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Research article

Spatial ecology and habitat utilization of American alligators in an urban-influenced ecosystem

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Abstract

Previous studies have explored spatial ecology and habitat use of alligators and other crocodilian species. However, few studies have explored these characteristics in urban environments. We studied an alligator population that occurred in an urban-influenced ecosystem, a habitat that has received little scientific attention. Our objectives were to determine spatial ecology and habitat use of American alligators within this urban system and to provide a template of methodology and analytical techniques that can be used by urban biologists, planners and researchers in order to assess and study urban crocodilian populations. We recorded 653 observations of alligators and their locations during 19 alligator surveys at an encounter rate of 0.6 alligators per km/survey. Results indicated that alligators exhibited clustering patterns of distribution. Thirteen different wetland types occurred within our survey area, but alligators were only observed in 10 of the 13. We found few differences in habitat use among size classes. We observed little segregation between adult and subadult size classes. However, there was spatial segregation between hatchlings and all other size classes, presumably due to female nest site selection. Alligators of all size classes seemingly avoided areas of high human activity; therefore, urbanization can influence alligator distribution and habitat use within wetland ecosystems. We provide methods and information that can be incorporated into future research and management of urban crocodilian populations. Utilizing this information, biologists can identify potential target areas for implementing management strategies, identify habitat and nesting areas, and mitigate human–alligator conflict.

Key words: crocodilian, Geographic Information Systems, habitat use, Texas, wetlands

Introduction

Population dynamics of wildlife species, such as population structure and distribution, are important demographic factors that result from the synergistic relationship between density-dependence and environmental factors (Langvatn and Loison 1999; Eversole et al. 2015a). Frequently, these parameters are limited or regulated by physiological factors such as thermoregulation, foraging demands, reproduction, predator avoidance, and territorial defense (Durtsche 2013). In particular, American alligator (*Alligator mississippiensis*) population structure, distribution and dynamics are thought to be diverse and affected by many factors, of which morphological variation, habitat requirements, and social structure of alligators are considered the most significant (Woodward and Marion 1978;

Subalusky et al. 2009; Eversole et al. 2015a,b). These factors result in differential habitat use and spatial ecology of alligators at each life history stage (i.e. hatchling, juvenile, subadult, adult). Few studies have examined these differences across size classes to determine the spatial distribution of alligator populations. Knowledge of spatial distribution aids in better understanding the role of predator avoidance, size segregation and habitat use in the population ecology of alligators.

American alligators inhabit wetland ecosystems throughout the southeastern USA. Their western range extends into the Gulf coast, southern, and central portions of Texas (Ross and Ernst 1994; Conant and Collins 1998). Many aspects of alligator ecology have been studied in a wide variety of habitats and locations (Saalfeld et al. 2008; Webb et al. 2009; Rosenblatt and Heithaus 2011; Nifong et al. 2014). Alligators that inhabit coastal areas have been known to utilize marshes and wet prairies interspersed with shallow open water and canals (Hines et al. 1968; Joanen and McNease 1972; Morea et al. 2002). Moreover, alligators in inland habitats often are more variable and diverse in regards to life history than their coastal counterparts (Joanen and McNease 1984; Ryberg et al. 2002; Eversole 2014). Although there is some information available about these characteristics, gaps in knowledge concerning habitat use, activity patterns, and how this affects alligator populations still exist. Alligator habitat use and activity may vary according to gender, size class and season (Chabreck 1965; Joanen and McNease 1970; Goodwin and Marion 1979; Taylor and Neal 1984; Rootes and Chabreck 1993). However, it is unknown how these parameters may differ in transition zones that contain variable habitat types. Ecotones often have greater abundance and density of species than are found in either flanking habitat type (Milne et al. 1996). However, it is unknown if intraspecific competition between size class and gender of alligators will alter ecotone theory. Additionally, few studies have focused intensively on alligator ecology in the western portion of their range, and more specifically in urban habitats. Most often, alligator populations are studied in rural areas or areas with few human inhabitants (Ryberg et al. 2002; Nifong et al. 2014; Eversole et al. 2015a). However, due to the increase in urban alligator populations and human–alligator conflicts, information concerning such populations is absolutely necessary in order to mitigate these problems and properly understand and manage urban alligator populations (Eversole et al. 2014). To our knowledge, there have been no studies of alligator ecology in urban-influenced ecosystems, and very few studies of crocodilian species in general in these environments. Smith et al. (2013) emphasized the need to consider anthropogenically altered habitats in herpetological research because such populations often occur at much higher densities and offer novel avenues for ecological study.

