman, 1999; McIlhenny, 1935). Populations became so rare and fragmented that the alligator was listed as an endangered species in 1967 and was listed as threatened until 1987 (Altrichter & Sherman, 1999). Major conservation efforts starting in the late 1960s have benefited wetland habitats and consequently, alligator populations. However, quantitative information on alligator population dynamics in Mississippi is presently unknown. An alternative explanation for the general increase in counts could be that observers are becoming better at detecting animals with experience. This is less likely than the trend reflecting an actual population process because observers were not held constant throughout the 15 years of surveying and 8 routes were included for analysis with different identities and combinations of observers.

The top competing models supported several variables that relate directly to detection and encounter rate or distribution of alligators. However, as confidence interval overlapped zero for all variables except year and wind, I am unable to ascertain their effect on counts. Increasing wind velocity had a negative effect on counts. This possibly relates to environmental conditions that may impair observer's ability to detect alligators on moving water which can obscure eyeshines (Woodward & Marion, 1978). Also, wind may negatively affect emergence rates as crocodilians seek shelter from inclement weather and high winds (Bugbee, 2008; Pacheco, 1996). Turbidity from recent precipitation and wave action associated with wind and rain events may also limit alligator feeding activity (Murphy, 1977). Other variables that were present in my competing models have been observed to affect alligator spotlight counts. Higher water levels affect movement patterns and consequently, encounter rates (especially subadults), by providing a larger area for alligators to disperse searching for food and avoiding predation (Webb, Zuur, Calkins, & Duguay, 2009; Woodward & Marion, 1978; Woodward, Rice, & Linda, 1996). Effect of water temperature on alligator activity and emergence rates varies, depending on season and its relation to air temperature (Bugbee, 2008; Woodward & Marion, 1978). However, the effect is stronger for water temperature than air temperature and stronger in colder periods than warmer periods (Woodward & Marion, 1978). Even though air temperature and the difference in air and water temperature may have different effects on activity and emergence, air temperature was not included in the models due to high collinearity (Bugbee, 2008). Another possible effect of water temperature is that emergence rates increase throughout the night as alligators lose heat, potentially confounding effects of survey start time leading to greater counts throughout the night (Bugbee, 2008).

A source of bias observed in the MDWFP surveys relates to departures from the route to better assign each observed animal to an estimated size class. Although no study has been performed on the misclassification rates of alligator sizes, trained observers may differ in their estimation abilities (B. Strickland, pers. obs.). Closing mode surveys, where the vessel leaves the transect to obtain more information about a sighting, may introduce uncertainty into survey estimates by not returning to the transect line and double counting individuals (Dawson et al., 2008). In addition, MDWFP surveys do not record time spent off the transect line, impacting estimates of total survey time and introducing bias. Typically, the choice of doing a closing mode survey may be based on more accurately estimating a detection level covariate (e.g., body size) than one could from the survey centerline. However, in my study almost one-third (32%) of detections were listed as unknown size or unknown over/under 2 m in size due to the submergence of wary animals when approached, which was similar to a previous estimate (Lutterschmidt & Wasko, 2006).

In addition, evasive action from disturbance such as a boat motor or spotlight by alligators is another behavioral variable that could potentially influence detection in this study. Wariness may be particularly problematic when surveys attempt to estimate size, requiring a closer approach to individual alligators. Wariness may also be related to hunting pressure and increase with age (Woodward & Marion, 1978). Therefore, changes in yearly harvest pressure and shifting age structures could lead to spurious results when comparing counts over time (Bayliss, 1987).

Distance sampling was not a feasible alternative to traditional alligator spotlight surveys given the sampling procedure and that I was not able to meet the assumptions in my trial study. Number of alligator detections increased with increasing distance from the transect centerline, therefore, I was unable to fit a decreasing detection function and determine a reliable estimate of density.

