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Habitat Use of American Alligators in East Texas

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ABSTRACT The American alligator (*Alligator mississippiensis*) has made a remarkable recovery throughout its range during the last half-century. In Texas, USA, current inland alligator population and harvest management strategies rely on generalized and often site-specific habitat and population data generated from coastal populations, because it is assumed that habitat and demographic similarities exist between inland and coastal populations. These assumptions have not been verified, however, and no studies have specifically examined inland alligator habitat use in Texas. We quantified alligator habitat use in East Texas during 2003–2004 to address this information gap and to facilitate development of regionally specific management strategies. Although habitat was variable among study areas, alligators used habitats with >50% open water, substantial floating vegetation, and emergent vegetation close (<12 m) to dry ground and cover. Adults used habitats further from dry ground and cover, in open water (75–85%), with less floating vegetation (6–22%) than did subadults, which used habitats that were closer to dry ground and cover, with less open water (52–68%), and more floating vegetation (8–40%). Although habitat use mirrored coastal patterns, we estimated alligator densities to be 3–5 times lower than reported in coastal Texas, likely a result of inland habitat deviations from optimal coastal alligator habitat, particularly in the preponderance of open water and floating vegetation. Our findings that 1) inland habitats varied among sites and did not exactly match assumed optimal coastal habitats, 2) alligators used these inland habitats slightly differently than coastal areas, and 3) inland alligator densities were lower than coastal populations, all highlight the need for regionally specific management approaches. Because alligator populations are influenced by habitat quality and availability, any deviations from assumed optimal habitat may magnify harvest impacts upon inland populations. (JOURNAL OF WILDLIF

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KEY WORDS Alligator mississippiensis, American alligator, habitat use, inland wetlands, Texas.

Market hunting, poaching, and wetland habitat losses reduced American alligators (Alligator mississippiensis) throughout Texas and the southeastern United States during the late 1800s and early 1900s, and by 1967 American alligators were listed as endangered (McIlhenny 1935, U.S. Department of Interior 1987). These declines prompted a surge of alligator research, management, and protection during the 1960s–1980s (Chabreck 1965, Joanen and McNease 1970, Chabreck 1971, Goodwin and Marion 1979, Taylor and Neal 1984), whereby alligator recovery is generally attributed to wetland conservation policies, translocation, and alligator harvest restrictions during this period (Johnson et al. 1985, Cooper 1997).

American alligator ecology and management has been well-researched throughout its range, but few published studies exist on alligator habitat use in its westernmost range (i.e., coastal [Cooper 1997] and inland TX wetlands [see Hayes-Odum et al. 2003, Lutterschmidt and Wasko 2006]). Regardless of geographic location, alligator habitat use, activity, and movement vary according to gender, age class, and season (Chabreck 1965, Joanen and McNease 1970, Goodwin and Marion 1979, Taylor 1984, Rootes and Chabreck 1993). In general, coastal alligators use marshes and wet prairies interspersed with shallow open water and canals with associated levees (Hines et al. 1968, Joanen and McNease 1972, Morea et al. 2002). Inland wetland habitats often are more diverse, characterized by bottomland hardwood wetlands, river and creek drainages, shallow emergent wetlands, and deep and shallow open water in both natural

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and manmade lakes and reservoirs (Joanen and McNease 1984, Ryberg et al. 2002). Although shallow and deep-water habitats interspersed with emergent marshes characterized alligator habitat, optimal (i.e., 20–40% open water, <20% open water >1.2 m, high interspersion, ponded water <15 cm deep) alligator habitat descriptions are based upon metrics developed in coastal Louisiana and Texas (Newsom et al. 1987). Neither inland habitat availability nor use has been well-described (see Joanen and McNease 1984, Ryberg et al. 2002), nor has the applicability of coastal habitat descriptions for inland alligator populations.

