Sexual Maturity in Male American Alligators in Southwest Louisiana

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Abstract. Very little is known about the attainment of puberty in reptiles. In the American alligator (*Alligator mississippiensis*) males are assumed to be sexually mature at about 1.8 m in total length, but it is not clear at what size they produce testosterone, spermatozoa and mate successfully. We re-examined this question by studying plasma testosterone levels in blood samples from a large sample of alligators (~1,500) collected every month of the year and ranging in size from approximately 61 cm (2 ft) to 360 cm (11.5 ft). Testosterone values ranged from 0.05–115.41 ng/mL. All size classes of alligators exhibited a seasonal cycle in testosterone levels, but the concentrations were size-dependent: the larger the alligator the higher the testosterone. In all size-classes testosterone reached a peak in the breeding season (March–May). Mean testosterone in the largest size-class during breeding was 75 ng/mL whereas in the smallest size-class peak testosterone was less than 3 ng/mL. The smallest size-class (59–89 cm) showed an additional rise in testosterone in late summer. The attainment of sexual maturity in alligators appears to be closely associated with growth and is a gradual process lasting several years. Sexually immature alligators show a seasonal pattern of testosterone secretion similar to that of adults, but the values are significantly lower.

Keywords. American alligator; Sexual maturity; Testosterone.

INTRODUCTION

Very little is known about the endocrinology of sexual maturation in reptiles, but in mammals there is a substantial body of research on the subject (Ebling, 2005; Plant and Wichel, 2006). In juvenile mammals the gonads are relatively quiescent and circulating reproductive pituitary and gonadal hormones remain low, but at the approach of puberty there is an increase in pulsatile gonadotropin-releasing hormone (GnRH) secretion from the hypothalamus, an activation of the gonadal-pituitary-hypothalamic axis and a rapid attainment of fertility (Ebling, 2005). There is no evidence for such a rapid onset of sexual maturity in reptiles; the data suggest rather that there is a slow, gradual attainment of fertility (see below).

In the Louisiana population of the American alligator (*Alligator mississippiensis* Daudin, 1802), males are assumed to be sexually mature at about 1.83 m in total length and 10–12 years of age (Joanen and McNease, 1980). The size and age at which alligators reach sexual maturity, however, is dependent on where they live. In the Everglades of southern Florida for example, female alligators are reported to be sexually mature at about 1.5 m and 14–18 years of age (Jacobsen and Kushlan, 1989; Dalrymple, 1996; F. Mazzotti, personal comm.), whereas in central Florida, growth rate and sexual maturity are similar to what has been reported for southwest Louisiana (Hines et al., 1969). At the northern extreme of its range, male alligators may reach sexual maturity at about 1.84 m and 15–16 years of age (Klause, 1983; Wilkinson and Rhodes, 1997). Murphy and Coker (1983), however, reported that in a sample of 251 male alligators caught in North Carolina, "no male alligators less than 2.2 m (7 ft) in total length were found to have sperm present" [in the penile groove].

The reason for these population differences in the number of years to reach sexual maturity is ambient temperatures during the "growing months", i.e. when the temperature is above 16°C and alligators are able to metabolize food and grow rapidly (Chabreck and Joanen, 1979). A second factor is the quality of the habitat, i.e. availability of food (Lance, 2003). In southern Florida the temperature rarely goes below 16°C, but the food resources are sparse (Dalrymple, 1996); hence, alligators in this region grow slowly and reach sexual maturity at a smaller size than in more northern regions where resources are abundant.

Joanen and McNease (1980) based their estimate of size at sexual maturity on the presence of semen in the penile groove from a sample of 14 alligators over 1.83 m in length caught during the mating season between April and June. However, it was not clear how many of these alligators were much larger than this estimated minimum size, or how many close to this size, but at least three were over 2.44 m in length.

We re-examined this question by studying plasma testosterone levels in blood samples from a large sample of alligators (~1,500) collected in every month of the year over a three-year period, and ranging in size from 61–360 cm total length.