Due to the complex habitat and impassible regions of the river channel, I traveled down the center of the Pearl River channel and violated one of the main assumptions of distance sampling in that transect lines were not randomly placed with respect to animal distribution. Commonly, wildlife surveys along rivers and other linear waterbodies travel down the center of a channel or talweg. Consequently, animals are not uniformly distributed along the survey strip and talweg surveys frequently sample unrepresentative habitat (i.e., unequal coverage probability) passing through areas of greater animal densities (Braulik et al., 2012; Dawson et al., 2008). In distance sampling surveys, transect lines are assumed to represent a sample of habitat in a survey block (i.e., equal coverage probability) and should be random with respect to an animal's distribution (Buckland et al., 2001; Dawson et al., 2008). Due to their fluvial geomorphology, river channels and other confined waters makes placing random transects difficult (Dawson et al., 2008). Parallel lines with systematic or random spacing or a zigzag design is recommended for these situations (Strindberg & Buckland, 2004). However, these designs are also problematic due to the dynamic nature of fluvial systems of Mississippi causing river channels to be narrow in some spots and, in other places, to open up into shallow wetlands or swamp habitats impassible by boat. Some areas of Mississippi's rivers may often be filled with debris and have high flow velocity making navigation, particularly in shallow areas outside the channel, dangerous for small motorboats especially at night.

In some sections of the routes there were defined riverbanks limiting detections past the bank. In other places there were large, inundated, and shallow wetlands impassible by boat where I was able to detect eyeshines as far as the spotlight reached. In sections with a well-defined riverbank, it would be feasible to establish strip transects and meet the assumption that nearly every animal is detected. However, in wetland areas my ability to detect animals likely declined with distance, meaning that line transects could be appropriate. Sighting conditions were likely different between these riverine habitats and with changing widths, distance bins may be unavailable or the bound of the last bin may change along the route (Dawson et al., 2008). Studies on the Amazon river dolphin (*Inia geoffrensis*) used strip transects at multiple distances from the bank and line transects perpendicular to the flow of the river to derive a detection function not confounded with a density gradient (Martin & da Silva, 2004; Vidal et al., 1997). However, in my case, logistics and navigational dangers of sampling across dynamic riverine and wetland habitats during the night preclude use of perpendicular strip transect surveys (Braulik et al., 2012).

Alligators likely are not evenly distributed throughout the channel, reflecting resource selection choices (e.g., foraging, risk avoidance) favoring use outside the non-vegetated main channel. Number of detections at a distance from the centerline transect in my study was not solely caused by the detection function but may be related to the detection process (observation model) and distribution of animals (state model). This prohibited assuming animal availability was uniform with respect to distance from the transect centerline. Thus, I would be required to estimate an alligator density gradient from the centerline, which is responsible for confounding the effect of distance on detectability. A *post hoc* solution to the non-uniform distribution would involve collection of detailed environmental data and a significantly more complex analysis (Buckland et al., 2007).

In distance sampling, exact distances are preferred to assigning observations to distance categories (i.e., bins) in the field (Buckland et al., 2001). Due to the nocturnal nature of crocodilian surveys, laser rangefinders were not practical to estimate distances due to reflectivity of the water and difficulty of aiming at a small target. Thus, observers placed detected alligators into distance intervals, introducing a source of observer bias and reducing information per observation. Another issue was use of a small number of distance bins (n = 3) plus the centerline for surveys; typically, survey transects should consist of a minimum of 4 bins, with 5 distance bins or greater generally recommended (Buckland et al., 2001). However, large numbers of bins make it difficult for observers, who are visually estimating interval cutoffs, to accurately place detections in the appropriate distance bin (Buckland et al., 2001). Another requirement of distance sampling design is the need for 10–20 transects within a study area, with a minimum of approximately 40 detections per transect for a robust analysis (Buckland et al., 2001). These sampling conditions make meeting basic survey design recommendations impractical for alligator spotlight surveys in rivers, creeks, and wetlands of Mississippi.

