RESEARCH ARTICLE

The Effects of Hurricane Rita and Subsequent Drought on Alligators in Southwest Louisiana

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ABSTRACT Hurricane Rita struck the coast of southwest Louisiana in September 2005. The storm generated an enormous tidal surge of approximately four meters in height that inundated many thousands of acres of the coastal marsh with full strength seawater. The initial surge resulted in the deaths of a number of alligators and severely stressed those who survived. In addition, a prolonged drought (the lowest rainfall in 111 years of recorded weather data) following the hurricane resulted in highly saline conditions that persisted in the marsh for several months. We had the opportunity to collect 11 blood samples from alligators located on Holly Beach less than a month after the hurricane, but were unable to collect samples from alligators on Rockefeller Wildlife Refuge until February 2006. Conditions at Rockefeller Refuge did not permit systematic sampling, but a total of 201 samples were collected on the refuge up through August 2006. The blood samples were analyzed for sodium, potassium, chloride, osmolality, and corticosterone. Blood samples from alligators sampled on Holly Beach in October 2005, showed a marked elevation in plasma osmolality, sodium, chloride, potassium, corticosterone, and an elevated heterophil/lymphocyte ratio. Blood samples from alligators on Rockefeller Refuge showed increasing levels of corticosterone as the drought persisted and elevated osmolality and electrolytes. After substantial rainfall in July and August, these indices of osmotic stress returned to within normal limits. *J. Exp. Zool. 313A:106–113, 2010.* © 2009 Wiley-Liss, Inc.

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Alligators are known to avoid salt water, but are occasionally found many miles from shore in the Gulf of Mexico (Elsey, 2005). Unlike crocodiles, which can tolerate salt water because of their ability to excrete excess sodium through salt glands in the tongue (Taplin et al., '82), alligators (and caimans) become dehydrated when exposed to salt water. In addition, crocodiles are able to excrete more salt than alligators via the cloaca (Pidcock et al., '97). The skin of caimans is permeable to water and sodium (Bentley and Schmidt-Nielsen, '65, '66) and it is likely that the skin of the closely related alligators is similarly permeable. However, some populations of alligators (Birkhead and Bennett, '81) and caimans (Taplin, '88; Grigg et al., '98) are found in estuarine habitats.

Under laboratory conditions we have shown that young alligators (~1 kg body mass) exposed to less than 50% seawater exhibit elevated plasma osmolality, an increase in plasma corticosterone, and increases in plasma sodium and chloride

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and an inhibition of growth (Morici, '96; Lance et al., 2000). One-year-old alligators (~50 cm total length) in the laboratory cannot survive a salinity of 20 ppt (Lauren, '85). There is no information, however, on the physiological responses of alligators to salt water under natural conditions.

Hurricane Rita produced an enormous storm surge when it came ashore directly at Sabine Pass, the Texas/Louisiana border, in September 2005. Many thousands of acres of coastal marsh were inundated with full strength seawater. The freshwater marsh vegetation was destroyed, cattle, deer, and other mammals were killed, and a large number of alligators were killed, but an accurate estimate of the total number was not possible. Preliminary reports on the destructive effect of the storm surge on regional habitat and alligator populations have been described in detail in Elsey et al. (2006). Anecdotal information from observers who were able to get into the marsh reported seeing numbers of dead animals along the coast and numbers of alligators in poor condition.

Salinity measurements in the marsh taken by the staff (when conditions permitted) at Rockefeller Refuge showed unusually high levels persisting for several months. Under these conditions, areas of fresh water were scarce or unavailable to the resident alligators. The persistent high salinity resulted in extreme dehydration in many of these animals. This physiological stress was exacerbated by a lack of rain. One aspect of this stress was the lack of reproduction and nesting on the refuge in 2006. High salinity conditions continued until June. In July and August 2006, substantial rainfall was recorded and freshwater conditions were re-established. This unusual environmental situation provided a unique opportunity to study how alligators reacted to a severe osmotic stress in nature.

MATERIALS AND METHODS

This study is composed of two groups of samples; those collected within three weeks after the hurricane from adult-sized and sub-adult alligators found on Holly Beach, and a series of samples from sub-adult alligators collected opportunistically from February through August 2006 on Rockefeller Wildlife Refuge (see map, Fig. 1).

