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Reproductive Cycle of the American Alligator¹

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SYNOPSIS. The reproductive cycle of the American alligator, *Alligator mississippiensis*, was studied using blood and tissue samples from wild alligators, and blood samples drawn from a captive breeding stock at the Rockefeller Wildlife Refuge in Louisiana. Generally the cycle commences in March as air and water temperatures increase. By early April the seminiferous tubules are full of actively dividing spermatocytes and maturing spermatozoa. Testis mass is greatest at this time and plasma testosterone is at a peak (>50 ng/ml), but mature spermatozoa do not appear until late April and mid May when mating takes place. Plasma testosterone levels decline rapidly in June after spermiogenesis, and are low to nondetectable in July and August when the testes are fully regressed. A second small peak in testosterone occurs in September without any obvious changes in testicular histology. In the female a similar temperature dependent initiation of the ovarian cycle occurs in late March. Plasma estradiol levels reach a peak (>600 pg/ml) in mid April, and ovarian follicles increase from 3 mm to 4.5 mm in diameter at ovulation in May. Plasma testosterone is also high in preovulatory females (ca. 1.5 ng/ml). Plasma progesterone shows a periovulatory surge to levels as high as 16 ng/ml, but declines rapidly during the 3/4 wk between ovulation and oviposition. During egg incubation (66 days) when the female remains close to the nest, ovarian steroids remain undetectable.

INTRODUCTION

The American alligator, *Alligator mississippiensis* (Daudin) is now firmly reestablished in many areas of the southeastern United States in which it was once believed close to extinction. Its present range (Fig. 1) is probably close to its historical range (Joanen and McNease, 1986, 1987a), with the densest populations occurring in the freshwater coastal marshes of Louisiana (Joanen, 1974; Joanen and McNease, 1978, 1986, 1987a, b), and the lakes of central Florida (Hines, 1979).

Despite its relative abundance and the intense interest shown by many travelers and zoologists during the past 200 years (see Reese, 1915; Kelloff, 1929; Neill, 1971; Joanen and McNease, 1987a, for a discussion on early literature), the reproductive biology of the alligator was, until recently, largely unknown. Although Clarke (1888) had described two nests in Florida with 29 and 31 eggs respectively, and had noted the approximate date of oviposition, and Reese (1907) had reported a mean clutch

size of 31 from 12 nests in Florida, most published information was wildly inaccurate (for an egregious example see Cope, 1900). Arthur (1928) and Kelloff (1929) thought that mating occurred in February and March, and as recently as 1961, Forbes stated (incorrectly) that alligators lay clutches of up to 200 eggs in April or May. The classic, but largely overlooked, work of McIlhenny (1934, 1935) gives an excellent account of the life history of the alligator in Louisiana, an accurate timetable of nest-building and egg-laying, and data on growth and age at sexual maturity. Giles and Childs (1949) estimated the time of year at which ovulation and egg-laying occurred by examining reproductive tracts of alligators killed by hunters during the summer months. However, not until the extensive studies of Joanen and McNease (1970, 1971, 1972, 1975, 1979, 1980) were the first reliable data on the annual reproductive cycle of both sexes collected.

In this paper I review data on the reproductive cycle of the male and female alligator in south Louisiana. Information on populations in other parts of its range and on other crocodylian species are discussed where data are available. Some of this information has appeared elsewhere (Joanen and McNease, 1975, 1980; Lance

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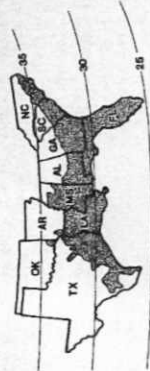


FIG. 1. Current distribution of *Alligator mississippiensis* (shaded area) in the southeastern United States. Lines of latitude are indicated.

et al., 1983; Lance, 1984, 1985, 1987; Ferguson, 1985).

ANNUAL CYCLE OF REPRODUCTIVE ACTIVITY IN LOUISIANA

The annual activity cycle of *A. mississippiensis* in Louisiana is critically dependent on seasonal changes in temperature (Joanen and McNease, 1979, 1980, 1987b). Alligators fast during the cooler months from October to March. They may emerge to bask on warm sunny days, but spend most of the winter months in dens or holes dug under the banks of small ponds or canals. In late March or early April, depending on temperature, the animals move from their winter habitat into the deeper open water of lagoons and canals. Members of both sexes bellow occasionally at this time, usually just before dawn. As air and water temperatures increase in mid-April, feeding resumes, and the intensity of bellowing increases. Courtship activities begin in mid-April, and continue until copulation takes place in late May or early June (Joanen and McNease, 1980; Vliet, 1987). After mating, females leave the deep water areas and move into open marsh to small isolated ponds where nesting takes place. Males and non-breeding females remain in deep water areas throughout the summer.

Only the female alligator builds and guards the nest, but in the closely related *Caiman latirostris* both sexes participate in nest building (Widholzer et al., 1986). Nesting in warmer years can begin as early as the first week in June, and in cool years may be delayed until the first week in July, but the bulk of the population nests and lays eggs within a two week period (Joanen and McNease, 1989). Peak nesting period

is directly correlated with mean ambient temperature during March through May (Joanen and McNease, 1979, 1989). A similar correlation between spring air temperature and date of nesting was reported for south Florida (Jacobsen and Kushlan, 1986). In North Carolina peak nesting occurs in mid July (Klausa, 1984). One clutch of eggs is produced which is laid in a single night. Incubation lasts 62–66 days. Clutch size can range from 2 to 50. Young, first time nesters and very old animals generally produce small clutches (Ferguson, 1985; Joanen and McNease, 1987b). Mean clutch size is 30 in south Florida (Jacobsen and Kushlan, 1986), 30 in northern Georgia (Mezzen, 1977), 38 in north central Florida (Diets and Hines, 1980), 39 in south Louisiana (Joanen and McNease, 1980), and 44 in South Carolina (Wilkinson, 1984). South Carolina females, which have the largest clutch size, are unusually large for this species (Wilkinson, 1984).

The breeding cycle, clutch size and incubation period of the Chinese alligator are remarkably similar to those of the American alligator (Gu and Zhang, 1983; Chen and Wang, 1984). There is no evidence of more than one clutch per year (Joanen, 1969; Joanen and McNease, 1971, 1975, 1980), although two clutches per year have been documented in captive Indian mugger crocodile, *Crocodilus palustris* (Whitaker and Whitaker, 1984).