MATERIALS AND METHODS

The study was carried out on Rockefeller Wildlife Refuge, a coastal marsh in southwestern Louisiana encompassing some 29,380 ha of fresh, intermediate, brackish and saline habitats that supports one of the densest populations of alligators in the USA. Alligators were caught by several different methods: at night from boats with outboard motors in canal habitat, or from airboats in shallow interior marsh habitat, by approaching the alligator after locating the characteristic reflective eye-shines with a powerful spotlight (Q-Beam®). A cable noose was then placed over the head and neck of the alligator, and the jaws secured with large rubber bands. In larger animals a second noose was used to secure the jaws before rubber bands were applied. During daytime, alligators were caught by use of heavy fishing tackle and casting a treble hook to snag the alligator, and reeling it close to the bank or beside an outboard and noosing the alligator as above. Each alligator was marked by use of monel web tags placed between the toes, measured to the nearest cm, and marked by removing a tail scute. Sex was determined by cloacal palpation (Joanen and McNease, 1978) before releasing the alligators at the capture site.

Blood samples were collected in the field from the dorsal spinal vein (Zippel et al., 2003) using heparinized syringes (10 cc) fitted with 18 gauge 3.8 cm needles. The syringes containing the blood were immediately placed on ice until they were transported to the laboratory. All blood samples included in the analysis were collected within 10 min of capture to avoid stress-induced suppression of testosterone secretion (Lance and Elsey, 1986; Lance et al., 2004). If a blood sample took longer than 10 min to collect it was not used in the analysis. Plasma was separated from red cells (within one to three hours after sampling) in a clinical desktop centrifuge and stored at -20°C. The blood plasma samples were shipped frozen to San Diego for hormone analysis.

Data on paired testicular mass from samples collected from adult male alligators during the breeding season at Rockefeller Refuge over the past 30 years were also used (Joanen and McNease, 1980; Lance, 1989; Lance and Elsey, unpublished data).

Hormone analysis

Duplicate 100 µL plasma samples (samples with concentrations greater than 4 ng/mL were diluted and re-assayed) were extracted in 2 mL of an ethyl acetate-hexane mixture (3:2) by shaking for 30 s on a vortex mixer (Lance and Elsey, 1986). The tubes were then snap-frozen in a dry-ice-methanol mixture, the organic phase decanted into 12 × 75 mm disposable glass tubes and evaporated to dryness under a stream of filtered air in a 37°C water bath. To the dry tubes 500 µL of PBS (phosphate-buffered saline w/0.1% gelatin; pH = 7.0) was added and the tubes were shaken for 30 s. Tritiated testosterone (~10,000 cpm) in 100 µL PBS and 100 µL antibody (ICN, Costa Mesa, CA) in PBS were added and the mixture was allowed to equilibrate overnight at 4°C. Unbound steroids were removed by addition of 250 µL of a dextran-charcoal mixture (6.25 g charcoal, 0.625 g dextran in 100 mL PBS) and allowed to sit for 30 min at 4°C. Following centrifugation at 8°C for 15 min and 3,000 rpm the supernatant containing the bound fraction was decanted into glass scintillation vials, 5 mL scintillation fluid added, and the radioactivity measured in a Beckman liquid scintillation counter, LS 6500.

RESULTS

Alligators in Louisiana grow at a rate of about 30 cm/year for the first six years of life until they reach a total length of approximately 1.8 m (McIllhenny, 1934; Chabreck and Joanen, 1979). The rate of growth for both males and female slows dramatically at this time, but the rate of growth differs thereafter; males grow at a faster rate than females and achieve a greater total length (Joanen and McNease, 1980).

We divided the samples into size classes by 30 cm intervals up to 1.8 m approximating the first six years (our smallest size class, 59–89 cm consists of alligators of approximately two years of age). As samples from alligators greater than 2 m are far less common than from smaller size classes these data were combined. Testosterone values ranged from 0.05–115.41 ng/mL. All size classes of alligators exhibited a seasonal cycle in testosterone levels, but the concentration was size-dependent: the larger the alligator, the higher the testosterone. In all size-classes testosterone reached a peak in the breeding season (March–May; see Figs. 1–5). Getting accurate hormonal data from very large males, however, is difficult. Not only are large males uncommon, but also getting a blood sample within 10 min is often impossible. The time to restrain an alligator that can weigh > 200 kg will often take up to 20 min, even with an experienced crew; thus, the stress to the animal suppresses circulating testosterone levels (Lance and Elsey, 1986; Lance et al., 2004). We did, however, get seven samples from alligators from 214–244 cm total length within the 10 min limit that showed a mean testosterone level of 43.8 ng/mL. Mean testosterone in the largest size class (< 214–244 cm) during breeding was 75 ng/mL, whereas in the smallest size-class peak testosterone was < 3 ng/mL. The smallest size class (59–89 cm) showed an additional rise in testosterone in late summer (Figs. 1–5). Paired testis mass vs. total body length for sexually mature alligators are plotted in Figure 6.

