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IMPORTANT HABITAT CHARACTERISTICS FOR AMERICAN ALLIGATORS (*ALLIGATOR MISSISSIPPIENSIS*) ON THE EDGE OF THEIR RANGE

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***Abstract.*—Once threatened with extinction, American Alligators (*Alligator mississippiensis*) have recovered across most of their historic range. Alligators reach the northwestern boundary of their range in Arkansas, where habitat characteristics might limit populations. Although low population densities have been dismissed by local managers as a consequence of poor habitat, no habitat studies of alligators have been performed to confirm this. It is crucial that habitat requirements of alligators throughout their range be understood for effective management and conservation. We conducted habitat assessments and population surveys for 19 bodies of water within the known range of American Alligators in southern Arkansas to determine which habitat characteristics were the most important predictors of relative population abundance. Ten habitat characteristics were incorporated into a stepwise multiple regression model with alligator relative population abundance as the dependent variable. Vegetative cover along the shoreline was the most important variable followed by land ownership (private or public). Water clarity and total vegetative cover were also important to the overall model, which explained 73% of the variation in relative population abundance. Although private water bodies had significantly higher population densities of alligators than publicly owned sites, a subsequent multi-response permutation procedure revealed no significant differences in measured habitat variables between private and publicly owned sites. Considering that measured habitat variables were not statistically different, there could be anthropogenic factors limiting American Alligators on public lands that have otherwise suitable habitat.**

Key Words.—anthropogenic stress; habitat use; shoreline vegetation

INTRODUCTION

Habitat loss and degradation are tremendous threats to biodiversity worldwide, and are among the most important threats facing reptiles (Gibbons et al. 2000). In response to high extinction rates brought about by habitat loss (Pimm et al. 1995), and considering that an organism can only survive in habitats that provide for its basic needs, such as food and refugia (Morrison et al. 1998), managers must strive to understand the critical habitats important for the protection of species. Worldwide, 927 of the 4,393 extant reptilian species evaluated by the IUCN (2014), including 11 of the 23 crocodilians, are critically endangered, endangered, or vulnerable. Of the 38 imperiled reptilian species Wilcove et al. (1998) recognized in the United States, 97% have experienced significant habitat loss.

The American Alligator (*Alligator mississippiensis*) is a prime example of significant habitat loss. In Arkansas (the northwestern edge of its range), the species has lost more than 70% of its wetland habitat since the 1780s, a larger percentage than any other state where alligators are found (Dahl 1990). Although the importance of habitat is obvious, key habitat variables for alligators remain ambiguous. Two habitat suitability indices have been constructed for alligators, one for coastal Louisiana (Newsom et al. 1987) and another for the Everglades in Florida (Rice et al. 2004). Alligator habitat in the northwestern part of their range is characterized by rivers, oxbow lakes, and forested wetlands and does not resemble coastal marshes and estuaries described in the Louisiana suitability index, nor does it resemble the Everglades. Rice et al. (2004) acknowledged the limitations of extrapolating the Everglades model to other areas, and Newsom et al. (1987) recommended that the Louisiana model be used only for coastal marshes in Louisiana and Texas. Researchers have acknowledged the paucity of data on inland populations of alligators (Subalusky et al. 2009; Dunham et al. 2014), especially considering that many of these populations now are exposed to sport hunts (Saalfeld et al. 2008). Although some new habitat studies for inland alligators exist (Webb et al. 2009; Lewis et al. 2014), the studies to date have included small numbers of sample sites and are hundreds of kilometers away from the northern boundary of the range of the alligator. Inland and riverine habitats