The female alligator guards the nest throughout incubation, then opens the nest in response to vocalization by the young at hatching (Kushlan, 1973; Herzog, 1975; Kushlan and Kushlan, 1980; Kushlan and Simon, 1981). Vocalization by females during nest opening has also been reported (Hunt, 1988). The female usually builds a den in the vicinity and does not return to the deeper water until the following spring. The young are believed to overwinter in the same den, often remaining at the nest site until their third year (Chabreck, 1965). Non-breeding adult females and males stay in the deep water canals and lagoons throughout the summer and then move to their winter habitat in late October (Joanen and McNease, 1970, 1972). In northern Louisiana movement is more restricted.

with mating and nesting occurring in the same area (Taylor, 1984).

THE MALE

Male alligators reach sexual maturity at a length of 1.8 m in south Louisiana (Chabreck and Joanen, 1979; Joanen and McNease, 1987b), and 2.2 m in South Carolina (Murphy and Coker, 1984), but alligators less than 2.7 m in length are rarely successful breeders (Murphy and Coker, 1984). Age at sexual maturity varies with geographic region: from 10 yr in Louisiana to 18 yr in North Carolina (Klausa, 1984). However, the number of high temperature "growing months" required to reach sexual maturity may be similar for all alligators (Joanen and McNease, 1987b). Thus, alligators reared in heated pens reached sexual maturity in only 6 yr (Coulson and Hernandez, 1983; Coulson et al., 1973; Joanen and McNease, 1987b).

Crocodile testes were first described by Hans Sloane in 1725, "testes of the crocodile were elongated and reddish . . . and 'lay over the kidneys'" (Ahrenfeldt, 1959). Similar brief descriptions of Nile crocodile testes were given by Cott (1961) and Graham (1968). Breeding alligator "testis is pinkish-cream color. A mature but inactive testis is a purplish-pink color" (Joanen and McNease, 1975).

Joanen and McNease (1975) collected male alligators throughout one breeding season in south Louisiana and showed that paired testis mass was greatest at the peak of courtship activity in May, and that the right testis was generally larger than the left. Indeed the right testis is usually larger and heavier (21.6 ± 1.9 g/100 g greater, $n = 14$) than the left (Lance, unpublished, see Fig. 2), and lies more anteriorly. Neither Cott (1961) nor Graham (1968) noted testicular asymmetry in *C. niloticus*. I have pooled all of the available gravimetric data collected in south Louisiana over the past 8 yr (Fig. 3). Peak testis mass occurs in April and May followed by a rapid decline in the last half of June, with complete regression evident by mid July. Testis mass remains low throughout the remainder of the year. Testis weights for the months of November to January are not available,

with only limited data for February and March. However, from measurements of fixed material from November (Lance, unpublished) and measurements of testes collected in February (R. Eisey, personal communication) it appears that little growth occurs during November, but that in warm years substantial testicular growth could occur as early as mid February.

Joanen and McNease (1980) checked for the presence of spermatozoa in the penial groove and identified living cells for a period of 43 days, from 9 May to 20 June. Semen samples examined at the beginning of the breeding season contained numerous round cells. Histologic sections of testes collected in February showed clumps of cells in the lumen of the seminiferous tubules (Fig. 4A, B). It is not certain whether these cells are residual from the previous spermatogenic cycle or are immature spermatozoa (see also Fig. 6).

Males longer than 1.9 m produced spermatozoa. Animals longer than 2.7 m produced spermatozoa earlier and for a longer period than shorter males (Joanen and McNease, 1980). Klausa (1984) noted that the vent region in sexually active male alligators becomes swollen and flaccid a few days before the beginning of spermiation and remains swollen until the end of spermiation 5 wk later.

Alligators living in ponds heated by effluent from a nuclear reactor had spermatozoa in the penial groove one month earlier than alligators living in adjacent ponds at ambient temperature (Murphy, 1980). Cardelino (1981) reported collecting motile spermatozoa in January from alligators kept in heated enclosures. This temperature-induced spermatogenesis appears to be independent of photoperiod, as male alligators have successfully mated in zoos and farms at a whole range of latitudes and photoperiods (Green, 1981; Wright, 1981; Ben-Moshe, 1987; Eriksen, 1987). Coulson and Hernandez (1964) showed that seasonal variation in blood glucose and feeding activity was independent of photoperiod in immature alligators. However, diurnal activity in young alligators is sensitive to changes in photoperiod, and this activity can be entrained

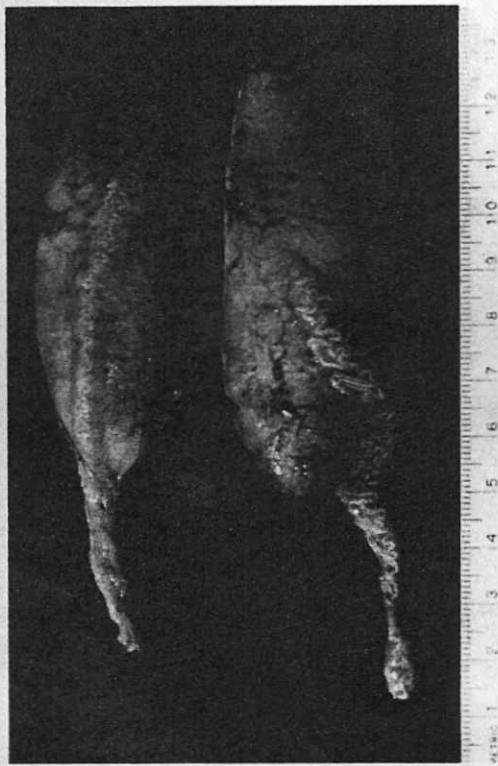


FIG. 2. Left (upper) and right (lower) testes with epididymis and portion of vas deferens of an alligator during the breeding season. Note difference in size.

to a particular light regimen (Kavaliers and Ralph, 1980). Although daily changes in photoperiod may influence daily activity cycles in alligators (Lang, 1976), photo-

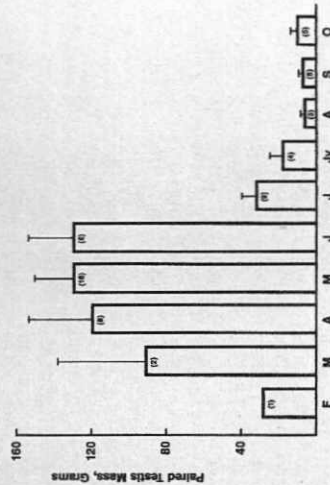


FIG. 3. Seasonal variation in absolute paired testis mass of *Alligator mississippiensis*. Months of the year indicated by a letter. The samples from the month of June have been divided into the first and second two weekly periods to emphasize the rapid decline in mass following spermiation. Monthly sample size is given within parentheses in the open bars. SEM indicated by the line above the open bar.

reproduction, but temperature alone is clearly the major environmental factor in temperate zones (see Licht, 1984 for review). Seasonal rains and seasonal changes in water levels of lakes and rivers are probably the stimuli for reproduction in the Nile crocodile (Cott, 1961; Modha, 1967).

