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American Alligator (Alligator Mississippiensis) Ecology Within Human-Dominated Landscapes

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AMERICAN ALLIGATOR (ALLIGATOR MISSISSIPPIENSIS) ECOLOGY WITHIN HUMAN-DOMINATED LANDSCAPES

by

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in partial fulfillment of the requirements for the degree of

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CERTIFICATE OF APPROVAL

The thesis “American alligator (*Alligator mississippiensis*) ecology within human-dominated landscapes” submitted by Eli Beal

Approved by the thesis committee: Date

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Abstract:

Urbanization is an ever-increasing threat to wildlife and their habitats, yet research has been limited to a small number of taxa. The American alligator (*Alligator mississippiensis*) is an apex predator that has surprisingly received minimal attention within urban areas. To investigate the potential effects of urban land use on spatial ecology, we conducted surveys of relative alligator abundance in nine tributaries surrounding the St. Johns River. We used these data to explore the potential effects of urban development on alligator spatial distribution and habitat selection. At the coarse scale, we found no correlation between percent developed land and relative alligator abundance. Instead, salinity is the primary driver of relative abundance. At the fine scale, we found that alligators prefer habitats characterized by more open water and highly vegetated shorelines and avoid anthropogenic structure. Only one out of 93 sighted individuals was an adult, and recent data suggests that adults are relatively rare in our study area. Thus, juveniles still occupy urban habitats because they are not being targeted and they face virtually no competition from adults. To investigate the potential effects of land development on trophic ecology, we performed gut content analysis on golf course alligators found on Jekyll Island, Georgia. We made comparisons with alligators found in more natural areas on Sapelo Island, Georgia. Percent index of relative importance values reveal that there may be functional differences in prey choice or availability, but analysis of similarity, non-metric multidimensional scaling, and simplified Morisita index analyses show no significant difference. Further land development and increasing human activity may therefore degrade available habitat and limit the distribution of breeding adult alligators in once suitable areas and possibly shift diets toward reliance on prey items usually of lesser importance. These potentially interacting spatial and trophic effects could lead to local population declines.

Introduction:

A major driver of land use change is urbanization, whereby the land surface of relatively small areas is hyper-developed to support high-density human populations. This type of development is a force of biotic homogenization, where the environment built to meet the relatively narrow needs of humans creates more homogenous habitat and species assemblages (McKinney 2006). Changes in habitat structure and distribution would therefore be expected to greatly influence the ecology of organisms in an urban setting. Urban areas are one of the fastest growing types of land use, with the size of these areas expected to increase 139% in the southeast U.S. alone by 2060 (Terando et al. 2014). Despite the rapid growth of urban areas, our understanding of the ecological effects of urbanization is still in its infancy. Filling this knowledge gap will be key for moving toward the development and implementation of sustainable urban growth practices.

One group of organisms that has been largely overlooked in the field of urban ecology is large predators. They are typically excluded from areas of dense human habitation, especially in developing regions, due to the costs associated with their presence such as human and livestock endangerment (Dickman et al. 2011). If large predators can find a way to subsist in an urban environment, they are faced with many challenges. For example, the limited availability and fragmented nature of suitable habitat in urban areas has been shown to limit intraspecific variation in predator home range size (Grinder and Krausman 2001), possibly leading to the exclusion of individuals that require larger ranges. If suitable habitat can be found, urban predators can also face higher densities of conspecifics in these areas (Bateman and Fleming 2012). Despite the challenges associated with living alongside humans, some species of predators persist in urban areas, however these tend to be small- to medium-bodied mesopredators like raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*), and coyotes (*Canis latrans*), which display cryptic behavior (Bateman and Fleming 2012). In contrast, large predators like leopards (*Panthera pardus*) and spotted hyena (*Crocuta crocuta*) are more frequently documented in peri-urban and rural areas where they rely almost exclusively on domestic animals for food (Abay et al. 2011; Athreya et al. 2016). These novel predation opportunities created by anthropogenic influence may provide predators with greater ease of hunting, decreased search effort, and increased capture success (Fleming and Bateman 2018). These effects may be more pronounced in nocturnal predators because of the artificial light generated by human development (Manfrin et al. 2018). Changes in land use within peri-urban and rural areas have also been found to affect the level of human-wildlife conflict with large predators like black bears (*Ursus americanus*; Evans et al. 2014). Despite the direct effects that large predators can have on humans and their domestic animals in peri-urban and rural areas, little research has been performed in highly urbanized areas. One reason it is difficult to assess the ecology of large predators in urban ecosystems in general may be because outcomes of these interactions appear to be highly context-specific (El-Sabaawi 2018), meaning more research is necessary before a broad understanding can be reached.

The American alligator (*Alligator mississippiensis*) is a widely abundant, large-bodied apex predator found across the southeastern U.S. but has received minimal attention within urban areas. This is particularly surprising because alligators, and crocodilians in general, are regularly sighted within 10 km of city centers (Turak et al. 2020). Furthermore, alligators are a well-known indicator species that have been used to track the health of other ecosystems like the Everglades due to their ability to integrate changes in habitat and water quality within their tissues and behaviors (Mazzotti et al. 2009). To our knowledge no studies have yet been published that investigate alligator ecology in a heavily urban landscape, despite relatively large increases in the number of reported nuisance alligator complaints and alligator bites on humans over the last few decades (Woodward et al. 2019). However, there have been two studies in “urban-influenced” areas: Eversole et al. (2018) investigated habitat selection and distribution of an alligator population in a nature preserve on the outskirts of Houston, TX and found that alligators tended to avoid areas with the highest levels of human activity. Similarly, Lewis et al. (2014) investigated alligator habitat selection and distribution in a nature preserve on the outskirts of Fort Worth, TX and found that alligator behaviors may be impacted by boat traffic. A significant knowledge gap also exists surrounding the trophic ecology of alligators in a heavily urbanized landscape. Delaney et al. (1988) reported on the food habits of nuisance alligators from six counties in northeast Florida, but to our knowledge, this is the only study that has investigated the diet of peri-urban crocodilians. Researchers found the relative importance of some food groups for nuisance alligators differed from those reported for non-nuisance alligators (Delaney et al. 1988).

The spatial ecology portion of our study took place along the St. Johns River, an iconic part of the Florida landscape. The water system is a source of sustenance and employment across 12 counties, and the waters support abundant and diverse flora and fauna. The river also runs directly through Jacksonville, the largest city by land area in the contiguous U.S. Previous studies have shown that urban development around this river has shifted overall ecosystem function through the alteration of hydrology, chemistry, and biotic richness (Chadwick et al. 2006). The health of the St. Johns River is also threatened by pollution, over-use, and mismanagement (Pinto et al. 2017). Monitoring programs for some species of animals and plants have been initiated in this region (Pinto et al. 2017), but alligators have received almost no attention from researchers within the lower St. Johns River system.

The trophic ecology portion of our study took place on Jekyll Island, Georgia. The island has an area of approximately 23 km^2 and the southern section is more developed, containing a residential area, multiple golf courses, and a water park. The northern section is less developed, broken only by a road which circles the perimeter of the island. Routine surveys of alligators by the Jekyll Island Authority (JIA) have revealed healthy populations of alligators living within both sections. Extensive mark-recapture work has already been done by JIA to establish population size and distribution, so a significant knowledge base already exists.

For the spatial component of this study, we hypothesized that alligators found in the lower St. Johns River system would avoid areas that have become intensively urbanized because of the associated alteration of natural habitat features and increased levels of human activity. We expected alligator density to instead be highest in the least developed areas, and in terms of habitat selection, we hypothesized that alligators would show avoidance of anthropogenic structure. Urban development alters the habitat that alligators have evolved in for millions of years, therefore we expected that any deviation in habitat quality, from an alligator's perspective, would influence their spatial ecology patterns. For the trophic component of this study, we hypothesized that alligators in the more developed landscape would have a significantly different and less diverse diet than individuals living in a more natural setting since development can lead to biotic homogenization.