Studies have recognized the need to incorporate observer bias and imperfect detection in crocodilian population surveys (Shirley et al., 2012; Subalusky et al., 2009). The double observer method is a cost effective and logistically feasible way to account for these issues (Nichols et al., 2000; Shirley et al., 2012; Subalusky et al., 2009). The double observer method addresses many of the issues related to detection and animal density gradient encountered in my distance sampling trials, while simultaneously accounting for observer and habitat effects on counts (Shirley et al., 2012). However, the approach would involve additional observers and, in some cases, a separate crew and watercraft.

Another approach to monitor alligators would be using a two-stage binomial-Poisson hierarchical model that can estimate detection and changes in abundance from typical spotlight data (Fujisaki et al., 2011; Kéry et al., 2009). The main limitation for this approach in historical datasets of spotlight counts is that it relies on replicate surveys of a route in the same season to calculate a method of moments estimate for detection probability (Fujisaki et al., 2011). Consequently, it would require a doubling of effort and cost compared to the present survey approach.

Survey recommendations

Analysis of MDWFP alligator survey data and the attempt of using distance sampling led to several recommendations for future surveys:

1. Accurate and generalized estimates of diving and emergence (surfacing) rates would improve abundance estimates from eyeshine counts. Availability bias of submerged animals missed is a significant issue facing crocodilian spotlight surveys (Braulik et al., 2012; Marsh & Sinclair, 1989). Even though I was able to quantify effects of environmental covariates on counts, without accurate and generalized measures of availability bias, an estimate from any survey approach (including distance sampling and even strip transects) only represents the available, surfaced portion of the population. Available emergence estimates for alligators are highly variable and environmental and demographic characteristics

influencing this behavior have not been well studied or quantified (Bugbee, 2008; Nifong et al., 2014; Woodward et al., 1996).

2. Increased standardization and closer adherence to standard practices would reduce number of covariates needed to predict counts (Fujisaki et al., 2011; Wood, Woodward, Humphrey, & Hines, 1985). I recommend future surveys should control sources of bias such as number and identity of observers as well as type and quantity of lights. If possible, watercraft including length and motor should be kept constant. Survey start time and boat speed should be standardized to keep the effort constant and account for the possibility of encounter rates changing throughout the night (Bugbee, 2008; Woodward & Marion, 1978). Accurate measurements of each survey level covariate would improve assessment of their influence on detection and abundance.
3. Based on observed variation of counts between years at some routes, I recommend multiple surveys conducted within a year to account for random environmental variation that may impact encounter rate and detection of animals. Replicate surveys for each route would allow evaluating the influence of the number of covariates currently recorded by MDWFP personnel, especially when modeling the influence of covariates by body size class.
4. I recommend consistently visiting each route every year and complete data collection for each survey to eliminate the issues of missing data and counts, which can complicate population models. Using automatic data recorders (e.g., Trimble Juno; Trimble Navigation Limited, Sunnyvale, California, USA) for real time and error-free data entry would be more efficient and likely cost effective in

the long term by reducing hourly cost of data entry and proofing.

5. Environmental variables may have site and population specific characteristics making comparisons in counts among different habitats and regions unreliable (Bayliss, 1987; Hutton & Woolhouse, 1989). State surveys in Mississippi include a range of habitats (e.g., river, bayou, canal, reservoir, lake). Thus, any state method would have to accommodate this variation and be applicable to all habitats. In addition, several survey routes include broadly different habitat types (e.g., creeks vs. reservoir), which may have different alligator density patterns and detection probabilities (Dawson et al., 2008). Further analyses of these routes should account for shifts in habitats by modeling and separately calculating parameters in homogenous segments (Wood et al., 1985). It is also important to consider the temporal component of alligator behavior in surveys, which may influence routes traveling multiple habitats that start and end the survey in the same order of habitat types. For abundance estimates, areas such as landmasses and islands that cannot be surveyed by boat should be excluded from area calculations (Dawson et al., 2008).