Social order favors breeding by alligators over 2.8 m in length (Garrick *et al.*, 1978; Joanen and McNease, 1980). Dominant males (generally the largest) mate with all receptive females in a captive group, but females may also mate with several subordinate males (Garrick and Lang, 1977; Garrick *et al.*, 1978; Vliet, 1987). It is not known if the clutch produced is the result of multiple fertilizations.

Rathke (1866) described the epididymis of *C. acutus* as very narrow, slim and brilliantly white. Alligator epididymis appears similarly poorly developed (see Fig. 2). Since the histological boundaries of alligator epididymis have not been defined, I shall use the terminology of Short *et al.* (1967) for the structures where spermatozoa are stored (excurent ducts, Wolffian ducts and ductus deferens). Joanen and McNease (1980) noted a close correlation between the condition of the ductus deferens and reproductive state in alligators. In sexually active males the duct was thickened and convoluted and packed with semen; in sexually inactive but mature males it was reduced to a ribbon-like tube. Larsen *et al.* (1984) estimated $> 1.5 \times 10^9$ spermatozoa/ml in alligator semen collected from the vas deferens.

Larsen and Cardelino (1981) attempted to collect alligator semen by electroejaculation and reported, during application of current, "a stream of clear fluid would run from two ducts bilaterally located on the lateral surface of the shaft of the penis." They termed this substance "accessory duct fluid," suggesting it might function as a diluter of the highly concentrated semen. No chemical analysis of this fluid was made and there is no anatomical basis for its source. Most probably it is urine. Reese's (1924) histological description of the inornitment organ of a 1.6 m caiman gave no indication of ducts other than the urethra and penial groove. I have been

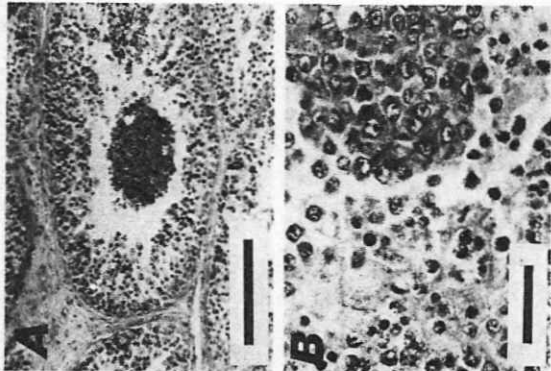


FIG. 4. A. Histological section of testis collected in February showing clump of cells in the lumen of the seminiferous tubule. Bar = 200 μ m. B. Same section at higher magnification. Bar = 20 μ m.

unable to detect lateral ducts in gross or histological examination of several alligator penes (Lance, unpublished).

The spermatogenic cycle can begin as early as November if the weather is unusually warm, but only divisions of primary spermatogonia have been seen in sections of testes collected at this time. Alligator testes collected in October showed no cell division, whereas testes collected in an exceptionally warm February had enlarged seminiferous tubules with actively dividing spermatogonia, and primary and secondary spermatocytes (Fig. 4A, B). Seminiferous tubules were greatly enlarged by late March and early April, contained abundant secondary spermatocytes, a few spermatozoa, but no mature spermatozoa (Fig. 5A, B). Mature spermatozoa were visible in the seminiferous tubules by late April and early May (Fig. 5C), but spermiation was not apparent until late May and June

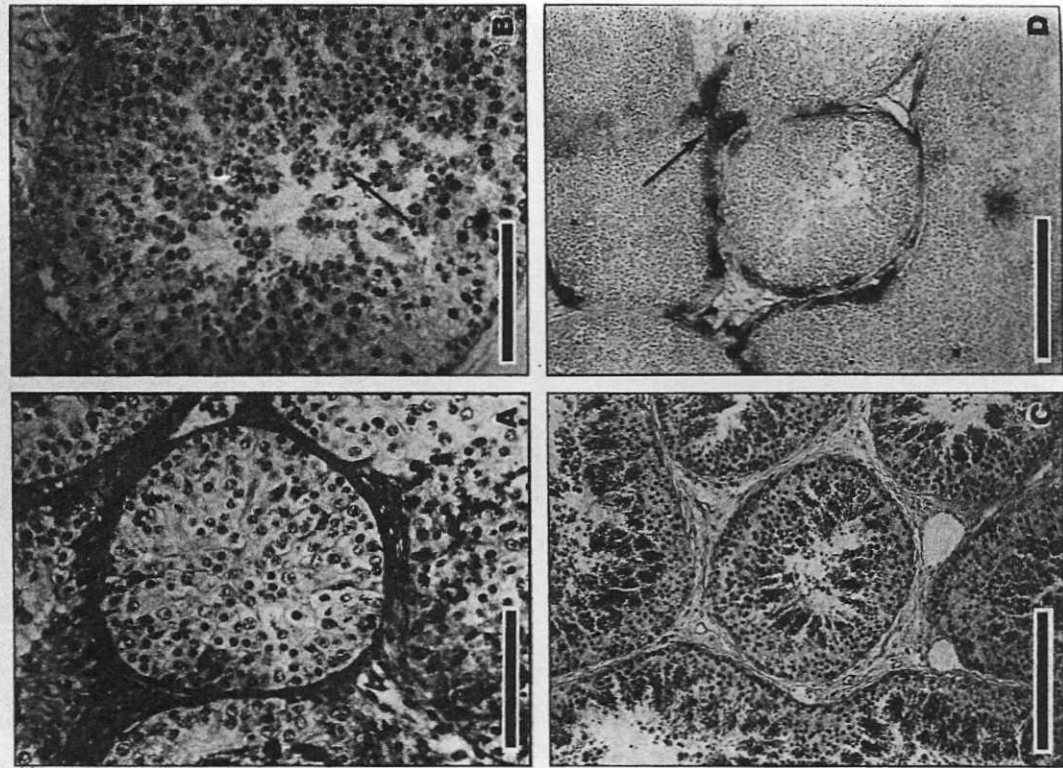


FIG. 5. A. Histological section of testis collected in March. Seminiferous tubules are packed with spermatogonia and spermatocytes. No late-stage spermatids or spermatozoa are present. Bar = 70 μ m. B. Cross section

(Fig. 6A). In mid June spermatogenesis ceased abruptly and testicular regression ensued (Fig. 6B). By late July testicular regression was complete: tubular diameter was greatly reduced, and the interstitium filled with connective tissue and islands of Leydig cells (Fig. 6C, D). Throughout September and October a similar picture was seen.