American alligators are apex predators, ecological engineers and keystone species within the wetland habitats that they occupy (Mazzotti and Brandt 1994; Mazzotti et al. 2009; Eversole et al. 2015a). They are an essential component in the trophic and non-trophic processes of these multidimensional systems (Subalusky et al. 2009). Due to the capability of the species to serve as a model of ecological condition, a complete understanding of their ecology, biology and life history across all habitat types and areas of their range is imperative. The objectives of this study were to (i) determine population abundance, structure, spatial distribution and habitat use of American alligators within an urban-influenced ecosystem and (ii) provide a template of methodology and analytical techniques that can be used by urban biologists, planners and researchers in order to assess and study urban occurring crocodilian populations. We hypothesized that these parameters occurred in relation to alligator size–class and that our results would spatially reflect the urban-influence of our study site location.

Materials and methods

Study area

Armand Bayou Nature Center (N 29°35.0529, W 95°4.5909; datum WGS1984; Fig. 1) is a privately operated, non-profit organization and nature preserve located in Pasadena, TX. This site is located within the Houston, TX, metropolitan area and is considered an island of habitat within a major urban environment (Fig. 1). The nature preserve and property consists of 1011 hectares located along Armand Bayou, a public tidal and brackish body of water that flows into Galveston Bay. Although the waterways are public and not owned by the Armand Bayou Nature Center, they are managed and maintained by nature center staff. Other public water bodies in the area include Horsepen Bayou, Big Island Slough, Mud Lake, Clear Lake and Galveston Bay. Our alligator survey transects and study area included Armand Bayou, Big Island Slough, Horsepen Bayou and the northern portion of Mud Lake. This area receives a mean annual rainfall of 130 cm. The temperature ranges from a maximum of 34°C to a minimum of 7°C. The average elevation of Armand Bayou Nature Center is 20.7 m above sea level. Higher salinity levels and urban influences on water quality and habitat availability are unique attributes of this study site. Thirteen different wetland habitat types occur within the alligator survey area at Armand Bayou (Fig. 2; Supplementary Appendix). These wetland habitat types range from freshwater to estuarine and include palustrine and lacustrine wetlands (Fig. 2; Supplementary Appendix). Vegetation types range from emergent persistent to deciduous hardwoods (Fig. 2; Supplementary Appendix). All habitat types are reported and listed in a categorical manner that corresponds to the National Wetlands Inventory Database categories so that habitat types can be easily cross-referenced (http://www.fws.gov/wetlands/Data/Wetland-Codes.html, accessed 11 August 2018).

Alligator surveys

Population characteristics were determined by conducting nighttime surveys along designated transects and used the methods outlined by Chabreck (1966), Thompson et al. (1984) and Webb et al. (2009). Each survey was conducted from a boat outfitted with an electric motor, and using 200 000 candle power spotlights at 6–8 km/hr. An estimation of total length (TL) of each observed alligator was determined by estimating the distance from the eyes to the nares in inches, which this length is similar to TL in feet (Chabreck 1966; Eversole et al. 2017). After which, English measurements were converted to metric units. We classified alligators into four size classes based on their TL: hatchlings (≤30.5 cm, TL), juveniles (30.6–121 cm, TL), subadults (121.1–182.9 cm, TL) and adults (183.0+ cm, TL) (Saalfeld et al. 2008). If observers were unable to place alligators into specific size classes, an attempt was made to place alligators into broader groups of adults (>183 cm TL) and non-adults (<183 cm TL). In cases when no size estimation could be made, individuals were recorded as unknown. We logged a global positioning system (GPS) point for each alligator at the location where it was sighted. Because there is no definitive or reliable estimate of detectability during nighttime surveys, we did not incorporate detectability estimates into our data. The survey transect