Chapter 1 – Alligators in the big city: Spatial ecology of American alligators

Materials and Methods:

Field Methods:

We performed nighttime spotlight surveys with an outboard motorboat throughout 2019 to determine alligator abundance, distribution, and habitat selection. This technique is an established method for estimating relative population sizes in crocodilians across heterogeneous habitat (Overton 1971). However, a limitation of spotlight surveys is the variation in detection probability caused by different environmental conditions or observers (Fujisaki et al. 2011). To control for these effects, we implemented a standardized survey protocol (Wood et al. 1985; Anderson 2001). All surveys covered the first 8 km of nine tributaries within the lower St. Johns River system, starting at the point where each tributary meets the main channel of the river (Figure 1). We limited our surveys to the first 8 km because some tributaries contained low bridges that blocked boat access after this point. We chose tributaries that were surrounded by different amounts of urban land cover such that our surveys spanned an urbanization gradient from approximately 5% to 80% urban land cover within 1 km of the river's edge (Figure 2). GIS analyses also revealed that land use patterns around the St. Johns River are dynamic, with different urban land cover proportions at 1, 3, and 5 km from the water's edge for each tributary (Tables 1, 2, and 3). To reduce temporal bias, we conducted surveys over the span of one year and segregated sampling periods into four distinct seasons (winter [Dec-Feb], spring [Mar-May], summer [Jun-Aug], and fall [Sep-Nov]. We surveyed each tributary one time during each season during the middle month of each season, resulting in a total of four surveys per tributary. We surveyed the tributaries in a quasi-random fashion because the tributaries closest to the mouth of the St. Johns River are under significant tidal influence, so we timed surveys of those tributaries during periods of high tide in order to access the full survey area. We only performed surveys when rainfall was absent and wind speeds were below 16 km/h since these factors have been shown to affect alligator detection probability (Strickland et al. 2018). Quasi-random sampling over the span of a year was best suited to randomize environmental conditions that affect nighttime spotlight survey counts, such as water level, temperature, moon phase, and moon illumination (Woodward and Marion 1978; Messel et al. 1981; Eversole et al. 2015; Strickland et al. 2018).

We began all surveys no earlier than 30 minutes after sunset and we maintained a constant boat speed of 10-12 km/hr. At the start and end of each survey we recorded moon phase, current weather conditions, visibility, ambient light, air temperature, water temperature, and salinity. We detected alligator eyeshine primarily using two 1200 lumen handheld spotlights, but we also used additional handheld lights (6000 lumens) often throughout the surveys. As soon as we detected eyeshine we approached the alligator at reduced speed. We placed each individual into a size class (30-90 cm [juvenile], 90-180 cm [sub-adult], 180-270 cm [adult], 270-360 cm [large adult], +360 cm [largest adult]) by estimating the distance between the eyes and the tip of the snout (Chabreck 1966; Magnusson 1983). If an alligator submerged before size estimation could take place, we recorded its length as unknown or simply larger or smaller than 180 cm. At each sighting we recorded global positioning system location using the on-deck boat navigation unit. We measured environmental characteristics at each sighting using a YSI meter (Pro2030; YSI; Yellow Springs, Ohio), a thermometer, and a sky quality meter (SQM; Unihedron; Grimsby, Ontario).

We recorded information about habitat characteristics for each sighting following previous studies (Webb et al. 2009; Lewis et al. 2014). We first visually characterized habitat in a 10 m radius circle centered on the alligator sighting location (“used habitat”). We recorded the proportion of open water, emergent vegetation, floating vegetation, anthropogenic structure, and dry ground within the circle, as well as the alligator’s distance from shore, vegetation, and anthropogenic structure. We then visually classified the same habitat characteristics in a 20×100 m plot centered on the alligator sighting location and stretching along the shoreline (“available habitat”). If an alligator sighting occurred entirely in open water, then we shifted the plot to the closest shoreline. For each used habitat circle and available habitat plot, we classified the respective shorelines as natural, hardened, or mixed, depending on if the shore was totally vegetated, subject to anthropogenic armoring, or a mixture of the two types respectively. We also estimated the proportion of shoreline found within these areas that were covered in naturally growing vegetation rather than anthropogenically altered lawns.

Land Use Classification:

We used ArcGIS Pro (ESRI; Redlands, CA) for all spatial data manipulation and visualization. We acquired land use and cover data from the St. Johns River Water Management District (SJRWMD) via the Florida Geographic Data Library. For all analyses we used data from the most recent SJRWMD dataset, which was from 2014.

We split a 100k definition polygon of the St. Johns River to create smaller units representing each tributary transect. The resulting features consisted of the main portion of each tributary surveyed where lower order streams that were not surveyed were deleted. Because the extent to which alligators respond to land use changes was not known, we buffered the transect polygon feature for each tributary to 1, 3, and 5 km to further clip the SJRWMD land cover and use data layer. By creating three buffers for each of the nine tributaries, we generated a total of 27 land cover and use layers.

We classified land use types through the Florida Land Use and Cover Classification System (FLUCCS), as cited in SJRWMD metadata documentation. This hierarchical coding scheme contains four levels, of which we used the highest level (level 1) designation. This particular level classifies land use into nine distinct categories. These categories included urban and built-up; agriculture; upland nonforested; upland forests; water; wetlands; barren land; transportation, communication, and utilities; and special classification. For the purposes of this study, we only included defined terrestrial land use types in statistical analyses. These land use types were urban and built-up (ex: residential, industrial, and recreational areas), agriculture (ex: cropland, pastures, aquaculture), upland nonforested (ex: shrub and brushland), upland forests (ex: coniferous forests, hardwood forests, tree plantations), wetlands (ex: freshwater/saltwater marshes, mangrove swamps, wet prairies), barren land (ex: beaches other than swimming beaches, borrow areas, spoil areas), and transportation, communication and utilities (ex: highways, electrical power facilities, wastewater treatment facilities).

We calculated the proportions of each land use type using each respective land use shape area divided by total shape area. The resulting data table contained the proportion of each general land use type surrounding each tributary at the 1, 3, and 5 km level.

Statistical Analyses:

To determine if environmental conditions and land use characteristics affect broad scale alligator distribution, we performed multiple analyses using SPSS (IBM; Armonk, New York).

We did not apply population estimate correction equations to the alligator counts because they tend to underestimate population numbers in crocodilians (Balaguera-Reina et al. 2018). Sighting data used in statistical analyses therefore represent relative alligator abundance, not a prediction of true alligator population size. We first checked normality for each variable using Kolmogorov-Smirnov and Shapiro-Wilk tests to determine if parametric or nonparametric tests were appropriate. Normality varied greatly across the suite of variables; therefore, Spearman's rho and Pearson's correlation coefficient were used when appropriate. We then performed simple linear regression to determine if there were any direct relationships between relative alligator abundance and individual variables. We performed these tests for alligator counts in each tributary by season and for the average number of sightings per tributary across seasons. We also averaged environmental variables for each tributary by season and for the average value per tributary across seasons. We tested for the effect of land use at all three buffer sizes for each tributary, including all terrestrial land use types.

We then performed multiple linear regression analyses in a stepwise manner. This modeling system excluded variables found to be highly correlated with other variables (multicollinear) and retained variables with significant contribution to the model ($p \leq 0.05$). We then performed these tests on modified datasets that did not contain the two most saline tributaries to further validate preliminary findings.

To evaluate habitat selection, we compared percent shoreline vegetation and the proportions of habitat characteristics found in the 10 m radius circle to those found in the remaining areas of each respective 20×100 m plot using the Wilcoxon signed rank test. When comparisons could be made between two normally distributed groups of data, we used a paired sample t-test instead. While comparing used to available habitat data was the basis of the tests, the amount of data per analysis differed between analysis groups. The first group was composed of all habitat selection data across time and space. This “global” dataset was the most robust in terms of sample size but may have been biased by double counting individuals across time. The second group was divided by season, so analyses were performed on all data collected within a season across space. This group removed the bias of double counting individuals but may be affected by variation in the number of sightings per season and tributary.