Forbes (1937, 1938a, b, 1939, 1940a, b) in a series of papers on gonadal development and the effect of hormones in immature alligators mentioned several times the absence of interstitial tissue in alligator testes. Forbes (1940a) stated, "It is possible that interstitial cells which can be identified as such never occur in the alligator testes: this point obviously should be settled by careful study of the testes of adult alligators." This misconception continued despite Cott's (1961) noting "a well organized and functional lipoidal interstitium" in the testis of a sub-adult *C. niloticus*. Graham (1968) also described Leydig cells in the Nile crocodile. In addition, Ramaswami and Jacob (1965) reported well developed Leydig cells in immature *C. palustris* as did Gouder and Nadkarni (1974) in two year old *C. porosus*. Hooker (1970) remarked on the reported absence of Leydig cells in crocodiles, but suggested that previous workers had merely failed to detect them.

Leydig cells are difficult to identify in wax sections of testis from alligators in breeding condition as the seminiferous tubules are greatly expanded (see Fig. 5). However, the presence of Leydig cells could be demonstrated in the interstitium of frozen sections by the intense reaction for delta-5- β -hydroxysteroid dehydrogenase (β -HSD), a key enzyme in steroid hormone biosynthesis (Fig. 5D).

Plasma testosterone concentrations in adult male alligators range from less than

10 ng/ml to over 100 ng/ml during the breeding season. Generally large males had higher plasma testosterone concentrations than smaller males (Murphy and Coker, 1984; Lance, unpublished). Some immature males (<1.8 m) also had elevated plasma testosterone at this time, but levels rarely exceeded 5 ng/ml (Lance, unpublished). Testosterone levels, already high by February and March, reached a peak in April, declined slightly in May, and then dropped to non-detectable concentrations in June, July and August. A second, but smaller peak occurred in September and October (Fig. 7). Individual variation in these months was much greater than in the summer months.

THE FEMALE

Female alligators reach sexual maturity at 10 yr in south Louisiana at a length of about 1.8 m (McClenny, 1984; Joanen and McNease, 1980), but do not reach peak breeding condition until about 20 yr (Ferguson, 1985; Joanen and McNease, 1987b).

A large literature exists on the breeding cycle of female crocodilians, including descriptions of the nests, eggs and maternal behavior (Ferguson, 1985), but very little information is available on the gross or microscopic anatomy of reproductive organs. Dutta (1949-1953) briefly described the ovaries of *C. palustris* and *Gavialis gangeticus*, and the ovary of *A. mississippiensis* was described by Joanen and McNease (1980). This elongate ovary is attached to the dorsal wall of the peritoneal cavity by a mesovarium. The right ovary (and oviduct) is generally larger than the left, and generally contains more follicles of preovulatory diameter (Lance, unpublished). Neither Cott (1961) nor Graham (1968) made note of any difference in size of the ovaries or oviducts of *C. niloticus*. Each ovary contains at least three

of a seminiferous tubule from testis collected in early April. Note the presence of late spermatid stages (arrow) near the lumen of the tubule. Bar = 70 μ m. C. Lower magnification view of testis cross section from mid-April. Mature spermatozoa are visible in the lumen of the tubule. Bar = 200 μ m. D. Frozen section of testis from late April. Note intense formazan deposits (arrow) in the interstitial region indicating β -HSD activity. Bar = 300 μ m.

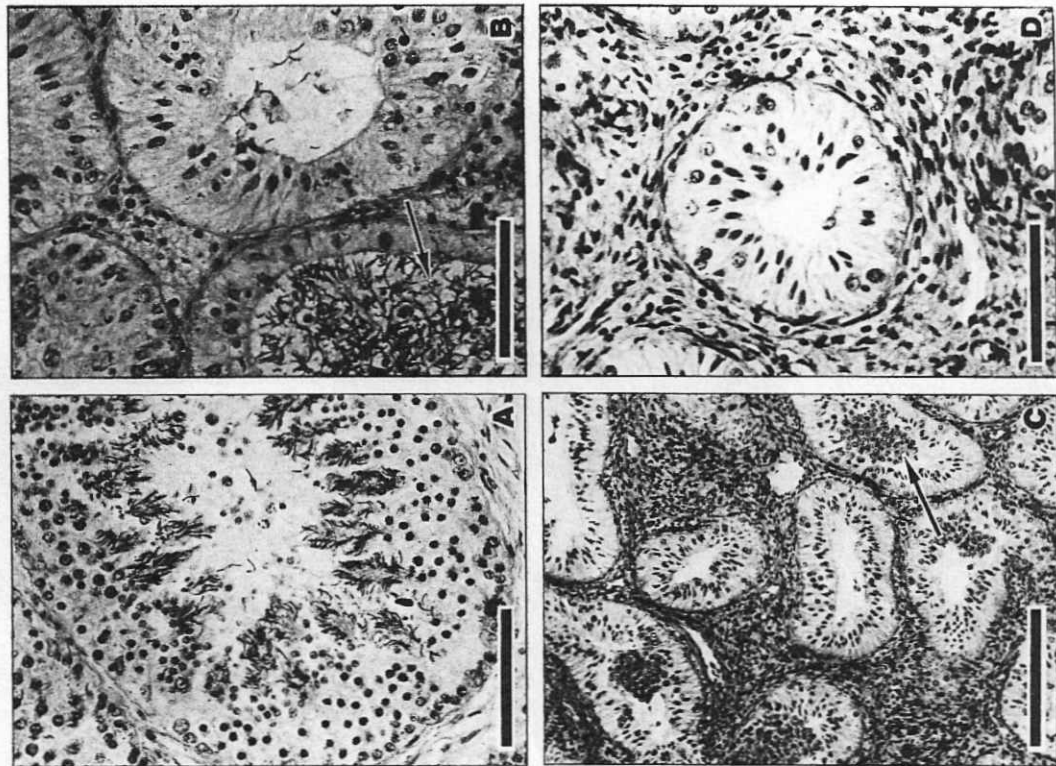


FIG. 6. A. Cross section of seminiferous tubule in early May. Abundant spermatozoa are present at the border of the lumen. Bar = 70 μ m. B. Cross section of testis from late June at late spermiation. Note tubule packed with spermatozoa (arrow) adjacent to empty tubule. The seminiferous epithelium is reduced to a single