Holly Beach

Alligators at Holly Beach were captured during daylight hours with a locking cable snare. A burlap sack was placed over the eyes of the alligator and the mouth was secured closed with large elastic bands. Samples of approximately 10 mL of blood were collected from the spinal (Zippel et al., 2003) vein using 20 cc syringes and 3.8 cm 18 gauge needles. The samples were transferred to 6 mL Vacutainer™ tubes containing heparin, stored on ice, and transferred to McNeese State University (Lake Charles, LA). For the blood samples collected from alligators at Holly Beach, total and differential peripheral leukocyte counts were obtained. To attain total white cell values, whole blood was treated with Gram-Wright stain and leukocytes were counted using a hemocytometer. Differential leukocyte values were acquired by smearing fresh whole blood onto a slide and manually identifying and counting 200 leukocytes under 40 × magnification. Following centrifugation, the plasma samples were shipped to San Diego for osmolality measurements and electrolyte and corticosterone analysis.

Rockefeller Wildlife Refuge

The biologists at the Rockefeller Wildlife Refuge were able to collect a total of 201 alligator blood samples opportunistically

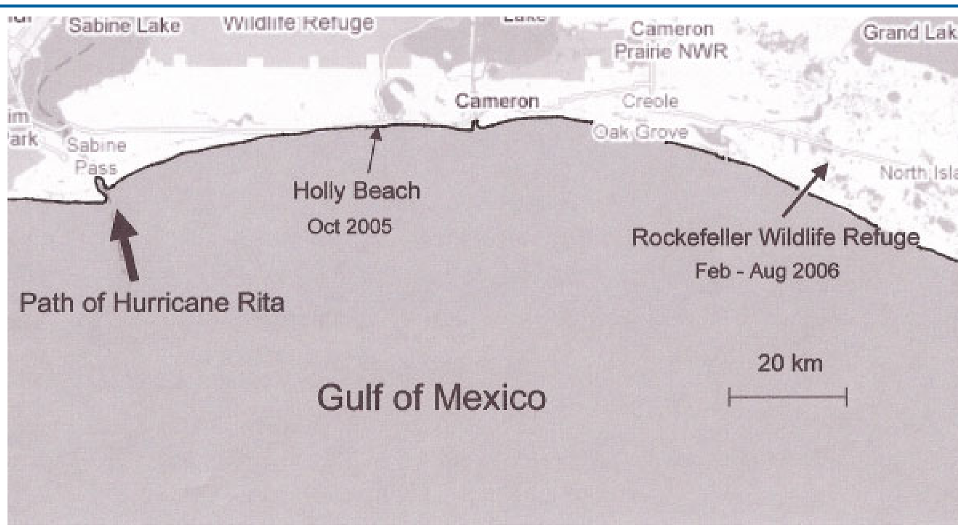

Figure 1. Map of coastal southwest Louisiana showing collecting sites and path of Hurricane Rita.

from February to August 2006. Rockefeller Wildlife Refuge encompasses some 29,380 hectares of coastal marsh. Joanen ('69) presented a detailed description of the predominant vegetation and the mixture of habitats within the refuge. The Louisiana coastal wetlands have been classified as fresh marsh, <2 ppt; intermediate marsh, 2–6 ppt; brackish marsh, 6–15 ppt; and saline wetlands, >15 ppt (Keddy et al., 2007). Alligators generally avoid saline wetlands but will feed and nest (but at a lower density than in fresh marsh) in brackish marsh.

The lack of a functioning infrastructure (no electricity, drinking water, functioning fuel stations, telephones, or gas, and many roads impassable) in the area for several months after the hurricane made systematic sample collection impossible. Alligators were caught opportunistically between February and August 2006; safety issues and mandatory curfews immediately after Hurricane Rita precluded earlier sampling.

Alligators on Rockefeller were caught mostly at night from airboats in shallow marsh habitat. Alligators were located by detecting the reflection from the retina with a powerful spotlight (Q-Beam®). A locking cable noose was then placed over the head and neck of the alligator, and the jaws secured with rubber bands. During daytime, alligators were caught by use of heavy fishing tackle, casting a treble hook to snare the alligator, and reeling it close to the bank and noosing the alligator as above.