Alligator field techniques, including population survey methods, have mostly been developed in the coastal portions of their range. However, site and habitat specific differences may lead to biases and error in detection probabilities and abundance measures when applied to inland systems (Ryberg, Fitzgerald, Honeycutt, & Cathey, 2002; Webb et al., 2009). The broad application of methods developed in coastal systems across the alligator's range may not be applicable given differences in habitat and environmental conditions, which may in turn impact detection probabilities (Subalusky et al., 2009). Research is needed in the inland riverine ecosystems of the southeastern United States to address these issues and develop robust evaluations of techniques across multiple habitat types and systems.

It is important that MDWFP alligator survey protocols and monitoring programs account for imperfect detection and standardize or model important covariates. Alligator monitoring programs should use standardized spotlight surveys while taking advantage of double observer or seasonally replicated hierarchical modeling approaches. This in turn requires that information needs and goals of alligator population management should be clearly outlined. A spotlight survey design could be implemented to meet the management goals and answer relevant questions at the appropriate spatial scale and with adequate inference. I recommend a stratified random design based on habitat type and management regime (i.e., harvest pressure) or systematic controlled surveys and these designs would be an improved approach to monitor alligator populations over time (O'Brien & Doerr, 1986). Effect of harvest levels and take of nuisance animals on alligator populations could be better evaluated if accurate population estimates exist. Therefore, implementing robust survey techniques that generate reliable abundance estimates with associated precision measures will improve the capabilities of MDWFP to manage alligator populations and would serve as a model to other conservation agencies in the southeastern United States.

Table 3.1 Alligator counts for each survey of all routes by year in Mississippi, USA, 1999–2013.

Year	**Big Black River**	**Little Sunflower River**	**Okatibbee Lake**	**Pelahatchie Bay**	**Percy Quinn**	**Pearl River - Highway 43**	**Pearl River - Lowhead Dam**	**Steele Bayou**
1999							20 (1.73)	
2000			7 (0.21)				17 (1.47)	24 (1.21)
2001		5 (0.27)	8 (0.24)			82 (4.77)	30 (2.60)	22 (1.11)
2002		27 (1.45)	12 (0.36)				39 (3.38)	21 (1.06)
2003			14 (0.42)				17 (1.47)	
2004		19 (1.02)	9 (0.27)	46 (6.39)	12 (1.88)	93 (5.41)	25 (2.17)	18 (0.91)
2005	15 (0.86)	14 (0.75)	17 (0.51)	36 (5.00)	36 (5.65)	117 (6.80)	26 (2.25)	32 (1.62)
2006	12 (0.69)	14 (0.75)	21 (0.63)	57 (7.92)	12 (1.88)	171 (9.94)	50 (4.34)	28 (1.41)
2007	20 (1.15)	16 (0.86)	19 (0.57)	30 (4.17)		128 (7.44)	38 (3.30)	
2008	18 (1.04)	23 (1.24)	15 (0.45)	28 (3.89)	15 (2.35)	102 (5.93)	27 (2.34)	27 (1.36)
2009	29 (1.67)	24 (1.29)	27 (0.82)	45 (6.26)	28 (4.39)	89 (5.17)	53 (4.60)	
2010	21 (1.21)	22 (1.18)	14 (0.42)	42 (5.84)		144 (8.37)	45 (3.90)	22 (1.11)
2011		46 (2.47)	15 (0.45)	34 (4.73)	19 (2.98)	183 (10.64)	58 (5.03)	16 (0.81)
2012		32 (1.72)	27 (0.82)	52 (7.23)			54 (4.68)	22 (1.11)
2013	32 (1.84)		14 (0.42)	42 (5.84)		134 (7.79)	38 (3.30)	31 (1.57)

The number in parentheses is the count divided by route length in km.

Table 3.2 Results from all competing negative binomial generalized linear mixed models from candidate set with delta $AIC_c \leq 2$ to describe alligator counts in Mississippi, USA, 1999–2013.

