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Effect of Drought on Clutch Size and Hatchling Production of American Alligators (*Alligator mississippiensis*) in Texas

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***Abstract*.—The American Alligator (*Alligator mississippiensis*) has made a remarkable recovery throughout its range during the last half-century. This recovery is attributed to management practices that are based on sound research. However, little research has focused on nest characteristics, nest success, and production of hatchling alligators in Texas. We quantified hatching success of 902 American Alligator nests collected from the wild during 2007–2012. Nests were hatched in farm facility incubators under optimum conditions to determine potential hatchling production of wild nests. The clutch size (mean ± SE: 37.1 ± 0.3; $F_{4,897} = 0.55$, $P = 0.700$) and the number of infertile eggs per nest (5.2 ± 0.2; $F_{4,897} = 0.63$, $P = 0.640$) did not differ by years, but significantly fewer hatchling alligators were produced in 2011 (18.1 ± 0.9) than the other years (23.5 ± 0.4; $F_{4,897} = 9.29$, $P < 0.001$), presumably due to drought conditions experienced during 2011.**

Key Words.—clutch characteristics; crocodilian; egg collection; nest success; reproduction; wildlife management

Introduction

The American Alligator (*Alligator mississippiensis*) is an endemic species that inhabits rivers, swamps, marshes, lakes, bayous, and ephemeral bodies of water along the Gulf coast of the United States (Conant and Collins 1998). After a period of heavy hunting pressure during the early part of the twentieth century (Thompson et al. 1984), the American Alligator has made an incredible comeback due to harvest regulations, intensive management strategies, and wetland conservation (Conant and Collins 1998; Saalfeld et al. 2008). This population decline initiated periods of extensive field research that aided in the recovery of the species. Various aspects of the autecology and biology of the American Alligator have been comprehensively examined including distribution, behavior, life history (Deitz and Hines 1980; Joanen and McNease 1989; Gabrey 2010; Saalfeld et al. 2012), captive maintenance and management (Chabreck 1978), and physiology (Joanen and McNease 1989). However, despite the numerous studies that have been conducted, there still remains much needed information about the ecology and population dynamics of the species, which is essential for sound management.

Alligator numbers have increased to the point that the species requires intense management to maintain these growing populations at appropriate levels (i.e., harvest programs) to preserve population health and habitat integrity, while also reducing the amount of human-alligator conflict. To maintain stable populations, harvest needs to be balanced with recruitment. By knowing how many individuals can potentially be recruited into a population annually, we can better understand how to manage populations with these goals in mind. Nest success, hatchling production, and hatchling survival are essential components in estimating recruitment (Saalfeld et al. 2012). There is limited knowledge of nesting success, ecology, and population dynamics of alligators in Texas (Hayes-Odum et al., 1993; Saalfeld et al. 2012). Hayes-Odum et al. (1993) stated that there are few data, specifically in Texas, on clutch sizes and fertility rates. Concurrently, Cooper and Slaughter (2008) indicated that there has been little research conducted in Texas concerning the nest success of the American Alligator. In addition, Ruckel and Steele (1984) indicate that variation in nesting parameters along geographic gradients suggests the need to collect baseline reproductive data within each geographic area for a population to be managed properly. Although overt, it is critical to distinguish the difference between nest success and hatchling production. Studies of nest success define a successful nest as one that produces ≥1 hatched egg (Woodward et al. 1989; Saalfeld et al. 2012). These data are commonly reported as binomial, either as successful or unsuccessful. While useful in some regards, this type of representation is qualitative but not quantitative. Therefore, beyond nest success, hatchling production confirms not only if a nest was successful, but also quantifies nest success by representing the number of hatchling alligators produced from a single nest. This information is arguably more useful in management and conservation than nest success alone and provides a better understanding of the dynamics of alligator populations. In addition, it is advantageous in employing more precise and accurate management strategies that target conservation and the sustainable use of American Alligators. Drought has been reported to cause desiccation of alligator eggs (Joanen and McNease 1989), as well as reduced reproduction and physiological stress on both adult and juvenile alligators (Lance et al. 2010). There is insufficient information however, on the effect drought has on reproductive output of alligator nests and clutch characteristics from a quantitative perspective. Therefore, the objectives of this study were to quantify clutch size and hatchling production of wild American Alligator nests in southeastern Texas, and to determine if these parameters are affected by drought.