Alligator populations in Texas currently are stable or increasing (Joanen and McNease 1984, Johnson et al. 1985); the first legal public alligator hunt was conducted in coastal Texas in 1984 (Cooper 1997). In Texas, original harvest and population management guidelines were constructed based on research conducted in coastal Louisiana (Thompson et al. 1984, Newsom et al. 1987). Currently, site-specific nocturnal surveys, aerial nest surveys, and local growth rate, size structure, and population demographic data from harvested populations are used to modify management strategies at local and regional scales. Statewide management strategies assume, however, that inland populations are similar to coastal populations (Thompson et al. 1984). Density and growth rates vary (Hines et al. 1968, Brandt 1991, Dalrymple 1996, Wilkinson and Rhodes 1997, Saalfeld et al. 2008); therefore, universal population and harvest models may not be appropriate. As inland Texas alligators continue to expand and harvest opportunities increase, understanding life-history characteristics such as habitat use becomes important, particularly because alligator

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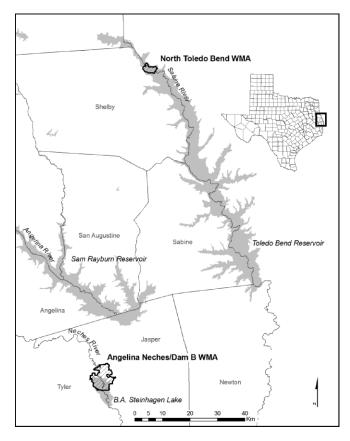


Figure 1. Location of Angelina/Neches Dam B and North Toledo Bend Wildlife Management Areas (WMA) in East Texas, USA, used as study sites to perform nocturnal surveys and quantify inland American alligator habitat use, May–August 2003 and May–September 2004.

population demographics are thought to vary among habitat types and habitat condition or quality (Ryberg et al. 2002; see Joanen and McNease 1984, Saalfeld et al. 2008). We quantified alligator habitat use in 2 large inland wetlands in East Texas to supplement development of regionally specific harvest and population management strategies and to address information gaps regarding inland alligator habitat use.

STUDY AREA

We conducted our study on portions of Toledo Bend and B. A. Steinhagen Reservoirs on the Sabine and Neches Rivers, respectively, in Texas (Fig. 1). The area was characterized by expansive bottomland hardwood forests and various wetland types adjacent to river floodplains with mixed pine and hardwood forests on uplands. Angelina-Neches/Dam B (Dam B) Wildlife Management Area (WMA) was 5,113 ha and included portions of B. A. Steinhagen Reservoir, in Jasper and Tyler counties, Texas, at the convergence of the Angelina and Neches rivers (Fig. 1). The reservoir was managed for flood control by the United States Army Corp of Engineers, and Dam B WMA was managed by the Texas Parks and Wildlife Department. We partitioned Dam B WMA into 2 study areas based on gross habitat differences. Dam B Park (2,266 ha) was characterized by shallow water (<1.5 m), abundant floating and emergent aquatic vegetation interspersed with deep channels, and open water in the Neches River and associated creeks. Dam B River (1,673 ha) was deep (>2.5 m) open water, associated with the Neches and Angelina River channels, adjacent swamps and sloughs, and bottomland hardwood forests. Aquatic habitats were dominated by water hyacinth (Eichhornia crassipes), common salvinia (Salvinia minima), alligatorweed (Alternanthera philoxeroides), hydrilla (Hydrilla verticillata), smartweed (Polygonum spp.), and water lotus (Nuphar luteum). Dominant woody species along wetland margins were baldcypress (Taxodium distichum), buttonbush (Cephalanthus occidentalis), black willow (Salix nigra), Chinese tallow (Triadica sebifera), water oak (Quercus nigra), overcup oak (Q. lyrata), water tupelo (Nyssa aquatica), and pine (Pinus spp.).

North Toledo Bend (NTB) WMA (1,400 ha), on Toledo Bend Reservoir in Shelby County, Texas (Fig. 1), contained baldcypress and water tupelo swamps, open water, emergent marshes, and a portion of the Sabine River with associated bottomland hardwood forests and upland pine ridges. A primary feature of NTB WMA was a shallow water (<1 m) impoundment (222.6 ha) managed primarily for wintering waterfowl, dominated by baldcypress and water hyacinth, hydrilla, and water lotus. The deepest (>2 m) open-water habitats in the NTB WMA were within the Sabine River channel, where baldcypress, buttonbush, planer-tree (*Planera aquatica*), water tupelo, water oak, overcup oak, and pine dominated the margins.