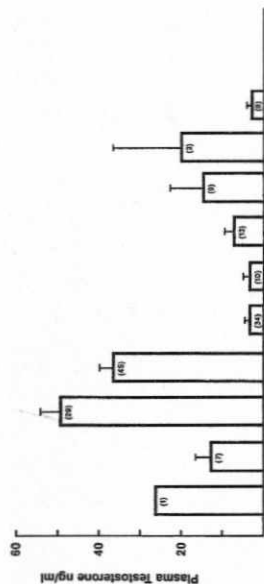


FIG. 7. Seasonal variation in plasma testosterone in male alligators sampled in south Louisiana. Bars represent the mean \pm SEM. Numbers in parentheses within the bars indicate sample size. Letters beneath bars indicate month.

size classes of follicles: <1 mm, 1 to 4 mm, and the current year's crop of preovulatory follicles of 5 to 45 mm in diameter (Fig. 8). These observations suggest that it takes at least 3 yr for a differentiated oocyte to grow to preovulatory diameter (Lance, 1985). The developing follicles protrude from the cortical surface of the ovary and are shed through a small opening directly into the fimbria of the oviduct (Figs. 8, 9); however, ectopic ova occasionally occur (T. Joanen, personal communication; Lance, unpublished). It is possible that ovulation is a reflex response to copulation, or is induced by the prolonged courtship, because isolated females do not lay eggs (T. Joanen, personal communication).

Loyez (1906) and Dutta (1949-1953) studied the histology of immature crocodilian oocytes. Dutta (1950) claimed "a well marked germinal epithelium is not recognizable" and that "the early oögonial stage is rarely found in crocodilians." Forbes (1940a), however, described germinal epithelium in the cortical region of the immature alligator ovary. In the ovaries of adult alligators examined by me, germinal epi-

thelium and abundant immature oögonia were easily recognizable in the outer stroma (Lance, unpublished).

Vitellogenesis begins in the early spring as temperature increases. The 4 to 5 mm follicles grow to about 20 mm by early April, then to 30 mm by early May, attaining a preovulatory diameter of 40 to 45 mm by late May (Lance, 1985). Few atretic follicles over 20 mm were seen. No statistical data have been collected, but most post-ovulatory ovaries seen by this author had between one and four large atretic follicles (see Fig. 9). Thus most follicles entering the vitellogenic stage of growth were ovulated. Atretic follicles from smaller size classes have not been studied.

Joanen and McNease (1980) and Lance (unpublished) examined reproductive tracts of female alligators during the reproductive cycle and estimated time between ovulation and oviposition as 3 to 3½ weeks. During this period the albumin and the calcareous egg shell are deposited. Following ovulation (late May to mid June) and oviposition (mid June to early July) primordial ovarian follicles remain unde-

layer. Bar = 70 μ m. C. Low magnification of testis tissue from late August. Note complete regression of seminiferous tubules and increase in the interstitial area which appears to be composed of connective tissue-like elements. In some tubules (arrow) remnants of germ cells still fill the lumen (see also Fig. 4). Bar = 200 μ m. D. Higher magnification of a single tubule from testis collected in September. There is no evidence of spermatogonial division. Bar = 70 μ m.

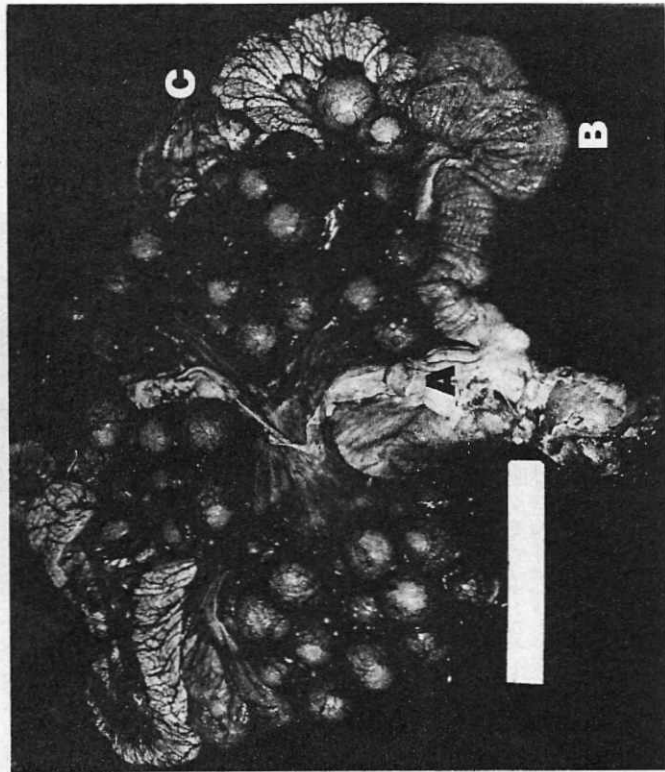


FIG. 8. Freshly dissected reproductive tract of a female alligator shortly before ovulation. Note the richly vascularized and hypertrophied oviduct and the stigma (clear area) on the ovarian follicles. The colon (A) has been removed for clarity. The glandular region of the oviduct is indicated by the letter C and the muscular, vaginal region by the letter B. The cloacal region is just below the letter A.

veloped until the following spring (see Fig. 9). Female alligators show no ovarian development in February and early March (Joanen and McNease, 1980; Lance, unpublished).

Follicular epithelium of developing alligator oocytes is composed of a single layer of granulosa cells resting on a basement membrane, similar to chelonians and birds. The thecal layer is poorly developed (Figs. 10A, 11). A positive reaction for 3β -HSD was found only in the granulosa layer (Fig. 10B). As the follicles increase in diameter, granulosa is reduced to a flattened, single layer of cells, but with an intense reaction

for 3β -HSD (Fig. 10B). Following ovulation the collapsed follicle forms a "corpus luteum," containing mostly connective tissue with a thin layer of granulosa-lutein cells in the core (Fig. 10C). These cells show no obvious signs of hypertrophy or hyperplasia but did give an intense reaction for 3β -HSD (Fig. 10D). Only five ovaries from animals with shelled eggs in the oviducts have been examined, and all were at the same stage of development, an estimated 2 wk post-ovulation. Alligator corpora lutea differ considerably from what has been described in other reptiles. In most of the Chelonians and Squamata the corpus luteum