Blood samples were collected in the field from the dorsal spinal vein (Zippel et al., 2003) using 10 cc heparinized syringes fitted with 18 gauge 3.8 cm needles and immediately placed on ice in the syringe until they were transported to the laboratory. All blood samples were collected within 10 min of capture. Plasma was separated from red cells (within one to three hours after sampling) in a clinical desktop centrifuge and stored at $-20°C$ for later hormone and electrolyte analysis. The blood plasma samples were sent to San Diego where corticosterone, sodium, chloride, potassium, and osmolality were measured.

Each alligator was marked by use of monel web tags (National Band and Tag Co., Newport, KY) placed between the toes, total length measured to the nearest centimeter and marked by removing a tail scute. Sex was determined by cloacal palpation/inspection and the alligator was released.

Hormone and Electrolyte Analyses

Corticosterone was measured in duplicate 50 μL plasma samples using an "Octeia" highly sensitive ELISA kit (Immunodiagnostic Systems Ltd., UK) designed for birds, but validated for alligators and other reptiles, following the manufacturer's protocol. Duplicate 50 μL samples of plasma were heat treated in a water bath at 80°C for 30 min to inactivate the corticosterone-binding protein that would interfere with the antibody–antigen reaction, and the cooled plasma then placed in an antibody-coated microtiter plate. After two hours, the reaction was stopped and a color reagent added. The resulting color reaction was then read on a micro-titer plate reader and the results calculated. Using this assay system accurate measurements of corticosterone concentrations from 0.1 to 30 ng/mL were obtained. Samples with hormone concentrations greater than 30 ng/mL were diluted and re-assayed.

Osmolality was measured using a vapor pressure osmometer (Wescor 5500 V.P.). Ten microliters of plasma was applied to an absorbent disc and placed into the instrument where vapor pressure was measured and an osmolality reading displayed. Each sample was measured twice.

Sodium and potassium were measured using a Perkin Elmer 3100 flame atomic absorption spectrometer. For sodium, 10 μL plasma samples were diluted 1:10,000 in distilled water and then measured at a wavelength of 589 nm. For potassium, 50 μL of plasma was diluted 1:200 and measured at a wavelength of 766.5 nm.

Chloride was measured in duplicate 50 μL plasma samples diluted in a color reagent (a mixture of ferric nitrate and mercuric thiocyanate) and absorption read in 1 cm diameter cuvettes in a spectrophotometer at 480 nm (Zahl et al., 1956).

Statistics

Monthly values for electrolytes, osmolality, and corticosterone were subjected to a one-way ANOVA.

RESULTS

Holly Beach

The results from the 11 blood samples collected from the Holly Beach alligators shortly after the hurricane are shown in Tables 1 and 2. Total white cell counts are elevated in 9 of the 11 samples, osmolality in 11, corticosterone in 9, sodium and chloride in all 11. Potassium was elevated in 10 of 11. It is likely that these alligators had been swept into the Gulf of Mexico and were attempting to return to the freshwater marsh after surviving a prolonged immersion in full strength seawater. Thirty-two dead

Table 1. Holly Beach alligators October 20, 2005.

I.D.	Sex	Length (cm)	Total WBC/mL	Het/lymph
HB-1	F	256.5	81,500	5
HB-2	F	180.3	93,000	3.5
HB-3	F	190.5	88,500	3.1
HB-4	F	231.1	98,000	3.6
HB-5	F	188.0	93,000	2.8
HB-6	F	175.3	57,500	1.4
HB-7	M	193.0	74,500	2.5
HB-8	F	167.6	81,500	2.3
HB-9	F	213.4	87,000	3.4
HB-10	M	180.3	12,500	2.6
HB-11	F	223.5	84,500	1.7
Normal			~60,000	~1.0

Table 2. Holly Beach alligators October 20, 2005.