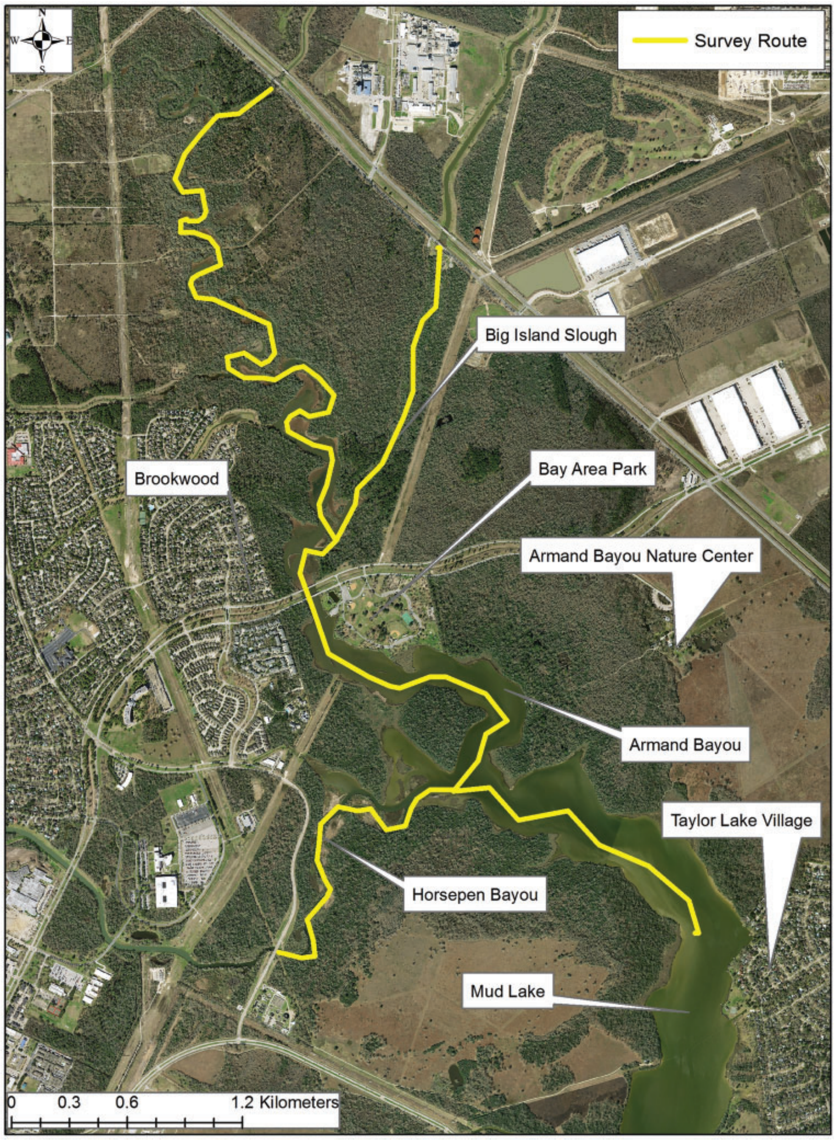

Figure 1: Map of survey transects and locations references for American alligator (Alligator mississippiensis) nighttime surveys conducted at Armand Bayou Nature Center in 2011 and 2012

included Armand Bayou, Horsepen Bayou, Big Island Slough and the northern portion of Mud Lake, all of which are interconnected (Fig. 2). We conducted 19 alligator nighttime surveys between 24 June 2011 and 30 October 2012. Surveys conducted in 2011 occurred monthly from 24 June to 21 October and surveys conducted in 2012 occurred monthly from 23 May to 30 October. We conducted surveys at 6–8 km/hr in a continuous straight line, with no overlap. This design eliminated the possibility of over-counting sighted alligators during surveys but still followed commonly employed methods for nighttime alligator surveys.

Data analysis

We calculated the relative abundance and encounter rate of alligators (number of alligators/km) for the survey area within our study area. Linear distance was calculated via handheld GPS and in ArcGIS 10.3 (ESRI, Redlands, CA, USA). We calculated descriptive statistics to summarize the alligator population structure using SAS 9.3 (SAS Institute, Inc., 2011). Point density analysis was used to determine and model areas of high use and clustering of observations with spatial analyst tools in ArcGIS 10.3. We tested the hypothesis (i.e. H_0: no spatial clustering of point data) of spatial distribution with nearest neighbor analysis and bounded the analysis to only include the wetland areas for which surveys were conducted (i.e. the study area polygon). Alligators of unknown size were included in the analyses irrespective of size but not included in the analyses relative to size-classes. For all test, $\alpha = 0.01$.

We performed the analysis of habitat use by first classifying wetland types that occurred within the survey area using the digital wetland basemap (i.e. National Wetlands Inventory) provided online by the United States Fish and Wildlife Service (UFWS) in ArcMap 10.3 (ESRI, Redlands, CA, USA). This system provides not only a classification of each wetland but also a detailed description of habitat and wetland type characteristics. We performed a spatial join between the wetland base map and alligator GPS locations in order to determine the wetland types