METHODS

Data Collection

We performed one nocturnal survey per month per study site during May-August 2003 and May-September 2004 to locate and mark alligator locations to quantify habitat use and to generate coarse alligator abundance and density values for each study area. Nocturnal survey transect lengths varied among study areas (17.5 km at Dam B Park, 25 km at Dam B River, 20 km at NTB) but were consistent among surveys and between years. We standardized surveys among study areas, months, and years with respect to observers, route, speed, and survey initiation time. Water level varied according to precipitation and water requirements of the managing water districts at each study area. We initiated surveys 30 minutes after sunset and detected alligators with ≥2 observers using 2 2-million-candlepower spotlights traveling 6-8 km/hour in either a 4.9-m Go-Devil® (Baton Rouge, LA) boat with a 20-horsepower Honda/Go-Devil® or a 4.9-m flat-bottom boat with a 40-horsepower outboard motor, depending upon study area. We counted all alligators observed during nocturnal surveys, estimated total body length (TL) with eye-to-nare length (Chabreck 1966), and recorded each into 30.5-cm (1-foot) categories. If an alligator submerged before we estimated TL, we recorded its length as unknown <1.8 m or unknown ≥1.8 m. We marked each alligator location with a uniquely numbered, weighted buoy for habitat data collection (see below). Perpendicular to the nocturnal survey transect, each observer estimated maximum visibility distances (m) every 2 minutes,

by estimating the maximum distance each could reliably see using spotlights. We estimated visibility distances during each survey.

We calculated average transect width (m) for each survey by averaging maximum estimated visible distances recorded during each nocturnal survey. We calculated area (ha) surveyed for each nocturnal survey as average transect width (m) multiplied by total transect length (m) and divided by 10,000 m². We estimated alligator densities (i.e., alligators/ha) for each survey as the total number of alligators observed during that survey divided by survey area. We also calculated a population index by dividing the total number of alligators observed by survey transect length (Woodward and Marion 1978).

We relocated numbered buoys the day after nocturnal surveys. Buoys served as plot centers for alligator microhabitat measures. We also randomly located 2 additional 10-m² plots within 20 m of each marked alligator location. We established random plots by tossing the weighted buoy in the direction of the second hand on a watch. We visually estimated cover (%) of the following microhabitat variables in each 10-m² plot (i.e., alligator plots and alligator-associated random plots): 1) open water, 2) emergent vegetation, 3) floating vegetation, 4) mud, and 5) dry ground. We also measured canopy cover presence or absence and water depth (m) at plot center and distances (m) from plot center to woody vegetation, cover (i.e., emergent, floating, and woody vegetation, or any combination thereof >1 m²), and dry ground.

We measured wetland macrohabitat along survey transects the day following each nocturnal survey. At 5-minute intervals traveling 10–15 km/hour along survey transects, we placed a weighted buoy to randomly locate each macrohabitat plot center. We traveled a 100-m transect from plot center in each cardinal direction and recorded habitat intersecting the bow of the boat every 10 m into the following categories: 1) open water, 2) emergent vegetation, 3) floating vegetation, 4) submerged vegetation, 5) woody vegetation, 6) dry ground, and 7) mud. We also recorded presence or absence of woody canopy cover >1 m above water surface and water depth (m) at each 10-m interval.

Data Analysis

We used an arcsine transformation on alligator microhabitat percentage data to meet normality assumptions (Zar 1999). We compared alligator microhabitat (irrespective of alligator size) among study areas with analysis of variance (ANOVA) and examined differences with least-squares mean separation. For all subsequent analyses, we 1) categorized alligators as either adult (individuals \geq 183 cm) or subadult (individuals <183 cm), 2) removed alligators of unknown size, and 3) removed NTB alligator microhabitat data, due to small numbers of alligators observed (n=41 for both yr combined). After these data-reduction procedures, we examined differences in alligator microhabitat between size classes, between Dam B River and Dam B Park, and between years with a series of ANOVAs. We examined differences between adult and subadult alligator micro-

habitat and alligator-associated random microhabitat, between Dam B River and Dam B Park, and between years with multivariate analysis of variance (MANOVA). We used least-squares mean separation tests to examine differences when ANOVAs were significant (P < 0.005) to maintain experiment-wide alpha rates of 0.05.

We calculated macrohabitat as percentage of 40 points per plot (i.e., 10 points/100-m transect) and used an arcsine transformation to meet normality assumptions (Zar 1999). We compared macrohabitat among study areas (NTB, Dam B Park, and Dam B River) and between years (2003 and 2004) with MANOVA. We used Wilks' λ as the test criterion because of its conservative power and analogy to univariate F statistics (Johnson and Wichern 2002). If differences (P < 0.05; i.e., Wilks' λ) occurred during MANOVA, we performed follow-up ANOVAs. We used a conservative approach, where we considered each ANOVA significant if P < 0.006, to maintain an experiment-wide alpha of 0.05. We also examined differences (P < 0.05) in water depth among study sites and between years with ANOVA. In all instances, we used least-squares mean separation tests if differences (P < 0.006 or P < 0.05) occurred during ANOVAs (Zar 1999).