Model[a]*	**df[b]**	**Log L[c]**	**AIC_c[d]**	**ΔAIC_c[e]**	**w_i[f]**
year + water temp. + wind	6	-314.54	642.18	0	0.17
year + water temp. + wind + rainfall	7	-313.48	642.43	0.25	0.15
year + water temp. + wind + water level	7	-313.52	642.52	0.34	0.15
year + wind + water level	6	-314.80	642.69	0.51	0.13
year + wind + rainfall	6	-314.92	642.92	0.75	0.12
year + wind	5	-316.18	643.12	0.95	0.11
year + water temp. + wind + rainfall + water level	8	-312.92	643.76	1.58	0.08
intercept only	3	-330.19	666.70	24.50	0.00

Covariates are scaled (mean = 0, SD = 1).

Water temperature is abbreviated "water temp.".

[a] Models are ranked from most to least supported with all including an intercept.

[b] Number of parameters with all models containing an intercept term, random term, and an error term.

[c] Log likelihood of the model.

[d] Akaike information criterion corrected for small sample sizes (AIC_c)

[e] Difference in AIC_c from the top model

[d] Weight of support for each model in a total of 1.

*Route is the single random effect in all mixed models.

Table 3.3 Full model-averaged coefficients with shrinkage of negative binomial generalized linear mixed models for candidate set with delta $AIC_c \leq 2$ to describe alligator counts in Mississippi, USA, 1999–2013.

Parameter	**β**	**SE**	**Pr(>|z|)**	**2.5%**	**97.5%**
intercept	3.38	0.21	<0.001	2.96	3.81
year	0.17	0.03	<0.001	0.10	0.24
wind	-0.09	0.04	0.029	-0.17	-0.01
water temp.	0.04	0.05	0.371	-0.05	0.13
water level	-0.02	0.03	0.554	-0.09	0.05
rainfall	-0.02	0.03	0.561	-0.08	0.04

Covariates are scaled (mean = 0, SD = 1).

Route is the single random effect in all mixed models.

Parameters are ranked in order of support for the full averaged model.

Water temperature is abbreviated "water temp.".