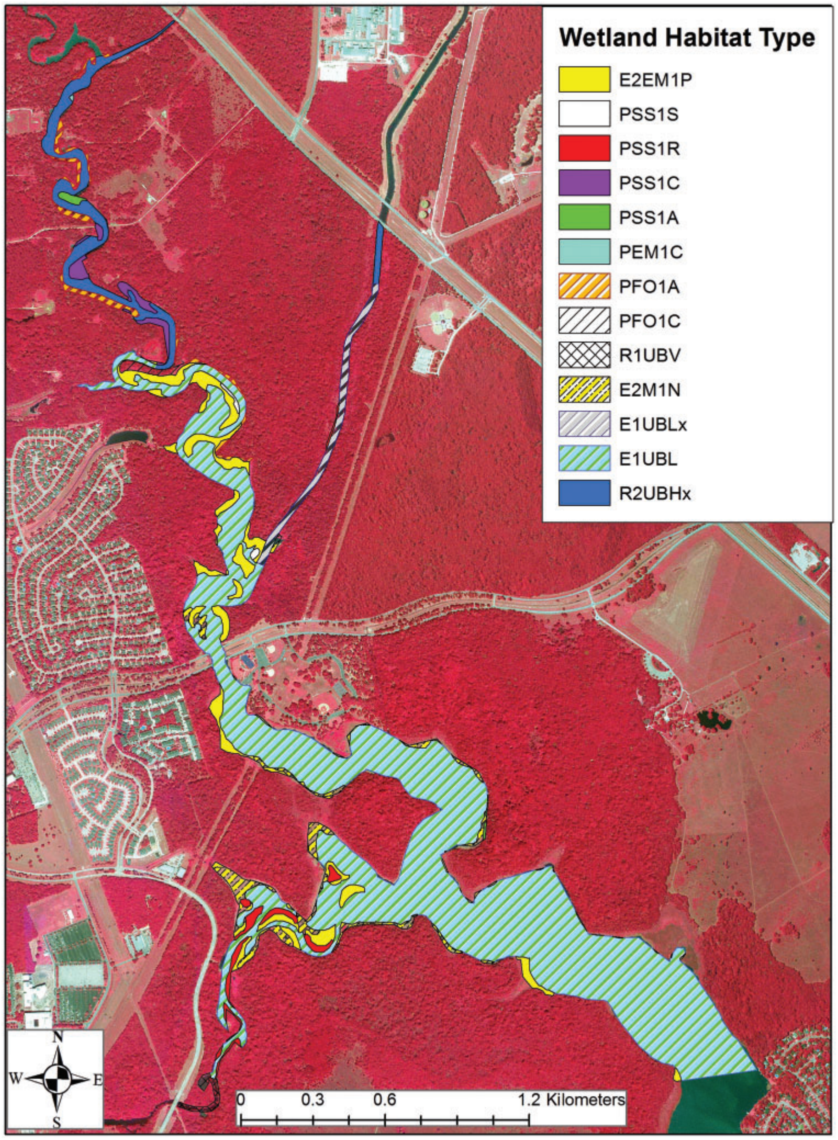

Figure 2: Map of wetland habitat types present within the American alligator (Alligator mississippiensis) survey area at Armand Bayou Nature Center, Pasadena, TX, USA

in which alligators occurred during the survey time. We determined habitat utilization using the methods described by Neu et al. (1974; i.e. chi-square analysis and Bonferroni Z-statistics to control the experiment-wise error probability at 0.10). We selected the methods of Neu et al. (1974) to analyze our data because McClean et al. (1998) found that this method was superior at predicting habitat utilization in comparison to other available methods. Additionally, Bingham and Brennan (2004) found that other methods for analyzing datasets for habitat utilization inflated the type 1 error rates, which biased the results. Conversely, Bingham and Brennan (2004) found that the Neu et al. (1974) method did not increase the type 1 error rates; thus providing confidence in our analysis. We calculated confidence intervals from the chi-square analysis using SAS 9.3 (SAS Institute, Inc., 2011). Habitat types were considered used more or less than expected if the proportion of observed alligator use was significantly different than the proportion of expected use based on the area of each habitat type. We did not include hatchling alligator data in this analysis because it is known that subsequent to hatching, they stay within close proximity to the nest site for the first year. Therefore hatchling alligator habitat use is more reflective of nest site location rather than hatchling habitat use and requirements.

Survey and habitat use data meets the assumption of independence for required in this analysis because (i) aurveys were conducted far enough apart in time and on a linear transect (i.e. this eliminated the possibility that individuals would be counted more than once during a single survey) and (ii) The home ranges of alligators are large enough, and wetland types spatially abundant enough that each individual had equal opportunity to select any habitat type.

Results

We recorded a total of 653 observations of alligators across all surveys conducted (Table 1). Overall mean encounter rate (alligators/km) on a per survey basis was 0.6/km (Table 1). The nearest neighbor analysis rejected the null hypothesis (i.e. H_0: no

Table 1: Results from American alligator (*Alligator mississippiensis*) nighttime surveys conducted at Armand Bayou Nature Center in 2011 and 2012

	Hatchlings	Juveniles	Subadults	Adults	Unk TL < 1.83m	Unk TL > 1.83m	Unk	Total
Mean ± SE per survey	4 ± 1.1	18 ± 2.1	5 ± 0.5	4 ± 0.5	1 ± 0.3	1 ± 0.3	14 ± 1.5	7 ± 2.5
Mean encounter rate per survey (alligators/km)	0.3/km	1.5/km	0.4/km	0.3/km	0.1/km	0.1/km	1.2/km	0.6/km
Total % population composition	10%	19%	15%	11%	3%	3%	40%	100
Total num. of obs.	68	122	101	73	21	21	268	653
Km. surveyed								12