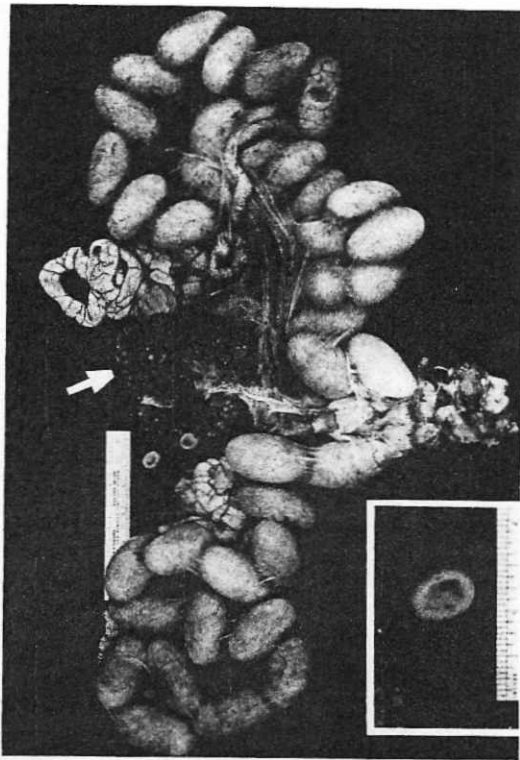


FIG. 9. Freshly dissected reproductive tract of a female alligator with shelled eggs in the oviduct. As in Figure 8 the colon has been removed and the cloaca is at the bottom of the picture. Note absence of yolked follicles in the ovary (arrow) and the presence of postovulatory follicles (inset). All the eggs are in the vaginal region. A loop of the glandular region is visible to the right of the arrow.

is a solid mass of hypertrophied granulosa-lutein cells exhibiting all the characteristics of steroid secreting tissue. Furthermore, in those species in which plasma progesterone has been measured, there is a significant correlation between histological appearance of the corpus luteum and plasma hormone level (Lance and Callard, 1978). The histology or ultrastructure of luteal cells of alligator do not indicate active steroid secretion (Fig. 12). The 12 hr post-ovulatory follicle of Japanese quail is strikingly similar to that of alligators in that there is an intense 3β -HSD activity restricted to granulosa-lutein cells. Quail ovarian enzyme activity disappeared by 60 hr post-ovulation (Colombo *et al.*, 1980).

Blood plasma from females with developing ovarian follicles contained high levels of the yolk precursor, vitellogenin, associated with high levels of calcium, magnesium, zinc, iron, cholesterol and protein

when compared to males or non-breeding females (Lance *et al.*, 1985). Similar plasma changes in immature alligators could be elicited by injections of estradiol-17 β (Van Brunt and Menzies, 1971; Eisey and Wink, 1986; Lance, unpublished). Plasma estradiol concentrations in reproducing female alligators are shown in Figure 13. Peak estradiol levels correlated with preovulatory follicular development, vitellogenesis and oviduct hypertrophy.

Both male and female alligators have a plasma sex-steroid binding protein (SSBP). In males, juveniles and non-breeding females circulating levels of SSBP remain unchanged throughout the year. However, in breeding females SSBP concentrations decline during the later stages of vitellogenesis and egg-laying (Ho *et al.*, 1987). This decrease in SSBP may result in an increase in unbound steroid and thus amplify the influence of the hormone on



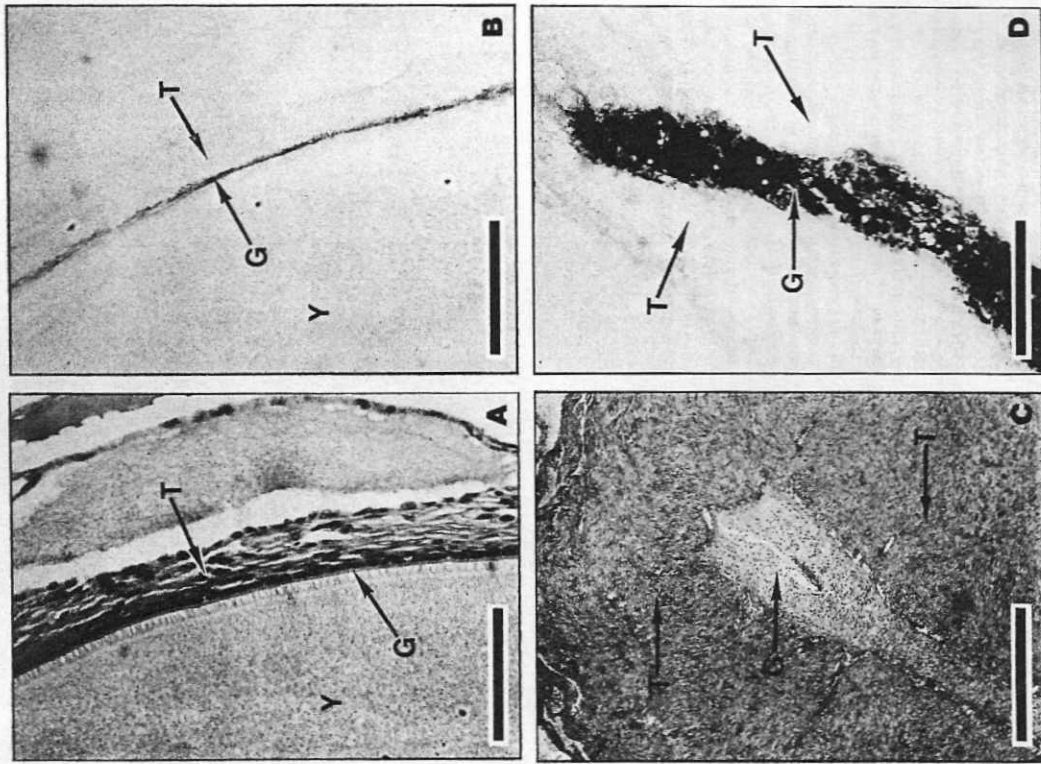
FIG. 11. Electron micrograph (8,000 \times) of granulosa cell from preovulatory follicle (approximately 10 mm in diameter). L = lipid droplets, Y = yolk. Compare same cell type in Figure 12.

reproductive functions (Ho *et al.*, 1987). Non-breeding females and post-ovulatory females had no detectable estradiol in the blood (Lance *et al.*, 1983). Shi *et al.* (1986) measured plasma estradiol in three captive, nonbreeding, female Chinese alligators at the Beijing Zoo, and, not surprisingly, found very low levels (2.4 to 25 pg/ml). In vitellogenic females plasma testosterone (Fig. 13) was also elevated during follicular growth, but less than 1/20th the concentrations seen in males. Although plasma testosterone appeared to be correlated with follicular growth and vitello-

genesis, a direct relationship between testosterone and estradiol was not observed (Lance, 1985). Plasma testosterone was high in some animals with very low plasma estradiol values. Female turtle (Callard *et al.*, 1978) and fowl (Erches and Cunningham, 1977) showed a discrete peak of testosterone preceding the estradiol peak. Testosterone is thought to be essential for normal oviduct development in chickens (Yu and Marquardt, 1973; Mika *et al.*, 1987) and may have a similar function in alligators.

