Effect of timing of egg collection on growth in hatchling and juvenile American alligators

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ABSTRACT – Many crocodilians are raised commercially for their valuable hides and meat. Stock is often obtained by collecting eggs from the wild, a practice known as egg ranching. Hatchlings are then obtained after incubating these eggs in a controlled setting. Alligators are raised in commercial facilities in Louisiana, and growth rates of hatchlings and juveniles can be an important economic factor for the producer. In this study we demonstrate that alligator eggs collected soon after deposition, and incubated at optimum temperatures for the majority of the incubation period produce hatchlings that are heavier (p = 0.029) and longer (p = 0.0072) than clutch mates collected later, and subjected to fluctuating diurnal temperatures in the wild. This accelerated growth associated with early egg collection can be an economic benefit to the alligator producer, and may reduce the impact of potential natural mortality factors (such as flooding, predation, and lightning fires) that eggs would otherwise be exposed to if not collected.

THE American alligator (*Alligator mississippiensis*) occurs in the southeastern United States and field studies have examined nesting in this species (Joanen, 1969; Deitz & Hines, 1980; Platt *et al.,* 1995). Alligators begin courtship and breeding in spring, and nest in early summer, with nest construction usually occurring in June followed by hatching in late August and into September (Joanen, 1969). Alligators construct a mound nest of vegetation with eggs deposited within the nest cavity; average clutch size in a five year study of 315 nests was 38.9 eggs (Joanen, 1969). Alligators are valuable commercially for their hides and meat, and alligator eggs are often collected from the wild and incubated in controlled settings, to avoid natural mortality factors such as predation and flooding (Elsey *et al.,* 2001). The practice of egg “ranching” has led to an intensive alligator culture program, which in Louisiana is valued at approximately US $60 million yearly for the hides and meat alone. In recent years some 350,000 alligator eggs have been collected annually in Louisiana, while in peak years over 500,000 eggs have been collected (Elsey *et al.,* 2006). Notably potentially high embryo mortality from Hurricanes Katrina and Rita was avoided as a result of prior egg collections for ranching operations.

Sex in all crocodilians studied thus far is determined by incubation temperature (Lang & Andrews, 1994). Additionally, hatchling and juvenile alligator growth can be affected by the temperature at which the eggs are incubated; growth rates are greatest when eggs are incubated at intermediate temperatures, rather than at the extremes needed which determine sex (Joanen *et al.,* 1987). In *Caiman latirostris*, hatchlings obtained from eggs incubated at 31°C were larger than those incubated at 29°C or 33°C; and growth after one year was best for those incubated at 29°C and 31°C than at 33°C (Pina *et al.,* 2007). A small study (six eggs each at 28°C and 30°C, seven eggs each at 32°C and 34°C) of *Caiman crocodilus yacare* (Miranda *et al.,* 2002) likewise showed faster growth at intermediate incubation temperatures (caiman monitored for 120 days at the temperatures noted above, after the initial 20 days of incubation at 30°C).

The incubation period of alligator eggs can vary from 63 days at constant high incubation temperatures (33°C) to 84 days at constant low (29°C) incubation temperatures (Lang & Andrews, 1994). Temperatures in natural nests in the wild fluctuate (range of 23.3°C–32.8°C in Joanen, 1969) and may have varying levels of exposure to sun or shade based on geographic location. Various types of nesting vegetation from which nests are constructed may affect incubation temperatures as well (Elsey *et al.,* unpubl. data). High and low incubation temperatures can cause developmental abnormalities (Ferguson, 1985) and embryo mortality in alligators (Lang & Andrews, 1994). In crocodiles, Webb & Cooper-Preston (1989) similarly noted more abnormal embryos developed at high incubation temperatures in *Crocodylus porosus.* The effect of incubation temperature on reptilian phenotype has recently been reviewed in detail (Rhen & Lang, 2004); references therein note the effects of incubation temperature on crocodilian hatchling morphology, pigmentation, egg dynamics, thermal responses, and growth. Another recent review specific to crocodilians noted temperature affects hatchling size, pigmentation patterns, post-hatching growth rates and thermoregulation in juveniles (Deeming & Ferguson, 1989).