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DISCUSSION

The remarkable similarity in the patterns of testosterone levels among sexually mature and immature alligators during the annual reproductive cycle is surprising and suggests that these juveniles are responding to the same environmental cues as the adults (and probably secreting GnRH and gonadotropins) but are not capable of producing spermatozoa. The secondary rise in testosterone in late summer in the 59–89 cm group is difficult to explain (none of the other groups showed any similar

rise in testosterone) but might be due to the growth spurt that occurs during the warmer months in alligators of this size (Chabreck and Joanen, 1979; Joanen and McNease, 1980). There is a gradual increase in circulating testosterone levels with increase in body size, an increase in paired testis mass (and presumably an increase in the Leydig cell population), but no evidence, as far as we can tell, of a sudden increase in these parameters around sexual maturity. We are not sure if our findings of a long, slow increase in testosterone applies to saurians (snakes and lizards), but it does seem to apply to the other extant archosaurs, the
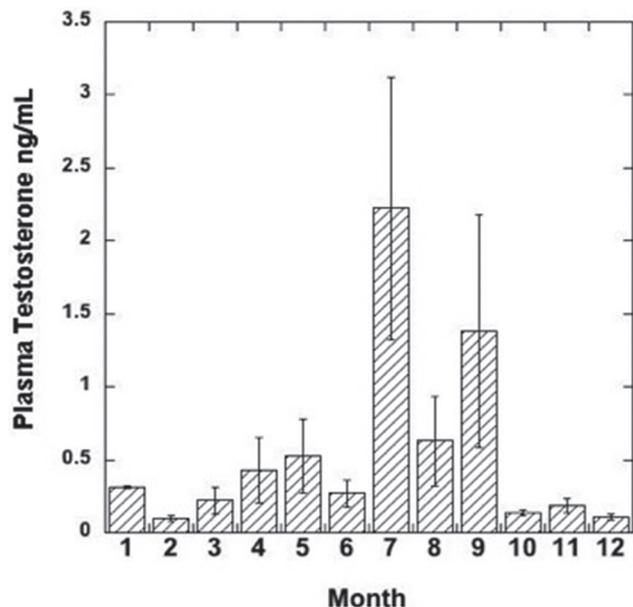

Figure 1. Plasma testosterone concentrations in the 2 ft (59–89 cm) size class.
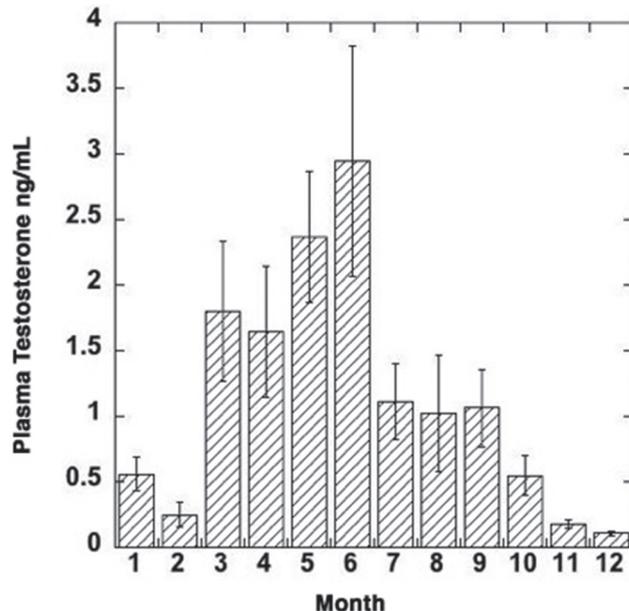