RESULTS

On the Dam B Park route we observed 31–41 alligators in 2003 and 35–90 alligators in 2004 (Table 1). On the Dam B River route we observed 19–29 alligators in 2003 and 10–53 alligators in 2004 (Table 1). We observed few alligators at NTB, ranging 5–8 in 2003 and 0–12 in 2004 (Table 1). Alligator density at Dam B Park tended to be higher than Dam B River, whereas both Dam B Park and Dam B River alligator densities exceeded NTB densities ($F_{2,22} = 26.6$; P < 0.001; Table 1).

Alligator microhabitat varied among study areas, but generally was similar between NTB and Dam B Park (Table 2). Alligators in Dam B River were closer to dry ground (<15 m), in areas with much greater canopy cover (>40%), than those in Dam B Park or NTB (>70 m and <20%, respectively; Table 2). Overall alligators occurred in areas with 60–75% open water, with little (<5 %) emergent vegetation, considerable (>30%, depending upon study area) floating vegetation, generally close (<5 m away) to cover (Table 2).

Alligator microhabitat varied from random habitat in Dam B River (Wilks' $\lambda = 14.3$; df = 10, 1,216; P < 0.001) and among study sites (Wilks' $\lambda = 55.2$; df = 10, 1,216; P < 0.001). We also found a study site × year (Wilks' $\lambda = 5.4$; df = 10, 1,216; P < 0.001), year × status (i.e., alligator or random habitat; Wilks' $\lambda = 1.9$; df = 10, 1,216; P < 0.001), and study site × status (Wilks' $\lambda = 3.2$; df = 10, 1,216; P < 0.001) interaction. We found alligators in Dam B River in areas that were shallower, closer to woody vegetation, and had nearly double the canopy cover than random habitat (Table 2). Within Dam B Park, alligator microhabitat was similar to random habitat, where alligators tended to occur in habitats that mirrored the Dam B Park area (Table 2).

Table 1. Number of American alligators observed (n), area surveyed (ha), densities (alligators/ha), population indices (alligators/km), and mean water depths (m) from nocturnal surveys conducted on the Dam B Park, Dam B River, and North Toledo Bend routes at the Angelina/Neches Dam B and North Toledo Bend Wildlife Management Areas, in East Texas, USA, 2003 and 2004.^a

| Study area | Yr | | | | | | | | | | | | |
|----------------------------|------|------|------|------|------|------|------|------|------|--|--|--|--|
| | | 20 | 003 | | 2004 | | | | | | | | |
| | May | Jun | Jul | Aug | May | Jun | Jul | Aug | Sep | | | | |
| Dam B Park route (17.5 km) | | | | | | | | | | | | | |
| Total alligators observed | 40 | 44 | 31 | 41 | 35 | 54 | 43 | 90 | 52 | | | | |
| Area surveyed | 155 | 112 | 123 | 125 | 232 | 158 | 160 | 167 | 166 | | | | |
| Density | 0.26 | 0.39 | 0.26 | 0.33 | 0.15 | 0.34 | 0.27 | 0.54 | 0.31 | | | | |
| Population index | 2.29 | 2.51 | 1.77 | 2.34 | 2.00 | 3.09 | 2.46 | 5.14 | 2.97 | | | | |
| Mean water depth | 1.7 | 2.0 | 1.5 | 1.9 | 1.9 | 1.8 | 2.0 | 1.3 | 1.8 | | | | |
| Dam B River route (25 km) | | | | | | | | | | | | | |
| Total alligators observed | 28 | 29 | 29 | 19 | 27 | 20 | 10 | 44 | 55 | | | | |
| Area surveyed | 292 | 243 | 239 | 246 | 247 | 349 | 307 | 175 | 198 | | | | |
| Density | 0.10 | 0.12 | 0.12 | 0.08 | 0.11 | 0.06 | 0.03 | 0.25 | 0.28 | | | | |
| Population index | 1.12 | 1.16 | 1.16 | 0.76 | 1.08 | 0.80 | 0.40 | 1.76 | 2.20 | | | | |
| Mean water depth | 2.1 | 2.7 | 2.4 | 2.6 | 2.6 | 2.5 | 2.6 | 2.4 | 2.3 | | | | |
| N Toledo Bend (20 km) | | | | | | | | | | | | | |
| Total alligators observed | 7 | 5 | 8 | 5 | 12 | | 0 | 4 | | | | | |
| Area surveyed | 239 | 234 | 198 | 191 | 291 | | 0 | 267 | | | | | |
| Density | 0.03 | 0.02 | 0.04 | 0.03 | 0.04 | | 0 | 0.01 | | | | | |
| Population index | 0.35 | 0.25 | 0.40 | 0.25 | 0.60 | | 0 | 0.20 | | | | | |
| Mean water depth | 1.6 | 1.3 | 1.6 | 1.3 | 2.0 | | 1.7 | 1.6 | | | | | |