I.D.	Osmolality (mmol/kg)	Corticosterone (ng/mL)	Sodium (mmol/L)	Chloride (mEq/L)	Potassium (mmol/L)
HB-1	388	7.67	231.9	198.6	7.88
HB-2	371	2.64	209.2	166.8	8.03
HB-3	424	25.62	223.8	179.8	7.95
HB-4	385	19.30	196.6	179.2	7.05
HB-5	454	19.82	247.3	198.6	8.25
HB-6	506	26.02	276.7	230.5	7.13
HB-7	336	4.95	185.4	172.7	7.05
HB-8	318	3.43	173.5	159.0	6.60
HB-9	348	2.10	193.2	169.4	7.65
HB-10	354	1.94	201.3	163.6	6.30
HB-11	348	0.27	196.4	172.7	7.43
Normal	290–310	1.00–2.00	~140.0	~120.0	4–6

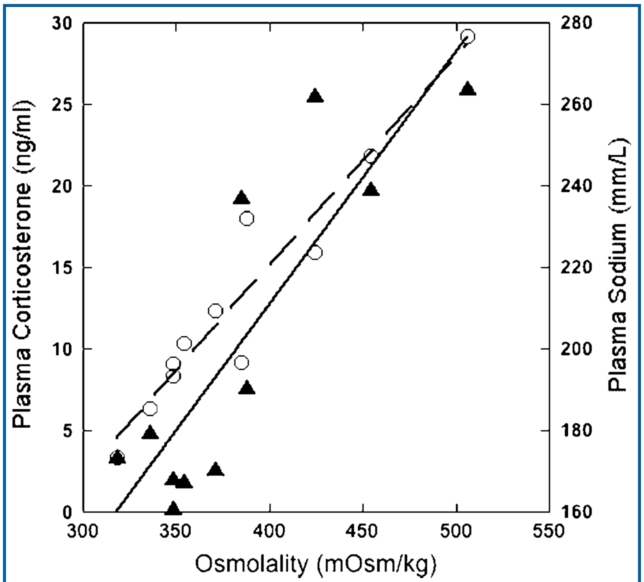

Figure 2. Plasma corticosterone and plasma sodium plotted against plasma osmolality for the samples collected at Holly Beach. Corticosterone values are represented by solid triangles and sodium by open circles. Slope for corticosterone (solid line) $y=-49.24+0.15488x$, $r^2=0.7367$ ($P<0.01$), slope for sodium (broken line) $y=14.43+0.5143x$, $r^2=0.9206$ ($P<0.01$).

alligators were counted in the vicinity (M. Merchant, unpublished). In Figure 2, osmolality values are plotted against plasma corticosterone and sodium. There is a highly significant correlation ($r^2=0.74$) of high corticosterone with elevated osmolality, and an even stronger relationship is seen with sodium ($r^2=0.92$). Chloride was also elevated and the relationship to osmolality was significant, but not as strong as that of sodium (Table 2). The osmolality values for samples HB 1, 3, 4, 5, and 6 are the highest recorded for this species. These extreme osmolality numbers were associated with elevated corticosterone levels and extremely high sodium and chloride. The principal component of the osmotic pressure appears to be sodium. The heterophil/lymphocyte ratios were also elevated (Table 1) in these alligators.

Rockefeller Refuge

On Rockefeller Refuge, 201 blood samples were collected (64 males and 130 females and 7 unidentified). Total body length ranged from 61 to 243.8 cm, mean 122.4±2.3 cm, $n=195$ (the length of six animals was not recorded).

In Figure 3, the monthly rainfall totals at Rockefeller Refuge from February to August 2006 and the corticosterone monthly means are shown. A rainfall total at Rockefeller Refuge for January 2006 was not available, but at Lake Charles, 80 km to the north, 4.87 cm were recorded (the January average for Lake Charles is 14.02 cm). Only a single alligator blood sample was collected in June 2006 so a mean value is not plotted for that month. There was an association of high corticosterone, high sodium, high chloride, and high osmolality levels with lack of rain. The single sample from an emaciated female alligator collected in June 2006, at the peak of the drought, had the highest ever corticosterone value (36.2 ng/mL) recorded from a wild alligator. The osmolality and plasma sodium values for this sample (431 mmol/kg and 202.4 mmol/L, respectively) were also extremely high. There was no difference between the sexes for corticosterone or osmolality, but in the May sample larger individuals had significantly lower ($P<0.01$) corticosterone than smaller animals (Fig. 4). When the monthly values of plasma corticosterone and plasma osmolality are plotted (Fig. 5), the highest values for both are seen in April and May after several months of drought. Similar to what was seen with the Holly Beach samples, there was a strong association with plasma sodium and osmolality in a large sample collected in May 2006 (Fig. 6).