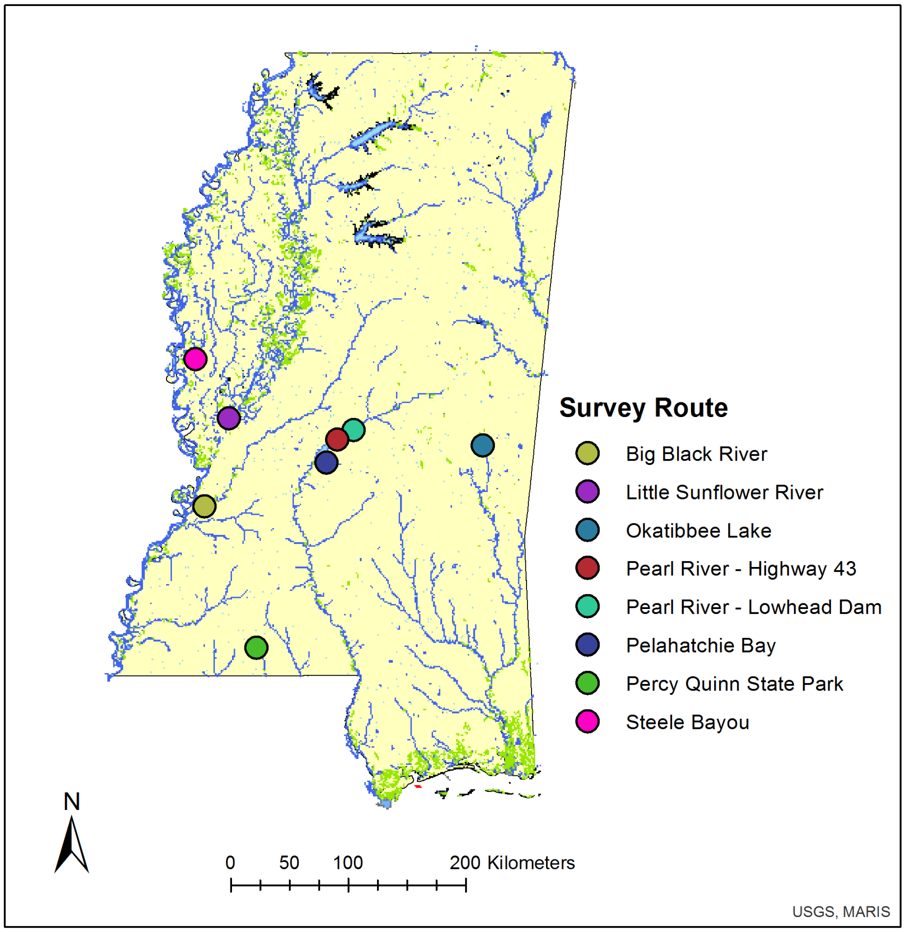

Figure 3.1 Map of selected state alligator spotlight survey routes in Mississippi, USA, 1999–2013.

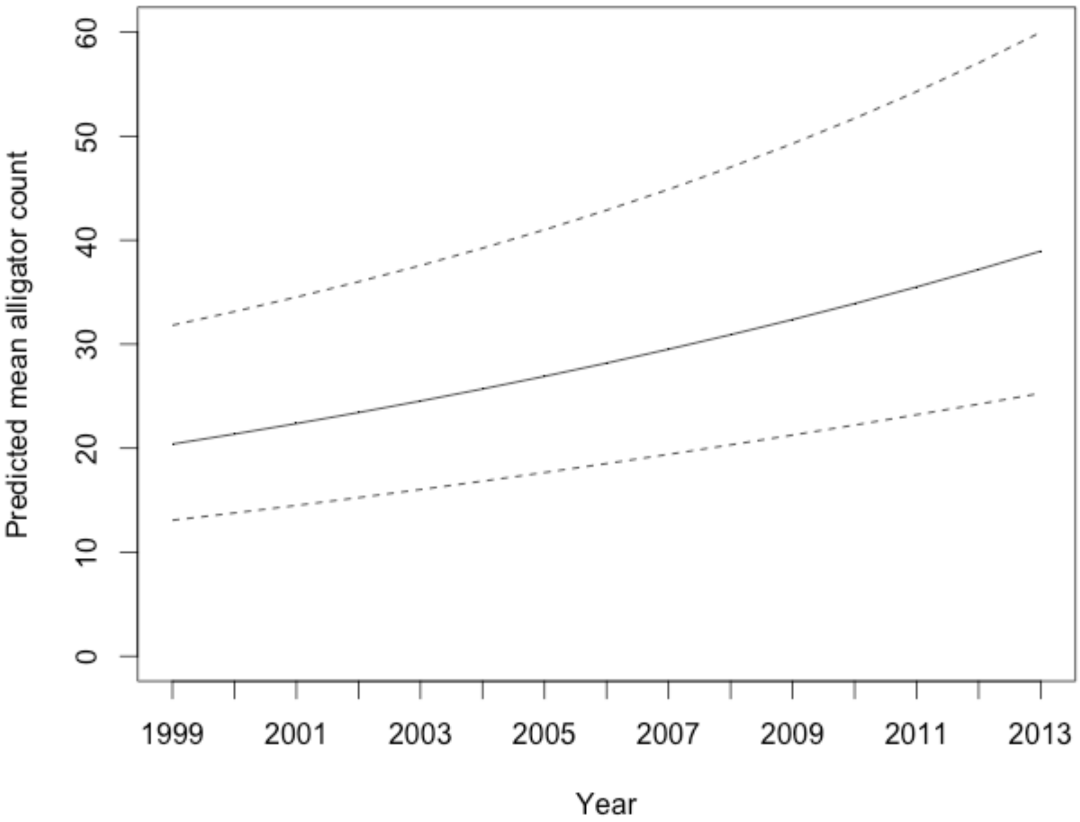

Figure 3.2 Predicted mean count of alligators per survey for all routes by year for the averaged model (solid line) and the 95% prediction interval (dotted lines) in Mississippi, USA, 1999–2013.