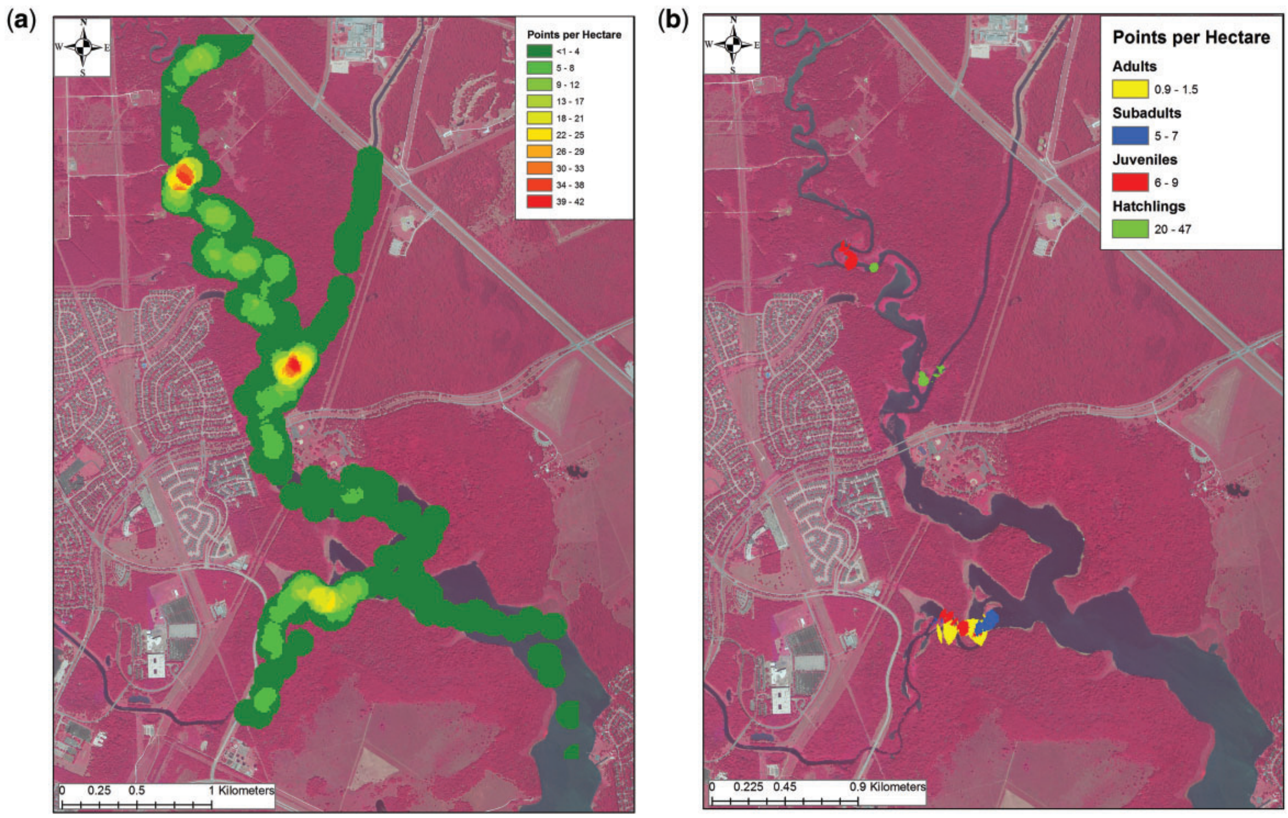

Figure 3: Point density analysis results of American alligator (Alligator mississippiensis) locations, (a) irrespective of alligator size–class and (b) by alligator size–class, at Armand Bayou Nature Center in 2011 and 2012

spatial clustering of point data) for combined size–classes ($P < 0.001$; $Z = -47.07$; ratio = 0.203), adults ($P < 0.001$; $Z = -14.35$; ratio = 0.122), subadults ($P < 0.001$; $Z = 10.05$; ratio = 0.472) and juveniles ($P < 0.001$; $Z = -11.56$; ratio = 0.453). The point density analysis indicated that there were areas of high point density for each size class (Fig. 3). Low and high point density areas identified from the point density analysis ranged from 1 to 47 points (i.e. observed alligators) per hectare (Fig. 3).

There were 13 different wetland types that occurred within the survey area (Fig. 2; Supplementary Appendix). All alligator size classes used coastal subtidal and excavated riparian habitats more than expected considering all available habitat types. Juvenile alligators used excavated coastal subtidal, commonly flooded coastal intertidal, and riparian habitats neutrally, and avoided all other habitat types (Tables 2 and 3). Subadults used excavated coastal subtidal and commonly flooded coastal intertidal habitats neutrally and avoided all other habitat types (Tables 2 and 4), while adult alligators used excavated coastal subtidal, commonly flooded coastal intertidal, seasonally flooded swamp, and riparian habitats neutrally, and avoided all other available habitat types (Tables 2 and 5).