Results:

Distribution:

We recorded a total of 93 alligator sightings during nighttime spotlight surveys across time and space (Table 4). Size classification was heavily skewed towards juveniles and sub-adults with only one individual falling into the 180-270 cm size class. The remaining individuals with confirmed total length estimations fell into the 30-90 cm size class (n = 50), the 90-180 cm size class (n = 12), or were coarsely estimated as less than 180 cm (n = 6). The remaining 24 individuals submerged before total length estimates could be taken. We found alligators in all tributaries at least once during the year except in Clapboard Creek, the least urbanized water system that was also closest to the inlet of the Atlantic Ocean. The summer season contained the most alligator sightings (n = 58). We encountered fewer animals in the spring season (n = 22), and even fewer in the fall and winter (n =8 and n = 5, respectively).

When investigating relative alligator abundance, we did not find any of the candidate explanatory variables to always be statistically significant across seasons or tributaries. However, we found salinity to be significant in three of the four sampling seasons and in the global dataset as well (Figure 3). We also found upland nonforested land use was correlated in three of the five datasets. We found other land use types and environmental conditions such as air temperature to be correlated, but not consistently. Because we found no land use type to be a consistently significant factor at one buffer size and percent coverage of individual land use types were highly correlated across buffer sizes, we only report analyses of land use at the 1 km buffer size. We could only generate multiple linear regression models for the spring and summer seasons as well as the global dataset based on the normality of their distributions. Salinity once again appeared to be a major driving force, but other covariates such as the level of ambient light and the presence of forested and nonforested land use types also appeared as significant factors in the spring season models (Table 5).

To ensure that the effects of salinity were not biased by environmental outliers, we removed the two most tidally influenced and saltiest tributaries (Clapboard Creek and Dunn Creek) from the dataset and both sets of analyses were repeated. Upon removing these two, the number of variables we found to be correlated with relative alligator abundances was highly reduced. We still found salinity to be a statistically significant predictor in the spring season and in the averaged global dataset. Stepwise multiple linear regression analyses on the tidally unbiased data still found salinity and air temperature to be significant predictive variables (all $p \leq 0.017$).

Habitat Selection:

Surveys of used and available alligator habitats produced a total of 89 paired data points across time and space. We found statistically significant differences between the used and available habitat within the data analysis groups. Using all data across time and space, we found alligators inhabited areas with greater expanses of open water, minimal anthropogenic structure, and heavily vegetated shorelines (Table 6; Figure 4; Figure 5). Results from using all data collected within a season across space were subject to inter-season variation, but anthropogenic structure was almost always avoided by sighted alligators (Table 7). On average, alligators were found more than 50 m from the nearest anthropogenic structure.

Discussion:

The lower St. Johns River system has not escaped the ever-expanding influence of urbanization. Tributaries such as the Arlington River, for example, are surrounded by land in which only about 13% is considered undisturbed (not used for urban, agriculture, or transportation purposes or left barren by human influence). Large predators in areas such as these are subject to intense anthropogenic pressures and have historically received little recognition or study, perhaps because they were assumed to be nonexistent. Our study demonstrates that one species of large predator, the American alligator, can still inhabit dense urban areas but that the spatial ecology and body size range of the species may be altered by shifts in land use and human activity.

At a coarse scale, alligator distribution within the lower St. Johns River system appears to be largely dependent on salinity, with alligators avoiding saltier tributaries across all seasons. Even more compelling, analyses which did not include the two most tidally influenced tributaries still found salinity to be a strong predictor of relative alligator abundance. This result is not particularly surprising since it is consistent with our existing understanding of alligator sensitivity to salinity (Rosenblatt and Heithaus 2011; Rosenblatt et al. 2013; Fujisaki et al. 2014, 2016; Gardner et al. 2016; Skupien and Andrews 2017; Mazzotti et al. 2019).

While salinity appears to be the primary driver of alligator distribution, we also found air temperature to be a significant predictor of alligator abundance in several cases at a coarse scale. Again, this is expected because warmer air temperatures are known to positively influence the number of alligators in a given area, especially when incorporating seasonality into analyses (Lutterschmidt and Wasko 2006; Fujisaki et al. 2014; Strickland et al. 2018). Additionally, we did find that some land use types, such as forested and nonforested areas, were significant predictors of alligator abundance in certain situations, but were subject to high levels of multicollinearity and failed to consistently appear in multiple linear regression models across data sets. Land use patterns may therefore have some effect on alligator distribution at a coarse scale but to a far lesser degree than that of environmental factors like salinity or temperature. Overall, alligators do not appear to be affected by urban land cover at a coarse scale.

At the finer scale of alligator habitat selection, our data suggests that individuals prefer more natural habitat features and tend to avoid anthropogenic structure. Specifically, alligators tended to select areas with more open water and shoreline vegetation. These factors have been reported to be important for other alligator populations in settings with less human impacts (Goodwin and Marion 1979; Webb et al. 2009; Gardner et al. 2016; Skupien and Andrews 2017). When statistically significant differences were observed in the proportion of anthropogenic structure, there was always less structure in the used habitat than in available habitat. Although no previous study has been performed in a mainly urban setting, alligator abundance has been shown to be reduced in areas that are heavily affected by human presence and activity, consistent with our results (Eversole et al. 2018). Neither emergent nor floating vegetation differed significantly between used and available habitats consistently, indicating little to no preference. However, the presence of emergent and floating vegetation is known to affect detectability in crocodilian spotlight surveys (Cherkiss et al. 2006; Fujisaki et al. 2011; Lewis et al. 2014). Tributaries we surveyed were bimodal in that they either had prevalent or minimal aquatic vegetation. Tributaries containing large amounts of aquatic vegetation, such as Black Creek, supported some of the largest alligator populations. If we underestimated alligator abundance in these areas because of limited detectability, corrections would only strengthen the results of this study.

We also found an incredibly strong bias toward sightings of small alligators across all tributaries. With 98.6% of all size-classified individuals falling below the length of 180 cm, adults were remarkably absent from the tributaries. This result is particularly surprising since a previous study in a human-disturbed area found no differences in habitat selection between alligator size classes and little segregation between size classes (Eversole et al. 2018). The most likely explanation for our result is that adult alligators in the lower St. Johns River system have been mostly removed by hunters or nuisance alligator trappers over time, and the small number of remaining adults has learned to avoid urban areas and human activity. Hunter harvest data from the Florida Fish and Wildlife Conservation Commission (FWC; myfwc.com/wildlifehabitats/wildlife/alligator/harvest/) shows that between 2011 and 2018, 155 alligators were harvested in Duval County, which has the same extent as the city of Jacksonville. The yearly average total length of the harvested alligators in Duval County never exceeded 245 cm, while 83% of the other counties in Florida had at least one yearly average total length of harvested alligators that exceeded this value. Of the counties with smaller yearly average values than Duval, two (Clay and St. Johns) border Duval and the St. Johns River. This suggests that adult alligators are relatively rare in the lower St. Johns River system and may have learned to be even more cryptic than they would be in less disturbed areas. Even more telling, nuisance alligator harvest data from FWC shows that between 2006 and 2018, average nuisance alligator total length in Duval County has steadily declined from 185 cm in 2006 to only 145 cm in 2018. The over-representation of immature alligators bolsters the validity of our survey regimen because animals less than 180 cm in total length typically do not move more than 6 km within 12 months (Chabreck 1965), which would represent tributary-level site fidelity in our study. However, juvenile movement patterns have only been examined in marsh habitats, while their movement patterns in rivers are largely unknown.