Figure 2. Plasma testosterone concentrations in the 3 ft (90–119 cm) size class.
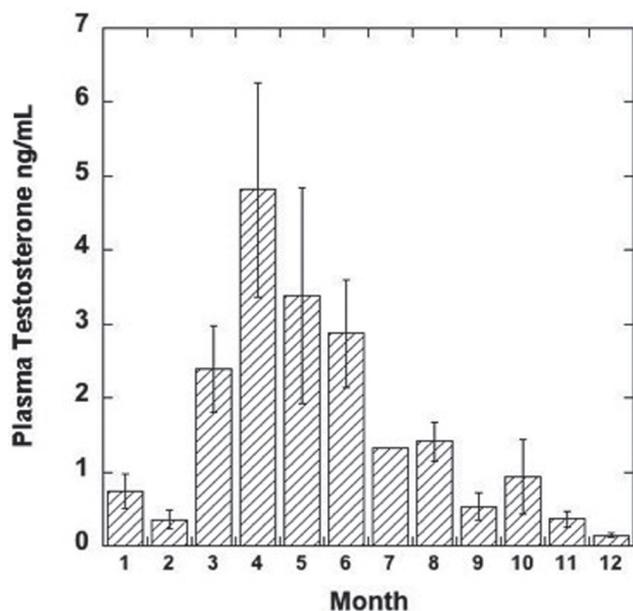

Figure 3. Plasma testosterone concentrations in the 4 ft (120–150 cm) size class.
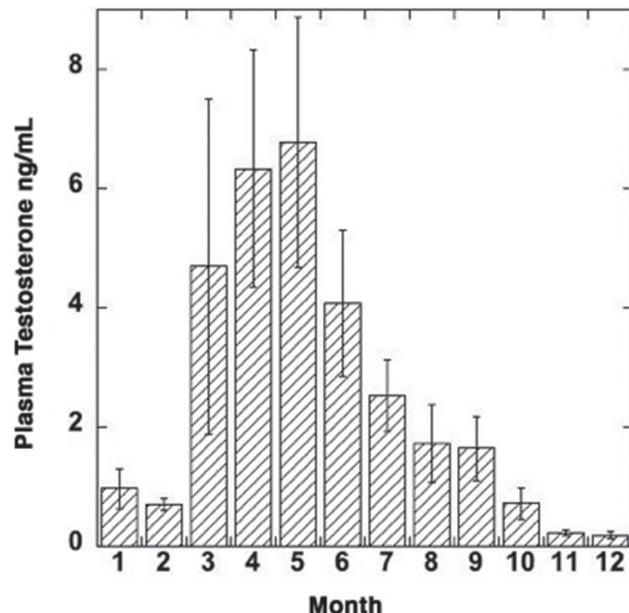

Figure 4. Plasma testosterone concentrations in the 5 ft (151–180 cm) size class.

birds. It is difficult to compare an animal in which it takes 10–12 years to reach sexual maturity with an animal in which it takes less than year, but a recent study looking at the onset of puberty in domestic ducks showed a similar, gradual increase in plasma testosterone during the weeks prior to sexual maturity in males (Yang et al., 2005). Birds, however, do exhibit the pulsatile secretion of GnRH from the hypothalamus at the approach of the breeding period that is characteristic of mammals (Vizcarra et al., 2004). Given the close relationship of birds and crocodilians, it is likely that a similar pulsatile secretion of GnRH occurs in alligators, but attempting to answer this question at present is almost impossible, as restraint of wild alligators results in an immediate shutdown of the reproductive system (Lance and Elsey, 1986; Lance et al., 2004).

While we are aware that our estimates of the age of the alligators in this population for the first six years of life are not exact, as growth among different animals can vary, our ability to age alligators over 1.8 m in length, and thus follow sexual maturation up to ten years, is even less certain. The use of counting bone growth rings in histological cross sections of femurs or from sections taken from the dorsal bony scutes can give reasonable estimates for male crocodilians up to about 10 years of age (Buffrénil, 1980; Hutton, 1986), but is far less accurate for adult females and males of greater age because of bone remodeling (Woodward et al., 2011).