Plasma progesterone, barely detectable

FIG. 10. A. Cross section of a previtellogenic ovarian follicle (8 mm in diameter). T = theca, G = granulosa, Y = yolk. Bar = 70 μ m. B. Frozen section of preovulatory follicle 35 mm in diameter. Note formazan deposit (arrow). Labels as in A. Bar = 500 μ m. C. Low magnification view of a post-ovulatory follicle from an alligator with shelled eggs in the oviduct. Note greatly thickened theca layer (T) and the poorly developed granulosa-lutein cells (G). Bar = 500 μ m. D. Frozen section from the same animal showing intense 3 β -HSD activity in the granulosa-lutein cells and absence of activity in the cells derived from the theca layers. Labels as in C. Bar = 500 μ m.



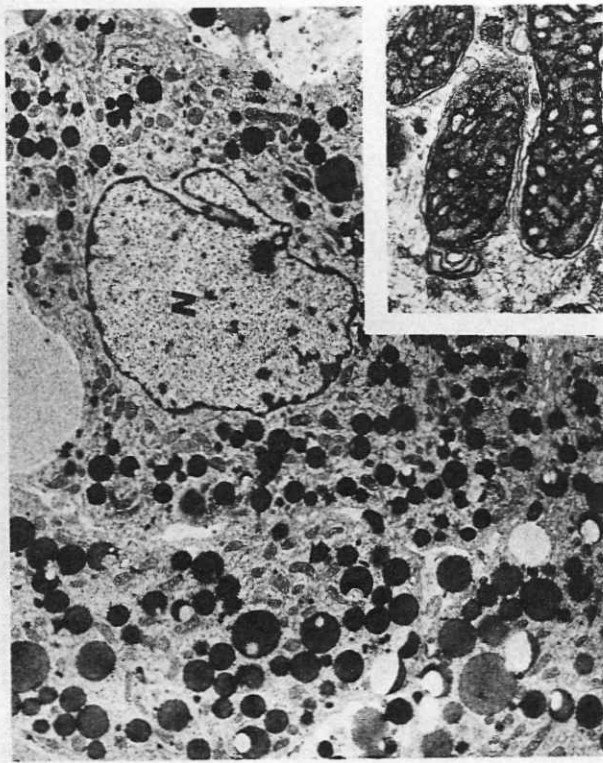


FIG. 12. Electron micrograph (2,000 \times) of granulosa-lutein cell from post-ovulatory follicle from the same animal as in Figure 10C. Nucleus is indicated by the letter N. Note unusual mitochondria (inset) and large electron dense granules.

throughout the year (Fig. 14), rose dramatically to 16 ng/ml just prior to ovulation. This preovulatory rise in progesterone appears to be of short duration as only two individuals close to the point of ovulation were found in 3 yr of sampling (Figs. 8, 14). Plasma progesterone in alligators with shelled eggs in the oviducts ranged from 0.5 to 2.5 ng/ml (Fig. 14). More data are needed to determine the duration of progesterone secretion during the 3/4 wk between ovulation and oviposition. Shi *et al.* (1986) measured progesterone throughout the year in three captive female *A. sinensis*, and found levels of 15–40 pg/ml. Breeding Nile crocodiles show preovulatory profiles of estradiol and testosterone similar to those of the alligator, but progesterone levels were no different in breeding and non-breeding females, ranging

from non-detectable to 300 pg/ml (C. Kofron, unpublished). The failure to detect significant progesterone levels in the Nile crocodile suggests that, as in the alligator, there is a transient surge of progesterone around the time of ovulation that is easily missed with monthly sampling.

Unlike female lizards in which close to 100% of the adult population reproduce in a given year (Tinkle, 1969) a significant number of adult female crocodilians fail to lay eggs each year. Joanan and McNease (1980) estimated that 63% of adult, size female alligators nested in one year in south Louisiana. Jacobsen and Kushlan (1986) reported that alligator nesting effort in south Florida varied from 16% to 58% with a mean of 29% over a 7 yr period. The percentage of female Nile crocodiles nesting increased with body size, with a max-

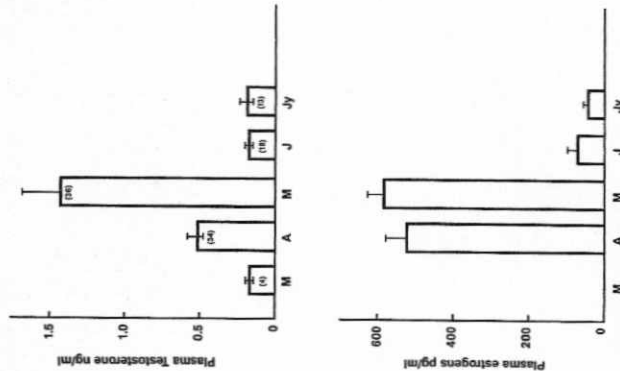


FIG. 13. Seasonal variation in plasma testosterone in female alligators (upper panel), and estradiol (lower panel). Bars represent the mean \pm SEM. Numbers in parentheses indicate sample size. Abbreviations for months are presented beneath the bars.

imum of close to 80% for the largest (>3 m) females (Cott, 1961). Using plasma calcium as an indicator of vitellogenesis in alligators, I have estimated nesting percentage from a low of <10% in a North Carolina population to a high of >50% in south Louisiana (Lance, unpublished). In South Carolina a sufficiently large sample was collected to break the results down into size classes, and, as with the Nile crocodile, nesting frequency increased with size: 0% nesting in those under 2 m in length; 14.8% in the 2–2.34 m class; 42.9% in the 2.34–2.95 m class (Wilkinson, 1984). Wild alligators in captivity showed considerable variability in annual nesting frequency: one nesting for 5 consecutive years, one every second year, another nesting for 3 yr with every fourth year skipped, and two others nesting only once in 5 yr (Joanan and McNease, 1971). More than 80% of a population of captive reared alligators, however, nested every year (Joanan and McNease, 1987b). Nesting frequency of wild alligators is unknown, but some marked individuals have nested at the same site for 2 yr (L. McNease, personal communication).