This study was initiated to determine if collecting alligator eggs early in the incubation period (so they can be incubated at the optimum steady incubation temperature for the maximum amount of time) leads to more rapid growth after hatching than eggs left in a natural setting and collected much later, and having longer exposure to fluctuating (and possibly sub-optimal) temperatures in the wild. If growth rates are accelerated, this information could be of great importance to commercial alligator farmers and ranchers. Harvest size could be attained sooner, thereby reducing the costs and time needed for rearing alligators to a commercially marketable size.

MATERIALS AND METHODS

This study was conducted on portions of Rockefeller Wildlife Refuge in Cameron Parish, Louisiana USA. The refuge boundaries were previously described (Joanen, 1969) although habitat losses due to saltwater intrusion and erosion are such that current land mass is estimated at 72,600 acres. This study was conducted in two phases, with a small pilot study done in 1999–2000 and an expanded study in 2003–04.

Alligator nests were generally located by helicopter and ground survey. Because post-hatching crocodilian growth can be strongly influenced by clutch of origin (Garnett & Murray 1986; Webb *et al.,* 1992; Pina *et al.,* 2007) each clutch was divided to serve as its own control. Half the clutch was collected early in incubation [to be incubated at optimum temperatures for post-hatchling growth (~ 31–32°C as per Joanen *et al.,* 1987) in a controlled environmental chamber] and the remaining eggs were left in the nest and collected just prior to hatching. The latter eggs were subjected to fluctuating temperatures under natural conditions.

During the pilot study, the experimental group (collected early) of the eggs from two of the three clutches (clutches A and C) were collected on 2 July 1999. Half the eggs from the third nest (clutch B) were collected on 7 July 1999 and treated as above. Near the estimated time to complete incubation, the control eggs remaining in the field were collected (clutch C collected on 5 August, and the remainder of clutches A and B were collected on 11 August).

During the follow up study, all six nests were visited and eggs divided into control and experimental groups earlier in incubation (18 June 2003), at which point the experimental half of each clutch was placed in the field laboratory incubator. The control group from each clutch was collected on 12 August 2003.

Two days after hatching, all hatchlings were weighed to the nearest 0.01 g and total length (TL) was measured to the nearest 0.1 cm. Hatchlings were permanently marked with removal of one or more tail scutes to indicate treatment and clutch of origin. Web tags were placed in the rear feet for individual identification. Hatchlings were maintained under identical conditions in grow-out chambers (Joanen & McNease 1976) with control and experimental alligators from each clutch kept in the same chamber, and fed a dry pelletized commercial ration approximately five days a week. Alligators were weighed and measured approximately every three months during the pilot study, and every two months for the duration of the 2003–04 study.

A mixed model analysis of variance was used to test for effects of collection time on the length and