Thus, juvenile and sub-adult alligators can still occupy urban areas of the lower St. Johns River system because humans are not targeting them for removal and they face virtually no competition or cannibalism from adults, while the few remaining adults appear to avoid urban areas almost entirely or become highly cryptic in nature. The young animals are then distributing themselves at a coarse scale to minimize the negative effects of high salinity on their smaller bodies (Lauren 1985) and are avoiding anthropogenic structure in favor of more natural habitat features at a finer scale. This represents a potentially significant shift in interactions between alligator size classes in urban areas relative to more natural areas.

Alligator occurrence and relative abundance across a heterogeneous habitat is multifaceted and complex, especially when considering variation between size classes and across study areas (Eversole et al. 2015). Overall, our study suggests that urban development adjacent to large river systems produces unfavorable habitat for alligators. Living in these areas, as well as the targeted removal of large individuals, has completely unknown consequences for alligator behavior, physiology, and population viability; more research is clearly needed to fully understand how these large predators may fare as urbanization continues across their range. Valuable insights could be made by studying possible differences in body condition between urban populations and those from more natural areas, along with dietary and contaminant studies. In general, large predators like alligators may actively avoid areas of human development due to habitat degradation and being targeted for removal, explaining why so few studies have been performed on large predators in urban areas.

Chapter 2 – What do alligators eat on golf courses?

Materials and Methods

Field Methods:

In conjunction with the Jekyll Island Authority (JIA), we performed monthly nighttime surveys of Jekyll Island's alligator population from April through October of 2019. After sunset, we used spotlights (6000 lumens) to detect alligators residing in golf course ponds. We captured individuals using a casted treble hook, a snare-pole, or a combination of both (McDaniel and Hord 1990). Once captured, we secured the mouth shut using electrical tape, freed the alligator from the fishing line, and dislodged the treble hook.

We measured the total length and snout-vent length of every captured alligator, marked the tail with a unique scute clipping pattern, determined sex by cloacal examination, and weighed each to the nearest 0.1 kg using a steel bar and a hanging scale. We then secured the animal to a spine board using nylon straps and used the hose-Heimlich technique as described by Fitzgerald (1989) to collect stomach contents. This technique is an established method and has been found to be more effective than other methods (Fitzgerald 1989; Nifong et al. 2012; Gonzalez-Jauregui et al. 2019). Stomach contents were collected in a bucket below the alligator's mouth and then filtered through a 4 mm mesh sieve. We then preserved the gut contents in glass jars with 95% ethanol. After processing of the alligator was complete, we released it back into the water where it was initially captured. We identified prey items in the laboratory to the lowest possible taxonomic level. We also recorded the wet weight and count of each prey type for each gut content sample.

Statistical Analyses:

We placed individual prey items into broad functional categories for analysis: birds, crustaceans, fishes, gastropods, insects/arachnids, mammals, reptiles, and seeds. To determine if there were any differences in the diets of alligators living in developed versus undeveloped areas, we compared data collected from Jekyll Island golf course alligators to data collected by Nifong et al. (2016) from alligators on low-development Sapelo Island, Georgia (Figure 6). Prey categories used by Nifong et al. included birds, crustaceans, fishes, gastropods, insects/arachnids, mammals, reptiles, amphibians, and horseshoe crabs (*Limulus polyphemus*).

We quantified the dietary composition of alligator stomach contents using the index of relative importance (IRI). This index is especially useful in dietary comparisons because it incorporates occurrence, frequency, and wet weight of prey items which accounts for biases like the differential digestion rates of hard-bodied and soft-bodied prey (Cortes 1997; Nifong et al. 2012). The average percentage of each prey group according to number (%N), wet weight (%W), and frequency of occurrence (%O, the number of alligator stomachs in which an item occurred) are used to calculate the IRI value:

$$IRI = \%O \times (\%N + \%W)$$

We calculated these values for all prey categories in both the Jekyll Island and Sapelo Island datasets. We then converted IRI values to a percentage (with *i* as each individual prey category):

$$\%IRI_i = \frac{IRI_i}{\sum_i^n IRI}$$

The %IRI values are useful for direct comparisons between the alligator populations living on the two islands.

To determine if there was a statistically significant difference between the diets of the two groups, we used analysis of similarity (ANOSIM) and non-metric multidimensional scaling

(NMDS) in R (RStudio Inc; Boston, Massachusetts). We calculated %IRI for each individual alligator in both groups, and we removed alligators with empty stomachs. We then used ANOSIM (function "anosim" from package "vegan") to determine if there was a significant difference between the %IRI values across all prey categories through 9999 permutations of Bray–Curtis dissimilarity calculations. As another measure of similarity and to better visualize the relationship between the diet preferences of both islands, we also performed NMDS (function "metaMDS" from package "vegan") across all prey categories. Lastly, we used the simplified Morisita index (Krebs 1999) to assess dietary overlap between the two groups using the following equation

$$C_H = \frac{2\sum_i^n p_{ij}p_{ik}}{\sum_i^n p_{ij}^2 + p_{ik}^2}$$

where C_H is the simplified Morisita index of overlap between population j and population k, p_{ij} is the %IRI value for prey category i in population j, p_{ik} is the %IRI value for prey category i in population k, and n is the total number of prey categories ($i = 1,2,3, \ldots ,n$). The value of the index varies between 0 and 1 and typically $C_H < 0.29$ indicates minimal dietary overlap, $0.30 < C_H < 0.65$ indicates moderate dietary overlap, and $C_H > 0.65$ indicates high dietary overlap (Langton 1982).

Results

We collected stomach content samples from 25 alligators on Jekyll Island golf courses, of which only one had an empty stomach. Alligators ranged from 56.8 – 237.0 cm in total length, and there was an approximately even sex ratio with 11 males, 13 females, and 1 unconfirmed individual. Data provided by Nifong et al. (2016) consisted of 93 alligators within our size range from Sapelo Island, of which only one had an empty stomach. Alligators from Sapelo Island ranged from 54.6 – 237.0 cm in total length. This data set was composed of 58 males, 33 females, and 2 unconfirmed individuals.

Calculations of %IRI showed heavy reliance on three prey categories (fishes, insects/arachnids, and crustaceans), with 95% of %IRI values coming from these categories for both island populations (Figure 7). However, the rank of each prey category differed between islands (Figure 7). ANOSIM showed no statistical difference ($p = 0.15$) and very little distance between data points ($R = 0.04$). The NMDS analyses also showed little indication of statistically significant difference with most permutations failing to reach convergence. The NMDS plots showed heavy overlap in data space between the two island populations (Figure 8). Finally, the simplified Morisita index value of dietary overlap was $C_H = 0.71$, indicating high dietary overlap between the two island populations.

Discussion

Land development is known to drastically affect different aspects of wildlife ecology, but the reported effects on large predator species have been highly variable. For example, some studies show declines in predation pressure (predation relaxation) while others show increases in predator abundance (predator proliferation) in response to urbanization (El-Sabaawi 2018). Our study demonstrates that one species of large predator, the American alligator, may alter its dietary preferences based on shifts in land use and human activity, thereby potentially altering its ecological role and influence on different prey communities.

Average %IRI values showed that alligators in the anthropogenically disturbed Jekyll Island population relied heavily on insects and arachnids, with over 70% of their diet composed of prey in this category. In contrast, insects and arachnids only made up 35.7% of the Sapelo

Island alligator population’s diet. This finding broadly agrees with Delaney et al. (1988) in that nuisance alligators relied more heavily on some types of invertebrate prey relative to “wild” populations. Sapelo Island alligators relied more heavily on crustaceans than the Jekyll Island alligators, possibly because the two populations are known to differ in their habitat use patterns. A study of alligator habitat use on Sapelo Island found that adult male home ranges are on average made up of 80% marine habitats and only 20% freshwater habitats (Nifong and Silliman 2017). In contrast, a study of alligator habitat use on Jekyll Island found that adult males on average only spend 26% of their time in marine habitats (Skupien et al. 2016). However, while average %IRI values indicate that there may be some dissimilarity between island population diets, statistical analyses such as ANOSIM, NMDS, and the simplified Morisita index suggest broad overlap in diet space. These incongruent findings may be a result of a relatively small sample size for the Jekyll Island population relative to the Sapelo Island population, as well as the fact that only two islands were used in the study. Significant variation in diets may not be detected from small sample sizes, and any observed variation may be a factor of regional differences and not from human development alone. Adding more samples from Jekyll Island and surveying across more islands in the future may lead to more robust conclusions.