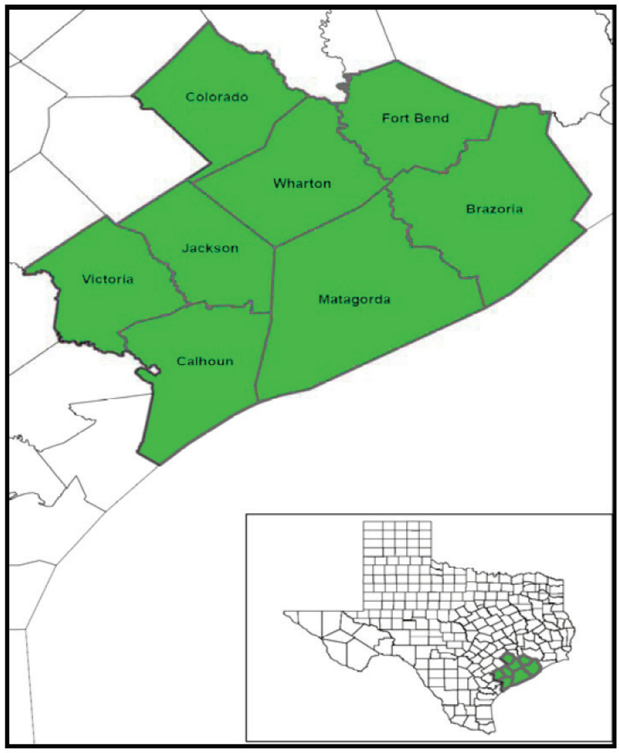

Figure 1. Counties in Texas, USA, where eggs of American Alligators (*Alligator mississippiensis*) were collected from 2007–2012.

Materials and Methods

Data on alligator nests were collected through collaboration with a Texas Parks and Wildlife Department (TPWD) contracted egg collector. Egg collectors throughout the state are contracted with TPWD to collect eggs from wild alligator nests. This is a common management practice among wildlife agencies in states that occur within the range of the American Alligator (Chabreck 1978; Thompson et al. 1984; Woodward et al. 1989). Once nests were located on a contracted property, a harvest of 50% of the total number of nests found was allowed by TPWD, regardless of egg presence or clutch size in each nest (i.e., collection allotment was based solely on the number of nests, not number of eggs). After collection, eggs were hatched in farm facility incubators and subsequently sold into the commercial market. In this study, we collected eggs from Matagorda, Calhoun, Brazoria, Victoria, Colorado, Fort Bend, Wharton, and Jackson counties, Texas from 2007–2012 (Fig. 1). We collected eggs from nests from a diverse array of habitats that are commonly found in southeastern Texas, including inland freshwater wetlands (e.g., lakes, ponds, swamps, freshwater marshes) and coastal brackish marshes.

We located alligator nests using methods similar to those of other studies (Klause 1984; Hunt 1987; Woodward et al. 1989; Hayes-Odum et al. 1993), and included walking the perimeter of all bodies of water located within each property. Nest characteristics such as debris piles, alligator tracks, slides, alligator scat, and the presence of avidly guarding females indicated the possible presence of a nest (Hayes-Odum et al. 1993). When possible, we located nests from the water by boat, and from the air via helicopter. We collected eggs during mid-incubation (i.e., late June into early July; Chabreck 1978; Woodward et al. 1989). Joanen and McNease (1987) found that by collecting eggs during mid-incubation, embryo mortality can be reduced substantially. However, Woodward et al. (1989) found that time of egg collection and hatch rate were unrelated. Additionally, Gutzke and Packard (1986) found that the hydric conditions of the nest during the first one-third of incubation had no effect on hatching success of Painted Turtles (*Chrysemys picta*). Therefore, assuming this is also true for alligator eggs, egg collection during mid-incubation not only reduced the risk of embryo mortality but also eliminated concerns that eggs were affected by the nest environment during early incubation. Subsequent to location, we opened and checked nests for the presence of eggs. Once eggs were found, we determined egg fertility by the presence of an opaque band, which appears within 24 h of deposition (Ferguson 1985; Webb et al. 1987). We determined egg viability through a comparison of the opaque band among all eggs in each clutch, and through examination of egg color and odor (Ferguson 1982; Woodward et al. 1989). Egg discoloration, egg odor, or the lack of an opaque band indicates an unfertile or non-viable egg. We recorded the total number of eggs per nest, number of fertile eggs, and number infertile eggs at the nest site.