Male alligators in Louisiana reach sexual maturity between 10–12 years of age (Joanen and McNease, 1980). As body mass increases, testis mass increases and circulating testosterone shows a correlated increase. Very large mal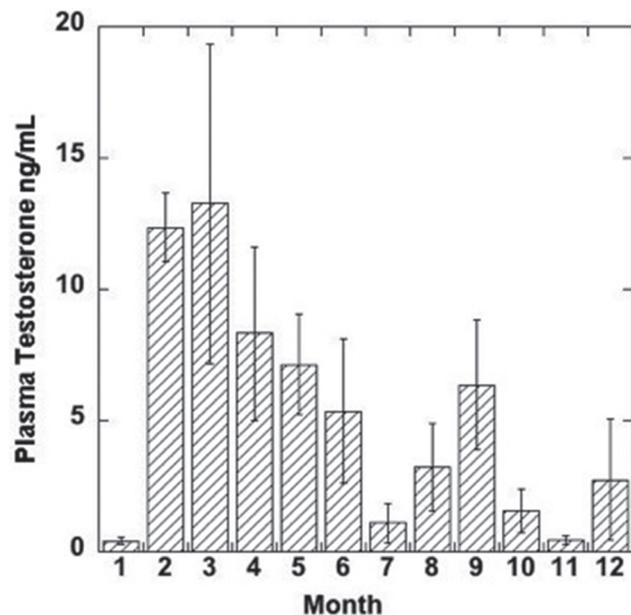es, up to 3.5 m in length, have the greatest paired testis mass (ca. 400 g) and, during the breeding season, the highest circulating testosterone levels (> 100 ng/mL; Lance, 1989). Despite variability due to the dissection techniques of different investigators in different years, body length and testis mass showed a robust, positive correlation (Fig. 6).

In southern Louisiana, some alligators at about 1.8 m in length are able to produce spermatozoa, but it was supposed unlikely that animals of this size mate successfully (Joanen and McNease, 1980). Larger males are known to drive smaller males away from females. However, recent observations of nocturnal behavior of alligators during the mating season have documented large mixed-sex assemblies of up to 80 animals (Dinets, 2010). Female alligators have been observed mating with more than one male in captivity (LeBuff, 1957) and multiple paternity has been documented in this population, in some cases up to three males contributed to a single clutch (Davis et al., 2001; Lance et al., 2009); therefore, the possibility that some of these smaller males succeed in mating cannot be ruled out.

Southern Florida alligators grow more slowly than do alligators from more northern populations having shorter growing seasons (Fogarty, 1974). Jacobsen and Kushlan (1989) suggest that higher metabolic costs, due to a higher ambient temperature and fewer available prey items in the Everglades, is responsible for the slower growth rates in this population.

Plasticity in size and age at sexual maturity is a well-known phenomenon among turtle populations (Tinkle, 1961; Gibbons et al., 1981) and is also well documented in crocodilians (Jacobsen and Kushlan, 1989; Lluch et al., 2004; Pitman, 1941; Shine et al., 2001; Webb, 1985). The

Figure 5. Plasma testosterone concentrations in the 6 ft (181–211 cm) size class. Note the different range of values in the x axis, from zero to 3.5 ng/mL in the 2 ft (59–89 cm) size class to 20 ng/mL in the 6 ft (181–211 cm) size class.
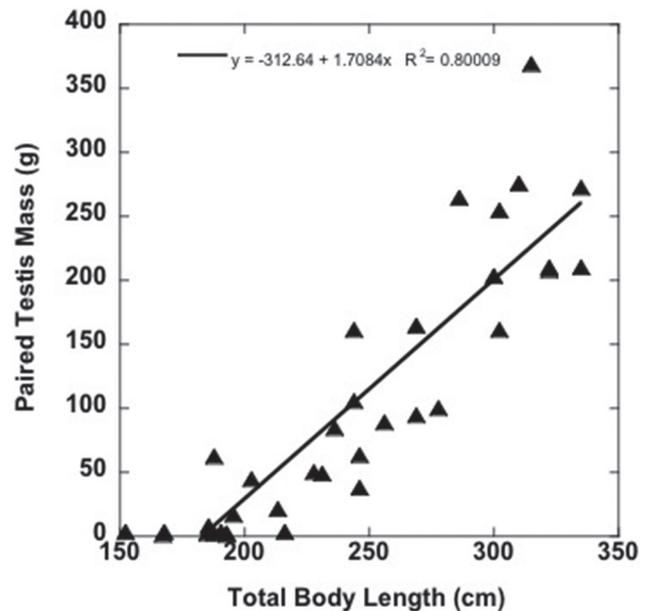
Figure 6. Relationship of paired testis mass to total body length in adult alligators.