Discussion

Our study indicates that alligators rely largely upon the tidal habitat with unconsolidated substrate that is continuously covered by tidal waters and <30% vegetative cover that occurs over much of the area that was surveyed (i.e. 1; E1UBL). These habitats were characterized by low gradient, no tidal influence, sand and mud substrate, oxygen depletion, true planktonic organisms and a well-developed floodplain (i.e. 13; R2UBHx). In the three areas of highest alligator point density, these habitats dominated the landscape. In the northern most area of high density point locations the majority of the habitat is described as habitat 13 (i.e. R2UBHx), while the two southernmost hotspots of alligator point location density fall within the habitat type 1 (i.e. E1UBL; Fig. 3). Alligator habitat use was similar

Table 2: Use of wetland habitat types, based on chi-square analysis with the Bonferroni Z-statistic (Neu et al. 1974), by differing size class of American alligator (*Alligator mississippiensis*) at Armand Bayou Nature Center during 2011–2012[a]

		Alligator size class[b]											
		Juvenile			Subadult			Adult			Overall		
Wetland type (number)	Wetland code	P	N	A	P	N	A	P	N	A	P	N	A
Coastal subtidal (1)	E1UBL	X			X			X			X		
Excavated coastal subtidal (2)	E1UBLx		X			X			X			X	
Occasionally flooded coastal intertidal (3)	E2EM1P			X			X			X			X
Commonly flooded coastal intertidal (4)	E2EM1N		X				X		X			X	
Occasionally flooded swamp (5)	PFO1A			X			X			X			X
Seasonally flooded marsh (6)	PEM1C			X			X			X			X
Occasionally flooded scrub marsh (7)	PSS1A			X			X			X			X
Seasonally flooded scrub marsh (8)	PSS1C			X			X			X			X
Seasonally flooded brackish marsh (9)	PSS1R			X			X			X			X
Seasonally flooded swamp (10)	PFO1C			X			X		X				X
Occasionally flooded brackish marsh (11)	PSS1S			X			X			X			X
Riparian zone (12)	R1UBV		X				X		X			X	
Excavated riparian zone (13)	R2UBHx	X			X			X			X		

[a]P-N-A refers to either preferred, neutral, and avoided habitat types by each size class of alligator. See Supplementary Appendix for habitat descriptions.
[b]Size classes were based on total length for hatchlings (≤30.5 cm), juveniles (30.6–121 cm), sub-adults (121.1–182.9 cm) and adults (≥183.0 cm).

Table 3: Habitat utilization results for juvenile American alligators (*Alligator mississippiensis*) during nighttime surveys at Armand Bayou Nature Center in 2011 and 2012[a]

Habitat type	Total area (ha)	Prop of area (%)	Num obs	Expected num obs	Proportion (%)	CI (–)	CI (+)	Use
Riparian zone (12: R1UBV)	2.7	2.2	4	2	3.4	0	0.079	Neutral
Coastal subtidal (1: E1UBL)	62.6	51.7	87	62	73	0.621	0.842	Greater
Excavated coastal subtidal (2: E1UBLx)	3.6	3	2	4	1.7	0	0.049	Neutral
Excavated riparian zone (13: R2UBHx)	0.8	0.7	17	1	14.3	0.056	0.230	Greater
Occasionally flooded swamp (5: PFO1A)	8.3	6.9	2	8	1.7	0	0.049	Less
Seasonally flooded marsh (6: PEM1C)	0.04	0.03	0	1	0	0	0	Less
Occasionally flooded scrub marsh (7: PSS1A)	6.9	5.7	0	7	0	0	0	Less
Seasonally flooded scrub marsh (8: PSS1C)	2.8	2.3	0	2	0	0	0	Less
Seasonally flooded brackish marsh (9: PSS1R)	6.5	5.4	0	6	0	0	0	Less
Occasionally flooded coastal intertidal (3: E2EM1P)	19	15.7	3	24	2.5	0	0.064	Less
Seasonally flooded swamp (10: PFO1C)	1	0.8	0	1	0	0	0	Less
Occasionally flooded brackish marsh (11: PSS1S)	0.3	0.2	0	1	0	0	0	Less
Commonly flooded coastal intertidal (4: E2M1N)	6.5	5.4	4	6	3.4	0	0.079	Neutral
Total	121.04	100	119					

[a]See Supplementary Appendix for habitat descriptions.

among each size, indicating that their use is similar (Table 2–5). In inland freshwater habitats, alligators of different size classes typically utilize different habitat types (Webb et al. 2009; Eversole et al. 2015a). Past studies of alligator habitat use in coastal systems of Louisiana and Texas have found that optimum habitats for American alligators included those with 20–40% open water with high interspersion of emergent vegetation, and ponded water ≤15-cm deep (Newsom et al. 1987). In addition, Webb et al. (2009) found that American alligators in east Texas used habitats with 50% open water, substantial floating vegetation and emergent vegetation near (12 m) dry ground and cover. Webb et al. (2009) found that adults used habitats further from dry ground and cover, in open water (75–85%), and with less floating vegetation (6–22%) than did sub-adults, which used habitats that were closer to dry ground and cover, with less open water (52–68%), and more floating vegetation (8–40%).