We gathered each clutch of eggs, as well as nest material from its respective nest, in wire baskets and transported eggs to captive hatching facilities in El Campo, Texas, USA, using the methods described by Chabreck (1978) and Woodward et al. (1989). Depending on the remoteness and accessibility of each nest, eggs were collected and transported through the use of airboats and vehicles. During collection, we carefully marked eggs with a waterproof marking pen along the dorsal axis of the egg shell before being transferred into the wire baskets (Woodward et al. 1989). We took care not to invert, rotate, or agitate the eggs in any way to decrease the likelihood of eggs experiencing disturbance or damage due to movement (Woodward et al. 1989). High mortality can result if embryos undergo excessive or intense movement following attachment to the shell membrane, specifically during the first few weeks post oviposition. We took extreme precaution to eliminate the risk of embryo mortality due to egg transportation. We added enough natural nesting material to each basket to confidently cover, cushion, and incubate each clutch. We were also careful to limit jarring while egg baskets were in transit. Eggs were successively deposited into a one room walk-in incubator. The ambient air temperature of the incubator was consistently maintained between 31.0–32.8° C, and the relative humidity was kept as close to 100% as possible. We periodically checked clutches during incubation to remove and record additional nonviable eggs (Woodward et al. 1989). Twice daily we inspected individual clutches for signs of hatching. We listened for sounds of pipping and hatchling vocalizations

Table 1. Clutch parameters, hatchling production, and nest totals of American Alligators (*Alligator mississippiensis*) for eight coastal counties in Texas, USA, from 2007–2012. Means (± SE) are shown for clutch size and other measures of production (listed below measure as per clutch).

Reproductive Trait	2007	2008	2010	2011	2012	Total
Number of Nests Collected	148	180	159	158	247	902
Total Eggs	5502	7017	6035	5757	9143	33454
Mean Clutch Size	37.2 ± 0.7	37.0 ± 0.7	38.0 ± 0.8	36.4 ± 0.7	37.0 ± 0.6	37.1 ± 0.3
Total Viable Eggs	4772	5997	5149	4910	7954	28782
Per Clutch	32.2 ± 0.8	32.0 ± 0.8	32.4 ± 0.8	31.1 ± 0.7	32.2 ± 0.6	31.9 ± 0.3
Total Non-Fertile Eggs	730	1020	886	847	1189	4672
Per Clutch	5.0 ± 0.4	5.4 ± 0.5	5.6 ± 0.5	5.4 ± 0.4	5.0 ± 0.4	5.2 ± 0.2
Hatchlings Produced	3479	4358	3958	2864	5715	20374
Per Clutch	24.0 ± 0.9	23.0 ± 0.8	25.0 ± 0.8	18.1 ± 0.9	23.1 ± 0.6	22.6 ± 0.4
Total Fertile Non-Hatching Eggs	1293	1639	1191	2046	2239	8408
Per Clutch	9.0 ± 0.7	8.6 ± 0.6	7.5 ± 0.6	13.0 ± 0.8	9.1 ± 0.5	9.3 ± 0.3
Total Non-Hatching Eggs	2023	2659	2077	2893	3428	13080
Per Clutch	14.0 ± 0.7	14.0 ± 0.8	13.1 ± 0.8	18.3 ± 0.9	14.0 ± 0.6	14.5 ± 0.3

from each nest basket, which indicated that the eggs were soon to hatch. In the wild, hatchling vocalizations from within the nest signals the maternal alligator to excavate the nest, aid neonates in hatching, and sometimes transport them to nearby water (Hunt 1987). Once we determined that a clutch was ready to hatch, we opened the nest and assisted the hatchlings in a manner similar to what would occur in a natural setting. We recorded the number of hatchlings produced and the number of viable eggs that did not succeed to full term. We obtained monthly rainfall data for all years of egg collection for each county (http://www.wunderground.com). We calculated mean monthly and yearly rainfall for the area using counties as replicates (Table 1).