Annual reproduction represents a considerable investment on the part of the female alligator: the mobilization of yolk proteins for a clutch of 30–40 eggs, weighing 50–70 g each; the mobilization of calcium from structural bone (Wink and Eilsey, 1986; Wink *et al.*, 1987) to produce 30–40 egg shells, each containing 3.0–5.0 g of calcium (K. Packard, personal communication); and the expenditure of energy during nest building and nest guarding. Inadequate energy reserves would preclude reproduction. Whether it is some metabolic end-product that inhibits the endocrine system of these females from responding to increasing temperature in spring or merely a behaviorally or genetically determined event is not known. The annual ovulatory cycle appears to be an all-or nothing phenomenon: young females at the very beginning of their reproductive life produce small clutches, and old females at the end of their reproductive life produce small clutches (see Hutton, 1984; Ferguson, 1985; Webb and Smith, 1987), but mature females produce a large clutch or

do not nest that year. In other words, animals that somehow sense they have inadequate energy reserves do not produce smaller clutches; they simply fail to ovulate.

Joanan and McNease (1980) noted that 3% of their sample of alligators, females over 2.7 m in length, was reproductively senescent or "barren." Graham (1968) reported a similar phenomenon in *C. niloticus*: a majority of females over 2.9 m had few enlarged oocytes and no corpora lutea. Oogonial proliferation may continue throughout adult life in the Crocodilia, but with a limit on the number of cell divisions, and hence, a limit on the number of oocytes

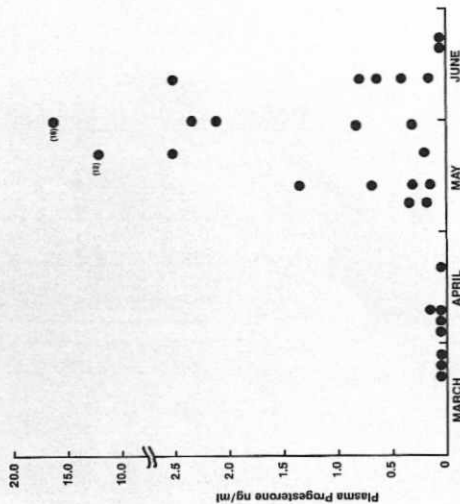


FIG. 14. Seasonal variation in plasma progesterone in female alligators. Black circles represent individual values. Note break in the scale. Numbers in parentheses next to the two highest points indicate progesterone concentration. The animal with a value of 12 ng/ml was preovulatory (see Fig. 8), and the animal with a value of 16 ng/ml had 48 eggs in the oviduct.

a female is capable of producing (see Tokarz, 1978 for a discussion on this topic in reptiles).

HORMONAL REGULATION OF REPRODUCTION

The endocrine glands and the hormones regulating reproduction in the alligator appear similar to those of other tetrapods (Lance, 1984): A portal system connecting hypothalamus and pituitary has been described (Green, 1951) and two forms of gonadotropin-releasing hormone (GnRH) immunologically and chromatographically identical to the two avian forms have been isolated from alligator brain (Lance *et al.*, 1985; Powell *et al.*, 1986). Although crocodilians are more closely related to birds than to other vertebrates, the morphology of the pituitary gland differs considerably. The intermediate lobe of the crocodile pituitary may comprise as much as 30% of the total gland (Saint Girons, 1970), whereas in birds an intermediate lobe is

responded to injections of mammalian FSH with increased testosterone secretion (Lance and Vliet, 1987). Male alligators also responded to injections of mammalian GnRH with increased testosterone secretion (Lance *et al.*, 1985).

Data on circulating levels of pituitary hormones and the pattern of gonadotropin secretion during follicular growth, ovulation and nesting are lacking. Preliminary data on plasma corticosterone indicate that breeding males have higher levels than females or immature males (Lance and Eley, unpublished). Circulating thyroxine also varies throughout breeding but its relationship to gonadal function is still unclear (P. Hall, personal communication).

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Social Displays of the American Alligator (*Alligator mississippiensis*)¹

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SYNOPSIS. Adult alligators perform two conspicuous social displays, bellows and headslaps. Both of these behaviors are performed from a "head oblique tail arched" (HOTA) posture. Bellow displays, by both males and females, involve the production of a loud, roaring vocalization. Male alligators also produce a "infrasonic signal, termed subsudible vibrations, just prior to the audible bellow. Bellowing occurs throughout the year, but is most frequent during the courting season, when alligators bellow daily in choruses. Chorus length appears to be correlated with the size of the adult population. Chorusing is frequently initiated by females but seems to be perpetuated by male alligators. Bellowing may serve to attract alligators of the opposite sex and possibly to space out animals of the same sex.

The headslap display is an assertion display consisting of eight component behavioral acts: the elevated posture, HOTA posture, subsudible vibrations, headslap, jawclap, growl, inflated posture, and tail wag. Each act component is variable in presence and intensity producing a highly variable, graded signal. The alligator typically remains motionless in the HOTA posture for about 16 sec before executing the headslap/jawclap acts. The headslap display involves a rapid clapping shut of the jaws as the undersurface of the head is slapped against the water surface. Headslapping is most common in early morning and afternoon hours. Analysis of 1,050 headslap displays by 91 known individuals indicates that 94.5% of the observed displays were performed by males. Headslap displays are generally performed from typical display sites which the alligator seeks out prior to the display. Responses to headslap displays include headslapping by others, lunges, approaches, and bellow growling. The headslap display functions as a declaration of presence.

A musky odor is commonly detected in association with both of these social displays, suggesting a possibly important, but little understood, pheromonal component of these behaviors.

The displays both involve complex signals including visual, auditory, olfactory and possibly tactile channels of communication. Most of the behaviors described are shared with many other species of crocodilians.

INTRODUCTION

The study of the social behavior of crocodilians is still in its infancy. Although crocodilians are large, conspicuous, and were, at least historically, common components of their aquatic communities, until recently little but anecdotal observations had been made on them. Accounts of encounters with the American alligator (*Alligator mississippiensis*) fill the notes of many early explorers and settlers of the southeastern United States. Most are highly embellished but include many interesting observations of the alligator's behavior and natural history. Records dating from the

late 1500s describe the roaring bellows of alligators resounding through the southern swamplands. Bartram's (1791) florid writings include accounts of bellowing, nesting and the aggressive nature of the alligator. Bartram (1791) and Audubon (1827) both comment on the enormous concentrations of alligators in large southern rivers.

Most early scientific studies of the alligator concentrated on descriptions of their morphology and physiology (Clarke, 1891; Reese, 1907, 1915; Coulson and Hernandez, 1964). However, Harper (1930) and McIlhenny (1935) contributed important observations of the natural history of the alligator obtained during years of close association with the animals in the wild.

In the 1960s, the detailed studies of the ecology of the Nile crocodile (*Crocodylus niloticus*) began to emerge, providing the first

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