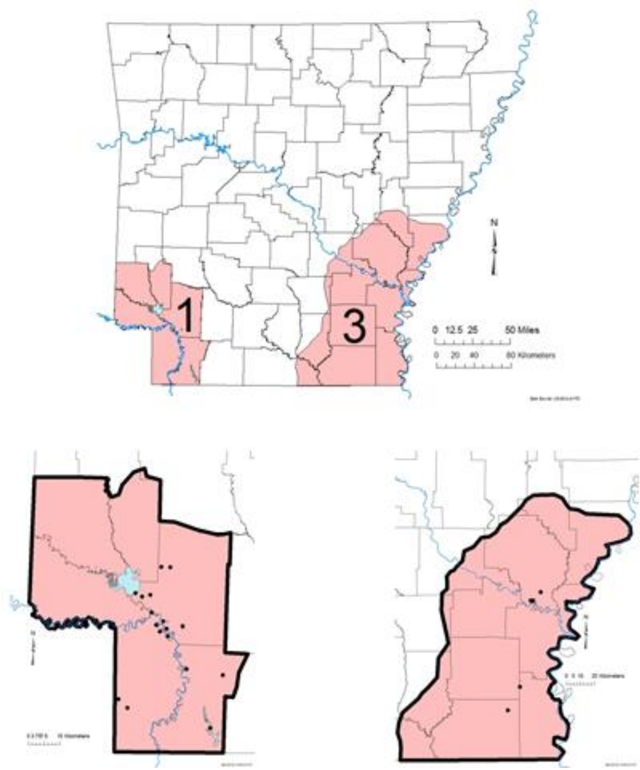

FIGURE 1. Study sites in southern Arkansas, USA, for habitat characteristics on the periphery of the range of the American Alligator (*Alligator mississippiensis*). Alligator Management Zones 2, 4, and 5 were closed to hunting and were thus omitted here.

make up a large portion of the range of this species, and for this reason should be analyzed to make informed management decisions at state or local levels. In addition, some critically endangered crocodilians require specific habitat types that are not well represented in the current literature. The Chinese Alligator (*Alligator sinensis*) is approaching extinction, and requires inland ponds and wetlands (Thorbjarnarson et al. 2002). The Gharial (*Gavialis gangeticus*), also on the verge of being lost, requires riverine systems (Hussain 2009).

Habitat use patterns from inland populations of the otherwise well-studied American Alligator could provide crucial insight to researchers and managers at the local as well as global level. The purpose of this study was to ascertain which habitat characteristics were most important for alligators in inland populations near the edge of their range. We also attempted to determine the role of land ownership (private or publicly owned) on alligator population densities.

MATERIALS AND METHODS

Study sites.—We collected habitat and relative population abundance data at 19 sites in southern Arkansas, USA (Fig. 1), where sport hunts have been allowed (Chastain and Irwin 2006). The areas were characterized by bottomland hardwood forests (*Taxodium distichum* and *Nyssa aquatica* to a lesser extent) and wetlands, although many wetlands have been lost or fragmented due to intense agricultural land use. The sites included oxbow lakes, bayous, and swamps and represented the diverse habitats used by alligators in this part of their range.

Relative population abundance.—We collected all data between May and August of 2009. Although this large timeframe encompasses both the mating and nesting seasons, our sites were complex and encompassed both deep channels (optimal breeding sites) and the edges of the water bodies (optimal nesting sites). We observed alligators of all size-classes in all habitat types throughout the course of this study. We determined relative abundance by performing nighttime surveys (Wood et al. 1985; Bayliss 1987) in which we selected a survey route for each body of water and followed a pre-programmed route by boat. We conducted two surveys 14 d apart for each water body and used the highest number for analysis to account for as many alligators as possible. We followed Arkansas Game and Fish Commission (AGFC) practices so our

TABLE 1. Mean (± SE) habitat variables and relative abundance of American Alligators (*Alligator mississippiensis*) across 13 public and six privately owned sites in southern Arkansas, USA.

Variable	Public	Private	Combined
Water Depth (cm)	243.4 ± 29.06	259.3 ± 39.54	248.4 ± 22.92
Secchi Depth (cm)	66.6 ± 6.31	82.4 ± 11.78	71.6 ± 5.77
Canopy Cover (%)	10.9 ± 3.00	20.0 ± 5.94	13.8 ± 3.17
Vegetative Cover (%)	22.1 ± 6.45	38.0 ± 10.56	27.1 ± 5.64
Edge Canopy Cover (%)	32.7 ± 8.67	42.6 ± 13.64	35.8 ± 7.19
Shoreline Development	3.61 ± 0.509	2.81 ± 0.479	3.36 ± 0.382
Area (ha)	1358.3 ± 1071.8	236.2 ± 192.9	1003.9 ± 36.5
Corridor Distance (km)	9.51 ± 2.817	0.85 ± 0.318	6.78 ± 2.129
Relative Abundance (APK)	3.31 ± 1.515	8.12 ± 2.916	4.84 ± 1.439

results could be informative to local managers. We approached the alligators as closely as possible to estimate size, and individuals 1.22 m (4 ft) or longer were included because this is the minimum length for harvest in Arkansas (Chastain and Irwin 2006). The survey routes did not overlap in an effort to avoid counting the same individual twice and inflating the value. We divided the number of observed individuals by the survey distance to generate alligators per kilometer (APK), following protocols used by local managers (Irwin and Wooding 2002). Although there was overlap among sites visited by the AGFC and the authors, five water bodies investigated have not been part of the alligator management program of the AGFC. We also compiled historical data on relative abundance, nuisance reports, permits issued, and harvested animals from eight years of annual reports of Chastain and Irwin (2008), Irwin and Chastain (2009), Irwin and Chastain (2010), Irwin and Chastain (2011), Irwin (2012), Barbee (2013), Barbee (2014) and Barbee (2015).