The plasma electrolyte values are presented in Table 3. There was a highly significant rise ($P<0.01$) in all components during

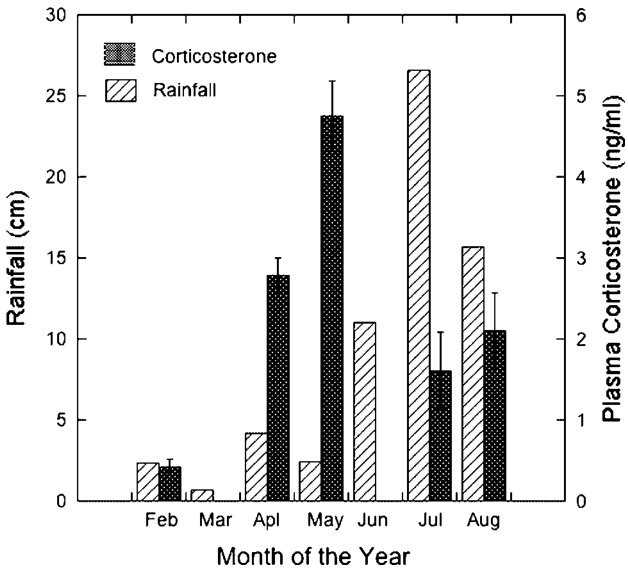

Figure 3. Monthly rainfall totals in 2006 at Rockefeller Refuge and monthly mean plasma corticosterone values. Standard error of the means (SEMs) for corticosterone is shown by the bars above and below the means.

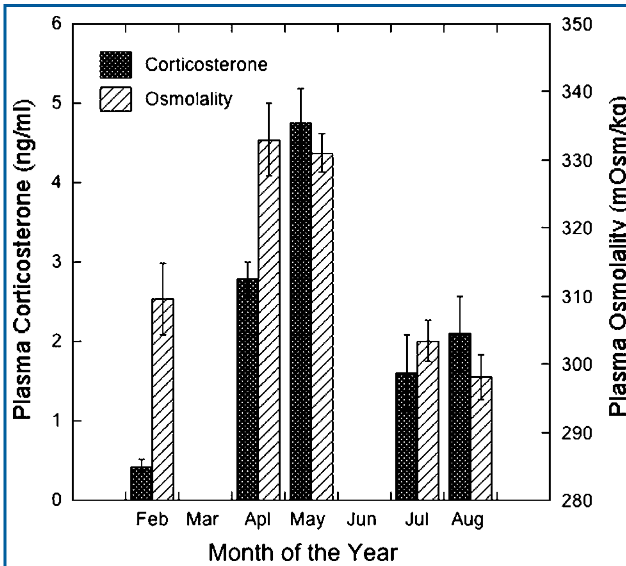

Figure 5. Monthly mean plasma corticosterone and plasma osmolality for alligators collected on Rockefeller Refuge during 2006. SEMs are represented by the bars above and below the mean values.

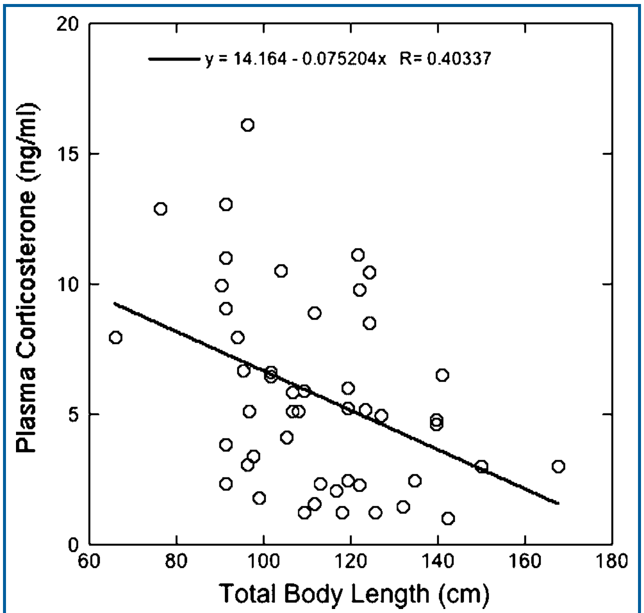

Figure 4. Plasma corticosterone plotted against total body length for samples collected on May 23, 2006 ($P<0.01$).