Trophic interactions of American alligators are known to vary widely among size classes, sexes, years, and habitats (Delaney and Abercrombie 1986; Nifong 2016). Our results suggest that alligators generally feed on similar prey items across Georgia barrier islands, even when one island is much more developed than the other. However, alligators found on golf courses tended to show higher values of relative importance for insect prey while alligators occurring in natural areas had a more even distribution of prey importance. This trend could possibly be explained by biotic homogenization of prey availability occurring on golf courses, or through island specific variation. These highly manicured and anthropogenically disturbed habitats may only support small insect prey, some fishes, and few crustaceans. Less developed areas may contain suitable habitat for a wider variety of prey species, giving alligators access to a more diverse menu. Alligators in developed landscapes would therefore be expected to have somewhat dissimilar diets to populations from more natural landscapes if the availability of prey species is different in urban environments (Delaney et al. 1988). Determining the potential strength of this effect would require sampling prey species availability and abundance (Delaney et al. 1988), but we were unable to incorporate this type of work into our research plan because of logistical issues.

Conclusions

Our study is one of the first to assess the effects of intense anthropogenic development on the spatial and trophic ecology of the American alligator, a large predator regularly sighted within 10 km of city centers (Turak et al. 2020). Our results suggest that urban development adjacent to large river systems may produce unfavorable habitat for alligators and that large alligators may be preferentially excluded from urban areas by hunters and trappers who target them. The repercussions of effectively removing a majority of the breeding alligator population in urban areas is unknown, but these could hinder future management and conservation strategies. Additionally, alligators living in human dominated and heavily manicured landscapes (e.g., golf courses) do not appear to shift their consumption patterns relative to less disturbed habitats, but larger sample sizes and study areas are needed to confirm these results. Our study indicates that alligator conservation efforts in human-dominated landscapes would require the preservation of riparian vegetation, potentially limiting the size and number of anthropogenic structures (e.g., docks) within aquatic areas, maintaining movement corridors between different habitat types, maintaining an adequate stock of breeding-size individuals, and protecting the biodiversity of prey species.

These types of conservation efforts could be strengthened by the development of holistic biodiversity plans at the city level, an idea which has protected natural areas in many cities internationally. A prime example of such a plan can be found in Singapore, one of the largest cities in southeast Asia. In September 2009, Singapore announced the development of the National Biodiversity Strategy and Action Plan as one of its obligations under the United Nations' Convention on Biological Diversity. Broadly, the plan was created to 1) conserve and enhance biodiversity at the genetic, species and ecosystem levels, 2) ensure sustainable use of biodiversity resources, and 3) ensure fair and equitable sharing of benefits that result from the use of their genetic resources. To achieve these goals, Singapore developed the city biodiversity index (CBI) to self-assess their progress. The CBI is used to assist the Singapore government in benchmarking biodiversity conservation efforts in urban areas, which is especially important to overcome geographical, location, and taxonomic biases in urban biodiversity conservation efforts (Shwartz et al. 2014).

The recovery of smooth-coated otter (*Lutrogale perspicillata*) populations within Singapore acts as a testament to the efficacy of the CBI and its associated changes to urban development. The otters reappeared in Singapore in the mid-1990s after an absence of approximately three decades, but the population remained small and isolated for many years until dramatic increases in both population size and range after 2007 (Theng and Sivasothi 2016). These trends were partially attributed to the slowed growth of coastal development (Theng and Sivasothi 2016). The inevitable interaction of humans with otters raises the probability of disturbance and conflict, so raising awareness and educating the public are considered vital for the future of these aquatic mammalian predators (Theng and Sivasothi 2016). A study conducted by Kawata and Ozoliņš (2018) found that perceived value by the public was higher for wild otters rather than tame individuals, given that their sighting frequency was high enough. If American alligator populations are to have successes in urban areas like the smooth-coated otter, they similarly would require the public to perceive them as highly valuable. While the perceived risk associated with alligators is relatively low, global views concerning crocodilian conservation have become less positive as populations recover (Caldicott et al. 2005; Hayman 2011). Education campaigns and public outreach are therefore key aspects of large predator conservation in urban areas.

In our rapidly urbanizing world, natural areas are being destroyed and hyper-developed to support high-density human populations. These changes usually come at the expense of wildlife species, many of which have inhabited such areas for thousands of years relatively unaffected by human activity. However, some species have adapted to live in anthropogenically dominated landscapes. Some small- to medium-bodied mesopredators which display cryptic behavior have flourished in these areas, yet large-bodied predators have often been displaced. Large predators that inhabit the periphery of human habitation typically sacrifice natural spatial and trophic patterns to survive. Our study has added to this body of knowledge with evidence that American alligators may avoid anthropogenically degraded habitats and alter prey consumption likely based on what is most available in these areas. Novel predation opportunities and anthropogenic avoidance appears to alter how large predators exist within their environment, but the adaptability of these species may enable them to persist in areas that we once thought were inhospitable to large predators. However, the process of adapting to a new environment may lead such predators to abandon their “wild” ecological roles.

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Table 1: Land cover and use across tributaries measured within 1km of the St. Johns River. Land cover and use descriptions are based on 2014 SJRWMD Level 1 FLUCCS codes.

Land Cover and Use Description	Arlington	Black	Broward	Clapboard	Doctors	Dunn	Julington	Ortega	Trout
Urban and Built Up	82.0	20.0	44.4	4.8	79.9	42.0	62.4	67.5	74.4
Agriculture	0.0	3.2	0.1	0.0	0.1	1.7	1.8	0.3	0.1
Upland Nonforested	0.6	0.4	11.5	1.9	0.0	10.1	2.6	0.2	0.3
Upland Forests	2.5	21.2	20.5	25.2	5.3	14.8	7.9	7.4	4.3
Wetlands	9.6	54.4	12.9	64.5	13.5	22.8	24.7	21.0	16.8
Barren Land	0.0	0.0	0.1	1.4	0.0	0.7	0.0	0.0	0.0
Transportation, Communication, and Utilities	5.3	0.8	10.5	2.2	1.2	7.9	0.6	3.6	4.1

Table 2: Land cover and use across tributaries measured within 3km of the St. Johns River. Land cover and use descriptions are based on 2014 SJRWMD Level 1 FLUCCS codes.

Land Cover and Use Description	Arlington	Black	Broward	Clapboard	Doctors	Dunn	Julington	Ortega	Trout
Urban and Built Up	81.5	34.3	47.6	11.4	79.0	40.7	62.2	72.7	70.7
Agriculture	0.2	4.6	0.6	0.9	0.4	2.8	0.8	0.8	0.2
Upland Nonforested	0.4	1.9	7.4	5.8	0.3	7.4	3.5	0.5	1.2
Upland Forests	2.7	27.1	16.1	21.9	4.7	15.4	8.3	10.7	8.5
Wetlands	9.2	29.6	15.9	52.4	12.1	18.3	22.8	12.0	14.9
Barren Land	0.1	0.1	2.0	0.6	0.0	2.8	0.1	0.0	0.0
Transportation, Communication, and Utilities	5.9	2.4	10.5	7.0	3.5	12.6	2.3	3.3	4.5

Table 3: Land cover and use across tributaries measured within 5km of the St. Johns River. Land cover and use descriptions are based on 2014 SJRWMD Level 1 FLUCCS codes.