We used the means procedure (PROC MEANS; Littell et al. 1991) in SAS to determine mean values of each clutch characteristic (e.g., clutch size, viable eggs, infertile eggs, hatchlings produced, and non-hatching viable eggs). This procedure additionally was used to determine mean yearly rainfall from 2007–2012. We used the general linear model procedure (PROC GLM; Littel et al. 2006) to compare differences between average clutch sizes, number of viable eggs, and hatchlings produced between years. Furthermore, this procedure was used to analyze rainfall data by month, year, and month-year interactions. If the comparison of means showed significant differences ($P < 0.05$), we used Tukey's studentized range (HSD) test to make pair-wise comparisons.

Results

From 2007–2012, 33,454 eggs were collected from 902 wild American Alligator nests (Table 1). No eggs were collected in 2009 due to a surplus of alligators in the commercial market, which resulted in a low demand for alligator products. On average each nest contained 37.1 ± 0.3 (mean ± SE) eggs, of which 31.9 ± 0.3 were viable eggs (86% of egg total), and 5.2 ± 0.2 were infertile (14% of egg total). Of the 32 viable eggs, on average 22.6 ± 0.4 hatched (71% of viable eggs, 61% of total eggs), and 9.3 ± 0.3 eggs did not hatch (29% of viable eggs, 25% of total eggs). On average 14.5 ± 0.3 eggs (infertile eggs + fertile non-hatching eggs) did not hatch from the mean nest total of 37.1 eggs. Collected nests had an average hatchling potential production rate of 61% per nest. The number of viable eggs ($F_{4,897} = 0.59$, $P = 0.710$), infertile eggs ($F_{4,897} = 0.63$, $P = 0.640$), and total eggs/nest ($F_{4,897} = 0.55$, $P = 0.700$) did not differ among years. However, the number of fertile non-hatching eggs ($F_{4,897} = 9.13$, $P < 0.001$), and the number of hatchlings produced ($F_{4,897} = 9.29$, $P < 0.001$) did differ significantly in 2011. We found that there were fewer hatchling alligators (18.13 ± 0.9, 49% of total eggs, 58% of viable eggs) and more fertile non-hatching eggs (12.9 ± 0.8, 35% of total eggs, 40% of viable eggs) in 2011 than in all other years (23.5 ± 0.4; 8.5 ± 0.3).

Mean annual rainfall from 2007–2012, excluding 2009, for the area in of our study was 179.5, 87.4, 129.4, 49.3, and 104.5 cm, respectively. The mean annual rainfall differed by year ($F_{4,420} = 65.85$, $P < 0.001$). There was also a significant difference detected by month ($F_{11,420} = 25.46$, $P < 0.001$), and month-year interaction ($F_{44,420} = 11.49$, $P < 0.001$; Table 2). In general, July was the wettest month, receiving approximately 16 cm of precipitation, while October was the driest month, receiving < 4 cm of precipitation on average.

Discussion

Clutch sizes of American Alligators vary by geographic region and year. Joanen (1969) reported a mean clutch size of 38.9 in Louisiana; Deitz and Hines (1980) determined a similar mean clutch size of 37.5 in Florida, and Ruckel and Steele (1984) found a mean clutch size of 38.0 in freshwater lake habitat in Georgia. However, Goodwin and Marion (1978), Metzen (1977), and Wilkinson (1983) reported mean clutch sizes of 30.3, 30.0, and 44.2, respectively, from Florida, Georgia, and South Carolina alligators. Conversely, we found a mean clutch size that was lower than the 40.7 reported by Ruckel and Steele (1984) and the 44.2 reported by Wilkinson (1983) in brackish marshland and coastal habitat. The fertility rate (i.e., the proportion of fertile eggs in a clutch) that we determined for Texas alligator nests (31.9 ± 0.3, 86.0%) was lower than the 92.1% and 92.7% that was found at two sites in Georgia by Ruckel and Steele (1984). Nevertheless, very few studies have investigated how fertility rates of the American Alligator may fluctuate along temporal and environmental gradients. There have been several studies that have investigated

Table 2. Average monthly (± SE) rainfall for eight coastal counties in southeast Texas from 2007–2012. Means with the same capital letters are not significantly different ($P > 0.05$) between years of the same month. Means with the same lowercase letter are not significantly different ($P > 0.05$) between months of the same year.