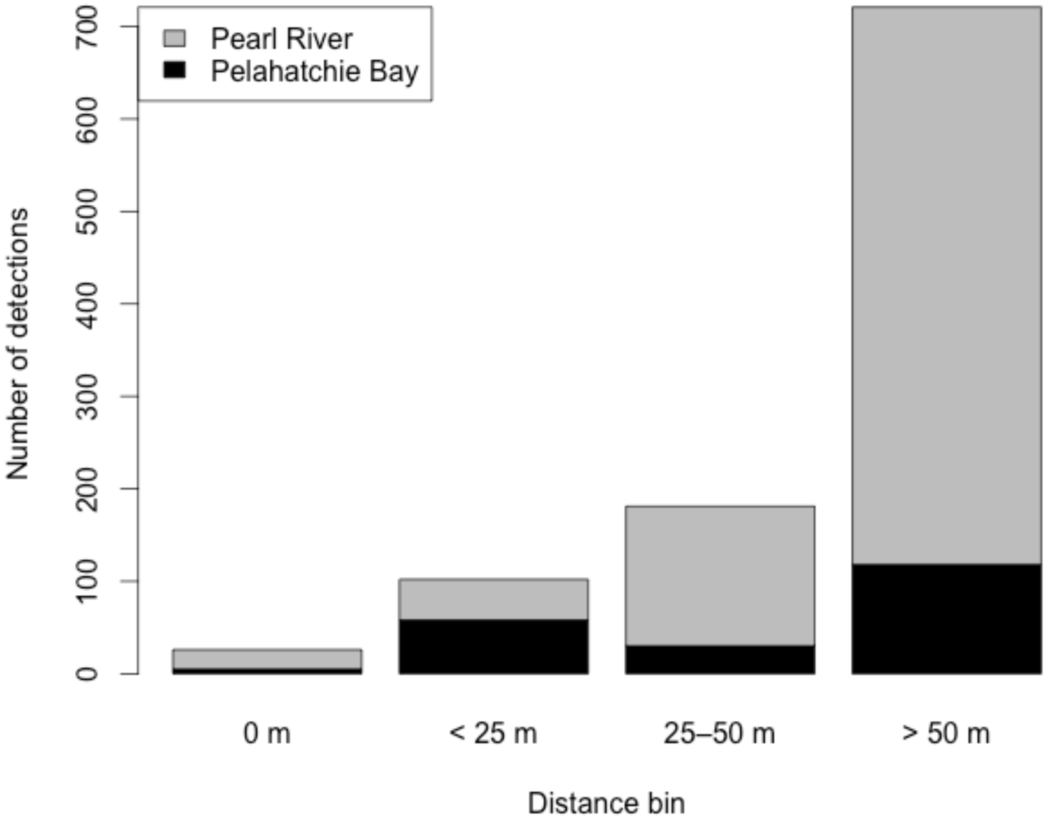

Figure 3.3 Number of detections of alligators in each distance bin for all distance sampling surveys on the Pelahatchie Bay (black bars) and Pearl River (gray bars) routes in Mississippi, USA, 2013.

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CHAPTER IV

CONCLUSION

Wildlife management and conservation frequently rely on understanding mechanisms that influence spatial distribution and accurately estimating population size. Alligators are generalist top predators that potentially have top-down effects, mobile vectors of nutrients between terrestrial and aquatic systems, and ecosystem engineers that manipulate water flow and influence plant communities (Mazzotti et al., 2009; Rosenblatt & Heithaus, 2011). Due to broad and diverse ecological roles of alligators, understanding their space use and social dominance can provide great insight into their functional role in the ecosystem. In addition, development and assessment of appropriate survey and monitoring techniques can give reliable information to manage and conserve alligator populations. Overall, the ecological information and potential improvements to population estimation approaches provided in this thesis will contribute to conservation and management actions for alligator populations and their habitats across the species' entire range.