		Mass (g)			
		Hatching	**1 December 1999**	**28 February 2000**	**19 May 2000**
A	**Experimental**	39.20 +/- 1.17 (10)	225.30 +/- 9.74 (10)	638.90 +/- 57.91 (10)	1126.60 +/- 95.50 (10)
	Control	37.10 +/- 1.07 (10)	206.88 +/- 25.55 (8)	586.50 +/- 90.61 (8)	991.75 +/- 148.19 (8)
B	**Experimental**	46.60 +/- 1.72 (14)	281.36 +/- 10.40 (14)	765.07 +/- 34.86 (14)	1272.64 +/- 54.38 (14)
	Control	48.55 +/- 1.49 (13)	252.15 +/- 33.13 (13)	675.69 +/- 87.52 (13)	1131.23 +/- 145.44 (13)
C	**Experimental**	49.77 +/- 1.75 (14)	232.25 +/- 17.45 (12)	559.23 +/- 41.17 (13)	795.69 +/- 76.53 (13)
	Control	47.98 +/- 2.04 (16)	206.07 +/- 17.33 (15)	502.94 +/- 53.96 (16)	795.19 +/- 158.92 (16)
			Total Length (cm)		
A	**Experimental**	23.9 +/- 0.4 (10)	42.3 +/- 0.7 (10)	58.9 +/- 1.4 (10)	73.5 +/- 1.9 (10)
	Control	23.5 +/- 0.5 (9)	40.9 +/- 1.7 (8)	56.6 +/- 2.8 (8)	70.6 +/- 3.0 (8)
B	**Experimental**	25.7 +/- 0.4 (14)	46.4 +/- 0.6 (14)	63.2 +/- 1.0 (14)	77.5 +/- 0.9 (14)
	Control	26.3 +/- 0.3 (13)	44.2 +/- 2.6 (13)	60.2 +/- 2.6 (13)	74.3 +/- 3.5 (13)
C	**Experimental**	25.6 +/- 0.8 (14)	42.4 +/- 1.5 (12)	56.1 +/- 1.8 (13)	66.3 +/- 2.5 (13)
	Control	24.9 +/- 0.7 (16)	39.8 +/- 1.0 (15)	52.7 +/- 1.7 (16)	63.0 +/- 2.3 (16)

Table 1. Mass and total length (TL) of alligator hatchlings from a pilot study conducted 1999 - 2000. Values presented as mean +/- 1 SE (n). A, B, and C designate three specific clutches.

weight of alligators, using the individual nests as random blocks. Means are presented as +/- 1 SE. Results considered significant at $p < 0.05$.

RESULTS

In the initial pilot study in 1999–2000, two of the early half sets of eggs hatched three days prior to the eggs from the same clutch which were collected later in incubation; in the remaining clutch three additional days were required for the experimental group to hatch compared to the control group. In the expanded study of 2003–04, all the experimental half clutches collected early hatched sooner (one to six days earlier; average 3.5 days earlier for hatchlings to pip/emerge) than their control counterparts (late collected) from the same nest.

In the pilot study in 1999, at the time of hatching two of the three clutches produced hatchlings that were heavier and longer when collected earlier than their controls collected close to hatching (Table 1). However, when the alligators were again weighed and measured on 1 December, 28 February, and 19 May the experimental hatchlings were heavier and longer in all cases than their paired control clutch mates (Table 1). By the last measurement, the sets from clutch “C” had nearly equal masses, but the experimental early collected half averaged 3.3 cm longer than their controls. Of note, the SEMs for the final two measurements (particularly for mass) were often greater for the controls, suggesting the experimental groups collected early were more uniform in size with less occurrence of runting, wherein some animals are smaller than clutch mates and growth remains poor despite aggressive husbandry practices.

In the larger study involving six clutches, experimental hatchlings were heavier than their control clutch mates; similar results were seen when they were weighed on 27 October 2003 (Table 2). By 17 December the control alligators from clutch B slightly exceeded the mass of those from the experimental half (454 g vs. 449 g). Similar findings were noted for clutch B and clutch E at the final measurement on 16 February 2004; although the additional masses were only 19 g for clutch E and 36 g for clutch B. In the other four clutches, the experimental alligators were heavier than their control counterparts by masses of 7 g, 85 g, 102 g, and 167 g (Table 2).