a Blank fields indicate those for which we performed no surveys due to low water, inclement weather, or dry conditions.

Within both Dam B Park and River, adults occurred in microhabitats with deeper (>1.5 m), more open water (>75%), and much less floating vegetation (8–22%) than did subadults, which were found in areas with shallow water (<1.5m), closer to dry ground and cover (<2 m), and with greater canopy cover (approx. 20–50%; Table 3). Subadults in Dam B River were closer to woody cover and dry ground, with more than double the canopy cover of subadults in Dam B Park, but subadults in both areas occurred in shallow

(<1.5 m) open-water (>50%) habitats (Table 3). Adults followed similar habitat patterns, where adults in Dam B River were closer to wood and dry ground in areas with >3 times the canopy cover (Table 3). Habitat variation between Dam B Park and Dam B River drove many of these comparisons (see below); however, regardless of study site, adults occurred in deeper, more open water, with less floating vegetation, and further from dry ground or cover than did subadults (Table 3).

Table 2. Means, standard errors, F- and P-values resulting from analysis of variance (ANOVA) for alligator microhabitat, irrespective of size class, among study areas and between alligator microhabitat and random habitat within each study area, at Dam B River and Dam B Park Wildlife Management Area, and North Toledo Bend Wildlife Management Area, in East Texas, USA, May-August 2003 and May-September 2004.

| Dam B River (n = 261) | | | | | | | | B Park | k (n = | N Toledo Bend (n = 41) | | | | | | |
|----------------------------|-------------------|-----|-----------|-----|------------------|---------|-----------|--------|-----------|------------------------|------------------|-------|------------------------|------|------------------|---------|
| | Alligator | | Random | | | | Alligator | | Random | | | | Alligator | | | |
| Habitat | \bar{x} | SE | \bar{x} | SE | F^{b} | P | \bar{x} | SE | \bar{x} | SE | F^{c} | P | \bar{x}^{d} | SE | F^{e} | P |
| Water depth (m) | 1.6A ^f | 0.1 | 2.0 | 0.0 | 10.2 | 0.002 | 1.4A | 0.0 | 1.5 | 0.0 | 2.9 | 0.087 | 1.5A | 0.2 | 5.2 | 0.006 |
| Distance to wood (m) | 6.7B | 0.9 | 10.5 | 0.1 | 12.7 | < 0.001 | 27.9A | 2.7 | 29.5 | 1.9 | 0.3 | 0.613 | 9.0B | 2.6 | 22.7 | < 0.001 |
| Distance to dry ground (m) | 12.2B | 1.3 | 15.8 | 0.6 | 6.0 | 0.015 | 76.1A | 5.1 | 76.9 | 3.6 | 0.0 | 0.889 | 70.3A | 12.9 | 54.3 | < 0.001 |
| Distance to cover (m) | 4.0A | 0.7 | 7.6 | 0.8 | 17.6 | < 0.001 | 3.0A | 0.5 | 4.7 | 0.4 | 6.6 | 0.010 | 4.5A | 3.6 | 0.8 | 0.433 |
| Open water (%) | 73.3A | 1.6 | 72.4 | 0.5 | 0.2 | 0.694 | 62.5B | 1.9 | 58.6 | 1.7 | 0.9 | 0.340 | 61.0B | 6.2 | 9.7 | < 0.001 |
| Emergent vegetation (%) | 1.8A | 0.4 | 0.9 | 2.1 | 9.0 | 0.003 | 2.2A | 0.5 | 2.9 | 0.5 | 0.1 | 0.824 | 4.5A | 2.6 | 1.3 | 0.273 |
| Floating vegetation (%) | 7.5B | 1.0 | 5.1 | 0.3 | 11.3 | < 0.001 | 31.7A | 1.9 | 30.5 | 1.6 | 1.1 | 0.302 | 31.6A | 6.1 | 58.0 | < 0.001 |
| Mud (%) | 4.9A | 0.7 | 3.2 | 0.9 | 12.6 | < 0.001 | 1.6B | 0.4 | 1.5 | 0.4 | 1.5 | 0.227 | 0.4B | 0.2 | 20.9 | < 0.001 |
| Dry ground (%) | 11.3A | 1.2 | 17.9 | 0.7 | 2.5 | 0.116 | 0.7B | 0.5 | 6.1 | 1.0 | 7.8 | 0.005 | 2.4B | 1.6 | 39.1 | < 0.001 |
| Canopy cover (%) | 43.2A | 2.9 | 25.4 | 1.8 | 27.1 | < 0.001 | 1.8B | 1.8 | 10.6 | 1.2 | 4.2 | 0.042 | 16.1B | 5.6 | 41.7 | < 0.001 |