Microhabitat characteristics.—We collected microhabitat data *in-situ* using a systematic sampling regime that divided the body of water into 10 equidistant transects. We collected data at 10 equidistant points along each transect. We arbitrarily placed the first point of each sampling transect 1 m from the shore to ensure representation of edge habitat. We located transects and sampling points in the field with a handheld GPS unit (Garmin International Incorporated, Olathe, Kansas, USA). At each sampling point, we quantified four microhabitat characteristics. We measured water depth (± 1.0 cm) with a weighted vinyl tape, water clarity (± 1.0 cm) with a Secchi disc, and canopy cover (± 1.0%) with a spherical densiometer. We measured vegetative cover (± 1.0%) consisting of emergent vegetation, floating vegetation, or algae, with a 1 m^2 quadrant. We used the points 1 m from the bank to represent shoreline vegetation and canopy.

Macrohabitat characteristics.—We measured three landscape level variables, total water body area (ha), shoreline development (D_L), and corridor distance, using mapping software (Delorme, Yarmouth, Maine, USA). Shoreline development is a measure of water body roundness or how dissected it is, and we measured this as the ratio of the shoreline divided by the circumference of the area of the water body as if the area was circular, following Mackie (2004). We defined corridor distance as the nearest straight line distance (km) to the nearest large river (seventh order or larger).

Statistical analysis.—We used bidirectional stepwise regression for analysis of all habitat data (including land ownership), with relative population abundance as the dependent variable. We used log-transformations as necessary to meet the assumption of normality, except for percentage data, which we logit-transformed. We addressed multicollinearity by constructing a correlation matrix, and the assumption of homoscedasticity was met. The probability to enter and leave the model was 0.25, and we selected an α of 0.05. We performed analyses in JMP 8.0 ™ (Statistical Analysis Software, Cary, North Carolina, USA).

Six study sites were privately owned and the remaining 13 were open to the public. To ensure privately owned and publicly owned sites could be analyzed together in the regression model, we performed a multi-response permutation procedure (MRPP) to determine if there was a difference in measured habitat between public and private sites following McCune et al. (2002). No transformations are necessary for this nonparametric test, and we used a Euclidian distance measure with groups defined by ownership (private or public). We chose an α of 0.05 and used the R (version 3.0.2) package VEGAN. We also performed a nonparametric Wilcoxon rank-sum test ($\alpha = 0.05$) to determine differences in relative population abundance between private and publicly owned sites due to differences in sample size with using JMP 8.0™.

RESULTS

Relative population abundance ranged from 0.25–19.88 APK, with a mean (± SE) of 4.84 ± 1.44. Habitat characteristics varied widely across the 19 sites (Table 1). The stepwise regression explained 72.6% of the variation in relative abundance (Table 2). Shoreline

TABLE 2. Bidirectional stepwise regression model of habitat variables affecting densities of American Alligators (*Alligator mississippiensis*).

Overall Model			Model Parameters		
r^2	F ratio	P-value	Variable	Estimate	$P > t$
0.726	$F_{4,18} = 9.276$	< 0.001	Shoreline Vegetation	5.267	< 0.001
			Land Ownership	0.903	0.002
			Water Clarity	-0.026	0.014
			Total Vegetation	-3.462	0.029

vegetation was the most important variable in the model (P < 0.001), followed by land ownership (P = 0.002). Water clarity (P = 0.014) and overall vegetative cover (P = 0.029) were both negatively related to relative abundance.

Land ownership was the second most important variable in the model and explains 20.5% of the variation in relative abundance. We found higher alligator population densities in privately owned bodies of water compared to public sites (Z = 1.974, P = 0.043, n = 19). Overall, private sites averaged 8.12 APK, while public sites averaged 3.31 (Fig. 2). The nine habitat characteristics did not differ significantly between private and public sites (Euclidian, A = -0.004, P = 0.420).