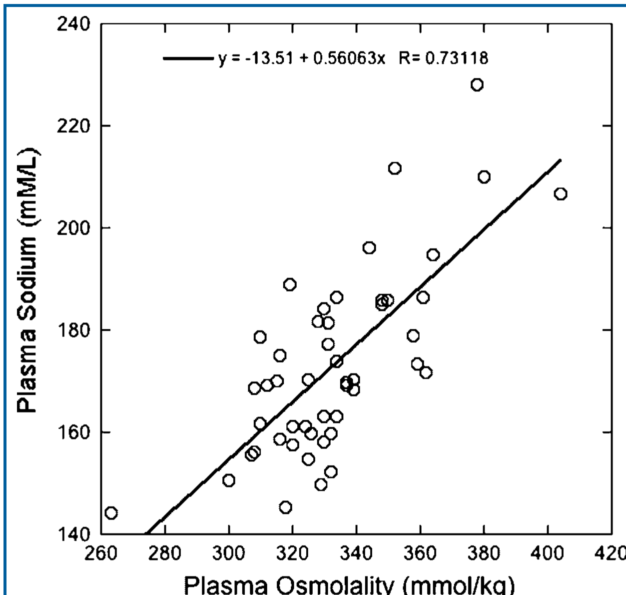

Figure 6. Alligator plasma sodium plotted against plasma osmolality for the May 23 sample ($P<0.01$).

April and May and a decline in July and August, but all remained slightly above baseline (baseline values are shown in the last row of Table 2). There were no differences between the sexes for any electrolyte.

DISCUSSION

The alligators sampled on Holly Beach showed all the physiological indices of severe stress; osmolality, sodium, and corticosterone were extremely high. These animals were in poor

Table 3. Alligator plasma electrolytes in 2006.

Month	Sodium	Chloride	Potassium
February	127.9+3.8 ($n=33$)	145.4+2.6 ($n=33$)	4.71+0.11 ($n=33$)
April	142.5+4.3 ($n=24$)	166.2+4.4 ($n=24$)	6.54+0.25 ($n=24$)
May	172.9+2.2 ($n=73$)	164.0+2.2 ($n=73$)	6.73+0.18 ($n=73$)
July	168.8+3.8 ($n=41$)	144.0+3.0 ($n=41$)	5.76+0.13 ($n=41$)
August	156.8+4.2 ($n=29$)	145.6+3.2 ($n=29$)	5.79+0.14 ($n=29$)

physical condition, some close to death. Lymphocyte numbers are depressed in reptiles under stress, whereas heterophil values remain unchanged (Aguirre et al., '95; Lance and Elsey, '99). The alligators on Holly Beach had heterophil/lymphocyte ratios of greater than two (Table 1), indicating that these alligators had been under severe stress prior to the time the blood samples were collected.

This study has demonstrated that alligators are susceptible to hyperosmotic stress under certain conditions in nature, and that they show the same responses as alligators subjected to salt water under laboratory conditions.

Alligators and caimans lack salt glands and, unlike crocodiles, are unable to adapt to salt water, but alligators are often found in intermediate marsh (salinity 2–6 ppt, Keddy et al., 2007). In fact, growth rates for alligators in intermediate marsh are greater than those in fresh water marshes (Rootes et al., '91). In captivity at 5 ppt seawater alligators thrived, but at a salinity of 10 ppt and above, they lost weight and showed elevated stress hormone levels (Lauren, '85; Morici, '96). Three "unusually fat and healthy" alligators from 122 to 152 cm total length were caught in salt water in Key West, Florida (Allen and Slatten, '45) and alligators have been observed in an estuary in North Carolina at a salinity of 24 ppt (Birkhead and Bennett, '81), but physiological data on these animals were not available. Wild populations of adult *Caiman latirostris* in southern Brazil were observed feeding in an estuary at 24 ppt without exhibiting any change in plasma osmolality; however, these same animals lost body weight when held in water at 33 ppt for 72 hr, and caiman less than 1 kg body mass were found only upstream in fresh water (Grigg et al., '98). The distribution of the American alligator in the coastal wetlands of Louisiana, however, often results in this population being exposed to unusually high salinities. When a large amount of salt water comes into the freshwater marshes during hurricanes, newly hatched alligators with extremely thin skin are subjected to an extreme osmotic stress and many die. Under laboratory conditions, small alligators died when exposed to 20 ppt seawater for two weeks (Lauren, '85). Larger alligators have a less permeable skin (Davis et al., '80) and are thus able to resist short-term exposure to seawater (e.g. Elsey, 2005). In our May sample at the height of the drought (Fig. 4), an effect of size was evident, even though these animals were less than 2 m total length. Under natural conditions, however, when hurricanes bring salt water into the coastal marshes, there is some mortality, but alligator populations as a whole seem relatively unaffected (Ensminger and Nichols, '57).