Land Cover and Use Description	Arlington	Black	Broward	Clapboard	Doctors	Dunn	Julington	Ortega	Trout
Urban and Built Up	77.5	39.6	50.0	14.0	64.3	39.0	59.1	75.2	64.4
Agriculture	0.2	10.7	1.2	0.6	0.9	2.0	0.9	0.7	1.1
Upland Nonforested	0.4	1.7	4.7	5.1	0.7	5.3	2.3	0.5	1.9
Upland Forests	3.7	23.2	14.8	21.0	7.4	15.9	12.6	8.0	11.8
Wetlands	10.0	22.3	17.7	49.6	23.2	22.6	21.3	10.9	13.6
Barren Land	0.1	0.1	1.3	0.5	0.0	1.5	0.1	0.0	0.0
Transportation, Communication, and Utilities	8.1	2.5	10.2	9.1	3.4	13.6	3.8	4.7	7.1

Table 4: Number of alligator sightings by tributary (listed from northeast to south) over the span of a year, separated by season in which the sighting occurred.

Tributary	Winter Sightings	Spring Sightings	Summer Sightings	Fall Sightings	Average Sightings
Clapboard	0	0	0	0	0.00
Dunn	0	0	0	1	0.25
Broward	0	0	3	0	0.75
Trout	0	1	0	0	0.25
Arlington	1	5	13	2	5.25
Ortega	0	4	14	0	4.50
Doctors	0	4	6	3	3.25
Julington	2	5	4	2	3.25
Black	2	3	18	0	5.75

Table 5: Significant multiple linear regression models for normally distributed alligator sightings by season that incorporate environmental cofactors and measures of land use (LU) at levels of 1, 3, and 5 km surrounding each transect.

Dependent Variable	Model Parameters	p-value
Spring Sightings	Salinity	0.004
	Salinity + Light	0.001
	Salinity + Forests LU (1km)	0.001
	Salinity + Forests LU (3km)	0.001
	Nonforested LU (5km)	0.003
	Nonforested LU (5km) + Salinity	0.002
	Nonforested LU (5km) + Salinity + Light	0.001
Summer Sightings	Salinity	0.035
Average Sightings	Salinity	0.003

Table 6: Results of Wilcoxon signed rank tests from the global dataset that independently compared all habitat characteristics from the used habitat to their respective value in available habitat. Average percent of each habitat type is represented for both used and available habitat. Statistically different results are marked with an asterisk (*).

	Used Habitat		Available Habitat		
Habitat Characteristic	x̄ (%)	SE	x̄ (%)	SE	p-value
Open Water	57	2.2	51	1.6	0.007*
Emergent Vegetation	10	1.7	13	1.7	0.19
Floating Vegetation	10	1.9	12	1.9	0.10
Anthropogenic Structure	4	1.1	8	1.2	< 0.001*
Dry Ground	19	2.0	16	1.7	0.56
Shoreline Vegetation	87	3.2	81	3.5	0.007*

Table 7: Results of Wilcoxon signed rank tests and paired samples t-tests independently comparing each habitat characteristic from the used habitat to the available habitat within a given season. Statistically different results are marked with an asterisk (*).

Season	**Habitat Characteristic**	**p-value**	**Average Percent Characteristic (used habitat)**	**Average Percent Characteristic (available habitat)**
Winter (n=5)	Open Water	0.59	34	32
	Emergent Vegetation	0.88	20	19
	Floating Vegetation	1.00	29	29
	Anthropogenic Structure	0.66	9	7
	Dry Ground	0.14	8	14
	Shoreline Vegetation	0.32	100	88
Spring (n=22)	Open Water	0.031*	63	52
	Emergent Vegetation	0.31	10	12
	Floating Vegetation	0.14	7	9
	Anthropogenic Structure	0.017*	5	11
	Dry Ground	0.48	16	17
	Shoreline Vegetation	0.26	80	79
Summer (n=54)	Open Water	0.33	56	52
	Emergent Vegetation	0.067	7	13
	Floating Vegetation	0.37	11	12
	Anthropogenic Structure	0.001*	3	7
	Dry Ground	0.029*	22	16
	Shoreline Vegetation	0.037*	89	82
Fall (n=8)	Open Water	0.23	61	53
	Emergent Vegetation	0.22	22	14
	Floating Vegetation	0.10	0	4
	Anthropogenic Structure	0.34	9	14
	Dry Ground	0.024*	8	15
	Shoreline Vegetation	0.22	91	77

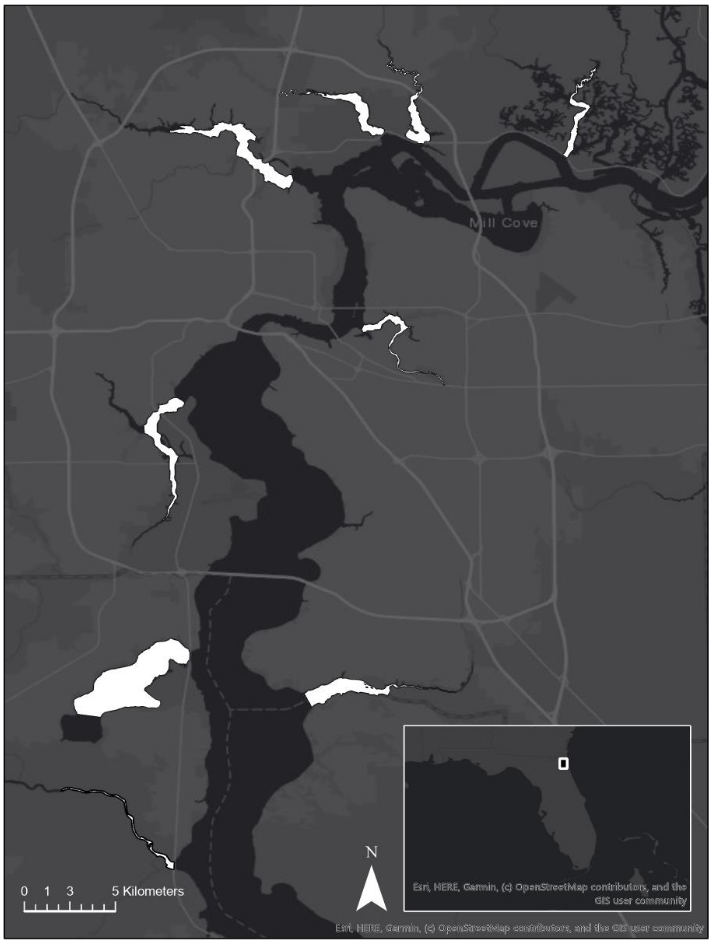

Figure 1: Tributary transects (white areas) surrounding the lower St. Johns River system. From northeast to south: Clapboard Creek, Dunn Creek, Broward River, Trout River, Arlington River, Ortega River, Doctors Lake, Julington Creek, and Black Creek.

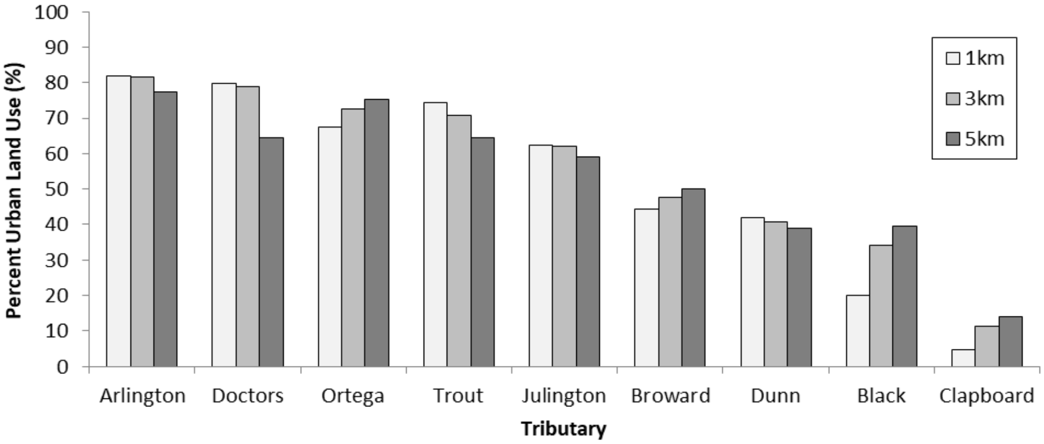

Figure 2: Levels of urban development (FLUCCS code 1000) surrounding the study area tributaries of the St. Johns River. Land use was quantified using 1km, 3km, and 5km buffers around each tributary transect.