DISCUSSION

The positive correlation with shoreline vegetation and negative correlation with total vegetation might help us better understand disparities in previous studies. For instance, some studies have suggested that open water (lacking vegetation) is preferable, especially for larger alligators (Newsom et al. 1987; Webb et al. 2009), while Lewis et al. (2014) found that alligators avoided open water. Although the latter example might be the result of a small sample of animals, it is likely that vegetation is differentially important depending on where it is and how it is being used. For instance, all pods of hatchling alligators observed in this study were observed in vegetation near the shore, and Tamarack (1988) has suggested that it is important refugia for young alligators. Critical nest materials also often consist of vegetation found near the shore (McIlhenny 1935; Joanen 1969; Brandt and Mazzotti 2000). Additionally, although adult alligators might be using open water to travel across their home range, they benefit from shoreline vegetation when hunting large, terrestrial predators. Similar to the current study, Villegas and Reynoso (2013) found that aquatic vegetation is important for all size-classes. The removal of such cover has even been suggested as a means of reducing alligator densities in areas where they are unwanted (Woodward and David 1994). Although there is a possibility that our negative correlation with total vegetation and relative abundance is explained by decreased visibility and sampling bias (Woodward and Moore 1993), this has been found to be less of a problem in complex habitats than open water systems (Subalusky et al. 2009). The negative relationship with water clarity (Secchi depth) and relative abundance is likely similarly explained by reduced visibility by potential predators (for young alligators) or prey (for larger ones) being beneficial for survival.

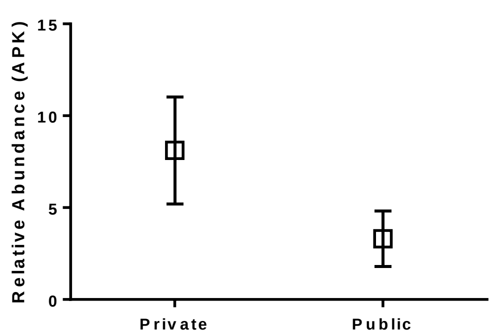

FIGURE 2. Mean relative abundances (± SE) for American Alligators (*Alligator mississippiensis*) at privately own and public sites in southern Arkansas, USA.

Ownership was a significant factor in this study and anthropogenic effects may have limited alligator populations in Arkansas. Land ownership was second only to shoreline vegetation in terms of predictive power, and privately owned sites had significantly higher population densities. There was only one privately-owned site that did not appear in top 50% of sites in terms of relative abundance, and this particular site had a pay-to-launch boat ramp and was readily accessible to the public, which made it legally private but functionally public. This site had the same potential anthropogenic threats associated with the public sites.

The second and fourth highest population densities (Moore's Bayou and Post Lake) were seen at publicly owned sites that were adjacent to the federally protected Arkansas Post National Memorial. Alligators are known to use the relatively small area (302 ha) of the Arkansas Post National Memorial for nesting (McCallum et al. 2003), and the federally protected sanctuary at Arkansas Post could be improving the population densities of the