Month	2007		2008		2010		2011		2012	
Jan	17.1 (0.1)	Abcd	10.3 (1.6)	Bab	7.9 (1.1)	BCbc	6.68 (4.7)	BCa	4.7 (0.9)	Cabc
Feb	1.0 (0.2)	Bg	4.8 (0.8)	ABc	8.3 (0.5)	Abc	1.57 (0.2)	Bbcd	8.2 (2.6)	Aabc
Mar	17.3 (0.6)	Abc	6.4 (1.0)	BCbc	5.8 (0.5)	BCbc	2.71 (0.3)	Cbcd	9.7 (1.9)	Ba
April	8.3 (6.7)	Acdefg	6.7 (0.4)	ABbc	4.0 (0.6)	BCbc	0.15 (0.1)	Cd	5.2 (2.0)	ABabc
May	20.4 (2.5)	Ab	2.2 (1.3)	Cc	12.2 (1.8)	Bb	3.33 (0.8)	Cabcd	10.2 (2.8)	BCa
Jun	12.0 (3.0)	Abcdef	3.0 (1.0)	Bc	12.7 (2.2)	Ab	3.55 (0.8)	Babc	4.0 (0.4)	Babc
Jul	34.9 (5.6)	Aa	6.5 (0.9)	Bbc	26.0 (4.2)	Aa	1.04 (0.3)	Bcd	10.8 (2.0)	Ba
Aug	12.9 (1.7)	Abcde	12.0 (1.4)	Aa	3.3 (0.85)	Bbc	0.85 (0.3)	Bcd	3.2 (0.7)	Babc
Sep	7.8 (1.0)	Bdefg	3.3 (1.0)	Bc	23.9 (4.2)	Aa	3.17 (0.4)	Bbcd	9.4 (1.6)	Bba
Oct	7.4 (1.0)	Aefg	4.9 (0.5)	Ac	0.1 (0.1)	Cc	4.49 (1.3)	ACab	1.4 (0.6)	BCc
Nov	5.8 (1.0)	Aefg	6.1 (1.6)	Abc	5.4 (0.8)	Abc	2.51 (1.0)	Abcd	1.8 (1.0)	Abc
Dec	3.0 (1.1)	Afg	2.1 (0.4)	Ac	4.8 (1.1)	Abc	4.83 (0.9)	Aab	3.7 (1.0)	Aabc

hatching or production success in the wild. Ruckel and Steele (1984) determined a mean hatchling production that ranged between 44.7–55.1% in Georgia. Hatchling production was estimated at 58.2% in Louisiana (Joanen 1969) and from 45% (Goodwin and Marion 1978) to 50.6% (Deitz and Heines 1980) in Florida. Ruckel and Steele (1984) indicate that the hatching rates in their study, and others, are most likely conservative estimates due to the high probability of not observing all hatchlings or finding all egg remnants at each nest site. In contrast, it is likely that our estimate of hatchling production is greater than what naturally occurs in the wild due to our controlled research methods (i.e., hatching eggs in captive farm facilities). However, it is plausible that the true value of hatchling production of wild alligator nests lies somewhere in between our "best case scenario" estimate and estimates from studies conducted in the wild. These differences also are likely a function of regional and geographic variability of life-history characteristics of the species (Brandt 1991; Wilkinson and Rhodes 1997).