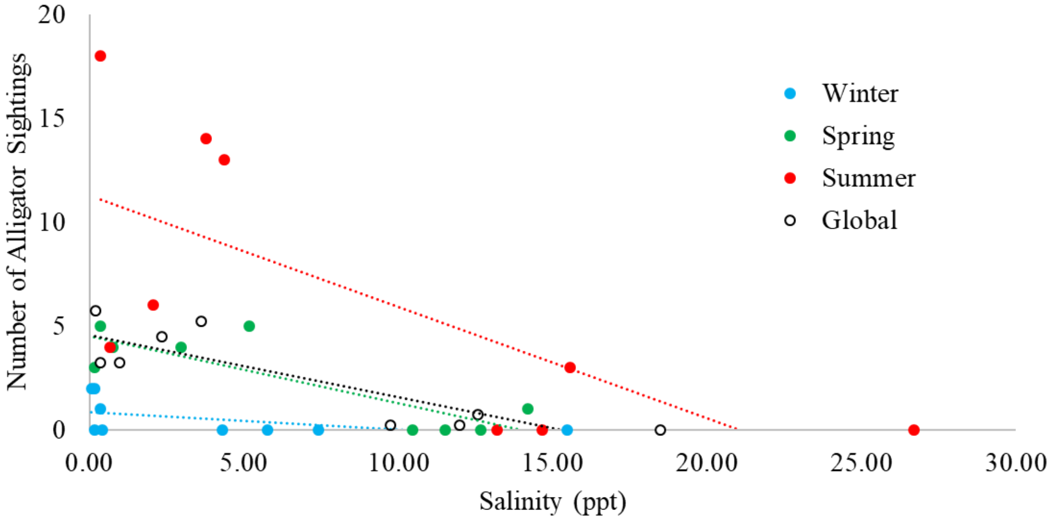

Figure 3: Correlation and simple linear regression results depicting the negatively correlated relationship of relative alligator abundance with salinity. Data is represented from winter (p=0.029), spring (p=0.004), and summer (p=0.035) sampling seasons, as well as in the averaged global dataset (p = 0.003).

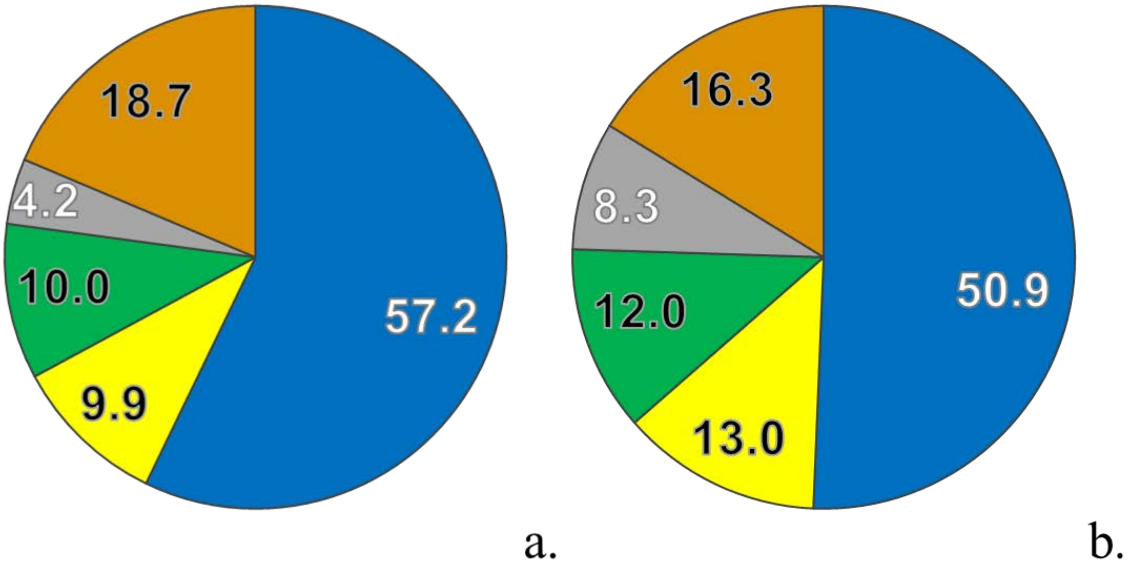

Figure 4: Average percent habitat characteristics in alligator used habitat (a.) and available habitat (b.) from the global data set. Significant differences were found in the proportion of percent open water (p=0.007) and percent anthropogenic structure (p=<0.001) through Wilcoxon signed rank tests and paired samples t-tests. Deviations from 100% are due to rounding error from averaged values.

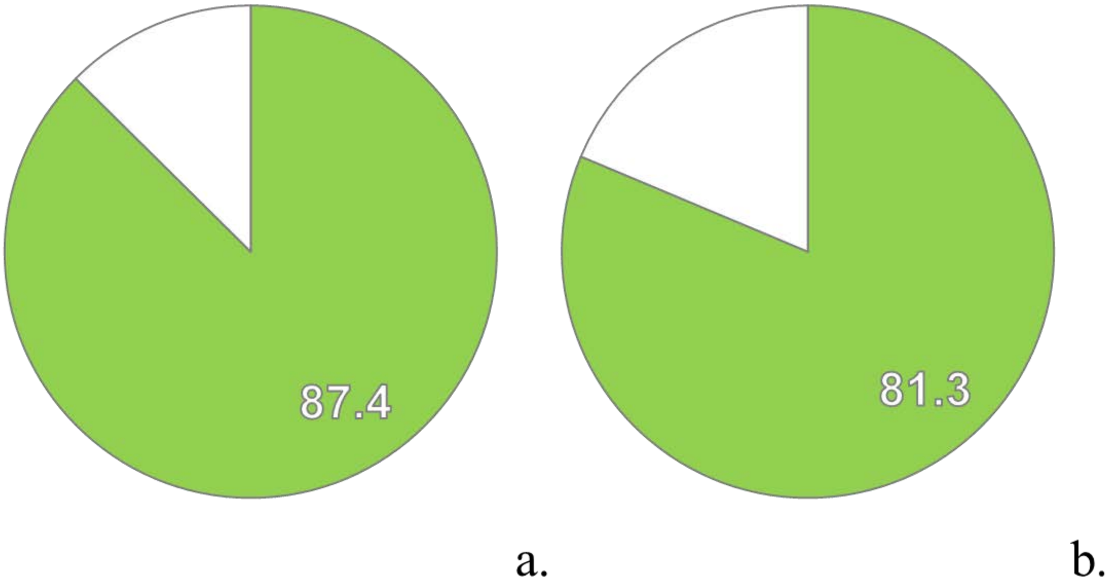

Figure 5: Average percent shoreline vegetation in alligator used habitat (a.) and available habitat (b.) from the global data set. Significant differences were found between the two habitat types (p=0.007) through Wilcoxon signed rank tests.