The freshwater crocodile of Australia, *Crocodylus johnstoni,* is known to undergo a period of dormancy or estivation during dry periods. Christian et al. ('96) reported that even after three months of estivation plasma osmolality had a mean of 310 mOsm/kg and plasma sodium a mean of 146 mmol/L in a population of *C. johnstoni* studied under natural conditions. The authors concluded that even after this long period without access to water, the crocodiles were not dehydrated, but did lose body mass. Estivating crocodiles had a slightly lower metabolic rate than actively feeding crocodiles, but did not appear to have any special adaptations for surviving drought conditions. The crocodiles were able to tolerate these dehydrating conditions by covering themselves with mud and hiding deep in holes, keeping cool and preventing water loss through the skin. The salt glands did not appear to be involved in this behavioral response to drought (Christian et al., '96).

Behavioral observations of alligators in Texas during drought (Hayes-Odum and Jones, '93) indicated that they do much the same as *C. johnstoni*, they stop feeding and stay within their dens. Similar behavior has been observed in Louisiana during drought; alligators travel long distances (up to several kilometers) in search of fresh water or stay within dens (Elsey et al., 2008a). Following Hurricane Rita, the alligators in Louisiana were subjected to a different form of dehydration stress in which it was impossible to avoid the salt water, thus the usual behavioral means of surviving drought were unavailable. The salinity in the marsh at Rockefeller Refuge, however, was not uniformly high, pockets of water with salinities of less than 10 ppt were seen close to areas of where the salinity was 24 ppt, even at the height of the drought in May. A few animals were thus able to avoid severe dehydration and maintain a relatively low plasma osmolality (and low corticosterone). Nonetheless, the lack of fresh water inhibited reproduction in this population. No nests were seen on Rockefeller Refuge in June 2006, the peak of the nesting season in southwest Louisiana.

Other crocodilian species have been reported to undergo estivation in long periods without rain, but there are no physiological data available. It would be particularly interesting to compare the physiological response of a caiman that estivates (Campos et al., 2006) with that of the Australian freshwater crocodile during prolonged dry spells.

In laboratory experiments we have previously shown that subjecting immature alligators to a series of different salinities resulted in elevated plasma electrolytes, elevated plasma osmolality, and elevated corticosterone (Lance et al., 2000). Our data on alligators in high salinities following Hurricane Rita nicely complement laboratory studies and clearly show that salt water results in extreme stress in alligators.

Abercrombie et al. (2001) discuss the life history strategy of alligators in environments that can alter radically in unpredictable ways. They state that, "Perhaps the basic alligator demographic strategy is to transcend habitat fluctuations by means of large, almost invulnerable adults." This strategy is constrained by a greatly protracted time to maturity, and a high pre-adult mortality, but is offset by the production of large numbers of offspring over the years following a catastrophic event. Following a major disruptive event such as hurricane, there is likely a high mortality of juvenile alligators, but many sub-adults and adults, especially reproductively active individuals, survive.

The coastal wetlands of Louisiana have experienced many hurricanes and many inundations by salt water in the past. Despite some mortality during these events, alligator populations have proved to be extremely resilient. Generally, when a hurricane comes ashore in the wetlands of southwest Louisiana it is followed by heavy rain, so saline conditions rarely persist. Following Hurricane Rita, there was a record-breaking drought creating an unusual situation in which fresh water was unavailable to most of the surviving alligators. Once fresh water conditions were restored, the alligators rapidly regained body condition and within months were capable of reproducing. A nice example of this ability of alligator population to recover following a devastating hurricane was seen in 2007. In 2006, there was little or no nesting on Rockefeller Refuge, whereas in 2007, nesting was higher than normal (Elsey et al., 2008b). In the case of Hurricane Rita, mortality numbers were impossible to estimate, but in the year following the hurricane and subsequent drought, large numbers of nests were seen.

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