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physiological mechanism for delayed sexual maturation and/or maturation at small size is unclear, but delayed sexual maturity at greater size occurs in most heterotherms inhabiting cooler environments (Berrigan and Charnov, 1994). Thus, alligators in the northern extreme of the range attain sexual maturity at a much larger size, and greater age than those in the southern part of the range. Theoretical ecologists have developed models for such variation, but these models lack physiological explanations (Stearns and Koella, 1986; Berrigan and Charnov, 1994; Barot et al., 2004).

Male and female crocodilians raised in captivity, provided warmth during the cooler months, and given free access to food attain sexual maturity several years earlier than animals in the wild (Joanen and McNease, 1975, 1980; Lance, 1989, 2003), suggesting that the accelerated increase in body mass is responsible, but how this increase in mass is detected by the hypothalamus and thus speeds up sexual maturation is unknown. In mammals, an increase in leptin secretion from fat deposits at puberty is involved in turning on the hypothalamo-hypophysial-gonadal axis (Henson and Castracane, 2003). A leptin-like molecule has recently been identified in birds and alligators (Prokop et al., 2014), but data on circulating levels of leptin during the reproductive cycle of alligators are not yet available.

The eventual attainment of sexual maturity by crocodiles living in extreme environments at very small body size and with reduced fat depots is difficult to explain. These animals mature slowly and produce much smaller clutches and smaller eggs than populations in more favorable habitats. A pristine population of the Australian freshwater crocodile, *Crocodylus johnstoni* Krefft, 1873, was discovered in the upper reaches of the Liverpool River, Arnem Land, Australia (Webb, 1985). The author remarked on the reduced size and poor body condition of adults of this population as compared to the same species in other parts of its range. This population also produced significantly smaller clutches than other populations (a mean of six versus 13.2 ± 3.2 for this species). In the Sahara (or the Sahel) there are isolated remnant populations of *Crocodylus niloticus* Laurenti, 1768, living in permanent bodies of water and ephemeral wetlands (Duveyrier, 1864; Pellegrini, 1911; Gautier, 1928; Joleaud, 1933; Le Berre 1989; de Smet, 1998; Lluch, 2001; Shine et al., 2001; Lluch et al., 2001). Maximum size attained by these crocodiles is stated as about 2 m, as compared to the 5 and 6 m of Nile crocodiles in other parts of Africa (Le Berre, 1989), although Gautier (1928) claimed that "The crocodiles do not exceed a meter in length." Gautier (1928) continues, "...but this reptile, so formidable in the Indies, is a languid and inoffensive creature in the Sahara." P. Lluch (personal comm.) stated that the Saharan crocodiles he had seen were good condition. The small size of these crocodilians is also associated with small eggs and

small clutches, but how many eggs in a clutch or egg size was not recorded (Shine et al., 2001; Hemmo Nickel personal comm.). There is evidence from molecular studies that these isolated populations of crocodiles are actually a separate species (Hekkala et al., 2011).

Other populations of Nile crocodiles with reduced adult body size have also been described. Pitman (1941) reported that dwarf races of *Crocodylus niloticus* occurred in Eastern Uganda with an adult size < 2 m, but with heads of 30 cm. He hypothesized that the small size of these animals was due to seasonal drying up of these rivers and the fact that they spent much of the time in deep cavities without food or water. These emaciated-looking crocodilians living on the edge are believed to reach sexual maturity at a much greater age than crocodilians living in relatively benign habitats. Le Berre (1989) stated, however, that the crocodiles in the Sahara attained sexual maturity in 12–15 years of age, but how he arrived at this estimate was not explained.

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