^a We measured alligator habitat in 10-m² plots centered upon weighted buoys located during monthly nocturnal surveys.

^b F- and P-values associated with ANOVA in alligator and random habitat within Dam B River.

^c F- and P-values associated with ANOVA in alligator and random habitat within Dam B Park.

^d We did not report F- and P-values for ANOVA in alligator and random habitat within N Toledo Bend, because there were no differences (P > 0.005) for any variable.

^e We reported F- and P-values for ANOVA in alligator habitat only among study areas.

f Alligator habitat means followed by the same letter within the same row are not different (P > 0.005) among study areas.

Table 3. Means, standard errors, F- and P-values, a resulting from analyses of variance for adult and subadult American alligator microhabitat at Dam B Park (DBP) and Dam B River (DBR; Dam B Wildlife Management Area), in East Texas, USA, May-August 2003 and May-September 2004.

| | DBP | | | DBR | | | | | | | | | | | | |
|----------------------------|------------------------------|-----|-----------|------|-----------|-----|------|-----|-------|----------------|-------------------|---------|----------------------|-------------|------|-------------|
| | Subad Ad (n = 161) (n = 121) | | | | | | | | | BR ad subad | Ad DBP vs. DBR | | Subad DBP vs. DBR | | | |
| Habitat | \bar{x} | SE | \bar{x} | SE | \bar{x} | SE | x | SE | F | P | F | P | F | P | F | P |
| Water depth (m) | 1.3 | 0.1 | 1.5 | 0.1 | 1.4 | 0.1 | 2.3 | 0.2 | 3.21 | 0.042 | 9.40 | < 0.001 | 23.4 | $< 0.001^1$ | 2.1 | 0.146^{1} |
| Distance to wood (m) | 22.9 | 3.2 | 34.4 | 6.2 | 4.1 | 0.8 | 11.3 | 2.0 | 1.23 | 0.295 | 6.47 | 0.002 | 9.8 | 0.002 | 24.3 | < 0.001 |
| Distance to dry ground (m) | 60.6 | 6.4 | 103.1 | 11.7 | 8.5 | 1.4 | 20.4 | 2.8 | 5.20 | 0.006 | 6.52 | 0.002 | 36.3 | < 0.001 | 45.9 | < 0.001 |
| Distance to cover (m) | 1.2 | 0.3 | 6.2 | 1.4 | 2.7 | 0.8 | 6.5 | 1.6 | 9.51 | < 0.001 | 2.62 | 0.076 | 0.0 | 0.885 | 3.8 | 0.053 |
| Open water (%) | 52.4 | 2.8 | 74.8 | 3.2 | 67.8 | 2.3 | 84.8 | 2.9 | 13.88 | < 0.001 | 10.48 | < 0.001 | 7.1 | 0.009 | 16.2 | < 0.001 |
| Emergent vegetation (%) | 2.4 | 0.8 | 2.3 | 0.9 | 1.7 | 0.6 | 1.1 | 0.7 | 0.11 | 0.893 | 2.50 | 0.085 | 1.5 | 0.232 | 0.0 | 0.911 |
| Floating vegetation (%) | 40.2 | 2.9 | 21.7 | 3.1 | 7.6 | 1.4 | 6.3 | 2.0 | 9.02 | 0.002 | 0.56 | 0.572 | 19.5 | < 0.001 | 88.6 | < 0.001 |
| Mud (%) | 2.7 | 0.7 | 0.4 | 0.3 | 6.4 | 1.2 | 2.1 | 0.9 | 4.28 | 0.015 | 4.53 | 0.012 | 6.9 | 0.010 | 17.0 | < 0.001 |
| Dry ground (%) | 1.9 | 0.6 | 0.7 | 0.7 | 14.6 | 1.9 | 5.3 | 1.7 | 0.78 | 0.046 | 4.6 | 0.011 | 8.8 | 0.004 | 57.9 | < 0.001 |
| Canopy cover (%) | 18.7 | 0.7 | 7.4 | 2.4 | 48.3 | 3.7 | 23.2 | 5.3 | 4.15 | 0.017 | 8.16 | < 0.001 | 9.8 | 0.002 | 40.2 | < 0.001 |

^a P-values ($P \ge 0.006$) indicate no difference.