We may not have observed structured use of habitat in our study for several reasons. Although there were numerous wetland types that occurred within the area that we surveyed, there may not have been large enough differences between each type to result in differences in alligator use. Alligators have been described as generalist predators (Rosenblatt et al. 2015), due to this they are likely habitat generalists as well (Ross and Ernst 1994; Conant and Collins 1998), at least during times of nighttime activity and possibly foraging. For example, we conducted all nighttime surveys at the same time of night. It is possible that on a broad scale, activity and therefore, habitat use was the same for all size classes during those times. If survey times were varied, we may have found this not to be true. For example, at an inland site, Eversole et al. (2015a,b) found activity to be highly variable by size and greatly affected by time of night and the environment. It has been found that habitat segregation among size classes in inland wetlands are partly the result of dietary needs (Subalusky et al. 2009); however, the production of alligator prey in coastal habitats is thought to be much greater (Valentine et al. 1972; Rootes et al. 1991). If the

Table 4: Habitat utilization results for subadult American alligators (*Alligator mississippiensis*) during nighttime surveys at Armand Bayou Nature Center in 2011 and 2012[a]

Habitat type	Total area (ha)	Prop of area (%)	Num obs	Expected num obs	Proportion (%)	CI (–)	CI (+)	Use
Riparian zone (12: R1UBV)	2.7	2.2	4	2	3.4	0	0.079	Less
Coastal subtidal (1: E1UBL)	62.6	51.7	87	62	73	0.621	0.842	Greater
Excavated coastal subtidal (2: E1UBLx)	3.6	3	2	4	1.7	0	0.049	Neutral
Excavated riparian zone (13: R2UBHx)	0.8	0.7	17	1	14.3	0.056	0.230	Greater
Occasionally flooded swamp (5: PFO1A)	8.3	6.9	2	8	1.7	0	0.049	Less
Seasonally flooded marsh (6: PEM1C)	0.04	0.03	0	1	0	0	0	Less
Occasionally flooded scrub marsh (7: PSS1A)	6.9	5.7	0	7	0	0	0	Less
Seasonally flooded scrub marsh (8: PSS1C)	2.8	2.3	0	2	0	0	0	Less
Seasonally flooded brackish marsh (9: PSS1R)	6.5	5.4	0	6	0	0	0	Less
Occasionally flooded coastal intertidal (3: E2EM1P)	19	15.7	3	24	2.5	0	0.064	Less
Seasonally flooded swamp (10: PFO1C)	1	0.8	0	1	0	0	0	Less
Occasionally flooded brackish marsh (11: PSS1S)	0.3	0.2	0	1	0	0	0	Less
Commonly flooded coastal intertidal (4: E2M1N)	6.5	5.4	4	6	3.4	0	0.079	Neutral
Total	121.04	100	119					

[a]See Supplementary Appendix for habitat descriptions.

Table 5: Habitat utilization results for adult American alligators (*Alligator mississippiensis*) during nighttime surveys at Armand Bayou Nature Center in 2011 and 2012[a]

Habitat type	Total area (ha)	Prop of area (%)	Num obs	Expected num obs	Proportion (%)	CI (–)	CI (+)	Use
Riparian zone (12: R1UBV)	2.7	2.2	5	1	7.2	–0.012	0.157	Neutral
Coastal subtidal (1: E1UBL)	62.6	51.7	50	36	72.4	0.578	0.871	Greater
Excavated coastal subtidal (2: E1UBLx)	3.6	3	3	2	4.3	–0.023	0.110	Neutral
Excavated riparian zone (13:R2UBHx)	0.8	0.7	8	1	11.6	0.011	0.221	Greater
Occasionally flooded swamp (5: PFO1A)	8.3	6.9	0	5	0	0.000	0.000	Less
Seasonally flooded marsh (6: PEM1C)	0.04	0.03	0	1	0	0.000	0.000	Less
Occasionally flooded scrub marsh (7- PSS1A)	6.9	5.7	0	4	0	0.000	0.000	Less
Seasonally flooded scrub marsh (8: PSS1C)	2.8	2.3	0	1	0	0.000	0.000	Less
Seasonally flooded brackish marsh (9: PSS1R)	6.5	5.4	0	4	0	0.000	0.000	Less
Occasionally flooded coastal intertidal (3: E2EM1P)	19	15.7	0	14	0	0.000	0.000	Less
Seasonally flooded swamp (10: PFO1C)	1	0.8	1	1	1.5	–0.025	0.054	Neutral
Occasionally flooded brackish marsh (11: PSS1S)	0.3	0.2	0	1	0	0.000	0.000	Less
Commonly flooded coastal intertidal (4: E2M1N)	6.5	5.4	2	4	2.9	–0.026	0.084	Neutral
Total	121.04	100	69					

[a]See Supplementary Appendix for habitat descriptions.

habitat at Armand Bayou is conducive to the dietary needs of all size classes, alligators may not need to segregate into different wetland types during times of foraging (i.e. nighttime), which would aid in explaining our results.