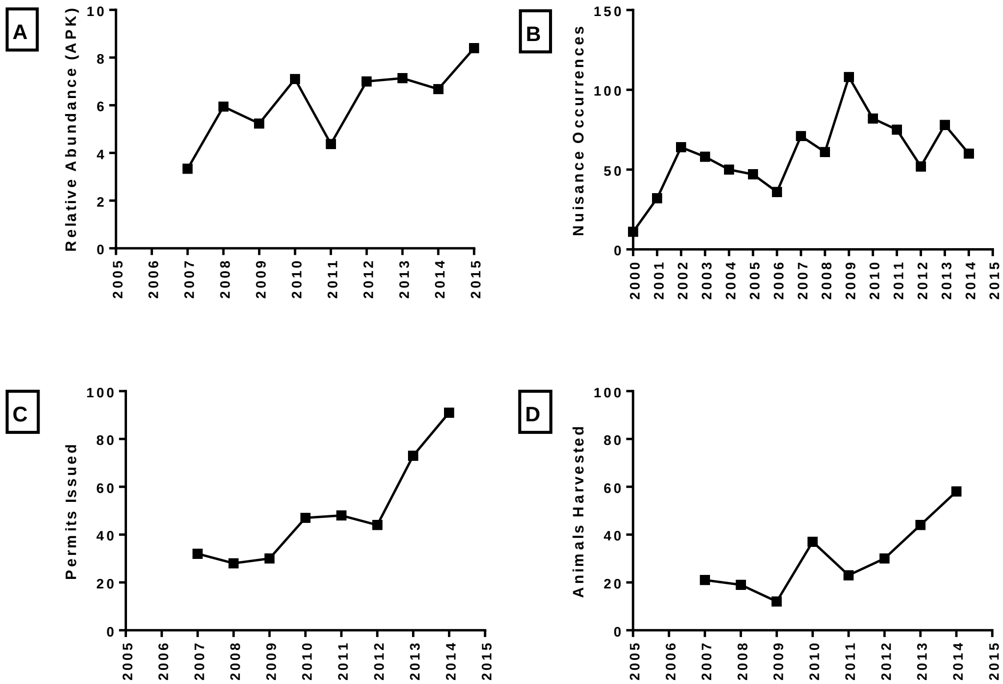

FIGURE 3. Historic American Alligator (*Alligator mississippiensis*) data from Arkansas, USA. (A) Mean relative abundance (APK) combined from Alligator Management Zones 1 and 3 (where harvests were permitted) 2007–2015. (B) Number of nuisance alligator occurrences 2000–2014. (C) Number of permits issued statewide 2007–2014. (D) Number of animals harvested statewide 2007–2014.

adjacent, state-managed sites. Higher densities were observed at privately-owned sites, but the habitat characteristics of private and publicly-owned sites were statistically similar. This indicates that accessibility and anthropogenic stress might be limiting alligator population densities at publicly-owned sites. In Arkansas, more alligators appear to be found in places less frequented by humans, although no empirical data have been collected to support this (Trauth et al. 2004). It has been observed that opening areas for recreational use can result in precipitous declines for turtle populations (Garber and Burger 1995), which suggests that even low impact use may play a role in the disparity of alligator population densities between public and privately owned sites. Physical injuries to turtles have been reported from boat propellers (Bulté et al. 2010), and Lewis et al. (2014) have suggested alligators avoid open water for this reason.

Aside from unintentional disturbance, human harassment and poaching also may contribute to lower population densities in publicly owned sites. Lance and Elsey (1999) found that alligators of both sexes showed marked decreases in sex hormones after being stressed. Additionally, frequently harassed alligators are less likely to defend their nests, which can further lower the probability of offspring survival (Kushlan and Kushlan 1980). Despite suitable habitat, anthropogenic effects could be limiting relative population abundance of American Alligators via increased mortality, reduced reproductive success, and increased emigration. All of these anthropogenic factors might help explain the seemingly high variability (4.84 ± 1.44) in relative abundance across the sites in this study. Although the habitat might be similar across these sites, being on the edge of their range might make them more sensitive to land-use, and proximity to public places of varying degrees of protection (from state wildlife management areas to National Wildlife Refuges and preserves), as well as private lands, might all influence population dynamics in this species.

The weather conditions during the course of this study were unusually rainy, but even given the wet conditions, post-harvest survey reports conducted by the AGFC across multiple sites show that 2009 was similar to other years. The mean encounter rates for Alligator Management Zones 1 and 3 (where harvests are permitted) in 2008, 2009, 2010, and 2011 were 5.94, 5.24, 7.11, and 4.38 APK, respectively, which can be explained by natural population fluctuation (Irwin and 2011; Fig. 3A). What was unusual about 2009 was the high number (108) of nuisance alligator occurrences (Fig. 3B), but this is likely explained by widespread flooding that displaced animals or allowed them to travel more easily to areas of human inhabitation. The number of permits issued and the number of animals harvested increased after this study was conducted (Fig. 3C and Fig. 3D), but this is likely due to management practices given that the relative abundances from the AGFC-conducted surveys did not increase as dramatically during this period of time (Fig. 3A).

Our study reveals two important habitat characteristics for alligators in Arkansas that should be given greater attention by researchers and, potentially, managers. First, shoreline vegetation provides refugia for juvenile alligators and cover for adults hunting terrestrial prey. Second, the higher population densities of American Alligators in privately owned bodies of water, even with statistically similar habitat, indicates that ownership (and likely disturbance) plays a role in alligator population dynamics. The effects of anthropogenic stress on wild alligators should be further explored to determine if human-induced stress is decreasing reproductive potential or immune function, which could affect population persistence.

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