Macrohabitat varied among study sites (Wilks' $\lambda = 24.2$; df = 24, 688; P < 0.001; Table 4), and there was a study site \times year interaction (Wilks' $\lambda = 2.4$; df = 16, 474; P = 0.002) due to differences between years in dry ground at NTB ($F_{1.86} =$ 10.84; P = 0.001). We combined macrohabitat data for both years, given the similarity in responses between years. Dam B River had the most (80%) open water and the least amount of emergent, floating, and submerged vegetation (<10%), whereas amounts of open water (42-52%) and floating vegetation (37–46%) were similar between Dam B Park and NTB, which had the most submerged vegetation (Table 4). Water depth also varied among study sites $(F_{3,10,063} = 598.9; P < 0.001)$ and between years $(F_{3,10,063} =$ 26.9; P < 0.001), and there was a site \times year interaction $(F_{2,10,063} = 598.9; P < 0.001)$. Among study sites, water was deepest in Dam B River, but water depths were similar between years within Dam B Park (2003 range 1.5-2 m; 2004 range 1.3-2 m) and within Dam B River (2003 range 2.1-2.6 m; 2004 range 2.3-2.6 m), although at NTB water was deeper in 2004 (range 1.6-2 m) than 2003 (range 1.3-1.6 m; $F_{1,3,518} = 67.4$; P < 0.001).

DISCUSSION

Within coastal Louisiana and Texas optimal alligator habitat contains 1) highly interspersed open water and emergent vegetation, 2) 20-40% open water, and 3) water depths >1.2 m in 10-20% of the area (Newsom et al. 1987). Habitat suitability declines as water-level fluctuations become more unpredictable (Joanen and McNease 1984, Kushlan and Jacobsen 1990) or with increasing exposed substrates (Newsom et al. 1987) due to water loss (Joanen and McNease 1970). Declining habitat quality affects food quality and quantity, as well as a suite of alligator demographics, such as growth rates, densities, reproductive success, and survival (McNease and Joanen 1974, Newsom et al. 1987); however, direct relationships among these variables are unclear. Inland wetland habitats in our study had more open (42-80%) and generally deeper water (1.6-2.5 m; Table 4) than considered optimal (Newsom et al. 1987), but our study wetlands had considerable floating vegetation (6-47%), which is poorly defined in optimal coastal alligator habitat descriptions (Newsom et al. 1987). Other habitat characteristics such as amount of emergent

Table 4. Means, standard errors, and resulting F- and P-values from analysis of variance for wetland macrohabitat collected after nocturnal American alligator surveys at North Toledo Bend Wildlife Management Area and Dam B River and Dam B Park in East Texas, USA, May–August 2003 and May–September 2004.

| Habitat | N Toledo (n = 8 | | Dam B : | | Dam B | | F | |
|--------------------------|---------------------|-----|-----------|-----|-----------|-----|-------|---------|
| | $	ilde{x}$ | SE | \bar{x} | SE | \bar{x} | SE | | P |
| Open water (%) | 42.4 B ^b | 3.6 | 80.3 A | 1.6 | 52.3 B | 3.0 | 29.9 | < 0.001 |
| Emergent vegetation (%) | 4.8 AB | 1.2 | 1.4 B | 0.3 | 8.3 A | 1.3 | 9.7 | < 0.001 |
| Floating vegetation (%) | 46.5 B | 3.8 | 6.1 A | 1.0 | 37.4 B | 3.4 | 36.3 | < 0.001 |
| Submerged vegetation (%) | 43.6 A | 3.8 | 0.0 C | 0.0 | 23.9 B | 3.3 | 43.9 | < 0.001 |
| Woody vegetation (%) | 6.5 A | 0.9 | 7.3 A | 0.9 | 4.3 B | 0.7 | 14.8 | < 0.001 |
| Mud (%) | 1.0 B | 0.2 | 2.0 A | 0.4 | 1.9 A | 0.5 | 54.0 | < 0.001 |
| Dry ground (%) | 6.1 B | 0.9 | 9.3 A | 1.0 | 2.0 C | 0.6 | 48.8 | < 0.001 |
| Canopy cover (%) | 16.5 A | 1.5 | 18.0 A | 1.4 | 8.5 B | 1.0 | 43.0 | < 0.001 |
| Water depth (m) | 1.6 C | 0.0 | 2.5 A | 0.0 | 1.8 B | 0.0 | 651.2 | < 0.001 |

^a Sample sizes indicate total no. of macrohabitat plots we measured at each study area for both yr combined.