The habitat selection of adult male alligators is a scale-dependent process and aquatic vegetation, water depth, and water temperature may be important factors influencing alligator foraging and thermoregulation (Goodwin & Marion, 1979; Joanen & McNease, 1972; Webb et al., 2009). At the coarser spatial scale, the limited evidence of resource selection in my study suggests that the study area is perceived as homogenous by alligators or that it meets their resource needs. An alternative explanation that deserves further exploration is that the wrong variables could have been measured and our habitat categories might not depict limiting factors to alligators. At finer scales, strong selection for certain variables such as floating, emergent vegetation and the avoidance of open water habitats could have management and conservation implications for alligators in inland rivers and reservoirs. For instance, state water management plans and programs for the local control of aquatic pests could consider: 1) allowing parts of the natural flood plain to flood seasonally for sub-adult dispersal and 2) maintaining patches of thick vegetation to help alligators mitigate their heat budgets. The lack of congruency among selection of resources at different scales reveals the importance of each resource for overall fitness and allows for an assessment of the overarching factors that drive differences in selection across scales. The most important variables of an individual's realized niche and the most significant limiting factors at the population level are the resources most critical for management at the appropriate scale. My study exposes that the biological significance of human disturbance, aquatic plant management, hunting pressures, and climate change is yet to be fully investigated, understood, or quantified for inland riverine alligator populations.

Though apparent habitat suitability and low alligator density did not manifest in an observed dominance hierarchy, a change in either could increase intraspecific interactions, facilitating a dominance hierarchy. The mechanisms by which social hierarchies form is an interesting area of behavioral evolutionary ecology that allows for improved understanding of animal distribution theory (Beacham, 2003; Estevez, Andersen, & Naevdal, 2007). Future studies of alligators could be designed to specifically test models of animal distribution theory including ideal despotic distribution or ideal preemptive distribution (Fretwell, 1972; Oro, 2008). Studies of adult male alligators have observed no aggressive behaviors, high interchange, and limited defense of territory (Joanen & McNease, 1972) as well as no defensive behaviors, close proximity, and large range overlap (Goodwin & Marion, 1979). In addition, riverine male crocodiles have no spatial partitioning and range overlap suggesting territoriality is not an important behavioral component (Kay, 2004). Based on the results of my research and other studies, assumptions regarding alligator territoriality and dominance hierarchies should be reviewed and the semantics clarified.

Results from modeling alligator count data in Mississippi from 1999 to 2013 show that counts per survey are increasing. Long-term data collection (15 years), diverse general habitat conditions at routes, survey standardization, and modeling effects of environmental covariates colligate to assume that predicted count change in the model is proportional to a change in population size. The observed positive response of alligator counts in Mississippi may reflect the benefit of listing the species for some time under the Endangered Species Act and long-term wetland conservation practices implemented in the state.

Even though distance sampling does not appear to be a feasible monitoring technique for riverine alligator population, it is important that survey protocols and monitoring programs account for imperfect detection and standardize or model important covariates. However, evaluating potential effects of environmental and observer variables on detectability will require a rigorously designed experimental approach to yield a higher statistical power than historical spotlight survey data. Alligator monitoring programs should use standardized spotlight surveys while taking advantage of double observer or seasonally replicated hierarchical modeling approaches. This in turn requires that information needs and goals of alligator population management should be clearly outlined. An alligator survey design could then be implemented to meet the management goals and answer relevant questions at the appropriate spatial scale. I recommend a stratified random design based on habitat type and management regime (i.e., harvest pressure) or systematic controlled surveys and these designs would be an improved approach to monitor alligator populations over time (O'Brien & Doerr, 1986). Effect of harvest levels and take of nuisance animals on alligator populations could be better evaluated if accurate population estimates exist. Therefore, implementing robust survey techniques that generate reliable abundance estimates with associated precision measures will improve the capabilities of MDWFP to manage alligator populations and would serve as a model to other conservation agencies in the southeastern United States.

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