In the 2003–2004 study, the TL of experimental hatchlings were longer at the initial time of

		Mass (g)			
		Hatching	27 October 2003	17 December 2003	16 February 2004
A	**Experimental**	45.73 +/- 0.79 (14)	211.57 +/- 13.62 (14)	454.78 +/- 43.32 (14)	815.93 +/- 94.89 (14)
	Control	43.14 +/- 1.24 (12)	193.08 +/- 13.85 (12)	441.08 +/- 30.55 (12)	808.75 +/- 60.03 (12)
B	**Experimental**	52.19 +/- 1.25 (17)	205.41 +/- 14.45 (17)	449.35 +/- 29.56 (17)	776.24 +/- 55.26 (17)
	Control	50.08 +/- 2.91 (13)	205.08 +/- 15.47 (13)	454.23 +/- 44.89 (13)	812.46 +/- 95.47 (13)
C	**Experimental**	53.79 +/- 0.97 (21)	255.29 +/- 10.63 (21)	547.52 +/- 33.12 (21)	920.43 +/- 70.85 (21)
	Control	50.91 +/- 1.68 (18)	232.39 +/- 18.42 (18)	489.94 +/- 42.33 (18)	835.39 +/- 81.69 (18)
D	**Experimental**	53.85 +/- 0.90 (16)	271.81 +/- 14.67 (16)	594.50 +/- 39.85 (16)	1156.50 +/- 83.64 (16)
	Control	51.26 +/- 0.98 (12)	231.27 +/- 9.61 (11)	517.27 +/- 31.01 (11)	989.09 +/- 50.83 (11)
E	**Experimental**	52.78 +/- 1.44 (23)	249.18 +/- 11.13 (22)	532.41 +/- 30.80 (22)	988.77 +/- 63.64 (22)
	Control	52.58 +/- 1.56 (22)	248.00 +/- 11.66 (22)	527.63 +/- 25.64 (22)	1007.82 +/- 40.85 (22)
F	**Experimental**	55.82 +/- 1.35 (11)	250.91 +/- 15.64 (11)	553.18 +/- 42.42 (11)	945.36 +/- 91.54 (11)
	Control	53.18 +/- 1.20 (8)	229.63 +/- 22.37 (8)	501.00 +/- 57.45 (8)	843.50 +/- 130.03 (8)

Table 2. Mass of hatchling alligators from six clutches of eggs, 2003–04. Values presented as mean +/- 1 SE (n). A - F designate six different clutches.

measurement as well as the third measurement (17 December 2003) in five of the six groups. In the other clutch the average lengths were the same whether collected early or late (Table 3, Clutch B). At the second measurement on 27 October 2003 the experimental sets had average totals lengths greater than their control clutch mates in all six cases. At the time of the final measurement, four of the experimental sets were longer than their controls for each clutch (Table 3, Figure 1).

Statistical analyses indicated there was a significant difference in weight between experimental and control collection ($p = 0.029$), with alligators from experimental eggs being heavier than those from control eggs. Similarly, there was a difference in average length of alligators obtained from experimental eggs as compared to the control counterparts ($p = 0.0072$) with greater lengths corresponding to experimental eggs collected and incubated early.

Figure 1. Two alligators from the same clutch of eggs that were raised under identical conditions. The larger alligator (right) was hatched from an egg that was collected early and incubated at optimum temperatures while the smaller alligator (left) was from an egg collected later, just prior to hatching, and exposed to fluctuating temperatures in a natural nest.

DISCUSSION

These results indicate that alligator size at hatching and post-hatching growth rates can be affected by the timing of egg collection, provided that maximum exposure time to optimum incubation temperatures is allowed. Early timing of egg collection might also allow egg ranchers to avoid natural mortality factors such as flooding (Platt *et*