^b Means followed by the same letter within the same row are not different (P > 0.05).

vegetation (5–8%) and little (1–9%) mud or dry ground were within reported ranges of optimal coastal habitat conditions (Newsom et al. 1987). How these slight variances and gross similarities in our habitat estimates directly influence population densities is not clear. Alligator densities in our study were 3–5 times lower than coastal estimates (Altrichter and Sherman 1999; G. Calkins, Texas Parks and Wildlife Department, unpublished data). Relationships between habitat characteristics and population densities should be explored.

Alligator microhabitats were used in proportion to their availability in Dam B Park and Dam B River. Alligators in Dam D River occupied areas near river shorelines, downstream from log jams and downed trees. In Dam B Park, water depths were fairly uniform (<2 m), and the site contained approximately equal open water:emergent and floating vegetation used by alligators in other studies. Adults occupied deeper, less vegetated open-water habitats, farther from cover than did subadults. Few studies report specific subadult habitat requirements (see Goodwin and Marion 1978); however, in our study subadults tended to occupy shallower more heavily vegetated habitats close to cover. Neither submerged nor floating vegetation are specifically mentioned in previous alligator habitat descriptions (e.g., Newsom et al. 1987). The combination of shallow water with equal coverage of open water and floating and submerged vegetation may hinder alligator movements, making these areas less suitable for adults, but may provide concealment for subadults. Advances in real-time Global Positioning System tracking systems may allow future work to focus upon spatial distribution of adults and subadults in these inland wetlands.

During late spring and early summer, mats of water hyacinth, alligator weed, and common salvinia created patchy networks of open water and cover, and during summer, these mats became larger. Alligators create holes in non-floating vegetation in other regions, which increases interspersion and maintains reliable water sources during drought (see Palmer and Mazzotti 2004). We did not find similar holes in our study areas, perhaps due to existing open water, negating the need for alligators to actually create holes. Information is needed about the distribution, arrangement, and extent of submerged and floating vegetation and relationships with water levels to understand if these habitat features affect alligator populations in inland wetlands.

Slight changes in water levels will influence the extent of suitable alligator habitat and affect alligator occupancy and habitat suitability (Woodward et al. 1996). Water levels in inland reservoirs and associated wetlands rapidly change, often unpredictably, during summer, due to natural (e.g., flooding) and man-made (e.g., withdraw) causes. During late summer 2004, water level at Dam B dropped 1.0 m in 3 days. Subsequently, we observed fewer adult alligators in shallow water in Dam B Park and found more alligators in deep water in Dam B Park. Although temporary, such fluctuations concentrate alligators into remaining habitats

and increase subadult susceptibility to predation (Joanen and McNease 1970, Woodward et al. 1987). Indeed, conservation and management of alligators may depend on restoration, or perhaps implementation, of more natural water fluctuations (Kushlan and Jacobsen 1990).

MANAGEMENT IMPLICATIONS

Alligator harvest and habitat management in Texas is implemented primarily through locally obtained data and a long-used management plan developed from coastal Louisiana and Texas (Thompson et al. 1984). As alligator populations and harvest opportunities continue to expand, modifications of this management approach may be required. We found alligators used inland habitats at densities 3-5 times lower than coastal areas, in proportion to their availability, similar to alligators in coastal areas, but habitats deviated from what is considered to be optimal in coastal wetlands (Newsom et al. 1987). It is unclear how habitat conditions, including distribution, arrangement, extent of submerged and floating vegetation, and water management affect movements, survival, and spatial distribution of alligators in these inland wetlands. Impacts of current harvest management strategies as related to habitat or densities in inland wetlands are presently unknown. If sustainable harvest management is a goal, conservative approaches should be used for these inland wetlands to minimize impacts on populations existing at lower densities and in slightly different habitats than coastal counterparts.

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