There were interesting differences in broad scale location of alligator size hotspots (Fig. 3). There was no size–class segregation between adults and subadults and a clear separation between hatchlings and adults and subadults. However, juvenile alligators appeared to be within a transition stage with some juveniles segregated from adults and subadults and other juveniles in proximity to adults and subadults. The hotspots of hatchling alligators occurred on the opposite end (i.e. 2.8 and 4.4 km separation) of the survey transect than that of adults (Fig. 3). However, the groups still occurred in the same habitat types. Additionally, a high density area of juvenile locations occurred along the northern end of the survey transect at a distance of 4.4 km from the adult, subadult and other juvenile hotspots. Although the results of the point density analysis of juvenile locations are unclear, it is likely that the areas of observed hatchling high density are the result of female nest site selection. It is unlikely that hatchlings travel to areas of low adult occurrence; as they typically stay within the vicinity of the nests from which they are hatched (Newsom et al. 1987). This may indicate that this area of the survey transect includes areas that provide increased availability of nesting space and habitat.

Another interesting aspect of the point density analysis is a seeming avoidance of areas with increased human activity (Fig. 3). For example, the areas of lowest point density occurred in the area around Bay Area Park (Fig. 3), where there is a large amount of human activity (i.e. kayaking, canoeing and general recreation), and the areas where the two subdivisions (i.e. Taylor Lake Village and Brookwood) extend to the edge of the survey area (Fig. 1). Although alligators can potentially become habituated to humans in certain circumstances (e.g. feeding; Eversole et al. 2014), crocodilians in general avoid humans, and are quite wary of their presence (Pacheco 1996; Ron et al. 1998). This suggests that human encroachment and urbanization may influence the distribution, resulting in differential habitat use, of alligators within the wetlands that they occupy. This is significant for this area in particular, because it is one of the fastest growing areas with one of the largest human populations in the USA (U.S. Census Bureau 2012). Furthermore, the Texas Gulf Coast area also hosts a large population of alligators and alligator habitat that is quickly being developed and usurped by humans (Eversole et al. 2014). This information along with a similar point density analysis approach could potentially be used in the future by urban biologists or planners in order to identify areas of potential human–alligator conflict. For example, Nichol and Lentic (2008) suggested a hotspot analysis of crocodile occurrence and distribution to be used to identify and target areas for additional trapping efforts and determining likely sources of problem crocodiles. They suggested that management strategies be employed in identified hotspots in order to avoid future human–crocodile conflict. This information coupled with future research also has the potential to be used in outreach to educate the general public about how alligators potentially respond to human activity on a spatial scale.

Webb et al. (2009) reported an average alligator density of 0.22 alligators/ha at an inland Texas site. As mentioned previously, this estimate was considered a low density because reports of alligator density in coastal populations were 3–5 times higher. Relative abundance on a per ha scale (using methods of Webb et al. 2009; not accounting for alligator detectability) in our study was 0.06 alligators/ha. This is interesting because our estimate of average relative abundance is much lower than that reported by Webb et al. (2009). Although we did not specifically test this, human encroachment could be a contributing factor in the low population densities and relative abundance of alligators observed in this study. For example, Armand Bayou Nature Center functions as a habitat island and refuge amid a major metropolitan area (Fig. 1). This area likely does not contain adequate nesting habitat or space to support the number of successful nests that would be required to increase or maintain a stable alligator population. The nesting propensity and number of nests produced annually have been found to be extremely important variables that can cause major increases or decreases in population size and are very sensitive to minor fluctuations (Eversole et al. 2019). During past nest surveys at Armand Bayou Center, researchers were only able to locate one alligator nest in the survey area, which supports this hypothesis (C. B. Eversole, pers. observation).

Conclusions

Information about alligator populations in varying habitat types and portions of their range, aids in collectively understanding the species in its entirety. Our study suggests that there are many factors that can contribute to the spatial ecology and habitat use of alligators and that these factors differ in urban environments. For example, as urbanization increases near wetlands, biologists should expect alligator avoidance of humans and increased nuisance alligator issues. Therefore, by incorporating this study into research, management, and planning, biologists and planners can identify potential target areas for the implementation of management practices (e.g. harvest, nuisance control, size-specific surveys), identify habitat and nesting areas or improve survey methods. By doing so, alligator populations can be more precisely managed in a way that promotes population persistence and human–alligator coexistence. This study highlights the need for future research to determine the effect of urbanization on alligator populations and the habitats that they commonly use. This information can aid in improving management of populations, reduction of human–crocodilian conflict and understanding of ecological differences in urban ecology. We demonstrate an analytical approach to identifying alligator occurrence, distribution and habitat use that can be replicated and used by urban biologists and planners that aim to incorporate alligator ecology in urban environments into planning and management activities. This approach is broadly applicable to not only American alligators but also other urban wildlife species for which this type of information is useful in identifying ecological patterns and developing science-based management and mitigation strategies. In addition, future studies should strive to further explore habitat use, requirements and spatial ecology of all size classes of alligators in urban ecosystems such as this. The ecological importance of this species warrants the need for research in order to definitively determine its requisite role and functioning within wetland ecosystems across all areas of the species' range.

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Supplementary data

Supplementary data are available at *JUECOL* online.

Conflict of interest statement. None declared.

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