		Total Length (cm)			
		Hatching	**27 October 2003**	**17 December 2003**	**16 February 2004**
A	**Experimental**	24.4 +/- 0.3 (14)	42.1 +/- 1.0 (14)	53.0 +/- 1.7 (14)	63.2 +/- 2.8 (14)
	Control	23.3 +/- 0.5 (12)	39.9 +/- 1.0 (12)	51.2 +/- 1.3 (12)	61.9 +/- 1.4 (12)
B	**Experimental**	25.2 +/- 0.5 (17)	42.6 +/- 1.1 (17)	53.6 +/- 1.4 (17)	63.6 +/- 1.5 (17)
	Control	25.2 +/- 0.5 (13)	42.2 +/- 1.0 (13)	53.6 +/- 1.6 (13)	64.0 +/- 2.1 (13)
C	**Experimental**	26.1 +/- 0.3 (21)	45.6 +/- 0.7 (21)	56.6 +/- 1.0 (21)	66.9 +/- 1.4 (21)
	Control	24.8 +/- 0.3 (18)	43.6 +/- 1.4 (18)	54.1 +/- 1.9 (18)	64.5 +/- 2.3 (18)
D	**Experimental**	26.0 +/- 0.4 (16)	46.0 +/- 1.0 (16)	57.8 +/- 1.5 (16)	70.6 +/- 1.9 (16)
	Control	25.2 +/- 0.3 (12)	43.1 +/- 0.5 (11)	54.7 +/- 0.9 (11)	67.2 +/- 1.3 (11)
E	**Experimental**	25.3 +/- 0.4 (23)	44.9 +/- 0.8 (22)	55.6 +/- 1.1 (22)	67.2 +/- 1.4 (22)
	Control	24.9 +/- 0.3 (22)	44.5 +/- 0.7 (22)	55.5 +/- 0.8 (22)	67.5 +/- 0.9 (22)
F	**Experimental**	25.6 +/- 0.4 (11)	44.8 +/- 1.2 (11)	57.0 +/- 1.7 (11)	67.2 +/- 2.4 (11)
	Control	25.2 +/- 0.4 (8)	42.4 +/- 1.8 (8)	53.6 +/- 2.7 (8)	63.4 +/- 3.7 (8)

Table 3. Total length (TL) of hatchling alligators from six clutches of eggs, 2003–04. Values presented as mean +/- 1 SE (n). A - F designate six different clutches.

al., 1995; Elsey *et al.,* 2006), predation, and lightning fires (Elsey & Moser, 2002), all of which are more likely to occur the longer the eggs are left in the field and exposed to these factors. Indeed, Platt *et al.* (1995) noted all alligator nests on his study site in southeastern Louisiana were lost to flooding from tropical storm Beryl in August 1988. We also received reports from several alligator ranchers noting losses of hundreds to thousands of alligator eggs from tropical storm Bill in late June/early July 2003 (Elsey, unpubl. data).

Accelerated growth of even a portion of an alligator rancher's crop could lead to a significant economic benefit for the business operation. The more rapidly an alligator reaches market size, the lower the costs incurred for continued heating, feeding, and labor for daily care and maintenance of the alligators. In Louisiana, alligator farmers must return a portion of juveniles back to the wild to the area from which wild eggs were collected, as part of a "head start" program (Elsey *et al.,* 2001). The larger the alligators are, the fewer that need be released to the wild to ensure recruitment. Thus, a few inches of additional growth could also allow Louisiana alligator farmers to complete their "release to the wild" obligations with fewer juvenile alligators, and allow them to harvest more for the valuable hides and meat (Elsey *et al.,* 2001). These juvenile alligators released to the wild have been shown to have accelerated growth rates relative to their wild counterparts (Elsey *et al.,* 2001), this may in part be due to optimal egg incubation temperatures under which they were incubated and maintained by the alligator farmer.

The large numbers of eggs collected by some commercial alligator farmers/ranchers necessitate that some eggs must be collected later in incubation, due to the relatively limited alligator nesting period (approximately 2–2.5 months). It is sometimes more efficient to conduct aerial helicopter surveys only when all nests have been constructed, rather than surveying too early, and missing nests yet to be constructed (for alligators in Louisiana, there is perhaps a two – three week period of time between the earliest and latest nests being completed). However, this study demonstrates the accelerated growth seen in hatchling and juvenile alligators simply by collecting eggs early (to maximize exposure time to optimum incubation temperatures) could be used to increase the profit margin in some commercial alligator ranches and avoid many natural mortality factors that limit nest success in the wild.

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