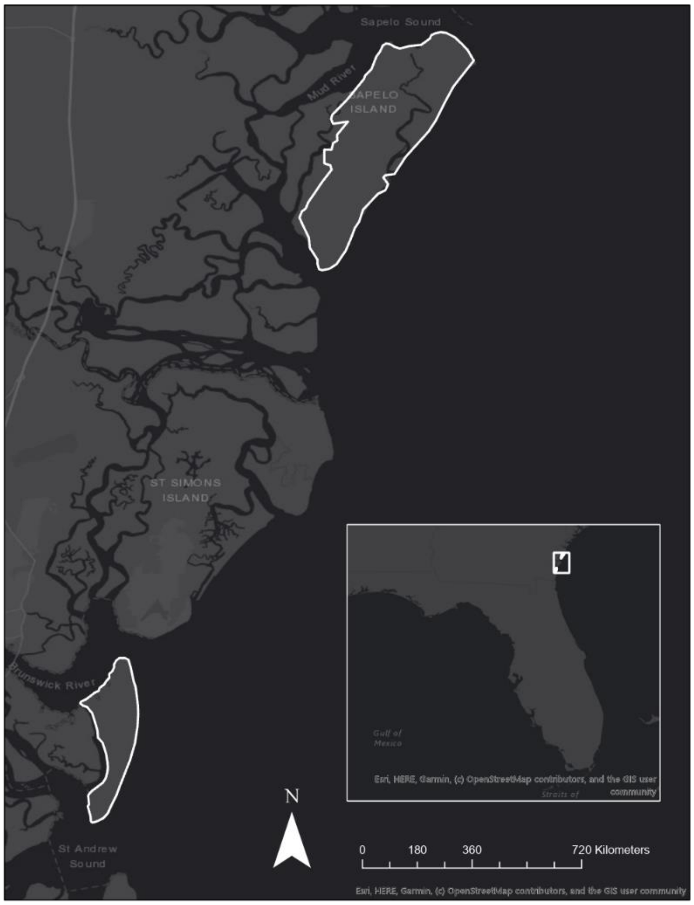

Figure 6: Study area of data collection for Chapter 2 (trophic ecology). Stomach contents were collected from alligators on golf courses on Jekyll Island, GA (southwestern island outlined in white). Data was provided for alligator gut contents from the lesser developed Sapelo Island, GA (northeastern island outlined in white).

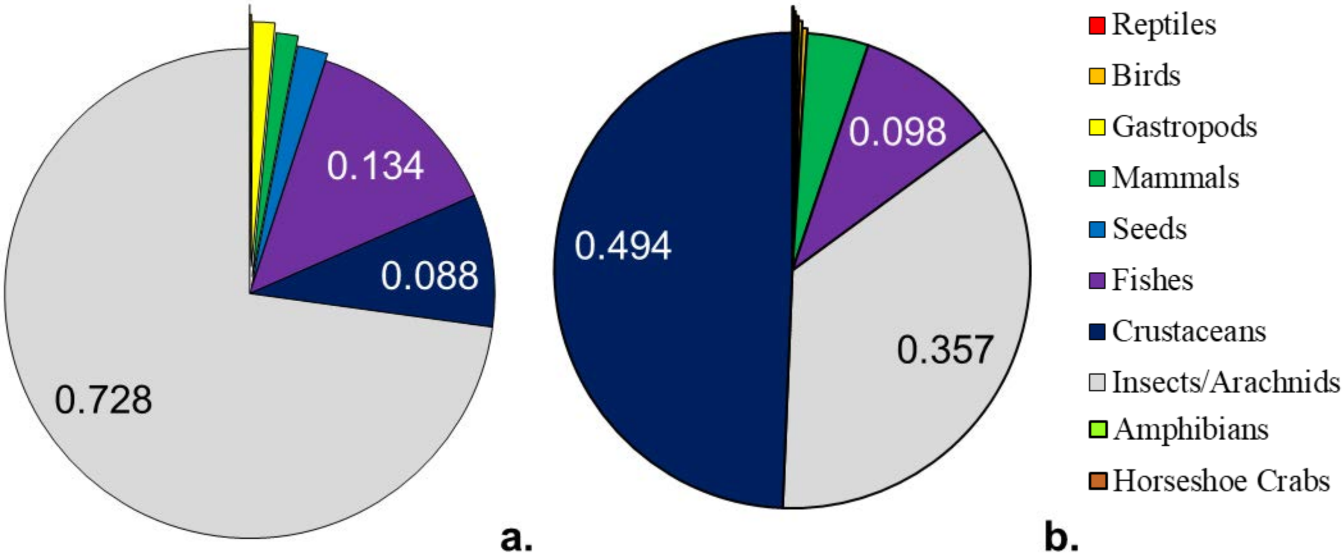

Figure 7: %IRI values for prey item categories found in Jekyll Island golf course alligators (a) and Sapelo Island alligators (b). ANOSIM and NMDS reveal no statistical differences for %IRI values calculated for each individual between the two island populations.

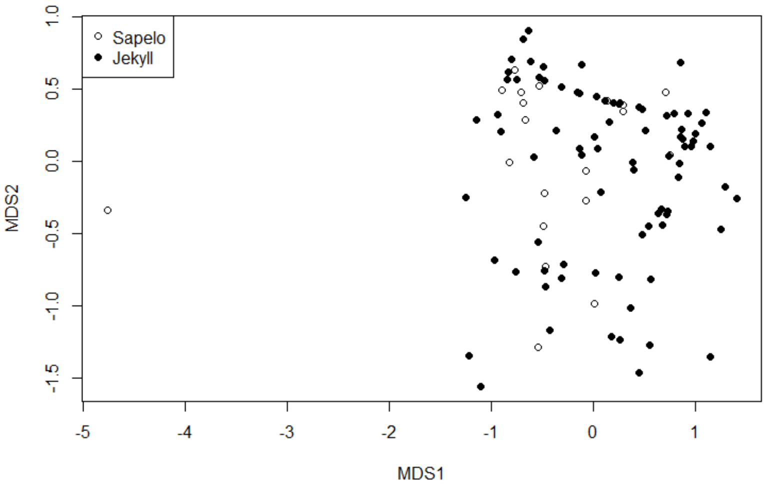

Figure 8: NMDS plot visualizing prey category %IRI values for all prey groups found in Jekyll Island golf course alligators and Sapelo Island alligators. Stress = 0.1357119 after 20 runs using Bray-Curtis dissimilarity.

Vitae

Eli Beal

Education

2018-2020	M.S. Biology University of North Florida (UNF), Jacksonville, FL
2014-2017	B.S. Biology: Ecology, Conservation, Environmental Biology Track Indiana University of Pennsylvania (IUP), Indiana, PA

Academic Positions

2019	Field Crew Leader, University of North Florida
2018-2020	Graduate Teaching Assistant, University of North Florida

Research Grants & Competitive Travel Grants

2020	UNF Coastal and Marine Biology Flagship Program Travel Award	$500
2019	ASIH Clark Hubbs' Travel Award	$600
2019	UNF Coastal and Marine Biology Flagship Program Travel Award	$500
2019	UNF Environmental Center Seed Grant	$5,754.20
2017	IUP School of Graduate Studies and Research Travel Grant	$375

First-authored Research Poster Presentations

E.R. Beal and A. Rosenblatt. *American alligator (Alligator mississippiensis) distribution across an urban landscape*.

E.R. Beal and D.J. Janetski. *Assessment of competition among sport fish in Two Lick Creek using gut content analysis*.

E.R. Beal and D.J. Janetski. *Pharmaceutical testing in and around waters of Presque Isle State Park, Erie Pennsylvania*.

Teaching & Mentoring Experience

Courses Taught

University of North Florida

2020	Principles of Biology Lab (Spring)
2019	Principles of Biology Lab (Fall)
2019	Crocodilian Behavioral Ecology (Summer)
2019	Principles of Biology Lab (Spring)
2018	Principles of Biology Lab (Fall)

Professional Affiliations

2019-Present	The Wildlife Society: Florida Chapter
2019-Present	American Society of Ichthyologists and Herpetologists
2014-2017	Strategies for Ecology Education, Diversity and Sustainability
2017-2018	Phi Kappa Phi (Honors Society)
2015-2018	Tri Beta (Biology Honors Society)
2015-2016	Phi Eta Sigma (National Honors Society)
2015-2016	Sigma Alpha Lambda (National Leadership and Honors Society)