It has been postulated that nest and hatching success vary temporally (Dietz and Hines 1980; Saalfeld et al. 2012). Our study suggests that more precisely, hatching success fluctuates along the temporal gradient of environmental variability, specifically drought (Joanen and McNease 1989; Lance et al. 2010). In 2011 Texas experienced the third driest year on record during the last four decades (Texas Agrilife Extension data; http://etweather.tamu.edu [Accessed 20 June 2013]), and especially for the counties included in our study area. Drought is known to be a limiting factor on alligators by decreasing hatching success and by increasing stress levels of adults (Joanen and McNease 1989; Lance et al. 2010). Alligator egg quality has been hypothesized to be a function of diet and stress (Wink et al. 1990). Environmental stochasticity occurs in time and space, and as a result, so does the quantity and quality of nutrition available to reproducing females (Seigel and Fitch 1985). This environmental variation is strongly linked to variation in reproduction, likely due to the effect of female nutritional condition on reproductive output and partitioning (Warner et al. 2007). Energy and nutritional reserves are also essential for the survival of adult reptiles during reproductive cycles and inauspicious environmental conditions, which can be greatly reduced during these times (Fox 1977; Duvall et al. 1982; Gregory 1982; Seigel and Ford 1987; Allsteadt and Lang 1994). It is likely that as a result of drought conditions experienced in 2011, females were physically stressed and, therefore, experienced nutritional and physiological effects that directly affected reproductive output through the decreased nutritional quality of egg yolks. It was noted that yolk mass of embryos that did not succeed to hatching were smaller in 2011 than in other years (Larry Janik and Cord Eversole, pers. obs.), presumably due to suboptimal nutritional or energetic quality. Wink et al. (1990) noted that overcrowding causes stress in captive alligators, which was found to inhibit and delay oviposition, as well as reduce egg quality. It is feasible that during drought alligators experience this same overcrowding stress due to a reduction in water and wetland habitat. This would seemingly result in a larger demand on prey items as a result of a large quantity of alligators converging into the remaining wetland habitat.

Although eggs in our study were housed in captivity, we believe that our results still illustrate the effect that drought has on wild alligator reproduction. This is because female stress levels, nutrition, and overall reproductive energy budget, rather than nesting conditions, are what set the stage for hatching success (Warner et al. 2007). By hatching eggs in captivity, we were able to remove the negative effects of nesting conditions and optimize hatching success to the level allowed by egg quality. Having done this, we likely observed the highest hatching success possible. It has been hypothesized that females that experience a decrease in resource availability during times of environmental stress may counter these suboptimal conditions by investing energy into fewer better-quality offspring (Warner et al. 2007). Because we did not observe a decrease in clutch size, but rather a decrease in the number of hatchlings produced per clutch, it is logical to assume that the energy investment per egg was less in the 2011 drought year than in other years. This indicates that this hypothesis does not hold true for alligators, at least not at the level of drought experienced in this study. If this were not the case, we would have most likely observed a smaller clutch size and hatching success would have remained constant across all years. Therefore, the decrease in hatching success during the 2011 nesting season was not the result of conditions experienced by the eggs, but instead the result of maternal energy investment and stress and thus an indirect effect of drought. Had the eggs in this study been left in the wild and subject to the environment, hatching success would have most likely been less than our estimate. However, the level from which hatching success would have begun to decline would have been less in the 2011 drought year than in all other years. Recent studies suggest that the environment and nutrition may play a much larger role in the complex reproductive biology of oviparous reptiles than what was once previously thought (Warner et al. 2007). We suggest that future research examine how threshold levels of climatic, environmental, and nutritional variation affect American Alligator reproduction across a diverse array of habitats, regions, and geographic localities.

Management implications.—Egg and hatchling production are important influences on American Alligator density (Deitz and Hines 1980). Understanding reproductive potential and survival to recruitment age is essential in the management of a harvested species. To do this, it is helpful for managers to understand the factors acting on nest production (e.g., climatic and environmental variation). Accordingly, managers can implement more precise management strategies as a way to offset stochastic events. With increasing urban pressure on alligators and their habitat, managers are faced with the challenge of balancing conservation and wide utilization of the species while reducing the amount of human-alligator conflicts. Ecological information such as nest success, hatchling production, survival, and recruitment are essential in facing conservation and management challenges.

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Picture
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